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Potential hydraulic efficiency in angiosperm trees increases with growth-site temperature but has no trade-off with mechanical strength

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ABSTRACT

Aim Xylem structures are closely related to a tree's hydraulic efficiency and mechanical stability, both of which affect the life history and ecological strategy of a species. Although mechanical strength and hydraulic capacity can be shaped by the environment, no such associations between hydraulic efficiency and climatic variables have been reported across a wide range of tree species.

Location Yunnan, south-west China.

Methods We compiled a data set for vessel density, vessel diameter (D), potential hydraulic conductivity (K_p), wood density (WD), modulus of rupture (MOR) and modulus of elasticity (MOE) from 316 angiosperm tree species. Our objective was to examine the correlations among xylem traits and climatic variables. We hypothesized that both hydraulic efficiency and mechanical strength would vary along climatic gradients, but that a trade-off would occur between them.

Results All xylem traits varied significantly across species, but the magnitudes of variation were greater for vessel traits than for mechanical properties. Values for K_p and D increased with mean annual temperature (MAT) in both evergreen and deciduous trees, but they were significantly correlated with aridity index (AI) in evergreen species only. Both WD and MOR were significantly correlated with MAT only in evergreen trees. MOR decreased with increasing AI in the evergreens, but not in deciduous trees. These findings indicated that xylem development in evergreens is more sensitive to environmental changes than in deciduous trees. However, stem hydraulic traits are independent of mechanical properties.

Main conclusions Consistent with our hypothesis, both hydraulic efficiency and mechanical strength of angiosperm trees are influenced by the environment, with temperature having a more important effect on hydraulic efficiency than precipitation. However, no trade-off exists between efficiency and strength. This absence of a link is explained because angiosperms have xylem tissue that specifically functions in either mechanical strength or water transport.

Keywords

Aridity index, climate, hydraulic efficiency, mechanical strength, temperature, xylem structure.

INTRODUCTION

Stem xylem structure, which is strongly related to hydraulic efficiency and mechanical stability, influences the growth, mortality, life history and geographical distribution of tree species

(Santiago *et al.*, 2004; Jacobsen *et al.*, 2007; Markesteijn *et al.*, 2011a). For example, the growth rate of rain forest trees is correlated positively with potential specific hydraulic conductance but negatively with wood density (WD), while their survival rate is positively related to WD (Poorter *et al.*, 2010). Both water

availability and air temperature can affect the development of xylem structure, which in turn influences the water supply and photosynthetic gas exchange in trees (Davis *et al.*, 1999; Sperry *et al.*, 2006; Gleason *et al.*, 2012). Shifts in rainfall patterns and increasing temperatures associated with climate change are likely to cause forest decline due to hydraulic failure in both arid and mesic habitats (Choat *et al.*, 2012). Therefore, understanding the influences of climatic factors on hydraulic efficiency and mechanical strength in trees is essential for predicting the processes and services of forest ecosystems.

Variations in xylem traits are examples of ecological strategies in trees (Preston *et al.*, 2006; van Gelder *et al.*, 2006). Vessel density and diameter vary with environmental gradients (Baas *et al.*, 2004), and drought and shade tolerance are related to hydraulic properties and WD (Markesteijn *et al.*, 2011a). Xeric-cultivated plants have a greater percentage of narrow vessels, whereas mesic-cultivated plants exhibit the opposite tendency (Stevenson & Mauseth, 2004). Smaller-diameter vessel lumens are produced in angiosperms when plants grow in habitats associated with dry soil or the risk of freezing (Sperry *et al.*, 2006; Fisher *et al.*, 2007). Xylem mechanical stability is correlated with tolerance to water stress (Jacobsen *et al.*, 2007), perhaps because of increased structural resistance against implosion (Jacobsen *et al.*, 2005). However, it is still unclear how vessel traits vary over a climatic gradient for a large number of species or geographic regions.

Both xylem hydraulic and mechanical traits are linked to the life-history 'strategy' of a tree (Choat *et al.*, 2005; Fu *et al.*, 2012). Whereas deciduous species drop their leaves during an unfavourable growing season, evergreen species maintain a canopy and transpire throughout the entire year (Eamus, 1999). Generally, deciduous species tend to possess lower WD, wider xylem vessels, higher hydraulic efficiency and greater susceptibility to embolism than do evergreen species (Eamus, 1999; Choat *et al.*, 2005; Fu *et al.*, 2012). However, Cavender-Bares & Holbrook (2001) have found that evergreen oaks have larger vessel diameters and higher hydraulic efficiency than deciduous oaks because the former have a lower ratio of leaf-to-sapwood areas.

