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Wood anatomical traits as a measure of plant responses to water availability: invasive *Acacia mearnsii* De Wild. compared with native tree species in fynbos riparian ecotones, South Africa

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Abstract Riparian ecotones in the fynbos biome of South Africa are heavily invaded by woody invasive alien species, which are known to reduce water supply to downstream environments. To explore whether variation in species-specific functional traits pertaining to drought-tolerance exist, we investigated wood anatomical traits of key native riparian species and the invasive *Acacia mearnsii* across different water availability proxies. Wood density, vessel resistance against implosion, vessel lumen diameter and vessel wall thickness were measured. Wood density varied significantly between species, with *A. mearnsii* having denser wood at sites in rivers with high discharge. As higher wood density is indicative of increased drought tolerance and typical of drier sites, this counter-intuitive finding suggests that increased wood density was more closely related to midday water stress, than streamflow quantity per se. Wood density was positively correlated with vessel resistance against implosion. Higher wood density may also be evidence that *A. mearnsii* is more resistant against drought-induced cavitation than the studied native species. The observed plastic response of *A. mearnsii* anatomical traits to variable water availability indicates the ability of this species to persist under various environmental conditions. A possible non-causal relationship between wood anatomy and drought tolerance in these riparian systems is discussed.

Keywords Drought tolerance · Wall-to-lumen ratio · Water potential · Wattle · Wood density · Xylem vessels

Introduction

The mechanical design of a plant is fundamental for survival and related functional traits can be plastic and directly influenced by the environment (Reich et al. 2003). There is much value in investigating variation in plant functional traits, especially under water limitation (Ackerly 2004). This type of information can provide crucial insights into the inter-specific variation that exists in communities that might experience changing environmental conditions, and whether differential, species-specific responses may confer a competitive advantage on some species. This is especially relevant in understanding the possible future persistence and distribution of biological invasions, especially with changing water availability. Wood anatomy, for example, is likely to be under strong selective pressure, thus the study of xylem anatomical functional traits that may determine plant responses to dry conditions in space and time has become an increasingly important research topic (Read and Stokes 2006).

Wood density, a key anatomical trait in tree species, is indicative of mechanical and physiological life history strategies and therefore a critical functional trait for understanding the evolution and ecology of whole plant performance in different environments (Swenson and Enquist 2007). This is mainly due to wood density being responsive to environmental factors such as water availability and temperature (Hacke et al. 2001; Thomas et al.

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2007; Martínez-Cabrera et al. 2009). Using landscape slope as a water availability proxy (steeper gradient = less water available), Barij et al. (2007) suggested that xylem structure was influenced by in situ hydrological properties—the less water available, the denser the wood (see also Preston et al. 2006). Mean annual precipitation (MAP) as a measure of water availability was also shown to have a significant negative correlation with wood density, as shown for *Eucalyptus grandis* in warm temperate regions of South Africa (Naidoo et al. 2006). However, wood density can also be positively correlated with MAP (Wiemann and Williamson 2002); Chave et al. (2006) hypothesised that dense wood in wet Neotropical forests is a safety mechanism against invertebrate attack. Still, as safe hydraulic transport is a crucial trait in plants, there is generally an important (positive) link between higher wood density and high resistance against drought-induced cavitation of xylem under water-stressed conditions (Hacke and Sperry 2001; Hacke et al. 2001; Meinzer 2003; Wheeler et al. 2005; Jacobsen et al. 2007a, b; Pratt et al. 2007; Stiller 2009).

Wood density can consequently be a valuable screening tool for identifying species that may be more vulnerable to variation in water availability in a specific community (Jacobsen et al. 2007a). Fynbos riparian zones in the south-western Cape of South Africa are predicted to endure severe future drought conditions (New 2002; Steynor et al. 2009). The invasive alien plant (IAP), *Acacia mearnsii*, an important forestry species in South Africa and known invader of especially riparian areas, aggravates this problem as it is a profligate water user (Dye et al. 2001; Dye and Jarmain 2004). An important question has been raised concerning the future invasion success of alien plants under global climate change—would IAPs become more invasive, and thus be even more competitive, or would their invasion success be reduced (Dukes and Mooney 1999). Using vulnerability to drought-induced cavitation, an important measure of drought tolerance in woody plants, Crous et al. (2012) showed the physiological advantage that xylem of *A. mearnsii* has in resisting hydraulic failure compared to key indigenous riparian tree species under proxies of decreasing water availability. This accentuates the invasive potential of *A. mearnsii*, however, a suite of complementary physiological and anatomical traits might better explain how a species adapt against hydraulic failure under water-stressed conditions (McCulloh et al. 2012).

Of interest, therefore, is the extent to which wood anatomy varies for native and invasive alien plants across a water availability gradient (Valladares et al. 2007; Funk 2008). A lack of anatomical variation (little or no plasticity) would suggest that species might endure significant stress under reduced water availability. IAPs in particular have displayed high trait plasticity in low resource environments, therefore differences in phenotypic plasticity between native and invasive species may provide insight into how co-occurring species could respond anatomically to changing environmental conditions (Funk 2008) and future geographic distributions (Hulme 2008). It would therefore be instructive to see how species, especially IAPs, can vary in structural adaptive strategy given different water availability proxies.

