

## WATER STRESS TOLERANCE OF SHRUBS IN MEDITERRANEAN-TYPE CLIMATE REGIONS: CONVERGENCE OF FYNBOS AND SUCCULENT KAROO COMMUNITIES WITH CALIFORNIA SHRUB COMMUNITIES<sup>1</sup>

ANNA L. JACOBSEN,<sup>2,5</sup> KAREN J. ESLER,<sup>3</sup> R. BRANDON PRATT,<sup>2</sup> AND FRANK W. EWERS<sup>4</sup>

<sup>2</sup>Department of Biology, California State University, Bakersfield, California 93311 USA; <sup>3</sup>Department of Conservation Ecology and Entomology and Centre for Invasion Biology, Stellenbosch University, Matieland, 7602, South Africa; and <sup>4</sup>Biological Sciences Department, California State Polytechnic University, Pomona, California 91768 USA

Mediterranean-type climate regions are highly biodiverse and predicted to be particularly sensitive to climate change. Shrubs of the Mediterranean-type climate region of South Africa are highly threatened, and their response to water stress has been comparatively little studied. Resistance to water stress induced xylem cavitation ( $P_{50}$ ) and xylem specific hydraulic conductivity ( $K_s$ ) were measured in 15 shrub species from fynbos and succulent karoo communities of South Africa. Species displayed a fivefold variation in cavitation resistance ( $P_{50}$  of  $-1.9$  to  $-10.3$  MPa) with succulent karoo species displaying greater interspecific variability in  $P_{50}$  than fynbos species. Principal components analysis (including  $P_{50}$ , minimum seasonal water potential,  $K_s$ , and xylem density) showed the response to water stress in fynbos species to be similar to chaparral species from the Mediterranean-type climate region of California. The data suggest convergence of community and species-specific water stress “strategies” between these Mediterranean-type climate regions with respect to their xylem traits. On the basis of the current study and reported plant death and dieback in these regions, woody species within the fynbos may be more susceptible to climate warming and drying than those within the succulent karoo that appear to be utilizing more diverse xylem strategies in response to water stress.

**Key words:** cavitation resistance; chaparral; dioecious; fynbos; Mediterranean-type climate; Mojave Desert; succulent karoo; water relations; xylem density.

The five Mediterranean-type climate regions are among the most biodiverse and threatened in the world. These five regions contain nearly 20% of all known vascular plant species but only occupy 5% of the earth’s surface (Cowling et al., 1996). In a recent study examining global biodiversity conservation priorities, these regions were recognized as highly vulnerable to losses in biodiversity and regions in which recovery of degraded ecosystems was highly unlikely (Brooks et al., 2006). Additionally, these regions have been identified as being particularly threatened by global climate change (IPCC, 2007).

The Mediterranean-type climate region of southwestern South Africa stands out as being uniquely diverse and particularly threatened. Additionally, predictions for future climate in the region point to significant changes in water availability (Shulze and Perks, 2000) and suggest that the ecology of the region may be highly threatened by such changes (Lovett et al., 2005; Midgely et al., 2006). However, seasonal water relations have only been studied among very few woody plant species of South Africa (Miller et al., 1983; Moll and Sommerville, 1985; van der Heyden and Lewis, 1989; Richardson and Kruger, 1990; Smith and Richardson, 1990; Jacobsen et al., 2007a). Published data on cavitation resistance of woody shrub species

from this region are also lacking (however, see Swift et al., 2008, for data on four riparian species).

The woody, evergreen, sclerophyllous shrubs that typify Mediterranean-type climate regions appear to undergo similar levels of water stress during the long summer droughts that characterize the climate of these regions (however, see Cowling et al., 2005 on climatic differences among these regions). This similarity is supported by the similar means and ranges of minimum seasonal water potential ( $\Psi_{\min}$ ) of plants in these regions (Martínez-Vilalta et al., 2002; Jacobsen et al., 2007a, c). The shrubs of these regions also have  $\Psi_{\min}$  similar to those reported for other arid and semiarid evergreen shrubland communities including species from the Great Basin Desert (Hacke et al., 2000), the Mojave Desert (Jacobsen et al., 2008), the coastal sage scrub (Jacobsen et al., 2008), and the Sonoran Desert (Pockman and Sperry, 2000). Although a mean  $\Psi_{\min}$  of approximately  $-4$  to  $-5$  MPa may represent a common physiological limit of these arid and semiarid shrub communities, it appears that species strategies for coping with this level of water stress may vary greatly among these communities (Jacobsen et al., 2008).

The Mediterranean-type climate region of South Africa contains many plant communities that differ in their average precipitation, topography, substrate, disturbance regimes, etc., but often grow adjacent to each other in a patchwork across the broader landscape (Rebello et al., 2006). Two of these communities are the fynbos and succulent karoo. Fynbos shrub species occur in areas that receive more rainfall than the succulent karoo, and the shrub species are usually taller in the fynbos compared to the woody shrub species of the succulent karoo. Fynbos communities grade into succulent karoo as one travels inland from the coast to areas of less precipitation and tend to occur on different substrates, with fynbos occurring predominantly on

<sup>1</sup> Manuscript received 16 December 2008; revision accepted 18 March 2009.

This work was supported by an NSF Graduate Research Fellowship and Doctoral Dissertation Improvement Grant to A.L.J. and Michigan State University Department of Plant Biology. The authors thank L. Alan Prather, D. W. Schemske, F. W. Telewski, S. D. Davis, and L. M. Moe for valuable advice and discussions. A.L.J. and R.B.P. thank the Andrew Mellon Foundation and NSF Grant IOS-0845125 to R.B.P. for support.

<sup>5</sup> Author for correspondence (e-mail: ajacobsen@csu.edu)

sandstones and the succulent karoo on shales. It is unknown whether shrub species in these communities are utilizing similar xylem strategies in response to protracted summer drought or whether they are using different strategies and may be differentially susceptible to climate change.

We examined vulnerability to cavitation of 15 shrub species from South Africa along a gradient that spans the ecotone between fynbos and succulent karoo vegetation communities. These data were analyzed in tandem with previously reported  $\Psi_{\min}$  data on these species to examine their response to water stress. Knowledge of the cavitation resistance of these shrubs as it relates to  $\Psi_{\min}$  may be useful in predicting species or communities that are particularly sensitive to extreme water stress events in this region. Additionally, we examined what anatomical traits are associated with increased cavitation resistance among these species. We predicted that xylem vessel and fiber structural traits would be associated with cavitation resistance as has been reported previously (Hacke et al., 2001; Jacobsen et al., 2005, 2007c).

Last, data from these South African species were compared to data from three semiarid plant communities from North America to ascertain whether communities in these climatically similar regions use similar strategies in response to water stress, that is, if there is convergence in water stress tolerance among shrub species and plant communities from different mediterranean-type climate regions (see Cowling et al., 2005, regarding differences in rainfall reliability among these regions). The plant communities of the mediterranean-type climate regions of South Africa and California have been compared previously; however, most of these studies have focused only on the dominant vegetation communities of these regions, the fynbos and chaparral communities, and on plant structure and diversity rather than physiological strategies of plants (e.g., Cody and Mooney, 1978; Barbour and Minnich, 1990; Keeley and Bond, 1997). Limited comparisons have also been made between plants of the succulent karoo and Mojave Desert (Esler and Rundel, 1999). Mojave Desert shrubs occur in sites that are somewhat more arid and more variable in precipitation than for the chaparral and coastal sage communities. Similarly, the succulent karoo occurs in sites that are more arid and variable in precipitation than the fynbos. We predicted that species from climatically similar communities would converge in their xylem functional traits related to water stress tolerance.