Xylem evolution can be viewed as a 'trade-off triangle' among mechanical strength, conductive efficiency and resistance to embolism. Such trade-offs result from the conflicting structural requirements for xylem design in trees (Baas *et al.*, 2004; Sperry *et al.*, 2008). Resistance to vessel implosion, induced by a pressure difference between air- and water-filled conduits, is positively correlated with cavitation resistance (Hacke & Sperry, 2001; Jacobsen *et al.*, 2007). Xylem mechanical strength, which is largely related to WD, is measured in terms of the modulus of rupture (MOR) and the longitudinal modulus of elasticity (MOE) (van Gelder *et al.*, 2006). All three traits are correlated positively with cavitation resistances, but negatively with hydraulic efficiency (Preston *et al.*, 2006; Sperry *et al.*, 2006; Poorter *et al.*, 2010). In the dry woodlands of California, species experiencing the most negative seasonal water potential have higher values for WD, MOR, fibre wall area, and cavitation resistance, all of which contribute to greater tolerance to drought stress (Jacobsen *et al.*, 2007). However, Larjavaara &

Muller-Landau (2010, 2012) have suggested that the associations among WD, risk of trunk breakage and xylem implosion are not causal, but instead reflect the correlated selection of other traits in long-lived trees.

The contrasting structural requirements for xylem design in trees also affect the evolution of water transport efficiency and mechanical strength (Pittermann, 2010). Xylem-specific conductivity (K_s), i.e. the rate of sap flow per cross-sectional area of xylem across a given pressure gradient, is used as a measure of transport efficiency in the sapwood. A high K_s is achieved by a high vessel diameter-to-number ratio or by a high vessel lumen fraction in the sapwood, as reported across a range of biomes in eastern Australia (Gleason *et al.*, 2012). Species with lower WD and MOE have a higher K_s (Markesteijn *et al.*, 2011a; Gleason *et al.*, 2012). Moreover, significant trade-offs have been confirmed between hydraulic conductivity and mechanical strength in some species (Wagner *et al.*, 1998; Hacke *et al.*, 2006; Markesteijn *et al.*, 2011b). This is because a high WD should imply denser cell packing that results from narrower vessel lumens (Zanne *et al.*, 2010; Markesteijn *et al.*, 2011a). Thus, those narrower vessels have a higher ratio of cell wall to lumen area and a lower hydraulic efficiency (Hacke & Sperry, 2001). By comparison, some studies have found no trade-off between strength and hydraulic efficiency due to the sophisticated relations among xylem structures (Woodrum *et al.*, 2003; Fan *et al.*, 2011). The risk of embolism is related to vessel diameter under freeze-thaw conditions, but is also associated with the size of membrane pores of the pits when plants are growing under drought. Consequently, a species can simultaneously achieve large vessels and high hydraulic conductivity as well as narrower membrane pores and stronger resistance to embolism (Westoby & Wright, 2006). Based on these conflicting reports, the evidence for a trade-off between mechanical strength and hydraulic efficiency is ambiguous, and this possible trade-off remains unknown across a wide range of species (Zanne *et al.*, 2010; Gleason *et al.*, 2012).

In the present study, we examined a data set for xylem traits of woody angiosperm species from a diverse array of forest ecosystems within Yunnan Province in south-western China. Our principal objectives were to determine how xylem traits vary over climatic gradients, and to identify any correlations between hydraulic efficiency and mechanical stability. We tested the following three predictions: (1) species from cold habitats would be hydraulically less efficient because of selection for smaller vessel diameters at a lower temperature; (2) species growing in environments with less precipitation would have greater mechanical strength and lower hydraulic efficiency to facilitate water extraction from drying soils but without creating a rise in the water-potential gradient; and (3) a trade-off would exist between efficiency and strength because of the conflicting structural requirements for xylem design.

MATERIALS AND METHODS

We compiled published data for xylem traits from 316 angiosperm species in 42 families within Yunnan Province in

Table 1 The variables of wood traits used in the present study.

Variables	Definition	Unit
VD	Vessel density (vessel number per cross-sectional area of sapwood)	Number mm ⁻²
<i>D</i>	Vessel lumen diameter	mm
<i>K_p</i>	Potential specific stem conductivity (estimated from sapwood vessel diameter and vessel density based on Poiseuille's law for fluid flow through pipes)	kg m ⁻¹ MPa ⁻¹ s ⁻¹
WD	Dry wood density (dry mass at 15% moisture content divided by fresh volume)	kg m ⁻³
MOR	Modulus of rupture of wood at 15% moisture content (breaking strength)	MPa
MOE	Modulus of elasticity of wood at 15% moisture content (resistance to bending)	GPa

south-western China (Luo, 1989; Zhang *et al.*, 1989; Ye *et al.*, 1999). Woody tissue was collected from 46 sites across the latitudes of 21°9' N to 29°15' N, where elevations ranged from 130 m to 2390 m (Appendix S1 in Supporting Information). At each site, 3 to 15 trees were sampled per species, and mean values were calculated from these references for vessel density (VD), vessel diameter (*D*), wood density (WD), modulus of rupture (MOR) and modulus of elasticity (MOE) (terms defined in Table 1). Values for WD, MOR and MOE were based on a 15% moisture content.

The mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) were calculated from regression models derived from data in climatic records (1961 to 2004) from 119 meteorological stations in Yunnan Province. These readings were based on the longitude, latitude and elevation of each sampling site (Appendix S1). Values for MAT ranged from 11.4 to 22.6 °C, while MAP was between 738.6 and 2250.8 mm. Potential evapotranspiration (PET, mm) was calculated according to the FAO Penman–Monteith equation (Allen *et al.*, 1998):

$$\text{PET} = \frac{0.408\Delta(R_n - G) + \gamma \frac{900}{T + 273} u_2 (e_s - e_a)}{\Delta + \gamma(1 + 0.34u_2)} \quad (1)$$

where R_n is net radiation (MJ m⁻² day⁻¹), G is soil heat flux (MJ m⁻² day⁻¹), T is air temperature (°C), u_2 is wind speed (m s⁻¹), e_s is saturation vapour pressure (kPa), e_a is actual vapour pressure (kPa), Δ is the slope of the saturation vapour pressure curve at air temperature T (kPa °C⁻¹) and γ is the psychrometric constant (kPa °C⁻¹). Rates of PET were calculated using *AWSET* software (Hess, 2002; Fan & Thomas, 2012). The aridity index (AI) was defined as the ratio of potential evapotranspiration to precipitation (Arora, 2002).

Potential hydraulic conductivity (K_p) of the sapwood can serve as an indicator of water transport efficiency. Values for K_p are generally higher than those for true conductivity because one discounts the resistances of the vessel perforation plates, pit apertures and cavitated vessels. However, Santiago *et al.* (2004) have reported that K_p determined from the anatomical characteristics of the xylem is positively correlated with leaf-specific hydraulic conductivity measured *in situ*. We calculated the potential conductivity (kg m⁻¹ MPa⁻¹ s⁻¹) for each sampled species according to the Hagen–Poiseuille law:

$$K_p = (\pi\rho/128\eta) \times \text{VD} \times D^4 \quad (2)$$

where ρ is the density of water (998.2 kg m⁻³ at 20 °C), η is the viscosity of water (1.002 × 10⁻⁹ MPa s⁻¹ at 20 °C) (Poorter *et al.*, 2010), and VD and *D* are vessel density and diameter, respectively.

All statistical analyses were performed with R software v. 2.15.0 (R Development Core Team, 2012). Relationships among xylem traits or between traits and environmental variables were examined by Pearson's correlations (*cor.test* function in R package). Aware of the possible correlation between environmental factors across sampling sites, we evaluated the relative contribution of AI and MAT on xylem traits by partial linear regression.

RESULTS

Xylem traits varied considerably across species (Table 2, Appendix S1). The magnitudes of variation were greater for hydraulics-related traits (VD, *D* and K_p) than for mechanical properties (WD, MOE and MOR). Variations in WD, MOR and MOE among species were more than seven-fold, while those in VD, *D* and K_p were more than 10-fold. Among these traits, the variation in K_p was the greatest (430.6-fold) while that of WD was the smallest (3.9-fold). The magnitudes of variation for K_p and VD were significantly greater in evergreen trees. No significant differences in vessel traits were found between evergreen and deciduous species, although the mean values for mechanical properties were larger in the former. The highest hydraulic conductivities were found in the taxa of Juglandaceae, Moraceae and Rutaceae, while the greatest wood densities were found in Fagaceae, Oleaceae and Clusiaceae.

Vessel density (VD) was negatively correlated while *D* and K_p were positively correlated with MAT across species (Fig. 1). Both WD and MOE were negatively correlated with MAT for evergreen species, but not for deciduous trees.

Across all species, MAP was weakly and negatively correlated with VD, and weakly but positively correlated with *D*, K_p , MOE and MOR (Fig. 2). When the sampled taxa were divided into evergreen and deciduous groups, MAP was significantly correlated with VD, *D*, K_p and MOR in the evergreens while only VD was significantly correlated with MAP in deciduous trees (Fig. 2). When all taxa were pooled together, AI was positively

Table 2 Variations in xylem traits and mechanical properties of 316 angiosperm tree species.

