Trade-offs between xylem hydraulic efficiency and mechanical strength in Chinese evergreen and deciduous savanna species

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Evergreen and deciduous species coexist in tropical dry forests and savannas, but differ in physiological mechanisms and life-history strategies. Hydraulic conductivity and mechanical support are two major functions of the xylems of woody plant species related to plant growth and survival. In this study, we measured sapwood-specific hydraulic conductivity (Ks), leaf-specific hydraulic conductivity (KL), modulus of rupture (MOR) and elasticity (MOE), xylem anatomical traits and fiber contents in the xylems of 20 woody species with contrasting leaf phenology (evergreen vs deciduous) in a Chinese savanna. Our results showed that deciduous species had significantly higher Ks and KL but lower MOR and MOE than evergreen species. Evergreen species experienced more negative seasonal minimum water potential (Pmin) than deciduous species during the dry season. Furthermore, we found trade-offs between xylem hydraulic efficiency and mechanical strength across species and within the evergreen and deciduous groups, and these trade-offs were modulated by structural and chemical traits. Both Ks and KL were significantly related to hydraulic weighted vessel diameter (Dh) across all species and within the deciduous group. Both MOR and MOE were significantly related to wood density, neutral detergent fiber and acid detergent fiber across species and within evergreen and deciduous groups. Our findings demonstrated that Chinese evergreen and deciduous savanna species diverged in xylem hydraulic and mechanical functions, reflecting conservative and acquisitive life-history strategies for evergreen and deciduous species, respectively. This study provides new information with which to understand the hydraulic and biomechanical properties and ecological strategies of savanna species in long-term dry-hot environments.

Keywords: Chinese savanna, fiber content, hydraulic conductivity, modulus of rupture, trade-off, vessel anatomy, wood density.

Introduction

The xylem of woody plants is of great importance in long-distance water transport, mechanical support, and the storage of water, carbohydrates and nutrients (Wagner et al. 1998, King et al. 2006, Pratt and Jacobsen 2017, van der Sande et al. 2019, Pratt et al. 2021a). The advantages of efficient water transport in the xylem can maintain leaf water potential at a relatively high value, keep the stomata open and maintain photosynthetic gas exchange (Brodribb and Feild 2000, Pratt and Jacobsen 2017, Liu et al. 2019). Previous studies have shown that xylem hydraulic conductivity is correlated with leaf photosynthetic capacity (Brodribb and Feild 2000, Santiago et al. 2004), plant growth rate (Fan et al. 2012, Hoeber et al. 2014, Qi et al. 2021), productivity (Zhao et al. 2021) and even species distribution (Markesteijn et al. 2011, Martin et al. 2013). In addition, xylem mechanical strength protects plants from abiotic and biotic damage, which affects plant survival, growth and reproductive performance (Wagner et al. 1998, King et al. 2006, Read and Stokes 2006, Onoda et al. 2010, Pratt et al. 2021a). A plant needs to maintain a certain level of
water transport to allow leaf transpiration and photosynthesis, as well as adequate mechanical support to resist breaking forces from physical disturbance and herbivores (Wagner et al. 1998, Onoda et al. 2010, Lachenbruch and McCulloh 2014). Both xylem hydraulic efficiency and mechanical strength are closely linked to the acquisition and use of water and nutrient resources, the competitive ability and the life-history strategies of the plants (Choat et al. 2005, Sterck et al. 2006, Marksteijn et al. 2011, Zhang et al. 2013, Pratt et al. 2021a). It is important for us to understand whether hydraulic efficiency and mechanical strength in the xylems of woody plants are related to each other and how anatomical traits shape the covariation of hydraulic and mechanical performance (Lachenbruch and McCulloh 2014, Pratt and Jacobsen 2017).

 Sapwood-specific hydraulic conductivity ($K_s$) can quantify the water transport ability in the xylem, whereas the leaf-specific hydraulic conductivity ($K_t$) indicates the hydraulic efficiency of the xylem to supply water to the leaves (Zimmermann 1978, Sperry and Tyree 1988). The anatomical traits of conductive tissues (vessel in angiosperm or tracheid in gymnosperm) affect hydraulic efficiency in the xylem (Tyree et al. 1994). In general, wider and longer vessels can support higher hydraulic efficiency than narrower and shorter vessels (Hacke et al. 2006, Lens et al. 2011). Moreover, the modulus of elasticity (MOE) and modulus of rupture (MOR) indicate the bending stiffness and resistance to breaking in the branched xylem (Gere and Timoshenko 1999, Pratt and Jacobsen 2017). Numerous studies have suggested that both MOR and MOE are well correlated with wood density (WD) across species (King et al. 2006, Pratt et al. 2007, Onoda et al. 2010, Santini et al. 2013, Xiao et al. 2021, Pratt et al. 2021a). In gymnosperm species, both water transport and mechanical support are provided by tracheid-based systems (Pittermann et al. 2006). In angiosperm species, fibers are involved in mechanical support, and xylem mechanical stiffness and resistance are related to fiber traits, such as the proportion of fibers in xylem cross section, fiber lumen diameter (FLD), fiber wall thickness (FWT), fiber arrangement and cellulose microfibril angle (Lachenbruch and McCulloh 2014, Pratt and Jacobsen 2017, L. Zhang et al. 2019, Pratt et al. 2021a). Furthermore, the fibers in leaf tissues can support the skeleton in cell wall composition (Kitajima et al. 2012), and lignin can increase the bending resistance (Alvarez-Clare and Kitajima 2007). Leaf fracture toughness was related to cellulose content per dry mass (DM) across species and within plants (Kitajima et al. 2016). To our knowledge, however, there have been no tests for the relationships between fiber content and mechanical strength in xylems.

 The division of labor between vessels for water transport and fibers for mechanical support suggests an interdependency between hydraulic efficiency and mechanical strength in the xylem of angiosperm species (Pratt and Jacobsen 2017). Some studies have shown a trade-off between water transport efficiency and mechanical strength (Wagner et al. 1998, Fan et al. 2017, Xiao et al. 2021), however, others have shown no relationship at all (Jacobsen et al. 2007a, L. Zhang et al. 2013). Furthermore, previous studies have also found trade-offs between xylem mechanical traits and starch storage, and between storage capacity and embolism resistance under drought, and these trade-offs were mitigated by the structural and functional basis of xylems (Chen et al. 2020, Pratt et al. 2021b). More studies are needed to make a comprehensive conclusion regarding the potential trade-offs or associations between xylem hydraulic efficiency and mechanical strength. Environmental conditions may put selective pressure on the trade-offs or associations among xylem xylems (Fu et al. 2012, Sanchez-Martinez et al. 2020, Pratt et al. 2021a). In seasonal environments, water limitation strongly influences xylem functions (Pratt et al. 2021b), and the minimum water potential experienced by plants during drought stress ($P_{min}$) indicates the drought exposure in the tissues, which is determined by multiple traits such as plant drought tolerance, hydraulic safety and leaf phenology (Bartlett et al. 2016, Zhang et al. 2017, Sanchez-Martinez et al. 2020, Pratt et al. 2021a). Pratt et al. (2021a) also revealed that $P_{min}$, as a hub trait, was linked to cellular trade-offs of fiber, vessel and parenchyma, which drove the functional trade-offs among xylem strength, transport and storage.