## MATERIALS AND METHODS

Xylem vulnerability to cavitation was measured in 15 species of evergreen sclerophyllous shrubs located on Jonaskop in the Riviersonderend Mountain Range in Western Cape Province, South Africa at ca. 33°56.08'S 19°31.26'E (Table 1; see Jacobsen et al., 2007a for site and species descriptions). Ten species were sampled from between 850 and 1020 m a.s.l. and typically receive ca. 420 mm of precipitation annually. Five species were sampled from between 540 and 660 m a.s.l. and typically receive ca. 315 mm of precipitation annually. These species represented the dominant woody plant species at this site that had been examined in a prior study (Jacobsen et al., 2007a) and which had straight, unbranched stem segments of suitable length for determining xylem vulnerability to cavitation using a centrifuge technique. This site occurs across an ecotone with the 10 higher elevation species occurring in fynbos vegetation, while the five lower elevation species are more strongly associated with the succulent karoo vegetation community (Agenbag et al., 2008). These sites are roughly comparable climatically to chaparral and coastal sage sites (ca. 460 mm of precipitation annually) and a Mojave Desert site (ca. 230 mm of precipitation annually) of the California mediterranean-type climate region and described in Jacobsen et al. (2007b). All sites, both in South Africa and California, experi-

TABLE 1. Species of evergreen shrubs located on Jonaskop in the Riviersonderend Mountain Range in the Western Cape Province, South Africa, including species families and the code used for each species in Figs. 1, 2, 4, and 5.

Species	Family	Code
Fynbos		
<i>Aspalathus hirta</i> E. Mey.	Fabaceae	Ah
<i>Aspalathus pachyloba</i> R. Dahlgren	Fabaceae	Ap
<i>Cliffortia ruscifolia</i> L.	Rosaceae	Cr
<i>Erica plukenetii</i> L.	Ericaceae	Ep
<i>Erica vestita</i> Thunb.	Ericaceae	Ev
<i>Leucadendron laureolum</i> (Lam.) Fourc., females	Proteaceae	LIF
<i>Leucadendron laureolum</i> (Lam.) Fourc., males	Proteaceae	LIM
<i>Leucadendron salignum</i> P. J. Bergius, females	Proteaceae	LsF
<i>Leucadendron salignum</i> P. J. Bergius, males	Proteaceae	LsM
<i>Metalasia densa</i> (Lam.) Karis	Asteraceae	Ld
<i>Nebelia laevis</i> O. Kuntze	Bruniaceae	NI
<i>Protea repens</i> (L.) L.	Proteaceae	Pr
Succulent karoo		
<i>Euclea</i> sp.	Ebenaceae	E
<i>Passerina obtusifolia</i> Thoday	Thymelaeaceae	Po
<i>Pteronia fasciculata</i> L.f.	Asteraceae	Pf
<i>Pteronia paniculata</i> Thunb.	Asteraceae	Pp
<i>Searsia undulata</i> (Jacq.) T. S. Yi, A. J. Miller & J. Wen <sup>a</sup>	Anacardiaceae	Su

<sup>a</sup> Formerly *Rhus undulata*

ence an extended summer dry period and receive primarily winter rainfall as is typical of mediterranean-type climate regions.

Unbranched, straight stem segments approximately 6–8 mm in diameter and 30 cm long were collected in the field during the early summer from 10 individuals per species. Two species were dioecious. For these species, stems were collected from 10 female and 10 male individuals. Stems were trimmed underwater in situ, wrapped in moist paper towels, sealed in plastic bags, and shipped on ice to California State University, Bakersfield, California, USA, via international express shipping. Vulnerability to cavitation was determined for stems as soon as they arrived, and all stems were measured within a week of being collected in the field.

Stems were trimmed under water from both ends until a segment 6–8 mm in diameter and 14 cm in length was obtained. Although we did not measure vessel length distributions of these species, vessel length is strongly correlated with vessel diameter (Ewers et al., 1990; Wheeler et al., 2005; Hacke et al., 2006), and all of these species had relatively narrow vessel diameters (17–33  $\mu\text{m}$  mean vessel diameters across all species; Jacobsen et al., 2007a), suggesting they also have relatively short vessels. Additionally, recent work has shown that estimates of cavitation resistance using the centrifuge technique are not impacted by vessels that may run the entire length of stem segments (Li et al., 2008).

Stems were connected to a tubing system and flushed for 1 h at 100 kPa, and the maximum hydraulic conductivity ( $K_{\max}$ ) of stems was measured gravimetrically (Sperry et al., 1988) using an analytical balance (CPI124S, Sartorius, Goettingen, Germany). After determination of  $K_{\max}$ , stems were spun in a centrifuge (Sorvall RC-5C, Thermo Fisher Scientific, Waltham, Massachusetts, USA) using a custom-made rotor (Alder et al., 1997). Vulnerability to cavitation curves were constructed by plotting the water potential (generated using the centrifuge) vs. the percentage loss in hydraulic conductivity (PLC). For each stem, curves were fit with a second order polynomial model (Jacobsen et al., 2007c). Cavitation resistance for each species was estimated using the pressure that resulted in 50% loss in hydraulic conductivity ( $P_{50}$ ) calculated from fatigue corrected curves using the conductivity after an initial spin of  $-0.25$  MPa in place of  $K_{\max}$  (Hacke et al., 2000; Jacobsen et al., 2007b). This calculation corrects for the vessels within a stem, which may exhibit flow after flushing under pressure, but which would not be functional at the pressures found within the intact plant. Unpaired  $t$  tests were used to compare xylem traits of males and females of dioecious species, a  $t$  test was used to compare cavitation resistance of fynbos vs. succulent karoo species, and an  $F$  test was used to compare the variability in cavitation resistance in fynbos vs. succulent karoo species (Minitab v.14.12; Minitab, State College, Pennsylvania, USA).

The xylem specific hydraulic conductivity ( $K_s$ ) of stems was determined using the methods described in Jacobsen et al. (2007a). Xylem area (not including the pith) was determined using a digital camera and image analysis software

