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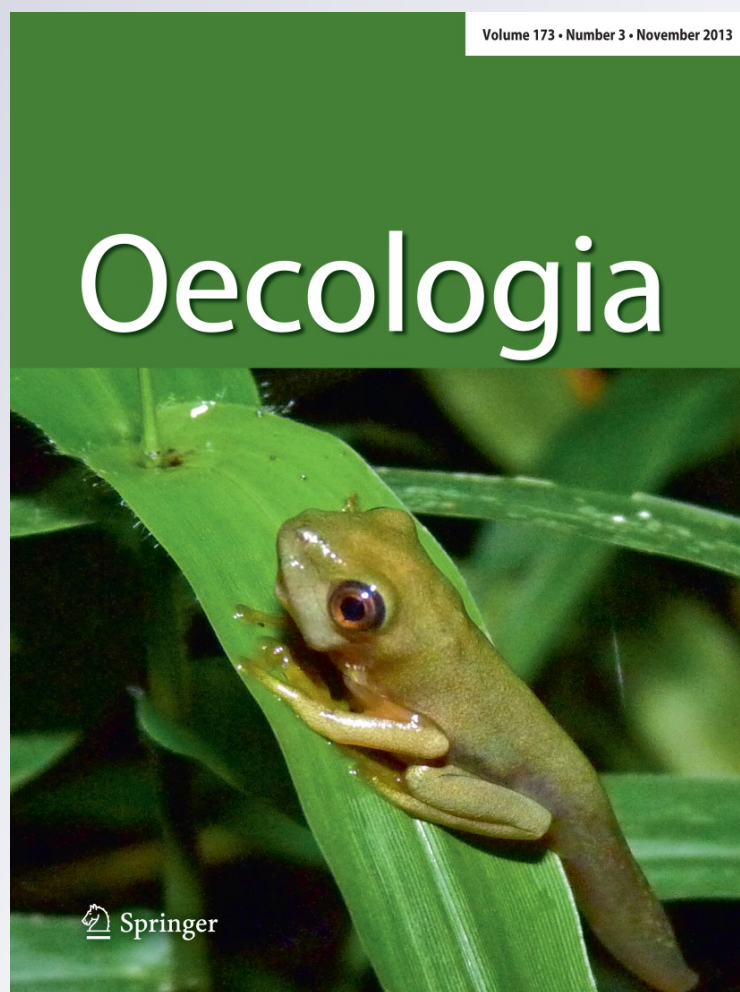Volume 173 · Number 3 · November 2013

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Xylem cavitation vulnerability influences tree species' habitat preferences in miombo woodlands

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Abstract Although precipitation plays a central role in structuring Africa's miombo woodlands, remarkably little is known about plant-water relations in this seasonally dry tropical forest. Therefore, in this study, we investigated xylem vulnerability to cavitation for nine principal tree species of miombo woodlands, which differ in habitat preference and leaf phenology. We measured cavitation vulnerability (Ψ_{50}), stem-area specific hydraulic conductivity (K_S), leaf specific conductivity (K_L), seasonal variation in predawn water potential (Ψ_{PD}) and xylem anatomical properties [mean vessel diameter, mean hydraulic diameter, mean hydraulic diameter accounting for 95 % flow, and maximum vessel length (V_L)]. Results show that tree species with a narrow habitat range (mesic specialists) were more vulnerable to cavitation than species with a wide habitat range (generalists). Ψ_{50} for mesic specialists ranged between −1.5 and −2.2 MPa and that for generalists between −2.5 and −3.6 MPa. While mesic specialists exhibited the lowest seasonal variation in Ψ_{PD}, generalists displayed significant seasonal variations in Ψ_{PD} suggesting that the two miombo habitat groups differ in their rooting depth. We observed a strong trade-off between K_S and Ψ_{50} suggesting that tree hydraulic architecture is one of the decisive factors setting ecological boundaries for principal miombo species. While vessel diameters correlated weakly ($P > 0.05$) with Ψ_{50}, V_L was positively and significantly correlated with Ψ_{50}. Ψ_{PD} was significantly correlated with Ψ_{50} further reinforcing the conclusion that tree hydraulic architecture plays a significant role in species' habitat preference in miombo woodlands.

Keywords Cavitation · Leaf specific conductivity · Miombo woodlands · Specific hydraulic conductivity · Xylem anatomy

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Introduction

Africa's miombo woodland is the most dominant vegetation of the Zambezian phytochorological region (White

1983). This vegetation formation covers an estimated land surface area of about 3.8 million km^2 (Frost 1996). In the north, miombo woodlands extend across Tanzania and southern fringes of the Democratic Republic of Congo, then across the continent from Angola, through Zambia, to Malawi and Mozambique. In the south, the woodlands extend to Zimbabwe (Campbell et al. 1996). The outstanding ecological feature of this seasonally dry tropical forest is that dominant tree species differ considerably in both biogeographical association and distribution extent (Chidumayo 1997; Frost 1996; Malaisse 1978). In this biome, there is a marked discontinuity in tree species composition between the relatively wet northern miombo woodlands and the semi-arid southern dry miombo woodlands (Frost 1996).

Using the 1,000-mm mean annual rainfall isohyet, White (1983) divided miombo woodlands into wetter and drier types. Wet miombo woodlands occur above 1,000 mm mean annual rainfall. Dry miombo woodlands occur in areas that receive less than 1,000 mm mean annual rainfall. Floristically, wet northern miombo woodlands are richer than the dry miombo woodlands. Not surprising, the majority of the principal tree species (mesic specialists) have their distribution effectively confined to the wet northern miombo woodland habitats and only a handful of the principal species (generalists) establish in both wet and dry miombo woodland habitats (Chidumayo 1987).

