

GEOGRAPHIC AND SEASONAL VARIATION IN CHAPARRAL VULNERABILITY TO CAVITATION

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ABSTRACT

Resistance of stem xylem to water stress-induced cavitation and embolism among chaparral shrub species in California has been extensively studied, providing the opportunity to examine broad patterns in cavitation resistance. We used previously published as well as unpublished vulnerability to cavitation curve data from 16 chaparral shrub species of southern California to examine the variability of cavitation resistance across sites, regions, and seasons. Additionally, these data provided a unique opportunity to address a recent methodological debate within the field of plant hydraulics. We found that different methods, specifically a centrifuge method and a dehydration method, produced similar results ($P = 0.184$). Vulnerability to cavitation varied seasonally, with species exhibiting greater susceptibility to water-stress induced cavitation during the wet season ($P = 0.003$). Cavitation resistance did not differ among sites that were less than 10 km apart even though these sites differed in their coastal exposure, precipitation, and temperatures ($P = 0.476$). However, across larger geographic distances and with increased climatic divergence, cavitation resistance significantly varied ($P = 0.005$), with populations from a higher rainfall mountain range exhibiting greater susceptibility to cavitation. These data suggest that species may be particularly susceptible to the onset of early summer drought before xylem has hardened. Variation in cavitation resistance may be limited locally, but broadly dispersed species may diverge in cavitation resistance across their range. Maintaining populations that vary in cavitation resistance may be an important component of species conservation planning in an era of increased climatic variability.

Key Words: Cavitation resistance, chaparral, drought, embolism, water potential, water relations, water stress, xylem.

Cavitation and subsequent embolism of xylem conduits can occur when plants experience water stress (Davis et al. 2002; Tyree and Zimmermann 2002) and results in reduced hydraulic transport efficiency. This may be particularly harmful during periods of extreme or protracted drought when catastrophic hydraulic failure may lead to plant dieback and death (McDowell et al. 2008). Cavitation-induced hydraulic failure has been linked to plant dieback and mortality during both long- and short-term droughts (Rice et al. 2004; Anderegg et al. 2013; Paddock et al. 2013; Pratt et al. 2014) and when plants were experimentally exposed to water stress (Pratt et al. 2008).

Xylem cavitation resistance is an important plant functional trait that varies among ecosystems (Maherali et al. 2004; Choat et al. 2012) and, at smaller scales, among plant communities (Jacobsen et al. 2007b; Hacke et al. 2009). For species with broad distributions, selection at drier

sites and during dry years may lead to intraspecific variation among populations in some species (Mencuccini and Comstock 1997; Kavanagh et al. 1999; Kolb and Sperry 1999b; Pratt et al. 2012), although previous studies have also found that some climatically divergent populations do not vary greatly in cavitation resistance (Mencuccini and Comstock 1997; Matzner et al. 2001; Stout and Sala 2003; Lamy et al. 2011). Species may also be phenotypically plastic in their xylem vulnerability to cavitation, although this has been relatively little studied (Holste et al. 2006; Beikircher and Mayr 2009; Mayr et al. 2010; Fichot et al. 2010; Awad et al. 2010; Plavcova and Hacke 2012).

Co-occurring species of chaparral shrubs in southern California exhibit highly divergent levels of cavitation resistance (Davis et al. 1999; Jacobsen et al. 2007a; Pratt et al. 2007b) and include some of the most cavitation resistant angiosperms ever measured (Maherali et al.

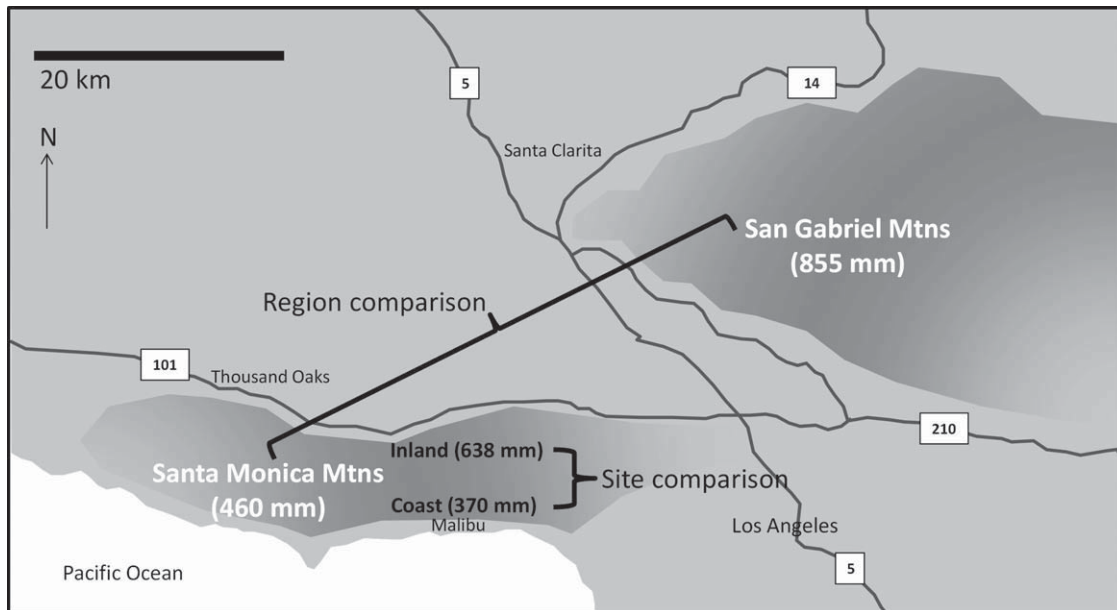


FIG. 1. Vulnerability to cavitation curves were analyzed from species occurring in southern California that had been measured at multiple locations. Data were divided into two regions, either the Santa Monica Mountains or the San Gabriel Mountains. Within the Santa Monica Mountains, vulnerability curves were further divided into subpopulations sampled at sites located near the coast and those sampled from inland sites. Selected highways and cities from the study area are indicated on the map and the mean annual precipitation for the sites and regions (as reported in the previously published studies included in Table 1) are shown.

2004). However, large scale mortality of chaparral shrubs has been reported during extreme drought years, particularly at a desert-chaparral ecotone (Paddock et al. 2013).

Chaparral shrubs exhibit multiple life history types, largely defined by their post-fire response. This includes species that resprout from underground storage structures following fire, species that recruit post-fire through the germination of fire-cued seeds, and species that employ both of these strategies. These differential life history types are related to large functional differences between some chaparral shrub species at both the adult (Jacobsen et al. 2007a; Pratt et al. 2007a, b) and seedling (Pratt et al. 2008, 2010, 2012) stages. Furthermore, drought-induced mortality of seedlings may be common, particularly among post-fire seeding species whose seedlings must survive the protracted summer dry period that occurs in the Mediterranean-type climate region of southern California (Frazer and Davis 1988; Thomas and Davis 1989). Selection for higher cavitation resistance may therefore be expected at drier and more interior sites, where mortality has been observed, compared to species occurring in more mesic or coastal sites that experience less water stress. These patterns may become more pronounced across broader, regional scales.

