



Comparative community physiology: nonconvergence in water relations among three semi-arid shrub communities

Anna L. Jacobsen¹, R. Brandon Pratt¹, Stephen D. Davis² and Frank W. Ewers³

¹Department of Biology, California State University, Bakersfield, 14 SCI, 9001 Stockdale Hwy, Bakersfield, CA 93311, USA; ²Natural Science Division, Pepperdine University, 24255 Pacific Coast Hwy, Malibu, CA 90263, USA; ³Biological Sciences Department, California State Polytechnic University, 3801 West Temple Ave, Pomona, CA 91768, USA

Summary

Author for correspondence:

Anna L. Jacobsen

Tel: +1 661 654 2572

Fax: +1 661 654 6956

Email: ajacobsen@csub.edu

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• Plant adaptations to the environment are limited, and therefore plants in similar environments may display similar functional and physiological traits, a pattern termed functional convergence. Evidence was examined for functional convergence among 28 evergreen woody shrubs from three plant communities of the semi-arid winter rainfall region of southern California.

• Both leaf and water relations traits were examined, including seasonal stomatal conductance (g_s), specific leaf area (SLA), leaf specific conductivity (K_l), seasonal water potential (Ψ_w), stem cavitation resistance (Ψ_{50}), and xylem density.

• Species display community-specific suites of xylem and leaf traits consistent with different patterns of water use among communities, with coastal sage scrub species utilizing shallow pulses of water, Mojave Desert scrub species relying on deeper water reserves, and chaparral species utilizing both shallow and deep moisture reserves. Communities displayed similar degrees of water stress, with a community-level minimum Ψ_w (Ψ_{wmin}) of c. -4.6 Mpa, similar to other arid communities. Pooled across sites, there was a strong correlation between Ψ_{wmin} and xylem density, suggesting that these traits are broadly related and predictive of one another.

• This comparative community physiology approach may be useful in testing hypotheses of functional convergence across structurally similar semi-arid communities.

Key words: cavitation resistance, chaparral, coastal sage, Mediterranean-type ecosystems, Mojave Desert, stomatal conductance, water potential, xylem density.

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Introduction

Plant functional convergence studies, at both the global and community levels, have suggested that plants may be limited in their physiological solutions to environmental stresses and that plants in similar environments may therefore display similar functional and physiological traits (Reich *et al.*, 1997, 2003; Pareulo *et al.*, 1998; Meinzer, 2003; Bucci *et al.*, 2004; Swenson & Enquist, 2007). At the global scale, strong correlations among species functional traits may represent necessary mechanistic relationships among traits. At the community level, separation of communities along these trade-off axes may differ among communities. Such findings

suggest that there is potential to predict plant traits and related ecological processes across broad regions based on environmental conditions. Additionally, such correlations may be useful in predicting plant traits in regions or communities that have been poorly studied. Many studies examining plant functional traits have examined plant form (Pareulo *et al.*, 1998), xylem density (Swenson & Enquist, 2007), water relations (Ackerly, 2004; Bucci *et al.*, 2004; Bhaskar & Ackerly, 2006), and leaf traits (Reich *et al.*, 1997; Ackerly, 2004) as traits associated with specific aspects of plant functional variation.

Across broad scales, plant form appears convergent, leading to the recognition of vegetatively similar biomes. A classic

example of this is convergence to a shrub-dominated landscape in Mediterranean-type climate regions (Aschmann, 1973; Pareulo *et al.*, 1998). These plant communities from around the world have often been compared with one another, although not in terms of the detailed physiological parameters used in the present study (Aschmann, 1973; di Castri & Mooney, 1973; Parsons & Moldenke, 1975; Cody & Mooney, 1978; Cowling & Campbell, 1980; Kruger *et al.*, 1983). While there appears to be great similarity in plant form among species occurring in these regions (i.e. shrubs with evergreen, tough leathery leaves), it is not clear that this morphological similarity corresponds with similar functional traits among species.

We examined evidence for functional convergence among the evergreen woody shrubs occurring in three semi-arid plant communities in the winter rainfall region of southern California. These communities included chaparral, coastal sage scrub, and Mojave Desert scrub. In the present study, we included leaf, stem, and water-relations traits. Leaf-level measurements included specific leaf area (SLA). Stem-level measurements included leaf and xylem specific conductivity (K_1 and K_s , respectively), xylem resistance to cavitation (Ψ_{50}), and xylem density (K_s and Ψ_{50} were previously reported by Jacobsen *et al.* (2007c)). To characterize plant water relations, seasonal measurements were made of stomatal conductance (g_s) and leaf branchlet water potential (Ψ_w) for 12–14 months. Additionally, temperature and precipitation were monitored at each site.

We predicted that the species occurring in these communities would display similar water-relations and functional traits in response to their common arid winter rainfall environment and that trait values of species among these communities would occupy similar ranges and fall along a common functional axis. We predicted that, among sites, species would experience dry season water potentials (Ψ_{wmin}) similar to their xylem cavitation resistance (Ψ_{50}) that have already been reported (Jacobsen *et al.*, 2007c). This would be consistent with the 1 : 1 relationship between Ψ_{wmin} and Ψ_{50} reported for arid communities, including 26 species of chaparral (Jacobsen *et al.*, 2007b; Pratt *et al.*, 2007a) and six shrubs from the Great Basin Desert (Hacke *et al.*, 2000). Based upon previously reported Ψ_{50} , a 1 : 1 relationship would result in differential Ψ_{wmin} among the sites such that the chaparral species would experience the lowest Ψ_{wmin} and species in the other two sites would experience less negative Ψ_{wmin} relative to the chaparral.

We predicted g_s would decline with declining Ψ_w during the course of the dry season when plant water status declined and the vapor pressure deficit increased (Poole & Miller, 1975; Davis & Mooney, 1985; Schulze, 1986; Thomas & Eamus, 1999; Brodribb & Holbrook, 2003, 2004; Barradas *et al.*, 2004; Ladjal *et al.*, 2005; Galmés *et al.*, 2007). Such a stomatal response is presumably necessary in order for plants to avoid extreme negative pressures and runaway cavitation during the dry season, especially among evergreen plants (Cochard *et al.*, 2002; Sperry *et al.*, 2002). Additionally, we predicted that

chaparral species would have a shallower slope in their relationship between Ψ_w and g_s (i.e. delayed stomatal closure), consistent with their more cavitation-resistant xylem (Ladjal *et al.*, 2005; Jacobsen *et al.*, 2007c).