 Evergreen and deciduous woody species coexist in seasonally dry tropical forests and savannas, because of the strong selective pressure of seasonal drought (Quigley and Platt 2003, Choat et al. 2005, Ishida et al. 2010, Fu et al. 2012, Zhang et al. 2017). Several studies have shown that co-occurring evergreen and deciduous species exhibit clear distinctions in stem hydraulic efficiency (Chen et al. 2009, Fan et al. 2011, Fu et al. 2012); however, others have failed to find this divergence (Ishida et al. 2010). The elucidation of this issue is further complicated by the lack of a direct test to compare the potential differences in biomechanical traits between evergreen and deciduous species.

 Savanna ecosystems are mainly distributed in tropical and subtropical regions, covering appropriately 20% of the land surface and accounting for 30% of the primary production of terrestrial vegetation (Solbrig et al. 1996, Grace et al. 2006). Valley-type savanna occurs widely in the deep, hot and dry valleys of several large rivers among the high mountains, in Southwest China (Jin and Ou 2000, Zhu et al. 2020). Because of strong seasonality in the precipitation of savanna ecosystem, the environmental pressure drives the differentiation in leaf phenology, and evergreen and deciduous woody species coexist in this Chinese savanna (Zhang et al. 2007, 2017). Our previous studies have shown that evergreen and deciduous tree species exhibit divergent strategies of drought tolerance and hydraulic safety under prolonged seasonal drought (Zhang et al. 2017, SB Zhang et al. 2019). However, the ecological
strategies in hydraulic efficiency and mechanical strength have not been well characterized for Chinese savanna woody species with contrasting leaf phenology.

In this study, we measured 14 xylem functional traits related to hydraulic efficiency and biomechanical strength, as well as P\textsubscript{min} in woody species (7 evergreen species vs 13 deciduous species) in a savanna ecosystem, Southwest China. We evaluated the potential differences in hydraulic and biomechanics between evergreen and deciduous savanna species, and elucidated the possible trade-offs and associations between hydraulic and biomechanical functions and underlying anatomical traits. Given phylogenetic conservatism, traits at the species level are influenced by evolutionary history, and closely related species are expected to have similar trait values (Blomberg et al. 2003, Losos 2008). Evolutionary correlations among hydraulic, biomechanical, anatomical traits and fiber contents were also analyzed using phylogenetically independent contrasts (PICs; Paradis and Schliep 2019).

We addressed the following questions: (i) do evergreen and deciduous species differ in terms of hydraulic efficiency and mechanical strength; (ii) is there an evolutionary trade-off between xylem hydraulic efficiency and mechanical strength across species and within evergreen and deciduous groups; and (iii) how is the hydraulic and mechanical trade-off, if any, determined by the structural traits?

**Materials and methods**

**Study sites**

This study was conducted at Yuanjiang Savanna Ecosystem Research Station (YSERS, 23°27′N, 102°10′E and 481-m elevation above sea level), Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, located in Yuanjiang County, Yunnan Province, Southwest China. The study site hosts a valley-type savanna (Jin and Ou 2000). The climate is characterized by two distinct seasons: rainy season (May–October) and dry season (November–April). According to the meteorological record of YSERS observed from 2012 and 2020, the mean annual temperature was 25.0 °C with a mean monthly temperature ranging from 17.7 °C (January) to 30.3 °C (June). The total annual precipitation was 675.8 mm, concentrated from June to September (see Figure S1 available as Supplementary data at Tree Physiology Online). Due to rock outcrops (60–70%), water leakage and shallow soil, this valley-type savanna lacks groundwater reserves, and water stress is a dominant selective pressure (Jin and Ou 2000). The soil is ferralic cambisol with pH of 7.2 ± 0.1. The concentrations of nitrogen, phosphorus, potassium and sulfur in the topsoil (0–20 cm) were 0.285 ± 0.022%, 0.086 ± 0.006%, 1.673 ± 0.012% and 0.031 ± 0.002%, respectively.

**Plant materials**

Based on the species composition of the 1 ha (100 m × 100 m) long-term monitoring Chinese savanna plot, we selected 13 deciduous and 7 evergreen plant species in this study, including 12 families and 20 genera (Table 1). These deciduous species shed their leaves during the dry season. These 20 dominant species account for >70% of the biomass in the woody species of this valley-type savanna in Southwest China. The hydraulic and mechanical traits of the plants may be affected by the availability of light over the crown (Raimondo et al. 2009, Markesteijn et al. 2011). Therefore, all the sampled trees were completely exposed to overhead light to minimize the effects of shade. Five sun-exposed terminal branches were sampled from three to five adult individuals of each species, during the rainy season (July–August) in 2014. Sampled branches with healthy leaves were wrapped in moist towels and transported in a sampling box to the YSERS laboratory for further measurements. In each sample and measurement cycle, we only collected the branches of two species and kept them at 4 °C before hydraulic measurements. We measured hydraulic traits within 2 days after sampling the branches in the field.

**Hydraulic traits**

The maximum vessel length (MVL) was determined using the air injection method (Greenidge 1952). To avoid any effect of open vessels on our measurements of hydraulic conductivity, we sampled branches longer than the MVL. However, previous studies have also suggested that sample length has very little effect on the measured hydraulic conductivity in cut stems (Sperry et al. 2005, Jacobsen et al. 2015). These branches were recut under distilled water and trimmed using a razor blade. Potassium chloride (0.1 mol l\textsuperscript{−1} KCl) solution was used to flush the stem segments for at least 20 min to remove the native emboli present within the xylem vessels. The pressure of the KCl solution was set at 100 kPa. We measured the water flow (F, kg m\textsuperscript{−1} s\textsuperscript{−1}) using the drop in pressure to generate a gravity-induced hydrostatic pressure (7.3 kPa), whereas the stem segments were connected to a hydraulic conductivity apparatus (Sperry and Tyree 1988). We determined hydraulic conductivity (K\textsubscript{h}, kg m MPa\textsuperscript{−1} s\textsuperscript{−1}) as the flow rate divided by the pressure gradient. Subsequently, the cross-sectional area of the distal end of the samples (A\textsubscript{s}, mm\textsuperscript{2}) was determined as the average value of the two ends of the stem segments measured for hydraulic conductivity. Sapwood-specific hydraulic conductivity (K\textsubscript{sp}, kg m\textsuperscript{−1} MPa\textsuperscript{−1} s\textsuperscript{−1}) was calculated by K\textsubscript{h} divided by A\textsubscript{s}.