The strong link between mean annual precipitation and tree species composition underlines the importance of water-deficit stress in structuring this seasonally tropical forest. In particular, the ability of tree species to withstand xylem cavitation (rapid phase change of xylem water under tension from liquid to vapour) is expected to play a pivotal role in promoting tree species' ecological competitive ability in this water-limited ecosystem. Although other factors such as fire (Lawton 1978), geomorphology (Cole 1963), fauna (Guy 1989) and anthropogenic disturbances (Gillespie et al. 2000) constrain the distribution of principal tree species, water-deficit stress may impose severe restrictions on the establishment of drought-sensitive principal tree species in dry miombo woodlands.

Many studies have demonstrated that xylem cavitation vulnerability is closely correlated with plant species' drought tolerance (Edwards and Diaz 2006; Kolb and Davis 1994; Stratton et al. 2000; Tyree and Zimmermann 2002). There is ample evidence suggesting that cavitation resistance is positively correlated with plant drought tolerance and defines the range of habitats a species can successfully colonize (Brodribb and Hill 1999; Pockman and Sperry 2000). As expected, pressure for selection in arid environments favours individuals with high cavitation resistance (Canham et al. 2009; Choat et al. 2007; Jacobsen

et al. 2007). Furthermore, there exists a trade-off between cavitation resistance and hydraulic efficiency such that individuals with wider vessels are more vulnerable to cavitation than those with thicker walls and fewer lumen areas (Pockman and Sperry 2000). Regardless of the conclusions drawn from these studies they have all demonstrated that the mechanism through which xylem cavitation vulnerability impacts plant ecological performance is the severe limitation it imposes on the long-distance xylem water transport (Tyree and Sperry 1989). In general, cavitation resistance reflects the range of water-deficit stress that an individual plant can tolerate in any given habitat.

Many authors have demonstrated the importance of plant-water relations in influencing tree species' ecological competitive ability in most seasonally dry tropical forests (Chen et al. 2009; Choat et al. 2005; Lopez et al. 2005; Sobrado 1997). These studies have also shown that, in seasonally dry tropical forests, the mixture of plant communities that exist in mesic habitats typically encompasses a range of hydraulic properties associated with plant adaptation to water-deficit stress. However, these ecophysiological traits remain poorly understood for Africa's miombo woodlands. Therefore, to explore the relationship between xylem cavitation vulnerability and principal tree species' habitat preference, we selected Zambia's miombo woodlands. The ecological structuring of this seasonally dry tropical forest offered us an opportunity to test the hypothesis that tree species differing in habitat preferences will differ significantly in xylem cavitation resistance with mesic specializing plants being more vulnerable to cavitation than individuals with a wide habitat range.

Materials and methods

Study site

The experimental site was Mwekera National Forest no. 6 located on the outskirts of Kitwe City (12°49′S and 28°22′E; elevation 1,295 m above sea level). The site has an average tree density of 880 stems ha^{-1} with a mean basal area of 39 m^2 ha^{-1}. The vegetation is predominantly *Brachystegia-Julbernardia* woodlands with the genera *Brachystegia*, *Isoberlinia*, *Julbernardia* and *Marquesia* as common canopy co-dominants (Chidumayo 1987). Weather pattern for the site is characterized by summer rains which occur between November and April. This is followed by a long seasonal drought lasting from May to October. Average annual precipitation was 1,200 mm with mean annual temperatures ranging between 14 and 28 °C (readings taken from the nearest Zambia Meteorological Department weather station located 20 km from the site at Kafironda, Mufulira district). The experimental site was

selected on the strength that nearly all the principal tree species of miombo woodlands were present and had substantial forest stands with minimum human disturbances.

Sampling

In this study, we examined vulnerability to cavitation in nine co-dominant tree species of miombo woodlands co-occurring in a wet miombo woodland site. The selected nine species varied substantially in habitat preference and distribution. *Brachystegia floribunda* Benth. (Fabaceae), *Isoberlinia angolensis* (Benth.) Hoyle and Brenan (Fabaceae), *Julbernardia paniculata* (Benth.) Troupin (Fabaceae), and *Marquesia macroura* Gilg (Dipterocarpaceae) have their distribution restricted mainly to wet miombo woodlands (Frost 1996; Smith and Allen 2004). *Brachystegia boehmii* Benth. (Fabaceae), *Brachystegia longifolia* Benth. (Fabaceae), *Brachystegia spiciformis* Benth. (Fabaceae), *Erythrophleum africanum* (Benth.) Harms (Fabaceae), and *Pericopsis angolensis* (Baker) Meeuwen (Fabaceae) are widely distributed with occurrence in both wet and dry miombo woodlands (Chidumayo 1987; Fanshawe 1971).

Twenty-five representative trees per species (giving a total of 225 trees) were sampled based on the criteria that they were healthy, actively growing, and at least 100 m apart. We controlled for local environmental variability by sampling individuals that co-occurred. Co-occurring individual trees were tagged, and their GPS coordinates recorded to facilitate repeat measurements.