Relationships among traits were also examined in order to determine the predictability of functional traits, employing traits that are commonly used as indices of plant functional variation across broad scales. We predicted that xylem density would be correlated with Ψ_{wmin} (Jacobsen *et al.*, 2007a,b), Ψ_{50} (Hacke *et al.*, 2000; Jacobsen *et al.*, 2007b), and g_s (Bucci *et al.*, 2004) when examined across sites. We predicted that SLA would be correlated with Ψ_{wmin} and Ψ_{50} since SLA is associated with increased aridity tolerance (Wright *et al.*, 2002). Lastly, we predicted that SLA, K_s , and K_1 would be associated with g_s (Sperry, 2000; Gullás *et al.*, 2003; Santiago *et al.*, 2004; Poorter & Bongers, 2006). Correlations between these traits were also analyzed using phylogenetic independent contrasts in order to account for the phylogenetic relationships among species in analyses (Felsenstein, 1985).

Materials and Methods

Sites and species

Three diverse aridland plant communities were selected based on their high diversity 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, also located in the Santa Monica Mountains; and the Mojave Desert site was located in Red Rock Canyon State Park (see Jacobsen *et al.*, 2007c for site descriptions).

All of the shrub species that occurred in sufficient numbers and for which we were able to obtain permission to sample were studied at each of these sites. This included 10 chaparral species, nine coastal sage scrub species, and 10 Mojave Desert species (see Table 1). Most of these species are evergreen (Jacobsen *et al.*, 2007c). At each site, six individuals of each species were tagged at the beginning of the study. All measurements throughout the course of this study were conducted on these same individuals.

Xylem specific conductivity (K_s) and vulnerability to cavitation (Ψ_{50}) were also measured on these same individuals or individuals of the same species located in close proximity to the sampled individuals. The Ψ_{50} used in the present study were calculated from fatigue-corrected vulnerability to cavitation curves (Jacobsen *et al.*, 2007c). These data were published as part of a separate study (Jacobsen *et al.*, 2007c).

Weather

Temperature and precipitation were monitored at sites via Remote Automated Weather Stations (RAWS) run by the

Table 1 Species listed by site, families, species codes, cavitation resistance (Ψ_{50}), xylem specific conductivity (K_s), specific leaf area (SLA), and xylem density for 28 shrub species from three sites in southern California

Vegetation type and species	Family	Species code	Ψ_{50} (MPa) ^a	K_s (m ² MPa ⁻¹ s ⁻¹ × 10 ³) ^b	SLA (mm ² mg ⁻¹)	Density (kg m ³)
Chaparral						
<i>Adenostoma fasciculatum</i> Hook. & Arn.	Rosaceae	Af	-7.33 ± 0.45	0.88 ± 0.13	5.91 ± 0.42	679.3 ± 12.8
<i>Adenostoma sparsifolium</i> Torrey	Rosaceae	As	-4.65 ± 0.27	1.55 ± 0.19	11.43 ± 1.38	619.8 ± 10.9
<i>Arctostaphylos glandulosa</i> Eastw.	Ericaceae	Ag	-5.09 ± 0.34	1.04 ± 0.18	5.20 ± 0.29	661.5 ± 18.5
<i>Ceanothus cuneatus</i> (Hook.) Nutt.	Rhamnaceae	Cc	-7.19 ± 0.58	0.83 ± 0.19	4.27 ± 0.13	678.1 ± 10.4
<i>Ceanothus megacarpus</i> Nutt.	Rhamnaceae	Cm	-6.44 ± 0.43	1.91 ± 0.27	4.06 ± 0.16	638.9 ± 11.4
<i>Ceanothus oliganthus</i> Nutt.	Rhamnaceae	Co	-4.05 ± 0.37	1.24 ± 0.11	11.06 ± 1.23	647.1 ± 8.2
<i>Ceanothus spinosus</i> Nutt.	Rhamnaceae	Cs	-4.14 ± 0.61	1.33 ± 0.21	6.91 ± 0.62	614.9 ± 10.8
<i>Malosma laurina</i> (Nutt.) Abrams	Anacardiaceae	Ml	-0.52 ± 0.12	5.55 ± 1.05	5.24 ± 0.16	496.6 ± 16.9
<i>Quercus berberidifolia</i> Liebm.	Fagaceae	Qb	-1.51 ± 0.24	1.59 ± 0.51	7.38 ± 0.37	724.2 ± 8.9
<i>Rhus ovata</i> S. Watson	Anacardiaceae	Ro	-0.56 ± 0.07	1.64 ± 0.36	4.41 ± 0.37	523.1 ± 8.9
Coastal sage scrub						
<i>Artemisia californica</i> Less.	Asteraceae	Ac	-2.15 ± 0.16	1.21 ± 0.20	20.09 ± 1.20	685.7 ± 14.7
<i>Encelia californica</i> Nutt.	Asteraceae	Eca	-0.82 ± 0.08	1.44 ± 0.29	14.01 ± 0.47	637.8 ± 16.9
<i>Eriogonum cinereum</i> Benth.	Polygonaceae	Eci	-1.97 ± 0.18	0.93 ± 0.13	5.41 ± 0.19	671.2 ± 24.0
<i>Hazardia squarrosa</i> (Hook. & Arn.) E. Greene	Asteraceae	Hs	-1.42 ± 0.16	0.64 ± 0.08	12.26 ± 0.59	557.9 ± 12.5
<i>Lotus scoparius</i> (Nutt.) Ottley	Fabaceae	Ls	-2.34 ± 0.25	1.41 ± 0.25	15.39 ± 0.85	613.7 ± 16.7
<i>Malacothamnus fasciculatus</i> (Torrey & A. Gray) E. Greene	Malvaceae	Mf	-0.94 ± 0.14	0.77 ± 0.13	12.03 ± 0.69	571.8 ± 19.2
<i>Malosma laurina</i> (Nutt.) Abrams	Anacardiaceae	Ml	-0.68 ± 0.10	4.80 ± 1.67	4.41 ± 0.18	467.2 ± 7.7
<i>Salvia leucophylla</i> E. Greene	Lamiaceae	Sl	-1.70 ± 0.07	2.07 ± 0.28	12.96 ± 1.36	503.1 ± 19.1
<i>Salvia mellifera</i> E. Greene	Lamiaceae	Sm	-2.39 ± 0.26	1.50 ± 0.21	8.89 ± 0.37	528.9 ± 10.0
Mojave Desert scrub						
<i>Ambrosia dumosa</i> (A. Gray) Payne	Asteraceae	Ad	-1.05 ± 0.24	0.65 ± 0.12	11.69 ± 1.09	711.2 ± 16.1
<i>Atriplex canescens</i> (Pursh) Nutt.	Chenopodiaceae	Ac	-0.97 ± 0.17	0.17 ± 0.03	4.92 ± 0.45	797.8 ± 9.9
<i>Atriplex polycarpa</i> (Torrey) S. Watson	Chenopodiaceae	Ap	-1.98 ± 0.14	0.36 ± 0.05	4.62 ± 0.83	810.7 ± 10.4
<i>Coleogyne ramosissima</i> Torrey	Rosaceae	Cr	-1.50 ± 0.21	0.39 ± 0.05	10.57 ± 1.35	678.3 ± 18.0
<i>Gutierrezia microcephala</i> (DC.) A. Gray	Asteraceae	Gm	No data	No data	7.03 ± 0.59	647.2 ± 10.0
<i>Hymenoclea salsola</i> A. Gray	Asteraceae	Hs	-2.09 ± 0.35	1.60 ± 0.40	10.75 ± 0.84	690.2 ± 18.3
<i>Isomeris arborea</i> Nutt.	Capparaceae	Ia	-2.51 ± 0.23	0.34 ± 0.04	8.97 ± 0.73	612.6 ± 10.7
<i>Larrea tridentata</i> (DC.) Cov.	Zygophyllaceae	Lt	-3.31 ± 0.32	0.63 ± 0.10	6.17 ± 0.43	854.1 ± 8.4
<i>Lepidospartum squamatum</i> (A. Gray) A. Gray	Asteraceae	Ls	-0.79 ± 0.06	1.54 ± 0.39	No data	566.1 ± 12.0
<i>Lycium andersonii</i> A. Gray	Solanaceae	La	-1.02 ± 0.10	0.60 ± 0.16	9.36 ± 0.76	706.9 ± 16.9