The cavitation resistance of chaparral shrubs has been extensively studied, particularly in southern California (Jarbeau et al. 1995; Redfeldt

and Davis 1996; Davis et al. 1999a, 2002; Jacobsen et al. 2005, 2007a, b; Pratt et al. 2007b), which enabled us to evaluate the impact of differences between sites and regions on vulnerability to cavitation within repeatedly measured species of this plant community. Using previously published and some previously unpublished data we examined if cavitation resistance of chaparral shrubs 1) varied locally among shrub subpopulations at sites that were located in close proximity but differed in their ocean exposure (coast vs. inland) and 2) varied regionally between shrub populations from two mountain ranges occurring in southern California (Santa Monica Mts. vs. San Gabriel Mts.) (Fig. 1). We predicted that populations from coastally exposed sites would be less cavitation resistant than inland sites, due to the stronger maritime climatic influence along the coast (Vasey et al. 2012). We predicted that populations from the Santa Monica Mountains would be more cavitation resistant than the San Gabriel Mountains due to higher mean annual precipitation occurring in the San Gabriel Mountains, consistent with previous studies examining the impact of precipitation or watering treatments on cavitation resistance (Mencuccini and Comstock 1997; Kolb and Sperry 1999b; Helms 2009; Awad et al. 2010).

This analysis was complicated by the recent suggestion that some methods used to construct

vulnerability to cavitation curves may not produce reliable data (Choat et al. 2010; Cochard et al. 2010). In particular, it has been suggested that centrifuge-based data may produce a measurement artifact, especially in species with long vessels. The dataset compiled for the present study provided an ideal test of this suggestion, because both dehydration and standard centrifuge curves have been used to construct vulnerability curves on the same chaparral species at the same sites and during the same season. Additionally, many chaparral shrub species have long maximum vessels, including several species with maximum vessel lengths greater than one meter in length (Jacobsen et al. 2012). We also evaluated the impact of the season (wet vs. dry) during which curves were constructed, because this has previously been reported to impact vulnerability to cavitation (Kolb and Sperry 1999a; Jacobsen et al. 2007b).

METHODS

Previously published vulnerability curves conducted on chaparral shrub species from the Santa Monica Mountains and the San Gabriel Mountains of southern California were compiled (Jarbeau et al. 1995; Redfeldt and Davis 1996; Davis et al. 1999a; Davis et al. 2002; Jacobsen et al. 2005, 2007a, b, Pratt et al. 2007b). Previously unpublished vulnerability curves measured by the authors from 2004–2012 were also included in analyses (Table 1). This included data for 16 species for which curves were reported that had been measured on the same species across multiple sites (coastal vs. inland within the Santa Monica Mts.), regions (Santa Monica Mts. vs. San Gabriel Mts.), and/or seasons (wet vs. dry) and using two different methods (dehydration vs. centrifuge) (Fig. 1). Wet season vulnerability curves were defined as those that were measured between December and May for any sample year across all of the studies listed above, when plants were hydrated in the field (Jacobsen et al. 2008). Rainfall typically occurs during November to April at these sites and regions, with plant water status declining in July following the use of soil moisture reserves (Jacobsen et al. 2008). Dry season vulnerability curves were defined as those that were measured during July to October when plants are dehydrated in the field and were no longer growing (Jacobsen et al. 2007b).

Dehydration vulnerability curves were constructed using the methods described in Jacobsen et al. (2007a). Briefly, large branches, longer than the longest vessels as determined via air injection, were collected in the field. Branches were allowed to dehydrate for varying periods of time in the laboratory before being tightly bagged overnight to allow them to equilibrate. Water potentials of branches were measured the next morning and

then branches were cut underwater, alternately at each end, to excise a 0.10–0.14 m central stem segment for measurement. This sampling protocol reduces the negative pressure in the xylem prior to the extraction of the measured sample, which may be important in order to avoid artifact when sampling some species (Wheeler et al. 2013). Hydraulic conductivity (K_h) of stem segments was measured both immediately following excision of the stem segment and following a one hour flush at 100 kPa using a degassed and ultra-filtered solution (Jacobsen et al. 2007a). The percentage loss in hydraulic conductivity (PLC) was determined for each stem segment (Sperry et al. 1988).

Centrifuge vulnerability curves were constructed using the methods described in Pratt et al. (2007a). Stem segments 0.14 m or 0.27 m in length were excised, underwater, from larger branches that had been harvested in the field. Segments were then flushed as described above before being subjected to increasing negative water potentials by being spun in a custom centrifuge rotor (Alder et al. 1997; Tobin et al. 2013). Hydraulic conductivity was measured following each spin and these were used to calculate the PLC at each imposed water potential relative to the initial flushed value.

Vulnerability curves, whether generated using dehydration or centrifuge based data, were plotted as the PLC with declining water potential. All data from previous studies were replotted and reanalyzed for the current study. Water potential and PLC data from each curve and study were fit using a Weibull curve (Microsoft Excel 2010, Microsoft, Redmond, WA). This curve was then used to calculate the water potential at 50% loss in hydraulic conductivity (P_{50}) for each curve. The P_{50} value was used as an estimate of species cavitation resistance, as this is the most commonly compared and reported value in species comparisons (Choat et al. 2012). Additionally, the alpha (shape parameter), which determines if a curve is concave or convex, and the beta (scale parameter), which determines the “stretch” of the curve along the x-axis, for the Weibull fit were recorded. These fit parameters were compared later, if we found that there was a significant shift in the P_{50} between our comparison groups, to determine if the change in cavitation resistance was due to a shift in the shape or scale of the vulnerability to cavitation curve.

Differences in the P_{50} of species as impacted by site, region, season, or method were analyzed using paired t-tests with data paired by species (Release 16.1.0, Minitab, State College, PA). For these comparisons, data were matched by the parameters that were not being evaluated in the current comparison and a single pair of mean P_{50} was generated for each species (e.g., the site comparisons were conducted on species data

TABLE 1. NUMBER OF VULNERABILITY TO CAVITATION CURVES REPORTED FOR CHAPARRAL SHRUB SPECIES OCCURRING IN SOUTHERN CALIFORNIA. Reported vulnerability curves have been included only for species that have been measured across multiple sites, regions, seasons, and/or using different methods. Species codes used in the present study (Fig. 1) are included and are consistent with those reported previously for these species (Jacobsen et al. 2007b). The mean pressure (± 1 SE) at 50% loss in hydraulic conductivity as determined across studies and pooled across site, region, season, and method and the sources for the included vulnerability curves are included. Data were compiled from multiple sources for each species. ¹Nomenclature follows Baldwin et al. (2012). ²Formerly *Rhamnus californica* Eschsch. ³Formerly *Rhus laurina* Nutt.

