Cavitation resistance and seasonal hydraulics differ among three arid Californian plant communities

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ABSTRACT

Vulnerability to water stress-induced cavitation was measured on 27 woody shrub species from three arid plant communities including chaparral, coastal sage and Mojave Desert scrub. Dry season native embolism and pre-dawn water potential, and both wet and dry season xylem specific hydraulic conductivity (K_s) were measured. Cavitation resistance, estimated as water potential at 50% loss in conductivity (Ψ_{50}), was measured on all species during the wet season and on a subset of species during the dry season. Cavitation resistance varied with sampling season, with 8 of 13 sampled species displaying significant seasonal shifts. Native embolism and water potential were useful in identification of species displaying seasonal shifts. The K_s was not different among sites or seasons. The Ψ_{50} varied among species and communities. Within communities, interspecific variation may be partially explained by differences in rooting depth or leaf habit (evergreen, semi-deciduous, deciduous). Communities diverged in their Ψ_{50} with chaparral species displaying the greatest cavitation resistance regardless of sampling season. The greater cavitation resistance of chaparral species is surprising, considering the greater aridity of the Mojave Desert site. Adaptation to arid environments is due to many plant traits, and aridity does not necessarily lead to convergence in cavitation resistance.

Key-words: cavitation fatigue; chaparral; coastal sage scrub; embolism; hydraulic conductivity; leaf habit; Mojave Desert scrub; native embolism; water stress; xylem.

INTRODUCTION

Woody plant species from arid communities are more resistant to water stress-induced cavitation than species from more mesic regions when compared across broad spatial scales (Brodribb & Hill 1999; Maherali, Pockman & Jackson 2004). This same pattern is present across smaller scales such as the transition from riparian to upland communities in the Sonoran Desert (Pockman & Sperry 2000). In addition to moisture availability, growth form and leaf habit may also influence cavitation resistance, with shrubs having greater resistance to cavitation than trees (Maherali *et al.* 2004) and a trend for evergreen shrubs to have greater resistance to cavitation than deciduous shrubs (Martínez-Vilalta *et al.* 2002; Maherali *et al.* 2004). Aridland shrub communities, particularly those with evergreen species, may be convergent in containing species that are highly cavitation resistant [water potential at 50% loss in hydraulic conducticity (Ψ_{50}) < –4 MPa].

There have been several studies examining cavitation resistance of species within arid plant communities (c.f. Sobrado 1997; Hacke, Sperry & Pittermann 2000; Pockman & Sperry 2000; Martínez-Vilalta *et al.* 2002; Sperry & Hacke 2002; Jacobsen *et al.* 2007b); however, there have been far fewer studies comparing species across different types of arid communities. These studies have often been limited to few species (Kolb & Davis 1994, however, see Pockman & Sperry 2000) or investigations of a few widely distributed generalist species whose ranges overlap different communities (Mencuccini & Comstock 1997; Kolb & Sperry 1999b; Stout & Sala 2003). While a recent meta-analysis compared resistance to cavitation across expansive vegetation types (Maherali *et al.* 2004), such broad studies can be problematical because they do not control for data gathered across different seasons and years, and the utilization of different methods. There have been few, if any, comparisons among arid plant communities utilizing common methods and taking into account seasonal variation.

Vulnerability of stems to cavitation has been shown to vary greatly over the course of the growing season (from a Ψ_{50} of approximately –1.6 to –4.5 MPa over 3 months for *Artemisia tridentata*; Kolb & Sperry 1999a) as well as following drought or freezing stress (Hacke *et al.* 2001; Sperry *et al.* 1994, respectively). Such shifts can lead to significant changes in the vulnerability of stems to cavitation seasonally and, if widespread, may have a great effect on species and community comparisons. The season in which species are sampled is rarely reported; however, for studies that do report sampling season, there is considerable variation (c.f. Sobrado 1997; Tyree, Patiño & Becker 1998; Kolb & Sperry 1999b; Hacke *et al.* 2000; Martínez-Vilalta *et al.* 2002; Stout & Sala 2003; Ewers *et al.* 2004; Jacobsen *et al.* 2007b). While techniques have been developed for correcting for freezing

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or water stress-induced cavitation fatigue, such as calculating loss in conductivity relative to the conductivity after application of a modest negative pressure (>–0.5 MPa; Hacke *et al.* 2000; Sperry & Hacke 2002; Maherali *et al.* 2006), it is possible that shifts occurring during the growing season may be harder to standardize.

In the current study, we examined, in the same year and season, the resistance to water stress-induced cavitation (estimated by Ψ_{50} and Ψ_{75}) among three arid plant communities of southern California including chaparral, coastal sage scrub and Mojave Desert scrub communities. Vulnerability to cavitation curves were determined for 27 shrub species including 12 for which no vulnerability curves have previously been published. In addition to vulnerability curves, native per cent loss in hydraulic conductivity (PLC) (i.e. native embolism) and pre-dawn water potential were measured on plants during the dry season, and xylem specific conductivity (K_s) was measured in both the wet and dry seasons. In order to evaluate the possibility of seasonal shifts in cavitation resistance among these species, which may complicate comparisons with previously published curves, vulnerability to cavitation curves were measured during both the wet and dry seasons on a subset of these species.

We predicted that among these three arid communities, species would show similar mean xylem resistance to water stress-induced cavitation and a similar range in values. This is consistent with findings of similar ranges and means in Ψ_{50} among woody species from Mediterranean-type climate regions compared to deserts in a recent meta-analysis (Maherali *et al.* 2004). Additionally, this is consistent with predictions of plant functional convergence in response to similar environments (Meinzer 2003).