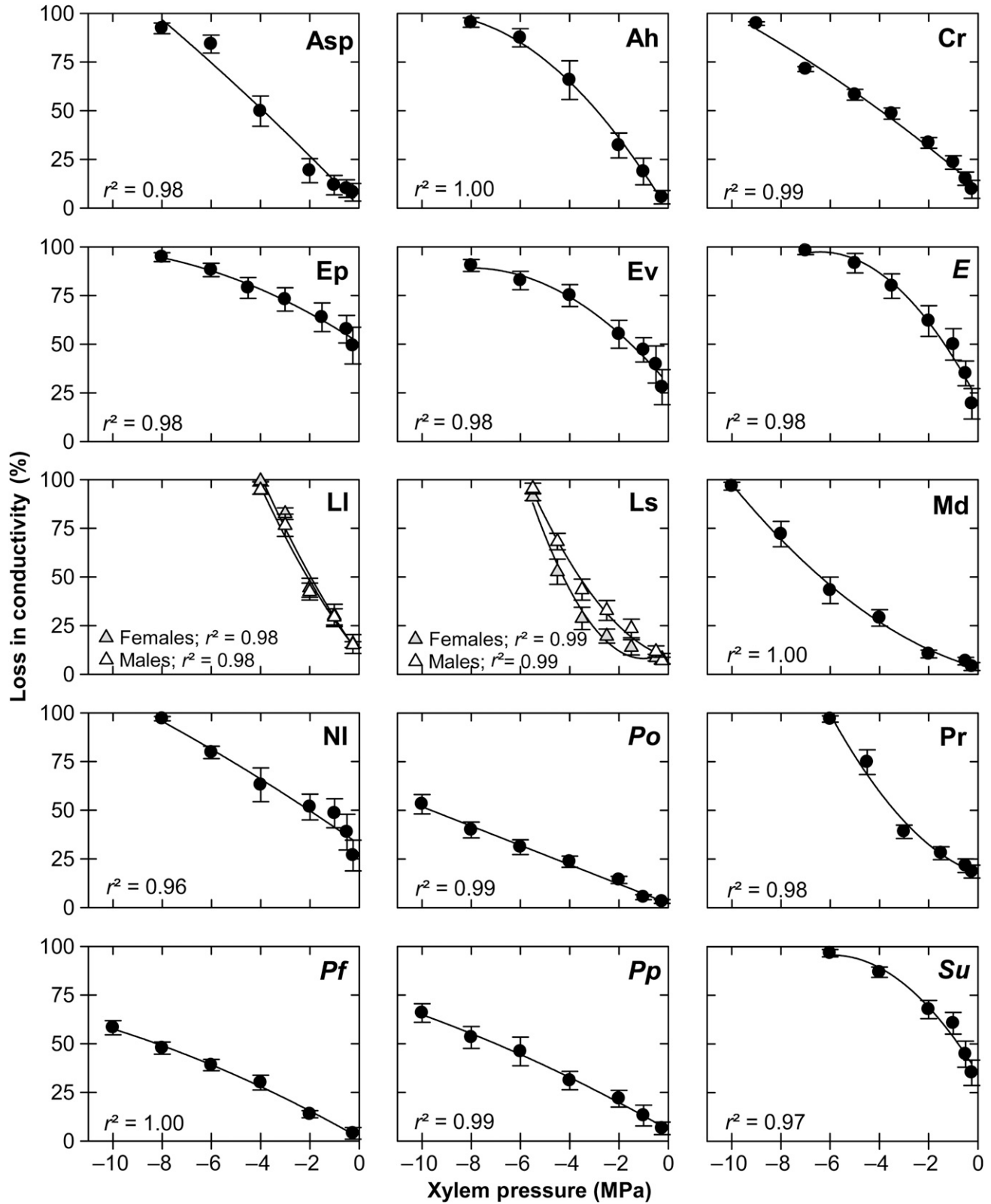


Fig. 1. Vulnerability to cavitation curves for 15 evergreen shrub species from South Africa depicting the percentage loss in hydraulic conductivity for a given decrease in xylem pressure generated using a customized rotor and centrifuge (see Materials and Methods for details). Curves for monoecious species are shown with black circles (means  $\pm$  1 SE), and for dioecious species, curves for females are shown with gray triangles and for males with open triangles (means  $\pm$  1 SE). Species abbreviations are in black type for fynbos species and in gray italic type for succulent karoo species. For code to species abbreviations, see Table 1.

(Olympus SP-500UZ, Olympus Imaging Corp., Center Valley, Pennsylvania, USA; Scion Image v. Beta 4.0.3, Scion Corp., Frederick, Maryland, USA). The  $K_{\max}$  was divided by the xylem area to obtain xylem specific conductivity ( $K_s$ ). Values of  $K_s$  obtained and used in analyses in the current study were strongly correlated to those reported previously for these species ( $F = 26.78$ ,  $df = 1$ ,  $P < 0.001$ ,  $r^2 = 0.67$ ; Jacobsen et al., 2007a).

Several anatomical and mechanical traits were previously reported for all the species included in the current study (Jacobsen et al., 2007a) except for *Erica vestita*. These include the fiber-associated traits of xylem density, modulus of rupture (MOR), fiber lumen diameter, fiber wall thickness, and the percentage fiber wall area per xylem cross-sectional area and the vessel-associated traits of vessel lumen diameter, vessel mechanical strength against implosion [ $(t/b)_h^2$ ; Hacke et al., 2001], and the percentage vessel area per xylem cross-sectional area. We examined which of these xylem traits were associated with  $P_{50}$ . We also examined the relationship between  $P_{50}$  and  $\Psi_{\min}$  and  $K_s$ . Correlations among  $P_{50}$  and these traits were examined using linear regression analyses of both raw trait values and phylogenetic independent contrasts (PICs; Felsenstein, 1985; Minitab v.14.12, Minitab). Phylogenetic independent contrasts were run using the phylogeny reported in Jacobsen et al. (2007a) and the program COMPARE (Martins, 2004).

A principal component analysis was used to examine whether South African species were utilizing similar water stress tolerating strategies to those used by species from Californian winter rainfall plant communities (Statview v.5.0.1; SAS Institute, Cary, North Carolina, USA). Cavitation resistance ( $P_{50}$ ),  $K_s$ , xylem density, and minimum seasonal water potential data ( $\Psi_{\min}$ ) were included in the analyses for 28 species from California from previously published studies (Jacobsen et al., 2007b, 2008). Data for these same four traits were included for 14 South African species, including  $P_{50}$  and  $K_s$  from the current study and xylem density and  $\Psi_{\min}$  as reported in Jacobsen et al. (2007a). A MANOVA was used to examine whether the relationships between these xylem traits differed among these communities and ANOVAs were used to determine if communities' multivariate components differed.

## RESULTS

**Cavitation resistance of fynbos and succulent karoo species**—Species varied in the shape and magnitude of their vulnerability to cavitation curves, displaying concave, convex, and

linear shapes (Fig. 1). In general, species displayed very little cavitation fatigue, consistent with our sampling in early summer after the growth of new xylem. Species varied considerably in resistance to cavitation, with a range in water potentials at 50% loss in hydraulic conductivity ( $P_{50}$ ) of  $-1.9$  MPa (*Searsia undulata*) to  $-10.3$  MPa (*Passerina obtusifolia*) (Fig. 2). The mean  $P_{50}$  across species was  $-4.5 \pm 1.5$  MPa (Fig. 2). Fynbos and succulent karoo species did not significantly differ in their resistance to cavitation ( $t = 1.26$ ,  $df = 4$ ,  $P = 0.277$ ), although the succulent karoo associated species displayed greater interspecific variability in cavitation resistance ( $F_{5,11} = 6.67$ ,  $P = 0.022$ ).

The males and females of the dioecious species *Leucadendron salignum* differed significantly in their cavitation resistance ( $t = -2.34$ ,  $df = 8$ ,  $P = 0.041$ ), but the shapes of their vulnerability curves were similar. The females were more resistant to cavitation than the males, with an average  $P_{50}$  of  $-4.4 \pm 0.1$  MPa for the females compared to  $-3.7 \pm 0.2$  MPa for the males. In contrast, the males and females of the dioecious species *L. laureolum* did not differ in cavitation resistance ( $t = 0.40$ ,  $df = 8$ ,  $P = 0.699$ ).