^aFrom Jacobsen *et al.* (2007c).^bFrom Jacobsen *et al.* (2007c).

Western Regional Climate Center for which temperature and precipitation at weather stations is monitored hourly and available online (<http://www.wrcc.dri.edu/wraws/>). Conditions at the chaparral site were approximated using the Malibu Canyon California RAWS, at the coastal sage scrub site using the Malibu Hills California RAWS, and for the Mojave Desert scrub site using the Jawbone California RAWS.

Seasonal water potential

Water potential (Ψ_w) was measured on all species approximately monthly, beginning in February 2006 and continuing through April 2007. Leaves or branchlets were removed from plants at midday, double-bagged, and placed in a cooler on ice. Samples were then rapidly transported to an air-conditioned laboratory at Pepperdine University (Malibu, CA, USA) for the chaparral and coastal sage scrub species, or

California State University, Bakersfield (CSUB) for the Mojave Desert scrub species. Samples were rapidly processed using a pressure chamber (Model 2000 Pressure Chamber Instrument, PMS Instruments, Corvallis, OR, USA). A previous study concluded that laboratory-measured Ψ_w samples were no different from those measured immediately in the field (Jacobsen *et al.*, 2007c).

Seasonal stomatal conductance

Stomatal conductance (g_s) was measured on all species approximately monthly, beginning in April 2006 and continuing through April 2007. Stomatal conductance was measured on a leaf or branchlet of six individuals per species at each sampling time using a steady-state porometer (Li-Cor, Inc., LI-1600 Steady State Porometer with a 1600-07 Cylindrical Chamber, Lincoln, NE, USA). For each sampling

time, all species within a site were measured within a single day, beginning at approx 10:00 h and ending around noon. Leaf and air temperatures were periodically checked using an infrared thermometer for leaf temperatures (Fluke 572 CF IR thermometer; Fluke Corporation, Berlin, Germany) and a thermocouple for air temperatures (4015 Traceable Total Range Thermometer with a beaded Type-K thermocouple probe; Control Company, Friendswood, TX, USA). Sampled leaves or branchlets were collected and the sampled leaf area determined using a leaf area meter (LI-3100, Li-Cor). Stomatal conductances of species were then corrected using the area of the leaves containing stomata (i.e. species with stomata on only one side of the leaf were corrected using the one-sided leaf area, species with amphistomatic leaves were corrected using the two-sided leaf area, and species with needle-like leaves were corrected by calculating the surface area of the leaf based on cross-sectional measures of leaf geometry).

Specific leaf area

Specific leaf area was measured on fully mature leaves at the start of the summer dry period. Branchlets were collected from individuals in the field, placed in plastic bags, and transported to the laboratory at CSUB. Individual leaves were then taken from each branchlet, with a total of 10 leaves from 10 individuals for each species, and their area was measured using a leaf area meter. Leaves were then placed in a drying oven at 60°C for 4 d and their dry mass was determined using an electronic balance (CP124S, Sartorius, Goettingen, Germany). Specific leaf area was calculated as the leaf area per dry leaf mass ($\text{mm}^2 \text{mg}^{-1}$). The SLA was not determined for *Lepidospartum squamatum* because of difficulty separating its small adherent scale-like leaves from the stem.

Leaf specific hydraulic conductivity

Leaf specific hydraulic conductivity was measured during the dry season in August and September 2006 on 24 of the 28 species included in the present study. The remaining four species had very small, scale-like, or adherent leaves which prevent accurate determination of leaf area. Stems approx. 0.5 m in length were collected predawn. Stems were cut from the plant while underwater, 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 laboratory and native conductivity was measured on a stem segment 10 cm in length and 4–8 mm in diameter within 5 h of collection following the methods in Jacobsen *et al.* (2007c). All leaves distal to the measured stem were collected and their leaf area determined using a leaf area meter. The native conductivity was then divided by this leaf area to determine the dry season leaf specific xylem conductivity (K_l).

Xylem density

Xylem density was determined as the dry mass per water saturated volume. Stem segments *c.* 5 cm long and 6–8 mm in diameter were collected adjacent to those used for determination of vulnerability to xylem cavitation in a prior study (Jacobsen *et al.*, 2007c). Stem segments were split longitudinally and their pith and bark removed. Xylem segments were then soaked in degassed water adjusted to a pH of 2 overnight, and saturated volume was determined using the methods of Hacke *et al.* (2000). Samples were then placed in a drying oven at 60°C for 4 d and their dry mass determined.

Data analysis

Statistical analyses were performed using Minitab (Release 14.12.0, Minitab Inc., State College, PA, USA) and/or Statview (v. 5.0.1, SAS Institute Inc., Cary, NC, USA). Alpha was set at 0.05 for all comparisons. Differences in minimum and maximum seasonal Ψ_w and minimum and maximum g_s were analyzed among species at a single site and among sites using ANOVAs followed by Bonferroni/Dunn post-hoc analyses when appropriate. Seasonal changes in Ψ_w and g_s were analyzed using repeated-measures ANOVAs followed by Bonferroni/Dunn post-hoc analyses when appropriate.

Linear regression models were used to analyze the within- and among-species relationships between g_s and Ψ_w , and ANOVAs were used to examine differences in the slopes and intercepts of these regressions among species and sites. Linear regressions were also used to examine the relationship between these seasonal measures and SLA, K_l , K_s , Ψ_{50} , and xylem density.