Stem water potential

Predawn stem water potentials (Ψ_{PD}) were measured at approximately fortnightly intervals between April 2007 and December 2008 ($n = 7$ trees per species) with a pressure bomb (SKPM 1405; Skye Instruments, Llandrindod Wells, UK). Ψ_{PD} measurements were made on all sampled species during the same day and time (0530–0800 hours standard local time). Given that plants have a tendency to equilibrate overnight with wetter zones in the bulk soil (Schmidhalter 1997); Ψ_{PD} was a better measure representing an estimation of soil water potential (Andrade et al. 1998; Williams and Araujo 2002). Ψ_{PD} measurements were taken from the same individual trees at each sampling period. Samples were kept in field plastic sample bags throughout the measurement procedure in order to reduce transpirational water loss during measurement.

Anatomical measurements

We determined maximum vessel length (V_L) by forcing air at a pressure of between 60 and 100 kPa through the basal end of the branch while at the same time keeping the distal end dipped into a bucket of water (Choat et al. 2005; Ewers and Fisher 1989; Zimmermann and Jeje 1981). The distal end of the twig was continuously cut back in sections of 1 cm until bubbles were seen forming at the cut end. Once bubbles appeared, the procedure was stopped and the total length of the remaining segment measured to the nearest centimetre. This was then recorded as the V_L for that particular twig.

Sample preparation prior to vessel diameter determination involved soaking segments for 3 weeks in a solution of ethanol, distilled water, and glycerol mixed in equal proportions (Beikircher and Mayr 2008). Cross-sections were cut between 15 and 30 μm thick using a manual sliding microtome. The cross-sections were, thereafter, stained with safranin and mounted with Canada balsam. In order to measure the three anatomical variables, slides were photographed using a digital camera mounted on a microscope. The photographs were prepared and analysed using the software Image J (freely available from www. http://rsb.info.nih.gov/ij/). From the prepared photographs, three variables were analysed to characterize vessel diameter, following the methods of Tyree and Zimmermann (2002). The three variables analysed were mean vessel diameter (D), hydraulic mean diameter (D_H), and mean vessel diameter accounting for 95 % of conductivity (D_{95}). D was calculated by averaging all vessels. D_H was calculated as:

$$D_H = \left[\frac{\sum_D^4}{N} \right] 1/4 \tag{1}$$

where N is the number of conduits.

D_{95} was calculated by ranking all the diameters raised to the fourth power in ascending order (D^4). These D^4 were then summed until their sum was equal to 95 % of the total conductance. An arithmetic mean was then calculated for diameters accounting for this conductance.

Hydraulic properties

Three healthy, leaf-bearing branches (under-bark diameter ranged from 4 to 10 mm) were sampled per individual tree for hydraulic conductivity measurements (Patino et al. 1995; Van der Willigen et al. 2000). The harvested branches were always covered in wet towels and sealed in dark plastic sample bags. At the laboratory, segments were cut from the branches approximately equal in length to the determined species' V_L plus 10 % allowance. Throughout sample preparation, segments were always kept totally immersed in distilled water. Hydraulic conductivity was gravimetrically determined by inserting the basal end of the segment into a custom-built water reservoir with a low delivery pressure head of 2 kPa. Segments were perfused

with de-gassed, filtered (to 0.2 µm) and acidified (with HCl, pH = 2) distilled water (Kolb et al. 1996; Sperry et al. 1988). Segments were allowed to equilibrate for between 15 and 30 min before initial flow determination. After initial sap flow determination, segments were flushed at a constant pressure of 150 kPa and re-measurement of conductivity without emboli immediately followed. At the end of each flow determination, segment under-bark diameter and length were accurately measured (using a digital micro caliper—accuracy 0.01 mm). Maximum hydraulic conductivity (K_H) was calculated as:

$$K_\mathrm{H} = \frac{J_\mathrm{V}}{\Delta P/l} \qquad (2)$$

where K_H is the maximum hydraulic conductivity, J_V is the flow rate (kg s^{-1}), ΔP is the delivery pressure (MPa), and l is segment length (m).

Stem-area specific hydraulic conductivity (K_S; kg s^{-1} m^{-1} MPa^{-1}) was derived by dividing hydraulic conductivity with effective sapwood cross-sectional area (m^2).

Cavitation induction

Cavitation resistance was determined on 25 individuals per tree species from April to July 2008 using the standard bench drying technique (Cochard et al. 1992). Branches were left to dehydrate naturally on laboratory benches and their water potentials periodically monitored. Cavitation resistance was determined on segments of six branches per individual tree in sequence of increasing dehydration. The branches were dehydrated to varying ranges of water potential corresponding to 0–>80 % loss of hydraulic conductance. Depending on species, the dehydrating periods ranged from 6 to 48 h. Prior to stem water potential determination using a pressure chamber (SKPM 1405), dehydrated branches were initially sealed in plastic bags for 30 min to allow for equilibration of water potential. For construction of vulnerability curves, hydraulic conductivity (K_H minimum) was initially determined on dehydrated segments using the gravimetric method described in the previous section. This was followed by flushing out emboli as already described and re-measurement of K_H to obtain K_H maximum. Percent loss in hydraulic conductivity (PLC) was then calculated as:

$$\mathrm{PLC} = \frac{K_\mathrm{H}\mathrm{max} - K_\mathrm{H}\mathrm{min}}{K_\mathrm{H}\mathrm{max}} \times 100 \qquad (3)$$

where K_H max is the maximum hydraulic conductivity without emboli, and K_H min is initial hydraulic conductivity with emboli. To confirm that the segments had been thoroughly freed of emboli, they were perfused with safranin dye at the end of each experiment.