**Cavitation resistance correlates to xylem structure and function**—Across all species, cavitation resistance was associated with anatomical traits of xylem fibers (Fig. 3). Increased resistance to cavitation was associated with increased xylem density (Fig. 3A;  $F = 9.24$ ,  $df = 1$ ,  $P = 0.007$ ,  $r^2 = 0.40$ ), greater percentage fiber wall area per cross sectional area (Fig. 3B;  $F = 19.64$ ,  $df = 1$ ,  $P = 0.001$ ,  $r^2 = 0.56$ ), and increased stem mechanical strength estimated by the modulus of rupture (MOR) (Fig. 3C;  $F = 40.87$ ,  $df = 1$ ,  $P < 0.001$ ,  $r^2 = 0.79$ ). Fiber lumen diameter was also correlated with  $P_{50}$  ( $F = 6.41$ ,  $df = 1$ ,  $P = 0.023$ ,  $r^2 = 0.30$ ; not shown). Fiber wall area and MOR remained correlated with  $P_{50}$  when relationships were analyzed using phylogenetic independent contrasts (PICs;  $F = 6.52$ ,  $df = 1$ ,

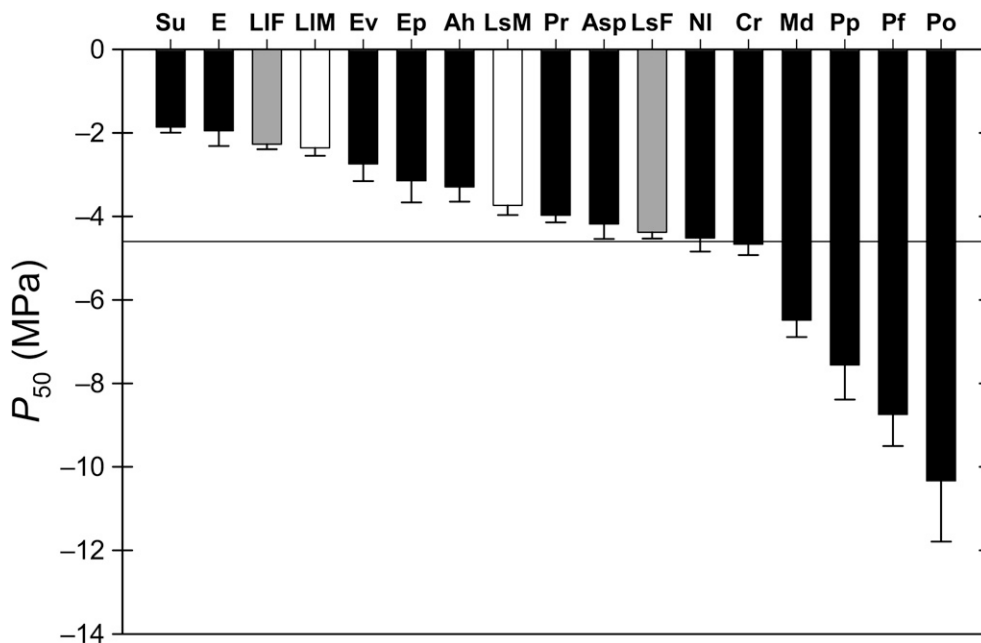


Fig. 2. Cavitation resistance ( $P_{50}$ ) of 15 evergreen shrub species from South Africa, estimated from fatigue-corrected vulnerability to cavitation curves (see Materials and Methods for details). Bars represent species means  $\pm 1$  SE (monoecious species values are represented as black bars, females from dioecious species as gray bars, and males from dioecious species as open bars). Horizontal line indicates the across species mean cavitation resistance of  $-4.5$  MPa. For code to species abbreviations, see Table 1.

$P = 0.024$ ,  $r^2 = 0.33$  and  $F = 6.51$ ,  $df = 1$ ,  $P = 0.029$ ,  $r^2 = 0.39$ , respectively); however, xylem density and fiber lumen diameter were not correlated to  $P_{50}$  when PICs were used ( $F = 0.21$ ,  $df = 1$ ,  $P > 0.05$  and  $F = 0.36$ ,  $df = 1$ ,  $P > 0.05$ , respectively). Fiber wall thickness was not correlated to  $P_{50}$  when either raw traits ( $F = 0.31$ ,  $df = 1$ ,  $P > 0.05$ ) or PICs were analyzed ( $F = 1.24$ ,  $df = 1$ ,  $P > 0.05$ ; not shown).

Cavitation resistance was also associated with vessel anatomical and functional traits (Fig. 3). Vessel lumen diameter (Fig. 3D;  $F = 25.02$ ,  $df = 1$ ,  $P < 0.001$ ,  $r^2 = 0.64$ ), theoretical vessel implosion resistance (the ratio of the vessel wall thickness to lumen diameter [ $(t/b)_h^2$ ]; Fig. 3E;  $F = 19.21$ ,  $df = 1$ ,  $P = 0.023$ ,  $r^2 = 0.58$ ), and the percentage cross sectional vessel area (Fig. 3F;  $F = 10.13$ ,  $df = 1$ ,  $P = 0.007$ ,  $r^2 = 0.42$ ) were correlated with  $P_{50}$ . Vessel lumen diameter and percentage vessel area were also correlated with  $P_{50}$  when PICs were analyzed ( $F = 10.62$ ,  $df = 1$ ,  $P = 0.006$ ,  $r^2 = 0.45$  and  $F = 5.96$ ,  $df = 1$ ,  $P = 0.030$ ,  $r^2 = 0.31$ , respectively); however, PICs of  $(t/b)_h^2$  and  $P_{50}$  were not correlated ( $F = 0.87$ ,  $df = 1$ ,  $P > 0.05$ ). Xylem specific conductivity also was correlated with  $P_{50}$  when raw traits were analyzed ( $F = 6.19$ ,  $df = 1$ ,  $P = 0.020$ ,  $r^2 = 0.31$ ), but not when PICs were analyzed ( $F = 0.23$ ,  $df = 1$ ,  $P > 0.05$ ; not shown).

**Response to water stress**—Fynbos and succulent karoo species included in the current study appear to use different strate-

gies to cope with summer water stress. All but one of the fynbos species had minimum seasonal water potentials that were the same or higher (less negative) than their  $P_{50}$ , which suggests that in a year of normal precipitation these species will have dry season losses in hydraulic conductivity that are near or less than 50% (Fig. 4). In contrast, the succulent karoo species are not more resistant to cavitation than the fynbos species, yet these species had much more negative dry season water potentials (Fig. 4). In a typical year, these species are likely to reach higher percentage losses in hydraulic conductivity during the dry season, especially *Searsia undulata* and the *Euclea* species.

**Convergence among mediterranean-type climate regions**—Across mediterranean-type climate regions, communities significantly differed in the suites of xylem traits used by species ( $F = 10.552$ ,  $df = 4$ ,  $P < 0.001$  and  $F = 6.753$ ,  $df = 4$ ,  $P < 0.001$  for PC1 and PC2, respectively). Xylem traits were associated with two axes of variation ( $df = 9$ ,  $P < 0.001$ ). The first principal component (PC1) was associated with  $\Psi_{min}$ , xylem density, and  $K_s$  and explained 57% of the variation among species. Positive PC1 values are associated with higher  $\Psi_{min}$ , lower xylem density, and higher  $K_s$ . The second principal component (PC2) was associated with  $P_{50}$  and explained 20% of the variation among species. Positive PC2 values are associated with lower cavitation resistance. The relationships among these traits