A principal-components analysis was used to examine differences among the suites of xylem traits used by species and communities. Factor scores of individual species were plotted to compare species from different communities. Minimum seasonal water potential (Ψ_{wmin}), Ψ_{50} , K_s , and xylem density were included in this analysis. A MANOVA was used to determine if communities differed in the relationships among these multiple traits.

The phylogeny used for phylogenetic independent contrast (PIC) calculations was constructed based on the relationships among families and species reported in published phylogenies. Relationships among species were based on recent molecular-based phylogenies (Morgan *et al.*, 1994; Bayer & Starr, 1998; Hardig *et al.*, 2000; Goertzen *et al.*, 2003; Hilu *et al.*, 2003; Urbatsch *et al.*, 2003; Soltis & Soltis, 2004; Soltis *et al.*, 2005). Contrasts were calculated using COMPARE (Martins, 2004) and linear regressions were used to examine the relationship between SLA, K_l , K_s , Ψ_{50} , and xylem density contrasts pooled across communities. Correlations among PICs were similarly significant or nonsignificant to correlations among raw trait values in most cases; therefore, only correlations of raw trait values, which have more easily interpretable

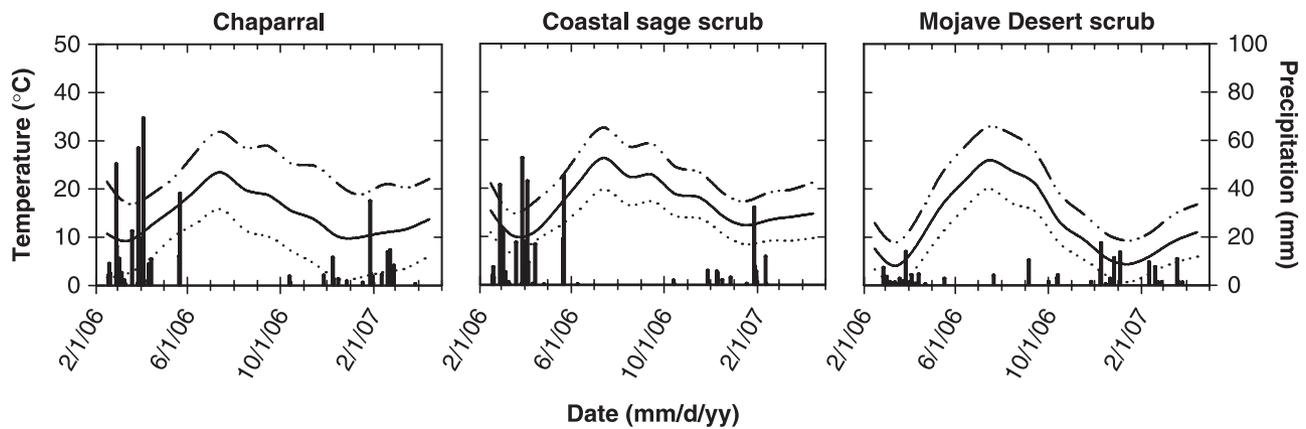


Fig. 1 Monthly average mean (solid line), minimum (dotted line), and maximum (dashed/dotted line) temperature and precipitation for three sites located in southern California (USA) from February 2006 through April 2007. Each bar represents the date and amount of a precipitation event recorded at a site.

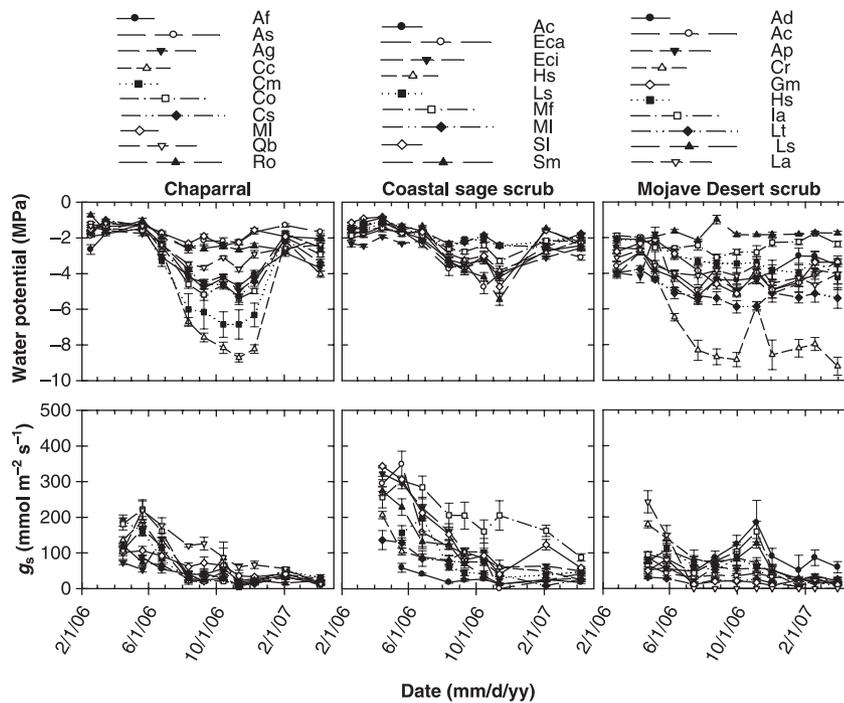


Fig. 2 Water potential and stomatal conductance (g_s) measured approximately monthly on species from three arid plant communities in southern California (USA). Water potential was measured on 29 species from February 2006 through April 2007, and g_s was measured on 28 species from April 2006 through April 2007. Within each panel, different symbols represent different species and the same symbols are used to represent the same species for water potential and g_s panels for each community (see Table 1 for species abbreviations). Symbols are species means ± 1 SE.

values, are discussed in the Results section. There was only one case in which the raw trait correlation and PICs correlation did not agree and this is discussed later.

Results

Weather

Spring rains occurred across all sites from February 2006 though May 2006 (Fig. 1). The summer rainless period began in June 2006 and extended through September 2006 for the Mojave Desert, and through October 2006 for the chaparral and coastal sage scrub, at which time a few small precipitation events occurred (< 10 mm). Substantial rain did not fall at the

sites until the months of December 2006 and January 2007 when several precipitation events (> 20 mm) occurred across the sites. Rainfall during the 2005–06 rainy season was 510 mm for the chaparral site, 460 mm for the coastal sage scrub site, and 230 mm for the Mojave Desert site. Rainfall for the 2006–07 rainy season was considerably lower and was 130, 80, and 100 mm for the chaparral, coastal sage, and Mojave Desert sites, respectively.