METHODS

Sites and Species

Three diverse aridland plant communities were selected based on their high prevalence of woody shrub species. All sites were located in the winter rainfall–summer dry area of southern California, USA. The chaparral site was located in Cold Creek Canyon Preserve in the Santa Monica Mountains. The coastal sage scrub site was located on the campus of Pepperdine University in an ecological preserve also located in the Santa Monica Mountains. These two sites experienced similar precipitation over the course of the study (February 2006–February 2007: 433 and 406 mm, respectively) and similar cold season mean temperatures (10 °C compared to 9 °C at the chaparral site), but the coastal sage scrub site had slightly higher mean summer temperatures (26 °C compared to 23 °C at the chaparral site) and a narrower daily temperature range (approximately 10 °C compared to 16 °C for the coastal sage and chaparral sites, respectively). The Mojave Desert site was located in Red Rock Canyon State Park and experienced less annual precipitation for the year sampled than the other two sites (138 mm). This site had similar summer

mean temperatures as the coastal sage scrub (26 °C) site but had cooler mean winter temperatures than either of the other two sites (4 °C).

All of the woody shrub species with unbranched, straight stems longer than 14 cm that had at least 12 individuals present at a site were included in the present study (Table 1) with two exceptions. *Arctostaphylos glauca* was excluded from the chaparral site because it is locally rare and we did not have permission to sample it, and *Gutierrezia microcephala* was excluded from the Mojave Desert site because we were unable to measure the hydraulic flow due to vessel blockage in this species. The remaining species included 10 chaparral species, 9 coastal sage scrub species and 9 Mojave Desert scrub species. These species represent 15 families and several leaf habits (Table 1). Nomenclature follows Hickman (1993). One species, *Malosma laurina*, occurred at both the chaparral and coastal sage scrub sites, and was sampled at both making the total number of sampled species 27.

Soil texture, which can influence xylem cavitation resistance (Sperry & Hacke 2002), was measured beneath one individual of each species at each site ($n = 9$–10 per site). Soil was collected from surface level to a depth of 30 cm, and the texture was determined using the hydrometer method (Soil hydrometer; VWR Scientific, West Chester, PA, USA) described in Sheldrick & Wang (1993). Soil texture was not different among sites, with no significant differences in the sand, clay or silt fractions among sites ($P > 0.05$ for all). All soil samples fell within the Sand to Loamy Sand categories.

Wet season vulnerability to cavitation

Wet season vulnerability to cavitation was measured from February through early July 2006 on at least six individuals per species. The last rainfall of the wet season at all sites occurred on 18–23 May, and water potentials of plants did not begin to decline until late July. Stems were trimmed underwater in the field to a length of approximately 30 cm, sealed in plastic bags with a moist paper towel, placed in a cooler on ice and transported to the laboratory at California State University, Bakersfield (CSUB) where they were refrigerated until measured (within 4 d of field collection). Stems were trimmed underwater from both ends until a segment 4–8 mm in diameter and 14 cm in length was obtained, except for stems of *Adenostoma fasciculatum*, *Ceanothus cuneatus*, *Ceanothus megacarpus* and *Larrea tridentata*. For these species, stem segments at least 50 cm long where collected in the field. These stems were then trimmed underwater to 27 cm in length in the lab. The longer stem sizes were needed for use in a larger rotor, which could generate more negative pressures because prior studies indicated this may be needed for these species (Pockman & Sperry 2000; Jacobsen *et al.* 2007b).

Vulnerability to cavitation was determined for stem segments as described in Jacobsen *et al.* (2005). In brief, stems were connected to a tubing system and were flushed for 1 h at 100 kPa, and the maximum hydraulic conductivity

Table 1. Vegetation community, location and sampled species within each community along with families, codes and leaf habits

Vegetation type and location	Species	Family	Species code	Leaf habit[d]
Chaparral – Cold Creek Canyon Preserve, Santa Monica Mountains, CA, USA (34.5 N 118.4 W)				
	Adenostoma fasciculatum Hook. & Arn.	Rosaceae	Af	E
	Adenostoma sparsifolium Torrey	Rosaceae	As	E
	Arctostaphylos glandulosa Eastw.	Ericaceae	Ag	E
	Ceanothus cuneatus (Hook.) Nutt.	Rhamnaceae	Cc	E
	Ceanothus megacarpus Nutt.	Rhamnaceae	Cm	E
	Ceanothus oliganthus Nutt.	Rhamnaceae	Co	E
	Ceanothus spinosus Nutt.	Rhamnaceae	Cs	E
	Malosma laurina (Nutt.) Abrams[a]	Anacardiaceae	Ml	E
	Quercus berberidifolia Liebm.	Fagaceae	Qb	E[b]
	Rhus ovata S. Watson	Anacardiaceae	Ro	E
Coastal sage scrub – preserve located at Pepperdine University, Malibu, CA, USA (34.2 N 118.4 W)				
	Artemisia californica Less.	Asteraceae	Ac	SD, FDD
	Encelia californica Nutt.	Asteraceae	Eca	D
	Eriogonum cinereum Benth.	Polygonaceae	Eci	E, FDD
	Hazardia squarrosa (Hook. & Arn.) E. Greene	Asteraceae	Hs	E, FDD
	Lotus scoparius (Nutt.) Ottley	Fabaceae	Ls	D, PS
	Malacothamnus fasciculatus (Torrey & A. Gray) E. Greene	Malvaceae	Mf	SD, FDD
	Malosma laurina (Nutt.) Abrams[a]	Anacardiaceae	Ml	E
	Salvia leucophylla E. Greene	Lamiaceae	Sl	SD, FDD
	Salvia mellifera E. Greene	Lamiaceae	Sm	SD, FDD
Mojave Desert scrub – Red Rock Canyon State Park, CA, USA (35.2 N 117.6 W)				
	Ambrosia dumosa (A. Gray) Payne	Asteraceae	Ad	SD, FDD
	Atriplex canescens (Pursh) Nutt.	Chenopodiaceae	Ac	E, FDD
	Atriplex polycarpa (Torrey) S. Watson	Chenopodiaceae	Ap	E
	Coleogyne ramosissima Torrey	Rosaceae	Cr	SD, FDD
	Hymenoclea salsola A. Gray	Asteraceae	Hs	SD, FDD, PS
	Isomeris arborea Nutt.	Capparaceae	Ia	SD, FDD, PS
	Larrea tridentata (DC.) Cov.	Zygophyllaceae	Lt	E
	Lepidospartum squamatum (A. Gray) A. Gray	Asteraceae	Ls	E[c]
	Lycium andersonii A. Gray	Solanaceae	La	D

[a]Formerly *Rhus laurina*; this species was present at both the chaparral and coastal sage scrub sites.
[b]May be facultatively drought deciduous during extreme drought events (Pratt and Davis, unpublished data) but was not during the studied time period in the present study.
[c]Scale-like leaves.
[d]E, evergreen; SD, semi-deciduous; FDD, facultatively drought deciduous; D, deciduous; PS, photosynthetic stems.