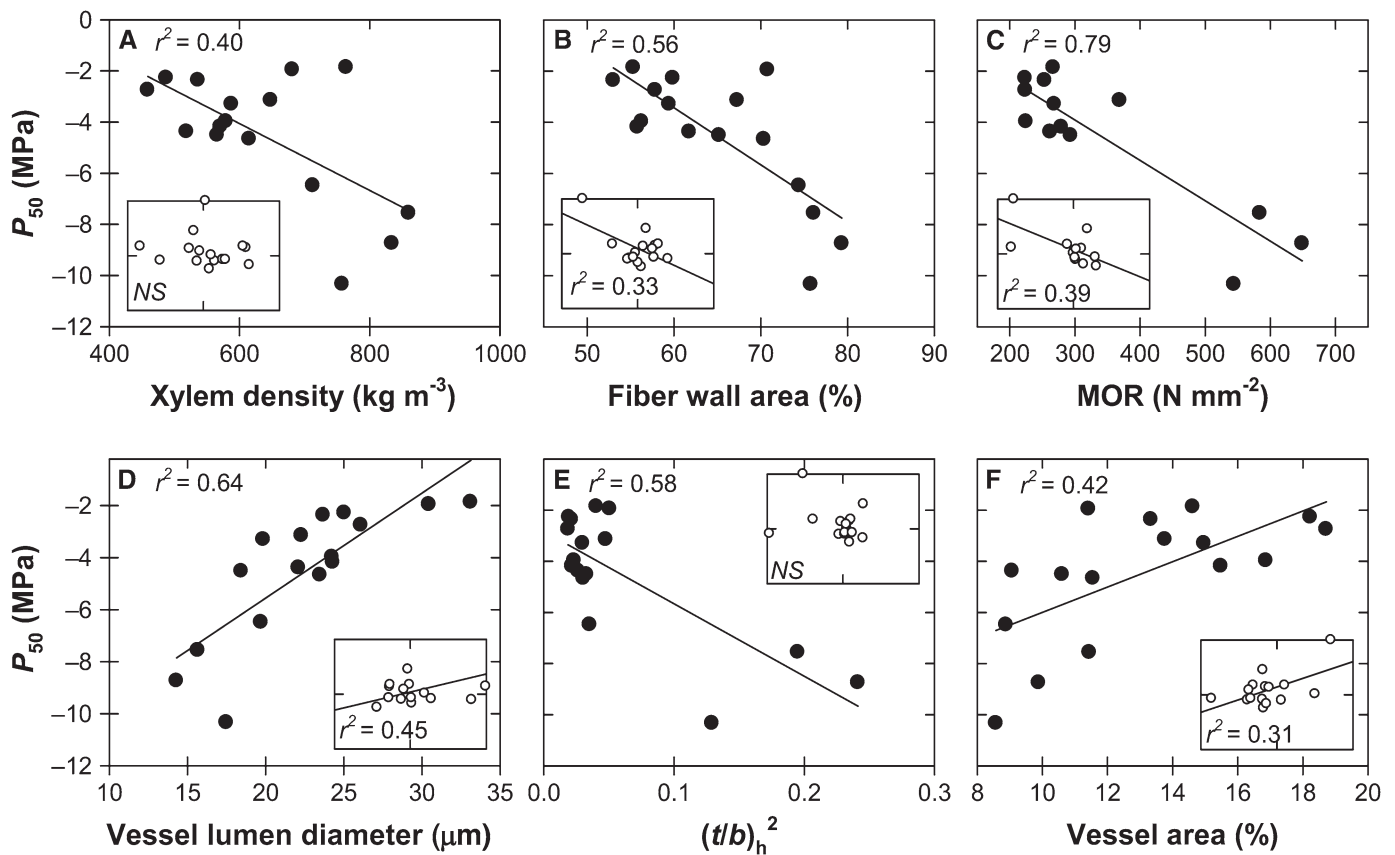


Fig. 3. Xylem fiber and vessel anatomical traits as predictors of cavitation resistance ( $P_{50}$ ) among 15 evergreen shrub species from South Africa. (A) Xylem-fiber-associated traits include xylem density, (B) percentage fiber wall area per xylem cross-sectional area, and (C) stem mechanical strength against breakage estimated by the modulus of rupture (MOR). Xylem-vessel-associated traits include (D) vessel lumen diameter, (E) theoretical vessel implosion resistance [ $(t/b)_h^2$ ], and (F) percentage vessel area per xylem cross-sectional area. Raw trait values are shown as solid circles and of phylogenetic independent contrasts in insets as open circles (see Materials and Methods). Only significant regression lines are shown.

are similar to those previously reported for Mediterranean shrub communities (Jacobsen et al., 2008).

Fynbos and chaparral shrub species use similar suites of xylem traits and did not differ in calculated values of either the first or second components of a principal components analysis (Fig. 5;  $P > 0.05$ ). Fynbos and chaparral species both tend to fall in the lower right corner of this figure (Fig. 5), consistent with a strategy of high cavitation resistance and comparatively low stress. The fynbos “strategy” significantly differed from the Mojave Desert species in both PC1 and PC2 ( $P > 0.05$  for both). Fynbos species did not differ from coastal sage in PC1 ( $P > 0.05$ ) but did differ in values of PC2 ( $P = 0.006$ ).

Succulent karoo shrub species had widely variable strategies, but were most closely associated with Mojave Desert species in PC1 (Fig. 5;  $P > 0.05$  between the Mojave Desert and succulent karoo) and with the chaparral and fynbos in PC2 ( $P > 0.05$  for PC2 between both the chaparral and fynbos compared to succulent karoo). These species undergo high water stress levels annually but are not very resistant to cavitation relative to these water stress levels. Succulent karoo species differed from coastal sage species in values of both PC1 and PC2 ( $P > 0.05$  for both).

## DISCUSSION

**Cavitation resistance of fynbos and succulent karoo species**—Cavitation resistance varied greatly among 15 species from the mediterranean-type climate region of South Africa. Species displayed cavitation resistances (estimated as the water potential at 50% loss in hydraulic conductivity;  $P_{50}$ ) ranging from  $-1.9$  to  $-10.3$  MPa and displayed as much variation within microsites as across the sampled ecotone. Species displayed a

mean cavitation resistance of  $-4.5$  which is not different from that reported for angiosperms from other Mediterranean-type climate regions (Martínez-Vilalta et al., 2002; Maherali et al., 2004; Jacobsen et al., 2007c).

The *Pteronia* species included in the current study have extremely low water potentials seasonally (less than  $-10$  MPa; Midgley and van der Heyden, 1999; Jacobsen et al., 2007a). These species are also very resistant to cavitation and have some of the lowest  $P_{50}$  reported for angiosperms (Davis et al., 1999; Maherali et al., 2004; Jacobsen et al., 2007c). The xylem of these species is very dense, and their vessels are relatively narrow in diameter and have very thick vessel walls. These traits may be related to the high cavitation resistance of these species.

Across all species, cavitation resistance was correlated with xylem anatomical and functional traits. Species with the greatest cavitation resistance have more fiber wall area per cross sectional xylem area and have greater stem mechanical strength against breakage. This is consistent with previous studies that have found strong and phylogenetically independent correlations between fiber traits and cavitation resistance and between stem mechanical properties and cavitation resistance in semi-arid shrubs (Jacobsen et al., 2005, 2007c). Species with greater cavitation resistance also tend to have increased xylem density than less resistant species, but these traits are not evolutionarily correlated. The lack of an evolutionary correlation among these traits may be due to the nature of the relationship between these traits and the wide range in xylem density that can be found among species that are not very resistant to cavitation; however, it is likely that species must have dense xylem to develop high levels of cavitation resistance. These correlations suggest that xylem fibers, which largely determine xylem density and mechanical strength in angiosperms, may play a role in cavita-

