Ecological Monographs, 77(1), 2007, pp. 99–115
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CAVITATION RESISTANCE AMONG 26 CHAPARRAL SPECIES OF SOUTHERN CALIFORNIA

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Abstract. Resistance to xylem cavitation depends on the size of xylem pit membrane pores and the strength of vessels to resist collapse or, in the case of freezing-induced cavitation, conduit diameter. Altering these traits may impact plant biomechanics or water transport efficiency. The evergreen sclerophyllous shrub species, collectively referred to as chaparral, which dominate much of the mediterranean-type climate region of southern California, have been shown to display high cavitation resistance (pressure potential at 50% loss of hydraulic conductivity; P_{50}). We examined xylem functional and structural traits associated with more negative P_{50} in stems of 26 chaparral species. We correlated raw-trait values, without phylogenetic consideration, to examine current relationships between P_{50} and these xylem traits. Additionally, correlations were examined using phylogenetic independent contrasts (PICs) to determine whether evolutionary changes in these xylem traits correlate with changes in P_{50}. Co-occurring chaparral species widely differ in their P_{50} (−0.9 to −11.0 MPa). Species experiencing the most negative seasonal pressure potential (P_{min}) had the highest resistance to xylem cavitation (lowest P_{50}). Decreased P_{50} was associated with increased xylem density, stem mechanical strength (modulus of rupture), and transverse fiber wall area when both raw values and PICs were analyzed. These results support a functional and evolutionary relationship among these xylem traits and cavitation resistance. Chaparral species that do not sprout following fire but instead recruit post-fire from seed had the greatest resistance to cavitation, presumably because they rely on post-fire survival of seedlings during the summer dry period to persist in the landscape. Raw values of hydraulic vessel diameter (d_h), maximum vessel length, and xylem-specific hydraulic conductivity (K_s) were correlated to P_{50}; however, d_h, maximum vessel length, and K_s were not correlated to P_{50} when analyzed using PICs, suggesting that these traits have not undergone correlated evolutionary change. We found no difference in xylem traits between species occurring at freezing vs. nonfreezing sites, although freezing has been shown to affect the survival and distributions of some chaparral species. Stem mechanical strength, fiber properties, and post-fire regeneration type appear to be key factors in the evolution of cavitation resistance among chaparral shrubs.

Key words: *biomechanics; California; cavitation; chaparral; embolism; water relations; xylem.*

Introduction

In a vascular plant, stem xylem must be able to withstand xylem cavitation and the mechanical stresses associated with negative pressure during water stress. This is especially true for evergreen species of chaparral shrubs in the mediterranean-type climate region of southern California that experience a predictable 6–8 month annual rainless period (di Castri 1973, Cowling et al. 2005). It is crucial that these species maintain functional xylem in order to sustain water transport to evergreen leaves throughout the dry summer months, when limited water availability results in the occurrence of extreme negative pressures in the stem xylem (Schlesinger et al. 1982, Williams et al. 1997, Davis et al. 2002, Ackerly 2004). Sustained function of xylem throughout the year may be particularly important among evergreen chaparral shrubs because there is no evidence of embolism repair among adults (Kolb and Davis 1994, Williams et al. 1997). Not all species are able to withstand the negative xylem pressures that develop and water-stress-induced cavitation and embolism have been implicated in branchlet dieback and whole-plant death in some chaparral species (Williams et al. 1997, Davis et al. 2002), as well as other woody plant species (Rood et al. 2000, Lloret et al. 2004). Embolism may also reduce hydraulic transport, which can result in declines in stomatal conductance (Pratt et al. 2005) and lowered photosynthetic capacity (Brodribb and Feild 2000). Thus, cavitation and embolism of stem xylem have the potential to affect plant growth, reproduction, and survival.

At the cellular level, xylem structure is thought to determine cavitation resistance. According to the air-

Manuscript received 29 November 2005; revised 21 June 2006; accepted 23 June 2006. Corresponding Editor: L. A. Donovan.
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seeding hypothesis, cavitation occurs when gas is pulled into a water-filled xylem conduit from an adjacent gas-filled cell or intercellular space. This occurs when negative pressures within the water-filled conduit exceed the cohesive bonds between water molecules at the gas–water interface of the largest pore in a xylem pit membrane (Zimmermann 1983, Sperry and Tyree 1988, Jarbeau et al. 1995). Risk of cavitation may therefore be linked to the pitted area of xylem conduits. A larger and longer conduit may have a greater likelihood of containing a more vulnerable pit pore somewhere along its length (Hargrave et al. 1994, Tyree et al. 1994, Sperry et al. 2005). Hydraulically efficient xylem with longer and wider conduits may thus be more suseptible to cavitation. Cavitation may also occur when negative pressures overcome the ability of xylem conduit walls to resist collapse (Carlquist 1975, Hacke et al. 2001, Donaldson 2002, Cochard et al. 2004, Brodribb and Holbrook 2005). The risk of cavitation due to cell wall collapse may explain correlations between wood density, xylem mechanical strength, and vessel and fiber anatomical properties with cavitation resistance (Wagner et al. 1998, Hacke et al. 2001, Sperry 2003, Baas et al. 2004, Jacobsen et al. 2005). These correlations suggest that species of chaparral shrubs that experience greater seasonal water stress may have to invest in denser, mechanically stronger stem tissue in order to resist water-stress-induced cavitation. This increased cost may negatively impact the competitive ability of some species, perhaps through reduced growth rate (Enquist et al. 1999, King et al. 2005).

Freezing also can cause xylem embolism formation, although by a mechanism independent from that of water-stress-induced cavitation. When xylem sap freezes, the gas dissolved in the sap comes out of solution. This process can lead to cavitation upon thawing if the bubbles do not go back into solution but instead expand through a process directly linked to vessel diameter (Ewers 1985, Yang and Tyree 1992, Langan et al. 1997, Davis et al. 1999*a*, Pittermann and Sperry 2003). For chaparral species occurring at freezing sites, increased resistance to freezing-induced cavitation may come at the cost of decreased vessel diameter, decreased vessel length (Ewers 1985), and a concurrent decrease in conductive efficiency.

While anatomical differences affect cavitation resistance, differential life history and the ecology of a species may also be linked to cavitation resistance. Chaparral species are often categorized into three post-fire regeneration types: (1) nonsprouting species, (2) facultative-sprouting species, and (3) obligate-sprouting species (Table 1). Nonsprouting (NS) chaparral species are also referred to as obligate-seeding species because adults are killed by fire and these species rely on post-fire recruitment from seed to persist in the landscape. Adults of obligate-sprouting (OS) species often survive fire, resprouting from underground lignotubers. Facultative-sprouting (FS) species resprout and also recruit from seed following fire. These differences in post-fire regeneration type have been linked to differences in rooting depth and microclimate. Nonsprouting species, particularly NS *Ceanothus* spp., have younger root systems (only as old as the most recent fire) and tend to be shallow rooted, whereas FS and OS species tend to have older and deeper roots (Hellmers et al. 1955, Kummerow et al. 1977, Burk 1978, Miller and Poole 1979, Thomas and Davis 1989). Additionally, NS species appear to occupy drier microsites, preferentially recruiting in open-canopy, post-fire gaps and thriving on drier south-facing slopes (Hanes and Jones 1967, Schlesinger et al. 1982, Frazer and Davis 1988, Thomas and Davis 1989, Odion and Davis 2000).

While increasing cavitation resistance among evergreen species has been found to correlate with decreased annual precipitation across broad scales (Maherali et al. 2004), cavitation resistance can vary widely among chaparral species growing at the same site (Kolb and Davis 1994, Redtfeldt and Davis 1996, Davis et al. 1998, 1999*b*, Jacobsen et al. 2005). In this study, we examined which xylem traits were correlated with increased resistance to cavitation among all the evergreen chaparral shrub species that occur in the Santa Monica Mountains of southern California. We examined relationships using both raw-trait values of species and the trait values after correcting for the evolutionary relationships among species using phylogenetic independent contrasts.

We predicted that species that are more vulnerable to cavitation would maintain higher seasonal pressure potentials than species that are more resistant to cavitation. Species differing in cavitation resistance would display differential xylem traits such that, with increasing cavitation resistance: (1) vessel diameter, vessel length, and conductive efficiency would decrease; and (2) xylem density, mechanical strength, and percentage of transverse fiber wall area would increase. We predicted that with increasing cavitation resistance, the theoretical resistance of vessels to collapse, based on the ratio of cell wall thickness to lumen diameter, also would increase (Hacke et al. 2001). For species occurring at freezing sites, vessel diameter and xylem conductive efficiency would decrease relative to species at nonfreezing sites.

We predicted that, among the three post-fire regeneration types of chaparral species, NS species, which have shallower roots and occupy drier microsites, would experience greater seasonal water stress and would be more resistant to cavitation. The different sprouting types would also exhibit differences among xylem traits related to cavitation resistance, such as xylem density, xylem mechanical strength, and xylem anatomical characteristics.

Phylogenetic independent contrasts (PICs) were used to test which xylem structural and functional traits have undergone correlated evolutionary change with cavitation resistance. Phylogenetic independent contrasts are calculated differences in trait values for each speciation event (or node) represented in a phylogeny. A correlation

TABLE 1. Species included in this study and the site, mean cavitation resistance, and, for each species, mode of recovery following fire.

