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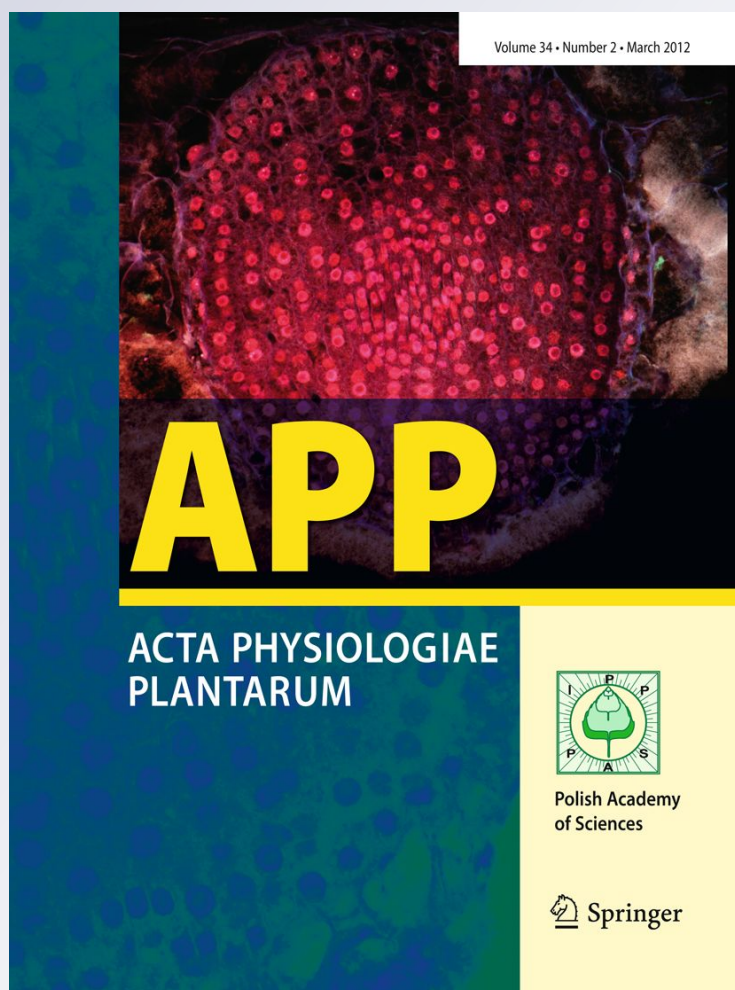
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Functional coordination between branch hydraulic properties and leaf functional traits in miombo woodlands: implications for water stress management and species habitat preference

Royd Vinya · Yadvinder Malhi · Nick Brown · Joshua B. Fisher

Abstract We investigated functional coordination between branch hydraulic properties and leaf functional traits among nine miombo woodlands canopy tree species differing in habitat preference and phenology. Specifically, we were seeking to answer the question: are branch hydraulic properties coordinated with leaf functional traits linked to plant drought tolerance in seasonally dry tropical forests and what are the implications for species habitat preference? The hydraulic properties investigated in this study were stem area specific hydraulic conductivity (K_S), Huber value (H_v), and xylem cavitation vulnerability (Ψ_{50}). The leaf functional traits measured were specific leaf area (SLA), leaf dry matter content (LDMC), and mean leaf area (MLA). Generalists displayed significantly ($P < 0.05$) higher cavitation resistance (Ψ_{50}) and SLA, but lower sapwood specific hydraulic conductivity (K_S), leaf specific conductivity (K_L), MLA, and LDMC than mesic specialists. Although MLA was uncorrelated with Ψ_{50}, we found significant ($P < 0.05$) positive and negative correlations between plant hydraulic properties and leaf functional traits linked to plant drought tolerance ability, indicating that the interactions between branch hydraulics and leaf functional traits related to plant drought tolerance ability may influence tree species habitat preference in water-limited ecosystems.

Introduction

Miombo woodlands in southern Africa are a significant transitional biome situated between the mesic tropical rainforests and the arid savannas (Malaisse 1978). In this seasonally dry tropical forest, plant productivity and distribution are largely restricted by water stress (White 1983). As expected, the majority of canopy tree species display narrow habitat range, with distribution effectively confined to the relatively wet northern miombo woodlands (occurring above 1,000 mm mean annual precipitation). A few canopy species are widely distributed, occurring in both wet and dry miombo woodlands (Chidumayo 1987). The narrow habitat range species (mesic specialists) are brevi-deciduous, whereas the wide habitat range species (generalists) are drought-deciduous, suggesting that the two groups of species employ different mechanisms in dealing with water stress.

Given the intensity and severity of drought in this seasonally dry tropical forest (Frost 1996; Murphy and Lugo 1986), interactions between plant physiological and morphological traits may play a crucial role in explaining differences in species habitat specialization. In particular, interactions between branch hydraulic properties and leaf functional traits associated with drought tolerance may

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Table 1 The nine miombo woodland principal tree species studied

Species	Genera	Leaf phenology	Functional group
Brachystegia boehmii Benth	*Fabaceae*	Fully deciduous	Generalist
Brachystegia longifolia Benth	*Fabaceae*	Fully deciduous	Generalist
Brachystegia spiciformis Benth	*Fabaceae*	Fully deciduous	Generalist
Erythrophleum africanum (Benth.) Harms	*Fabaceae*	Fully deciduous	Generalist
Pericopsis angolensis (Baker) Meeuwen	*Fabaceae*	Fully deciduous	Generalist
Brachystegia floribunda Benth	*Fabaceae*	Brevi-deciduous	Mesic specialist
Isoberlinia angolensis (Benth.) Hoyle & Brenan	*Fabaceae*	Brevi-deciduous	Mesic specialist
Julbernardia paniculata (Benth.) Troupin	*Fabaceae*	Brevi-deciduous	Mesic specialist
Marquesia macroura Gilg	*Dipterocarpaceae*	Brevi-deciduous	Mesic specialist

play a significant role in structuring such ecosystems (Reich et al. 1997). Separate pieces of evidence point in the direction of both branch hydraulic properties and leaf functional traits as reflecting a balance between plant water stress management and species ecological performance (Engelbrecht et al. 2000; Mencuccini 2003; Wright et al. 2002). Since the greatest impact of predicted climate change in seasonally dry tropical forests is likely to be in the magnitude and frequency of drought (IPCC 2007), understanding the relationships between branch hydraulic properties and leaf functional traits would add more insight into how these ecosystems will respond to future climate trends.