(K_{hmax}) of stems was measured gravimetrically (Sperry, Donnelly & Tyree 1988) using an analytical balance (CP124S; Sartorius, Goettingen, Germany). Following the determination of their K_{hmax}, stems were spun in a centrifuge (Sorvall RC-5B Refrigerated Superspeed Centrifuge or RC-5C; Thermo Fisher Scientific, Waltham, MA, USA), using either a small (for 14 cm stem segments) or a large (for 27 cm stem segments) custom-built rotor (Alder *et al.* 1997). Vulnerability to cavitation curves were constructed by plotting the water potential (generated using the centrifuge) versus the PLC. For each stem, curves were fit with a second-order polynomial model (Jacobsen *et al.* 2007b).

Additionally, PLCs were calculated, and curves were generated using the K_h from an initial spin of −0.25 to −0.5 MPa in place of the K_{hmax} in order to correct for cavitation fatigue of the xylem (Hacke *et al.* 2000; Sperry & Hacke 2002; Maherali *et al.* 2006). This is performed because xylem conduits that were previously embolized or damaged may become conductive following flushing, resulting in an elevated K_{hmax}. Using K_h following a relatively mild pressure (>−0.5 MPa) embolizes these non-functional conduits while leaving functional conduits intact, thus yielding a more realistic K_{hmax}. These corrected curves were then used to predict the water potential at 50 and 75% loss in hydraulic conductivity (Ψ_{50} and Ψ_{75}, respectively) for each stem, and these values were averaged to get a species mean ($n = 6$–12 per species with a greater number of samples for those species for which no prior data existed on vulnerability to cavitation).

The xylem specific hydraulic conductivity (K_s) of stems was determined using the methods described in Jacobsen *et al.* (2007a). Stained active xylem area was determined using a digital camera and image analysis software (Olympus SP-500UZ; Olympus Imaging Corp., Center Valley, PA, USA, and Scion Image v. Beta 4.0.3; Scion Corp., Frederick, MD, USA). The whole xylem area in cross-section (minus the pith) was also determined. The K_{hmax} was then divided by either the active (stained) xylem area or the whole xylem area to obtain two different measures of xylem specific conductivity (K_s).

Dry season pre-dawn water potential and native PLC

In September 2006, branchlets from six individuals of each of four species, *Atriplex polycarpa*, *Hymenoclea salsola*, *Isomeris arborea* and *L. tridentata*, were collected pre-dawn, and water potential was immediately determined in the field using a pressure chamber (Model 2000 Pressure Chamber Instrument; PMS Instrument Company, Albany, OR, USA). A second set of branchlets were collected at the same time from the same individuals, double bagged, placed in a cooler on ice and transported to CSUB where they were rapidly processed in an air-conditioned lab using the same pressure chamber. Additionally, stem segments from the same individuals were collected pre-dawn. Leaves were removed from these branches prior to the branches being removed from the plant, stems were then double-bagged, placed in a cooler on ice and transported to CSUB where xylem segments of approximately 4 mm were rapidly excised and placed into calibrated psychrometers (PST-55-30-SF; Wescor Inc., Logan, UT, USA) connected to a microvolt meter (HR-33T Dew Point Microvoltmeter; Wescor Inc., Logan, UT, USA) for determination of the stem xylem water potential. For these four species, there was no significant difference between water potential measured on branchlets in the field or laboratory ($P > 0.05$ for all); therefore, for the remaining 23 species, branchlets were transported to the lab at CSUB (for the Mojave Desert species) or Pepperdine University (for the chaparral and coastal sage scrub species) for measures of branchlet water potential.

Pre-dawn water potential was measured during the dry season (measurements made on 30 August 2006 through 6 September 2006). Six individuals were measured per species. On the same mornings that pre-dawn branchlet water potential was determined, stems approximately 0.5 m in length were collected from the same individuals to determine native embolism. Stems were cut from the plant while underwater to prevent the introduction of air into the xylem. The end of each stem was covered with a small piece of moist paper towel and sealed with parafilm laboratory film, and the whole branch was double-bagged in plastic bags containing moist paper towels. Branches were rapidly transported to the lab at CSUB or Pepperdine University and were measured within 5 h of collection. Stems were trimmed underwater from both ends until an unbranched straight stem segment 10 cm in length and 4–8 mm in diameter was obtained. These stems were connected to a tubing manifold, and the native K_h was determined gravimetrically. Stems were then flushed following the procedure described previously, and K_{hmax} was determined. Using these values, the native PLC of stems was determined. Native PLC was not measured on *Malacothamnus fasciculatus* because of mucilaginous clogging of stems. Stems were then sectioned at their midpoint, and whole xylem area in cross-section (minus the pith) was determined. The K_{hmax} was then divided by the whole xylem area to obtain the xylem specific conductivity (K_s) for the dry season.

Dry season vulnerability to cavitation

Four or five species were selected at each site for determination of dry season vulnerability to cavitation. We attempted to measure the species with the most negative wet season Ψ_{50} in order to determine the species with the greatest cavitation resistance at each site and also to sample phylogenetically diverse species. Dry season vulnerability curves were constructed using the same methods as described for the wet season vulnerability curves. Dry season curves were measured during November and December 2006 when plants were at or near their annual minimum water potential (Jacobsen, unpublished data). Dry season measures were halted after the onset of significant winter rain in mid-December, and for this reason, we were unable to measure dry season curves on additional species.