Vulnerability curves were constructed by plotting the determined branch water potential versus PLC. The vulnerability curves were fitted with the following sigmoidal function:

$$\mathrm{PLC} = 100 / (1 + \exp(a(\Psi - \Psi_{50}))) \qquad (4)$$

where Ψ_{50} is the water potential associated with 50 % loss in hydraulic conductance, and a represents the slope of the vulnerability curve (Pammenter and Willigen 1998).

Statistics

A linear mixed-effects ANOVA model was employed in determining variations in xylem cavitation vulnerability, K_S, leaf specific hydraulic conductivity (K_L), D and V_L between the two miombo woodlands habitat groups (Zar 2010). The relationship between cavitation resistance, hydraulic efficiency, xylem anatomy and seasonal variation in water potential, was analysed using linear regression analysis. Prior to any statistical analysis all data was tested for normality and variance constant. K_S data failed both the normality and variance constant tests, and were, therefore, log transformed. All statistical analyses were performed in Minitab (version 14, Minitab, State College, PA).

Results

Predawn stem water potential

Between the two habitat groups, there were significant ($P < 0.05$) variations in Ψ_{PD} during the period of measurement (April–November 2008). On average Ψ_{PD} for drought-deciduous generalists was significantly ($P < 0.05$) more negative than the brevi-deciduous mesic specialists (Fig. 1). While Ψ_{PD} for the five drought-deciduous generalist species showed substantial fluctuations over the period of measurement, brevi-deciduous mesic specialists showed very little fluctuations in Ψ_{PD} during the same period of measurement.

Variations in hydraulic properties, cavitation resistance and xylem anatomic traits

There were substantial variations in K_S and K_L between the two habitat groups. On average K_S varied almost twofold between mesic specialists and drought-deciduous generalists. K_L varied nearly threefold between the two miombo habitat groups (Table 1).

The nine principal tree species of the miombo woodlands differing in habitat preferences and leaf phenology differed substantially in cavitation resistance, measured as water potential leading to 50 % loss in hydraulic
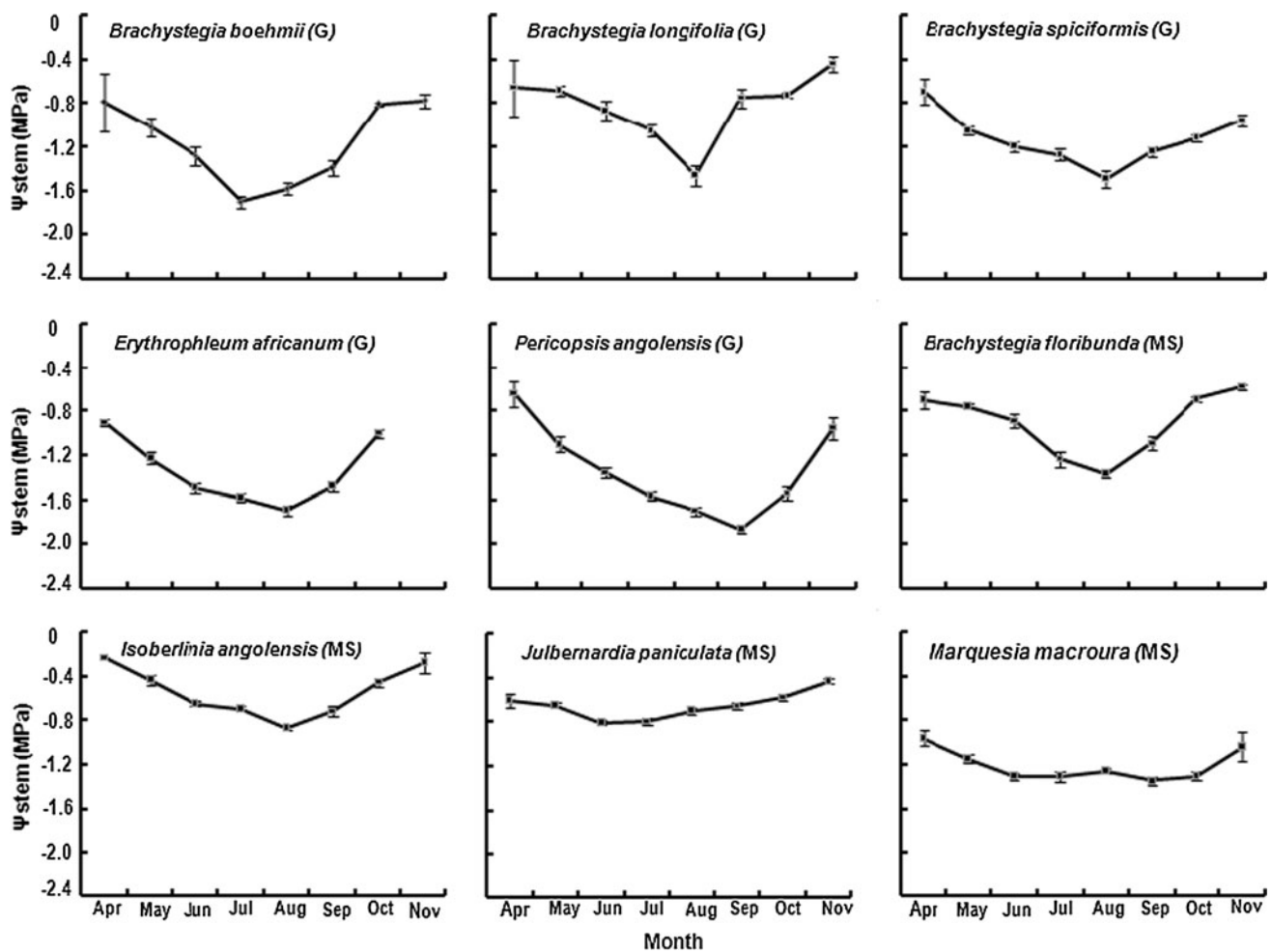
Fig. 1 Mean predawn water potentials (Ψ) for the nine principal tree species of miombo woodlands ($n = 7$ trees per species). *G* generalist, *MS* mesic specialist