Comparative studies have shown that plant hydraulic conductivities tend to be higher under mesic sites than arid ones (Engelbrecht et al. 2000; Van der Willigen et al. 2000). Conversely, cavitation resistance (rapid phase change by xylem water under tension from liquid to vapour) has been observed to increase with increasing habitat aridity (Tyree and Zimmermann 2002). Consistent with these observations, it has been proposed that pressure for selection under arid environments favours plants with low hydraulic efficiency, but with high cavitation resistance (Canham et al. 2009; Zimmermann 1983). Ideally, this relationship suggests that plant hydraulic architecture has the potential to set species ecological boundaries by limiting hydraulically efficient individuals to the mesic habitats, while the less efficient but with secure xylems may compete in both mesic and arid habitats (Brodribb and Hill 1999; Lopez et al. 2005; Pockman and Sperry 2000).

Besides hydraulic response to drought, plants are also known to respond to water stress by modulating patterns of leaf carbon allocation (Niinemets 2001). For instance, it is a well-established fact that plants respond to water stress by modulating leaf size relative to leaf mass (Fonseca et al. 2000; Lamont et al. 2002; Reich et al. 1997). Available evidence also shows a trend towards smaller compact leaves, which are thicker and denser in arid environments than under mesic ones (Ackerly et al. 2002). Although

significant amount of evidence has coalesced in support of the hypotheses that both hydraulic properties and leaf functional traits are responsive to soil water variability, very little is known about the interactions between these two suites of traits for most dry tropical forests in Africa.

Therefore, the primary aims of this study were to evaluate the relationships between branch hydraulic properties and leaf functional traits associated with plant drought tolerance and to examine the extent to which these relationships influence species habitat preference. For examining these relationships, miombo woodlands, a seasonally dry tropical forest in southern Africa, was selected.

Materials and methods

Study site

In this study, two forest reserves with known forest management history were chosen to represent wet and dry miombo woodlands (White 1983). The two forest reserves experience summer rains, which occur between November and April followed by marked seasonal drought lasting from May to October. The wet site is Mwekera National Forest No. 6 located on the outskirts of City of Kitwe (12°49′S and 28°22′E; elevation of 1,295 m above sea level). The vegetation of the wet site is typically *Brachystegia-Julbernardia* woodlands with the genus *Brachystegia, Isoberlinia, Julbernardia*, and *Marquesia* as common canopy co-dominants (Chidumayo 1987). Average stand basal area and stand height are 39 m^2 ha^{-1} and 21 m, respectively. The wet site receives an average annual precipitation of 1,200 mm with average annual temperatures ranging from 14 to 28°C. The dry site is Siamambo local forest, located in Choma District at 16°50′S and 27°03′E with an average elevation of 1,266 m above sea level. The vegetation of the dry site has *Brachystegia boehmii, Brachystegia spiciformis*, and *Julbernardia globiflora* as the common canopy co-dominants. Mean stand

Table 2 Summary of species leaf and stem hydraulic traits

Site	Species	SLA (cm²/g)	MLA (cm²)	LDMC (g g^{-1}) × 10^{-2}	Ψ_{50} (MPa)	K_S (kg s^{-1} MPa^{-1} m^{-1})	H_v	K_L (kg s^{-1} MPa^{-1} m^{-1}) × 10^{-4}
Wet	*B. boehmii*	433 ± 14	30 ± 1	8.1 ± 0.4	−3.2 ± 0.11	5.74 ± 0.3	2.9 ± 0.02	1.66 ± 0.12
	B. longifolia	470 ± 13	27 ± 2	8.6 ± 0.3	−2.5 ± 0.08	5.17 ± 0.3	2.8 ± 0.02	1.41 ± 0.12
	B. spiciformis	522 ± 15	89 ± 4	7.8 ± 0.3	−2.8 ± 0.08	7.47 ± 0.5	2.3 ± 0.02	1.71 ± 0.15
	E. africanum	562 ± 34	33 ± 1	6.6 ± 0.6	−3.1 ± 0.09	9.97 ± 0.4	2.0 ± 0.01	1.98 ± 0.15
	P. angolensis	504 ± 18	73 ± 3	6.3 ± 0.3	−3.2 ± 0.10	9.43 ± 0.4	2.4 ± 0.02	2.27 ± 0.22
	B. floribunda	488 ± 43	112 ± 4	11.3 ± 1	−1.7 ± 0.20	13.73 ± 0.6	2.4 ± 0.01	3.32 ± 0.27
	I. angolensis	383 ± 13	202 ± 8	12.1 ± 0.5	−2.0 ± 0.22	24.19 ± 1.3	2.8 ± 0.01	6.86 ± 0.05
	J. paniculata	403 ± 12	157 ± 6	13.6 ± 0.6	−2.2 ± 0.10	15.58 ± 0.9	2.1 ± 0.01	3.33 ± 0.24
	M. macroura	418 ± 13	122 ± 4	11.3 ± 0.4	−1.5 ± 0.34	21.07 ± 0.8	2.5 ± 0.02	5.32 ± 0.44
Dry	*B. boehmii*	629 ± 42	24 ± 0.8	7.2 ± 0.5	−3.6 ± 0.14	2.77 ± 0.07	2.2 ± 0.1	0.59 ± 0.03
	B. spiciformis	620 ± 14	44 ± 1	7.0 ± 0.3	−3.6 ± 0.12	5.33 ± 0.18	1.4 ± 0.1	0.7 ± 0.04
	E. africanum	474 ± 8	32 ± 0.7	7.4 ± 0.5	−3.0 ± 0.10	8.19 ± 0.28	2.1 ± 0.2	1.59 ± 0.09
	P. angolensis	562 ± 18	57 ± 2	7.0 ± 0.5	−2.8 ± 0.13	10.53 ± 0.35	2.2 ± 0.1	2.21 ± 0.1