Wood density per se only represents the bulk measure of the multiple functions of xylem, i.e. it is an important broad indicator of xylem "construction cost". Therefore, wood density needs to be examined in relation to its functional and structural correlates (e.g. vessel traits), as together they can explain the variation that exists within communities (Preston et al. 2006). Important vessel traits are vessel lumen diameter, vessel wall thickness and then combined as wall-to-lumen ratios $(t/b)^2$ (vessel mechanical resistance against implosion, Fig. 1). Density correlates significantly and positively with wall-to-lumen ratios $(t/b)^2$ (Hacke et al. 2001; Hacke and Sperry 2001). So, plants that grow in places with lower water potentials require higher wall thickness (stronger walls) to resist implosion and drought-induced cavitation (Sperry et al. 2006). Larger lumens, although hydraulically more efficient, are seen as indicative of less dense wood (Wagner et al. 1998; Tyree and

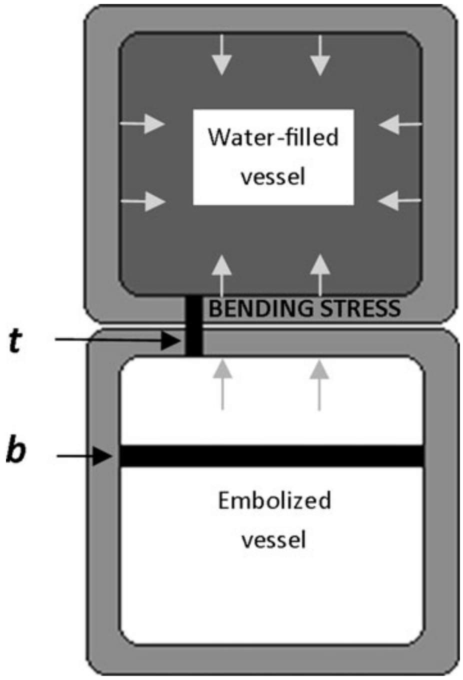

Fig. 1 Diagram defining wall thickness (t) and lumen diameter (b), showing b as the width of a hypothetical, minimum-area end wall between a full and an embolized vessel, and t as the thickness of their common wall. Bending stress due to negative water pressures can result in wall bending. This bending stress may cause walls to implode, subsequently letting air in (adapted and simplified from Hacke et al. 2001)

Zimmerman 2002). It is therefore helpful to seek ecological correlations between vessel lumen diameter, vessel wall thickness, $(t/b)^2$ (among others) and wood density, as a method of investigating the link between wood density and mechanical strength against drought stress.

Another valuable correlation with wood density is minimum water potential ($\Psi_{\min}$). Minimum water potential ($\Psi_{\min}$) is a good indicator of different plants' access to soil water (Ackerly 2004; Bhaskar and Ackerly 2006). Therefore, if density values are correlated with the water potential where the plant is most stressed, one will find that plants that experience the highest amount of stress, due to very low water potentials, are likely to have denser wood (Ackerly 2004; Jacobsen et al. 2007a).

The rationale of our study was therefore to investigate whether plastic responses in wood anatomical traits occur in the invasive alien species *A. mearnsii* (a major threat to functioning of riparian zones in the south-western Cape, South Africa), across proxies of water availability, and how co-occurring natives compare with that of the IAP. This was done at a catchment scale (a narrow geographic range with a similar Mediterranean-type climatic regime), where we investigated wood density and its components $(t/b)^2$, lumen width and wall thickness among three river systems, with streamflow volume as the surrogate for water availability (sensu Swift et al. 2008). Additionally we investigated whether *A. mearnsii* showed variation in wood density across a biome scale (a wide geographic range), with mean annual precipitation as the surrogate for water availability. Ultimately the following key questions were investigated:

1. Experiment 1: At a catchment scale, how do the woody invasive tree *A. mearnsii* and two key native riparian tree species respond with regards to wood density across three sites that differ in streamflow? Which anatomical traits contribute to this variation, and what could this mean for species under changing environmental conditions?
2. Experiment 2: At a biome scale, how plastic is *A. mearnsii* across sites with different precipitation, and within sites, how does its wood density compare to that of a co-occurring native species?

Methods

Description of species and study sites

We studied the evergreen tree *Acacia mearnsii* De Wild. (Fabaceae). This Australian species is highly invasive and a threat to riparian zones in the south-western Cape, South Africa (Enright 2000; Dye and Jarmain 2004).

For the catchment scale study (Experiment 1), the anatomy of *A. mearnsii* was contrasted with that of native riparian species *Brabejum stellatifolium* (L.) (Proteaceae) and *Metrosideros angustifolia* (L.) (Myrtaceae), key species in south-western Cape Mediterranean-type riparian systems, and critical for replanting and restoration in degraded riparian ecotones (Prins et al. 2004; Galatowitsch and Richardson 2005). The study sites were the Eerste River at Jonkershoek (33°57.621′S, 18°55.037′E; 200 m a.s.l.), Wit River at Bainskloof (33°34.217′S, 19°08.452′E; 279 m a.s.l.) and Molenaars River at DuToitskloof (33°41.778′S, 19°13.263′E; 297 m a.s.l.). Sites were selected according to the presence of the target species, and streamflow volumes—i.e. ranging from high to low flow. Jonkershoek represents the low flow site, Bainskloof the intermediate flow site and DuToitskloof the high flow site (data shown in Crous et al. 2012). The three sites occupy slightly different relative positions in the catchment: at Bainskloof the site is situated in the mountain stream transitional zone, while the two other sites are in the upper foothills, which have a lower gradient. The sampled trees at the different sites also occupy different elevations above and distances away from the active channel (during low flow conditions). Jonkershoek catchment has been considerably modified over the last century, in contrast to the other two catchments, where streamflows likely reflect conditions closer to the natural regime. This may impact long-lived vegetation at Jonkershoek.

For the biome scale study (Experiment 2), we compared the wood density of *A. mearnsii* along six riparian systems that fell within regions that differed in mean annual precipitation (MAP) (Table 1). Using the MAP as the surrogate for water availability gradient (e.g. Naidoo et al. 2006), the sites were divided into two mesic, two xeric, and two intermediate rainfall sites (Table 1). Additionally, within each site, we compared wood density of the invasive woody tree *A. mearnsii* against one native co-occurring species, as listed in Table 1. The biogeographic differences between sites necessitated the use of different native species at the different sites. Native species selection within sites was therefore based on the most important species (aerial cover) co-occurring along with the IAP, even though none of the species are obligate riparian species, similar to the invader. This means that only *A. mearnsii* was tested across the water availability gradient, whilst the native species were used to study differences in wood density within each site.