Seasonal water potential

All chaparral, coastal sage, and Mojave Desert species experienced significant changes in their water potential over the course of this study (Fig. 2; $P < 0.05$ for all). Chaparral

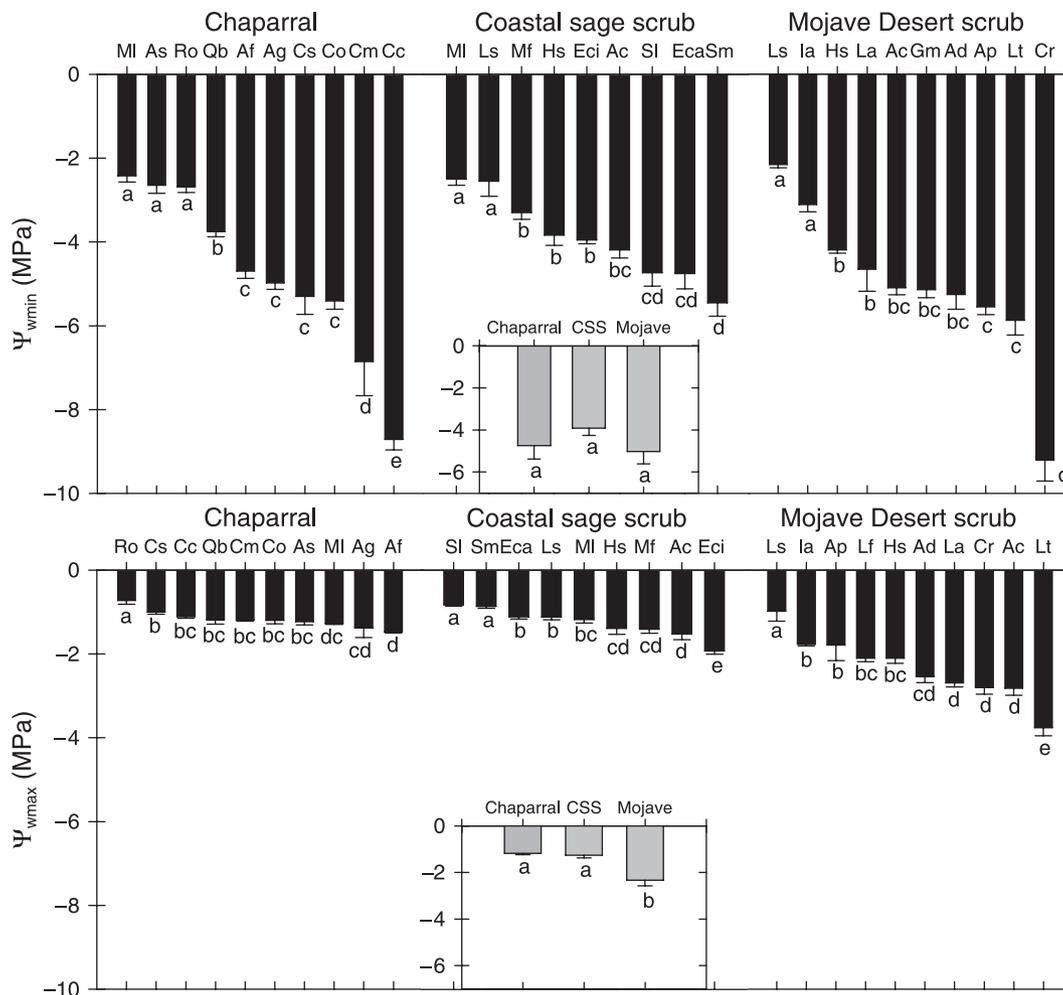


Fig. 3 Maximum and minimum water potential (Ψ_{wmax} and Ψ_{wmin} , respectively) as measured from February 2006 through April 2007 on 28 shrub species from three plant communities in southern California (USA): chaparral, coastal sage scrub (CSS), and Mojave Desert scrub. Each black bar represents a different species mean \pm 1 SE (see Table 1 for species codes). Different letters below bars indicate significant differences among species within a community. Insets: gray bars represent means \pm 1 SE across communities and different letters indicate significant differences.

species reached their maximum Ψ_w (Ψ_{wmax}) during the wet season in February, April, or May 2006. Most chaparral species reached their minimum Ψ_w (Ψ_{wmin}) during the dry season in August, October, or November 2006. *Rhus ovata* differed from these species in reaching its Ψ_{wmin} during the wet winter months (February 2007). All coastal sage scrub species experienced their Ψ_{wmax} during the wet season in April 2006. Most coastal sage scrub species experienced their Ψ_{wmin} at the end of the summer dry season in October and November 2006. Only one species, *M. laurina*, experienced its seasonal low during the winter cool period (February 2007). Most Mojave Desert scrub species reached their Ψ_{wmax} during the wet season in April and May 2006 and January and February 2007. *Lepidospartum squamatum* differed from these species in displaying its Ψ_{wmax} during the dry summer period (August 2006). Most species reached their Ψ_{wmin} during the dry summer season in July, August, and September

2006. However, a few species displayed seasonal lows during the wet winter months of January 2007 (*H. salsola*), February 2007 (*L. andersonii*), and March 2007 (*C. ramosissima*).

The average monthly Ψ_{wmax} occurred in the coastal sage scrub and Mojave Desert scrub in April 2006, and in the chaparral in May 2006 (Fig. 2). The three sites differed in their Ψ_{wmax} values (Fig. 3; $P < 0.001$), with the chaparral and coastal sage scrub species experiencing significantly less negative water potentials than the Mojave Desert species ($P < 0.001$ for both). The chaparral species and coastal sage scrub species did not differ significantly in their Ψ_{wmax} ($P > 0.05$).

The average monthly minimum water potential (Ψ_{wmin}) occurred in the chaparral and coastal sage scrub in November 2006 and in the Mojave Desert in September 2006 (Fig. 2). There was no difference among sites in Ψ_{wmin} (Fig. 3; $P > 0.05$).

Seasonal stomatal conductance

All chaparral and coastal sage species experienced significant changes in their stomatal conductance (g_s) over the course of this study (Fig. 2; $P < 0.05$ for all). All of the chaparral species experienced their maximum g_s (g_{smax}) in the spring in April and May 2006. Several species displayed their minimum g_s (g_{smin}) at the end of the summer dry period in November 2006 (*A. glandulosa*, *C. cuneatus*, *C. megacarpus*, *C. oliganthus*, and *C. spinosus*). Several other species displayed their g_{smin} in February (*R. ovata*) and April 2007 (*A. fasciculatum*, *M. laurina*, and *Q. berberidifolia*). All of the coastal sage scrub species displayed their g_{smax} in the spring season during April, May, and June 2006. Several coastal sage scrub species experienced their g_{smin} at the end of the summer dry season in November 2006 (*A. californica*, *L. scoparius*, *S. leucophylla*, and *S. mellifera*). However, several other species did not experience their g_{smin} until February (*E. californica* and *M. laurina*) and April 2007 (*E. cinereum*, *H. squarrosa*, and *M. fasciculatus*).