Standard errors of the mean are at 95% confidence interval

SLA specific leaf area, *MLA* mean leaf area, *LDMC* leaf dry matter content, Ψ_{50} cavitation resistance at 50% loss in conductivity, K_S specific leaf conductivity, H_v Huber value, K_L leaf specific conductivity

basal area and stand height are 14 m² ha^{-1} and 15 m, respectively. The dry site receives 800 mm of mean annual precipitation with mean annual temperatures ranging between 12 and 27°C.

Sampling

To examine the relationship between branch hydraulic properties and leaf functional traits, nine miombo woodlands canopy tree species were selected (Table 1).

The nine canopy tree species were selected on the basis that: (1) they differed substantially in habitat preference (Chidumayo 1987; Smith and Allen 2004), (2) they had contrasting leaf phenology, (3) there was no substantial taxonomical difference between them and, (4) they formed much of the canopy throughout the miombo woodlands. We sampled 25 GPS-referenced trees per species (giving a total of 225 trees at the wet site and 100 trees at the dry site). Generalists were sampled on both the wet and dry sites. Mesic specialists were only sampled on the wet site. Leaf measurements were carried out in June 2007 and April to June 2008. Data collection coincided with the end of the rainy season, by which time the leaves had reached full maturity and the soils were still well hydrated.

Leaf measurements

Three leaf-bearing, light-exposed branches were harvested per tree (between 0530 and 0730 hours local time) and quickly wrapped in wet towels. The samples were always placed in opaque plastic bags to ensure that leaves remained well hydrated. The full procedures for specific leaf area (SLA) and leaf dry matter content (LDMC) determination followed those of Westoby (1998) and Garnier et al. (2001). At the laboratory, one healthy and fully expanded leaf was harvested from each branch. The main criteria for selecting a leaf for measurement were that it had not suffered any leaf blade damage, was mature (hardened leaf blade), and actively photosynthesizing (green in colour). Prior to scanning (using Flatbed scanner—Packard Bell Diamond 1200 Plus, Packard Bell, UK) the leaves were initially weighed to get wet weight. The scanned leaves were then oven-dried at a constant temperature of 72°C for 48 h to a constant oven-dry weight (Ackerly et al. 2002; Sellin and Kupper 2006; Westoby and Wright 2003).

Leaf areas for the scanned images were determined using the software Image J (freely available from http://rsb.info.nih.gov/ij/). SLA (cm² g^{-1}) was calculated as the ratio of leaf area to its oven-dry mass. LDMC (g g^{-1}) was calculated as the ratio of leaf oven-dry weight to its wet weight.

Hydraulic properties measurement

Xylem hydraulic conductivity was measured on morphologically identical leaf-bearing branches (Patino et al. 1995). The branches were harvested in the early hours of the morning (between 0530 and 0830 hours). The under-bark diameter for the harvested twigs ranged from 4 to 10 mm. The harvested branches were always covered with wet towels and sealed in dark plastic sample bags to

Table 3 Results of linear mixed effects analysis of variance for co-occurring generalists and mesic specialists in wet and dry miombo woodland sites

Variable	Source	df	MS	F ratio	P value	VC
SLA (g cm^{-2})	Functional type	1	1.0602	12.68	0.009	7.53
	Species (functional type)	7	0.0836	2.96	0.006	4.16
	Individual (functional type species)	216	0.0282	2.01	<0.001	43.35
LDMC (g g^{-1})	Functional type	1	1.9077	48.08	<0.001	28.67
	Species (functional type)	7	0.0396	3.65	0.001	4.17
	Individual (functional type species)	216	0.0108	2.31	<0.001	35.30
MLA (cm^2)	Functional type	1	43.3102	14.32	0.007	54.55
	Species (functional type)	7	3.0239	65.68	<0.001	26.66
	Individual (functional type species)	216	0.0460	4.17	<0.001	12.53
K_S (kg s^{-1} MPa^{-1} m^{-1})	Functional type	1	25.4633	661.33	<0.001	49.72
	Species (functional type)	7	1.1288	29.32	<0.001	15.43
	Individual (functional type species)	216	0.0385	1.82	<0.001	16.24
H_v	Functional type	1	0.0125	0.66	0.417	0.14
	Species (functional type)	7	0.0678	3.58	0.001	5.40
	Individual (functional type species)	216	0.0189	2.02	<0.001	46.52
K_L (kg s^{-1} MPa^{-1} m^{-1})	Functional type	1	6.9027	234.3	<0.001	32.07
	Species (functional type)	7	0.2375	8.06	<0.001	7.72
	Individual (functional type species)	216	0.0294	2.01	<0.001	29.57
Ψ_{50} (MPa)	Functional type	1	65.3256	12.18	0.01	7.63
	Species (functional type)	7	5.3625	3.10	0.004	4.18
	Individual (functional type species)	216	1.7298	1.84	<0.001	41.58