Taxon†	Symbol‡	Site no.§	P_{50} (MPa)||	Postfire regeneration type¶	Citations#
Anacardiaceae					
Malosma laurina (Nutt.) Abrams††	a	1	−1.6	FS	E, K, P
Rhus integrifolia (Nutt.) Brewer and S. Watson	b	1	−1.8	OS	E, L, P
R. ovata S. Watson	c	2	−1.4	FS	A, B, E, P
R. trilobata Torrey and A. Gray	d	3	−3.0	FS	E, F, J
Ericaceae					
Arctostaphylos glandulosa Eastw.	e	2	−4.4	FS	B, E, G, I, M, N, O
A. glauca Lindley	f	2	−4.7	NS	B, D, E, G, M, N
Comarostaphylis diversifolia (C. Parry) E. Greene	g	4	−5.6	OS	J
Fagaceae					
Quercus agrifolia Nee	h	5	−2.0	OS	O
Q. berberidifolia Liebm.‡‡	i	2	−5.1	OS	B, E, M, N, O, P
Q. wislizeni A. DC.	j	6	−2.5	OS	E, M, P
Garryaceae					
Garrya veatchii Kellogg	k	7	−6.0	OS	D, E, M, P
Lauraceae					
Umbellularia californica (Hook. and Am.) Nutt.	l	2	−0.9	OS	E, P
Rhamnaceae					
Ceanothus crassifolius Torrey	m	8	−9.6	NS	B, D, E, M, O
C. cuneatus (Hook.) Nutt.	n	9	−9.5	NS	E, M, O
C. leucodermis E. Greene	o	5	−4.7	FS	B, E, N, O
C. megacarpus Nutt.	p	1	−11.0	NS	K, M
C. oliganthus Nutt.	q	5	−6.2	NS	D, E, O
C. spinosus Nutt.	r	1	−7.2	FS	K, M, N, P
Rhamnus californica Eschsch.	s	10	−1.5	OS	E, N
R. crocea Nutt.	t	10	−5.4	OS	E, M, N, P
R. ilicifolia Kellogg	u	10	−7.2	OS	B, D, E, N
Rosaceae					
Adenostoma fasciculatum Hook. and Am.	v	9	−8.3	FS	B, C, D, E, H, M, N, P
A. sparsifolium Torrey	w	9	−4.6	FS	C, M
Cercocarpus betuloides Torrey and A. Gray	x	2	−7.5	OS	D, E, M, P
Heteromeles arbutifolia (Lindley) Roemer	y	2	−6.2	OS	E, M, N, O, P
Prunus ilicifolia (Nutt.) Walp.	z	8	−4.4	OS	B, D, E, M, N, P

† Nomenclature follows Hickman (1993).
‡ Symbol used to represent species in Figs. 4 and 5.
§ Site numbers correspond to those in Table 2.
|| Pressure at 50% loss in hydraulic conductivity (see Fig. 2).
¶ Indicates mode of recruitment following wildfire for each species (see *Introduction* for details): NS, nonsprouting species; FS, facultative sprouting species; OS, obligate sprouting species (OS).
# Citations refer to literature documenting postfire regeneration type for each species: A, Stone and Juhren (1951); B, Horton and Kraebel (1955); C, Hanes (1965); D, Hanes and Jones (1967); E, Hanes (1971); F, Vogl and Schorr (1972); G, Keeley (1977); H, Keeley and Zedler (1978); I, Fulton and Carpenter (1979); J, Keeley (1987); K, Davis (1989); L, Lloret and Zedler (1991); M, Keeley (1992); N, Keeley (1995); O, Zedler (1995); P, Keeley (2000).
†† Formerly *Rhus laurina*.
‡‡ Formerly *Quercus dumosa*.

among PICs for two traits indicates that these traits have undergone changes of similar direction and magnitude across the phylogeny, and therefore they exhibit correlated evolutionary change (Felsenstein 1985, Ackerly 1999, 2000, Webb et al. 2002). Such a correlation suggests a possible functional link between these traits. Using both PIC and raw-trait analyses allowed us to assess which traits are correlated at present but have not experienced correlated evolutionary change.

MATERIALS AND METHODS

We measured xylem structural and functional traits in all of the species of evergreen sclerophyllous shrubs located in the Santa Monica Mountains of southern California (Fig. 1, Table 1). Sites were chosen (a total of 10) so as to minimize the number needed to include all 26 species (Table 2). All sites were located within 10 km of one another. We assumed that precipitation at these sites was similar due to their close proximity. Temperature varied among sites, with inland canyons (Table 2, sites 3, 7, 8, and 10) experiencing colder nighttime temperatures (Langan et al. 1997). Plants were tagged at each site and, when possible, the same individuals of each species were used for each of the measured parameters. It was not always possible to use the tagged individuals in some of the hydraulic conductivity and

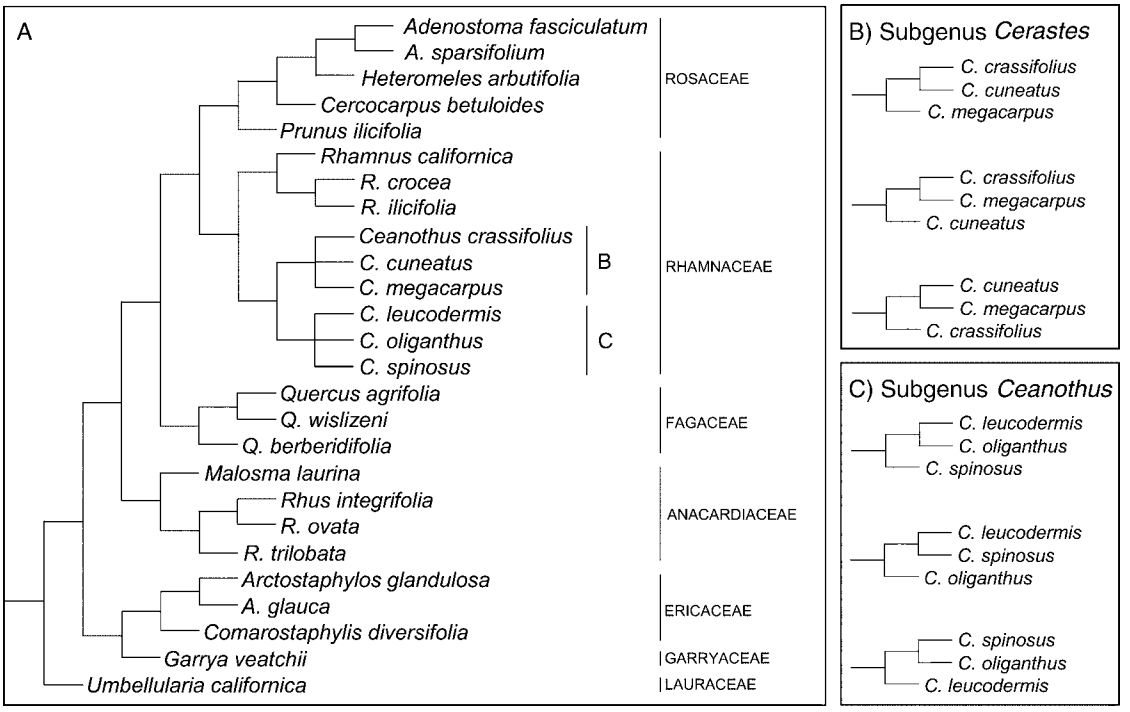

FIG. 1. (A) Phylogeny used for the determination of phylogenetic independent contrasts among 26 species of chaparral shrubs that occur in the Santa Monica Mountains of southern California, USA. (B, C) The three alternative resolutions for each of the two polytomies existing in the phylogeny. All nine possible alternative trees were analyzed. The phylogeny was constructed using published results referenced in the text. All branch lengths are assumed to be equal. Nomenclature is based on Hickman (1993).

vulnerability measures. In such cases, individuals in close proximity to the tagged plants were used.

Maximum vessel length was estimated from the mean maximum vessel length measured on a minimum of six individuals per species. A large branch, longer than the maximum vessel length, was cut from a plant and both the proximal and distal ends were trimmed with a razor blade to open all vessels. The proximal end of the stem was then attached to a pressurized gas chamber (~100 kPa) and the distal end (~6 mm in diameter) was submerged in water. Sequentially, 0.01-m lengths were cut from the proximal end until gas bubbles were detected emerging from the submerged distal end, suggesting that the single longest vessel had been opened at both ends of the branch. The remaining branch length plus one half the length of the final segment removed was then used to estimate the maximum vessel length (Greenidge 1952, Zimmermann and Jeje 1981, Ewers and Fisher 1989).

Xylem-specific hydraulic conductivity (K_s) was calculated as the maximum rate of water flow (with all embolisms removed) through a stem segment per xylem cross-sectional area, following the methods of Sperry et al. (1988), Kolb and Davis (1994), and Martinez-Vilalta

TABLE 2. Study sites located in the Santa Monica Mountains in Los Angeles County, California, USA.

