

Drought induced xylem embolism in four riparian trees from the Western Cape Province: Insights and implications for planning and evaluation of restoration

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Abstract

In Mediterranean climates, rainfall is restricted to periods of low evaporative demand, leaving plants to survive the summer drought. The purpose of this study was to determine the contribution of drought tolerance to the distribution of riparian species. These physiological insights will assist in developing target species lists for restoration of riparian ecosystems in the Western Cape, currently heavily degraded due to land clearing and invasive aliens. We estimated P_{50} and P_{100} from vulnerability curves and Ψ_x in four species across a range of summer water availability estimated by streamflow. As expected, decreasing streamflow resulted in lower predawn and mid-day xylem water potential, and species identified in previous studies as having broad distributions, such as *Brabejum stellatifolium* and *Metrosideros angustifolia*, sustained greater decreases in mid-day xylem water potential and were less vulnerable to cavitation than *Rapanea melanophloeos* or *Brachyleana neriifolia*, species with more restricted distributions. These results provide preliminary evidence that a consideration of drought tolerance might be useful in refining lists of target species for active restoration and evaluation of restoration success across projects in streams and rivers with different fluvial regimes.

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1. Introduction

The contribution of riparian habitats to ecosystem function and ecosystem services has been well documented (Malanson, 1993; Naiman and Décamps, 1997; Naiman et al., 2005). Water availability and disturbance are identified as important determinants of riparian community structure (Hupp and Osterkamp, 1996; Van Coller et al., 2000; Ross and Swift, 2003). Riparian habitats in Mediterranean-type ecosystems, characterized by summer drought, are less well understood than riparian habitats

in temperate ecosystems (Gasith and Resh, 1999; Salinas et al., 2000). Intense disturbance associated with peak flows during rainfall events in winter months is coupled with water deficits in summer months. As stream power diminishes and disturbance intensity decreases, water availability decreases during the period of greatest evaporative demand. This is in contrast to temperate areas with summer rainfall where water availability remains highest during periods of greatest evaporative demand. The combination of summer drought and winter disturbance creates a narrow recruitment niche making restoration of native species to degraded riparian ecosystems difficult (Salinas et al., 2000; Petit and Freund, 2001).

In riparian habitats of the Western Cape of South Africa, the invasion of woody exotics has decreased surface flow, eliminated native species important for wildlife, increased nutrient availability,

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and altered seed banks available for regeneration of riparian species following the natural disturbance regime that characterizes riparian habitats (Rowntree, 1991; Brown, 1998; Prinsloo and Scott, 1999; Le Maitre et al., 2002; Dye and Jarman, 2004; Richardson et al., 2007; Vosse et al., 2008-this issue). The near complete elimination of native species from many watersheds is complicating efforts to create a list of target species for restoration. This is a particular problem since a large part of the effort to restore riparian habitats in the Western Cape is devoted to the removal of non-natives dominating many riparian habitats by the Working for Water Programme (Van Wilgen et al., 1998). Species lists for restoration of degraded Fynbos-riparian ecotones in the Western Cape have been derived using ordination techniques (e.g. Galatowitsch and Richardson, 2005; Prins et al., 2005). While these studies have been successful in identifying co-occurring groups of species, and the physical factors associated with their presence or absence, no species-level, mechanistic understanding exists to indicate how the relationship between disturbance and drought might determine the distribution of riparian species across stream channels, between reaches, and between watersheds. Such a mechanistic understanding would involve understanding how drought, disturbance and substrate interact to determine survivorship.

Vulnerability to cavitation, interpreted in combination with water stress levels that plants experience in the field, is a useful measure of drought tolerance (Kolb and Davis, 1994; Linton et al., 1998; Pockman and Sperry, 2000; Maharali et al., 2004). Cavitation via the air-seeding mechanism occurs when root or stem xylem water pressure decreases to a point where capillary forces responsible for the adhesion of the water column to the vessel wall are overwhelmed, and air is pulled into the vessel at the pit membrane forming an embolism that blocks water transport (Zimmerman, 1983; Sperry et al., 1988; Jarbeau et al., 1995; Hacke and Sperry, 2001). Xylem with vessels that have thicker walls and less vessel lumen area are generally resistant to cavitation, but the cost of increased wall to lumen ratio may be a reduction in xylem conducting area (Pockman and Sperry, 2000; Hacke and Sperry, 2001; Hacke et al., 2001). Furthermore, there is a trade-off between resistance to cavitation and water transport such that xylem conduit construction, and therefore resistance to cavitation reflect the range of minimum xylem water potentials experienced *in situ* (Pockman and Sperry, 2000; Hacke and Sperry, 2001; Hacke et al., 2001).

We examined vulnerability to cavitation in four tree species across streams with different hydrologic regimes. The selected species varied in distribution extent and biogeographical affinity. *Rapanea melanophloeos* (L.) Mez has afro-montane affinities, while the other three species are restricted to the Western Cape province (Coates Palgrave, 2002). *Metrosideros angustifolia* (L.) and *Brabejum stellatifolium* (L.) are widespread in riparian habitats in the Western Cape occurring in each of the four groups of species identified in Prins et al. (2005) and identified as having ubiquitous distribution by Galatowitsch and Richardson (2005). The other two species, *R. melanophloeos* (L.) Mez. and *Brachylaena neriifolia* (L.f.) R. Br., were positively associated with factors indicating higher stream power in Galatowitsch and Richardson (2005). We hypothe-

sized that the four species selected, because of differences in distribution suggested by previous studies, would show differences in their vulnerability to cavitation across a range of minimum water availabilities. Previous work on *B. neriifolia* and *B. stellatifolium* revealed small differences in diurnal patterns of stomatal conductance with *B. neriifolia* sustaining higher mid-day xylem water potentials than *B. stellatifolium* (Richardson and Kruger, 1990).