Wood anatomical properties

Wood density (D_t) (Experiments 1 and 2) was determined using the method described in Hacke et al. (2000) and Pratt and Black (2006). Stem segments were cut according to a

Table 1 Description of the biome scale study sites, indicating the gradient in mean annual precipitation and species with which *Acacia mearnsii* was compared with regard to xylem density

Site	MAP (mm)	Gradient description	Native species compared	Latitude (S)	Longitude (E)	Elevation (m a.s.l.)
Eerste River, Stellenbosch	688	Mesic	*Brabejum stellatifolium* (L.) (Proteaceae)	33°56.266′	18° 53.260′	210
Witteklip River, Kareedouw	714	Mesic	*Cliffortia* spp. (Rosaceae)	33°49.331′	24°25.723′	377
Buffeljags River, Buffeljagsrivier	551	Intermediate	*Kiggelaria africana* (L.) (Achariaceae)	34°03.350′	20°32.343′	64
Buffeljags River, Heidelberg	413	Intermediate	*Kiggelaria africana* (L.) (Achariaceae)	34°00.500′	20°46.614′	179
Keisie River, Montagu	334	Xeric	*Psoralea pinnata* (L.) (Fabaceae)	33°41.232′	19°53.969′	789
Congo River, Oudtshoorn	241	Xeric	*Noltea africana* (L.) Rchb.f. (Rhamnaceae)	33°27.478′	22°20.711′	551

standardized canopy position, compass direction and position on branch, to reduce possible within tree variation (data not shown). Five to six stem segments from five replicate trees of each species were cut and trimmed to around 2–3 cm. Stems were then dissected longitudinally so that the pith and bark could be removed. Segments were then immersed in water and degassed for 12–24 h, or until no more air bubbles were observed. Saturated volume (xylem saturated with water after degassing) was determined using the water displacement method (Archimedes' principle) (Hacke et al. 2000). Dry weight was determined from measuring segments after dehydration in an oven at 75 °C for 48 h. Density values were calculated by the ratio of dry weight to saturated volume (g/cm^3). Density data (at both scales) were statistically compared using a factorial ANOVA followed by a Fisher LSD post hoc test (Statistica Release 8, StatSoft Inc.) to identify any between site and species differences. At the biome scale (Experiment 2), a one-way ANOVA was also used to compare *A. mearnsii* across sites. At the catchment scale (Experiment 1), multiple correlations were made between density and vessel traits.

Vessel traits were measured using methods described in Hacke et al. (2001) and Jacobsen et al. (2007a). Transverse sections were shaved from one stem segment per individual, and mounted on a slide. Several images were taken of each transverse section with a digital camera (Leica DFC425, Leica Microsystems, Solms, Germany) attached to a light microscope (Leica DM1000, Leica Microsystems, Solms, Germany). Images were analysed using the Leica Application Suite (LAS) software. In total, 100 measurements of vessel lumen diameter (d) and wall thickness (t) were made per individual stem segment, rendering 500 measurements per species per site. As our main interest was wood specific density and not whole stem conductivity, we used the unweighted average vessel lumen diameter as opposed to the hydraulically weighted average diameter (Preston et al. 2006). The $(t/b)^2$, a function of two adjacent xylem vessels, where t is the thickness of the common wall and b the length of the largest lumen, was obtained by measuring at least 20 adjacent vessels per individual, giving a total of 100 $(t/b)^2$ measurements per species per site. A factorial ANOVA, followed by a Fisher LSD post hoc test (Statistica Release 8, StatSoft Inc.) was used to determine significant differences between species across different streamflow sites (Experiment 1). To investigate any possible pattern in wood anatomical traits for tree species in the Mediterranean-climate south-western Cape riparian zones [e.g. if high wood density would also indicate high $(t/b)^2$, and how each species contributes to this relationship] (Iovi et al. 2009), average lumen diameter and wall thickness were separately correlated with wood density as d and t, and combined as $(t/b)^2$, and examined using regression analysis. Data were transformed as necessary to adhere to statistical models.

Xylem water potentials in the field

For the catchment scale study (Experiment 1), stem xylem water potential was measured using a pressure chamber (Pockman et al. 1995) (PMS instruments, Model 1000, Oregon, USA). Measurements were made in summer (December–February, 2008–2009), when plants experience drought stress. Midday (1200–1400 hours) measurements were made to obtain minimum water potentials ($\Psi_{\min}$), and were carried out on the same individuals ($n = 5$) used for wood density measurements. Three healthy stems (with leaves) from each individual were cut and measured immediately on site (one treatment). Three replicates of each treatment, measured over three different days, were made for each species across all sites. Data were calculated as mean ± SD ($n = 9$), and the relationships between $\Psi_{\min}$ and both wood density and vessel traits were examined using regression analysis.

Results

Catchment scale study

Twig wood density values from the three species investigated ranged from 0.484 to 0.641 g cm^{-3} (Table 2), within the range of average wood density values according to Chave et al. (2009). Wood density differed significantly across species ($P < 0.001$, Table 3). Specifically, *B. stellatifolium* and *M. angustifolia* did not differ in wood density across all sites whereas *A. mearnsii* presented variable results (Table 2). *A. mearnsii* consistently had significantly higher wood density compared to both native species at the intermediate streamflow (Bainskloof) and high streamflow (DuToitskloof) sites. Within sites, the intermediate streamflow site (Bainskloof) was the only site where all the species differed significantly in wood density.

Lumen diameters differed significantly across species and sites ($P < 0.01$, Table 3). *B. stellatifolium* and *M. angustifolia* showed a consistent trend in lumen diameter, with both species having significantly smaller diameters at the low streamflow site (Jonkershoek) as opposed to the other sites (Table 2). Within sites, lumen diameters did not differ between the native species. In contrast, *A. mearnsii* consistently had significantly larger lumen diameters than both native species across and within all sites. In addition, *A. mearnsii* did not differ in vessel lumen diameter between sites.

Vessel wall thickness showed significant differences within and between sites ($P < 0.001$, Table 3). All species had their greatest wall thickness at the low streamflow site, Jonkershoek. Wall thickness of *A. mearnsii* differed significantly across all sites. *A. mearnsii* was the only species to react in this way (Table 2). *M. angustifolia* had on average the smallest wall thickness (1.13 µm) and *B. stellatifolium* on average the greatest (2.89 µm).