Statistical analyses

Statistical analyses were preformed using Minitab (Release 14.12.0; Minitab Inc., State College, PA, USA) and/or Stat-view (v. 5.0.1; SAS Institute Inc., Cary, NC, USA). Alpha was set at 0.05 for all comparisons. Water potential as measured on branchlets using the pressure chamber in the lab or field, or on stem xylem using psychrometers were compared within species using analyses of variance (ANOVAS), followed by a Fisher's PLSD post hoc analysis when appropriate. Interspecific differences in Ψ_{50} were analyzed within site using ANOVAS, and ANOVAS were also used to analyze across site differences in Ψ_{50}, Ψ_{min} and K_s. For comparisons of Ψ_{50} and Ψ_{75} among species with different leaf habits, species were grouped into three categories: evergreen, semi-deciduous or deciduous; and ANOVAS were used.

Non-fatigue-corrected vulnerability to cavitation curves were used to predict the expected PLC at the pre-dawn water potential for comparison with the dry season field-measured native PLC. For comparison of the measured native PLC with the wet and/or dry season calculated PLC, *t*-tests were used. For seasonal comparisons of wet and dry season Ψ_{50} and Ψ_{75} within species, *t*-tests were used, and species were considered to have a significant seasonal shift in their vulnerability to cavitation if either of those parameters differed significantly. For comparisons within individual species of wet season-stained K_s, wet season K_s and dry season K_s, ANOVAS were used.

RESULTS

Wet season vulnerability to cavitation

The 27 species showed a range of cavitation resistances. This is indicated by the variation in the size and magnitude of their wet season vulnerability to cavitation curves, with curves ranging in shape from convex to linear to concave (Figs 1–3). In regression analyses of these vulnerability to cavitation curves, water potential described more than 82% of the variation in PLC in all cases (i.e. $r^2 > 0.82$), and often much more (most $r^2 > 0.95$).
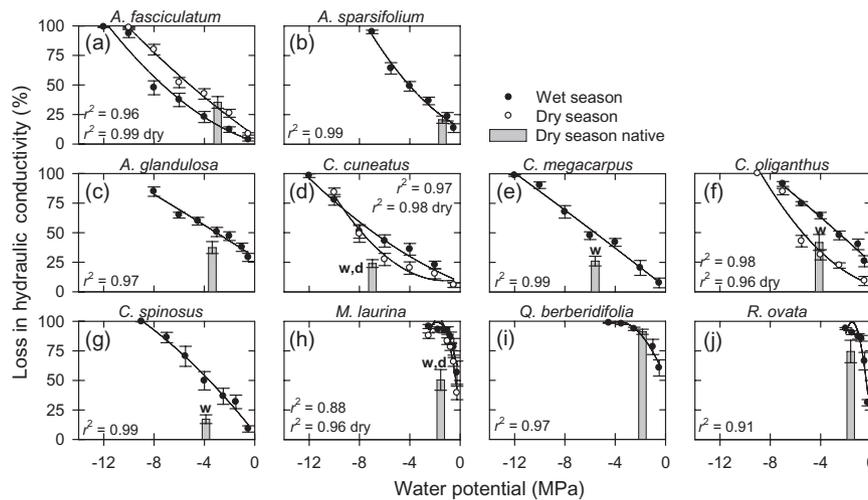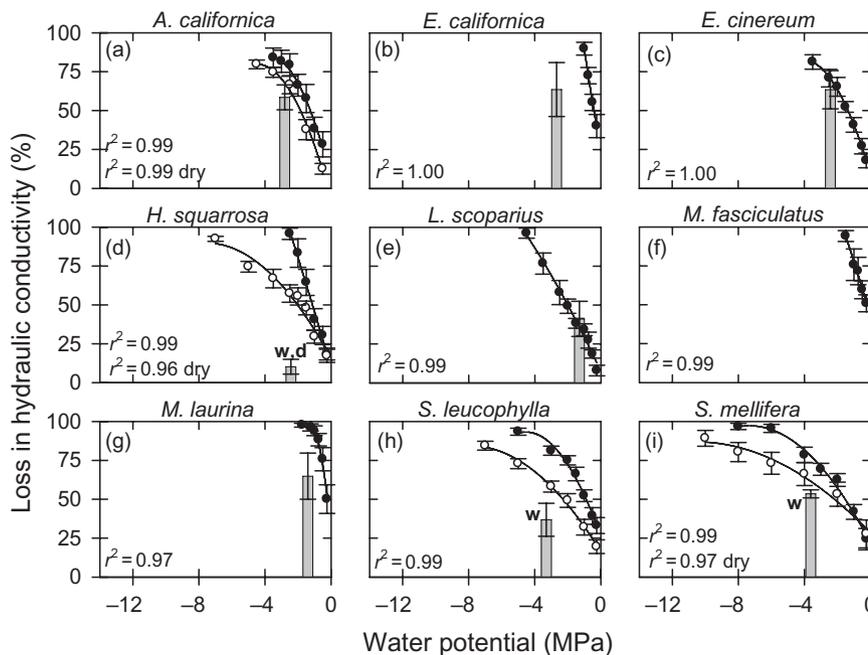
Figure 1. Vulnerability to cavitation curves measured on 10 chaparral shrub species (a–j; see Table 1 for full species names) during the wet season (February–May 2006; closed circles, mean ± 1 SE; $n = 6$–12) and for four species measured during the dry season (August–December 2006; open circles, mean ± 1 SE; $n = 6$). Curves shown are uncorrected for xylem fatigue (see Methods). Native per cent loss in conductivity (PLC) and pre-dawn water potential from the dry season are also shown (grey bars, mean ± 1 SE; $n = 6$). A 'w' indicates that native PLC are significantly different from those predicted by wet season vulnerability curves, and a 'd' indicates that native values are significantly different from those predicted by dry season vulnerability curves.
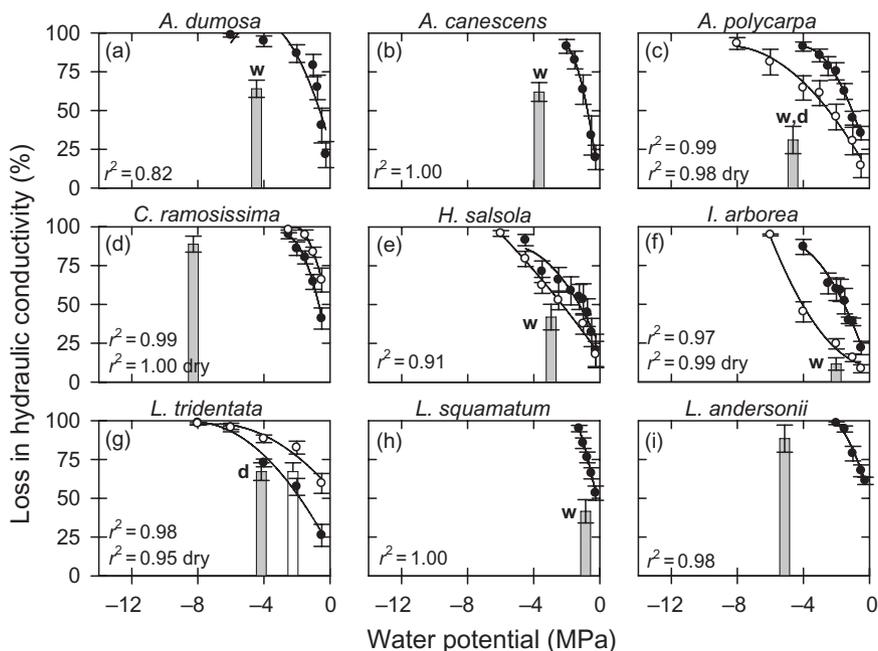
Wet season vulnerability to cavitation (estimated by the mean water potential at 50% loss in hydraulic conductivity; Ψ_{50}) was significantly different among the three arid communities ($P = 0.003$). The Ψ_{50} ranged from –0.5 (*M. laurina*) to –9.5 MPa (*A. fasciculatum*) (Fig. 4). The chaparral species were significantly more cavitation-resistant (lower Ψ_{50}) than the coastal sage scrub ($P = 0.003$) and the Mojave Desert scrub species ($P = 0.003$), with 7 out of 10 chaparral species displaying greater resistance than the most resistant species of either of the other two communities. The Mojave Desert and coastal sage scrub species were not different