Species ¹	Studies (n)												P ₅₀ (MPa)	Sources			
	Region (Mtn Range)						Method										
	Santa Monica			Inland			San Gabriel			Season					Dehydration		
	Coast	Inland	San Gabriel	Wet	Dry	Centrifuge	Dehydration										
<i>Adenostoma fasciculatum</i> Hook. & Arn. (Rosaceae)	Af	0	4	1	1	4	4	1	4	4	1	1	1	-5.57 \pm 1.05	Redfield and Davis 1996; Jacobsen et al. 2005, 2007b, unpublished data		
<i>Adenostoma sparsifolium</i> Torr. (Rosaceae)	As	0	4	0	1	3	2	2	3	2	2	2	2	-4.61 \pm 0.54	Redfield and Davis 1996; Jacobsen et al. 2005, 2007a, b		
<i>Arctostaphylos glandulosa</i> Eastw. (Ericaceae)	Ag	0	2	1	1	2	2	2	1	2	2	1	1	-2.86 \pm 0.57	Jacobsen et al. 2007a, b, unpublished data		
<i>Ceanothus crassifolius</i> Torr. (Rhamnaceae)	Ccr	0	2	2	2	1	3	3	1	3	3	1	1	-6.31 \pm 1.86	Davis et al. 1999, 2002; Pratt et al. 2007b		
<i>Ceanothus cuneatus</i> Nutt. (Rhamnaceae)	Ccu	0	4	0	1	3	3	3	1	3	3	1	1	-7.66 \pm 0.64	Davis et al. 1999; Jacobsen et al. 2007b; Pratt et al. 2007b		
<i>Ceanothus leucodermis</i> Greene (Rhamnaceae)	Cl	0	1	2	0	3	2	2	1	3	2	1	1	-2.80 \pm 1.05	Davis et al. 1999; Pratt et al. 2007, unpublished data		
<i>Ceanothus megacarpus</i> Nutt. (Rhamnaceae)	Cm	2	2	0	1	3	3	3	1	3	3	1	1	-8.32 \pm 1.15	Kolb and Davis 1994; Jacobsen et al. 2005, 2007b; Pratt et al. 2007b		
<i>Ceanothus oliganthus</i> Nutt. (Rhamnaceae)	Co	0	4	0	1	3	3	3	1	3	3	1	1	-3.74 \pm 1.00	Davis et al. 1999; Jacobsen et al. 2007b; Pratt et al. 2007b		
<i>Ceanothus spinosus</i> Nutt. (Rhamnaceae)	Cs	2	2	0	1	3	3	3	1	3	3	1	1	-4.46 \pm 0.85	Davis et al. 1999; Jacobsen et al. 2005, 2007b; Pratt et al. 2007b		
<i>Frangula californica</i> (Eschsch.) A. Gray ² (Rhamnaceae)	Fc	0	2	0	0	2	1	1	1	2	1	1	1	-1.68	Jacobsen et al. 2007a; Pratt et al. 2007b		
<i>Heteromeles arbutifolia</i> (Lindl.) M. Roem. (Rosaceae)	Ha	2	0	1	0	3	2	2	1	3	2	1	1	-4.39 \pm 2.06	Jarbeau et al. 1995; Jacobsen et al. 2007a; unpublished data		
<i>Malosma laurina</i> (Nutt.) Abrams ³ (Anacardiaceae)	MI	3	3	0	3	3	5	5	1	3	5	1	1	-0.77 \pm 0.31	Jarbeau et al. 1995; Jacobsen et al. 2005, 2007b, unpublished data		
<i>Quercus agrifolia</i> Née (Fagaceae)	Qa	1	2	0	2	1	2	2	1	1	2	1	1	-1.29 \pm 0.24	Jacobsen et al. 2007a, unpublished data		
<i>Quercus berberidifolia</i> Liebm. (Fagaceae)	Qb	1	4	1	4	2	5	5	1	4	5	1	1	-0.70 \pm 0.37	Jacobsen et al. 2007a, b, unpublished data		
<i>Rhamnus ilicifolia</i> Kellogg (Rhamnaceae)	Ri	2	1	1	0	4	2	2	1	0	2	2	2	-4.68 \pm 0.88	Jacobsen et al. 2007a; Pratt et al. 2007b, unpublished data		
<i>Rhus ovata</i> S. Watson (Anacardiaceae)	Ro	1	3	1	2	3	4	4	1	2	3	1	1	-0.70 \pm 0.20	Jacobsen et al. 2005, 2007a, b, unpublished data		