K_S stem area specific hydraulic conductivity, H_v Huber value, K_L leaf specific conductivity, SLA specific leaf area, MLA mean leaf area, LDMC leaf dry matter content, MS mean square, VC variance component

minimize transpiration and emboli development. At the laboratory, the segments were trimmed to approximately equal length as the determined species maximum vessel length plus 10% allowance in order to avoid open vessels (Vinya et al. unpublished). Throughout the process of sample preparation, segments were always kept wholly immersed in water. Prior to hydraulic determination, segments were flushed with distilled water at a constant pressure of 150 kPa for periods ranging from 20 to 30 min depending on species and extent of xylem embolism. Hydraulic conductivity was gravimetrically determined by inserting the basal end of the trimmed twig into a custom-built water reservoir with a low delivery pressure head of 2 kPa. Maximum hydraulic conductivity was determined by forcing degassed, filtered (to 0.2 μm) and acidified (with HCl, pH 2) distilled water through the segments (Kolb et al. 1996; Sperry et al. 1988). Each segment was allowed to equilibrate for 30 min before initial flow rate was measured. Sap flow was measured by attaching a pre-weighed cotton wool onto the free distal end of the segment. At the end of each flow determination, segment underbark diameter and length were accurately measured. Maximum hydraulic conductivity (K_H) was calculated as:

$$K_H = \left(\frac{J_V}{(\Delta P/l)} \right) \ (\text{Kg} \cdot \text{s}^{-1} \, \text{MPa}^{-1} \, \text{m}) \tag{1}$$

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

Huber value (H_v; cm^2 cm^{-2}) was calculated as the ratio of the sapwood cross-sectional area to the total supported leaf area:

$$H_V = \frac{A_W}{A_L} \tag{2}$$

where A_L (m^2) is the total leaf area supported by the twig.

Determination of xylem vulnerability to cavitation

We used the standard laboratory bench air-drying technique to induce cavitation in branches (Cochard et al. 1992). Branches were progressively dehydrated to various water potentials over a period of 6–48 h depending on

Table 4 Results of two-way ANOVA comparing wet and dry miombo woodland sites generalists

	Scale	df	MS	F ratio	P value	VC
SLA (g cm^{-2})	Site	1	0.142	18.7	<0.001	7.3
	Species	3	0.026	3.4	0.019	4
	Interaction	3	0.090	11.83	<0.001	13.8
	Error	192	0.007			75
LDMC (g g^{-1})	Site	1	0.0004	0.08	0.77	0.04
	Species	3	0.014	2.89	0.036	4.2
	Interaction	3	0.0117	2.41	0.068	3.5
	Error	192	0.0048			92.3
MLA (cm^2)	Site	1	0.829	69.08	<0.001	8.7
	Species	3	1.926	160.46	<0.001	60.8
	Interaction	3	0.198	16.5	<0.001	6.3
	Error	192	0.012			24
H_v	Site	1	0.0823	12.05	0.001	5
	Species	3	0.055	8.06	<0.001	10
	Interaction	3	0.035	5.16	0.002	6
	Error	192	0.007			79
K_S (kg s^{-1} MPa^{-1} m^{-1})	Species	3	1.6	197.84	<0.001	60
	Site	1	0.738	91.29	<0.001	9.3
	Interaction	3	0.279	34.5	<0.001	11
	Error	192	0.008			20
K_L (kg s^{-1} MPa^{-1} m^{-1})	Species	3	0.358	47.16	<0.001	30
	Site	1	0.586	77.21	<0.001	16
	Interaction	3	0.160	21.11	<0.001	13
	Error	192	0.0076			40
Ψ_{50} (MPa)	Species	3	0.0193	0.41	0.74	0.62
	Site	1	0.0043	0.09	0.76	0.05
	Interaction	3	0.081	1.73	0.16	2.6
	Error	192	0.047			97

SLA specific leaf area, *MLA* mean leaf area, *LDMC* leaf dry matter content, Ψ_{50} cavitation resistance at 50% loss in conductivity, K_S specific leaf conductivity, H_v Huber value, K_L leaf specific conductivity

species. We dehydrated the branches to varying range of water potentials corresponding to 0 to >80% loss of hydraulic conductance. Prior to water potential determination, small distal segments were excised from the main twig and placed in airtight plastic bags for 30 min to allow for water potential equilibration. This was then followed by water potential determination (Ψ) using a pressure chamber (SKPM 1405, Skye Instruments Ltd, UK).

For construction of vulnerability curves, hydraulic conductivity (K_{Hmin}) was initially determined on dehydrated segments using the gravimetric technique. This was followed by flushing out emboli as described above and re-measurement of K_H to obtain K_{Hmax}. Percent reduction in hydraulic conductivity (PLC) was then calculated as:

$$\text{PLC} = \frac{K_{Hmax} - K_{Hmin}}{K_{Hmax}} \times 100 \qquad (3)$$

where K_{Hmax} is the maximum hydraulic conductivity without emboli and; K_{Hmin} is initial hydraulic

conductivity with emboli. To confirm that the segments had thoroughly been freed of emboli, they were perfused with Safranin dye at the end of each experiment. Vulnerability curves were fitted with the following sigmoid function:

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

where Ψ_{50} is the water potential causing 50% reduction in hydraulic conductance, and *a* represents the slope of the vulnerability curve (Pammenter and Van der Willigen 1998).

Statistics

Differences between functional groups (generalists vs. specialists) were analysed using a linear mixed-effects model ANOVA (Zar 2010). We used a two-way ANOVA to test for the effects of site and species (Hofmann and

Franco 2003). Intra-species differences between wet and dry site generalists were analysed using two-sample t tests. We used linear regression analysis to determine the relationship between hydraulic properties and leaf functional traits. Data were log transformed because these failed both the normality and constant variance tests. Huber value data were arcsine transformed prior to log transformation, because these were in proportion format. All statistical analyses were performed in Minitab (Version 15, Minitab Inc., PA, USA).

Results

Hydraulic properties and leaf functional traits

There were significant ($P < 0.05$) differences in the range of branch hydraulic properties and leaf functional traits measured for the principal miombo woodland tree species in this study (Table 2).