Table 1 Variations in hydraulic and xylem anatomic properties between miombo woodlands' habitat groups ($n = 25$ trees per species)

Trait	Drought-deciduous generalists (mean ± SE)	Brevi-deciduous mesic specialists (mean ± SE)	ANOVA	
			P-value	VC (%)
Ψ_{50} (MPa)	-2.96 ± 0.41	-1.85 ± 0.31	**	7.63
K_S (kg s^{-1} MPa^{-1} m^{-1})	7.56 ± 0.38	17.83 ± 1.18	***	49.72
K_L (kg s^{-1} MPa^{-1} m^{-1}) $\times 10^{-5}$	18.06 ± 1.78	45.03 ± 4.13	***	32.07
V_L (m)	0.26 ± 0.01	0.30 ± 0.00	***	32.45
D (μm)	25.13 ± 0.76	26.12 ± 0.85	n.s.	0.12
D_H (μm)	31.20 ± 0.89	31.72 ± 0.98	***	3.25
D_{95} (μm)	34.77 ± 1.11	34.46 ± 0.97	***	5.00

SEs of the mean are at 95 % confidence interval

Mean cavitation resistance (Ψ_{50}), stem-area hydraulic conductivity (K_S), leaf specific conductivity (K_L), mean maximum vessel length (V_L), mean diameter (D_H), hydraulic mean diameter (D_H), and mean diameter accounting for 95 % flow (D_{95}), variance components (VC)

** $P < 0.01$, *** $P < 0.001$, *ns* non-significant

conductivity (Table 1). Generalists displayed significantly (ANOVA, $P = 0.01$) higher cavitation resistance than mesic specialists. There were clear differences in vulnerability curves between mesic specialists and habitat generalists (Fig. 2).

Mean V_L varied substantially between the two habitat groups. Mesic specialists' V_L was 15 % longer than that of drought-deciduous generalists. Although both D_H and D_{95} showed significant ($P = 0.001$) statistical variations, the actual differences were very marginal (Table 1). However, D did not vary significantly ($P = 0.6$) between the two habitat groups. Both mesic specialists and generalists possessed aggregated vessels. The only species which showed solitary vessels was *M. macroura* (Fig. 3).

Relationships between cavitation resistance, hydraulic efficiency, vessel traits and minimum seasonal water potential

Cavitation resistance was positively and significantly ($P < 0.05$) correlated with K_S. A linear regression explained 54 % of the variations in specific hydraulic conductivity (Fig. 4).

As cavitation resistance increased there was a corresponding decrease in hydraulic efficiency. There was a positive and significant ($P < 0.05$) correlation between cavitation resistance and mean V_L. A linear regression explained 53 % of the variations in cavitation resistance (Fig. 5). The relationship between V_L and Ψ_{50} remained significant ($P < 0.05$) even after removing the influential species (*M. macroura*) from the analysis. However, neither D_H nor D_{95} was significantly ($P > 0.05$) related to Ψ_{50}.

Ψ_{PD} was significantly ($P = 0.02$) correlated with Ψ_{50} (Fig. 6). A linear regression explained 55 % of the variations in Ψ_{50}.