If drought tolerance is an important factor in determining species composition in riparian habitats in the Western Cape, *M. angustifolia* and *B. stellatifolium* should show greater resistance to cavitation across the range of minimum water availabilities sampled and should sustain lower mid-day water potentials than *B. neriifolia*, since Galatowitsch and Richardson (2005) identified both of these species as ubiquitous (Alder et al., 1996; Davis et al., 1999; Pockman and Sperry, 2000). We expected *R. melanophloeos* to be more resistant to cavitation than *B. stellatifolium*, *M. angustifolia* or *B. neriifolia* because it usually occurs in upstream portions of catchments where minimum stream discharge is generally lower than for downstream portions of catchments. We expected *B. neriifolia* to be the most vulnerable to cavitation based on its significant association with less invaded reaches, and with factors consistent with higher stream power and therefore greater summer water availability.

Understanding the relationship between drought tolerance and fluvial regime would then lead to a more refined assessment of restoration success and could contribute to a more refined species palette for restoration projects in the Fynbos-riparian ecotone.

2. Methods

The study sites were all within the Jonkershoek valley (33° 57'47"S, 18° 55'32"E) in the Western Cape Province of South Africa. Four study sites were identified: a high streamflow site on the Eerste River at Swartbrug just below the Kleinplaas dam, a medium streamflow site on the Eerste River at Witbrug, and low streamflow sites at Biessievlei and Bosboukloof, both tributaries of the Eerste River. Four species native to Fynbos riparian zones were studied: *Metrosideros angustifolia* (Myrtaceae), *B. stellatifolium* (Proteaceae), *R. melanophloeos* (Myrsinaceae) and *B. neriifolia* (Asteraceae). *M. angustifolia* and *B. stellatifolium* occurred at all sites, *R. melanophloeos* occurred at all sites except Bosboukloof, and *B. neriifolia* occurred only on the Eerste River at Swartbrug and Witbrug. Five individuals of each species were flagged at each location, with the exception of *B. stellatifolium* and *M. angustifolia*, which were not sampled at Biessievlei because there were not enough individuals represented.

Vulnerability to cavitation was determined using the bench drying method (Davis et al., 1999; Pockman and Sperry, 2000; Brodribb et al., 2003). Preliminary determination of vessel length for all study species using the "air flow" method (Zimmerman and Jeje, 1981; Ewers and Fisher, 1989) indicated that no species had vessel lengths greater than 1.0 m. Eight to ten branches, 0.5 to 1.0 m in length or greater were cut from all individuals of one species at a study site before dawn. One

branch from each individual was bagged in the field for the 0 h measurements, and the rest were returned in separate bags to the laboratory where they were allowed to dehydrate for approximately 1, 2, 4, 6, 8 and 10 h or until 90–100% of hydraulic conductivity was lost. For *M. angustifolia*, branches were allowed to dehydrate for an additional period of 12 and 24 h to achieve the desired loss of conductivity. Branches were sealed in separate bags for approximately 1.5 h to equilibrate before measuring hydraulic conductivity and xylem water potential.

For each sample branch, a side branch was removed for measurement of xylem water potential, and the sample branch was immediately submerged in water and cut from each end [in 10 cm sections to a final 10 cm segment] to measure hydraulic conductance. Branch segments used to measure hydraulic conductance were always distal to side branches used to measure xylem water potential (Ψ_x). Ψ_x was measured using a PMS Model 600 Pressure Chamber Instrument (PMS Instruments, Oregon, USA). The percentage loss of hydraulic conductance was measured using the method described in Sperry et al. (1988). Vulnerability curves for each individual were constructed by plotting percent embolism as a function of Ψ_x , and fitting the points to a curve using a third order polynomial (Pockman and Sperry, 2000); R^2 values for curves of individuals ranged from 0.61 to 0.99 (Table 1). Vulnerability curves for the study species differed in shape, and the third order polynomial explained the largest amount of variation in percent loss of hydraulic conductance (highest R^2 values) for most species at most sites. A review of the literature reveals multiple curve-fitting equations including exponential (Pammenter and Vander Willigen, 1998), second order polynomial (Jacobsen et al., 2007), and third order polynomial (Pockman and Sperry, 2000). All vulnerability curves should show an increase in percent loss of hydraulic conductance with decreasing water potential; the equation used to fit data to a vulnerability curve is less important than the R^2 value obtained.