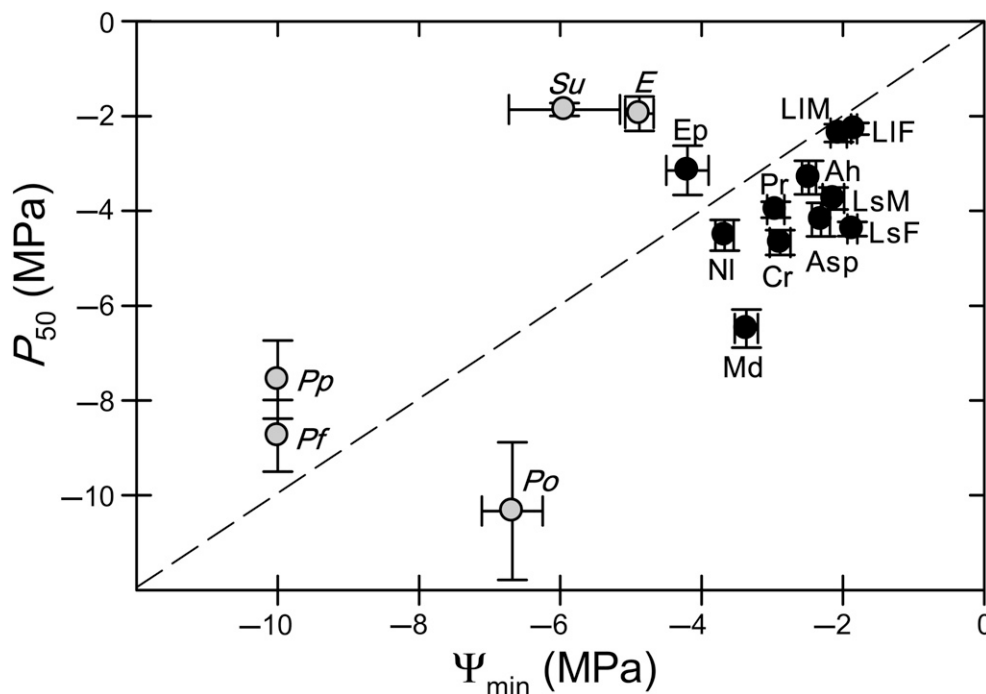


Fig. 4. Cavitation resistance ( $P_{50}$ ) plotted against minimum seasonal water potential ( $\Psi_{\min}$ ) for 15 species of evergreen shrubs from South Africa. Succulent karoo species are represented by gray circles and italic type and fynbos species are represented by black circles. Note, the  $\Psi_{\min}$  values for the two *Pteronia* species (Pf and Pp) shown are only approximate because they exceeded the limits of the pressure chamber ( $\Psi_{\min} \leq 10$  MPa). The dashed line represents a 1:1 line. For code to species abbreviations, see Table 1.

tion resistance, perhaps through mechanical reinforcement of xylem vessel walls (Jacobsen et al., 2005).

Species with the greatest resistance to cavitation have narrower vessel lumen diameters and less vessel area per cross section than species that are less resistant to cavitation. These combined traits likely result in more resistant species also displaying decreased xylem efficiency (i.e., lower  $K_s$ ), although the lack of an evolutionary correlation between  $K_s$  and  $\Psi_{50}$  suggests that there may be changes occurring at the pit-level that uncouple these traits. Changes in vessel diameter and cross-sectional area also modify the mechanical strength of vessels and xylem tissue and, as with the fiber traits above, are likely important in the mechanical resistance of vessels to the extreme negative pressures that develop in the xylem of arid and semi-arid shrubs. The presence of small vessels may also decrease the probability of a vessel containing large and less resistant pit pores (Hacke et al., 2006).

**Divergence in cavitation resistance among the sexes of a dioecious species**—Species of the genus *Leucadendron* are dioecious with some species displaying vegetative dimorphism between sexes. We examined two vegetatively dimorphic *Leucadendron* species, *L. lauroleum* and *L. salignum*, and found that females of the species *L. salignum* were more resistant to cavitation than males of the same species. To our knowledge,

this is the first time that a difference in cavitation resistance has been reported between the sexes of a dioecious species, although previous studies have examined the differences in water use and water use efficiency between males and females of dioecious species (Dawson and Bliss, 1989; Dawson and Ehleringer, 1993; Correia and Diaz Barradas, 2000; Hultine et al., 2007).

Within the genus *Leucadendron*, species differ in the degree to which they exhibit sexual dimorphism. Some species display large differences between sexes in leaf morphology and branching, while in other species the sexes are similar (Bond and Midgley, 1988; Bond and Maze, 1999; Rebelo, 2001). High dimorphism among sexes, as seen in *L. salignum*, may be linked to xylem functional dimorphism. Xylem functional and structural dimorphism among the sexes in *L. salignum* but not in *L. lauroleum* is supported by previous research that found males of *L. salignum* have greater xylem specific conductivity ( $K_s$ ), hydraulic vessel diameters ( $d_h$ ), and percentage vessel area and lower fiber wall area compared to females, while these traits did not differ between males and females of *L. lauroleum* (Jacobsen et al., 2007a).

*Leucadendron salignum* females and males co-occur in the same microsites and have similar water potentials (Jacobsen et al., 2007a). Differential cavitation resistance of the sexes in this species may have profound implications for population structure in this species if it is associated with differential drought-induced dieback or plant death among the sexes.

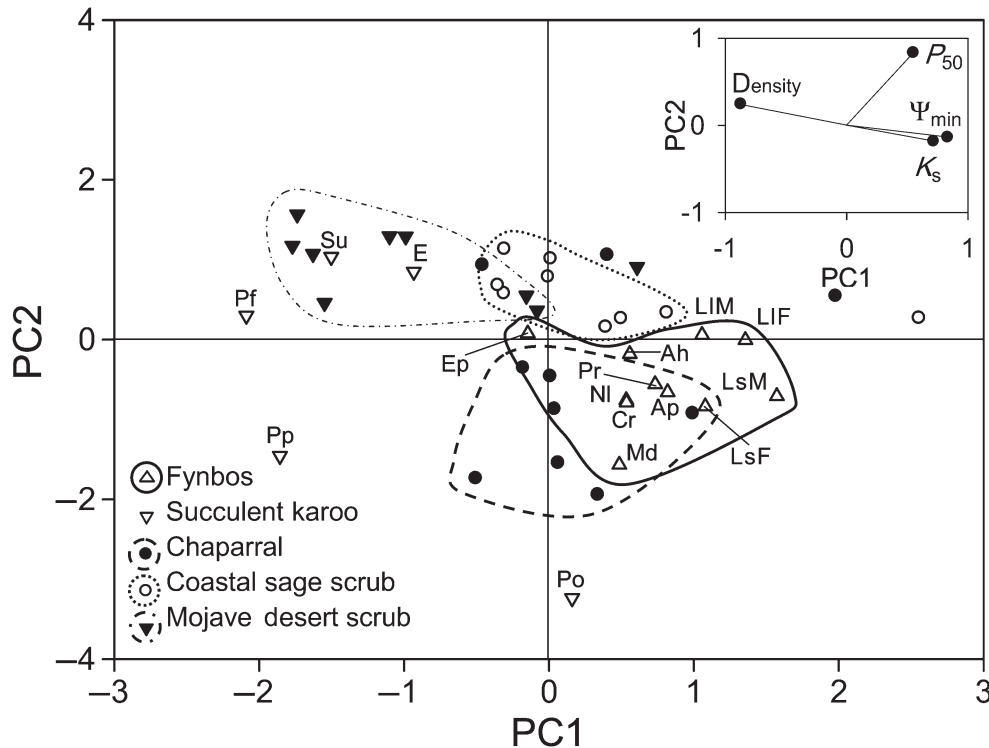


Fig. 5. Relationships among species from South Africa to those from climatically similar plant communities in California, USA, as determined by principal component analysis. The first principal component (PC1) was associated with minimum seasonal water potential ( $\Psi_{min}$ ), xylem density, and xylem specific conductivity ( $K_s$ ), and the second principal component (PC2) was associated with cavitation resistance ( $P_{50}$ ) (see inset for factor loadings). Positive PC1 values are associated with high seasonal  $\Psi_{min}$ , relatively high  $K_s$ , and low xylem density. Positive values of PC2 are associated with low cavitation resistance (high  $P_{50}$ ). Species from South Africa are shown as open triangles, with fynbos species as upward-pointing triangles and succulent karoo species as downward-pointing triangles. For the code to South African species abbreviations, see Table 1. Communities included from California are the chaparral (solid circles), the coastal sage scrub (open circles), and the Mojave Desert scrub (solid triangles). See Jacobsen et al. (2008) for identification of species within the California plant communities. Some California species are not included in circled California communities for clarity (see Jacobsen et al. [2008] for more discussion of these species), but these species were included in all analyses and in tests of community convergence.