from one another ($P = 0.909$) (Fig. 4b inset). Water potential at 75% loss in hydraulic conductivity followed the same pattern as Ψ_{50} (not shown), and non-fatigue-corrected values were positively correlated with fatigue-corrected values ($P < 0.001$; not shown). *M. laurina* was the only species that occurred at more than one site, in both the chaparral and coastal sage scrub, and its Ψ_{50} and Ψ_{75} did not vary between sites ($P = 0.471$ and 0.652 for Ψ_{50} and Ψ_{75}, respectively).

Species displaying different leaf habits (i.e. species with evergreen, semi-deciduous or deciduous leaves) did not

Figure 2. Vulnerability to cavitation curves measured on nine coastal sage scrub species (a–i; see Table 1 for full species names) during the wet season (February–May 2006; closed circles, mean ± 1 SE; $n = 6$–12) and for four species measured during the dry season (August–December 2006; open circles, mean ± 1 SE; $n = 6$). Curves shown are uncorrected for xylem fatigue (see Methods). Native per cent loss in conductivity (PLC) and pre-dawn water potential from the dry season are also shown (grey bars, mean ± 1 SE; $n = 6$). A 'w' indicates that native PLC are significantly different from those predicted by wet season vulnerability curves, and a 'd' indicates that native values are significantly different from those predicted by dry season vulnerability curves.

Figure 3. Vulnerability to cavitation curves measured on nine Mojave Desert scrub species (a–i; see Table 1 for full species names) during the wet season (February–May 2006; closed circles, mean ± 1 SE; $n = 6$–12) and for five species measured during the dry season (August–December 2006; open circles, mean ± 1 SE; $n = 6$). Curves shown are uncorrected for xylem fatigue (see Methods). Native per cent loss in conductivity (PLC) and pre-dawn water potential from the dry season are also shown (grey bars, mean ± 1 SE; for pre-dawn water potential as measured with psychrometers, white bar ± 1 SE; $n = 6$). A 'w' indicates that native PLC are significantly different from those predicted by wet season vulnerability curves, and a 'd' indicates that native values are significantly different from those predicted by dry season vulnerability curves.

significantly differ in either Ψ_{50} or Ψ_{75} ($P = 0.186$ and 0.188, respectively; see Table 1 for leaf habits of individual species). However, there was a trend for evergreen species to be more resistant to cavitation. Evergreen species had a mean Ψ_{50} of -3.1 ± 0.6 MPa compared to -1.8 ± 0.2 and -1.4 ± 0.5 MPa for the semi-deciduous and deciduous species, respectively.

Dry season pre-dawn water potential and native PLC

Mean native PLC measured in September was near 50% for all communities and was not different among communities (Figs 1–3; $P = 0.417$). Mean native PLC for the chaparral was $41.8 \pm 7.6\%$ versus $49.0 \pm 6.7\%$ for the coastal sage scrub and $55.6 \pm 7.7\%$ for the Mojave Desert scrub. Among individual species, native PLC ranged from 10.2% in *Hazardia squarrosa* to 91.9% in *Quercus berberidifolia*. Native PLC significantly differed from the PLC predicted

by wet season vulnerability curves and pre-dawn branchlet water potential in 14 out of 26 species (Figs 1–3; $P > 0.05$). Note, only 26 species were included in this analysis because we were unable to measure the native PLC on *M. fasciculatus* (see Methods).

Pre-dawn branchlet water potential (Ψ_{pd}) measured in September during the collection of native PLC values was not different among the three communities ($P = 0.151$). The mean $\Psi_{pd} \pm 1$ SE was -3.32 ± 0.59 MPa for the chaparral, -2.42 ± 0.26 MPa for the coastal sage scrub and -4.06 ± 0.70 MPa for the Mojave Desert scrub (grey bars in Figs 1–3).