The total leaf area (A\textsubscript{l}) distal to the base of the cut stem was scanned using a Li-3000A leaf area meter (Li-cor, Lincoln, NE, USA). We calculated leaf-specific hydraulic conductivity (K\textsubscript{ls}, kg m\textsuperscript{−1} MPa\textsuperscript{−1} s\textsuperscript{−1}) by K\textsubscript{h} divided by A\textsubscript{l}. The Huber value (HV, mm\textsuperscript{2} m\textsuperscript{−2}) is the ratio of sapwood area to leaf area, which indicates the relative allocation to sapwood area and leaf area.
Table 1. Characteristics of 20 evergreen and deciduous species included in the present study.

| Species                             | Code | Family       | Phenology | Growth form | Canopy height |
|-------------------------------------|------|--------------|-----------|-------------|---------------|
| Haldina cordifolia (Roxb.) Ridsd.   | Hc   | Rubiaceae    | Deciduous | Tree        | 5–7 m         |
| Cipadessa cinerascens (Pellegr.) Hand | Cc   | Meliaceae    | Deciduous | Shrub       | 3 m           |
| Polyalthia cerasoides (Roxb.) Benth. & Hook.f. exBedd. | Pc   | Annonaceae   | Deciduous | Tree        | 3–5 m         |
| Vitex negundo L.                    | Vn   | Verbenaceae  | Deciduous | Shrub       | 4 m           |
| Trigonostemon tuberculatum F.Du et J.He sp. nov. | Tt   | Euphorbiaceae | Deciduous | Shrub       | 3 m           |
| Bauhinia brachycarpa Benth.         | Bb   | Anacardiaceae | Deciduous | Tree        | 3 m           |
| Lannea coromandelica (Houtt.) Merr. | Lc   | Anacardiaceae | Deciduous | Tree        | 5–8 m         |
| Terminalia franchetii Gagnep.       | Tf   | Combretaceae | Deciduous | Tree        | 5 m           |
| Bridelia stipularis (L.) Blume      | Bs   | Euphorbiaceae | Deciduous | Liana       | 4 m           |
| Stryphnodendron zeylanicum (Hand.)   | Sf   | Euphorbiaceae | Deciduous | Shrub       | 3 m           |
| Termisina paniculata (Wall. ex G. Don) C. Y. Wu et T. L. Ming | Tp   | Anacardiaceae | Deciduous | Tree        | 5 m           |
| Woodfordia fruticosa (L.) Kurz      | Wf   | Lythraceae   | Deciduous | Tree        | 2–4 m         |
| Campylotropis delavayi (Franch.) Schindl. | Cd   | Leguminosae  | Deciduous | Tree        | 3 m           |
| Tarenna depauwetera Hutch.          | Td   | Rubiaceae    | Deciduous | Shrub       | 3 m           |
| Pistacia weinmannifolia J. Poiss. ex Franch. | Pw   | Anacardiaceae | Evergreen | Tree        | 5–7 m         |
| Diospyros yunnanensis Rehd. & E. H. Wilson | Dy   | Ebenaceae    | Evergreen | Tree        | 4–5 m         |
| Olea europea L.                     | Oe   | Oleaceae     | Evergreen | Tree        | 4–6 m         |
| Psidium guajava L.                  | Pg   | Myrtaceae    | Evergreen | Tree        | 6–8 m         |
| Carissa spinarum L.                 | Cs   | Apocynaceae  | Evergreen | Tree        | 3 m           |
| Burretiodendron kydifolium Hsu et Zhuge | Bk   | Malvaceae    | Evergreen | Tree        | 6 m           |

and is central to the plant water balance of the branches and leaves of the canopy (Maurizio et al. 2019).

Young’s modulus

Following the determination of hydraulic traits, the same stem segments that had been used for hydraulic measurements were used to measure the MOE and MOR with a three-point bending method using a universal testing machine (Model 3343, Instron, Illinois Tool Works Inc., Norwood, MA, USA). The diameter-to-length ratio was set to 1:20. The vertical force was applied at a speed of 20 mm min⁻¹. The bark, including the outer bark, phloem and cambium layers, was carefully removed before mechanical measurements. For each sample without bark, we measured the diameters at the midpoint and at both ends with a caliper (0.01 mm) and calculated its radius (R). The MOR was estimated by:

\[ \text{MOR} = F_{\text{max}} \times L \times R / 4I \] (1)

where \( F_{\text{max}} \) is the maximum force (N) when the debark stems are broken, \( L \) is the span length of the supports (m), \( R \) is the mean radius of debark stems (m) and \( I \) is the second moment of area (m⁴), which was calculated as follows (Gere and Timoshenko 1999):

\[ I = \pi R^4 / 4 \] (2)

The MOE was calculated from the linear region of the relationships between the load force (\( F, \) N) and its corresponding deflection (\( \delta, \) mm; Gere and Timoshenko 1999):

\[ \text{MOE} = FL^3 / 48\delta \] (3)

Wood density and anatomy

After measuring the hydraulic and mechanical traits, one 5-cm segment from each debarked stem was used to measure the WD (g cm⁻³). The volume of the fresh wood (\( V_{\text{wood}} \)) was measured using the water displacement method. The DM was weighed after drying in an oven at 70 °C for 72 h. Wood density was calculated as follows:

\[ \text{WD} = \text{DM} / V_{\text{wood}} \] (4)

Five segments per species were sampled for anatomical traits. Segments 3 cm in length were sampled from the debarked stems used for the mechanical and hydraulic traits. Transverse sections, 20-μm thick, were made with a microtome and stained with a mixture of safranin and Alcian blue. Digital photographs of the xylem transverse sections were recorded using a DM2500 light microscope (Leica Inc., Bensheim, Germany) connected to a computer. Three digital images per stem were taken to analyze the anatomical traits using ImageJ software (http://rsbweb.nih.gov/ij/). At least 100 vessel and fiber cells per species were used to determine the vessel and fiber traits.