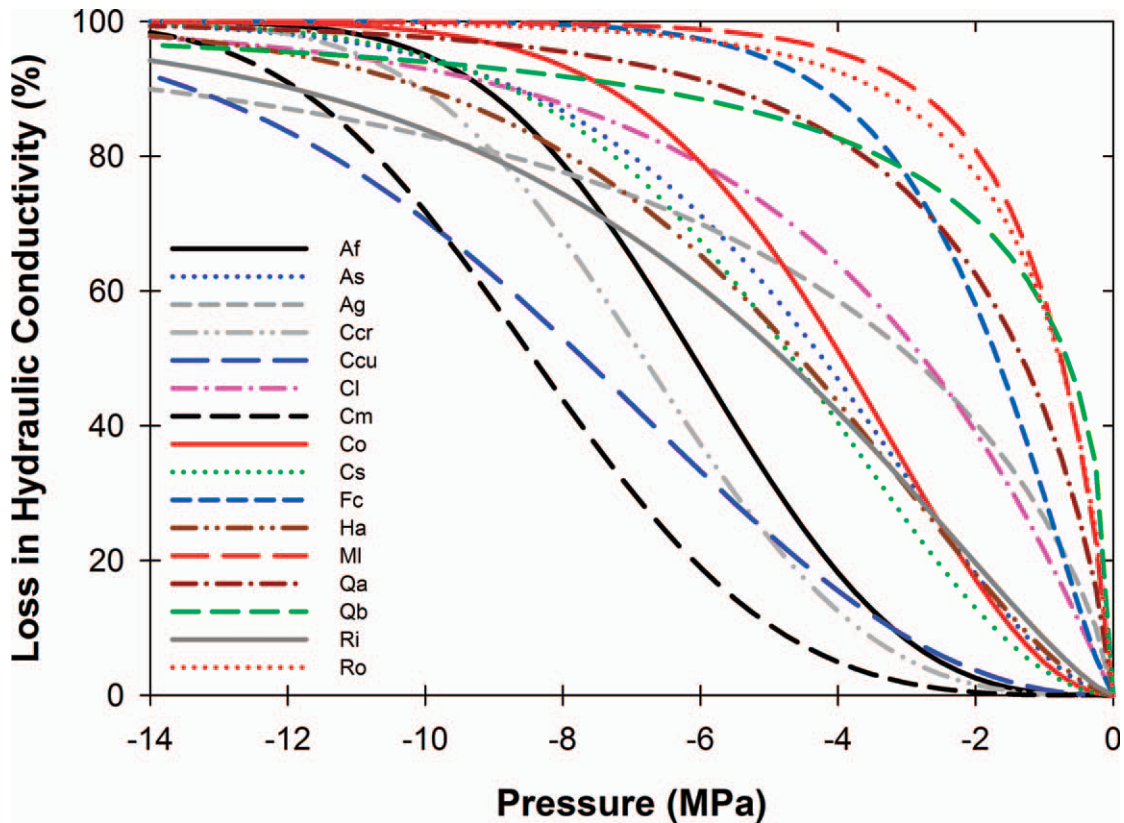


FIG. 2. Vulnerability to cavitation curves for 16 chaparral species, showing the increase in the percentage loss in hydraulic conductivity with decreasing pressure. Curves represent pooled data from all reported vulnerability curves for these species from the Santa Monica Mountains and San Gabriel Mountains of southern California. The shown curve is a Weibull curve fit to pooled data for each species. See Table 1 for species abbreviations.

matched for season and method, the season comparison was conducted on data matched for site and method, and the method comparison was conducted on data matched for site and season). It was not possible to use a more complicated model to analyze these data due to a lack of replication for many species and comparisons (Table 1). In most cases, this lack of replication was most commonly due to limited species range, for instance some species occur only along the coast or only within the Santa Monica Mountains.

To further examine the influence of site, region, season, and method on cavitation resistance, we plotted species pairs of P_{50} as they were calculated above. These data were analyzed using SMA regression (R Statistical Software, SMATR package, Warton et al. 2006). We compared whether the slopes of these regressions were different than one and whether the intercept was different from zero as an additional way to examine if site, season, region, or method influenced chaparral shrub cavitation resistance.

RESULTS

Sixteen chaparral shrub species varied greatly in their resistance to cavitation (Fig. 2). When pooled across studies, species cavitation resistance (as estimated by the water potential at 50% loss in hydraulic conductivity; P_{50}) ranged from -0.7 MPa to -8.32 MPa (Table 1), with values as high as -0.04 MPa and as low as -10.48 MPa for mean species values from individual studies.

The use of different methods (i.e., centrifuge-based curves vs. dehydration-based curves) did not result in a significant difference in P_{50} (Fig. 3A, B; $P = 0.184$, $T = -1.44$, $n = 10$ matched species pairs).

The season in which species were sampled significantly impacted P_{50} (Fig. 3C, D; $P = 0.003$, $T = -3.70$, $n = 12$ matched species pairs). This difference was due primarily to a shift in the scale of the vulnerability curve (beta parameter; $P = 0.002$, $T = 3.93$) rather than a change in the shape of the curve (alpha parameter; $P = 0.053$, $T = 2.17$). Vulnerability curves measured during

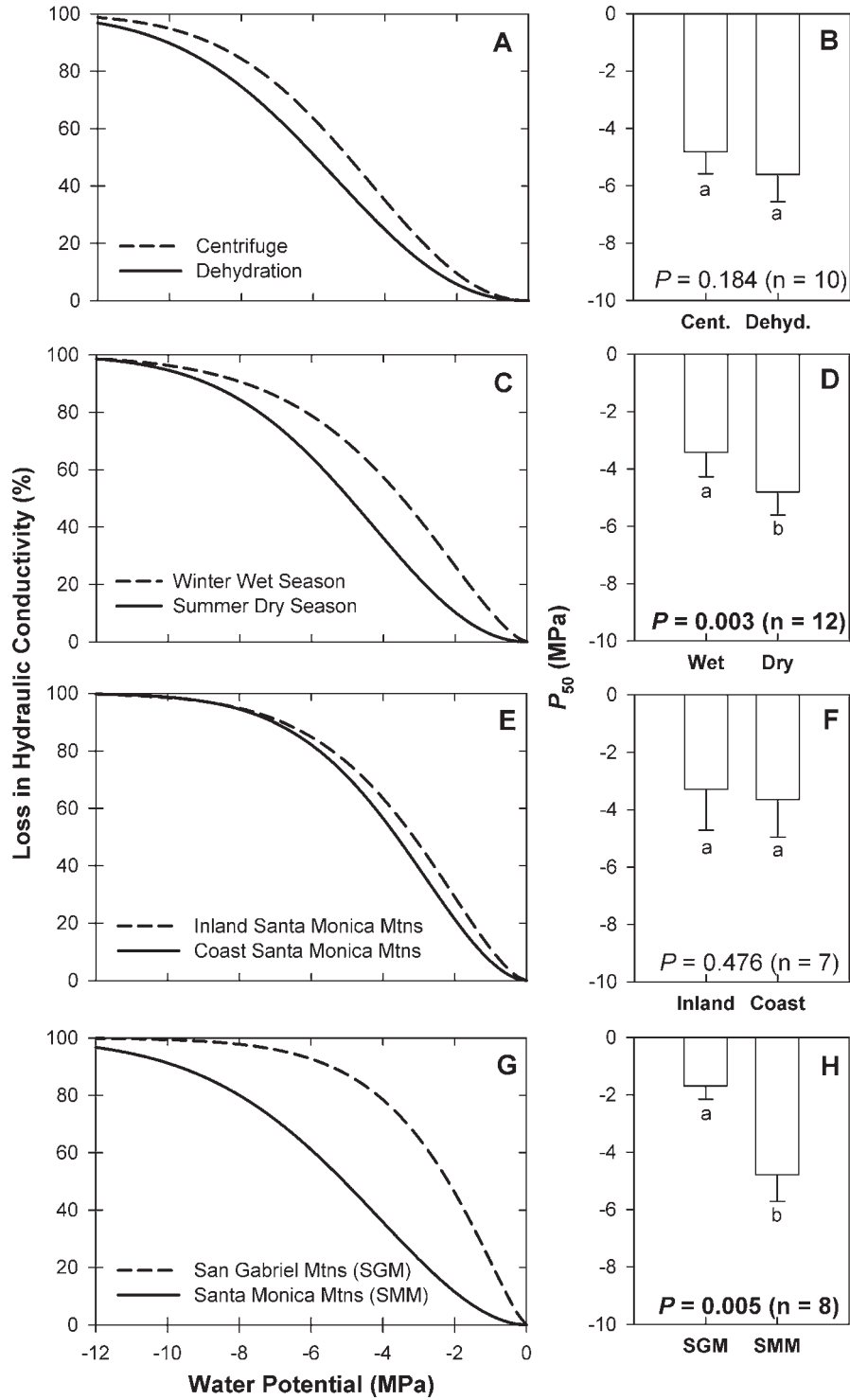


FIG. 3. Vulnerability to cavitation curves pooled across species of chaparral shrub species as they vary with the method used to construct curves (A, B), the season of measurement (C, D), the site from which species were sampled (E, F), or the region that was sampled (G, H). Vulnerability to cavitation curves are shown in panels A, C, E, and G and the mean ± 1 SE pressure at 50% loss in hydraulic conductivity (P_{50}) is shown in panels B, D, F, and H. The n indicates the number of species for which vulnerability curves were sampled using different methods or in different seasons, sites, or regions and different lowercase letters indicate significant differences.