Table 1
 R^2 values for fitted curves for individuals used to calculate P_{50} and P_{100} values

Species	High streamflow	Medium streamflow	Low streamflow
<i>Brabejum stellatifolium</i>	1. 0.94 (10)	1. 0.99 (5)	1. 0.90 (4)
	2. 0.84 (7)	2. 0.98 (4)	2. 0.99 (4)
	3. 0.96 (8)	3. 0.98 (5)	3. 0.99 (4)
	4. 0.96 (7)	4. 0.98 (5)	4. 0.97 (6)
<i>Meterosideros angustifolia</i>	1. 0.99 (5)	1. 0.91 (8)	1. 0.88 (7)
	2. 0.86 (9)	2. 0.89 (10)	2. 0.97 (6)
	3. 0.97 (6)	3. 0.99 (7)	3. 0.89 (5)
	4. 0.90 (8)	4. 0.90 (6)	4. 0.84 (7)
	5. 0.98 (7)		
<i>Brachyleana neriifolia</i>	1. 0.98 (4)	1. 0.89 (7)	
	2. 0.98 (6)	2. 0.81 (5)	
	3. 0.88 (4)	3. 0.64 (7)	
	4. 0.66 (5)		
	5. 0.61 (4)		
<i>Rapanea melanophloeos</i>	1. 0.94 (11)	1. 0.99 (5)	1. 0.99 (4)
	2. 0.91 (10)	2. 0.88 (6)	2. 0.97 (6)
	3. 0.92 (9)	3. 0.99 (5)	3. 0.99 (5)
	4. 0.71 (7)		4. 0.80 (4)
	5. 0.89 (10)		

Sample sizes for vulnerability curve points are in parentheses.

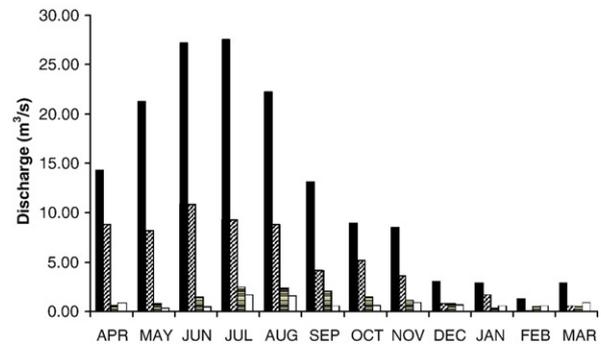


Fig. 1. Mean monthly discharge at the study sites (black bars represent Swartbrug, high streamflow; cross hatched bars represent Witbrug, medium streamflow; horizontal bars represent Bosboukloof, low streamflow; open bars represent Biessievlei, low streamflow).

The fitted curves for individuals were used to calculate 50% (P_{50}), corresponding to the constant b in Pammenter and Vander Willigen (1998), and 100% (P_{100}) loss of hydraulic conductivity. P_{50} values for the high and medium streamflow sites were analyzed using a factorial ANOVA, and the low streamflow sites were analyzed using a one-way ANOVA (Statistica Version 7.0, StatSoft Inc.). The low streamflow site was excluded from the factorial ANOVA because *B. neriifolia* did not occur at this site, resulting in an unbalanced model. The choice to exclude the site rather than the missing species was based on the fact that the low and medium streamflow sites had very similar summer water availabilities, and that we were interested in comparing species with different patterns of distribution. Means were separated using Fisher's LSD multiple range test ($P < 0.05$). Individuals were excluded from statistical analysis when curves did not allow extrapolation to 100% embolism. Points from all individuals of each species at each site were combined and EXCEL was used to fit a third order polynomial curve to create vulnerability curves for each species at each site (Pockman and Sperry, 2000). In the field, pre-dawn (Ψ_{max}) and mid-day xylem water potential (Ψ_{min}) for all individuals at each site was measured in late November and early December using a PMS Model 600 Pressure Chamber Instrument (PMS Instruments, Oregon, USA). Mid-day water potentials were measured several times between 11:30 and 14:00 in order to ensure that the lowest water potential was captured. Pre-dawn and mid-day xylem water potential data were analyzed separately using a factorial ANOVA (high and medium streamflow sites) and a one-way ANOVA (low streamflow site), as described for P_{50} .

Mean streamflow data for Swartbrug were obtained from Department of Water Affairs and Forestry, while those for Biessievlei, and Bosboukloof were obtained from the Council for Scientific and Industrial Research (CSIR; Stellenbosch office). Witbrug mean streamflow data values were estimated by subtracting the streamflow of the main tributary in the area, Langrivier (obtained from the CSIR, Stellenbosch office) from streamflow measured just upstream of Kleinplaas Dam (obtained from Department of Water Affairs and Forestry). Mean monthly streamflow was averaged from 1989–2006. There are some minor tributaries contributing to flow, but these

Table 2
Factorial ANOVA results for P_{50} , Ψ_{\min} and Ψ_{\max} , excluding the low streamflow site

Trait	Factor	df	F	P
P_{50}	Site	1	13.69	0.001
	Species	3	10.56	0.000
	Site × species	3	4.64	0.010
Ψ_{\max}	Site	1	3.92	0.057
	Species	3	4.46	0.011
	Site × species	3	10.49	0.000
Ψ_{\min}	Site	1	15.87	0.000
	Species	3	7.02	0.001
	Site × species	3	2.69	0.065

are not gauged, and so the Witbrug streamflow is only an estimated value and is likely lower than that given.

3. Results

3.1. Comparison of sites

Mean monthly streamflow differed among the three sites, and this difference was most pronounced in the wet season (April–November) (Fig. 1). Differences between the sites diminished in the summer months of December–March;

however, Swartbrug, the high streamflow site, maintained high flow relative to the other sites over all months. Differences between the lowest streamflow sites, Bosboukloof and Biessievlei, and the medium streamflow site, Witbrug, decreased substantially during the dry season, and in February and March, the low streamflow sites actually experience higher mean streamflow than the medium streamflow site (Fig. 1).