We observed significant ($P < 0.05$) variations in both hydraulic properties and leaf functional traits between the two miombo woodlands functional groups (generalists versus mesic specialists) examined in this study (Table 3).

However, Huber value (H_v) did not vary significantly ($P > 0.05$) between the two miombo woodlands functional groups.

Shift in hydraulic and leaf functional traits between wet and dry miombo woodlands

Across generalist populations, LDMC and Ψ_{50} varied insignificantly ($P > 0.05$) over the examined spatial scale (Table 4).

By contrast, K_S, K_L, MLA, and H_v varied significantly ($P < 0.05$) between the examined sites in this study (Table 4).

At the intra-species level, there were significant ($P < 0.05$) reductions in K_S from wet to dry miombo woodland sites for three (*B. boehmii*, *B. spiciformis*, and *Erythrophleum africanum*) out of the four generalists (Fig. 1).

Among the four generalists, only *B. spiciformis* showed a significant (two-sample t test assuming equal variances, $P = 0.006$) intra-species increase in cavitation resistance from wet to dry site. However, for the other three generalists (*B. boehmii*, *E. africanum* and *P. angolensis*) examined in this study, we observed an insignificant ($P > 0.05$) intra-species differences in Ψ_{50} between wet and dry sites.

Brachystegia boehmii, *B. spiciformis*, and *P. angolensis* showed a trend of increasing SLA from wet to dry site, with *E. africanum* being the only generalist species showing the opposite trend (Figs. 1, 2). LDMC followed a similar trend as SLA from wet to dry miombo woodland sites for the four generalists. As expected, MLA showed a declining trend from wet to dry miombo woodland site in *B. boehmii*, *B. spiciformis*, and *P. angolensis*.

Relationships between branch hydraulics and leaf functional traits

Across species, sapwood specific hydraulic conductivity (K_S) was negatively correlated to SLA ($r = 0.76$, $P = 0.02$), but positively correlated to both LDMC ($r = 0.74$, $P < 0.02$) and MLA ($r = 0.90$, $P = 0.001$). A linear regression analysis explained 58, 54, and 82% of the variability in SLA, LDMC, and MLA, respectively (Fig. 3).

There was a significant ($r = 0.75$, $P = 0.02$) negative correlation between Ψ_{50} and SLA. Ψ_{50} was, however, significantly and positively correlated to LDMC ($r = 79$, $P = 0.01$). On the contrary, Ψ_{50} was not correlated to MLA ($r = -0.56$, $P = 0.12$). A linear regression explained 56, 63, and 31% of the variability in SLA, LDMC, and MLA, respectively (Fig. 4).

However, Huber value was not correlated to any of the three leaf functional traits (SLA, LDMC, and MLA).

Discussion

As expected, miombo woodland tree species with wide habitat selection (generalists) converged towards high cavitation resistance, low hydraulic efficiency, and high SLA, but low LDMC and mean leaf area (MLA) (Table 2). By comparison, mesic specialists exhibited high hydraulic efficiency, but are more vulnerable to xylem cavitation with low SLA but high LDMC and MLA. Our findings on plant hydraulic properties are consistent with other studies (Brodribb and Hill 1999; Pockman and Sperry 2000).

It has been proposed that pressure for selection under arid environments favour plants with low SLA (Fonseca et al. 2000) and high cavitation resistance (Tyree and Zimmermann 2002). Consistent with these observations, one expects a positive relationship between SLA with Ψ_{50}. By contrast, our results showed a negative association between SLA with both Ψ_{50} and K_S, (Figs. 3, 4) indicating that species with low leaf mass per area were more resistant to drought-induced xylem cavitation than ones with high leaf mass per area. The most plausible explanation for the seemingly contradictory result may be attributed to the differences in leaf phenology between the two miombo woodlands functional groups. Several pieces of evidence point in the direction of leaf construction costs and leaf life span being negatively correlated with SLA (Eamus et al. 1999; Kikuzawa 1995; Sabrado 1991; Villar and Merino
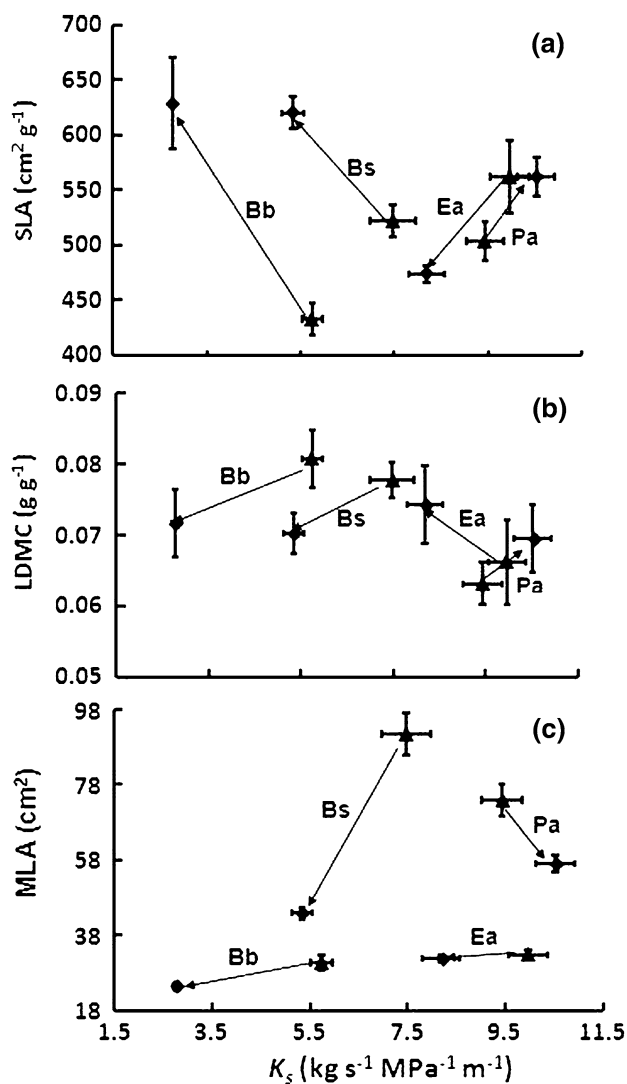
Fig. 1 Shifts in specific hydraulic conductivity and leaf functional traits between wet and dry miombo woodland habitats: **a** specific leaf area (SLA); **b** leaf dry matter content (LDMC); **c** mean leaf area (MLA). Chart symbols are: *arrows* represent trait shift from wet to dry miombo woodland sites