**Convergence among South African and Californian plant communities**—The fynbos “strategy” in response to water stress appears similar to that of other mediterranean-type climate region sclerophyllous shrubland species including the California chaparral and mixed oak forests of the Mediterranean Basin. Shrubs in these regions typically reach water potentials equivalent to 50% loss in hydraulic conductivity or less during the dry season (Martínez-Vilalta et al., 2002; Jacobsen et al., 2007b, c). Thus, in typical years, these species employ a relatively safe strategy consistent with their maintenance of full canopies of leaves year round; however, this strategy may be risky during extremely dry years.

Evergreen shrubs in California and the Mediterranean Basin appear susceptible to drought-induced mortality during dry years (Lloret et al., 2004; Paddock, 2006). Drought-induced dieback has also been reported for some fynbos shrub species (Hannah et al., 2007). Additionally, individuals occurring at ecotones at the drier end of communities may be particularly susceptible as suggested by the high mortality observed among chaparral species at a chaparral-desert ecotone during a drought year in California (Paddock, 2006). Shrubs in these communities may rely on avoidance of large declines in hydraulic conductivity, and most may not be able to adjust other traits, such as canopy area, in response to declining water availability. Species that retain a nearly full canopy often have dieback, while co-occurring species that are able to facultatively thin their canopy appear to avoid extensive dieback (R. B. Pratt [California State University, Bakesfield] and S. D. Davis [Pepperdine University], unpublished data).

The succulent karoo woody shrub “strategy” appears most similar to that of desert shrubs that also undergo high levels of embolism seasonally (Pockman and Sperry, 2000; Jacobsen et al., 2008). In drier areas, woody plants may be unable to avoid high levels of water stress and concomitant losses in hydraulic conductivity and must therefore rely on traits other than increased cavitation resistance, such as tight stomatal control or adjustment of leaf area seasonally (Jacobsen et al., 2008). Indeed, the species associated with the succulent karoo appear to be utilizing more variable strategies in response to water stress than fynbos species. Succulent karoo shrub species may therefore be more able to deal with annual rainfall variability than fynbos species.

**Conclusion**—Morphologically and climatically similar plant communities from the mediterranean-type climate regions of South Africa and California appear to be convergent in the suites of xylem traits used by species in relation to water stress. Chaparral and fynbos communities, which are morphologically similar (i.e., they are woody, evergreen, sclerophyllous shrubs) appear to converge in their water use “strategy” as defined by their cavitation resistance, minimum seasonal water potential, xylem density, and hydraulic efficiency. The five shrub species from the succulent karoo included in the current study appear to be utilizing divergent strategies in regards to their xylem water use, although they share some overlap with sclerophyllous shrubs from the Mojave Desert consistent with these being drier and more variable regions.

The mediterranean-type climate regions of California and South Africa have been identified as being particularly threatened by the warming and drying predicted for these regions (IPCC, 2007). In southern Africa, both the fynbos and succulent karoo have been identified as the most vulnerable ecosystems to projected climate change (IPCC, 2007). On the basis of the current study, woody species within the fynbos may be

more susceptible than those within the succulent karoo. Dieback of fynbos shrubs has been observed following drought and chaparral shrub death has also occurred in California during drought. The ability to apply data measured in more thoroughly studied mediterranean-type climate regions and vegetation communities to those that have been less studied and to combine data across convergent communities could greatly enhance our ability to detect and minimize the impact of climate change on biodiversity in these regions. Observed plant death and dieback in these communities under current extreme droughts in mediterranean-type climate regions support predictions of substantial climate change effects on woody plant species in these areas. The more arid shrub communities of the succulent karoo and Mojave Desert may be less susceptible to climate warming and drying due to the more variable strategies among species in these communities in response to water stress and their ability to cope with an already more variable rainfall regime.

#### LITERATURE CITED

- AGENBAG, L., K. J. ESLER, G. F. MIDGLEY, AND C. BOUCHER. 2008. Diversity and species turnover on an altitudinal gradient in Western Cape, South Africa: baseline data for monitoring range shifts in response to climate change. *Bothalia* 38: 161–191.
- ALDER, N. N., W. T. POCKMAN, J. S. SPERRY, AND S. NUISMER. 1997. Use of centrifugal force in the study of xylem cavitation. *Journal of Experimental Botany* 48: 665–674.
- BARBOUR, M. G., AND R. A. MINNICH. 1990. The myth of chaparral convergence. *Israel Journal of Botany* 39: 453–463.
- BOND, W. J., AND K. E. MAZE. 1999. Survival costs and reproductive benefits of floral display in a sexually dimorphic dioecious shrub, *Leucadendron xanthoconus*. *Evolutionary Ecology* 13: 1–18.
- BOND, W. J., AND J. MIDGLEY. 1988. Allometry and sexual differences in leaf size. *American Naturalist* 131: 901–910.
- BROOKS, T. M., R. A. MITTERMEIER, G. A. B. DA FONSECA, J. GERLACH, M. HOFFMANN, J. F. LAMOREUX, C. G. MITTERMEIER, ET AL. 2006. Global biodiversity conservation priorities. *Science* 313: 58–61.
- CODY, M. L., AND H. A. MOONEY. 1978. Convergence versus non-convergence in mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics* 9: 265–321.
- CORREIA, O., AND M. C. DIAZ BARRADAS. 2000. Ecophysiological differences between male and female plants of *Pistacia lentiscus* L. *Plant Ecology* 149: 131–142.
- COWLING, R. M., F. OJEDA, B. B. LAMONT, P. W. RUNDEL, AND R. LECHMERE-OERTEL. 2005. Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone mediterranean-climate ecosystems. *Global Ecology and Biogeography* 14: 509–519.
- COWLING, R. M., P. W. RUNDEL, B. B. LAMONT, M. K. ARROYO, AND M. ARIANOUTSOU. 1996. Plant diversity in mediterranean-climate regions. *Trends in Ecology & Evolution* 11: 362–366.
- DAVIS, S. D., F. W. EWERS, J. WOOD, J. J. REEVES, AND K. J. KOLB. 1999. Differential susceptibility to xylem cavitation among three pairs of *Ceanothus* species in the Transverse Mountain Ranges of southern California. *Ecoscience* 6: 180–186.
- DAWSON, T. E., AND L. C. BLISS. 1989. Patterns of water use and the tissue water relations in the dioecious shrub, *Salix arctica*: The physiological basis for habitat partitioning between the sexes. *Oecologia* 79: 332–343.
- DAWSON, T. E., AND J. R. EHLERINGER. 1993. Gender-specific physiology, carbon isotope discrimination, and habitat distribution in boxelder, *Acer negundo*. *Ecology* 74: 798–815.
- ESLER, K. J., AND P. W. RUNDEL. 1999. Comparative patterns of phenology and growth form diversity in two winter rainfall deserts: The Succulent Karoo and Mojave Desert ecosystems. *Plant Ecology* 142: 97–104.