Discussion

Many authors have demonstrated cavitation resistance to vary considerably between plants from contrasting habitats, with xeric individuals being more resistant than mesic ones (Brodribb and Hill 1999; Choat et al. 2005; Engelbrecht et al. 2000; Maherali, et al. 2004; Mencuccini and Comstock 1997; Van der Willigen et al. 2000). In this study, we hypothesized that tree species differing in habitat preferences and leaf phenology will differ in xylem cavitation resistance with brevi-deciduous mesic specialists being more vulnerable to cavitation than drought-deciduous generalists. Findings of this study are consistent with the hypothesis as drought-deciduous generalists converged towards higher cavitation resistance than co-occurring
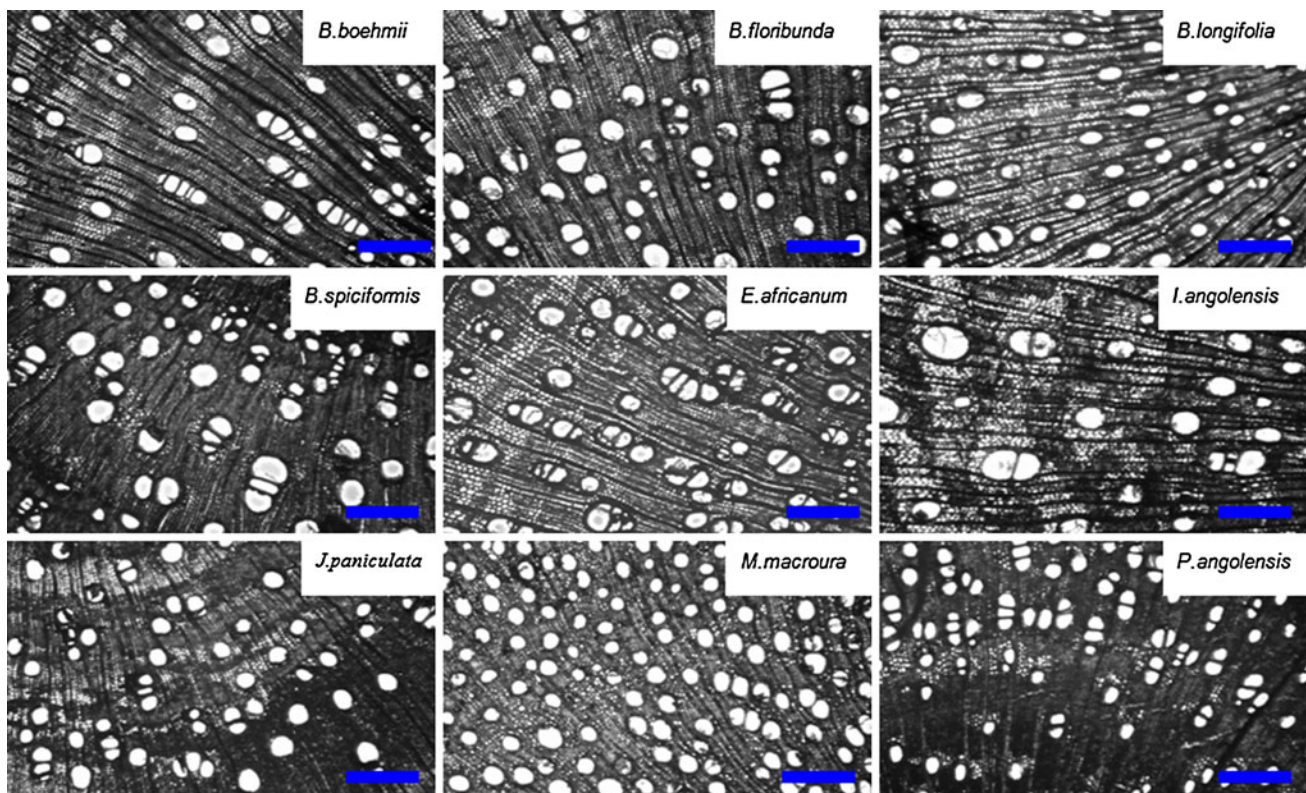
Fig. 2 Cross-sections of branch wood of principal canopy tree species of miombo woodlands. *Scale bar* 100 μm
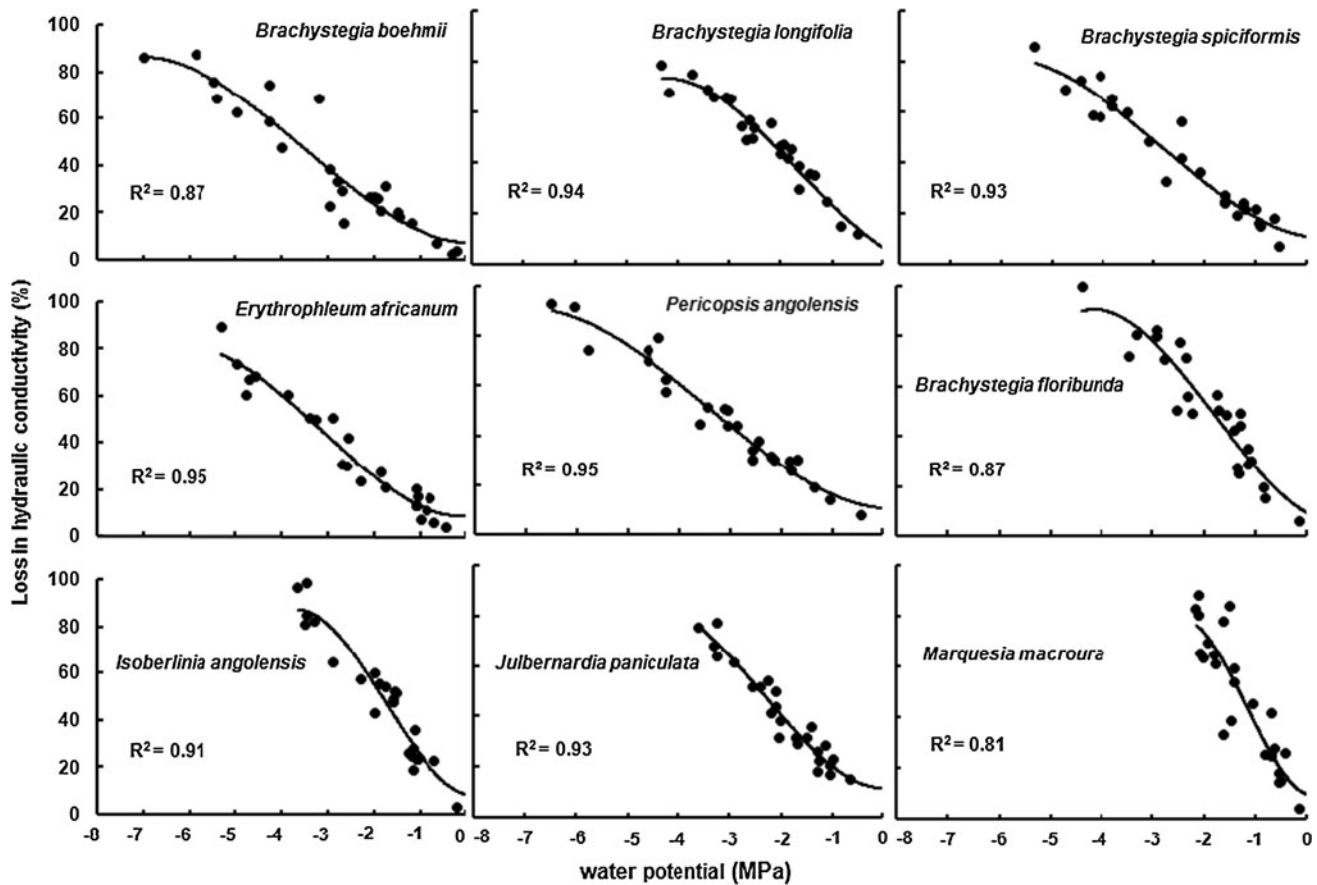
Fig. 3 Cavitation vulnerability curves for nine co-occurring tree species of miombo woodlands growing on a wet miombo woodlands site ($n = 25$ trees per species)