The ability of vessels to resist implosion $(t/b)^2$ varied significantly within and between sites ($P < 0.01$, Table 3). *B. stellatifolium* had significantly lower $(t/b)^2$ ratios than the other species (0.0143–0.0176 µm; Table 2). *A. mearnsii* in turn had the highest $(t/b)^2$ ratios (ranging from 0.0291 to 0.0372 µm), but only significantly higher than both natives at Jonkershoek and DuToitskloof. *M. angustifolia* was the only species that differed significantly in $(t/b)^2$ across all sites; the other two species, *B. stellatifolium* and *A. mearnsii*, did not vary across sites. Within sites, species had their highest $(t/b)^2$ values at either the intermediate or high streamflow sites.

Measurements of wood density across all species and sites showed a significant and positive relationship with the ability of vessels to resist implosion or $(t/b)^2$ ($R^2 = 0.77$; $P < 0.005$) and lumen diameter ($R^2 = 0.47$; $P < 0.05$) (Fig. 2a, b). However, no relationship existed between

Table 3 Factorial ANOVA results for measured wood anatomical traits at the catchment scale study (Experiment 1)

Trait	Factor	*df*	*F*	*P*
Wood density	Site	2	2.39	0.107
	Species	2	30.66	**<0.001**
	Site*Species	4	2.10	0.102
Lumen diameter	Site	2	11.6	**<0.001**
	Species	2	61.0	**<0.001**
	Site*Species	4	3.7	**<0.005**
Wall thickness	Site	2	2779.79	**<0.001**
	Species	2	283.37	**<0.001**
	Site*Species	4	166.63	**<0.001**
$(t/b)^2$	Site	2	15.05	**<0.001**
	Species	2	142.29	**<0.001**
	Site*Species	4	3.65	**<0.006**

Values in bold indicate statistical significance

Table 2 Mean values for wood anatomical traits measured across species and sites (Experiment 1)

Trait Streamflow	Species	Jonkershoek Low	Bainskloof Intermediate	DuToitskloof High
Wood density ($n = 5$)	*B. stellatifolium*	0.490^{a} (0.010)	0.487^{a} (0.027)	0.484^{a} (0.021)
	M. angustifolia	0.535^{ab} (0.015)	0.546^{b} (0.016)	0.528^{ab} (0.017)
	A. mearnsii	0.551^{b} (0.021)	0.641^{c} (0.022)	0.626^{c} (0.012)
Lumen diameter ($n = 5$)	*B. stellatifolium*	39.63^{a} (0.46)	42.53^{b} (0.51)	42.48^{b} (0.57)
	M. angustifolia	38.85^{a} (0.39)	42.23^{b} (0.46)	41.78^{b} (0.52)
	A. mearnsii	46.03^{c} (0.65)	45.23^{c} (0.70)	46.15^{c} (0.60)
Wall thickness ($n = 5$)	*B. stellatifolium*	2.89^{a} (0.033)	1.24^{b} (0.024)	1.23^{b} (0.012)
	M. angustifolia	1.80^{c} (0.024)	1.14^{df} (0.018)	1.13^{df} (0.015)
	A. mearnsii	2.69^{e} (0.041)	1.14^{f} (0.016)	1.33^{g} (0.016)
$(t/b)^2$ ($n = 5$)	*B. stellatifolium*	0.0143^{a} (0.001)	0.0151^{ab} (0.001)	0.0176^{b} (0.001)
	M. angustifolia	0.0207^{c} (0.001)	0.0348^{df} (0.002)	0.0288^{e} (0.002)
	A. mearnsii	0.0291^{d} (0.001)	0.0372^{f} (0.002)	0.0352^{df} (0.001)

Wood density values are in g cm^{-3}, lumen diameter and wall thickness are in µm. Standard errors are given in parentheses. A factorial ANOVA was used to compare species and sites, with means separated using a Fisher LSD post hoc test. Within and between sites, means with different superscripts differ significantly ($P < 0.05$)

wood density and wall thickness (t) (Fig. 2c). The strongest correlation between wood density and its component anatomical traits was with $(t/b)^2$. Measurements of minimum water potential ($\Psi_{\min}$) as an indicator of plant water stress were significantly and negatively correlated with $(t/b)^2$ and wood density (Fig. 3a, b). The $\Psi_{\min}$ explained 80 % of the variation in $(t/b)^2$, while it only explained 67 % of the variation in wood density. All correlations showed species occupying different parts of the curve, indicating species-specific trends in the relationship between wood anatomical characteristics.

Biome scale study

A one-way ANOVA of wood density of *A. mearnsii* vs. precipitation (across sites) showed significant intra-specific variation ($P < 0.001$, Fig. 4). Wood density of *A. mearnsii* was significantly the lowest at the two mesic sites (ranging from 0.487 to 0.511 g cm^{-3}; $P < 0.05$), and on average the highest at the xeric sites, as well as one coastal site, Buffeljagsriver (ranging between 0.572 and 0.593 g cm^{-3}). Significant differences were observed between wood density of *A. mearnsii* and the selected co-occurring native species within sites ($P < 0.05$; Table 4). Densities ranged between 0.451 and 0.564 g cm^{-3} for the native suite of species, and between 0.487 and 0.593 g cm^{-3} for the IAP (Table 4). A comparison between *A. mearnsii* and the chosen native species within each site showed that *A. mearnsii* had denser wood at both xeric sites, and at one mesic site (Stellenbosch).

Discussion

At the catchment scale, we examined how key fynbos riparian tree species co-occurring with the alien invasive tree *A. mearnsii* vary (if at all) in twig wood density across three sites where streamflow quantity was the proxy for water availability. Wood anatomical traits, such as vessel mechanical resistance to prevent implosion $(t/b)^2$, vessel lumen diameter and wall thickness were also assessed at this scale as they represent important correlates of wood density and thus have ecological relevance in explaining variation in wood density associated with water availability, both intra- and inter-specifically (Preston et al. 2006).