Stomatal conductance for the Mojave Desert species *A. dumosa* and *L. andersonii* did not change significantly over the course of this study (Fig. 2; $P > 0.05$ for both), although this includes only 2 months of data from *L. andersonii* as a result of it being fully drought deciduous. For the remaining Mojave Desert species, g_s underwent significant seasonal change (Fig. 2; $P < 0.001$ for all). Most species reached their g_{smax} in the wet spring season in April 2006 (*A. canescens*, *C. ramosissima*, and *L. tridentata*) and May 2006 (*H. salsola* and *G. microcephala*). However, several species reached their g_{smax} later in the dry season including *A. polycarpa* (August 2006), *I. arborea* (November 2006), and *L. squamatum* (November 2006). All species reached their g_{smin} during the cool winter months in December 2006 (*G. microcephala*), January 2007 (*C. ramosissima*, *H. salsola*, *I. arborea*, and *L. tridentata*), and March 2007 (*A. canescens*, *A. polycarpa*, and *L. squamatum*).

The average monthly high stomatal conductance (g_{smax}) occurred in the coastal sage scrub and Mojave Desert scrub in April 2006 but was delayed in the chaparral until May 2006 (Fig. 2). These months also coincided with the average monthly high water potentials across sites; however Ψ_{wmax} is not correlated with g_{smax} either within or across communities ($P > 0.05$ for all). The three sites differed in their g_{smax} values (Fig. 4; $P = 0.007$), with the coastal sage scrub species experiencing significantly greater g_{smax} than the chaparral or Mojave Desert species ($P = 0.019$ and 0.002 for coastal sage compared with the chaparral and Mojave Desert, respectively). Chaparral and Mojave Desert species did not significantly differ in their g_{smax} values ($P > 0.05$).

The average monthly minimum stomatal conductance (g_{smin}) occurred in the chaparral and coastal sage scrub in April 2007, and in the Mojave Desert in January 2007 (Fig. 2). There was no difference among sites in g_{smin} ($P > 0.05$).

Water potential and stomatal conductance

Among the different sites, the relationship between Ψ_w and g_s varied (Fig. 5; $P = 0.001$ for both slopes and intercepts across communities). For the chaparral and coastal sage scrub, Ψ_w was correlated to g_s pooled across species ($P < 0.001$ for both, $r^2 = 0.27$ and 0.22 , respectively); however, there was no relationship between Ψ_w and g_s pooled across species from the Mojave Desert ($P > 0.05$). Species from the coastal sage scrub had a significantly greater slope (64.89 ± 13.49) than either the chaparral (27.08 ± 4.60) or the Mojave Desert scrub species (12.07 ± 6.18) (Fig. 5; $P = 0.007$ and 0.001 for the coastal sage scrub compared to the chaparral and Mojave Desert scrub, respectively). Species from the chaparral and Mojave Desert did not differ significantly in their slopes of Ψ_w and g_s pooled across species ($P > 0.05$). Species from the coastal sage scrub also had significantly greater intercepts (273.77 ± 40.36) than either the chaparral (141.54 ± 13.67) or the Mojave Desert scrub species (106.56 ± 29.91) (Fig. 5; $P = 0.004$ and 0.001 for the coastal sage scrub compared with the chaparral and Mojave Desert scrub, respectively). Species from the chaparral and Mojave Desert did not differ significantly in their intercepts (Fig. 5; $P > 0.05$).

Specific leaf area

Specific leaf area was different among sites ($P = 0.014$), the coastal sage having significantly higher SLA compared with the chaparral ($P = 0.004$) and the Mojave Desert scrub ($P = 0.047$). Specific leaf area was not different between the chaparral and Mojave Desert scrub ($P > 0.05$). Specific leaf area of species was not correlated with Ψ_{wmax} , Ψ_{wmin} , K_s , K_l , or g_{smin} , either within or across communities ($P > 0.05$ for all; data not shown). Specific leaf area was also not correlated with g_{smax} across communities ($P > 0.05$ for all; data not shown); however, SLA was correlated with g_{smax} among Mojave Desert species ($P = 0.016$, $r^2 = 0.59$; data not shown) such that species with lower SLA also had lower g_{smax} . Specific leaf area was not correlated with g_{smax} among species in either chaparral or coastal sage scrub communities ($P > 0.05$ for both; data not shown).

Xylem density

Xylem density was significantly different among the sites ($P = 0.007$), with the Mojave Desert scrub having significantly denser xylem than the chaparral ($P = 0.035$) or coastal sage scrub ($P = 0.002$). Xylem density was not different between the coastal sage and chaparral ($P > 0.05$). Xylem density was correlated with Ψ_{wmax} and Ψ_{wmin} when pooled across communities such that species with denser xylem had more negative Ψ_{wmax} and Ψ_{wmin} (Fig. 6; $P < 0.001$, $r^2 = 0.52$ for Ψ_{wmax} and $P = 0.012$, $r^2 = 0.21$ for Ψ_{wmin}). Xylem density was not correlated with Ψ_{wmax} and Ψ_{wmin}