Fig. 2 Shifts in xylem vulnerability to cavitation and leaf functional traits between wet and miombo woodland habitats: **a** specific leaf area (SLA); **b** leaf dry matter content (LDMC); **c** mean leaf area (MLA). Chart symbols are: *arrows* represent trait shift from wet to dry miombo woodland sites

2001). In the case of this seasonally dry tropical forest, the drought-tolerant miombo woodlands generalist tree species are fully deciduous, whereas mesic specialists are characteristically brevi-deciduous (Table 1). Thus, in terms of leaf carbon economics, it is cheaper for the fully deciduous generalists to support leaves with low SLA because of the presumably low construction costs. It is, therefore, not surprising that in this seasonally dry tropical forest, there is a pronounced trend towards low SLA and high cavitation resistance from wet to dry sites (Fig. 2).

LDMC has often been linked to leaf adaption to withstand desiccation, such that high LDMC leaves are thicker and stiffer than low ones (Groom and Lamont 1997). As expected, plants adapted to arid habitats tend to develop
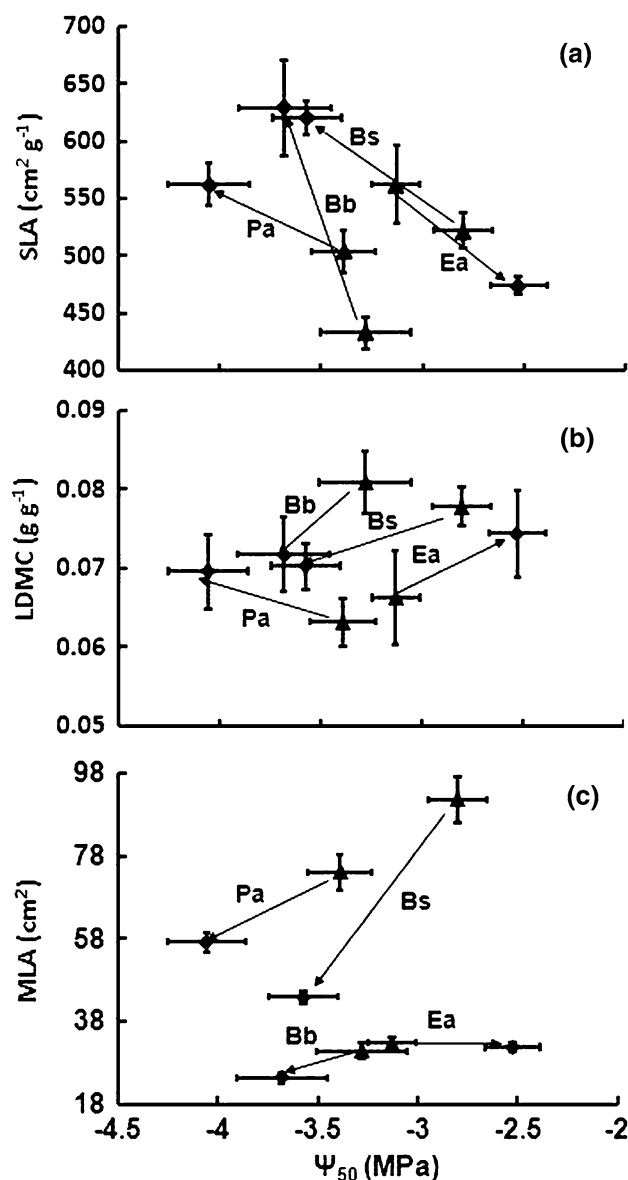
leaves high in LDMC and those from mesic habitats display an opposite trend. Thus, LDMC has repeatedly been viewed as a good predictor of plant ecological strategy (Wilson et al. 1999). Ideally, the general hypotheses, which propose a convergence towards increased cavitation resistance and high LDMC under arid environments, expect an inverse relationship between LDMC and Ψ_{50} and K_S. Surprisingly, we found an opposite pattern in which LDMC was positively associated with both Ψ_{50} and K_S (Figs. 3, 4).