Inter-specific differences in wood density were significant, with the invasive species *A. mearnsii* showing significantly denser branch wood at the two higher streamflow sites (Bainskloof and DuToitskloof). This adds to other supportive evidence that considerable phylogenetic variation in wood density exists (Chave et al. 2006; Read and Stokes 2006). Variation observed within this trait is mainly attributed to the distribution of species in relation to water availability gradients (Ackerly 2004; Preston et al. 2006; Poorter et al. 2009; Stiller 2009), though there is evidence that temperature could also contribute (Thomas et al. 2004, 2007). In view of this, Meinzer (2003) suggested that functional convergence towards higher wood density in

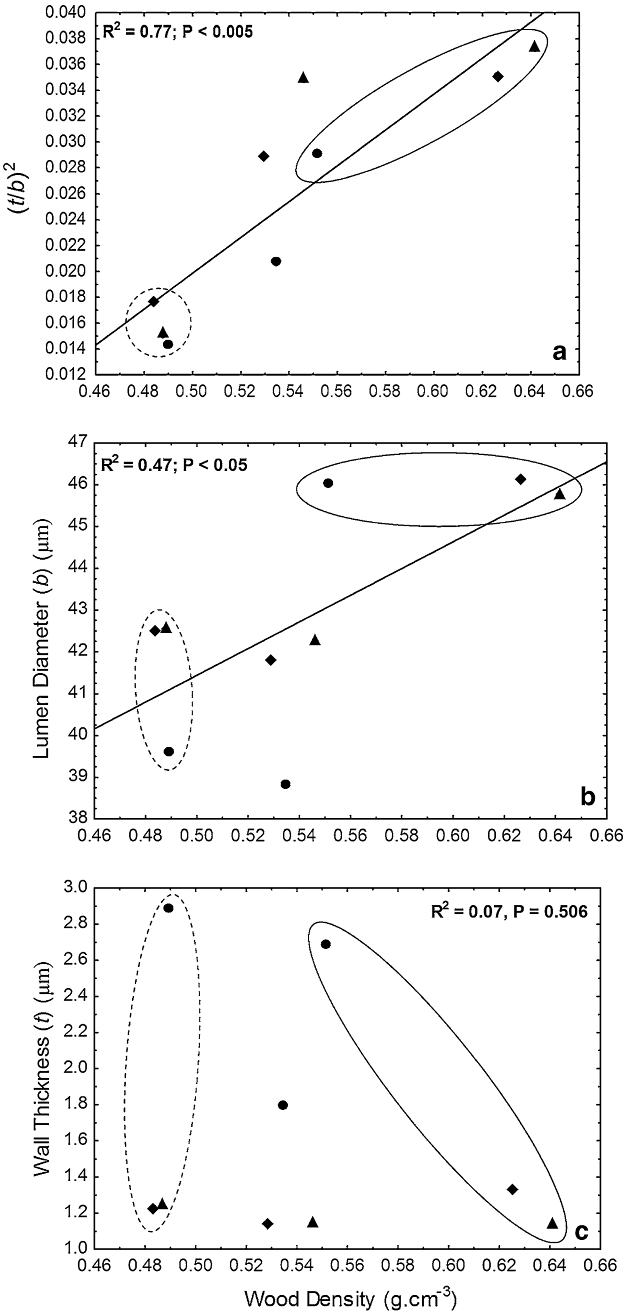

Fig. 2 Plots of **a** vessel resistance to implosion or $(t/b)^2$, **b** vessel lumen diameter, and **c** vessel wall thickness as functions of wood density across all species and sites. In each graph the *solid line shape* represents *Acacia mearnsii*, the *dotted line shape Brabejum stellatifolium*, and *open* is *Metrosideros angustifolia*. The low streamflow site (Jonkershoek) is represented by *circles*, the intermediate streamflow site (Bainskloof) by *triangles*, and the high streamflow site (DuToitskloof) by *diamonds*

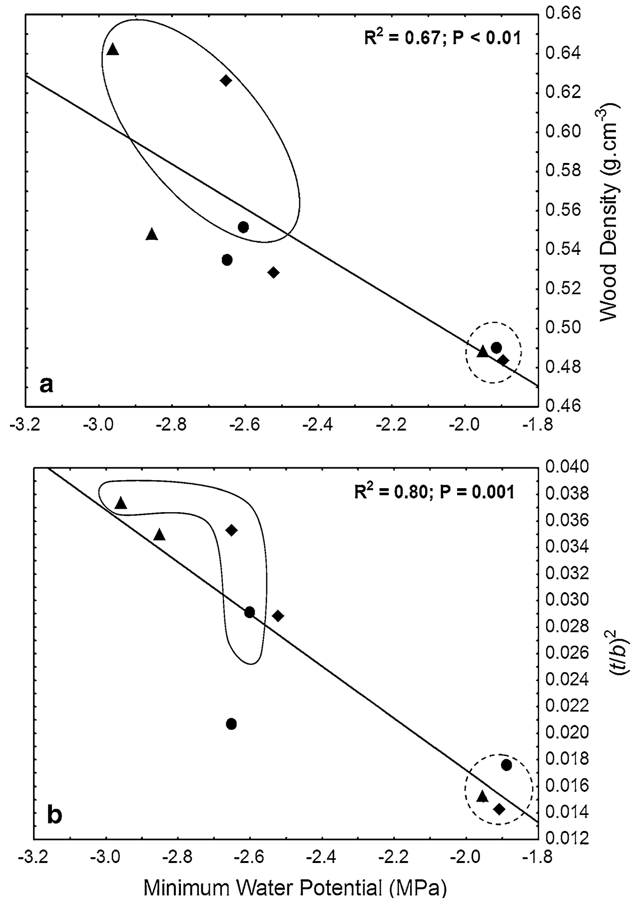

Fig. 3 Plots of **a** wood density and **b** vessel resistance to implosion or $(t/b)^2$ as a function of minimum water potential (Ψ_{min}) across all species and sites. In each graph the *solid line shape* represents *Acacia mearnsii*, the *dotted line shape Brabejum stellatifolium*, and *open* is *Metrosideros angustifolia*. The low streamflow site (Jonkershoek) is represented by *circles*, the intermediate streamflow site (Bainskloof) by *triangles*, and the high streamflow site (DuToitskloof) by *diamonds*

drier areas is a safety measure against drought-induced cavitation. Therefore, as denser wood is seen as a broad indicator of adaptation to water-stressed conditions, it is clear that for these riparian systems, *A. mearnsii*, at least at two sites, might functionally be more responsive towards limiting drought stress than co-occurring native species. The significant positive correlation between wood density and $(t/b)^2$ found in our study supports this argument, as species with high resistance against vessel implosion (less vulnerability to drought-induced cavitation) are likely to have high $(t/b)^2$ values (Hacke et al. 2001; Pratt et al. 2007). This result is consistent with the findings of Jacobsen et al. (2007a).