Vessel density (VD, no. of vessels mm⁻²) was calculated as the number of vessels per xylem area. Moreover, we measured...
the diameter of each vessel ($D_i$) and calculated the hydraulic weighted vessel diameter ($D_h$, μm) as follows:

$$D_h = \left(\frac{\sum D_i^4}{N}\right)^{1/4}$$

where $N$ is the number of vessels (Tyree and Zimmermann 2002).

In addition, we measured the FLD (μm) and FWT (μm) from the digital photographs. We measured the inter-FWT from two adjacent fiber cells; this was halved to calculate the FWT (Antonio et al. 2017).

**Fiber content**

Fresh wood without bark was sampled to measure the fiber content. After drying at 70 °C for at least 96 h, the wood samples were ground to a fine powder with a crusher and passed through a 20-mesh sieve. Neutral detergent fiber (NDF) indicates the total content of hemicellulose, cellulose and lignin, and acid detergent fiber (ADF) indicates the total contents of cellulose and lignin (Van Soest 1994, Onoda et al. 2011). We measured the proportions of NDF and ADF on an ash-free mass basis using the Van Soest method (Van Soest 1994). Then, NDF (g cm$^{-3}$) and ADF (g cm$^{-3}$) were recalculated by the product of WD and their proportions of NDF and ADF in wood DM. Thus, NDF and ADF were expressed per unit volume.

**Seasonal minimum water potentials**

The seasonal minimum water potential ($P_{min}$) was measured between 12:00 h and 14:00 h on sunny days during the dry season from November 2013 to April 2014. We wrapped the leaf-bearing branches for evergreen species and leafless terminal twigs for deciduous species with plastic bags and aluminum foil in the evening before the measurement days. We assumed that the leaf and branch water potentials were equilibrated. The midday water potentials of bagged leaves were measured using a pressure chamber (PMS). Because of leaf-shedding in deciduous species, we used leafless terminal twigs to determine stem $P_{min}$ during the dry season. Our recent study in this Chinese savanna found that the were no significant differences when determining stem water potentials using leaf and leafless terminal twigs after fully equilibrium (Chen et al. 2021). Seasonal minimum water potential ($P_{min}$) was the lowest midday water potential under natural conditions during dry periods.

**Phylogeny tree**

We present phylogenetic analyses of rbcL sequences (see Table S3 available as Supplementary data at *Tree Physiology* Online) from 20 species from GenBank (https://www.ncbi.nlm.nih.gov/). The alignments were carried out in Clustal X (Aiyar 2000). Maximum likelihood analysis was carried out using IQ-TREE v.2.1.1 software (Minh et al. 2020). The DNA substitution models was chosen as ‘GTR + F + R3’. One thousand bootstrap replicates were performed for each analysis to obtain confidence support. Finally, a phylogeny tree at the species level was constructed for all 20 species in this study (Figure S2 available as Supplementary data at *Tree Physiology* Online).

**Data analysis**

All statistical analyses were conducted using Rstudio with R 3.6.3 (R Development Core Team 2017). We compiled a dataset with species mean functional trait values. Species with greater absolute values of $P_{min}$ ($-P_{min}$) would experience more severe seasonal water stress. The values of $P_{min}$ were converted from negative to positive ($-P_{min}$) in principal component analysis (PCA) and correlation analyses. All traits were tested for normality using the Shapiro–Wilks test (Patrick 1982), and logarithm-transformed as necessary to improve normality and homoscedasticity before statistical analyses (Table S1 available as Supplementary data at *Tree Physiology* Online). The differences in traits between the deciduous and evergreen groups were tested using one-way analysis of variance (ANOVA). Principal component analysis was performed to evaluate the multiple relationships among functional traits and species, using the ‘FactoMinerR’ package (Lê et al. 2008).

Pearson’s correlation analyses were conducted to determine the bivariate relationships among traits using the ‘corr.test’ function of the ‘psych’ package. The phylogenetic signal was tested for every trait using Blomberg’s $K$ statistic (Blomberg et al. 2003). A value of $K > 1$ indicated a strong phylogenetic signal of traits, whereas a value of $K$ close to 0 indicated no phylogeny signal of traits (Blomberg et al. 2003). Furthermore, we assessed whether these correlations were the result of repeated evolutionary divergences using PICs combining the ‘APE’ package (Paradis and Schliep 2019), and ‘Picante’ package in R (Webb et al. 2010).

Standardized major axis (SMA) regression was used to test the bivariate relationships between hydraulic efficiency traits ($K_s$ and $K_L$) and biomechanical traits (MOE and MOR). The relationships of hydraulic and biomechanical traits with structural and anatomical traits were also analyzed using the ‘smatr’ package (Warton and Weber 2002). We compared the differences in the slopes and intercepts between the deciduous and evergreen groups.

**Results**

Deciduous species had higher $K_s$, $K_L$ and $D_h$, but lower MOR, MOE, VD, VWT and FLW, than evergreen species ($P < 0.05$, Table 2). In addition, evergreen species had a more negative $P_{min}$ ($-2.94 \pm 0.17$ MPa) compared with the deciduous group ($-4.03 \pm 0.27$ MPa; $P < 0.05$, Table 2). Evergreen and deciduous species did not, however, significantly differ in HV,
MVL and FLD (P > 0.05, Table 2). For all traits, Blomberg’s K-values were <1, and the corresponding P-values were higher than 0.05 (see Table S4 available as Supplementary data at *Tree Physiology Online*), indicating no phylogenetic signal.

Principal component analysis results based on the 15 traits of 20 savanna woody species showed that the first axis and second axis accounted for 56.7 and 13.7% of the total variance, respectively (Figure 1). The first axis was positively correlated with traits representative of high mechanical strength (i.e., MOR, MOE, WD, NDF and ADF) and strong drought exposure (−P$_{\text{min}}$). The traits related to high hydraulic efficiency (i.e., $K_s$, $K_l$, and $D_h$) clustered negatively on the first axis. The second axis was loaded by HV, MVL and FLD (Figure 1a). In addition, evergreen and deciduous woody species were well separated along the first PCA axis. Deciduous species mainly tended to be positioned on the negative side of the first axis with high hydraulic efficiency, whereas evergreen species tended to be positioned on the positive side of the first axis with high mechanical strength and strong drought exposure (−P$_{\text{min}}$; Figure 1b). However, there was some overlap between a deciduous shrub species (*Strophiolechia fimbrialyx*) and two evergreen tree species (*Psidium guajava; Figure 1b*).