- EWERS, F. W., J. B. FISHER, AND S.-T. CHIU. 1990. A survey of vessel dimensions in stems of tropical lianas and other growth forms. *Oecologia* 84: 544–552.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125: 1–15.
- HACKE, U. G., J. S. SPERRY, AND J. PITTERMANN. 2000. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic and Applied Ecology* 1: 31–41.
- HACKE, U. G., J. S. SPERRY, W. T. POCKMAN, S. D. DAVIS, AND K. A. MCCULLOH. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126: 457–461.
- HACKE, U. G., J. S. SPERRY, J. K. WHEELER, AND L. CASTRO. 2006. Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiology* 26: 689–701.
- HANNAH, L., G. MIDGLEY, S. ANDELMAN, M. ARAÚJO, G. HUGHES, E. MARTINEZ-MEYER, R. PEARSON, AND P. WILLIAMS. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* 5: 131–138.
- HULTINE, K. R., S. E. BUSH, A. G. WEST, AND J. R. EHLERINGER. 2007. Population structure, physiology and ecohydrological impacts of dioecious riparian tree species of western North America. *Oecologia* 154: 85–93.
- IPCC [INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE]. 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. M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson [eds.]. Cambridge University Press, Cambridge, UK.
- JACOBSEN, A. L., L. AGENBAG, K. J. ESLER, R. B. PRATT, F. W. EWERS, AND S. D. DAVIS. 2007a. Xylem density, biomechanics, and anatomical traits correlate with water stress in seventeen evergreen shrub species of the Mediterranean-type climate region of South Africa. *Journal of Ecology* 95: 171–183.
- JACOBSEN, A. L., F. W. EWERS, R. B. PRATT, W. A. PADDOCK III, AND S. D. DAVIS. 2005. Do xylem fibers affect vessel cavitation resistance? *Plant Physiology* 139: 546–556.
- JACOBSEN, A. L., R. B. PRATT, S. D. DAVIS, AND F. W. EWERS. 2007b. Cavitation resistance and seasonal hydraulics differ among three arid Californian plant communities. *Plant, Cell & Environment* 30: 1599–1609.
- JACOBSEN, A. L., R. B. PRATT, S. D. DAVIS, AND F. W. EWERS. 2008. Comparative community physiology: non-convergence in water relations among three semi-arid shrub communities. *New Phytologist* 180: 100–113.
- JACOBSEN, A. L., R. B. PRATT, F. W. EWERS, AND S. D. DAVIS. 2007c. Cavitation resistance among twenty-six chaparral species of southern California. *Ecological Monographs* 77: 99–115.
- KEELEY, J. E., AND W. J. BOND. 1997. Convergent seed germination in South African fynbos and Californian chaparral. *Plant Ecology* 133: 153–167.
- LI, Y., J. S. SPERRY, H. TANEDA, S. E. BUSH, AND U. G. HACKE. 2008. Evaluation of centrifugal methods for measuring xylem cavitation in conifers, diffuse- and ring-porous angiosperms. *New Phytologist* 177: 558–568.
- LLoret, F., D. SISCART, AND C. DALMASES. 2004. Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). *Global Change Biology* 10: 2092–2099.
- LOVETT, J. C., G. F. MIDGLEY, AND P. BARNARD. 2005. Climate change and ecology in Africa. *African Journal of Ecology* 43: 167–169.
- MAHERALI, H., W. T. POCKMAN, AND R. B. JACKSON. 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* 85: 2184–2199.
- MARTÍNEZ-VILALTA, J., E. PRATT, I. OLIVERAS, AND J. PIÑOL. 2002. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia* 133: 19–20.
- MARTINS, E. P. 2004. COMPARE, version 4.6b. Computer programs for the statistical analysis of comparative data. Distributed by the author at website <http://compare.bio.indiana.edu/>. Department of Biology, Indiana University, Bloomington, Indiana, USA.
- MIDGLEY, G. F., G. O. HUGHES, W. THULLER, AND A. G. REBELO. 2006. Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. *Diversity & Distributions* 12: 555–562.
- MIDGLEY, G. F., AND F. VAN DER HEYDEN. 1999. Form and function in perennial plants. In W. R. J. Dean and S. J. Milton [eds.], *The Karoo: Ecological patterns and processes*, 91–106. Cambridge University Press, Cambridge, UK.
- MILLER, P. C., J. M. MILLER, AND P. M. MILLER. 1983. Seasonal progression of plant water relations in fynbos in the Western Cape Province, South Africa. *Oecologia* 56: 392–396.
- MOLL, E. J., AND J. E. M. SOMMERVILLE. 1985. Seasonal xylem pressure potentials of two South African coastal fynbos species in three soil types. *South African Journal of Botany* 51: 187–193.
- PADDOCK, W. A. III. 2006. Adult mortality of chaparral shrubs following severe drought. M.Sc. thesis, Michigan State University, East Lansing, Michigan, USA.
- POCKMAN, W. T., AND J. S. SPERRY. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany* 87: 1287–1299.
- REBELO, A. G., C. BOUCHER, N. HELME, L. MUCINA, AND M. C. RUTHERFORD. 2006. Fynbos biome. In L. Mucina, and M. Rutherford [eds.] *The vegetation of South Africa, Lesotho and Swaziland*. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria, South Africa.
- REBELO, T. 2001. *Proteas: A field guide to the proteas of southern Africa*. Fernwood Press, Vlaeberg, South Africa.
- RICHARDSON, D. M., AND F. J. KRUGER. 1990. Water relations and photosynthetic characteristics of selected trees and shrubs of riparian and hillslope habitats in the south-western Cape Province, South Africa. *South African Journal of Botany* 56: 214–225.
- SHULZE, R. E., AND L. A. PERKS. 2000. Assessment of the impact of climate change on hydrology and water resources in South Africa. Report to South African Country Studies for Climate Change Programme. ACRUcons Report 33. School of Bioresources Engineering and Environmental Hydrology, University of Natal, Pietermaritzburg, South Africa.
- SMITH, R. E., AND D. M. RICHARDSON. 1990. Comparative post-fire water relations of selected seeding and resprouting plants in the Jonkershoek Valley, Cape Province, South Africa. *South African Journal of Botany* 56: 683–694.
- SPERRY, J. S., J. R. DONNELLY, AND M. T. TYREE. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell & Environment* 11: 35–40.
- SWIFT, C. C., S. M. JACOBS, AND K. J. ESLER. 2008. Drought induced xylem embolism in four riparian trees from the Western Cape Province: Insights and implications for plant and evaluation of restoration. *South African Journal of Botany* 74: 508–516.
- VAN DER HEYDEN, F., AND O. A. M. LEWIS. 1989. Seasonal variation in photosynthetic capacity with respect to plant water status of five species of the mediterranean climate region of South Africa. *South African Journal of Botany* 55: 509–515.
- WHEELER, J. K., J. S. SPERRY, U. G. HACKE, AND N. HOANG. 2005. Inter-vessel pitting and cavitation in woody Rosaceae and other vesselless plants: A basis for a safety versus efficiency trade-off in xylem transport. *Plant, Cell & Environment* 28: 800–812.