Variables	Number	Minimum	Maximum	Mean	<i>n</i> -fold variation
All taxa					
Vessel density	241	1.00	250.00	21.69	255.00
Vessel diameter	244	21.00	290.00	135.51	13.81
Potential specific conductivity	193	1.13	485.27	83.77	430.59
Wood density	283	0.31	1.19	0.659	3.85
Modulus of rupture	194	35.70	249.20	82.09	6.98
Modulus of elasticity	192	5.40	21.90	11.69	4.06
Evergreen trees					
Vessel density	157	1.00	255.00	20.51	255.00
Vessel diameter	154	21.00	290.00	133.45	13.81
Potential specific conductivity	123	1.13	448.22	82.83	396.65
Wood density	184	0.32	1.19	0.68	3.72
Modulus of rupture	127	35.70	249.20	104.84	6.98
Modulus of elasticity	126	5.40	20.40	12.09	3.78
Deciduous trees					
Vessel density	84	2.00	175.00	24.07	87.50
Vessel diameter	90	28.00	287.00	139.40	10.25
Potential specific conductivity	70	2.64	485.27	85.43	183.81
Wood density	99	0.31	1.15	0.63	3.71
Modulus of rupture	67	42.30	195.40	92.69	4.62
Modulus of elasticity	66	5.90	21.90	10.95	3.72

correlated with VD, but negatively with K_p , MOR and MOE (Fig. 3). However, significant correlations of AI with K_p and MOR were found only in the evergreens.

When we controlled for AI, MAT was significantly correlated with all tested xylem traits in evergreen trees, but only with the hydraulics-efficiency traits VD, D and K_p in deciduous species (Table 3). However, when we controlled for MAT, AI was significantly correlated with MOR and VD in the evergreen species but not with any xylem traits in the deciduous trees.

Contrary to our prediction, WD, MOR and MOE were not significantly correlated with the hydraulics-related traits VD, D and K_p across species (Fig. 4). Moreover, separating the data into evergreen and deciduous groups did not improve the significance of these correlations.

DISCUSSION

Correlations have been reported between the mechanical strength of xylem and climatic variables on both global and regional scales (Chave *et al.*, 2006; Zhang *et al.*, 2011). Moreover, a trade-off between hydraulic efficiency and mechanical strength has been found in some species (Davis *et al.*, 1999; Hacke *et al.*, 2006). Here we found that, on a regional scale, potential hydraulic conductivity in angiosperms was correlated significantly with temperature, and no trade-off was noted between efficiency and strength.

Hydraulic efficiency in relation to environment

Our results showed that hydraulic efficiency, as indicated by K_p and D , increased with rising MAT (Fig. 1). This is consistent

with the finding that stem hydraulic conductivity in 26 *Pinus* species is positively correlated with temperature (Creese *et al.*, 2011), and that species native to colder habitats generally have narrower xylem conduits than those from warmer regions (Fisher *et al.*, 2007; Wheeler *et al.*, 2007). The development of vessels and their size and density during cambial growth are thought to be linked to water viscosity in the xylem, which is affected by growth temperature (Thomas *et al.*, 2007). Greater hydraulic capacity at a high temperature may have evolved through selection for increased conduit size in plants growing in environments where the atmospheric evaporative demand is elevated (Maherali & DeLucia, 2001). This change may be advantageous to trees in warm climates because increased specific hydraulic conductivity in the absence of a reduced leaf-to-sapwood area ratio enhances plant conductivity without incurring the negative effects of premature leaf-shed on carbon gain (Maherali & DeLucia, 2001; Creese *et al.*, 2011). Likewise, lower conductivity in cold climates, if associated with smaller conduits, is likely to increase plant resistance to freezing-induced xylem cavitation (Creese *et al.*, 2011).

Pearson analyses demonstrated that potential hydraulic conductivity was improved with increasing MAP or decreasing AI across all species as well as in evergreen trees alone. However, these significant relationships between K_p and MAP or AI did not remain when we controlled for MAT. This indicated that temperature has a greater effect on hydraulic conductivity than does moisture level. Previous studies have also shown that vessel diameter and stem hydraulic conductivity are not responsive to moisture levels for trees in humid forests (Villar-Salvador *et al.*, 1997; Creese *et al.*, 2011). Arend & Fromm (2007) have