Xylem specific conductivity (K_s) did not differ among the three communities (Fig. 5c inset; $P = 0.107$). None of the measured species experienced a significant change in xylem specific conductivity from the wet season to the dry season (grey versus open bars in Fig. 5). For several species, not all growth rings in the xylem area were active as indicated by a significant difference between the stained area wet season
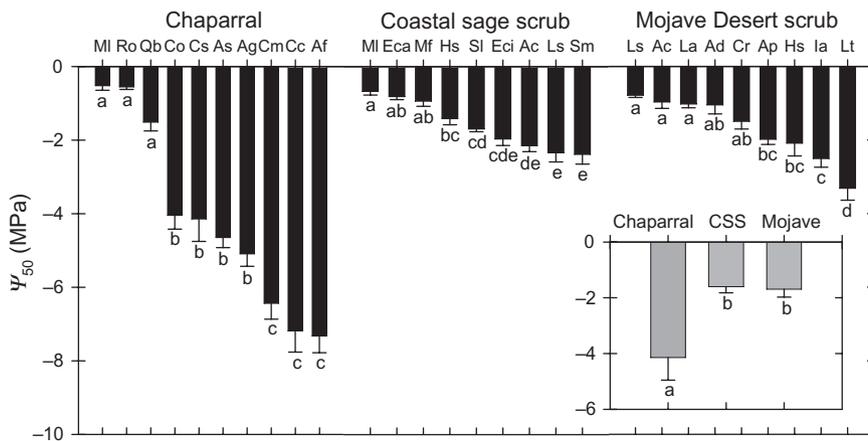
Figure 4. Water potential at 50% loss in hydraulic conductivity (Ψ_{50}) for 27 species from three arid plant communities (black bars, mean ± 1 SE; $n = 6$–12) corrected for fatigue (see Methods). Different letters indicate significant differences between species within a community. See Table 1 for species codes. Inset shows the mean Ψ_{50} for each community (grey bars ± 1 SE), and unique letters indicate significant differences among communities.
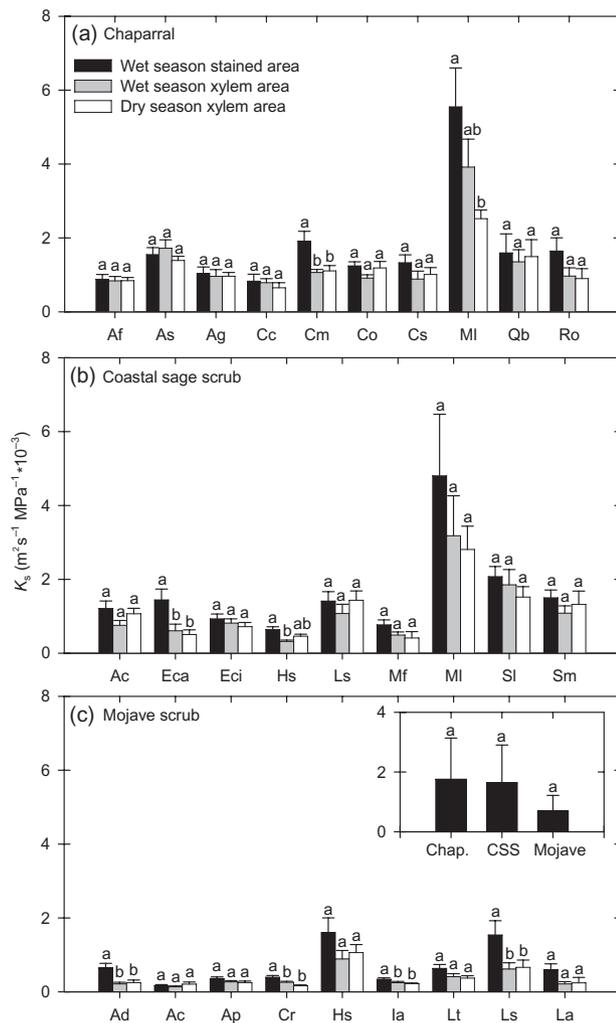
Figure 5. Xylem specific conductivity (K_s) for 27 species from three different arid plant communities: chaparral (a), coastal sage scrub (b) and Mojave scrub (c), as determined during the wet season (black and grey bars, mean ± 1 SE; $n = 6–12$) and dry season (open bars, mean ± 1 SE; $n = 6$). See Table 1 for species codes. Wet season K_s was determined by dividing the maximum hydraulic conductivity (K_{hmax}) by either the stained active area (black bars) or the whole xylem area (grey bars). Dry season K_s was determined by dividing K_{hmax} by the whole xylem area only (open bars). Unique letters indicated significant differences between measures within a species. Inset in c shows the mean wet season stained K_s for each community (black bars, mean ± 1 SE), and letters indicate that there was not a significant difference in K_s among communities.

K_s versus the whole xylem area wet season K_s (black versus grey bars in Fig. 5).

For four species in which water potentials were measured on branchlets in the field and laboratory, there was no significant difference between these water potentials ($P > 0.05$ for all; data not shown). For three out of four species, these branchlet water potentials were also not different from stem xylem water potentials as measured with psychrometers ($P > 0.05$; data not shown); however, for one species, *L. tridentata*, the stem xylem water potential measured

by psychrometers was significantly more hydrated than branchlet water potential measured using a pressure chamber ($P < 0.001$ for stem water potential compared to both the lab- and field-measured branchlet water potentials; data not shown).

Dry season vulnerability to cavitation

Among the 13 species for which dry season vulnerability to cavitation curves were measured, there was great variability in seasonal response when compared with wet season vulnerability curves. In some species, the dry season curve was more vulnerable (Figs 1a & 3g), in others, there was no significant difference (Figs 1d, 2a & 3d,e), and in others, the dry season curve was more resistant (Figs 1f, 2d,h,i & 3c,f). Of the 13 species for which dry season vulnerability to cavitation curves were measured, five had predicted PLC that was significantly different from the measured native PLC (Figs 1–3; $P > 0.05$). However, if the stem xylem water potential for *L. tridentata* is used instead of the branchlet value, both the dry season and wet season curves predict PLC for *Larrea* (open bar, Fig. 3g), reducing this to four of 13 species that have predicted PLC that are different from the measured native PLC.