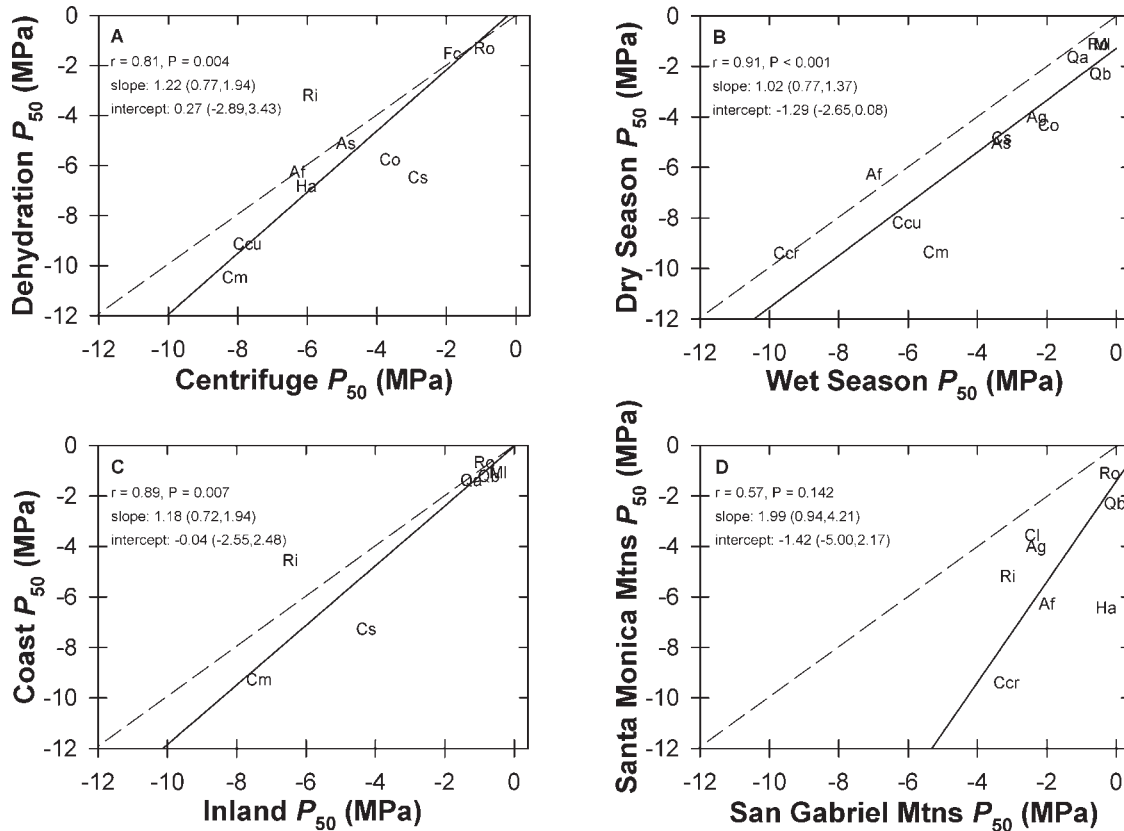


FIG. 4. Vulnerability to cavitation estimated as the pressure at 50% loss in hydraulic conductivity (P_{50}) for chaparral shrub species as it varied by vulnerability curve method (A), measurement season (B), site (C), and region (D). For each regression, species data were matched for all of the parameters not included in a given comparison (e.g., species data for vulnerability curve methods were matched for season, site, and region) and a species mean was calculated from the matched data. Data were fit using SMA regression and the slope and intercept for regressions are shown in each panel along with the 95% confidence intervals for these parameters in parentheses. The dashed line in each panel is the 1:1 line. Species abbreviations are listed in Table 1.

the wet season had P_{50} that were approximately 1.4 MPa more vulnerable to cavitation than P_{50} measured from the same subpopulation during the dry season (Fig. 3D).

Within a single mountain range, the Santa Monica Mountains of southern California, P_{50} did not vary among subpopulations of species occurring along the coast versus those occurring inland (Fig. 3E, F; $P = 0.476$, $T = -0.76$, $n = 7$ matched species pairs).

Across larger geographic distances, the P_{50} of populations occurring in the Santa Monica Mountains differed significantly from those occurring in the San Gabriel Mountains (Fig. 3G, H; $P = 0.005$, $T = -4.04$, $n = 8$ matched species pairs). This difference was due to a change in the shape of the vulnerability curve (alpha parameter; $P = 0.004$, $T = 4.16$), rather than a shift in the scale of the vulnerability curve (beta parameter; $P = 0.553$, $T = 0.62$). Vulnerability curves measured on populations occurring in the San Gabriel Mountains were approximat-

ly 3.1 MPa more vulnerable to cavitation compared to populations of the same species occurring in the Santa Monica Mountains (Fig. 3H).

Across all comparisons (method, season, site, and region), the slopes of regressions were not different from one in any case ($P > 0.05$ for all; see slope and intercepts with 95% confidence intervals in Fig. 4). Similarly, the intercepts of regressions were not different from zero in any case (Fig. 4; $P > 0.05$ for all).

DISCUSSION

Methodological Considerations

We found that both centrifuge and dehydration based vulnerability curves produced similar estimates of cavitation resistance. This is consistent with several recent studies that have shown that these methods produce similar results (Jacobsen and Pratt 2012; Sperry et al. 2012;

Tobin et al. 2013). Some prior reports of disagreement between methods may be due to the use of a different centrifuge technique (Cochard et al. 2010) or the confounding of technique comparisons with the pooling of data generated from both flushed and non-flushed curves (Cochard and Delzon 2013). Dehydration curves are most often based on percentage loss in conductivity (PLC) obtained by taking initial, or native, measurement of conductivity (K_s) followed by the flushing of samples to measure the maximum potential conductivity (K_{smax}) (however, see Jacobsen and Pratt 2012). These curves would not be expected to be comparable to centrifuge curves generated using non-flushed stems, because non-flushed curves begin at the K_s native rather than the K_{smax} (see Sperry et al. 2012). This results in non-flushed centrifuge curves exhibiting a flat initial portion of their curve, until the point that the centrifuged pressure exceeds the native pressure of the samples, which often results in a sigmoidal in shape. Non-flushed centrifuge curves may drastically differ in shape compared to flushed curves (Sperry et al. 2012). Thus, the agreement of methods in the present study may be at least partially due to the careful matching of samples and the inclusion of only flushed-sample centrifuge curves.