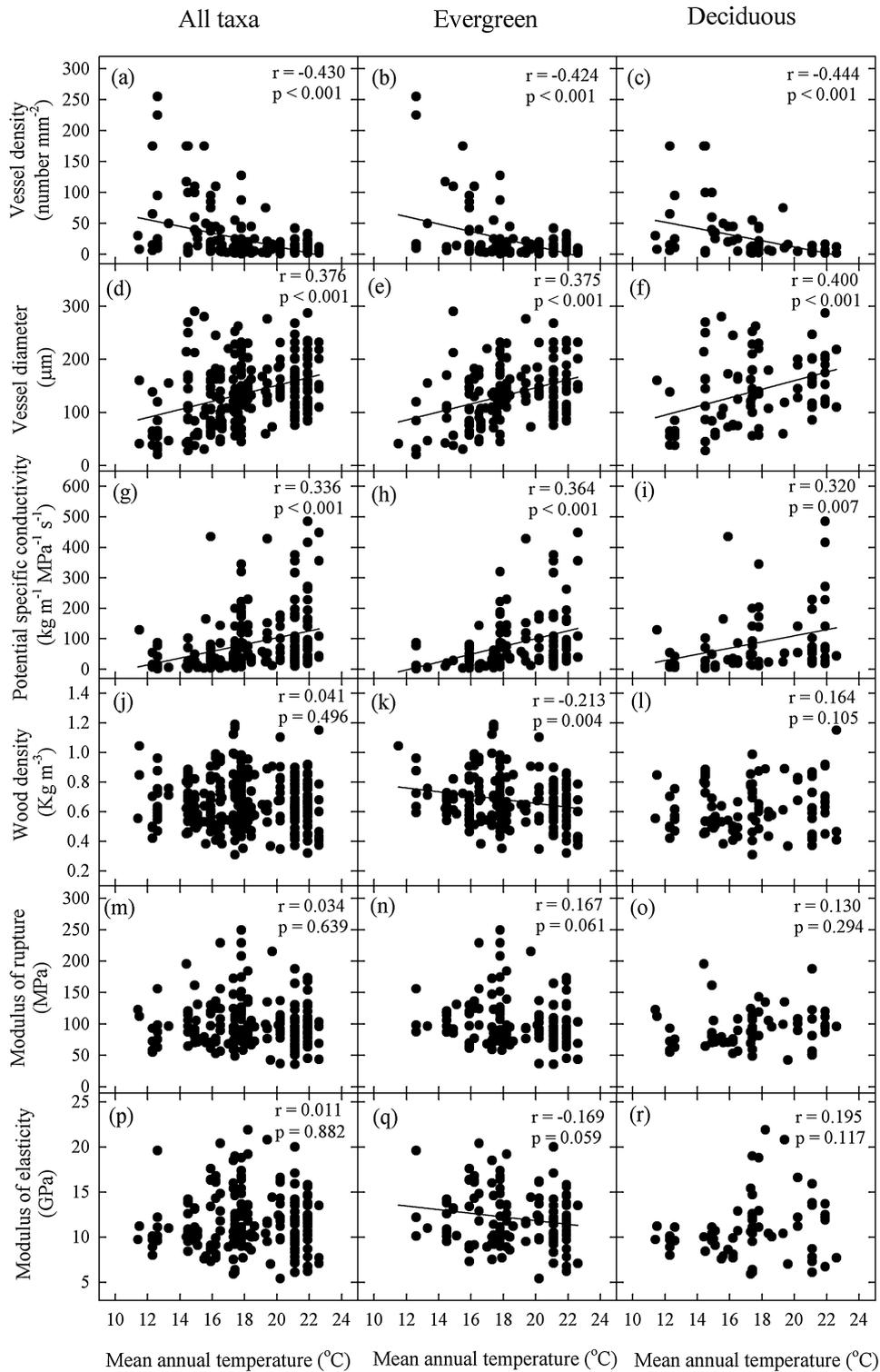


Figure 1 Relationships between mean annual temperature and vessel density, vessel diameter, potential specific conductivity, wood density, modulus of rupture and modulus of elasticity analysed using Pearson correlation for all taxa (left), evergreen species (middle) and deciduous species (right).

suggested that the ratio of vessel lumen area to xylem area is not affected by water stress because any drought-induced decrease in vessel size is matched by an increase in the number of newly formed vessel cells.

Xylem mechanical strength in relation to environment

Traits for xylem mechanical strength (MOE and MOR) were decreased with increasing MAT in evergreen trees, but not