Dry season Ψ_{50} and Ψ_{75} values differed significantly from wet season values in eight of 13 species (Fig. 6). In most of these cases, the dry season value was lower than the wet season value, indicating a shift towards being more resistant to cavitation during the dry season. However, in two cases, the dry season value was higher than the wet season value (*A. fasciculatum* and *L. tridentata*). Wet season and dry season Ψ_{50} were significantly correlated ($P < 0.001$).

DISCUSSION

Non-convergence of cavitation resistance

Across three arid plant communities, shrub species appear to diverge in their cavitation resistance in spite of similar growth form and environment. Among 27 woody shrub species from three arid shrub plant communities, there is considerable variability in vulnerability to water stress-induced cavitation. Within communities, this variability may be due to differences in rooting depth or heterogeneity of soil moisture availability within sites (Jacobsen *et al.* 2005; Jacobsen *et al.* 2007b). While soil texture of shallow soils was similar among sites and did not vary greatly within sites, deeper soil layers may exhibit greater heterogeneity (c.f. Davis & Mooney 1985). Differences in rooting depths and physiological traits among species are likely primary determinants of variability in vulnerability to cavitation. Indeed, a previous investigation found a similar range in cavitation resistance (Ψ_{50}) as found in the current study when comparing six co-occurring species of even-aged chaparral shrubs growing at the same microsite (Jacobsen *et al.* 2005).

While all three communities include species that are relatively vulnerable, the chaparral has many more species that are highly resistant to cavitation including seven species with
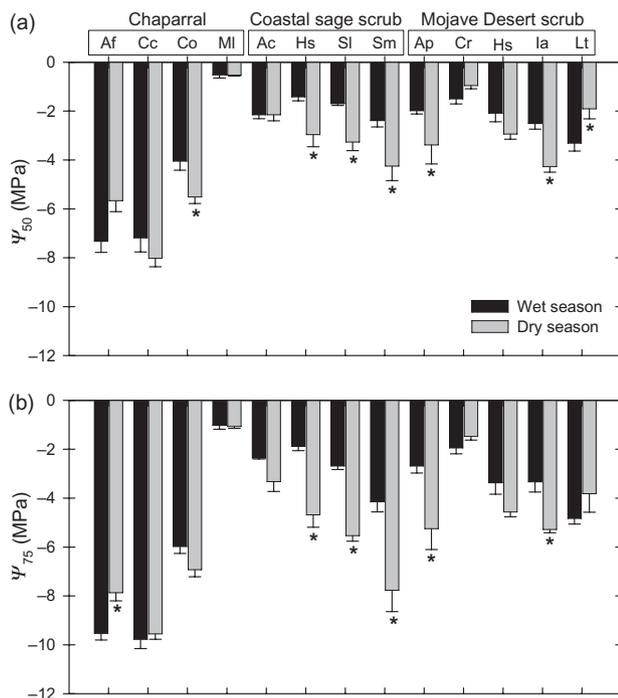
Figure 6. Mean water potential at 50% loss in hydraulic conductivity (Ψ_{50}) (a) and Ψ_{75} (b) for 13 species from three arid plant communities (black and grey bars ±1 SE) corrected for fatigue (see Methods for details). See Table 1 for species codes. Species means were determined from vulnerability to cavitation curves measured during the wet season (black bars) and dry season (grey bars). See Figs 1–3 for vulnerability to cavitation curves. An asterisk beneath the dry season bar indicates that the dry season and wet season Ψ_{50} or Ψ_{75} values were significantly different for that species. See Table 1 for species codes.

Ψ_{50} lower than –4 MPa. These species are more resistant than any species measured in either the coastal sage or Mojave Desert scrub. Indeed, chaparral species are, on average, more resistant to water stress-induced cavitation than species from the other two arid communities. This contrasts with findings of similar ranges and means in Ψ_{50} among woody species from deserts and winter rainfall regions when compared across a much broader scale (Maherali *et al.* 2004). Thus, species in these communities do not converge to a common level of xylem cavitation resistance as predicted. Additionally, the greater resistance of chaparral species to water stress-induced cavitation is surprising, considering the greater aridity of the Mojave Desert site (Maherali *et al.* 2004). This highlights that habitat aridity is not necessarily a good predictor of species resistance to water stress-induced cavitation across arid ecosystems.

Species in the coastal sage scrub and Mojave Desert scrub may have traits allowing them to mitigate extreme water stress in xylem tissues. This is supported by similar levels of native embolism among species in all three communities of approximately 50% loss in hydraulic conductivity during the dry season. This suggests that species are similarly avoiding high levels of xylem cavitation in spite of differences in cavitation resistance. Variation in leaf habit or

rooting depth among the sampled species may partially explain the different water stress-tolerating strategies among species, both within communities as well as between them. For instance, while the chaparral retain a near complete canopy throughout the dry season, many of the shrub species of the coastal sage and Mojave Desert are semi-deciduous or facultatively drought deciduous, and adjust their canopy size during the dry season. Additionally, chaparral species tend to be larger and have fuller canopies than species occurring in the other two communities (Jacobsen, unpublished data).

Seasonal shifts in cavitation resistance

Vulnerability to water stress-induced cavitation significantly varied depending on the season in which stems were measured. In many cases, non-fatigue-corrected wet season vulnerability curves were predictive of dry season native PLC. Native PLC values agreed with the PLC predicted by 13 out of 26 wet season curves, suggesting that seasonal shifts are not likely in these species. However, in 13 other species, native PLC was significantly different than that predicted by wet season vulnerability to cavitation curves. This suggested that shifts were likely, or alternatively, that branchlet water potential was in disequilibrium with stem xylem water potential in these other species. Indeed, of the 13 species for which vulnerability to cavitation curves were measured in both the wet and dry seasons, eight species displayed significant seasonal shifts. Most species shifted to become more resistant later in the season as was observed previously in *A. tridentata* (Kolb & Sperry 1999a), whereas a few species became more vulnerable during the dry season. Species in the present study experienced as much as a twofold change in vulnerability to cavitation from the wet season to the dry season, and seasonal shifts appear to be relatively common among shrub species in all three communities.