Site number and name	GPS location	Elevation (m)‡	Year of last burn§
1) Pepperdine University	34°2.37′ N, 118°42.07′ W	90	1996
2) Upper Cold Creek	34°5.33′ N, 111°39.29′ W	510	1993
3) Dark Canyon†	34°5.05′ N, 118°41.29′ W	180	1970
4) Mesa Peak	34°4.05′ N, 118°43.15′ W	480	1996
5) Murphy Ranch	34°5.05′ N, 118°39.08′ W	660	1993
6) Castro Crest	34°4.96′ N, 118°45.65′ W	610	1982
7) Tapia Park†	34°5.10′ N, 118°42.48′ W	160	1996
8) Malibu Forestry†	34°5.04′ N, 118°42.21′ W	180	1996
9) Lower Cold Creek	34°5.85′ N, 118°39.19′ W	340	1993
10) Soka University†	34°6.17′ N, 118°41.70′ W	220	1996

† Site where hard frosts (below −6°C) occur.
‡ Elevation is rounded to the nearest 10 m.
§ Most recent year site experienced a fire.

et al. (2002). One branch from a minimum of six different individuals per species was collected from the field. The collected branches were longer than the maximum vessel length for each species to prevent air from artificially being introduced into the cut branches. Branches were submerged in water and trimmed from alternate ends until a final stem segment, 0.1 m in length and between 6 and 8 mm in diameter, was obtained. Stems were connected to a tubing system and flushed with low-pH degassed HCl solution adjusted to a pH of 2 that had been passed through a 0.1-μm filter. The stems were flushed at a pressure of 100 kPa for one hour to remove gas emboli from the xylem vessels. The K_h (kg m MPa^{-1} s^{-1}) was then measured gravimetrically and the high-pressure perfusion process repeated until a maximum value (K_{hmax}) was obtained for each segment (Sperry et al. 1988). The segments were then attached to a tubing system that allowed uptake of a 0.1% (mass/volume) dye solution of crystal violet or basic fuchsin under a suction of 5–6 kPa for 25 min. Prior to uptake, the dye solution had been passed through a 0.1-μm filter. The midpoints of the distal segments were transversely sectioned at a thickness of 40 μm with a sliding microtome. The active sapwood area, indicated by the dye, was measured with a light microscope (Nikon microscope, model Microphot-FX, Tokyo, Japan; Spot RT Color camera, Diagnostic Instruments, Sterling Heights, Michigan, USA) and analyzed using image analysis software (Image version 1.61, National Institutes of Health, Bethesda, Maryland, USA). The K_s value (kg m^{-1} MPa^{-1} s^{-1}) was then calculated as K_{hmax}/active sapwood area.

In order to determine resistance to water-stress–induced cavitation, estimated by the water potential at 50% loss of hydraulic conductivity (P_{50}), either the dehydration (Sperry et al. 1988) or the centrifugation technique (Alder et al. 1997) was used. The use of these techniques depended on when the P_{50} was measured (dehydration technique was used prior to 1997). We have found that these techniques produce very similar results when used on the same species (e.g., Fig. 2P). Most, although not all, curves were constructed during the summer dry period; however, P_{50} values among these species have been consistent across several studies completed in different seasons and years (cf. Redtfeldt and Davis 1996, Davis et al. 2002, Jacobsen et al. 2005, Pratt et al. 2007; A. L. Jacobsen, *unpublished data*). For the dehydration technique, one branch was collected from each of 30–60 individuals per species and brought to the laboratory. The collected branches were longer than the maximum vessel length for each species to prevent air from artificially being introduced into the cut branches. The branches were left exposed on tabletops in an air-conditioned laboratory to dehydrate for up to six days to achieve increasing levels of water stress. On the night before conductivity measurements were made, branches were tightly bagged to allow the water content of the branch to equilibrate. The following day, stem pressure potentials were measured from leaves or branchlets using a pressure chamber (Model 1001, PMS Instrument Company, Corvallis, Oregon, USA). The branches were then cut under water, alternately at each end, to lengths of 0.1 m. The percentage loss of hydraulic conductivity (PLC) was determined for each stem segment (Jarbeau et al. 1995). Vulnerability curves were constructed by plotting percentage loss of hydraulic conductivity as a function of xylem pressure potential.

For the centrifuge technique, one branch per plant from a minimum of six plants per species, ~2 m in length, was excised, bagged in the field, and taken to the laboratory. The branch was recut under water to obtain one stem segment 6–8 mm in diameter and either 0.271 m long (for use with a large centrifuge rotor) or 0.14 m long (for use with a smaller rotor). The larger rotor was needed to create greater centrifugal force for the species that, based upon previous studies, required greater tensions to induce embolism (Kolb and Davis 1994, Redtfeldt and Davis 1996, Davis et al. 1999*b*, Jacobsen et al. 2005). Stems were flushed at a pressure of 100 kPa for one hour to remove gas emboli, and K_{hmax} was determined. Following determination of their K_{hmax}, stems were spun in a centrifuge (RC5G Plus, Sorvall, Kendro Laboratory Products, Asheville, North Carolina, USA), using a modified rotor to accommodate stem segments. Stems were spun at a prescribed speed of rotation in order to generate a known negative pressure on the water column in the xylem vessels (Alder et al. 1997) and PLC was determined for each stem after each successive spin. Vulnerability curves were constructed by plotting decreasing values of xylem pressure potential vs. PLC. For each species, PLC values were fitted with a second-order polynomial model, which was used to predict the P_{50}. We used this model to fit vulnerability curves because it was the most flexible model that was easily applied to our data. We sampled a large number of species that were divergent in their resistance to cavitation as well as the shape of their vulnerability curves, which ranged from linear, to concave or convex. In addition, data from both the dehydration and centrifugation techniques are readily analyzed using polynomial models.

Xylem pressure potentials were monitored several times yearly, at predawn and midday, on species beginning in 1989 and continuing through 2004. At each sampling time, we measured the pressure potentials (P_x) on branchlets on a minimum of six plants per species with the pressure chamber technique (Scholander et al. 1965). The most negative xylem pressure potentials (P_{min}) occurred yearly at the very end of the summer drought period, usually late in the fall (October to early December), prior to the onset of winter rains (Kolb and Davis 1994, Redtfeldt and Davis 1996, Davis et al. 1999*b*). For each of 25 species, P_{min} was estimated as the lowest mean branchlet water potential ($N \geq 6$) measured at midday from a single sample date in the specified

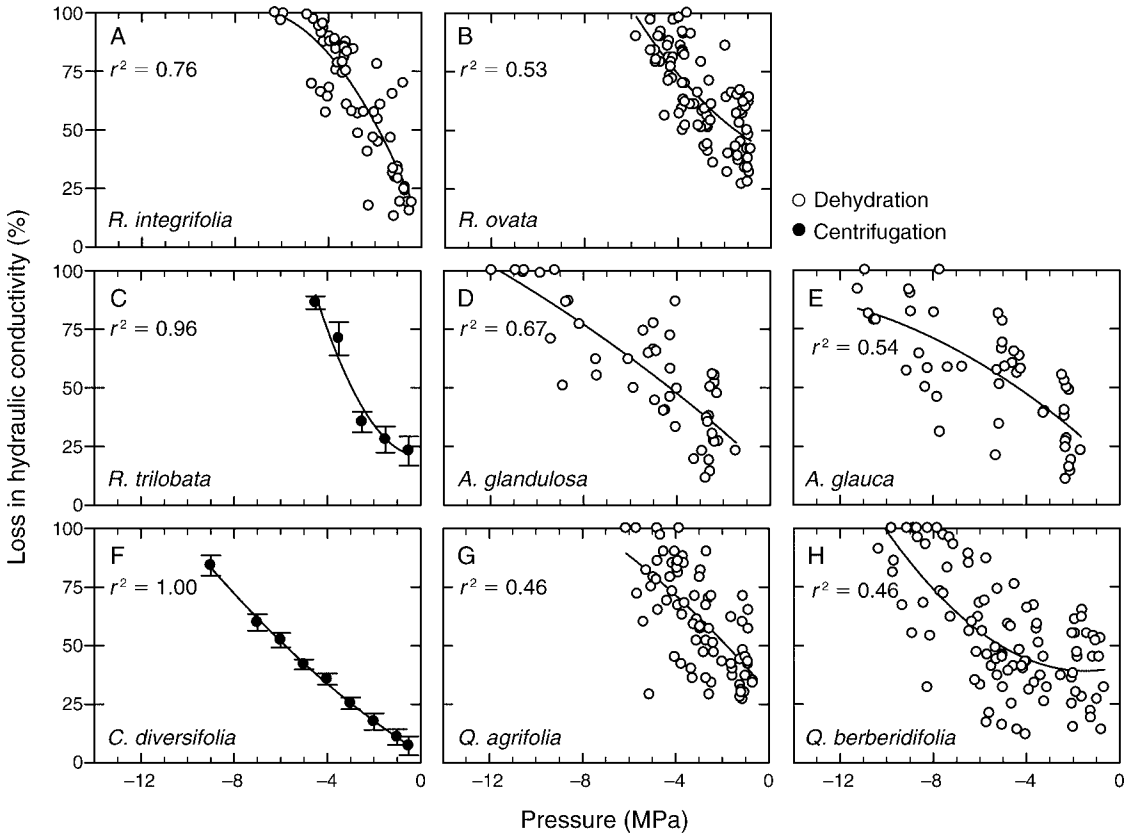

FIG. 2. Percentage loss in hydraulic conductivity as a function of pressure for stems of 17 species, using either a dehydration (open circles) or centrifugation (solid circles) technique. A second-order polynomial model was used to determine resistance to water-stress-induced cavitation estimated as the pressure at 50% loss in hydraulic conductivity (P_{50}). Data from both techniques are shown for *H. arbutifolia* in panel (P) (the data for the centrifugation technique for this species have previously been published in Jarbeau et al. [1995]). Data used to calculate P_{50} for the nine species not shown (see Fig. 1B, C) were obtained from the following sources: *C. crassifolius,* Davis et al. (2002); *M. laurina*, Jarbeau et al. (1995); *C. megacarpus*, Kolb and Davis (1994); *A. fasciculatum*, Redtfeldt and Davis (1996); *C. cuneatus*, *C. oliganthus*, and *C. spinosus*, Davis et al. (1999*b*); *C. leucodermis* and *R. crocea*, Pratt et al. (2007). For full genus names, see Fig. 1.

sample period. The mean P_{min} for a 26th species, *Garrya veatchii*, was measured only in 2002. The driest year in recorded history for southern California occurred between 2001 and 2002 (110 mm compared to a 125-year mean of 380 mm, recorded at the Los Angeles Civic Center since 1877) and provided the opportunity to measure the century-low P_{min} on these species (Thornton 2005). In 2002, values for P_x were measured between 29 and 31 October prior to the onset of the first winter rains on 7 November. We were able to measure these record low pressure potentials on 23 of the 26 species included in this study (P_{min} in 2002 was not measured on *Comarostaphylis diversifolia*, *Rhus integrifolia*, or *Rhus trilobata*).