brevi-deciduous mesic specialists (Table 1; Fig. 3). Variation in cavitation resistance between the two miombo woodlands' habitat groups can be interpreted as a plant adaptive response to water availability in this water-limited ecosystem (Canham et al. 2009). Pockman and Sperry (2000) drew similar conclusions on the distribution of the Sonoran vegetation.

Furthermore, the existence of a strong trade-off between K_S and Ψ_{50} for the nine canopy tree species of the miombo woodlands underlines the fundamental ecological role that plant hydraulic architecture plays in this water-limited ecosystem. This result is consistent with those of other authors (Markesteijn et al. 2011). Given the severity of the dry season in this seasonally dry tropical forest, the high K_S and K_L values among mesic specialists can be interpreted as an adaptation meant to offset the potential negative impacts of embolism (Tyree and Zimmermann 2002; Vinya et al. 2012). However, high cavitation resistance combined with low hydraulic efficiency enables generalists to be competitive in both wet and dry miombo woodland habitats.

Zimmermann (1983) proposed that large conduits were hydraulically more efficient than smaller ones and were, therefore, more vulnerable to xylem cavitation.
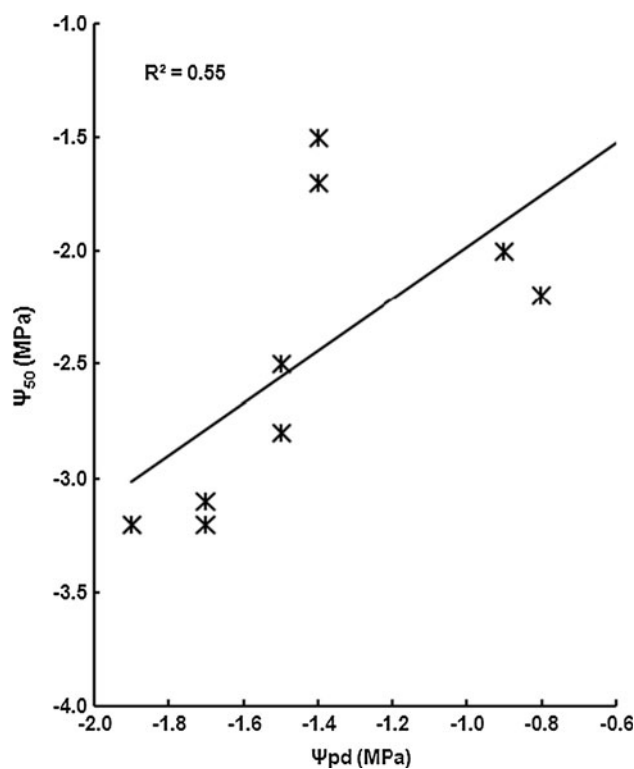
Surprisingly, results from this study show lack of a trade-off between Ψ_{50} and conduit diameter (Fig. 5). These findings are consistent with those of many authors who too have observed a lack of trade-off between conduit diameter and Ψ_{50} (Van der Willigen et al. 2000; Wheeler et al. 2005). The lack of a trade-off between Ψ_{50} and conduit diameters further reinforce the idea that the origins of cavitation lie outside conduit diameter (Tyree and Sperry 1989). However, the strong trade-off observed in this study between V_L and Ψ_{50} (Fig. 5) suggests that in this seasonally dry tropical forest selection may have acted on conduit length rather than conduit diameter in order to reduce hydraulic resistance.