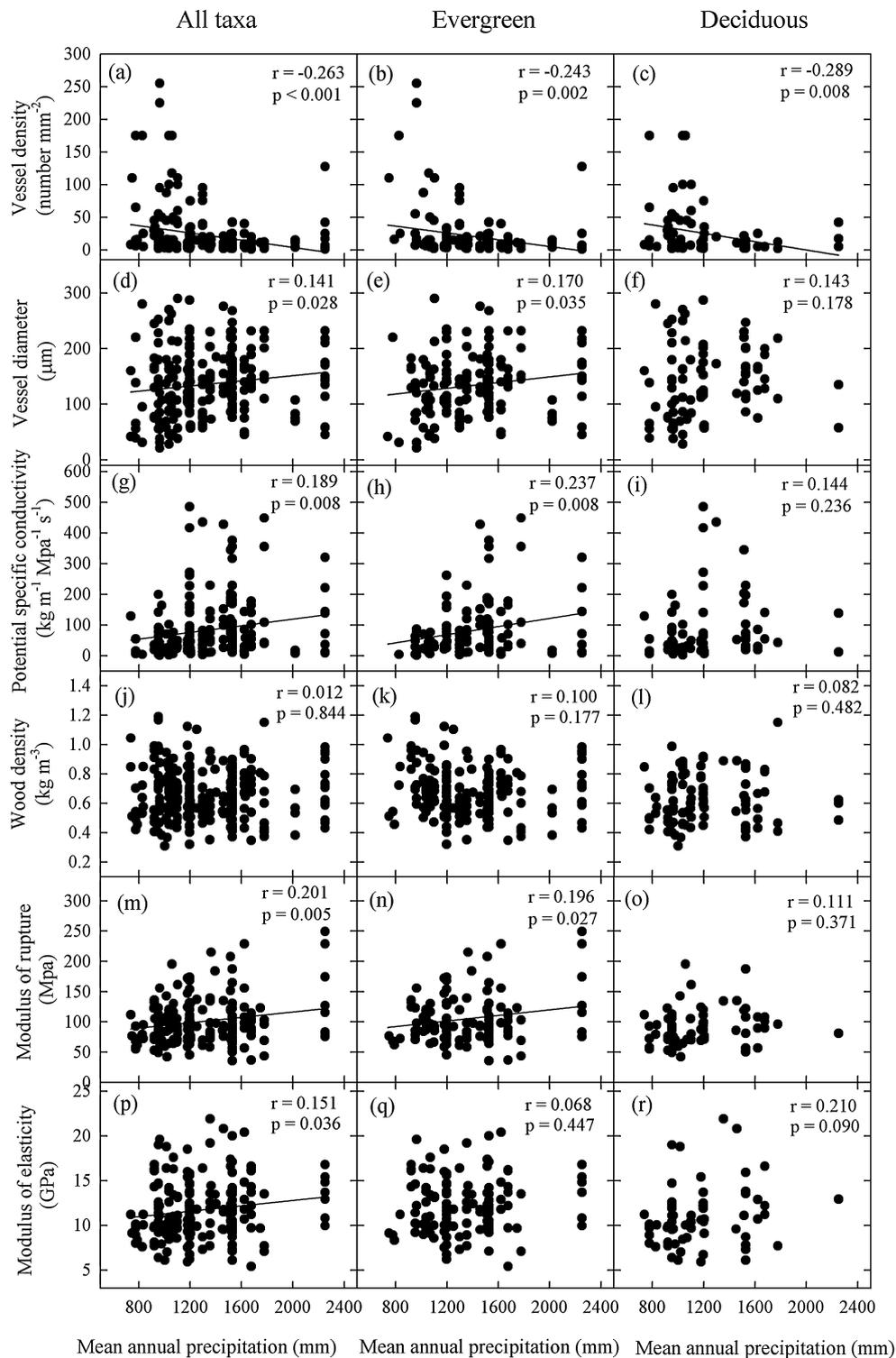


Figure 2 Bivariate correlations between mean annual precipitation and vessel density, vessel diameter, potential specific conductivity, wood density, modulus of rupture and modulus of elasticity analysed using Pearson correlation for all taxa (left), evergreen species (middle) and deciduous species (right).

in deciduous species. Meanwhile, MOR was reduced as AI increased in evergreen trees but, again, not in deciduous species. However, Onoda *et al.* (2010) have reported that, although precipitation does not affect MOE and MOR, WD is higher in trees

on Australian sites receiving less rainfall compared with sites in high-rainfall regions. Our findings indicated that the sensitivity of xylem mechanical traits to environmental conditions is related to leaf phenology, and that xylem development is