Another issue of repeated concern with centrifuge-based curves has been the influence of open vessels (i.e., vessels that are longer than the measured sample length and therefore do not contain a terminal vessel element within the sample) (Choat et al. 2010; Cochard et al. 2010). This issue has been experimentally examined using both alteration of the number of open vessels (Jacobsen and Pratt 2012) and short and long vessel comparisons (Sperry et al. 2012; Tobin et al. 2013) and open vessels have not been found to impact vulnerability curves when the standard Alder et al. (1997) centrifuge technique is used. Additionally, this issue has been tied to the shape of vulnerability curves, with particular concern raised about “r” shaped (or exponential shaped) vulnerability curves (Cochard and Delzon 2013), although careful study of r-shaped curve species, including single vessel air injection measures, have confirmed the validity of r-shaped curves (Sperry et al. 2012; Christman et al. 2012; Tobin et al. 2013).

Chaparral species exhibit a wide range in the shape and scale of their vulnerability curves and are also very divergent in the length of xylem vessels found among species, providing the opportunity for us to evaluate both the impact of long vessels on curves as well as the validity of vulnerability curves of differing shapes. Centrifuge and dehydration based vulnerability curves were not different across species. This included species with maximum vessel lengths as long as

1.4 m (Ro), 1.1 m (Fc), and 1.2 m (Ri) (Jacobsen et al. 2012; See Table 1 for species codes), which would clearly have vessels open through the measured samples. There was also methodological agreement between species with shorter maximum vessel lengths, including 0.3 m (Af), 0.5 m (Cm), and 0.3 m (Cs) (Jacobsen et al. 2012; See Table 1 for species codes). Additionally, when matched for region and season, we found good agreement between dehydration and centrifuge curves, including for species with r-shaped curves. Consistent with the findings of previous studies (Sperry et al. 2012; Christman et al. 2012; Tobin et al. 2013), this suggests that these curves describe a genuine species strategy. This finding highlights the diversity of hydraulic strategies employed by plants, including many chaparral shrub species.

Seasonal Effects

Cavitation resistance differed depending on the season during which measurements were conducted. Across species there was a general shift toward increased resistance from the wet season to the dry season. This is consistent with a general “hardening” of the xylem as plants reduced growth, produced latewood, and transitioned into the dry season during which they experience lower water potentials. This same pattern has been described previously in arid and semi-arid plant communities (Kolb and Sperry 1999a; Jacobsen et al. 2007b; Helms 2009). Changes in xylem function seasonally have also been described for other hydraulic traits and in other plant communities, including large seasonal changes in hydraulic conductivity (Sperry et al. 1987; Tibbetts and Ewers 2000; Jacobsen et al. 2007b; Choat et al. 2010). This suggests that plant hydraulics may be quite variable intra-annually and that measurements of plant hydraulics conducted at a single sampling time may not present a complete picture of the hydraulic strategy of a species. Additionally, measurement of PLC or conductivity across seasons may not be comparable to measurements, such as vulnerability curves, that are measured at a single time point. Finally, increased resistance later in the season suggests that plants may be particularly sensitive to early season drought and this may be an important area of research in predicting plant responses to more variable climate patterns.

Geographic Variability

Across shorter distances and between subpopulations within a single mountain range (i.e., sites), we did not find that cavitation resistance varied even though both the mean annual precipitation and temperature differed among coastal and inland sites. This is consistent with

recent research on a single chaparral lineage, *Arctostaphylos* Adans., that found that cavitation resistance did not differ between foggy coastal sites and non-foggy inland sites along the central coast of California (Jacobsen and Pratt 2013), even though the water potentials of plants at these sites differed (Vasey et al. 2012). It may be that across relatively short distances (<10 km), enough genetic material is exchanged to prevent subpopulations from diverging in response to local climatic conditions. This may also partially explain the high mortality observed among some species during drought where they occur at the drier end of their range (Paddock et al. 2013).

Across larger distances and among disjunct populations occurring within two mountain ranges, cavitation resistance significantly differed. Populations occurring in the San Gabriel Mountains, which receive considerably more mean annual precipitation (855 mm) than the Santa Monica Mountains (460 mm), were more vulnerable to cavitation. This was consistent with our prediction and with a previous study that compared two chaparral shrub species between these two regions (Helms 2009). This is also consistent with previous studies that have described populations from more mesic areas as being more vulnerable to cavitation in some species (Mencuccini and Comstock 1997; Kavanagh et al. 1999; Kolb and Sperry 1999b) as well as findings from shrub species occurring in other Mediterranean-type climate regions (Pratt et al. 2012). Additionally, the San Gabriel Mountains sites experience winter freezing and freeze-thaw events that may impact the hydraulics of plants from the San Gabriel Mountains (Davis et al. 1999b; Cordero and Nilsen 2002), although it is not clear the impact this may have on the present comparison because freezing also occurs in some sites within the Santa Monica Mountains (Pratt et al. 2005). Finally, soil properties have also been shown to impact vulnerability to cavitation (Sperry and Hacke 2002) and it should be noted that soil composition was different between these regions, with the Santa Monica Mountains composed predominantly of sedimentary derived soils and the San Gabriel Mountains composed predominantly of plutonic derived soils (Schoenherr 1992).

Hydraulic Trait Diversity

It is not clear whether these differences represent phenotypic plasticity in xylem function or if they represent genetic differences, and it would require establishment of a common garden with plants from both regions to determine. However, these data suggest that there is intraspecific variability in cavitation resistance among these chaparral shrub species. California climate is expected to warm significantly under

most climate change scenarios and patterns of precipitation are expected to change, although California topography makes fine-scale predictions difficult (Cayan et al. 2008). Thus, preservation of hydraulic trait diversity among chaparral species and populations may be key to long-term resilience of chaparral shrub species and communities.

CONCLUSIONS

Chaparral species vary in their cavitation resistance seasonally and among populations that occurred in regions with varying mean annual precipitation, suggesting that the timing of water stress and the traits of different populations are both important factors likely to influence the long-term resilience of chaparral communities. Additionally, chaparral species are highly variable in their vulnerability to cavitation, including the presence of some highly vulnerable species that exhibit r-shaped (or exponential shaped) vulnerability curves as well as more resistant species. More research is needed to more fully understand these very different, yet co-occurring, hydraulic strategies.