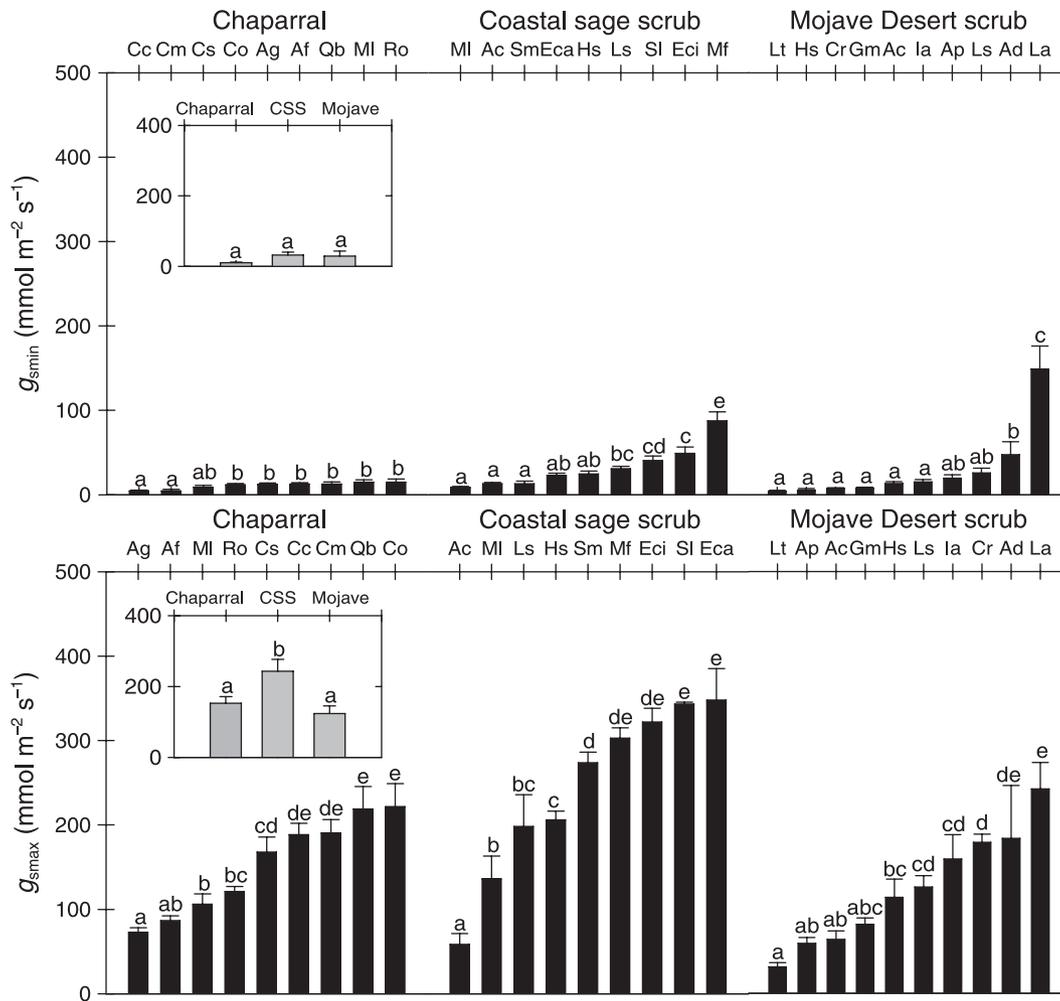


Fig. 4 Maximum and minimum stomatal conductance (g_{smax} and g_{smin} , respectively) as measured from April 2006 through April 2007 on 27 shrub species from three plant communities in southern California (USA): chaparral, coastal sage scrub (CSS), and Mojave Desert scrub. Each black bar represents a different species mean ± 1 SE (see Table 1 for species codes). Different letters below bars indicate significant differences among species within a community. Insets: gray bars represent means ± 1 SE across communities and different letters indicate significant differences.

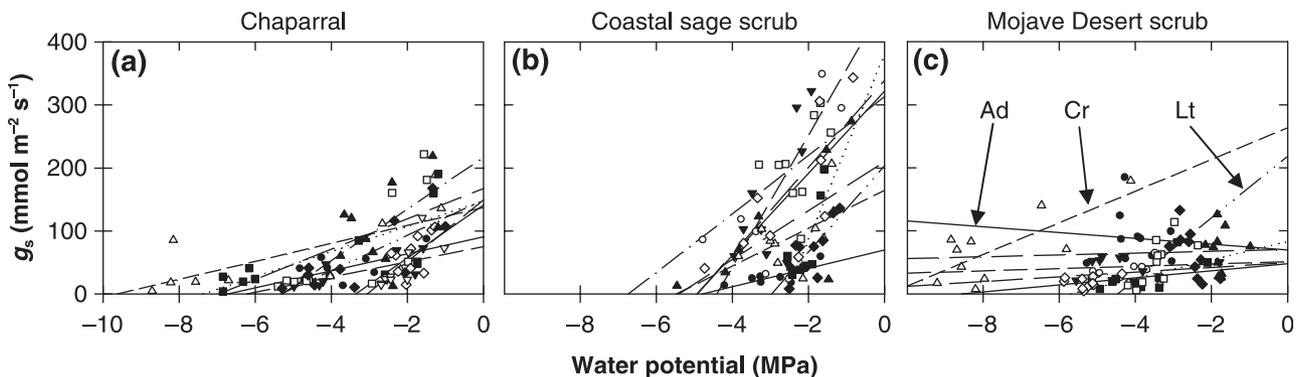


Fig. 5 Water potential as a predictor of stomatal conductance (g_s) for 28 species from three arid plant communities of southern California (USA): chaparral (a), coastal sage (b), and Mojave Desert scrub (c). Linear regressions were modeled for each species. Species from the coastal sage scrub had significantly greater slopes and intercepts when compared with either the chaparral or the Mojave Desert scrub species. Species from the chaparral and Mojave Desert did not differ significantly in their slopes or intercepts. Within each community, different symbols represent different species. See Table 1 for species codes in (c) and see Fig. 2 for species legend for (a)–(c).

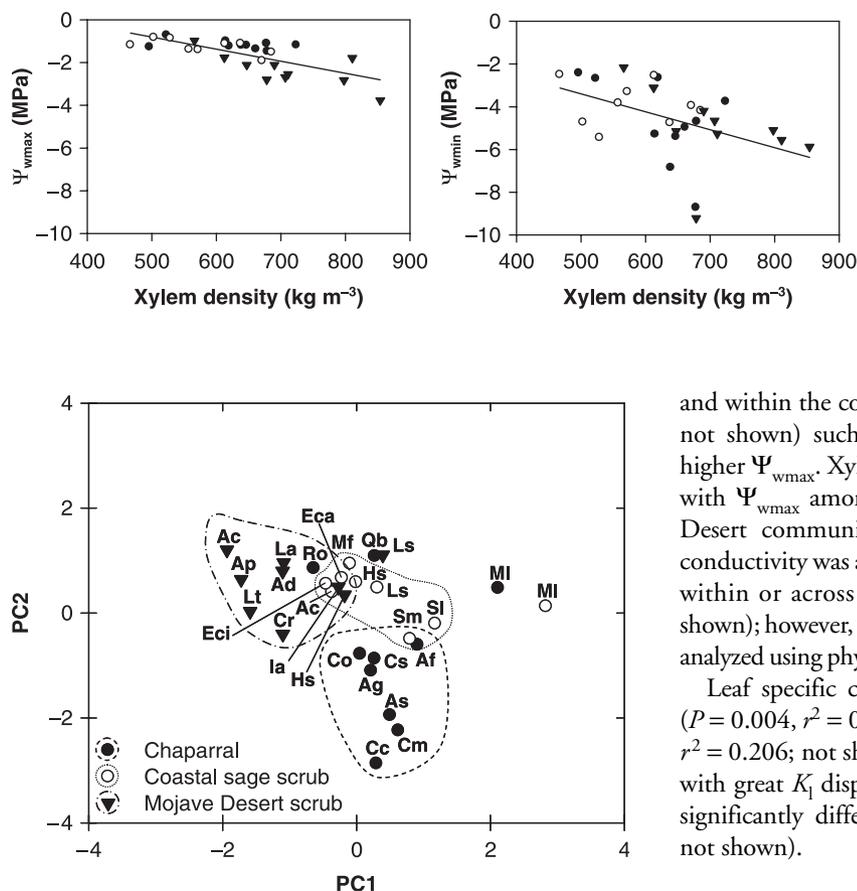


Fig. 6 Xylem density as a predictor of Ψ_{wmax} and Ψ_{wmin} ($P < 0.001$, $r^2 = 0.52$ for Ψ_{wmax} and $P = 0.012$, $r^2 = 0.21$ for Ψ_{wmin}). Xylem density was not correlated with Ψ_{wmax} and Ψ_{wmin} within individual communities. Different symbols indicate data from different arid plant communities: closed circles, chaparral; open circles, coastal sage scrub; triangles, Mojave Desert.