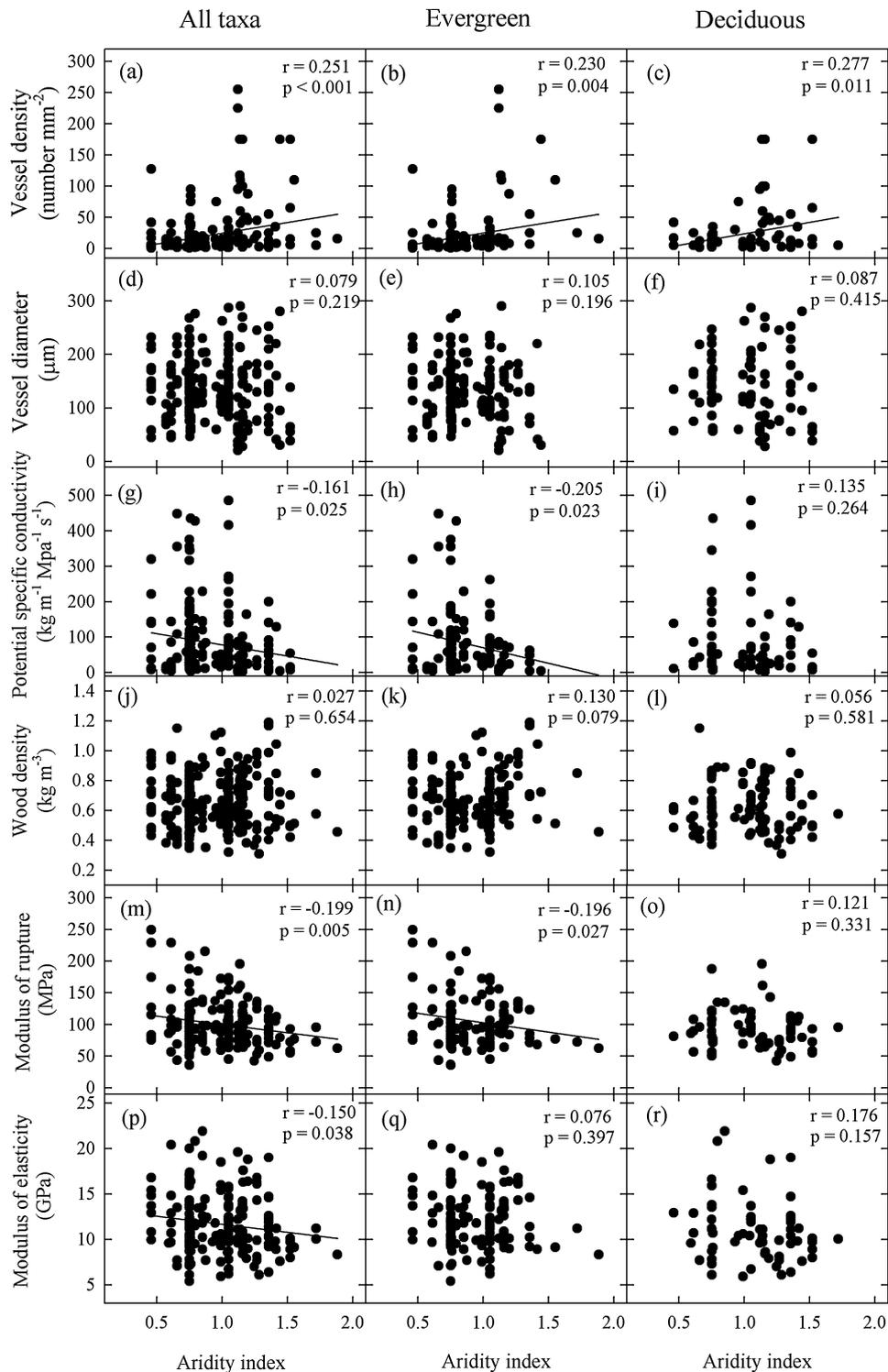


Figure 3 Bivariate correlations of aridity index with vessel density, vessel diameter, potential specific conductivity, wood density, modulus of rupture and modulus of elasticity analysed using Pearson correlation for all taxa (left), evergreen species (middle) and deciduous species (right).

more sensitive to changes in temperature and moisture in evergreens than in deciduous trees. Some studies have found that stem hydraulic traits also differ between deciduous and evergreen species (Cavender-Bares & Holbrook, 2001; Fan *et al.*,

2011; Fu *et al.*, 2012). Evergreen trees must maintain water transport to their leaves during the winter despite the risk of xylem dysfunction induced by freezing and drought. Deciduous species, by contrast, can avoid the stress of water loss and the

	MAT (controlling AI)			AI (controlling MAT)		
	All taxa	Evergreen	Deciduous	All taxa	Evergreen	Deciduous
Vessel density	-0.386***	-0.420***	-0.368***	0.151*	0.222**	0.090
Vessel diameter	0.375***	0.362***	0.416***	0.036	0.016	0.151
Potential specific conductivity	0.302***	0.342***	0.294**	0.047	0.157	0.030
Wood density	0.034	-0.197*	0.156	0.016	0.104	0.021
Modulus of rupture	0.104	-0.213*	0.090	-0.220**	-0.235**	0.074
Modulus of elasticity	0.041	-0.188*	0.135	-0.155*	0.113	0.105

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

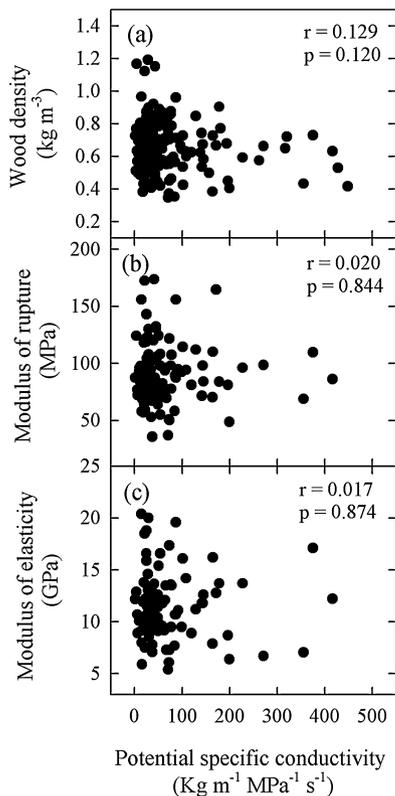


Figure 4 Bivariate correlations of potential specific conductivity with wood density, modulus of rupture and modulus of elasticity analysed using Pearson correlation for all taxa.