Values of P_{50} , Ψ_{\max} and Ψ_{\min} differed significantly among species (Table 2), and values of P_{50} and Ψ_{\min} differed significantly among sites (Table 2). There was a significant site-by-species effect for both Ψ_{\max} and P_{50} (Table 2). Although the site effect for Ψ_{\max} was not quite significant ($P=0.057$, Table 2), large differences between mean values for three of four species examined, the significant site-by-species interaction, and a probability value just above the arbitrary 0.05 value lead us to consider the results of this analysis further and include post hoc comparisons.

3.2. Individual species across high and medium streamflow sites

Values of P_{50} for *B. stellatifolium* varied between -2.5 MPa at Bosboukloof, the lowest streamflow site, and -2.3 MPa at Swartbrug, the highest streamflow site (Fig. 2a; Table 3), but did not differ significantly across sites (Table 3). Curves for this

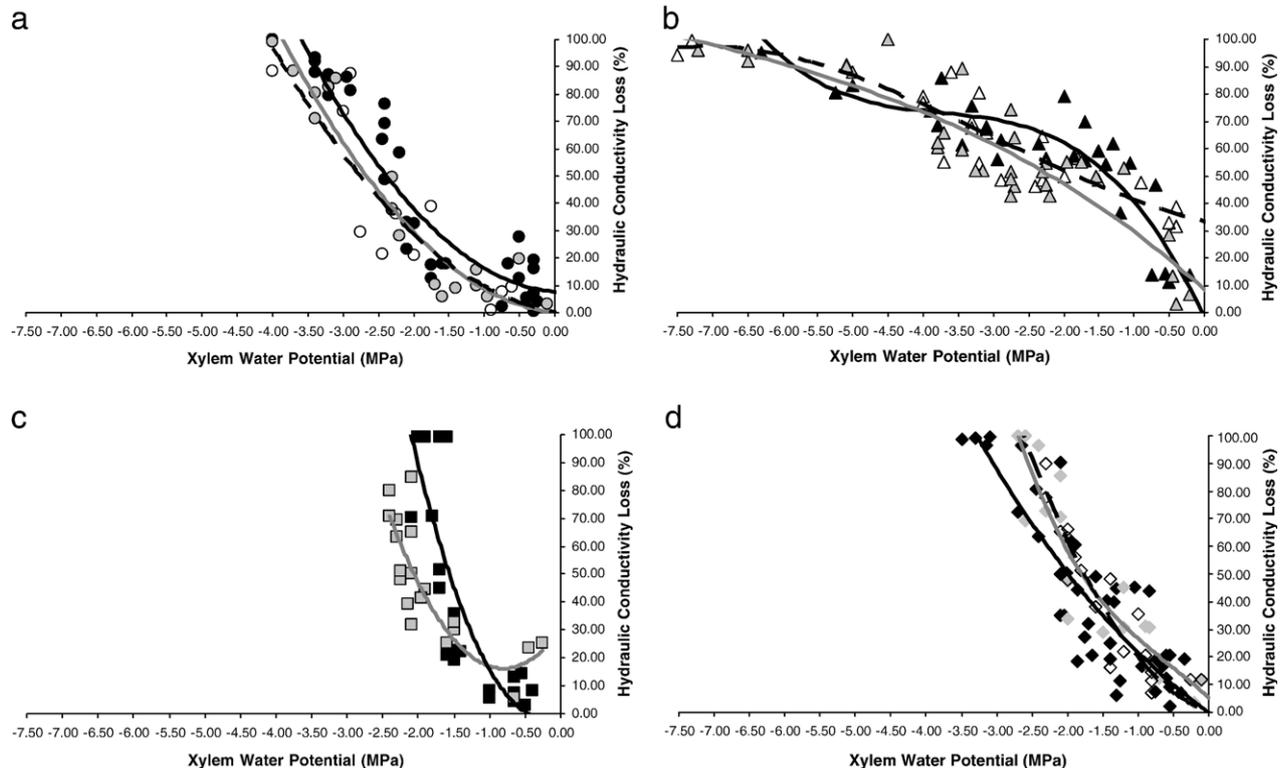


Fig. 2. Loss in hydraulic conductivity as a function of xylem water potential for the four species investigated. (a) *B. stellatifolium*. Closed black symbols and the solid dark line represent data points and the fitted curve ($R^2=0.87$, $n=41$) for Swartbrug, grey symbols and line represent data and fitted curve ($R^2=0.92$, $n=23$) for Witbrug, and the open symbols and dotted line represent data points and the fitted curve ($R^2=0.78$, $n=18$) for Bosboukloof. (b) *M. angustifolia*. Closed black symbols and line represent data and fitted curve ($R^2=0.82$, $n=35$) for Swartbrug, grey symbols and line represent data and fitted curve ($R^2=0.81$, $n=31$) for Witbrug, and open symbols and dotted line represent data and fitted curve ($R^2=0.81$, $n=25$) for Bosboukloof. (c) *B. neriifolia*. Closed black symbols and solid dark line represent data and fitted curve ($R^2=0.67$, $n=23$) for Swartbrug, grey symbols and line represent data and fitted curve ($R^2=0.70$, $n=19$) for Witbrug. (d) *R. melanophloeos*. Closed black symbols and line represent data and fitted curve ($R^2=0.78$, $n=47$) for Swartbrug, grey symbols and line represent data and fitted curve ($R^2=0.88$, $n=21$) for Witbrug, and open symbols and dotted line represent data and fitted curve ($R^2=0.88$, $n=19$) for Biessievlei.