Both MOR and MOE were negatively related to $K_s$ either across the 20 studied species, or separately within evergreen and deciduous species (Figure 2, Tables S2 and S5 available as Supplementary data at *Tree Physiology Online*). For the regressions of $K_s$ and mechanical traits (MOR and MOE), the SMA slopes were significant, but the intercepts were no significant between the deciduous and evergreen groups (Table S2 available as Supplementary data at *Tree Physiology Online*).

There was a significant correlation between MOR and $K_l$, and between MOE and $K_l$ across all species (Figure 2 and Table S2 available as Supplementary data at *Tree Physiology Online*). Both MOE and MOR were also negatively correlated with $K_s$ and $K_l$ when analyzed using PICs (P < 0.001, Table S5 available as Supplementary data at *Tree Physiology Online*). Species with higher xylem mechanical strength tend to have lower hydraulic efficiency. We found trade-offs between xylem hydraulic efficiency and mechanical strength irrespective of the effects of phylogeny.

The SMA regressions across all 20 species showed that $K_s$ was significantly and positively associated with $D_h$, but negatively correlated with WD, NDF and ADF (P < 0.05, Figure 3, Table S2 available as Supplementary data at *Tree Physiology Online*). Both MOR and MOE were significantly correlated with WFT (P < 0.05), but were not significantly related to FLD across species (P > 0.05, see Table S5 available as Supplementary data at *Tree Physiology Online*). MOR was positively related to WD, NDF and ADF across all 20 species or within evergreen and deciduous species, respectively (P < 0.05, Figure 4). Furthermore, the SMA slopes were marginally different between the deciduous and evergreen groups for the regressions of mechanical traits (MOR) with WD and fiber contents (NDF and ADF; see Table S2 available as Supplementary data at *Tree Physiology Online*).

**Discussion**

In this study, we compared the hydraulic efficiency and mechanical strength of evergreen and deciduous woody species in a Chinese savanna ecosystem, and tested the relationships...
Xylem hydraulic efficiency and mechanical strength

Figure 1. Factor loadings (a) and species scores (b) PCA for 15 functional traits and 20 species in a savanna ecosystem, Southwest China. Species codes and trait abbreviations are given in Tables 1 and 2, respectively.

Figure 2. Relationships between hydraulic efficiency and biomechanical traits in the xylems of evergreen and deciduous species in a savanna ecosystem, Southwest China. Trait abbreviations are shown in Table 2. Standardized major axis (SMA) regression was fitted for the evergreen and deciduous groups, respectively. See Table S2 available as Supplementary data at Tree Physiology Online for SMA regression results.
between hydraulic and mechanical functions and underlying structural and anatomical traits. Our results revealed a distinct divergence in hydraulic and mechanical traits between the evergreen and deciduous groups. Specifically, deciduous species had a higher xylem hydraulic efficiency, whereas evergreen species had higher mechanical strength. In addition, xylem anatomical traits and fiber contents could explain the hydraulic and mechanical functioning of the Chinese savanna evergreen and deciduous species.

In this study, none of the hydraulic, mechanical, anatomical or chemical traits showed phylogenetic signals. Moreover, the bivariate correlations between traits using PICs were similar to those with raw values of functional traits, suggesting that pairwise relationships between traits were phylogenetically independent in Chinese savanna woody species. Our result was consistent with previous studies in chaparral shrubs of southern California (Pratt et al. 2021a), and tree and liana species of tropical seasonal rainforest in Southwest China (L. Zhang et al. 2019). These results suggested that phylogeny cannot explain the associations among the plant xylem functions well. Here, we discuss the differences between evergreen and deciduous species, and the trade-offs between hydraulic efficiency and mechanical strength and the underlying anatomical and chemical traits irrespective of phylogeny.

**Evergreen and deciduous species differ in hydraulic efficiency and mechanical strength**

Our study was conducted in a semiarid savanna ecosystem where there was a seasonal drought from November to April (Figure S1 available as Supplementary data at Tree Physiology Online). This strong environmental pressure drove ecological differentiation in the leaf phenology of savanna species (Zhang et al. 2007, 2017). Co-occurring evergreen and deciduous species differ in terms of stem hydraulic conductivity and
Figure 4. Relationships between MOR and structural traits within evergreen and deciduous groups in a savanna ecosystem, Southwest China. Trait abbreviations are shown in Table 2. Standardized major axis (SMA) regression was fitted for the evergreen and deciduous groups, respectively. See Table S2 available as Supplementary data at Tree Physiology Online for SMA regression results.

Water use strategies in seasonally tropical dry forests and savannas (Eamus 1999, Chen et al. 2009, Ishida et al. 2010, Markesteijn et al. 2011, Fu et al. 2012, Zhang et al. 2017, S.B. Zhang et al. 2019). Previous studies have shown that $P_{\text{min}}$ acts on plant functional trade-offs under drought stress (Jacobsen et al. 2007, Pratt et al. 2007, Bartlett et al. 2016, Pratt et al. 2021b). In the present study, deciduous woody species exhibited higher $K_w$, $K_l$, and $D_v$, whereas evergreen woody species had higher VD and VWT values. Moreover, the xylems experienced more negative water potential ($P_{\text{min}}$) in evergreen species than in deciduous species under seasonal drought stress. These results suggest that evergreen and deciduous woody species adopt conservative and acquisitive water use strategies, respectively (Eamus 1999, Ishida et al. 2010, Poorter et al. 2010, Qi et al. 2021). Drought-deciduous tree species maintain higher water transport via an efficient vascular system and carbon gain in the rainy seasons, and maintain a high $P_{\text{min}}$ and drop their leaves to avoid drought damage during seasonal drought (Bartlett et al. 2016); in contrast, on average, evergreen trees can maintain a more negative $P_{\text{min}}$ to tolerate seasonal drought, but this comes at the cost of lower xylem hydraulic efficiency throughout the year (Goldstein et al. 1989, Choat et al. 2005, Chen et al. 2009, Ishida et al. 2010, Fu et al. 2012).

We also found significant differences in MOR, MOE, WD, FWT, NDF and ADF values between the evergreen and deciduous groups, indicating a divergence in mechanical strength in the xylem of Chinese savanna woody species with contrasting leaf phenology. In this study, evergreen species developed high-density xylem (higher WD) and thicker walled vessels and fibers (VWT and FWT), as well as investing more support...
costs in xylem DM (higher NDF and ADF), to enhance xylem biomechanical strength (higher MOR and MOE) compared with the deciduous group. Greater xylem mechanical stability in evergreen species can promote higher resistance to bending and twisting, and can reduce damage by herbivores compared with that experienced by deciduous species (Niklas 1992, Read and Stokes 2006, Onoda et al. 2010).