Wood density was determined as the mean dry mass per fresh volume of mature stems from 10 individuals per species (Wagner et al. 1998, Hacke et al. 2001). The pith was removed from the stems by cutting the stems longitudinally with a razor blade. The stems were saturated in degassed HCl solution adjusted to a pH of 2 until they reached their maximum wet mass. Water-saturated volume was determined by water displacement in a graduated cylinder. The stems were dried at 60°C to a constant mass, and dry mass was determined.

Stem mechanical strength as modulus of rupture (MOR) was determined for a minimum of 10 individuals per species using a four-point bending test on an Instron Universal Machine (Model 4202, Instron Corporation, Canton, Massachusetts, USA) at Michigan State University following the methods of Jacobsen et al. (2005). Stem segments were kept at ~10°C until MOR was measured. All stems were measured within three days of being collected in the field. A four-point bending test was conducted with a compression load cell of 500 N. The load was applied at two points along the span length with a crosshead speed of 20 mm/min, and stems were stressed until the load reached a maximum value, determined as the maximum force obtained in the bending test prior to stem failure.

When possible, the same stems used in the determination of P_{50} or K_s were also used for xylem anatomical measures. When this was not possible, a stem of similar

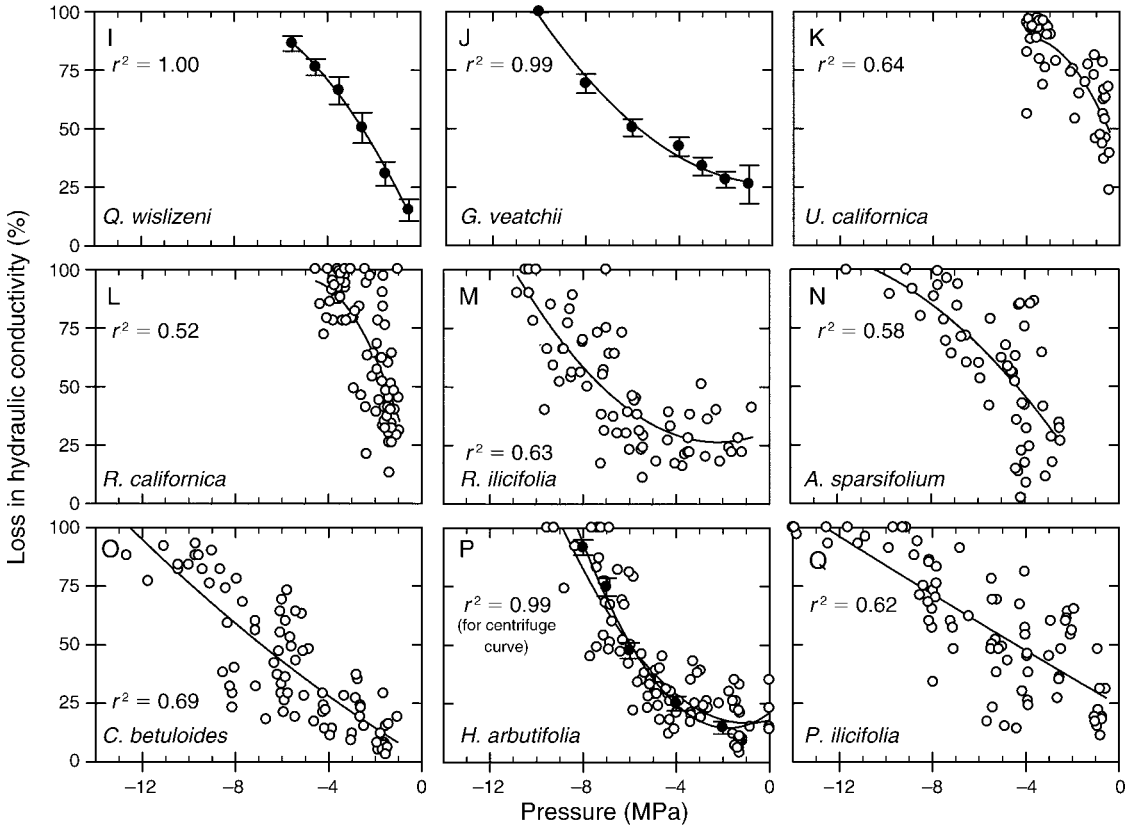

FIG. 2. Continued.

diameter from the same plant was used. For each stem, images were taken of several wedge-shaped sectors to sample for vessel and fiber features. Vessel lumen diameter (d in micrometers), fiber lumen diameter, fiber wall thickness, total transverse lumen area (vessel + fiber lumen area/sapwood area), and transverse fiber wall area/sapwood area were measured with these images. All of the vessels and fibers in sectors were measured until a sample size of 200 vessels and 100 fibers was obtained for a stem. The hydraulic vessel diameter (d_h) was calculated from the formula $d_h = (\Sigma\ d^5)/(\Sigma\ d^4)$, based upon all the sampled vessels in a stem. The vessel implosion resistance, $(t/b)^2_h$ (Hacke et al. 2001), was determined for those vessels within the sampled 200 vessels per stem that formed pairs from which one or both vessels fell within ± 5 μm of the calculated d_h, where t was the thickness of adjoining vessel walls and b was the lumen diameter of the vessel.

Phylogenies for regression analyses were constructed by hand using published phylogenetic data. Relationships among families were based on recent molecular-based phylogenies (Soltis et al. 1997, Hilu et al. 2003). Within families and genera several papers were used to support relationships (Anacardiaceae, Miller et al. 2001; Ericaceae, Hileman et al. 2001; Fagaceae, Manos et al. 2001, Nixon 2002; Rhamnaceae, Richardson et al. 2000, Hardig et al. 2000; Rosaceae, Morgan et al. 1994, Campbell et al. 1995, Potter et al. 2002). We were unable to find support for resolution below the level of subgenus within the genus *Ceanothus* (Rhamnaceae) resulting in two polytomies within the phylogeny (Fig. 1). Resolving these polytomies to create fully bifurcated trees resulted in nine possible trees. Since we combined several trees to create these final trees, our phylogenies lacked branch length information; therefore, all analyses were run assuming equal branch lengths (Ackerly 2000). This is a conservative approach, thus there is less certainty associated with a lack of correlation among contrasts but high confidence when there is a significant correlation among contrasts. Additionally there may be increased error in these analyses due to nonrandom species sampling (we sampled only woody chaparral shrubs) (Donoghue and Ackerly 1996, Ackerly 2000).

We calculated phylogenetic independent contrasts to test for patterns of correlated evolutionary change between traits (Felsenstein 1985) using COMPARE, version 4.6b (Martins 2004). Contrasts were calculated for all nine fully resolved trees (Fig. 1). For determination of trait correlation, regressions were run on trait contrasts for all nine trees and P-values were corrected using a sequential Bonferroni technique (Rice 1990) in order to maintain a comparison-wide α-value of 0.05.

PICs were not used to analyze differences among species with different post-fire regeneration modes because we were unable to assign post-fire regeneration modes to deep nodes in the phylogeny. To compare slopes of regressions of P_{min} and P_{50}, an ANCOVA was used and differences were considered to be significant if $\alpha \leq 0.05$ (Minitab version 14.12 [2004] and Statview version 5.0.1 [1998]). Unpaired t tests were used to compare xylem traits of species occurring at freezing and nonfreezing sites. In order to determine if traits differed among post-fire regeneration types, ANOVAs were used, followed by a Fisher's post hoc analysis if significant differences were detected. Data were transformed as necessary to meet the assumptions of statistical models.

Results

The 26 species of chaparral examined exhibited a wide range in cavitation resistance with a mean P_{50} of -5.1 ± 0.5 MPa (mean ± SE). *Umbellularia californica* was the least resistant to cavitation (Fig. 2K, Table 1; $P_{50} = -0.9$ MPa) and *Ceanothus megacarpus* was the most resistant (Table 1; $P_{50} = -11.0$ MPa).

The greatest water stress experienced by plants on an annual basis in the field (minimum seasonal pressure potential at midday, P_{min}) was correlated to cavitation resistance (Fig. 3A; $r^2 = 0.77$, $P < 0.001$, $N = 25$ for 1989–2001 and 2003–2004). The slope of the regression between P_{50} and P_{min} did not differ from a 1:1 relationship (based on 95% confidence interval, $N = 25$) for minimum seasonal pressure potentials measured from 1989–2001 and 2003–2004 (Fig. 3A). In 2001–2002, southern California experienced the lowest annual precipitation on record (since 1877). Minimum seasonal pressure potentials (P_{min}) in 2002 were significantly lower than the P_{min} that had been recorded on the same chaparral shrub species from 1989–2001 and 2003–2004 (mean P_{min} of -6.8 ± 0.6 MPa for 2002 and -4.9 ± 0.4 MPa for 1989–2001 and 2003–2004; paired t test, $P < 0.001$, $N = 22$). The lowering of P_{min} in 2002 significantly altered the relationship between P_{min} and P_{50} (Fig. 3A) with slopes being significantly different between data from 2002 and the other sample years (ANCOVA, $P = 0.017$, $N = 22$). In the driest year in recorded history, P_{50} was correlated to the minimum seasonal pressure potential experienced by these chaparral shrubs (Fig. 3A; $r^2 = 0.67$ for 2002 P_{min}, $P < 0.001$, $N = 23$).