Table 3
Mean values for P_{50} across species and streamflow regimes

Species	High streamflow	Medium streamflow	Low streamflow
<i>Brabejum stellatifolium</i>	-2.30 ^{ab} (0.06) $n=4$	-2.48 ^a (0.13) $n=4$	-2.50 ¹ (0.26) $n=4$
<i>Meterosideros angustifolia</i>	-1.29 ^c (0.09) $n=5$	-2.09 ^{abc} (0.29) $n=4$	-1.76 ² (0.29) $n=4$
<i>Brachyleana neriifolia</i>	-1.53 ^d (0.07) $n=5$	-2.07 ^{abc} (0.04) $n=3$	
<i>Rapanea melanophloeos</i>	-1.96 ^{bc} (0.11) $n=5$	-1.85 ^{cd} (0.12) $n=3$	-1.77 ² (0.06) $n=4$

Values are in MPa. Standard errors are given in parentheses. Two separate ANOVA procedures were carried out. A factorial ANOVA was used to compare the high and medium streamflow regimes and a one-way ANOVA to determine differences within the low streamflow regime. In both cases, means were separated using the Fishers's LSD multiple range test. Within and between the high and medium streamflow regime, means with different alphabetical superscripts differ significantly ($P<0.05$). Within the low streamflow regime, means with different numerical superscripts differ significantly ($P<0.05$).

species at all sites were J-shaped. Ψ_{\max} was similar and not significantly different among sites, but mean Ψ_{\min} decreased by almost an order of magnitude ($P=0.034$, Table 4). Mean Ψ_{\min} and Ψ_{\max} observed for *B. stellatifolium* were consistent with previously published work where Ψ_{\min} and Ψ_{\max} were about -0.2 and about -2.0 MPa respectively (Richardson and Kruger, 1990; Table 4).

The shape of the vulnerability curve of *M. angustifolia* differed from that of *B. stellatifolium*. Individuals from the high streamflow site exhibited a very steep increase in percent embolism until Ψ_x dropped below between -1.0 and -1.5 MPa; at lower values of Ψ_x , the rate of increase in percent embolism leveled off until Ψ_x dropped below -3.5 to -4.5 MPa, at which point rates of increase in percent embolism increased again (Fig. 2b). A less pronounced, but similarly-shaped curve described individuals at the two drier sites. Mean P_{50} values decreased significantly with decreasing streamflow (Table 3). Ψ_{\min} for *M. angustifolia* individuals was significantly lower at the high streamflow site (Table 4), and Ψ_{\max} decreased by almost two orders of magnitude from the high to medium streamflow site ($P=0.000$; Table 4).

The pattern of vulnerability to cavitation for *B. neriifolia* was similar to that for *M. angustifolia*. Individuals growing at the high streamflow site showed increased embolism relative to individuals growing at the medium streamflow site, especially at more negative xylem water potentials (Fig. 2c). The mean values for P_{50} differed significantly between the two sites sampled for this species (Table 3). This species did not occur at the low streamflow sites. Ψ_{\max} did not differ significantly and Ψ_{\min} was very similar across the two sites ($P=0.325$; Table 4). As with *B. stellatifolium*, mean values of Ψ_{\max} , and Ψ_{\min} at the high and medium streamflow sites, -0.66 and -0.55 MPa, and -1.95 and -1.81 MPa

respectively, were consistent with values in Richardson and Kruger (1990).

The shape of the curves of *R. melanophloeos* shifted from almost linear to J-shaped with decreasing water availability (Fig. 2d), but there was no significant difference in mean values of P_{50} , Ψ_{\max} , and Ψ_{\min} at the high streamflow or medium streamflow sites, although Ψ_{\min} did decrease by an order of magnitude ($P=0.058$; Table 4).

3.3. Across-species comparisons

Both *B. stellatifolium* and *R. melanophloeos* had significantly lower values of P_{50} than *M. angustifolia* or *B. neriifolia* at the high streamflow site (Table 3). At the medium streamflow site, *B. stellatifolium* values of P_{50} were significantly lower than *R. melanophloeos* (Table 3), and were close to being significantly lower than *M. angustifolia* ($P=0.05$) and *B. neriifolia* ($P=0.056$). At the lowest streamflow site, the mean P_{50} value for *B. stellatifolium* was close to being significantly lower than the mean for *M. angustifolia* and *R. melanophloeos*, ($F=3.508$, $P=0.075$, $df=2$; Table 3).

Species showed considerable differences in Ψ_{\max} at all sites. At the high streamflow site, *B. neriifolia* had significantly lower mean Ψ_{\max} , than *M. angustifolia* or *B. stellatifolium* (Table 4). At the medium streamflow site, mean Ψ_{\max} of *M. angustifolia* is significantly lower than the other three species, while the mean Ψ_{\max} of *R. melanophloeos* was higher than all other species (Table 4). Ψ_{\min} is less variable at the medium streamflow site; mean Ψ_{\min} of *R. melanophloeos* is significantly higher than Ψ_{\min} of *B. stellatifolium* (Table 4). However, at the high streamflow site Ψ_{\min} of *M. angustifolia* is significantly lower than all other species. At the low streamflow sites, neither

Table 4
Mean values for Ψ_{\max} and Ψ_{\min} across species and streamflow regimes