In fact, Ψ_{min} was also significantly correlated with both $(t/b)^2$ and wood density. There is a tight negative correlation between wood density, its structural correlates and minimum water potentials for species in the south-western Cape riparian zones. The influence of the environment at the plant tissue level is thus linked to changes that promote drought tolerance at the cellular level (Jacobsen et al. 2007b; Pratt et al. 2007). Importantly, it is also clear that this is a species-specific response because species clumped on different parts of the curves that explained the relationship between different functional traits (see also Iovi et al. 2009). It is therefore possible to determine different plant responses to water availability within a community, and in so doing be able to broadly predict drought tolerance of species under climate change scenarios (*A. mearnsii* in this case) as argued by Jacobsen et al. (2007a).

Interestingly, *A. mearnsii* also exhibited significantly larger lumen diameters and thinner walls compared to the native species, an indication that it might anatomically select for hydraulic efficiency rather than hydraulic safety through being drought tolerant (Hargrave et al. 1994; Kolb and Sperry 1999). Preston et al. (2006) found an inverse relationship between vessel lumen area and wood density, which they attributed to vessel lumen conductivity which increases with the fourth power of lumen diameter (see also Tyree and Zimmerman 2002; Sperry et al. 2006). The result is less dense wood, as the percentage of lumen area per transverse section of xylem is increased, ultimately limiting mechanical strength (Wagner et al. 1998). However, departure from this trend does exist, where vessel traits such as lumen diameters were found to vary independent of xylem wood density (Martínez-Cabrera et al. 2009).

In support of this indistinct relationship between vessel traits and wood density, we found that lumen diameters were positively correlated with wood density. This suggests that species with denser wood would be less adapted to drought-induced cavitation, and better equipped at transporting water, a counter-intuitive response to the hydraulic safety versus efficiency relationship (e.g. Kolb and Sperry 1999). In angiosperms, however, one cannot readily correlate conduit diameter per se against water-stress vulnerability as this was found to be a weak relationship (Hacke et al. 2000; Hacke and Sperry 2001; Jacobsen et al. 2005). This is because vulnerability to drought-induced cavitation is primarily influenced by the porosity of inter-conduit pit membranes (Hacke et al. 2000; Tyree and Zimmerman 2002; Woodruff et al. 2008; Choat and Pittermann 2009). Also, Woodrum et al. (2003) found that for *Acer* spp. in mesic environments (similar to our catchment scale study), there were no direct trade-offs between hydraulic conductivity and mechanical properties, as water transport at their study sites might not have been limited, and therefore had no selective influence on anatomy (Sperry et al. 2006).

This suggests a non-causal relationship between specific traits such as measured wood density and vulnerability to drought-induced cavitation (Larjavaara and Muller-Landau 2010). The observed variation in vessel diameter and wood density at the catchment scale, thus adds to our

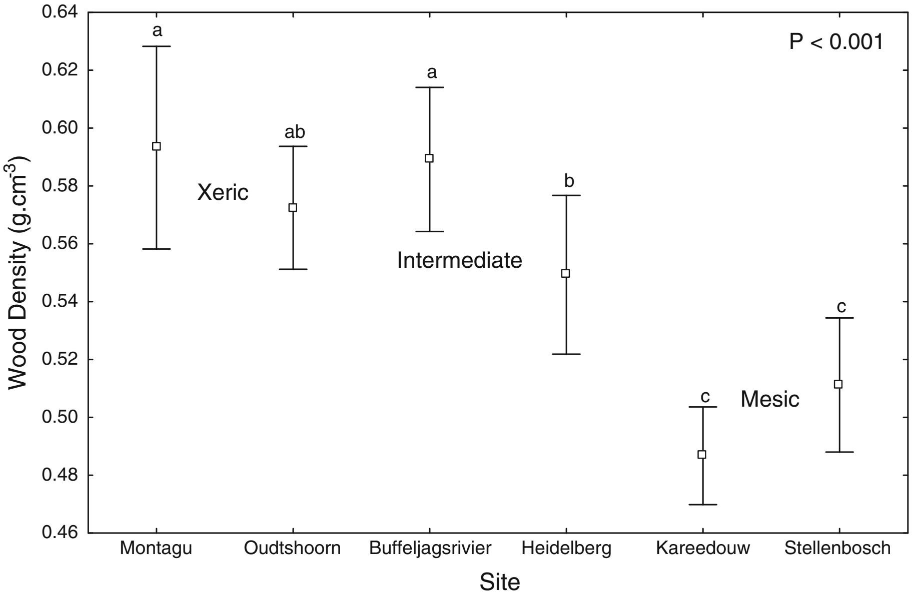

Fig. 4 Mean wood density with 95 % confidence intervals for *Acacia mearnsii* as a function of water availability along an environmental gradient (as described in Table 1). A One-way ANOVA was used to compare density between sites, with means separated using a Fisher LSD test. Means with different superscripts differ significantly ($P < 0.05$). $n = 5$

Table 4 Mean values for wood density of *Acacia mearnsii* across a precipitation gradient and between the selected native species (Experiment 2, as described in Table 1)

Site	Selected Native	*A. mearnsii*
Montagu (Xeric)	0.453^{a} (0.012)	0.593^{b} (0.017)
Oudtshoorn (Xeric)	0.511^{c} (0.005)	0.572^{bd} (0.010)
Buffeljagsrivier (Intermediate)	0.542^{bd} (0.007)	0.589^{b} (0.012)
Heidelberg (Intermediate)	0.564^{d} (0.010)	0.549^{d} (0.013)
Kareedouw (Mesic)	0.544^{d} (0.011)	0.487^{c} (0.008)
Stellenbosch (Mesic)	0.451^{a} (0.010)	0.511^{c} (0.011)

All values are in g cm^{-3}. Standard errors are given in parentheses. A factorial ANOVA was used to compare within and between species and sites, with means separated using a Fisher LSD post hoc test. Within and between sites, means with different superscripts differ significantly ($P < 0.05$). $n = 5$

understanding of plant strategies in mesic areas, and provides insight on how plants balance water availability, leaf evaporative demand and ultimately wood anatomical traits (Shume et al. 2004).