The species experiencing the most negative pressure potentials from 1989–2001 and 2003–2004 were typically the same species that exhibited the greatest decline in their pressure potentials in 2002 relative to other sample years (Fig. 3B). The slope of the regression of P_{min} from 1989–2001 and 2003–2004 vs. P_{min} in 2002 significantly differed from that of a 1:1 line (based on 95% confidence interval, $N = 22$), but the intercept was not different from the origin (based on 95% confidence interval, $N = 22$). The minimum seasonal pressure potential from 1989–2001 and 2003–2004 was strongly correlated to the P_{min} in the record drought year of 2002 (Fig. 3B; $r^2 = 0.76$, $P < 0.001$, $N = 22$).

Several xylem traits were correlated with cavitation resistance, including xylem density, percentage of transverse fiber wall area, and modulus of rupture (MOR) (Fig. 4). Increased xylem density and fiber wall area were associated with decreased P_{50} for both raw values (Fig. 4A, B; $r^2 = 0.39$ and 0.27, respectively, $P < 0.001$ for both, $N = 26$) and PICs (Fig. 4D, E; $P < 0.001$ for regressions of PICs for all phylogenetic trees for both, $N = 25$). Whole-stem mechanical strength, estimated by MOR, was also correlated with cavitation resistance for both raw values (Fig. 4C; $r^2 = 0.45$ for MOR, $P < 0.001$, $N = 26$) and PICs (Fig. 4F; $P < 0.001$ for regressions of PICs for all phylogenetic trees, $N = 25$).

The mechanical strength of vessels to resist implosion, $(t/b)_h^2$ (Hacke et al. 2001), calculated from vessel anatomical traits, was correlated to resistance to cavitation (P_{50}) when raw-traits values were analyzed (Fig. 5A; $r^2 = 0.18$; $P = 0.032$, $N = 26$); however, these traits were not correlated when analyzed using PICs (Fig. 5C; P from 0.136 to 0.578 for regressions of PICS for all nine phylogenetic trees, $N = 25$). All species except two, *Ceanothus crassifolius* and *Cercocarpus betuloides*, fell well above the theoretical threshold of implosion (dashed line in Fig. 5A).

Measurements of vessel size, including mean hydraulic vessel diameter (d_h) and maximum vessel length were correlated with cavitation resistance ($r^2 = 0.39$, $P = 0.001$, $N = 26$ for d_h and $r^2 = 0.20$, $P = 0.021$, $N = 26$ for maximum vessel length; not shown). However, d_h and maximum vessel length were not correlated with cavitation resistance when analyzed using PICs (P from 0.100 to 0.187 for d_h and from 0.262 to 0.414 for maximum vessel length for regressions of PICS for all nine phylogenetic trees for each, $N = 25$; data not shown). Xylem-specific conductivity (K_s) was also not correlated with cavitation resistance when analyzed using PICs (Fig. 5D; P from 0.246 to 0.377 for regressions of PICS for all phylogenetic trees, $N = 25$) but P_{50} and K_s were correlated when raw data were analyzed using a power function (Fig. 5B, $P = 0.002$, $N = 26$; exponent $= -0.51$).

Species occurring at freezing sites did not differ in their xylem traits from species occurring at nonfreezing sites. There was no difference between species at freezing and nonfreezing sites in d_h (34.6 ± 3.0 and 42.3 ± 3.2 μm for freezing and nonfreezing sites, respectively; t test, $P = 0.094$, $N = 7$ for freezing and 19 for nonfreezing; not shown), maximum vessel length (0.80 ± 0.12 and 0.88 ± 0.21 m for freezing and nonfreezing sites, respectively; t test, $P = 0.74$, $N = 7$ for freezing and 19 for nonfreezing; not shown), or K_s (2.15 ± 0.29 and 1.93 ± 0.62 kg m^{-1} MPa^{-1} s^{-1} for freezing and nonfreezing sites, respectively; t test, $P = 0.76$, $N = 7$ for freezing and 19 for nonfreezing; not shown).

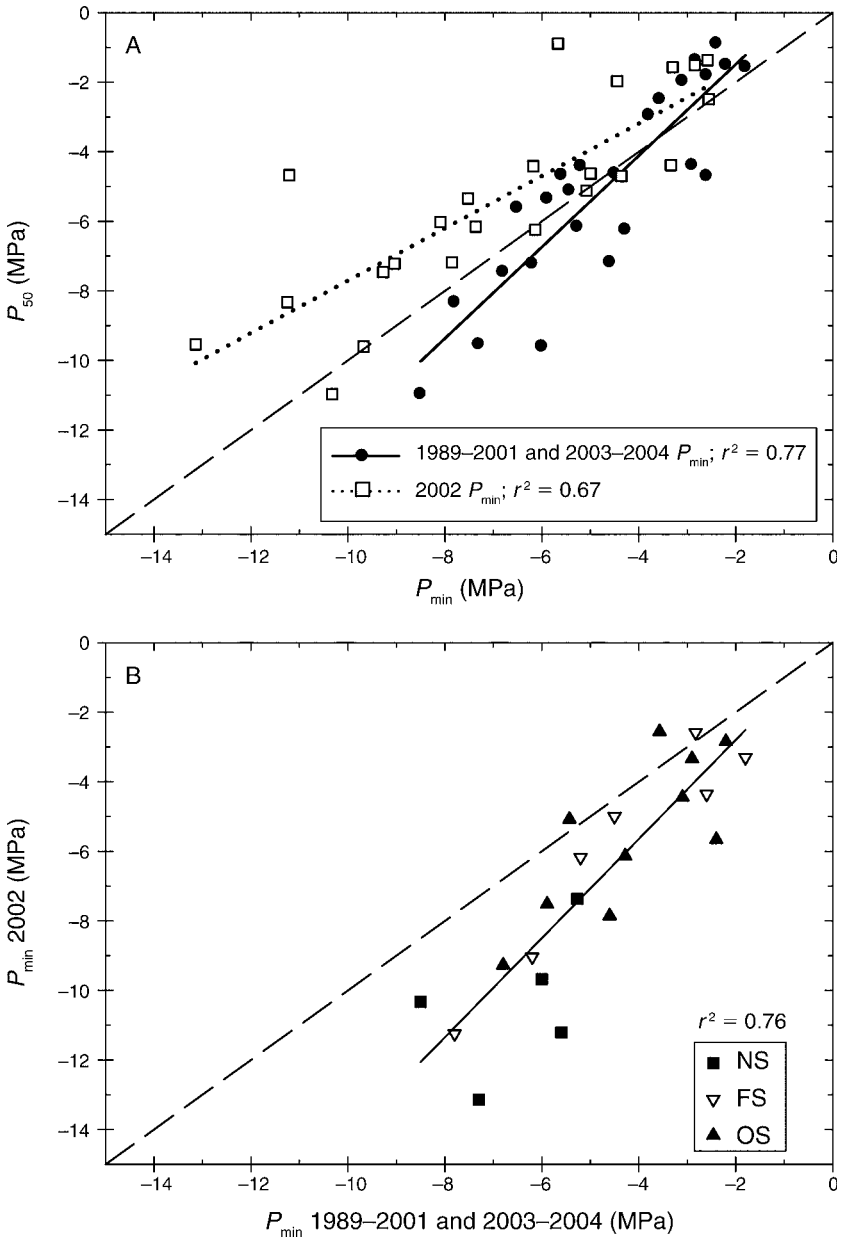

FIG. 3. (A) Pressure potential at 50% loss of hydraulic conductivity (P_{50}) as a function of minimum seasonal pressure potential of branchlets (P_{min}) measured in 1989–2001 and 2003–2004 (solid circles and solid line) and from 2002 (open squares and dotted line). Slopes of the regression lines differ significantly ($P = 0.017$), but the intercepts do not ($P = 0.19$). The slope of P_{50} vs. P_{min} from 1989–2001 and 2003–2004 is not different from a slope of 1.0 ($P = 0.20$), but the slope of P_{50} vs. P_{min} from 2002 does differ from 1.0 ($P = 0.012$). (B) Minimum seasonal pressure potential in 2002, the year of the lowest annual rainfall on record (since 1877), vs. P_{min} from 1989–2001 and 2003–2004. Symbols indicate modes of post-fire regeneration: solid square, NS (nonsprouting); open triangle, FS (facultative-sprouting); and solid triangle, OS (obligate-sprouting) (see Table 1 for details). For both panels, the dashed line represents a 1:1 relationship. The slope of the solid (fitted) line in panel (B) differs from the 1:1 line ($P = 0.016$), but the intercept does not differ from the origin ($P = 0.940$).