Species	High streamflow		Medium streamflow		Low streamflow	
	Ψ_{\max}	Ψ_{\min}	Ψ_{\max}	Ψ_{\min}	Ψ_{\max}	Ψ_{\min}
<i>Brabejum stellatifolium</i>	-0.27 ^{cd} (0.05) $n=5$	-2.09 ^{bc} (0.10) $n=5$	-0.50 ^b (0.06) $n=5$	-1.99 ^{bc} (0.10) $n=5$	-0.40 ¹ (0.07) $n=5$	-2.08 ¹² (0.06) $n=5$
<i>Meterosideros angustifolia</i>	-0.24 ^d (0.03) $n=5$	-2.43 ^a (0.08) $n=5$	-0.79 ^a (0.03) $n=5$	-1.85 ^{bcd} (0.15) $n=5$	-0.38 ¹ (0.12) $n=4$	-2.26 ¹ (0.11) $n=4$
<i>Brachyleana neriifolia</i>	-0.66 ^{ab} (0.14) $n=5$	-1.95 ^{bc} (0.08) $n=5$	-0.55 ^b (0.07) $n=4$	-1.81 ^{bcd} (0.12) $n=4$		
<i>Rapanea melanophloeos</i>	-0.47 ^{bc} (0.09) $n=5$	-1.86 ^{bcd} (0.04) $n=5$	-0.23 ^{cd} (0.02) $n=3$	-1.55 ^d (0.03) $n=3$	-0.13 ² (0.03) $n=4$	-1.73 ² (0.19) $n=4$

Values are in MPa. Standard errors are given in parentheses. Two separate ANOVA procedures were carried out for Ψ_{\max} and similarly for Ψ_{\min} . A factorial ANOVA was used to compare the high and medium streamflow regimes and a one-way ANOVA to determine differences within the low streamflow regime. In both cases, means were separated using the Fishers's LSD multiple range test. Within and between the high and medium streamflow regime, means with different alphabetical superscripts differ significantly ($P<0.05$). Within the low streamflow regime, means with different numerical superscripts differ significantly ($P<0.05$).

Ψ_{\max} nor Ψ_{\min} of *B. stellatifolium* and *M. angustifolia* differed significantly. Mean Ψ_{\max} of *M. angustifolia* was significantly lower than *R. melanophloeos* ($F=4.10$, $P=0.050$, $df=2$; Table 4), and both *B. stellatifolium* and *M. angustifolia* mean Ψ_{\min} were significantly lower than *R. melanophloeos* ($F=10.21$, $P=0.004$, $df=2$; Table 4).

When mid-day xylem water potential, Ψ_{\min} , a measure of plant water stress, is plotted as a function of values of P_{50} for individuals of all species, two groups of species emerge. Individuals that reach mid-day water potentials below measured P_{50} values, the point at which 50% of xylem conducting capacity is lost, may risk catastrophic embolism. Individuals of *M. angustifolia* at both the high and low streamflow sites had high Ψ_{\max} indicating greater water availability and fall below the line that indicates equal values of mid-day water potential

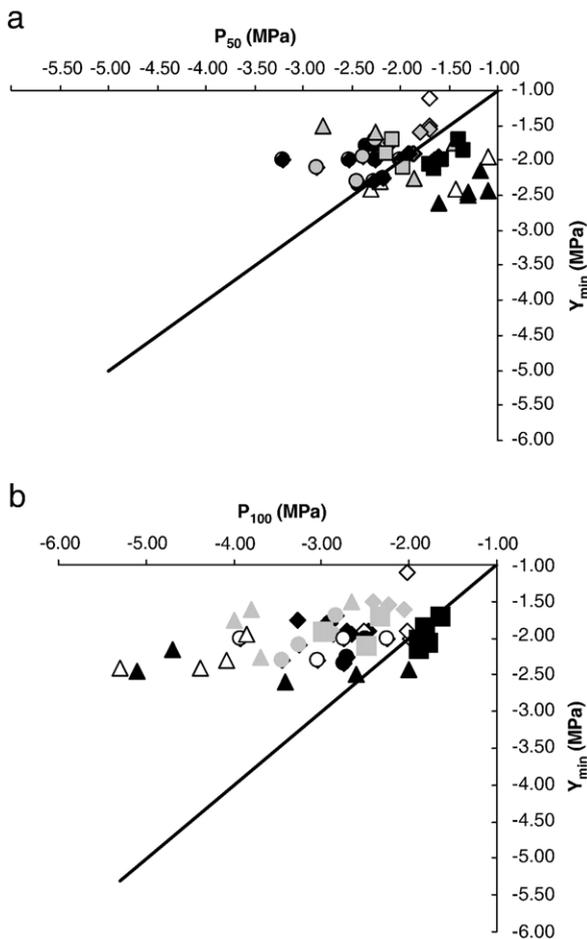


Fig. 3. Measured Ψ_{\min} for individuals plotted against xylem water potential at different levels of hydraulic conductivity. (a) P_{50} . *R. melanophloeos* is represented by diamonds, *B. stellatifolium* by circles, *M. angustifolia* by triangles and *B. neriifolia* by squares. For all species, closed symbols are Swartbrug (high streamflow) individuals, grey symbols are Witbrug (medium streamflow) individuals, and open symbols are either Bosboukloof (*M. angustifolia* and *B. stellatifolium*) or Biessievlei (*R. melanophloeos*). (b) P_{100} . *R. melanophloeos* is represented by diamonds, *B. stellatifolium* by circles, *M. angustifolia* by triangles and *B. neriifolia* by squares. For all species, closed symbols are Swartbrug (high streamflow) individuals, grey symbols are Witbrug (medium streamflow) individuals, and open symbols are either Bosboukloof (*M. angustifolia* and *B. stellatifolium*) or Biessievlei (*R. melanophloeos*).