For a few species, *C. cuneatus*, *M. laurina*, *H. squarrosa* and *L. tridentata*, dry season vulnerability to cavitation curves predicted PLC values significantly higher than the measured dry season native PLC. This pattern has been reported previously for tropical shrubs and trees (Lopez *et al.* 2005), and may be due to branchlet water potentials that are more negative than the pressure experienced by the stem xylem on which native PLC is measured. This leads to artificially high predictions of PLC similar to the pattern seen in these species. Nighttime transpiration and solutes in the xylem sap have been found to partially explain this disequilibrium in arid plants (Donovan *et al.* 1999; Donovan, Linton & Richards 2001; Donovan, Richards & Linton 2003); however, solutes in the xylem sap do not seem likely for the species in the current study because we did not find significant xylem sap osmotic potential in individuals in which this was examined (Jacobsen, unpublished data). Evidence of pre-dawn disequilibrium between stem xylem and branchlets was found in one species. For *L. tridentata*, native PLC was not different from that predicted by either wet or dry curves if the water potential of stem xylem measured by psychrometers was used instead of branchlet water

potential measured by pressure chamber (Fig. 3g). For the five species in the present study for which native PLC differed significantly from predictions based on wet season vulnerability curves, but for which dry season vulnerability curves were not measured, seasonal shifts and/or disequilibrium are likely.

Shifts in vulnerability to cavitation may explain some of the variability among published curves. Vulnerability to cavitation of chaparral species, both from the wet and dry seasons are similar in range to those previously reported for these species (c.f. Jacobsen *et al.* 2005, 2007b; Pratt *et al.* 2007). There have been relatively few vulnerability curves published for coastal sage scrub species, but for the species for which there are published curves, *M. laurina* and *Salvia mellifera*, our results are within the same range of published values (Kolb & Davis 1994; Langan, Ewers & Davis 1997; Jacobsen *et al.* 2005, 2007b). For the Mojave Desert species, the curves for *L. tridentata* and *H. salsola* are similar and within the range of other published curves for these species (Pockman & Sperry 2000 and Mencuccini & Comstock 1997, respectively). For the other two species for which curves have been published, *Ambrosia dumosa* and *Atriplex canescens*, the curves in the present study were more vulnerable than those reported elsewhere (Mencuccini & Comstock 1997 and Hacke *et al.* 2000, respectively). This may have resulted because the curves in the present study for these species were wet season curves. A shift in *A. canescens* of similar magnitude to that found in the closely related species *A. polycarpa* would produce a dry season curve similar to that reported by Hacke *et al.* (2000).

Influence of seasonal shifts on interspecific and community comparisons

Wet season cavitation resistance was correlated to dry season cavitation resistance in the present study, and similar differences were found among communities when data were compared within a season (i.e. mean Ψ_{50} is approximately 2 MPa lower in the chaparral compared with the other two communities when either wet or dry season values were compared). However, results could be altered significantly if Ψ_{50} values from different seasons were used to compare communities. This suggests that care must be taken in comparison of vulnerability curves completed during different seasons or for which no sampling season is reported. This may complicate attempts to use published values in broad-scale meta-analyses. Measures of native embolism and water potential may be useful in identifying species in which seasonal shifts are likely or to validate existing curves.

Physiology of seasonal shifts

Seasonal shifts in vulnerability to water stress-induced cavitation are likely of physiological significance and may be due to maturation of xylem as suggested by Kolb & Sperry (1999a) or to changes in pit membranes or mechanical strength. Several of the species that experienced significant shifts in xylem vulnerability to cavitation in the present study also have a large portion of inactive xylem as indicated by the significant difference between stained xylem specific hydraulic conductivity (K_s) and whole xylem K_s in these species including *C. megacarpus*, *A. dumosa* and *I. arborea*. This suggests that vulnerability to cavitation curves in these species largely measure the vulnerability of newer xylem, and may therefore be sensitive to maturation of the xylem over the course of the growing season. It is unlikely that the shifts seen in the present study are the result of loss of function or sealing off of old wood or early wood over the course of the growing season, as is seen in ring-porous species because these would likely affect K_s or would result in high levels of cavitation fatigue, neither of which were observed. Additionally, such shifts could be explained by seasonal hydrogel or other pit membrane changes (Gascó *et al.* 2006, 2007) although such changes would also likely have resulted in significant differences in K_s seasonally.

Seasonal changes in xylem mechanical strength may influence xylem cavitation without affecting seasonal hydraulic conductivity. Young xylem may not contain enough mature and mechanically robust cells to buttress newly functional vessels against implosion when exposed to high tensions (Jacobsen *et al.* 2005). Indeed, seasonal changes in mechanical strength against stem breakage have been found among several species of Rhamnaceae shrubs of the California chaparral including the four *Ceanothus* species included in the present study (Pratt, unpublished data). These species experienced significant increases in modulus of rupture (MOR) from the wet season to the dry season. Seasonal changes in xylem biomechanics may have important implications for dry season acclimation of woody shrubs, perhaps through increased resistance to implosion (Jacobsen *et al.* 2005). This suggests that care should be taken in interpreting vulnerability curves collected on non-hardened xylem, which may not be indicative of dry season values. Thus, dry season vulnerability to cavitation curves may be preferable in determination of the resistance to cavitation of the hardened xylem that actually tolerates low-seasonal water potentials. Additionally, while dry season curves are likely to have greater levels of xylem fatigue compared with wet season curves, a standard fatigue correction can be applied to curves minimizing the influence of fatigue on comparisons (Hacke *et al.* 2000; Sperry & Hacke 2002; Maherali *et al.* 2006).

In the present study, the greater resistance to cavitation of chaparral shrub species compared to coastal sage or Mojave Desert shrub species is similar regardless of whether wet or dry season curves are examined. Curves for all 27 species were completed during the wet season, providing a more comprehensive comparison of these communities, and similar differences in cavitation resistance were also found when the fewer dry season curves were compared. To conclude, in spite of environmental similarities and the common stress of summer drought, species from

these three communities have diverged in their xylem physiology with chaparral species displaying the greatest resistance to water stress-induced xylem cavitation regardless of sampling season. Among these communities, species are likely utilizing differing suites of whole plant traits in order to persist in these arid environments.

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