The three post-fire regeneration types (nonsprouting, facultative-sprouting, and obligate-sprouting) differed in their degree of seasonal water stress experienced and in their resistance to cavitation. Nonsprouting (NS) species experienced significantly greater water stress (lower P_{min}) in 2002 than facultative-sprouting (FS) and obligate-sprouting (OS) species (Table 3; ANOVA, $P = 0.008$ and 0.003 for NS compared to FS and OS, respectively; $P = 0.84$ for FS compared to OS, $N = 5$, 7, and 11 for NS, FS, and OS, respectively). Although there were no significant differences among regeneration types in 1989–2001 and 2003–2004 P_{min}, the data follows

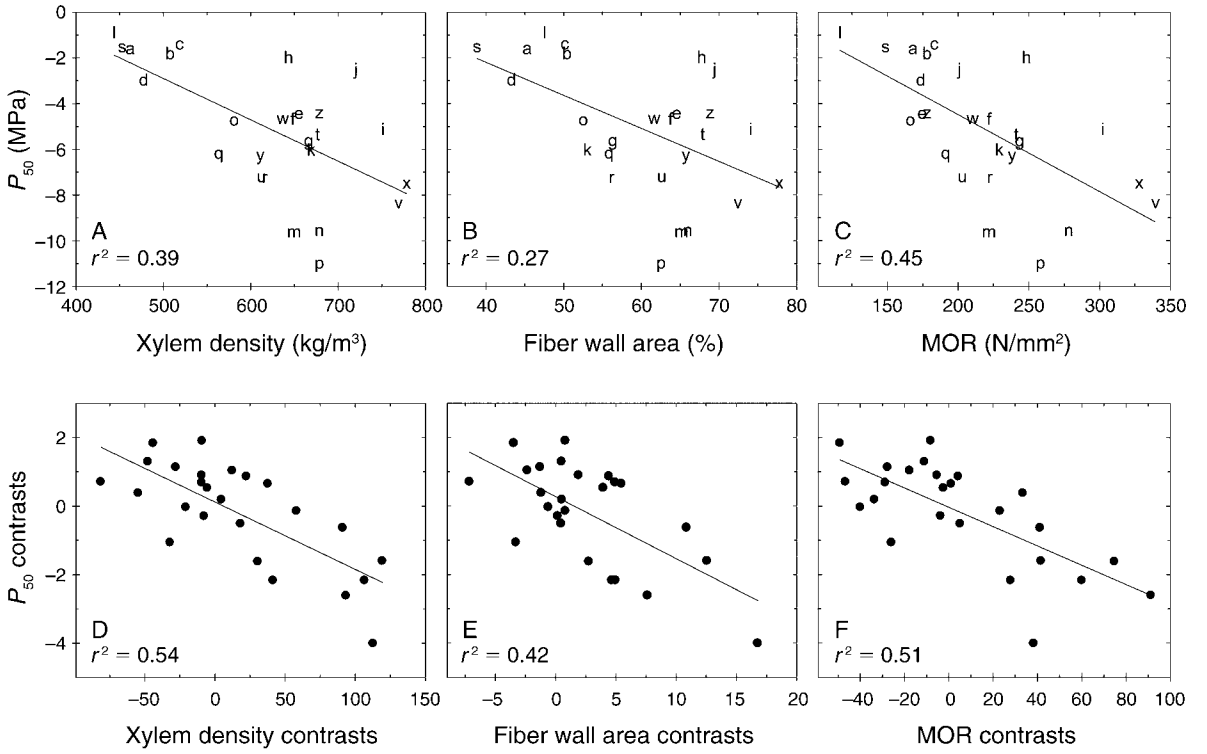

FIG. 4. (A) Pressure potential at 50% loss of hydraulic conductivity (P_{50}) as a function of xylem density, (B) transverse fiber wall area, and (C) modulus of rupture (MOR). Different lowercase letters represent different species (see Table 1 for species symbols). (D–F) Relationships between phylogenetic independent contrasts of these traits are shown for one representative tree of the nine analyzed phylogenetic trees.

the same pattern as that observed in 2002 (Table 3; ANOVA, $P = 0.096$, $N = 5$, 8, and 12 for NS, FS, and OS, respectively). Nonsprouting species also had significantly greater cavitation resistance than either FS or OS (Table 3; ANOVA, $P = 0.011$ and 0.006 for NS compared to FS and OS, respectively; $P = 0.94$ for FS compared to OS, $N = 5$, 8, and 13 for NS, FS, and OS, respectively). Maximum vessel length was also different among these three regeneration types with OS having longer maximum vessel lengths than either NS or FS species (Table 3; ANOVA, $P = 0.019$ and 0.047 for OS compared to NS and FS, respectively; $P = 0.51$ for FS compared to NS, $N = 5$, 8, and 13 for NS, FS, and OS, respectively).

Xylem traits associated with cavitation resistance including xylem density, MOR, and transverse fiber wall area, did not differ among the three post-fire regeneration types (Table 3; ANOVA, $P = 0.54$, 0.38, 0.64, and 0.20, respectively, $N = 5$, 8, and 13 for NS, FS, and OS, respectively). Xylem specific conductivity (K_s) and d_h were also not different among regeneration types (Table 3; ANOVA, $P = 0.24$ and 0.22, respectively, $N = 5$, 8, and 13 for NS, FS, and OS, respectively).

DISCUSSION

Cavitation resistance (estimated by P_{50}) varied considerably among 26 species of chaparral shrubs all occurring within 10 km of each other in the same geographical region. Cavitation resistance ranged from −0.9 to −11.0 MPa, with a mean resistance of −5.1 MPa. This range of resistances is similar to what has been reported in the literature for mediterranean-type climate regions (Maherali et al. 2004) and it is also consistent with the range in resistance reported for six species of chaparral shrubs growing at a common microsite having similar soil, precipitation, microclimate, and stand age (Jacobsen et al. 2005). Although rainfall was similar among sites in the current study, there may be a high heterogeneity in moisture availability among co-occurring species in the mediterranean-type climate region of southern California, perhaps due to differential rooting depth (Hellmers et al. 1955, Kummerow et al. 1977, Burk 1978, Miller and Poole 1979, Thomas and Davis 1989). The heterogeneity of moisture availability in this region and its exploitation by a diverse range of angiosperm species may partially explain the high woody plant diversity of the southern California chaparral.

The wide range of resistances found among these upland chaparral species contrasts with that reported for woody angiosperms in other arid plant communities. In a study of riparian and upland Sonoran Desert species (Pockman and Sperry 2000), mean cavitation pressures were scaled to the native percentage loss in conductivity

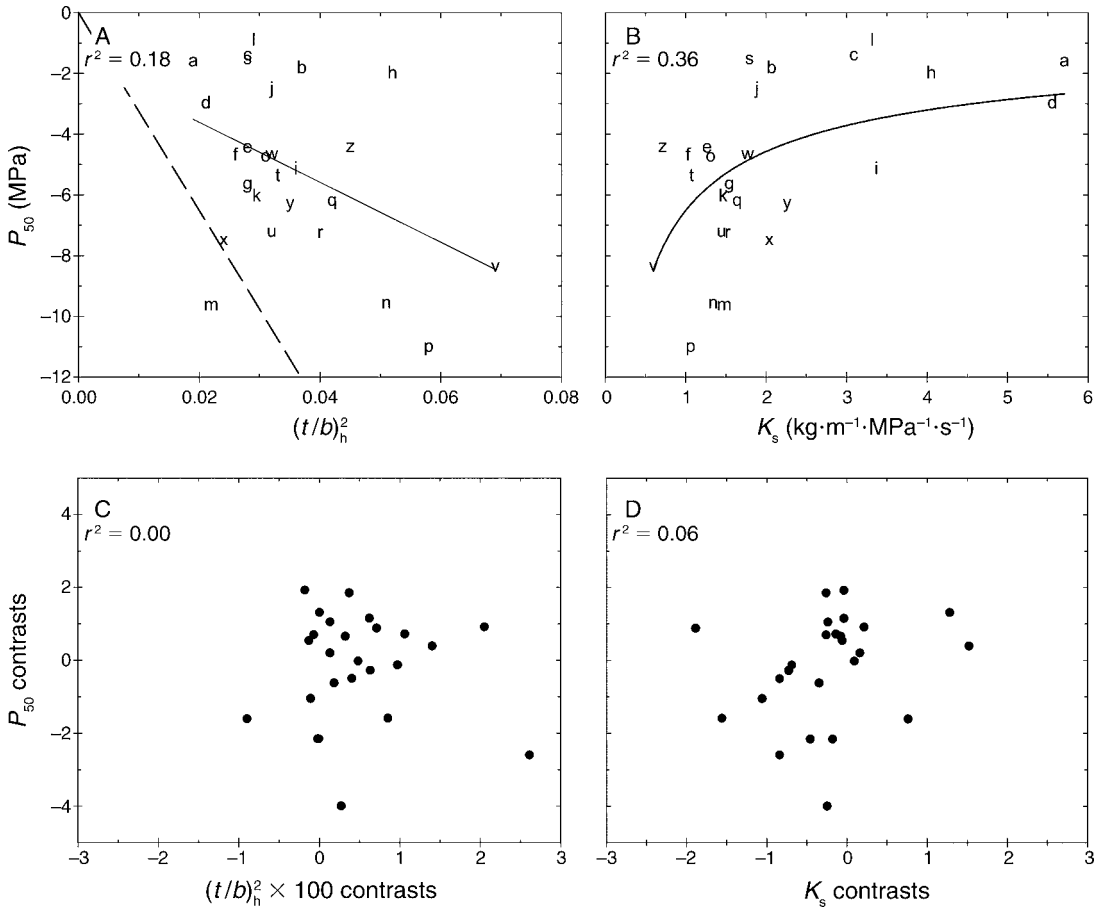

FIG. 5. (A) Cavitation resistance (P_{50}) as a function of estimated vessel implosion resistance, $(t/b)^2_h$, shown as a solid line, where t is the thickness of the double vessel wall between two vessels, b is the vessel lumen diameter, and subscript h indicates that only vessels near the mean hydraulic vessel diameters are used in determining the t and b. The dashed line represents the minimum conduit $(t/b)^2_h$ necessary to withstand a given P_{50} without cell wall collapse (modified from Hacke et al. [2001]). Most of the species have values that are near or above this theoretical implosion threshold. (B) Cavitation resistance (P_{50}) as a function of xylem-specific hydraulic conductivity (K_s). The curved line is a power function ($y = -6.52x^{-0.51}$). Different lowercase letters represent different species (see Table 1 for species symbols). The phylogenetic independent contrasts of (C) P_{50} vs. $(t/b)^2_h$, and (D) P_{50} vs. K_s. Results were obtained by analyzing each of nine phyletic trees; data from one tree is shown. The contrasts are not correlated in either case (contrasts from zero out of nine trees displayed a significant regression).