wintertime risk of xylem embolism by shedding their leaves (Cavender-Bares & Holbrook, 2001). Likewise, evergreen species have greater xylem cavitation resistance and higher MOE than deciduous trees (Cavender-Bares & Holbrook, 2001; Fu *et al.*, 2012). Values for WD, MOR and MOE are positively correlated with minimum seasonal water potential at sites prone to periodic drought, where trees show enhanced tolerance to water stress because of strong correlations between these traits and resistance to vessel implosion and cavitation (Jacobsen *et al.*, 2005; Preston *et al.*, 2006; Sperry *et al.*, 2006; Poorter *et al.*, 2010). Thus, increased cavitation resistance is an important survival strategy for evergreen trees (Maherali *et al.*, 2004).

Table 3 Partial correlations of xylem traits with mean annual temperature (MAT) and aridity index (AI) across species.

No trade-off between hydraulic efficiency and mechanical strength

We found no trade-off between hydraulic efficiency and mechanical strength across a wide range of angiosperm species over a large region (Fig. 4). This contradicts many previous reports (Wagner *et al.*, 1998; Hacke *et al.*, 2006; Markesteijn *et al.*, 2011a). Gleason *et al.* (2012) have shown that low WD and MOE are associated with high xylem specific conductivity in Australian angiosperm species. Those earlier descriptions about such a trade-off probably resulted because various species can have conflicting structural requirements for their xylem design (Pittermann, 2010).

Consistent with our conclusions, some researchers have observed no trade-off between efficiency and strength in fern, gymnosperm or angiosperm species (Fan *et al.*, 2011; Pittermann *et al.*, 2011). Woodrum *et al.* (2003) have suggested that differences in mechanical properties in *Acer* species are due to variations in fibre lumens that do not influence the efficiency of water transport. Here, we found that WD, MOR and MOE are not correlated with either vessel size or density, thereby indicating that the development of vessel traits is independent of wood mechanical traits.

When explaining the lack of this trade-off, one must note that xylem mechanical strength and vessel traits in angiosperms are theoretically uncoupled. A large portion of their hydraulic conductivity can be attributed to a relatively few, large vessels. Those larger vessels occupy only a small share of the stem cross-section and have a limited effect on WD (Westoby & Wright, 2006). Intervessel components, such as fibres and cell walls, account for the majority of the variation in mechanical strength (Jacobsen *et al.*, 2007; Zanne *et al.*, 2010), and vessel conductivity can be compensated by vessel length (Meinzer *et al.*, 2003; Fan *et al.*, 2011). An increase in fibre wall thickness might protect trees against implosion induced by embolism without causing a decline in hydraulic conductivity (Jacobsen *et al.*, 2005; Markesteijn *et al.*, 2011a).

Wood density has other roles in the life-history strategy. For example, Larjavaara & Muller-Landau (2010) have suggested that WD reflects maintenance costs of the trunk rather than mechanical strength; i.e. a high WD is associated with reduced trunk surface area and maintenance respiration. Furthermore,

trees can employ multiple strategies to increase their resistances to water stress and cavitation. Some species avoid catastrophic embolism through partial leaf-shedding during drought periods, as well as stronger stomatal regulation of leaf water potential and the production of deep root systems (Hoffmann *et al.*, 2011). Species with high WD tend to be more shallow-rooted (Bucci *et al.*, 2004). In addition, greater hydraulic capacitance in low-WD species can buffer leaf water potentials against temporary water shortages, maintaining gas exchange at higher levels or when under more prolonged drought cycles (Meinzer *et al.*, 2003). Consequently, this buffering effect of capacitance on the magnitude of transpiration-induced xylem tension appears to be coupled to cavitation resistance, possibly alleviating mechanical strength without necessitating a trade-off in hydraulic efficiency (Sperry *et al.*, 2008).

CONCLUSIONS

Our analysis showed that, over a broad range of angiosperm species, xylem hydraulic traits are influenced by temperature rather than by precipitation. Xylem development in evergreen trees was more sensitive to changes in temperature and moisture when compared with deciduous trees. No trade-off was found between mechanical strength and hydraulic efficiency. This is because angiosperms have specialized xylem tissue for strength and for water transportation. Thus, it is inevitable that traits related to these would not be linked. Our results have important implications for understanding xylem functional diversity and the ecological strategy of trees.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Stem xylem traits and environmental variables of 316 angiosperm tree species.

BIOSKETCHES

Shi-Bao Zhang is a senior researcher in plant physiological ecology. His research focuses on the evolution of plant functional traits, plant functional differentiation and ecological adaptation.

Kun-Fang Cao is a principal research scientist in plant physiological ecology. He interests in plant physiological ecology, especially plant hydraulics, water relations, evolution of plant functional traits and ecological adaptation, photosynthesis and photoprotection of tropical and subtropical plants in response to chilling temperature.

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