In contrast to expectations, wood density of the native species did not differ intra-specifically between sites differing in streamflow, despite considerable inter-specific variation. Clearly streamflow per se cannot be solely used to describe differences in wood density between riparian species. More evidence to strengthen this argument comes from the relationship between wood density and Ψ_{min}. Minimum water potential (Ψ_{min}) was significantly negatively correlated with wood density across species, similar to Jacobsen et al.'s (2007a) findings for evergreen shrubs in the Mediterranean-type climate region of South Africa. They found that plants differed significantly in their soil water use with those experiencing a greater seasonal water stress developing a higher wood density. In the Mediterranean-type climate of California, Preston et al. (2006) also argued that the best possible ecological correlate for wood density is soil water content. It would therefore be instructive to incorporate Ψ_{min} when investigating a possible driver of wood density, as plants' relative access to soil water (as measured by Ψ_{min}) (Ackerly 2004; Bhaskar and Ackerly 2006) is a more accurate measure than streamflow quantity (see e.g. Dawson and Ehleringer 1991), although the two might be interdependent. Also, not only are measurements like density and minimum water potentials relatively easy to obtain (Jacobsen et al. 2007a), but also, when applied to the South African fynbos, which is predicted to undergo influential climate change, they could provide vital information on different drought adaptive abilities of species and thus insights on possible range changes in response to reductions in water availability.

To further investigate whether we can broadly predict drought tolerance of species using wood density of species, we asked whether geographically derived differences in wood density (using MAP as a proxy for plant water availability) existed within *A. mearnsii*; also, how the wood density of *A. mearnsii* compares to that of a co-occurring native species, to see if functional trait convergence exists inter-specifically. There was clear evidence that there were significant intra-specific differences in wood density for *A. mearnsii*, with mesic sites having less dense wood than xeric sites, indicative of higher plasticity for the IAP. As less dense wood is correlated with increased hydraulic conductance (Wagner et al. 1998; Stratton et al. 2000), this species thus show functional trait adaptive responses across a water availability gradient. However, Swenson and Enquist (2007) suggested that the evolution of wood density is mostly correlated with variation in temperature (see also Thomas et al. 2004, 2007), and not necessarily MAP. Minimum water potential might therefore have a more prominent role in determining wood density, as suggested by the catchment scale study and literature. It is evident that the specific environmental factor that determines wood density is variable, and could be influenced by a combination of MAP, temperature and Ψ_{min}, depending on in situ microsite conditions.

Additionally, *A. mearnsii* had significantly denser wood compared to the native species at both xeric sites, an indication of inter-specific variation. Thus, in sites where plants have less access to soil moisture, this species should have an advantage in resisting xylem failure associated with drought conditions compared to the studied native species. This is consistent with what was found at the catchment scale study. The observed plastic response of *A. mearnsii* to variable water availability is very likely to have a positive influence on how this species responds to changes in hydrological and climatological conditions (Funk 2008) projected for the fynbos region.

Conclusion

At the catchment scale, wood density showed considerable inter-specific variation, but to a lesser extent intra-specific variation, indicating a higher degree of plasticity as opposed to functional convergence in this parameter of wood anatomy between taxonomically different species across these three riparian zones. In fact it was the invasive *A. mearnsii* which showed denser wood than the native species, particularly at the higher streamflow sites. As wood density also positively correlated with vessel resistance against implosion $(t/b)^2$, it seems that under certain site-specific conditions, *A. mearnsii* is apparently the most cavitation-resistant species amongst the three. This agrees with the physiological findings from Crous et al. (2012), emphasising the ability of this species to optimise structure and function under water-stressed conditions. These findings were also evident at the biome scale which again accentuated the invasive potential of this species in a changing environment. At this scale, there were distinct differences in wood density between species (*A. mearnsii* versus the native species within sites), and between sites (plastic response of *A. mearnsii* across an environmental gradient). These results support the argument that water availability has a strong selective effect on wood anatomy (Read and Stokes 2006; Sperry et al. 2006). To summarize, based on our results, it seems that this invasive species shows generally greater plasticity in anatomical traits compared to the studied native species, a finding of which relatively little information exists in literature. Further, for *A. mearnsii* at least, wood anatomical traits can be an easily obtainable screening tool of possible adaptation under different environments.

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References

Ackerly DD (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecol Monogr 74:25–44

Barij N, Stokes A, Bogaard T, Van Beek R (2007) Does growing on a slope affect tree xylem structure and water relations? Tree Physiol 27:757–764

Bhaskar R, Ackerly DD (2006) Ecological relevance of minimum seasonal water potentials. Physiol Plantarum 127:353–359

Chave J, Muller-Landau HC, Baker TR, Easdale TA, Ter Steege H, Webb CO (2006) Regional and phylogenetic variation of wood density across 2456 Neotropical tree species. Ecol Appl 16(6):2356–2367

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. Ecol Lett 12:351–366

Choat B, Pittermann J (2009) New insights into bordered pit structure and cavitation resistance in angiosperms and conifers. New Phytol 182:557–560

Crous CJ, Jacobs SM, Esler KJ (2012) Drought-tolerance of an invasive alien tree, *Acacia mearnsii* and two native competitors in fynbos riparian ecotones. Biol Invasions 14:619–631

Dawson TE, Ehleringer JR (1991) Streamside trees that do not use stream water: evidence from hydrogen isotope ratios. Nature 350:335–337

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? Trends Ecol Evol 14:135–139