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LITERATURE CITED

- 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.
- ANDEREGG, W. R. L., L. PLAVCOVÁ, L. D. L. ANDEREGG, U. G. HACKE, J. A. BERRY, AND C. B. FIELD. 2013. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased risk. *Global Change Biology* 19:1188–1196.
- AWAD, H., T. BARIGAH, E. BADEL, H. COCHARD, AND S. HERBETTE. 2010. Poplar vulnerability to xylem cavitation acclimates to drier soil conditions. *Physiologia Plantarum* 139:280–288.
- BALDWIN, B. G., D. H. GOLDMAN, D. J. KEIL, R. PATTERSON, T. J. ROSATTI, AND D. H. WILKEN, (eds.). 2012. *The Jepson Manual: vascular plants of California*, 2nd ed. University of California Press, Berkeley, CA.
- BEIKIRCHER, B. AND S. MAYR. 2009. Intraspecific differences in drought tolerance and acclimation in hydraulics of *Ligustrum vulgare* and *Viburnum lantana*. *Tree Physiology* 29:765–775.
- CAYAN, D. R., E. P. MAURER, M. D. DETTINGER, M. TYREE, AND K. HAYHOE. 2008. Climate change scenarios for the California Region. *Climate Change* 87:S21–S42.
- CHOAT, B., W. M. DRAYTON, C. BRODERSEN, M. A. MATTHEWS, K. A. SHACKEL, H. WADA, AND A. J. MCELDRONE. 2010. Measurement of vulnerability to water stress-induced cavitation in grapevine: a

- comparison of four techniques applied to long-vesselled species. *Plant, Cell & Environment* 33:1502–1512.
- , S. JANSEN, T. J. BRODRIBB, H. COCHARD, S. DELZON, R. BHASKAR, S. J. BUCCI, T. S. FIELD, S. M. GLEASON, U. G. HACKE, A. L. JACOBSEN, F. LENS, H. MAHERALI, J. MARTÍNEZ-VILALTA, S. MAYR, M. MENCUCINI, P. J. MITCHELL, A. NARDINI, J. PITTERMANN, R. B. PRATT, J. S. SPERRY, M. WESTOBY, I. J. WRIGHT, AND A. E. ZANNE. 2012. Global convergence in the vulnerability of forest to drought. *Nature* 491:752–756.
- CHRISTMAN, M. A., J. S. SPERRY, AND D. D. SMITH. 2012. Rare pits, large vessels and extreme vulnerability to cavitation in a ring-porous species. *New Phytologist* 193:713–720.
- COCHARD, H. AND S. DELZON. 2013. Hydraulic failure and repair are not routine in trees. *Annals of Forest Science* 70:659–661.
- , S. HERBETTE, T. BARIGAH, E. BADEL, M. ENNAJEH, AND A. VILAGROSA. 2010. Does sample length influence the shape of xylem embolism vulnerability curves? A test with the Cavitron spinning technique. *Plant, Cell & Environment* 33:1543–1552.
- CORDERO, A. R. AND E. T. NILSEN. 2002. Effects of summer drought and winter freezing on stem hydraulic conductivity of *Rhododendron* species from contrasting climates. *Tree Physiology* 22: 919–928.
- DAVIS, S. D., F. W. EWERS, J. S. SPERRY, K. A. PORTWOOD, M. C. CROCKER, AND G. C. ADAMS. 2002. Shoot dieback during prolonged drought in *Ceanothus* chaparral of California: a possible case of hydraulic failure. *American Journal of Botany* 89:820–838.
- , J. WOOD, J. J. REEVES, AND K. J. KOLB. 1999a. Differential susceptibility to xylem cavitation among three pairs of *Ceanothus* species in the Transverse Mountain Ranges of southern California. *Écoscience* 6:180–186.
- , J. S. SPERRY, AND U. G. HACKE. 1999b. The relationship between xylem conduit diameter and cavitation caused by freezing. *American Journal of Botany* 86:1367–1372.
- FICHOT, R., T. S. BARIGAH, S. CHAMAILLARD, D. LE THIEC, F. LAURANS, H. COCHARD, AND F. BRIGNOLAS. 2010. Common trade-offs between xylem resistance to cavitation and other physiological traits do not hold among unrelated *Populus deltoides* × *Populus nigra* hybrids. *Plant, Cell & Environment* 33:1553–1568.
- FRAZER, J. M. AND S. D. DAVIS. 1988. Differential survival of chaparral seedlings during the first summer drought after wildfire. *Oecologia* 76:215–221.
- HACKE, U. G., A. L. JACOBSEN, AND R. B. PRATT. 2009. Xylem function of arid-land shrubs from California, USA: an ecological and evolutionary analysis. *Plant, Cell & Environment* 32:1324–1333.
- HELMS, A. M. 2009. The effect of severe drought on xylem water transport in two chaparral species in the San Gabriel and Santa Monica Mountains. Honors thesis, Pepperdine University, Malibu, CA.
- HOLSTE, E. K., M. J. JERKE, AND S. L. MATZNER. 2006. Long-term acclimatization of hydraulic properties, xylem conduit size, wall strength and cavitation resistance in *Phaseolus vulgaris* in response to difference environmental effects. *Plant, Cell & Environment* 29:836–843.
- JACOBSEN, A. L. 2008. Comparative community physiology: nonconvergence in water relations among three semi-arid shrub communities. *New Phytologist* 180:100–113.
- . 2013. Vulnerability to cavitation of central California *Arctostaphylos* (Ericaceae): a new analysis. *Oecologia* 171:329–334.
- , 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.
- AND R. B. PRATT. 2012. No evidence for an open vessel effect in centrifuge-based vulnerability curves of a long-vesselled liana (*Vitis vinifera*). *New Phytologist* 194:982–990.
- , 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.
- , F. W. EWERS, AND S. D. DAVIS. 2007a. Cavitation resistance among 26 chaparral species of southern California. *Ecological Monographs* 77:99–115.
- , M. F. TOBIN, U. G. HACKE, AND F. W. EWERS. 2012. A global analysis of xylem vessel length in woody plants. *American Journal of Botany* 99:1583–1591.
- JARBEAU, J. A., F. W. EWERS, AND S. D. DAVIS. 1995. The mechanism of water-stress-induced embolism in two species of chaparral shrubs. *Plant, Cell & Environment* 18:189–196.
- KAVANAGH, K. L., B. J. BONDS, S. N. AITKEN, B. L. GARTNER, AND S. KNOWE. 1999. Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. *Tree Physiology* 19:31–37.
- KOLB, K. J. AND J. S. SPERRY. 1999a. Transport constraints on water use by the Great Basin shrub, *Artemisia tridentata*. *Plant, Cell & Environment* 22:925–935.
- . 1999b. Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). *Ecology* 80:2373–2384.
- LAMY, J.-B., L. BOUFFIER, R. BURLETT, C. PLOMION, H. COCHARD, AND S. DELZON. 2011. Uniform selection as a primary force reducing population genetic differentiation of cavitation resistance across a species range. *PLoS ONE* 6:e23476, doi:10.1371/journal.pone.0023476
- 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.
- MATZNER, S. L., K. J. RICE, AND J. H. RICHARDS. 2001. Intra-specific variation in xylem cavitation in interior live oak (*Quercus wislizenii* A. DC.). *Journal of Experimental Botany* 52:783–789.
- MAYR, S., B. BEIKIRCHER, M. A. OBKIRCHER, AND P. SCHMID. 2010. Hydraulic plasticity and limitations of alpine *Rhododendron* species. *Oecologia* 164: 321–330.
- MCDOWELL, N., W. T. POCKMAN, C. D. ALLEN, D. D. BRESHEARS, N. COBB, T. KOLB, J. PLAUT, J. SPERRY, A. WEST, D. G. WILLIAMS, AND E. A. YEPEZ. 2008. Mechanisms of plant survival and

- mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178:719–739.
- MENCUCINI, M. AND J. COMSTOCK. 1997. Vulnerability to cavitation in populations of two desert species, *Hymenoclea salsola* and *Ambrosia dumosa*, from different climatic regions. *Journal of Experimental Botany* 48:1323–1334.
- PADDOCK, W. A. S., III, S. D. DAVIS, R. B. PRATT, A. L. JACOBSEN, M. F. TOBIN, J. LÓPEZ-PORTILLO, AND F. W. EWERS. 2013. Factors determining mortality of adult chaparral shrubs in an extreme drought year in California. *Aliso* 31:49–57.
- PLAVCOVÁ, L. AND U. G. HACKE. 2012. Phenotypic and developmental plasticity of xylem in hybrid poplar saplings subjected to experimental drought, nitrogen fertilization, and shading. *Journal of Experimental Botany* 63:6481–6491.
- PRATT, R. B., F. W. EWERS, M. C. LAWSON, A. L. JACOBSEN, M. BREDIGER, AND S. D. DAVIS. 2005. Mechanisms for tolerating freeze-thaw stress of two evergreen chaparral species: *Rhus ovata* and *Malosma laurina* (Anacardiaceae). *American Journal of Botany* 92:1102–1113.
- , A. L. JACOBSEN, F. W. EWERS, AND S. D. DAVIS. 2007a. Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of California chaparral. *New Phytologist* 174:787–798.
- , ———, K. A. GOLGOTIU, J. S. SPERRY, F. W. EWERS, AND S. D. DAVIS. 2007b. Life history type and water stress tolerance in nine California chaparral species (Rhamnaceae). *Ecological Monographs* 77:239–253.
- , ———, S. M. JACOBS, AND K. J. ESLER. 2012. Xylem transport safety and efficiency differ among fynbos shrub life history types and between two sites differing in mean rainfall. *International Journal of Plant Sciences* 173:474–483.
- , ———, R. MOHLA, F. W. EWERS, AND S. D. DAVIS. 2008. Linkage between water stress tolerance and life history type in seedlings of nine chaparral species (Rhamnaceae). *Journal of Ecology* 96:1252–1265.
- , ———, A. R. RAMIREZ, A. M. HELMS, C. A. TRAUGH, M. F. TOBIN, M. S. HEFFNER, AND S. D. DAVIS. 2014. Mortality of resprouting chaparral shrubs after a fire and during a record drought: physiological mechanisms and demographic consequences. *Global Change Biology* 20:893–907.
- , G. B. NORTH, A. L. JACOBSEN, F. W. EWERS, AND S. D. DAVIS. 2010. Xylem root and shoot hydraulics is linked to life history type in chaparral seedlings. *Functional Ecology* 24:70–81.
- REDTFELDT, R. A. AND S. D. DAVIS. 1996. Physiological and morphological evidence of niche segregation between two co-occurring species of *Adenostoma* in California chaparral. *Écoscience* 3:290–300.
- RICE, K. J., S. L. MATZNER, AND W. BYER. 2004. Patterns of tree dieback in Queensland, Australia: the importance of drought stress and the role of resistance to cavitation. *Oecologia* 139:190–198.
- SCHOENHERR, A. A. 1992. A natural history of California. University of California Press, Berkeley, CA.
- SPERRY, J. S., M. A. CHRISTMAN, J. M. TORREZ-RUIZ, H. TANEDA, AND D. D. SMITH. 2012. Vulnerability curves by centrifugation: is there an open vessel artifact, and are “r” shaped curves necessarily invalid? *Plant, Cell & Environment* 35:601–610.
- , J. R. DONNELLY, AND M. T. TYREE. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell & Environment* 11:35–40.
- AND U. G. HACKE. 2002. Desert shrub water relations with respect to soil characteristics and plant functional type. *Functional Ecology* 16:367–378.
- , N. M. HOLBROOK, M. H. ZIMMERMANN, AND M. T. TYREE. 1987. Spring filling of xylem vessels in wild grapevine. *Plant Physiology* 83:414–417.
- STOUT, D. L. AND A. SALA. 2002. Xylem vulnerability to cavitation in *Pseudotsuga menziesii* and *Pinus ponderosa* from contrasting habitats. *Tree Physiology* 23:43–50.
- THOMAS, C. M. AND S. D. DAVIS. 1989. Recovery patterns of three chaparral shrub species after wildfire. *Oecologia* 80:309–320.
- TIBBETTS, T. J. AND F. W. EWERS. 2000. Root pressure and specific conductivity in temperate lianas: exotic *Celastrus orbiculatus* (Celastraceae) vs. native *Vitis riparia* (Vitaceae). *American Journal of Botany* 87:1272–1278.
- TOBIN, M. F., R. B. PRATT, A. L. JACOBSEN, AND M. E. DE GUZMAN. 2013. Xylem vulnerability to cavitation can be accurately characterized in a species with long vessels using a centrifuge method. *Plant Biology* 15:496–504.
- TYREE, M. T. AND M. H. ZIMMERMANN. 2002. Xylem structure and the ascent of sap. 2nd ed. Springer-Verlag, Berlin, Germany.
- VASEY, M. C., M. E. LOIK, AND V. T. PARKER. 2012. Influence of summer marine fog and low cloud stratus on water relations of evergreen woody shrubs (*Arctostaphylos*: Ericaceae) in the chaparral of central California. *Oecologia* 170:325–337.
- WARTON, D. I., I. J. WRIGHT, D. S. FALSTER, AND M. WESTOBY. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews* 81:259–291.
- WHEELER, J. K., B. A. HUGGETT, A. N. TOFTE, F. E. ROCKWELL, AND N. M. HOLBROOK. 2013. Cutting xylem under tension or supersaturated with gas can generate PLC and the appearance of rapid recovery from embolism. *Plant, Cell & Environment* 36:1938–1949.