Our results showed that hydraulic and mechanical traits differed between deciduous and evergreen species in the Chinese savanna, which was driven by the selective pressure of seasonal drought. These results provide insights into conservative and acquisitive life-history strategies for evergreen and deciduous species, respectively. Specifically, deciduous species maintained a higher water transport capacity and promoted fast growth during the rainy season when water availability was abundant, whereas they shed leaves when water was limiting; in contrast, evergreen species exhibited a higher mechanical strength at the cost of a reduction in hydraulic efficiency.

The trade-offs between hydraulic efficiency and mechanical strength are related to structural and anatomical traits

With or without considering phylogenetic effects, there was a significant and negative correlation between $K_s$ and MOR across species or within evergreen and deciduous species, separately. This result revealed a trade-off between hydraulic efficiency and mechanical strength, with or without considering phylogeny, which is consistent with previous studies (Wagner et al. 1998, Fan et al. 2017, Xiao et al. 2021). It has been suggested that this trade-off reflects the conflicting structural requirements for xylem design and fitness in plant species (Baas et al. 2004, Zhang et al. 2013). At the xylem tissue scale, the partitioning of vessels and fibers provides dual functionality of water transport and mechanical support (Lachenbruch and McCulloh 2014, Pratt and Jacobsen 2017, Pratt et al. 2021a). Moreover, the traits related to mechanical strength (MOR, MOE, WD, NDF, ADF and FWT) and drought exposure ($P_{\text{min}}$) clustered together on the positive site of PC axis 1, whereas the traits related to water transport efficiency ($K_s$, $K_t$ and $D_h$) clustered together on the negative site of PC axis 1 (Figure 1). Thus, our results imply that the trade-offs between hydraulic efficiency and mechanical strength are related to structural and anatomical traits.

Hydraulic conductivity increases with the fourth power of vessel diameter according to the Hagen-Poiseuille law (Tyree and Zimmermann 2002), and wider and longer vessels would contribute to a greater water flow rate for a given pressure gradient (Choat et al. 2005). A small increase in $D_h$ can greatly alter xylem hydraulic efficiency (Tyree and Ewers 1991, Tyree et al. 1994). In the present study, we found that the water transport ability in the xylem ($K_t$) was significantly and positively associated with $D_h$ across 20 savanna woody species and within the deciduous group (Figure 3). However, $K_s$ was affected by MVL in neither Pearson’s correlation nor PICs. This result suggested that xylem hydraulic efficiency was determined by $D_h$, rather than by MVL, which was consistent with previous studies (Sperry et al. 2005, Jacobsen et al. 2015). The reason for this result may be that the vessel length was not directly connected to vessel width, and xylem water transport was determined not only by vessel size but also by the inter-vessel pit properties, such as pit area and pit ultra-microstructure (Sperry et al. 2005, Wheeler et al. 2005, Lens et al. 2011, Jacobsen et al. 2015). In this study, we found a close correlation between $K_t$ and $D_h$ across 20 species and within deciduous group, but no relationship between $K_t$ and HV. Xylems with wider $D_h$ can have a higher $K_s$, and a concurrent increase in $K_t$ in Chinese savanna woody species.

The present study also reveals that there is a close correlation between mechanical strength (e.g., MOR and MOE) and fiber content in the xylem (e.g., NDF and ADF), both across species and within evergreen and deciduous species. A previous study has shown that a high fiber content contributes to higher mechanical resistance in leaves (Onoda et al. 2011). To our knowledge, this is the first study to test the associations between fiber chemical composition and xylem mechanical traits. High mechanical strength of the xylem can be achieved by increasing the support cost (e.g., hemicellulose, cellulose and lignin). Our results show that a greater allocation to fiber indeed enhances xylem stiffness and mechanical stability. Moreover, the SMAs results showed marginally different slopes for the regression of mechanical traits and fiber contents between evergreen and deciduous species. Although both MOR and MOE increased with increasing NDF and ADF, there was a higher mechanical strength and stiffness for a given fiber content per volume in the evergreen group than in the deciduous group. Plants may alter the anatomical design of the xylem to enhance mechanical strength, e.g., increasing FWT, altering cellulose microfibril angle and fiber arrangement (Chave et al. 2009, Pratt and Jacobsen 2017). In this study, we found correlations between MOR and FWT, and between MOE and FWT across species; however, these correlations weakened or became insignificant when only considering the evergreen or deciduous group. The significant relationship between MOR and FWT, and between MOE and FWT across species may be due to the divergence of evergreen and deciduous species in mechanical and fiber traits, and was clustered at different positions. Our results suggest that fiber content per volume, rather than fiber anatomical traits, strongly affects xylem mechanical strength.

Our results showed that WD was negatively associated with hydraulic conductivity, but positively associated with mechanical strength and stiffness. Wood density is a comprehensive functional trait that can be used to indicate the conflicting demands for water transport and biomechanics (Santiago et al. 2004, Pratt et al. 2007, Markesteijn et al. 2011, Rosell et al. 2014, Pratt and Jacobsen 2017). It has been suggested that WD is
mainly affected by the fiber wall and lumen fractions in the xylem (Ziemińska et al. 2013). With wider vessels in the xylem, there is less space for lignified fiber cells (Wagner et al. 1998). In this study, there was a negative correlation between WD and D\text{h}, but a positive correlation between WD and FWT, and between WD and VWT across species in both Pearson’s analyses and PICs. A high WD was associated with a thicker fiber wall and higher fiber content, but a lower D\text{h}, which has been proposed to provide higher mechanical strength against breakage at the cost of hydraulic efficiency (Jacobsen et al. 2005, Plavcová et al. 2019). These structural and chemical constraints govern the trade-offs between xylem hydraulic efficiency and mechanical strength (Pratt and Jacobsen 2017).