A positive relationship between LDMC and Ψ_{50} in this study arose due to differences in leaf phenology between
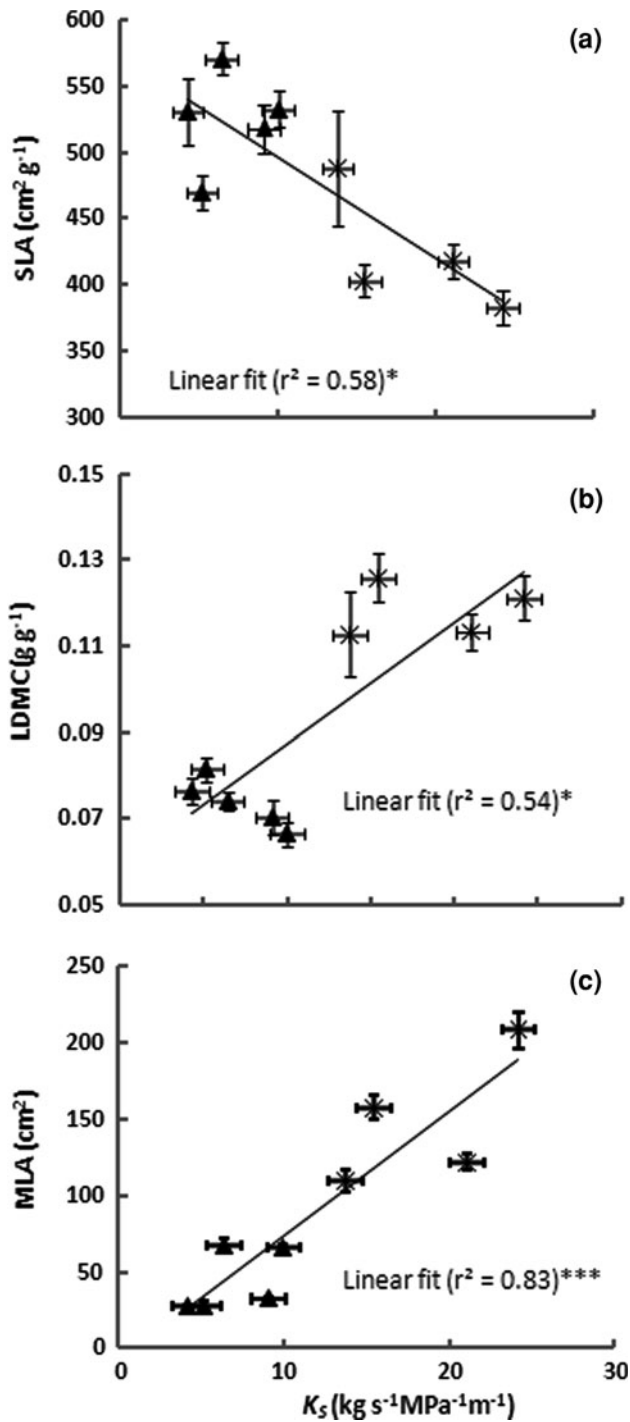
Fig. 3 Relationship between stem area specific hydraulic conductivity (K_S) and leaf functional traits: **a** specific leaf area (SLA); **b** leaf dry matter content (LDMC); **c** mean leaf area (MLA). Regression line data points are tree species mean ± SE ($n = 25$ trees per species). The fitted lines for graphs **a**, **b** and **c**, respectively, have the equations: $y = 2.83 - 0.17\chi$ ($F = 9.69$, $P = 0.017$); $y = 1.07 + 0.16\chi$ ($F = 8.37$, $P = 0.023$) and; $y = 0.71 + 1.13\chi$ ($F = 31.36$, $P = 0.001$). Chart symbols are: *closed triangles* generalists, *multi symbols* mesic specialists, **P < 0.05, **P < 0.01, ***P < 0.001, ns* not significant

Fig. 4 Relationship between xylem vulnerability to cavitation and leaf functional traits: **a** specific leaf area (SLA); **b** leaf dry matter content (LDMC); **c** mean leaf area (MLA). *Regression line* data points are tree species mean ± SE ($n = 25$ trees per species). Regression models describing the relationships are: $y = 2.54 - 0.053\chi$ ($F = 8.72$, $P = 0.021$); $y = 1.37 + 0.057\chi$ ($F = 11.87$, $P = 0.011$); and $y = 2.38 + 0.23\chi$ ($F = 3.18$, $P = 0.118$). Chart symbols are: *closed triangles* generalists, *multi symbols* mesic specialists, **P < 0.05, **P < 0.01, ***P < 0.001, ns P > 0.05*

the two miombo woodlands functional groups. Firstly, high LDMC leaves are generally expensive to construct as they entail greater leaf carbon investment to reinforce desiccation resistance (Williams et al. 1989). Secondly, numerous

studies have suggested that high LDMC confers the ability to plants to withstand lower negative leaf water potentials, hence enabling such species to maintain physiological processes under drought conditions (Kursar et al. 2009; Oertli et al. 1990; Zimmermann 1978). We believe that a combination of high LDMC with an efficient hydraulic architecture allows the low cavitation resistant mesic specialists to be physiologically active throughout the year. The net benefit of being productive throughout the year is the increased carbon investment in the photosynthetic apparatus, which gives rise to increased foliar carbon investment. On the other hand, low LDMC among the fully deciduous miombo woodlands generalists results in low desiccation resistance and as such these respond to seasonal drought by shedding leaves. Therefore, ability to limit seasonal water losses through leaf shedding, coupled with a xylem structure that is resistant to cavitation, enables miombo generalists to be successful in both the mesic and arid miombo woodland habitats.

Across species, we did not find a significant association between Ψ_{50} and MLA suggesting that these two traits are not functionally coordinated in this water-limited tropical forest. The advantages of small leaves under arid environments have been emphasized in a number of studies. For instance, it has been suggested that small leaves are better adapted to minimize leaf overheating under drought-prone environments than large ones (Parkhurst and Loucks 1972). Therefore, the lack of correlation between Ψ_{50} and MLA is quite surprising given the tight relationship between leaf size and transpiration rate (Hopkins and Hüner 2009). Interesting enough, K_S was strongly associated with MLA suggesting the existence of a physiological link between average leaf size and hydraulic efficiency. This is consistent with numerous studies that have demonstrated a positive relationship between hydraulic efficiency and stomatal conductance (Brodribb et al. 2002; Hubbard et al. 2001). As expected in this seasonally dry tropical forest, both hydraulic efficiency and MLA demonstrated significant reductions from wet to dry habitats, suggesting a significant shift towards reductions in plant water losses under arid habitats.

Conclusions

This study has demonstrated that differences in habitat preference between the two miombo woodland functional groups are as a result of variations in plant hydraulic properties as well as leaf functional traits. Tree species with wide habitat occurrences have xylem structures that are more resistant to cavitation than narrow habitat range of mesic specialists. Furthermore, generalists display high SLA, but low LDMC and MLA in comparison to mesic specialists. These results suggest that the interaction between plant hydraulic properties and leaf functional traits may exert some influence on the range of habitats that any given tree species can successfully colonize in seasonally dry tropical forests.