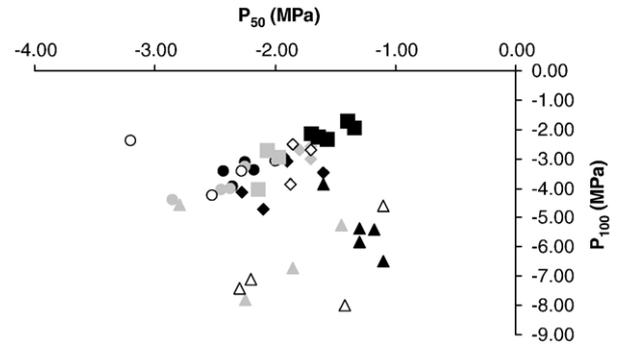


Fig. 4. Correlation between P_{50} and P_{100} . *R. melanophloeos* is represented by diamonds, *B. stellatifolium* by circles, *M. angustifolia* by triangles and *B. neriifolia* by squares. For all species, closed symbols are Swartbrug (high streamflow) individuals, grey symbols are Witbrug (medium streamflow) individuals, and open symbols are either Bosboukloof (*M. angustifolia* and *B. stellatifolium*) or Biessievlei (*R. melanophloeos*).

and values of P_{50} , as do all individuals of *B. neriifolia* occurring in high streamflow (Fig. 3a). But, at the medium streamflow site where Ψ_{\max} is lower for both *M. angustifolia* and *B. neriifolia*, individuals are either above the line equating P_{50} and Ψ_{\min} or on the line, as are all individuals of *B. stellatifolium* and most *R. melanophloeos* individuals at all streamflows. Moreover, mean Ψ_{\min} exceeds mean P_{50} for all species at lower water availability as indicated by Ψ_{\max} , but Ψ_{\min} for both *M. angustifolia* and *B. neriifolia* was below P_{50} at higher water availability.

If P_{100} , the Ψ_x at which a total loss of conductivity occurs, is plotted against mid-day water potential, a different pattern emerges. *M. angustifolia*, with a few exceptions maintains a larger safety margin against 100% loss of conductivity than the other species, but *B. neriifolia* sustained Ψ_{\min} at 100% loss of conductivity (Fig. 3b).

If P_{50} is plotted against P_{100} , the Ψ_x at which a total loss of conductivity occurs, two groups emerge. Most species at most sites form one group, and *M. angustifolia* individuals from all sites form a second group with the exception of two individuals (Fig. 4). *M. angustifolia* individuals experience much lower Ψ_x at 100% loss of conductivity than other species at the same sites even though the Ψ_x at 50% loss of conductivity is higher. A single *B. stellatifolium* individual from the low streamflow site belongs to neither group.

4. Discussion

The large differences between Ψ_{\max} at the high and medium sites suggests that water availability did decrease between those two sites, at least for two of the four species examined, *B. stellatifolium* and *M. angustifolia*. The other two species did not exhibit decreased Ψ_{\max} , while *R. melanophloeos* showed an increased Ψ_{\max} at the medium streamflow site. Although *R. melanophloeos* is considered a riparian species, unlike the other species, it has afromontane affinities. Lower Ψ_{\max} at higher water availability might suggest that this species may be less tolerant of saturated soils than the other species examined (Kozłowski, 1997).

B. stellatifolium, identified as ubiquitous and *R. melanophloeos*, identified as sensitive to invasion and associated with less disturbed riparian habitats (Galatowitsch and Richardson, 2005), exhibited similar responses to decreasing summer water availability across sites, since P_{50} values were not statistically different across sites (although, *R. melanophloeos* did sustain higher Ψ_{\min} than *B. stellatifolium* at all sites). Mean values of Ψ_{\min} always exceeded mean P_{50} values at all sites. This is in contrast to *B. neriifolia* and *M. angustifolia*, which both exhibited significantly lower mean P_{50} values, and mean Ψ_{\min} values that were more negative than P_{50} values at the medium streamflow site. Vulnerability to cavitation is related to xylem anatomy which may be phylogenetically constrained (Vander Willigen and Pammenter, 1998; Mahareli et al., 2004; Jacobsen et al., 2007) and may explain the observation that vulnerability to embolism in *B. stellatifolium* and *R. melanophloeos* does not change with increasing or decreasing water availability. These results lend some support to xylem anatomy being constrained by phylogenetic factors. However, the finding that *B. neriifolia* and *M. angustifolia* are able to change xylem anatomical traits in response to decreased water availability suggests greater phenotypic plasticity for these species or that phylogenetic constraints may not apply to all taxa, and needs further investigation.