Conclusions

In summary, we found a distinct divergence in hydraulic efficiency and mechanical strength in Chinese savanna species with contrasting leaf phenology, revealing conservative and acquisitive life-history strategies for evergreen and deciduous species, respectively. Our results also showed trade-offs between hydraulic efficiency and mechanical strength across Chinese savanna species, and these trade-offs were modulated by a suite of traits, including WD, vessel and fiber traits and fiber content. Taken together, xylem hydraulic efficiency was mainly driven by D\text{h}, whereas high levels of xylem mechanical strength were associated with WD, NDF and ADF. The pairwise relationships between traits were phylogenetically independent. The differentiation in stem hydraulics and biomechanics between evergreen and deciduous species suggests divergent life-history strategies, which are closely linked to plant growth and performance. These findings illustrate the hydraulic and biomechanical adaptations of Chinese evergreen and deciduous savanna species to long-term dry-hot environments. It is increasingly critical for future research to explore how hydraulic and mechanical functions affect plant performance in terms of growth, survival and reproduction, and so species fitness. Furthermore, previous studies have suggested some coordination or trade-offs among mechanical support, hydraulic efficiency and safety, storage of water, carbohydrates, nutrients and defensive secondary chemical compounds in wood (Pratt et al. 2007, Chave et al. 2009, Zhang et al. 2013, Plavcová et al. 2019, van der Sande et al. 2019, Pratt et al. 2021a). Therefore, further studies are needed to test the potential associations of the efficiency–safety–mechanics–capacitance correlations in xylems to understand the conflicting structural and functional requirements for xylem design and, correspondingly, on plant performance within ecosystems and across ecosystems.

Authors’ contributions

S.-B. Z. designed the experiment; S.-B. Z., G.-J. W., Y.-Y. Q. and L.-Y.Y. collected the data; S.-B. Z. and Y. S. analyzed the data; and S.-B. Z. led the writing. All authors contributed critically to the drafts and gave final approval for publication.

Supplementary data

Supplementary data for this article are available at Tree Physiology Online.

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Conflict of interest

The authors declare that there are no conflicts of interest.

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References

Aiyar A (2000) The use of CLUSTAL W and CLUSTAL X for multiple-sequence alignment. Methods Mol Biol 132:221–241.
Alvarez-Clare S, Kitajima K (2007) Physical defence traits enhance seedling survival of neotropical tree species. Funct Ecol 21:1044–1054.
Antonio JB, Silvia M, Javier G, Alejandro M, Karen M, Natalia T, Maria EF (2017) Wood density and anatomy of three Eucalyptus species: implications for hydraulic conductivity. Forest Systems 26:e010.
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.
Bartlett MK, Klein T, Jansen S, Chaot B, Sack L (2016) The correlations and sequence of plant stomatal, hydraulic, and wilting responses to drought. Proc Natl Acad Sci USA 113:13098–13103.
Blomberg SP, Garland T, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745.
Brodrribb TJ, Feld T (2000) Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. Plant Cell Environ 23:1381–1388.
Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. Ecol Lett 12:351–366.
Chen JW, Zhang Q, Cao KF (2009) Inter-species variation of photosynthetic and xylem hydraulic traits in the deciduous and evergreen Euphorbiaceae tree species from a seasonally tropical forest in south-western China. Ecol Res 24:65–73.

Tree Physiology Online at http://www.treephys.oxfordjournals.org
Chen YJ, Chaot B, Sterck F et al. (2021) Hydraulic prediction of drought-induced plant dieback and top-kill depends on leaf habit and growth form. Ecol Lett 24:2350–2363.

Chen ZC, Zhu SD, Zhang YT, Luan JW, Li S, Sun PS, Wan XC, Liu SR (2020) Tradeoff between storage capacity and embolism resistance in the xylem of temperate broadleaf tree species. Tree Physiol 40:1029–1042.

Choa B, Marilyn CB, Jon GL, Joseph AMH (2005) Hydraulic architecture of deciduous and evergreen dry rainforest tree species from north-eastern Australia. Trees 19:305–311.

Eamus D (1999) Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. Elsevier Ltd, Oxford, pp 11–16.

Fan DY, Jie SL, Liu CC, Zhang XY, Xu XW, Zhang SR, Xie ZQ (2011) The trade-off between safety and efficiency in hydraulic architecture in 31 woody species in a karst area. Tree Physiol 31:865–877.

Fan ZX, Sterck F, Zhang SB, Fu PL, Hao GY (2017) Tradeoff between stem hydraulic efficiency and mechanical strength affects leaf–stem allometry in 28 Ficus tree species. Front Plant Sci 8:1619.

Fan ZX, Zhang SB, Hao GY, Slík JWF, Cao KF (2012) Hydraulic conductivity traits predict growth rates and adult stature of 40 Asian tropical tree species better than wood density. J Ecol 100:732–741.

Fu PL, Jiang YJ, Wang AY, Brodribb TJ, Zhang JL, Zhu SD, Cao KF (2012) Stem hydraulic traits and leaf water-stress tolerance are coordinated with the leaf phenology of angiosperm trees in an Asian tropical dry karst forest. Ann Bot 110:189–199.

Gere JM, Timoshenko SP (1999) Mechanics of materials, 4th SI edn. Tanley Thones (Publisher) Ltd, Cheltenham, UK.

Goldstein G, Rada F, Rundel P, Azocar A, Orozco A (1989) Gas exchange and water relations of evergreen and deciduous tropical savanna trees. Ann Sci Forest 46:448s–453s.

Grace J, Jose JS, Meir P, Miranda HS, Montes RA (2006) Productivity and carbon fluxes of tropical savannas. J Biogeogr 33:387–400.

Greenidge JM, Ishida YJ, Leuschner C (1992) Plant biomechanics: an engineering approach to plant form and function. University of Chicago Press, Chicago, Illinois, USA.

Hoeber S, Leuschner C, Köhler L, Arias-Aguilar D, Schuldt B (2014) The importance of hydraulic conductivity and wood density to growth performance in eight tree species from a tropical semi-dry climate. For Ecol Manage 350:126–136.

Ishida A, Hayaraya H, Yazaki K et al. (2010) Seasonal variations of gas exchange and water relations in deciduous and evergreen trees in monsoonal dry forests of Thailand. Tree Physiol 30:935–945.

Jacobsen AL, Ewers FW, Pratt RB, Paddock WA, Davis SD (2005) Do xylem Fibers affect vessel cavitation resistance? Plant Physiol 139:546–556.

Jacobsen AL, Agenbag L, Esler KJ, Pratt RB, Ewers FW, Davis SD (2007a) Xylem density, biomechanics and anatomical traits correlate with water stress in 17 evergreen shrub species of the Mediterranean-type climate region of South Africa. J Ecol 95:171–183.

Jacobsen AL, Pratt RB, Ewers FW, Davis SD (2007b) Cavitation resistance among 26 charpalar species of southern California. Ecol Monogr 77:99–115.