(PLC) measured in the field in July. This difference makes it difficult to compare the mean cavitation pressures reported in Pockman and Sperry (2000) with those in the present study. Thus, we recalculated P_{50} for the species included in their study using common methods and without scaling values to native PLC (Pockman and Sperry 2000) as was done by Maherali et al. (2004). For Sonoran Desert angiosperms, excluding the gymnosperm *Juniperus monosperma*, the recalculated P_{50} range from a maximum of close to 0 MPa (moist, riparian species) to a minimum of approximately −7 MPa (dry, upland species). This is a smaller range in P_{50} than that found among the chaparral shrub species in the current study, but is similar to the range found among shrubs of the Great Basin Desert (Hacke et al. 2000, Sperry and Hacke 2002) and the Mojave Desert (A. L. Jacobsen, *unpublished data*). Thus, it appears that chaparral angiosperms may display a greater range of cavitation resistance than angiosperms of neighboring arid plant communities.

For estimating cavitation resistance, the xylem pressure potential at 50% loss of hydraulic conductivity (P_{50}) is somewhat arbitrary, and some authors have chosen to use other values, such as P_{75}. However, P_{50} is the value that has most often been used in comparisons across many species (Tyree et al. 1994, Hacke et al. 2001, Maherali et al. 2004). Additionally, in chaparral plants, we have found that the P_{50} is a good predictor of minimum seasonal pressure potential (P_{min}) during years with average precipitation, with P_{50} corresponding directly to P_{min} in a 1:1 relationship. This implies that, in most years, species are able to tolerate a 50% reduction in conductivity due to water stress and to maintain evergreen leaves during a 6–8 month summer drought

TABLE 3. Xylem functional and anatomical traits for species of three postfire regeneration types (±SE).

Postfire regeneration type†	1989–2001 and 2003–2004 P_{min} (MPa)‡	2002 P_{min} (MPa)§	P_{50} (MPa)||	Maximum vessel length (m)
NS	-6.5 ± 0.6^a	-10.3 ± 1.0^a	-8.2 ± 1.2^a	0.46 ± 0.08^a
FS	-4.3 ± 0.7^a	-6.0 ± 1.2^b	-4.4 ± 0.9^b	0.63 ± 0.14^a
OS	-4.5 ± 0.5^a	-5.7 ± 0.7^b	-4.3 ± 0.6^b	1.07 ± 0.16^b

† See Table 1 for description of the three post-fire regeneration types and the species representing each.
‡ Minimum seasonal pressure potential measured in 1989–2001 and 2003–2004, which were years of normal rainfall.
§ Minimum seasonal pressure potential measured in 2002, the year of the lowest rainfall in recorded history for southern California.
|| Pressure potential at 50% loss in hydraulic conductivity.
¶ Modulus of rupture.
# Xylem-specific hydraulic conductivity.
†† Mean hydraulic vessel diameter.

period. Thus, although species experience different absolute levels of seasonal water stress, they all experience a relatively similar loss in hydraulic conductivity seasonally. A similar relationship was found by Hacke et al. (2000) among Great Basin shrub species. They found a 1:1 relationship between the mean cavitation pressure (approximately P_{50}) and midday P_{min} in roots and shoots of six shrub species. This suggests stems of shrubs in arid communities may be similar in the level of embolism that they typically tolerate, while still surviving and remaining competitive in the community.

The driest year in recorded history for southern California occurred in 2001 and 2002 (110 mm compared to a 125-year mean of 380 mm; Thornton 2005) during which some species experienced significantly greater water stress than typical (e.g., 1989–2001 and 2003–2004). During this year, minimum seasonal pressure potentials were ~2 MPa more negative than prior years, although species differed in the magnitude of their P_{min} adjustment. Species that typically maintain higher seasonal pressure potentials generally did not experience as great a decline in seasonal pressure potential in 2002 (e.g., *Rhamnus californica* 1989–2001 and 2003–2004 $P_{min} = -2.2$ MPa compared to 2002 $P_{min} = -2.9$ MPa). In contrast, species that typically experience relatively low seasonal pressure potentials had considerably lower pressure potentials in 2002 (e.g., *Ceanothus cuneatus* 1989–2001 and 2003–2004 $P_{min} = -7.3$ MPa compared to 2002 $P_{min} = -13.1$ MPa). This rare drought event highlights an important functional consequence of the species-specific relationship between pressure potential and conductivity defined by the shape of the vulnerability curve. In species that display a steep-sloped portion of their vulnerability, a relatively small decrease in pressure potential results in a much greater loss of hydraulic conductivity than a similar decrease in pressure in a species with a less steep slope or more even loss in conductivity across pressure intervals (Kavanagh et al. 1999, Pockman and Sperry 2000). For example, *Rhamnus californica*, a relatively susceptible chaparral species may experience a nearly 40% increase in embolism with decrease in P_x from −2 MPa to −3 MPa (Fig. 2L), while the more resistant species, *Rhamnus ilicifolia*, may experience <5% embolism with the same change in P_x (Fig. 2M). Measurements of seasonal changes in percent embolism in species occurring in the field agree with these predicted patterns based on the shape of vulnerability curves (S. D. Davis, *unpublished data*).

Variability in seasonal water stress among species implies that the water status of species differs greatly even though they co-occur (Kolb and Davis 1994, Redtfeldt and Davis 1996, Davis et al. 1998, 1999*b*, Jacobsen et al. 2005). Species that maintain higher P_{min} and that experienced relatively little change in water stress in 2002 may occupy moister microsites (Hanes and Jones 1967, Schlessinger et al. 1982) or have deeper roots (Hellmers et al. 1955, Kummerow et al. 1977, Burk 1978, Miller and Poole 1979, Thomas and Davis 1989, Canadell and Zedler 1995), allowing them to access a greater water supply than co-occurring shallow-rooted species. This is consistent with the trend for sprouting species that have larger and older root systems to experience less severe water stress than shallow-rooted nonsprouting species. Alternatively, species that maintain higher P_{min} may have greater ability to conserve water such as the low minimum leaf conductance found in the chaparral shrub *Rhus ovata* (Pratt et al. 2005). Therefore, while mean annual precipitation may predict patterns of seasonal water stress and cavitation resistance across broad geographic scales (Maherali et al. 2004), it is noteworthy that microsite and species-specific traits may facilitate co-occurrence of species that are similarly divergent in their seasonal water stress and cavitation resistance within a single community and small geographical region.

In the present study, species with high resistance to cavitation have characteristic xylem traits, including greater wood density, increased transverse fiber wall area, and greater stem mechanical strength (MOR). This agrees with previous studies that have found a relationship between xylem density and cavitation resistance (Hacke et al. 2001, Baas et al. 2004, Jacobsen et al. 2005) and MOR and cavitation resistance (Wagner et al. 1998, Jacobsen et al. 2005). Our results indicate that changes in these xylem traits are correlated to changes in cavitation resistance across the phylogeny, suggesting

TABLE 3. Extended.

Xylem density (kg/m^3)	MOR (N/mm^2)¶	Fiber wall area (%)	K_s ($kg\ m^{-1}\ MPa^{-1}\ s^{-1}$)#	d_h (m)††
644 ± 21^a	234 ± 15^a	62.7 ± 1.8^a	1.31 ± 0.12^a	32.5 ± 1.6^a
589 ± 36^a	205 ± 21^a	55.7 ± 3.5^a	2.60 ± 0.71^a	42.3 ± 4.6^a
632 ± 29^a	220 ± 16^a	61.6 ± 3.2^a	2.08 ± 0.27^a	42.0 ± 4.1^a

that increased xylem density, MOR, and fiber wall area may be functionally linked to increased cavitation resistance. Mechanical reinforcement of xylem vessels by neighboring cells, specifically the fiber matrix, may be necessary to avoid vessel collapse under negative pressure (Niklas 1997, Hacke et al. 2001, Jacobsen et al. 2005). Cell wall collapse has not yet been reported for evergreen chaparral shrubs, possibly because cavitation occurs before critical pressures are achieved (Sperry 2003) or there is nondetectible microfracture of cell walls or pit membranes that induce cavitation prior to complete collapse (Jacobsen et al. 2005). Cell wall collapse resulting from the negative pressures of water stress has been observed in gymnosperm leaf tracheids (Cochard et al. 2004, Brodribb and Holbrook 2005). In these cases, preferential cell wall collapse occurred in tracheids lacking mechanical reinforcement by adjacent cells, while mechanically supported tracheids in stems and leaf midveins did not exhibit collapse. Our findings highlight the importance of matrix tissue strength in the prevention of conductive cell implosion under negative pressure.

While the evolutionary correlation between xylem mechanical strength (MOR and transverse fiber wall area) and resistance to cavitation is compelling, vessels of most species appear to be relatively safe from implosion. Based upon $(t/b)_h^2$ measurements, all but two of the species (*Ceanothus crassifolius* and *Cercocarpus betuloides*) have much greater vessel resistances to implosion than they would need to withstand pressures equaling their P_{50} (Hacke et al. 2001). Even during episodic drought events, such as the lowest rainfall in recorded history for Los Angeles County (2001–2002), $(t/b)_h^2$ vs. P_{min} in 2002 indicated that only three species experienced pressures more negative than their theoretical implosion threshold (*C. crassifolius*, *C. betuloides*, and *Arctostaphylos glauca*; not shown). However, species that have less implosion-resistant vessels may still be able to avoid implosion if their fiber matrix provides additional reinforcement against cell wall collapse. Interestingly, the two species, *C. crassifolius* and *C. betuloides*, which seemingly operate at high risk of vessel implosion, also have some of the highest transverse fiber wall area and xylem density among the species examined. Mechanical reinforcement by the fiber matrix surrounding vessels may be the more critical requirement for implosion resistance than the $(t/b)_h^2$ value in some dry-land species (Jacobsen et al. 2005).