Vulnerability curve shapes suggest that *M. angustifolia* is less drought tolerant than *B. stellatifolium* (Kolb and Davis, 1994; Kavanagh et al., 1999; Kolb and Sperry, 1999). Hacke et al. (2006), however, make the point that, despite initial rapid losses of hydraulic conductance, this curve shape leads to sustained hydraulic conductance at lower Ψ_x and this appears to be true for *M. angustifolia*. This is consistent with Vander Willigen and Pammenter's (1998) point that remaining hydraulic conductivity may be more important than P_{50} in explaining the ability to tolerate low water availability without hydraulic failure. Mean P_{50} for *M. angustifolia* was greater than for *B. stellatifolium* at all sites, but mean Ψ_{\min} of *M. angustifolia* was either significantly lower (high streamflow site) or not significantly different from *B. stellatifolium*. In fact, at all sites, *M. angustifolia* requires much more negative Ψ_x to reach 100% embolism than all other species, again supporting the idea that it is not the hydraulic capacity lost but the hydraulic capacity remaining that is important to drought tolerance (Vander Willigen and Pammenter, 1998). *M. angustifolia* maintains a larger safety margin between Ψ_{\min} and P_{100} because of the shallow slope of the vulnerability curve at more negative Ψ_x , which may result in increased hydraulic transport, and is typical of diffuse porous species (Alder et al., 1996). Continued conductivity under drought conditions in *M. angustifolia* may reflect a range of xylem conduits with different susceptibility to embolism (Alder et al., 1996; Hacke et al., 2006). Native embolism has been reported for other riparian species (Alder et al., 1996; Rood et al., 2000), and may be adaptive when coupled with branch or leaf shedding as a result of hydraulic segmentation (Rood et al., 2000).

The four species studied showed marked differences in response to water availability. *B. stellatifolium* and *R. melanophloeos* appear to maintain large safety margins against embolism by not allowing Ψ_{\min} to become more negative than P_{50}

regardless of water availability. Alternatively, both *B. neriifolia* and *M. angustifolia* maximize hydraulic transport at the expense of embolism, but only when water availability is high. The two species may therefore differ with respect to degree of vulnerability to 100% embolism under those conditions since *B. neriifolia* Ψ_{\min} hovers near 100% embolism. These results suggest that the similar distributions of these species may be the result of different strategies to cope with increasing drought. Under high water availability, *B. stellatifolium* and *R. melanophloeos* may limit stomatal conductance to maintain values of Ψ_{\min} that exceed P_{50} . However, Richardson and Kruger (1990) found no overall difference in stomatal conductance between *B. stellatifolium* and *B. neriifolia*, although *B. stellatifolium* maintained more constant rates of diurnal stomatal conductance than *B. neriifolia*. The fact that P_{50} for *B. stellatifolium* and *R. melanophloeos* did not mirror changes in water supply in this study might suggest that phylogenetic constraints, which dictate wood density, may be responsible for increased safety margins at high water availability (Vander Willigen and Pammenter, 1998; Brodribb and Holbrook, 2004; Mahareli et al., 2004). The ability of *M. angustifolia* and *B. neriifolia* to “relax” safety margins when water availability is high may translate into higher stomatal conductance which would translate into greater carbon gain, growth, and enhanced ability to compete for light. However, *B. neriifolia* runs a greater risk of catastrophic embolism than *M. angustifolia* which retains a greater capacity for hydraulic transport even with a greater than 50% loss of hydraulic transport.

Both *M. angustifolia* and *B. stellatifolium* are more likely to persist with invasion (Galatowitsch and Richardson, 2005; Pretorius et al., 2008-this issue) perhaps because they are able to tolerate decreases in water availability with invasion (Dye and Jarmain, 2004). In the case of *B. stellatifolium*, xylem anatomy may confer a greater safety margin against catastrophic embolism. In the case of *M. angustifolia*, xylem traits allow continued competition for light by maintaining higher stomatal conductances which translate into carbon gain and growth when water availability is high, but adjusts xylem traits when water is more limiting to avoid catastrophic embolism. This is in contrast to species less likely to co-exist with invasives such as *R. melanophloeos*, which exhibited significantly higher Ψ_{\min} than most other species examined at all sites, suggesting possible limitations on stomatal conductance, or *B. neriifolia* which might be highly vulnerable to water limitation or reduced light availability imposed by invasive species (Pockman and Sperry, 2000). A strategy involving a high risk of catastrophic embolism, but greater gas exchange capacity, would be useful if seasonal flood disturbance removed old branches, and kept competing species from establishing. Field observations indicate that this species is largely restricted to the stream edge and is not ubiquitous across all streams in the Western Cape (Charlie Boucher, pers. comm.).

The results of this study suggest that *B. stellatifolium* and *M. angustifolia* would be good candidates for inclusion in plant palettes for post-clearing restoration areas, especially in streams with low summer water availability since they appear to be more drought tolerant than the other two species examined. A similar recommendation was made by Galatowitsch and Richardson

(2005), based on the presence of *B. stellatifolium* and *M. angustifolia* in open or cleared sites in their study. Alternatively, *B. neriifolia* would not be a good candidate for inclusion in a plant palette unless water and light availability are high. The small safety margin of this species at both P_{50} and P_{100} is consistent with other studies of vulnerability to cavitation in riparian species and is related to predictable water supply typical of streams (Pockman and Sperry, 2000). This species may be a good candidate for judging restoration of fluvial regime as a measure of restoration success.

These are preliminary results, and additional research is needed to describe stomatal behavior and anatomical traits of xylem of these species in these different fluvial regimes (Kolb and Davis, 1994; Brodribb and Holbrook, 2004). This work does, however, begin to describe potential mechanisms underlying the distribution of these four species. Understanding drought tolerance facilitates refined targets for restoration that are realistic in terms of water availability requirements of native species, as well as illustrates the need for continued removal of non-native invasive species in order to restore fluvial conditions appropriate for successful restoration (Rood et al., 2003).

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