Dye P, Jarmain C (2004) Water use by black wattle (*Acacia mearnsii*): implications for the link between removal of invading trees and catchment streamflow response. S Afr J Sci 100:40–44

Dye P, Moses G, Vilakazi P, Ndlela R, Royappen M (2001) Comparative water use of wattle thickets and indigenous plant communities at riparian sites in the Western Cape and Kwazulu-Natal. Water SA 27:529–538

Enright WD (2000) The effect of terrestrial invasive alien plants on water scarcity in South Africa. Phys Chem Earth Part B 25(3):237–242

Funk JL (2008) Differences in plasticity between invasive and native plants from a low resource environment. J Ecol 96:1162–1173

Galatowitsch S, Richardson DM (2005) Riparian scrub recovery after clearing of invasive alien trees in headwater streams of the Western Cape, South Africa. Biol Conserv 122:509–521

Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. Perspect Plant Ecol Evol Syst 4:97–115

Hacke UG, Sperry JS, Pittermann J (2000) Drought experience and cavitation-resistance in six shrubs from the Great Basin, Utah. Basic Appl Ecol 1:31–41

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126:457–461

Hargrave KR, Kolb KJ, Ewers FW, Davis SD (1994) Conduit diameter and drought-induced embolism in *Salvia mellifera* Greene (Labiatae). New Phytol 126:695–705

Hulme PE (2008) Phenotypic plasticity and plant invasions: is it all Jack? Funct Ecol 22:3–7

Iovi K, Kolovou C, Kyparissis A (2009) An ecophysiological approach of hydraulic performance for nine Mediterranean species. Tree Physiol 29:889–900

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

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

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

Kolb KJ, Sperry JS (1999) Differences in drought adaptation between subspecies of Sagebrush (*Artemisia tridentata*). Ecology 80:2373–2384

Larjavaara M, Muller-Landau HC (2010) Rethinking the value of high wood density. Funct Ecol 24:701–705

Martínez-Cabrera HI, Jones CS, Espino S, Jochen Schenk H (2009) Wood anatomy and wood density in shrubs: responses to varying aridity along transcontinental transects. Am J Bot 96(8):1388–1398

McCulloh KA, Johnson DM, Meinzer FC, Voelker SL, Lachenbruch B, Domec J (2012) Hydraulic architecture of two species differing in wood density: opposing strategies in co-occurring tropical pioneer trees. Plant Cell Environ 35(1):116–125

Meinzer FC (2003) Functional convergence in plant responses to the environment. Oecologia 134:1–11

Naidoo S, Zboňák A, Ahmed F (2006) The effect of moisture availability on wood density and vessel characteristics of *Eucalyptus grandis* in the warm temperate region of South Africa. Paper presented in IUFRO symposium “Wood structure and Properties 2006”, 3–6 Sept 2006, Sielnica, Slovakia

New M (2002) Climate change and water resources in the southwestern Cape, South Africa. S Afr J Sci 98:1–8

Pockman WT, Sperry JS, O’Leary JW (1995) Sustained and significant negative water pressure in xylem. Nature 378:715–716

Poorter L, McDonald I, Alarcón A, Fichtler E, Licona J, Peña-Claros M, Sterck F, Villegas Z, Sass-Klaasen U (2009) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. New Phytol 185:481–492

Pratt RB, Black RA (2006) Do invasive trees have a hydraulic advantage over native trees? Biol Invasions 8:1331–1341

Pratt RB, Jacobsen AL, Ewers FW, Davis SD (2007) Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. New Phytol 174:787–798

Preston KA, Cornwell WK, DeNoyer JL (2006) Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. New Phytol 170:807–818

Prins N, Holmes PM, Richardson DM (2004) A reference framework for the restoration of riparian vegetation in the Western Cape, South Africa, degraded by invasive Australian Acacias. S Afr J Bot 70:767–776

Read J, Stokes A (2006) Plant biomechanics in an ecological context. Am J Bot 93(10):1546–1565

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB (2003) The evolution of plant functional variation: traits, spectra, and strategies. Int J Plant Sci 164(S3):S143–S164

Shume H, Grabner M, Eckmüllner O (2004) The influence of an altered groundwater regime on vessel properties of hybrid polar. Trees Struct Funct 18:184–194

Sperry JS, Hacke UG, Pittermann J (2006) Size and function in conifer tracheids and angiosperm vessels. Am J Bot 93:1490–1500

Steynor AC, Hewitson BC, Tadross MA (2009) Projected future runoff of the Breede River under climate change. Water SA 35(4):433–440

Stiller V (2009) Soil salinity and drought alter wood density and vulnerability to xylem cavitation of bald cypress (*Taxodium distichum* (L.) Rich.) seedlings. Environ Exp Bot 67:164–171

Stratton L, Goldstein G, Meinzer FC (2000) Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. Plant Cell Environ 23:99–106

Swenson NG, Enquist BJ (2007) Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. Am J Bot 94:451–459

Swift CC, Jacobs SM, Esler KJ (2008) Drought induced xylem embolism in four riparian trees from the Western Cape Province: insights and implications for planning and evaluation of restoration. S Afr J Bot 74:508–516

Thomas DS, Montagu KD, Conroy JP (2004) Changes in wood density of *Eucalyptus camaldulensis* due to temperature—the physiological link between water viscosity and wood anatomy. Forest Ecol Manag 193:157–165

Thomas DS, Montagu KD, Conroy JP (2007) Temperature effects on wood anatomy, wood density, photosynthesis and biomass partitioning of *Eucalyptus grandis* seedlings. Tree Physiol 27:251–260

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

Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. New Phytol 176:749–763

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

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

Wiemann MC, Williamson GB (2002) Geographic variation in wood specific gravity: effects of latitude, temperature and precipitation. Wood Fiber Sci 34:96–107

Woodruff DR, Meinzer FC, Lachenbruch B (2008) Height-related trends in leaf anatomy and shoot hydraulic characteristics in a tall conifer: safety versus efficiency in water transport. New Phytol 180:90–99

Woodrum CL, Ewers FW, Telewski FW (2003) Hydraulic, biomechanical, and anatomical interactions of xylem from five species of *Acer* (Aceraceae). Am J Bot 90(5):639–699