Not surprising, Ψ_{PD} fluctuated remarkably little over the course of the 8-month study period among the four brevi-deciduous mesic specialists (Fig. 1). On the contrary, drought-deciduous generalists experienced significant fluctuations in Ψ_{PD}. Differences in Ψ_{PD} may be attributed to differences in rooting depth between the two miombo woodlands' habitat groups (Timberlake and Calvert 1993). Therefore, the plausible explanation for the observed differences in seasonal minimum Ψ_{PD} between the two habitat groups may be that brevi-deciduous mesic specialists
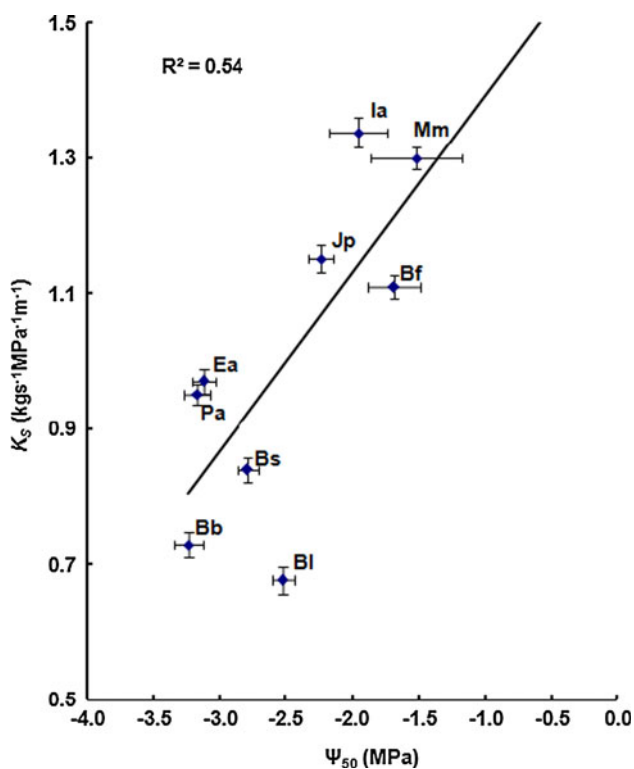
Fig. 4 Stem-area sapwood specific hydraulic conductivity (K_S) versus stem water potential threshold causing 50 % loss in hydraulic conductivity (Ψ_{50}). *Points are species mean* $\pm$ SE ($n = 25$ trees per species). K_S is log transformed. *Error bars* are SEMs at 95 % confidence interval

Fig. 6 Cavitation resistance (Ψ_{50}) plotted against minimum seasonal water potential (Ψ_{PD}) for the nine principal tree species of miombo woodlands. *Points are species mean* $\pm$ SE ($n = 25$ trees per species)

are accessing soil water from much deeper soil horizons than the drought-deciduous generalists. The variations in minimum seasonal Ψ_{PD} reflect the maximum water-stress deficit (Bhaskar and Ackerly 2006) that the two miombo woodlands' habitat groups can tolerate. Numerous studies have demonstrated the existence of a trade-off between

cavitation resistance and minimum seasonal water potential that any given plant experiences (Hacke et al. 2000; Sperry and Hacke 2002). Consistent with these studies we observed a significant correlation between Ψ_{50} and minimum seasonal Ψ_{PD} (Fig. 6). The existence of a strong trade-off between Ψ_{50} and Ψ_{PD} underpins the adaptive significance of cavitation vulnerability in this seasonally dry tropical forest.
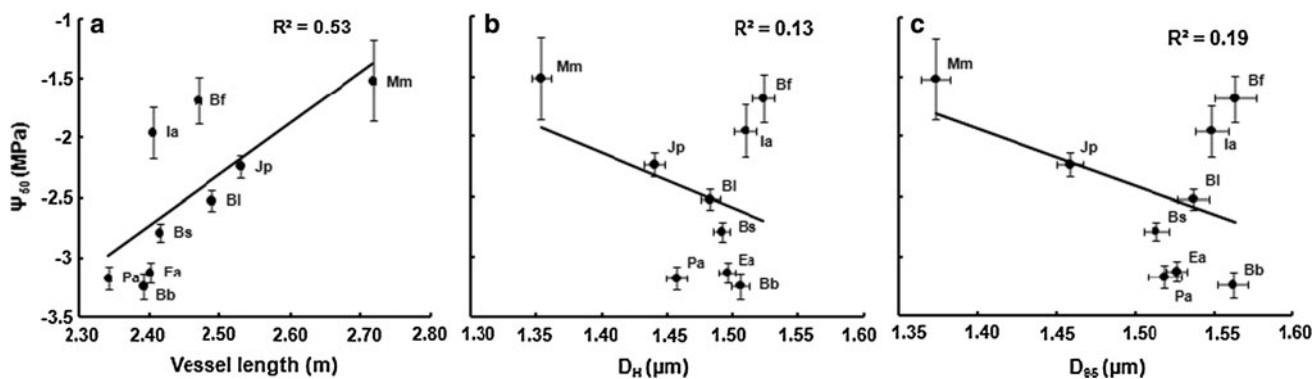
Fig. 5 Relationship between water potential at 50 % loss in hydraulic conductivity (Ψ_{50}) and **a** vessel length (V_L), **b** mean hydraulic diameter (D_H), **c** mean hydraulic diameter accounting for 95 % flow (D_{95}). *Points are species mean* $\pm$ SE ($n = 25$ trees per species). *Error bars* are SEMs at 95 % confidence interval

Conclusion

This study has demonstrated that xylem cavitation vulnerability is one of the key determinants setting tree species' ecological boundaries in miombo woodlands. The eco-physiological traits displayed by mesic specialists (low cavitation resistance combined with high K_S and K_L) compromise their competitive ability in dry miombo woodland habitats. In general, stem hydraulic architecture constrains the establishment of mesic specialists in dry miombo woodlands. Generalists owe their wide distribution in miombo woodlands to their physiologically adapted hydraulic architecture which can withstand xylem cavitation. The observed strong trade-offs that exist between K_S and Ψ_{50}, and between Ψ_{50} and Ψ_{PD}, confirm the adaptive significance of xylem cavitation vulnerability in influencing habitat preferences among principal tree species of the miombo woodlands. Although this study has established the potential mechanism through which drought sets limits to the distribution of principal miombo species, further research must be carried out to establish the ecological significance of interspecific variations in root cavitation resistance between mesic specialists and generalists.

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