Estimated implosion resistance ($(t/b)_h^2$) was correlated with P_{50}; however, these traits do not display correlated evolutionary change. That is, these traits were not correlated when analyzed using PICs. The correlation between the raw-trait values is consistent with previous findings (Hacke et al. 2001, Sperry 2003, Jacobsen et al. 2005). Vessels must be able to avoid implosion and cavitation in order to function so $(t/b)_h^2$ should not fall below the implosion threshold for a given pressure; however, there is no limit, other than mechanical and construction costs, to having a $(t/b)_h^2$ greater than the threshold as seen among many of the chaparral species in this study. There may be little selection for a change in $(t/b)_h^2$ with changing P_{50} as long as the $(t/b)_h^2$ is above the necessary implosion threshold. The $(t/b)_h^2$ value may prove to be a valuable tool for the identification of species in which fibers, rather than vessel wall to lumen ratios, are particularly important in resistance to implosion (e.g., *C. crassifolius* and *C. betuloides*).

Water-stress-induced xylem cavitation is caused by air seeding through pit pores, which we predicted would be more likely to occur in wider and longer vessels. These large vessels would have more pitted area, and, therefore, would have greater likelihood of containing a large noncavitation-resistant pit pore (Wheeler et al. 2005, Hacke et al. 2006). Consistent with this, we found that vessel size was correlated to cavitation resistance, with both hydraulic diameter and maximum vessel length correlating to P_{50}. This suggests that among these species, vessel diameter and length are correlated with pitted area. Additionally, it suggests that maximum vessel length may be a good predictor of average vessel length, as has been shown previously in other species (Ewers et al. 1990). However, a more thorough test of this hypothesis requires measuring the pitted area of vessels and vessel length distributions, which was not done in the current study (Wheeler et al. 2005).

The correlation between measures of vessel diameter and length and of cavitation are consistent with the correlation between xylem hydraulic efficiency (K_s) and cavitation resistance. Increased cavitation resistance appears to come at the cost of decreased K_s. A power function was used to analyze the relationship between these two parameters following Martínez-Vilalta et al. (2002), who applied this function to nine evergreen species from the Mediterranean Basin. Their model predicted a curve exponent of −2.0 and was partially based on the assumption that conduit diameter scaled linearly with size of pit pores. In our analysis, the

exponent of the power curve that best fit our data was −0.51. It differed significantly from the −2.0 predicted by the model of Martínez-Vilalta et al. (2002) ($P > 0.05$, based on 95% confidence intervals). The most likely explanation for this difference is that mean conduit diameter and the size of the largest pit pore in a conduit are not linearly linked among the chaparral species we examined. This is consistent with the findings of Hacke et al. (2006) that cavitation pressure, which is dependent on the largest pit pore, is not related to the mean pit membrane porosity.

Although measures of hydraulic efficiency are correlated to cavitation resistance when raw-trait values are analyzed, d_h, maximum vessel length, and K_s are not correlated to P_{50} when analyzed using PICs. This is consistent with a previous study that found that P_{50} varies independently of K_s among evergreen angiosperms when data are analyzed using techniques that correct for the evolutionary nonindependence of species (Maherali et al. 2004). This indicates that correlations among raw values of these traits are partially dependent on the evolutionary relationships among the species sampled and are likely not directly linked.

Larger vessels are more susceptible to freezing-induced cavitation than smaller vessels (Ewers 1985, Langan et al. 1997, Davis et al. 1999*a*, Pittermann and Sperry 2003); thus, at freezing sites, selection should favor reduced vessel size among evergreen species that are winter active, as is characteristic of many chaparral species. Susceptibility to freezing-induced cavitation is directly related to vessel diameter, with vessels more than ~44 μm in diameter being susceptible (Langan et al. 1997, Davis et al. 1999*a*, 2005, Pittermann and Sperry 2003). We did not find a difference in vessel diameter between species occurring at freezing and nonfreezing sites. Chaparral vessel diameters are generally smaller than the 44-μm threshold of freezing-induced cavitation susceptibility (mean $d_h = 40.3 \pm 2.5$ μm for all species), reducing the likelihood that many of the species occurring in freezing sites would experience selection to further reduce vessel diameter. In fact, the diminutive vessel diameters of chaparral shrub species relative to species of other plant associations have been described previously (Carlquist and Hoekman 1985, Carlquist 1989). It is worth noting, however, that vessel diameters at nonfreezing sites tend to be larger than vessel diameters at freezing sites ($d_h = 34.6 \pm 3.0$ and 42.3 ± 3.2 μm for freezing and nonfreezing sites, respectively), and there are several chaparral species that do have large enough vessel diameters to be susceptible to freezing-induced cavitation. Where these species occur at freezing sites, they experience a high level of embolism following a freeze–thaw (e.g., *Rhus ovata* and *Malosma laurina*; Pratt et al. 2005; *Quercus agrifolia* and *Q. berberidifolia*; S. D. Davis, *unpublished data*). Additionally, species that have small vessel diameters may still be at risk of freezing-induced cavitation if freezing is combined with water stress (Ewers et al. 2003) and freezing can affect plants through damage to living cells independent of xylem cavitation. Previous studies have well documented the effect of freezing in the chaparral on function, survivorship, and species distribution (Langan et al. 1997, Boorse et al. 1998, Davis et al. 1999*a*, 2005, Ewers et al. 2003, Pratt et al. 2005), and functional and structural adaptations to freezing remain an active area of research.

Cavitation resistance among species of chaparral shrubs appears to be associated with different types of post-fire regeneration. Nonsprouting species (NS) have greater cavitation resistance than either facultative-sprouting (FS) or obligate-sprouting (OS) species. High cavitation resistance may be important for NS because they recruit preferentially into open sites post-fire and must rely entirely on the survivorship of these seedlings to persist (Frazer and Davis 1988, Thomas and Davis 1989, Odion and Davis 2000). The high drought tolerance of NS seedlings and its relationship to seedling survivorship have been observed previously (Miller and Poole 1979, Frazer and Davis 1988, Thomas and Davis 1989, Davis et al. 1998). Cavitation resistance may also be important at the adult stage. We found that nonsprouting (NS) species experienced greater seasonal water stress than either OS or FS in 2002. In 2002, the driest year in recorded history for Los Angeles County, adults of NS chaparral shrubs that were not able to withstand the increased stress of the extreme drought suffered mortality, while co-occurring, and presumably more deeply rooted, sprouting species were able to persist (Paddock 2006). This agrees with previous studies that have found that NS are more shallowly rooted and occur in drier microsites, while sprouting species are more deeply rooted (Hellmers et al. 1955, Hanes and Jones 1967, Kummerow et al. 1977, Burk 1978, Miller and Poole 1979, Schlesinger et al. 1982, Thomas and Davis 1989, Davis et al. 1998).

Differences in maximum vessel length may be related to post-fire regeneration type. Although species from the three different regeneration types differ in their maximum vessel length, they do not differ in hydraulic vessel diameter or conductive efficiency when these traits are measured on stems of the same size, suggesting that longer maximum vessel lengths are not related to increased hydraulic efficiency. Instead, differences among these regeneration types may be related to differential growth-rates and stem diameters, since it has been shown that maximum vessel length increases with increasing stem diameter (Ewers et al. 1990). Resprouting FS and OS grow rapidly after a fire, with shoots quickly increasing in length and diameter (Horton and Kraebel 1955, Thomas and Davis 1989). In contrast, NS seedlings grow slowly and have shoots much smaller than those of co-occurring resprouts (Thomas and Davis 1989). Thus, it may be that in stands containing even-aged aboveground material, OS have larger stems and concurrently greater maximum vessel lengths due to more rapid early growth.

Among the evergreen species of chaparral shrubs of southern California, there is great variability in resistance to cavitation (P_{50}) as well as variability in maximum seasonal water stress (P_{min}). These large differences illustrate the heterogeneity that can exist within a single plant community of superficially similar species. Within the chaparral community, water-stress tolerance is related to several xylem traits, including xylem density, stem strength, and fiber anatomy. Resistance to cavitation is also correlated with traits associated with conductive efficiency. However, based on PIC analyses, our data suggest that evolutionary tradeoffs with cavitation resistance (P_{50}) among species of chaparral shrubs occur primarily in xylem construction costs (wood density) and fiber reinforcement (transverse fiber wall area and MOR), and not vessel dimensions ($(t/b)_h^2$, d_h, maximum vessel length) or hydraulic efficiency (K_s). For most species, selection for freezing tolerance does not appear to have strongly influenced the xylem traits we examined. The greater cavitation resistance of nonsprouting chaparral species relative to facultative- and obligate-sprouting species suggests that traits associated with post-fire regeneration type, such as rooting depth and microsite preference, may also be associated with differential cavitation resistance.

Acknowledgments

The authors thank the National Science Foundation (NSF) for supporting this research with grants DBI-0243788, IBN-0130870, and IBN-0131247. We also thank NSF for a Graduate Research Fellowship supporting the primary author. We thank David D. Ackerly for valuable advice, William A. Paddock III and Kristine A. Kern for their assistance in making stem mechanical measures, and Brad Marks and Steve Marquie for Instron Universal Machine use.

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