References

Ackerly DD, Knight CA, Weiss SB, Barton K, Starmer KP (2002) Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. Oecologia 130:449–457

Brodribb T, Hill RS (1999) The importance of xylem constraints in the distribution of conifer species. New Phytol 143:365–372

Brodribb JT, Holbrook NM, Gutierrez MV (2002) Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. Plant Cell Environ 25:35–44

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

Chidumayo EN (1987) Species structure in Zambian miombo woodland. J Appl Ecol 3:109–118

Cochard H, Cruiziat P, Tyree MT (1992) Use of positive pressure to establish vulnerability curves. Plant Physiol 100:205–209

Eamus D, Myers B, Duff G, Williams R (1999) A cost–benefit analysis of leaves of eight Australian savanna tree species of differing leaf lifespan. Photosynthetica 36:575–586

Engelbrecht BMJ, Velez V, Tyree MT (2000) Hydraulic conductance of two co-occuring neotropical understorey shrubs with different habitat preferences. Ann For Sci 57:201–208

Fonseca CR, Overton JM, Collins B, Westoby M (2000) Shifts in trait-combination along rainfall and phosphorus gradients. J Appl Ecol 88:964–977

Frost P. (1996) The ecology of miombo woodlands. In: Campbell B (ed) The miombo in transition: woodlands and welfare in Africa. CIFOR, Bogor, pp 11–57

Garnier E, Shipley B, Roumet C, Laurent G (2001) A standardized protocol for the determination of specific leaf area and dry matter content. Funct Ecol 15:688–695

Groom PK, Lamont BB (1997) Xerophytic implications of increased sclerophylly: interactions with water and light in *Hakea psilorrhyncha* seedlings. New Phytol 136:231–237

Hofmann WA, Franco AC (2003) Comparative growth 378 analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. J Ecol 91:475–484

Hopkins W, Hüner PAN (2009) Introduction to plant physiology. Wiley, New Jersey, p 503

Hubbard RM, Ryan MG, Stiller V, Sperry JS (2001) Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. Plant Cell Environ 24:113–121

IPCC (2007) Climate Change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Kikuzawa K (1995) The basis for variation in leaf longevity of plants. Vegetatio 121:89–100

Kolb KJ, Sperry JS, Lamont BB (1996) A method for measuring xylem hydraulic conductance and embolism in entire root and shoot systems. J Exp Bot 47:1805–1810

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

Lamont BB, Groom PK, Cowling RM (2002) High leaf mass per area of related species assemblages may reflect low rainfall and carbon isotope discrimination rather than low phosphorus and nitrogen concentrations. Funct Ecol 16:403–412

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

Malaisse F (1978) The Miombo Ecosystem. In: UNESCO (ed) Tropical forest ecosystems: a state-of-knowledge report prepared by UNESCO/UNEP/FAO. UNESCO, Paris, pp 589–606

Mencuccini M (2003) The ecological significance of long-distance water transport: short term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. Plant Cell Environ 26:163–182

Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. Ann Rev Ecol Syst 17:67–88

Niinemets U (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. Ecology 82:453–469

Oertli JJ, Lips SH, Agami M (1990) The strength of sclerophyllous cells to resist collapse due to negative turgor pressure. Acta Oecol 11:281–289

Pammenter NW, Van der Willigen C (1998) A mathematical and statistical analysis of the curves illustrating vulnerability to xylem to cavitation. Tree Physiol 18:589–593

Parkhurst FD, Loucks OL (1972) Optimal leaf size in relation to environment. J Ecol 60:505–537

Patino S, Tyree MT, Herre EA (1995) Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to free standing and hemi-epiphytic Ficus species from Panama. New Phytol 129:125–134

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

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. Proc Natl Acad Sci USA 94:13730–13734

Sabrado MA (1991) Cost–benefit relationships in deciduous and evergreen leaves of tropical dry forest species. Funct Ecol 5:608–616

Sellin A, Kupper P (2006) Spatial variation in sapwood area ratio and specific leaf area within a crown of silver birch. Trees 20:311–319

Smith P, Allen Q (2004) Field guide to trees and shrubs of the miombo woodlands. Royal Botanical Gardens Kew, London

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

Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap, 2nd edn. Springer, Berlin

Van der Willigen C, Sherwin HW, Pammenter NW (2000) Xylem hydraulic characteristics of subtropical trees from contrasting habitats grown under identical environmental conditions. New Phytol 145:51–59

Villar R, Merino J (2001) Comparison of leaf construction costs in woody species with differing leaf life-spans in contrasting ecosystems. New Phytol 151:213–226

Westoby M (1998) A leaf–height–seed (LHS) plant ecology strategy scheme. Plant Soil 199:213–227

Westoby M, Wright IJ (2003) The leaf size–twig size spectrum and its relationship to other important spectra of variation among species. Oecologia 135:621–628

White F (1983) The vegetation of Africa: a descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa. UNESCO, Paris

Williams K, Field CB, Mooney HA (1989) Relationships among leaf construction cost, leaf longevity, and light environment in rain forest plants of the genus *Piper*. Am Nat 133:198–211

Wilson PJ, Thompson K, Hodgson JG (1999) Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. New Phytol 143:155–162

Wright IJ, Westoby M, Reich PB (2002) Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. J Ecol 90:534–543

Zar JH (2010) Biostatistical analysis, 5th edn. Pearson Education International, London

Zimmermann U (1978) Physics of turgor- and osmoregulation. Ann Rev Plant Physiol 29:121–148

Zimmermann MH (1983) Xylem structure and the ascent of sap. Springer-Verlag, Berlin