Jacobsen AL, Rodriguez-Zaccaro FD, Lee TF, Valdivinos J, Toschi HS, Martinez JA, Pratt RB (2015) Grapevine xylem development, architecture, and function. In: Hacke U (ed), Functional and ecological xylem anatomy (pp. 133–162). Springer, Cham, pp 133–162.

Jin, Ou XK (2000) Vegetations in the hot and dry Valleys along the Yuanjiang, Nuijiang, Jinshajiang, and Lanchangjiang Rivers. Yunnan University Press, Kunming.
Pratt RB, Jacobsen AL (2017) Conflicting demands on angiosperm xylem: tradeoffs among storage, transport and biomechanics. Plant Cell Environ 40:897–913.

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, Percolla MI, De Guzman ME, Traugh CA, Tobin MF (2021a) Trade-offs among transport, support, and storage in xylem from shrubs in a semiarid chaparral environment tested with structural equation modeling. Proc Natl Acad Sci USA 118:e2104336118.

Pratt RB, Tobin MF, Jacobsen AL et al. (2021b) Starch storage capacity of sapwood is related to dehydration avoidance during drought. Am J Bot 108:91–101.

Qi JH, Fan ZX, Fu PL, Zhang YJ, Sterck F (2021) Differential determinants of growth rates in subtropical evergreen and deciduous juvenile trees: carbon gain, hydraulics and nutrient-use efficiencies. Tree Physiol 41:12–23.

Quigley M, Platt W (2003) Composition and structure of seasonally deciduous forests in the Americas. Ecol Monogr 73: 87–106.

R Development Core Team (2017) R: a language and environment for statistical computing.: R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Raimondo F, Trifilo P, Guillo M, Buffa R, Nardini A, Saileo S (2009) Effects of reduced irradiance on hydraulic architecture and water relations of two olive clones with different growth potentials. Environ Exp Bot 66:249–256.

Read J, Stokes A (2006) Plant biomechanics in an ecological context. Am J Bot 93:1546–1565.

Rosell JA, Gleason S, Méndez-Alonzo R, Chang Y, Westoby M (2014) Bark functional ecology: evidence for tradeoffs, functional coordination, and environment producing bark diversity. New Phytol 201:486–497.

Sanchez-Martinez P, Martinez-Vilalta J, Dexter KG, Segovia RA, Mencuccini M (2020) Adaptation and coordinated evolution of plant hydraulic traits. Ecol Lett 23:1599–1610.

Santiago LS, Goldstein G, Meinzner FC, Fisher JB, Machado K, Woodruff D, Jones T (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. Oecologia 140:543–550.

Santini NS, Schnitz N, Bennion V, Lovelock CE (2013) The anatomical basis of the link between density and mechanical strength in mangrove branches. Funct Plant Biol 40:400–408.

Solbrig OT, Medina E, Silva JF (1996) Biodiversity and savanna ecosystem processes: a global perspective. Springer, Berlin.

Sperry JS, Tyree MT (1988) Mechanism of water-stress-induced xylem embolism. Plant Physiol 88:581–587.

Sperry JS, Hacke UG, Wheeler JK (2005) Comparative analysis of end wall resistivity in xylem conduits. Plant Cell Environ 28: 456–465.

Sterck FJ, Van Gelder HA, Poorter GL (2006) Mechanical branch constraints contribute to life-history variation across tree species in a Bolivian forest. J Ecol 94:1192–1200.

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

Tyree MT, Zimmermann M (2002) Xylem structure and the ascent of sap. Springer, Berlin, Heidelberg.

Tyree MT, Davis SD, Cochard H (1994) Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? IAWA J 15:335–360.

Van Soest PJ (1994) Nutritional ecology of the ruminant. Cornell Press, Ithaca, NY.

van der Sande MT, Poorter L, Schnitzer SA, Engelbrecht BMJ, Markesteijn L (2019) The hydraulic efficiency-safety trade-off differs between lianas and trees. Ecology 100:e02666.

Wagner KR, Ewers FW, Davis SD (1998) Tradeoffs between hydraulic efficiency and mechanical strength in the stems of four co-occurring species of chaparral shrubs. Oecologia 117:53–62.

Warton DI, Weber NC (2002) Common slope tests for bivariate errors-in-variables models. Biom J 44:161–174.

Webb CO, Ackerly DD, Morlon H, Helmus MR, Cowan PD, Blomberg SP, Kembel SW, Cornwell WK (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464.

Wheeler J, Sperry J, Hacke U, Hoang N (2005) Inter-vessel pitting and cavitation in woody Rosaceae and other vellushed plants: a basis for a safety versus efficiency trade-off in xylem transport. Plant Cell Environ 28:800–812.

Xiao Y, Song Y, Wu FC, Zhang SB, Zhang JL (2021) Divergence of stem biomechanics and hydraulics between Bauhinia lianas and trees. AoB Plants 13:plab016.

Zhang JL, Zhu JJ, Cao KF (2007) Seasonal variation in photosynthesis in six woody species with different leaf phenology in a valley savanna in southwestern China. Trees 21:631–643.

Zhang L, Chen YJ, Ma KP, Bongers F, Sterck FJ (2019) Fully exposed canopy tree and liana branches in a tropical forest differ in mechanical traits but are similar in hydraulic traits. Tree Physiol 39: 1713–1724.

Zhang SB, Cao KF, Fan ZX, Zhang JL (2013) Potential hydraulic efficiency in angiosperm trees increases with growth-site temperature but has no trade-off with mechanical strength. Glob Ecol Biogeogr 22:971–981.

Zhang SB, Zhang JL, Cao KF (2017) Divergent hydraulic safety strategies in three co-occurring Anacardiaceae tree species in a Chinese savanna. Front Plant Sci 7:2075.

Zhang SB, Weng JG, Yang DX (2019) Drought-induced mortality is related to hydraulic vulnerability segmentation of tree species in a savanna ecosystem. Forests 10:697.

Zhao H, Liang ZM, Zhang YJ, Jiang B, Cai J (2021) Hydraulic efficiency at the whole tree level stably correlated with productivity over years in 9 poplar hybrids clones. For Ecol Manage 496:119382.

Zhu H, Tan YH, Yan LC, Liu FY (2020) Flora of the savanna-like vegetation in hot dry valleys, southwestern China with implications to their origin and evolution. Bot Rev 86:102–127.

Ziemiańska K, Butler DW, Gleason SM, Wright IJ, Westoby M (2013) Fibre wall and lumen fractions drive wood density variation across 24 Australian angiosperms. AoB Plants 5:plt046.

Zimmermann MH (1978) Hydraulic architecture of some diffuse-porous trees. Can J Bot 56:2286–2295.