Fig. 7 Results of a principal-components analysis using multiple traits measured on species occurring in three shrub communities of the winter rainfall area of southern California (USA). Component 1 (PC1) is strongly associated with water-relations traits, including minimum seasonal water potential (Ψ_{wmin}), xylem density, and xylem specific conductivity (K_s), such that species with higher values have greater K_s , lower xylem density, and higher (less negative) Ψ_{wmin} . Component 2 (PC2) is strongly associated with water stress tolerance (Ψ_{50}), such that higher values are less resistant to cavitation (i.e. have higher Ψ_{50}). The suites of traits utilized by each community differ significantly ($P = 0.006$). Each symbol represents a different community and species codes are shown in Table 1.

within individual communities ($P > 0.05$ for all). Xylem density was correlated with g_{smax} across communities such that species with denser xylem had lower maximum stomatal conductance ($P = 0.046$, $r^2 = 0.14$; data not shown). Xylem density was not correlated with g_{smax} within communities ($P > 0.05$ for all; data not shown). Xylem density was not correlated to g_{smin} within or across communities ($P > 0.05$ for all; data not shown).

Hydraulic conductivity

Xylem specific conductivity was correlated with Ψ_{wmax} ($P < 0.001$, $r^2 = 0.46$; data not shown) across communities

and within the coastal sage scrub ($P = 0.036$, $r^2 = 0.55$; data not shown) such that species with greater K_s experienced higher Ψ_{wmax} . Xylem specific conductivity was not correlated with Ψ_{wmax} among species within the chaparral or Mojave Desert communities ($P > 0.05$ for both). Xylem specific conductivity was also not correlated with Ψ_{wmin} , g_{smax} , or g_{smin} within or across communities ($P > 0.05$ for all; data not shown); however, K_s was correlated with Ψ_{wmin} when data were analyzed using phylogenetic independent contrasts ($P = 0.039$).

Leaf specific conductivity (K_l) was correlated with g_{smax} ($P = 0.004$, $r^2 = 0.337$, data not shown) and g_{smin} ($P = 0.030$, $r^2 = 0.206$; not shown) across communities such that species with great K_l displayed higher g_{smax} or g_{smin} . The K_l was not significantly different among communities ($P > 0.05$, data not shown).

Xylem vulnerability to cavitation

The xylem and leaf traits included in the present study were not generally good predictors of species vulnerability to xylem cavitation. Minimum seasonal Ψ_w was predictive of resistance to water stress-induced cavitation (Ψ_{50}) across communities ($P = 0.013$, $r^2 = 0.22$, not shown) and within the chaparral community ($P = 0.013$, $r^2 = 0.56$) but not within the coastal sage or Mojave Desert communities ($P > 0.05$ for both). Other traits included in the present study, including Ψ_{wmax} , g_{smax} , g_{smin} , SLA, xylem density, and K_s , were not predictive of Ψ_{50} either across or within communities ($P > 0.05$ for all; data not shown), with one exception. Minimum g_s was predictive of Ψ_{50} within the coastal sage scrub community, with species experiencing lower g_{smin} also having more negative Ψ_{50} ($P = 0.032$; $r^2 = 0.50$; data not shown).

Water-use 'strategies'

Communities differed in the suites of xylem traits utilized by species ($P = 0.006$). A principal-components analysis resulted in two components ($P < 0.001$, Fig. 7). Component 1 was mainly associated with Ψ_{wmin} , K_s , and xylem density and accounted for 63, 65, and 64% of the variability in these traits, respectively. Component 2 was mainly associated with Ψ_{50} and accounted for 55% of the variability among species

in Ψ_{50} . Species from the chaparral, coastal sage, and Mojave Desert communities occupy largely nonoverlapping areas when the species values of these components are graphed, consistent with the significant difference in multivariate strategies utilized by species within these communities (Fig. 7).

Discussion

Among shrub species occurring in three different winter rainfall plant communities of southern California, plants experienced similar patterns in their seasonal water status and stomatal conductance (g_s), such that, across sites, species tended to reach their seasonal high water potentials (Ψ_{wmax}) and maximum g_s (g_{smax}) in spring during the wet season. Species tended to reach their seasonal low water potentials (Ψ_{wmin}) at the end of the dry season and seasonal low g_s (g_{smin}) during the cool winter months. This matches the annual precipitation and temperature pattern for these sites and indicates that species are responding similarly to rainfall events and that cooler winter temperatures may limit gas exchange in Californian winter rainfall communities.

Several species from each of the three sites deviated from these average patterns of seasonal water status, illustrating phenological diversity among species. These included *R. ovata*, *M. laurina*, *H. salsola*, *L. andersonii*, and *C. ramosissima*, which reached their minimum seasonal water potentials (Ψ_{wmin}) during the winter wet season in 2007. This pattern has been described previously for *R. ovata* (Pratt *et al.*, 2005) and is likely caused by high winter embolism in the stems of this species, which reduces water supply to leaves. However, below-ground factors may be involved in other species, including root phenology and soil moisture distribution. *Lepidospartum squamatum* differed from other species in displaying its maximum seasonal water potential (Ψ_{wmax}) during the dry summer period (August). The range of this species extends into summer rainfall regions and this species appears to be tuned to a summer rainfall regime. A similar pattern was also evident in the Mojave Desert shrub *C. ramosissima*, which was able to respond rapidly to a small late summer rain pulse in the present study but which slowly responded to a pulse of winter rain. This pattern has been previously described for this species (Lin *et al.*, 1996; Gebauer & Ehleringer, 2000).

While across sites species tended to respond similarly to seasonal changes in precipitation, plant water status varied significantly among the sites during the wet season. Species in the chaparral and coastal sage scrub experienced similarly high Ψ_{wmax} , while species from the Mojave Desert did not reach similarly high water potentials. This may be the result of lower wet season soil moisture in the Mojave Desert site compared with the other two sites (A. L. Jacobsen, unpublished). Relatively low soil moisture values of shallow soil layers have been previously reported for the Mojave Desert (Smith *et al.*, 1995; Yoder & Nowak, 1999) and comparatively higher soil moisture values have been reported for the chaparral (Johnson-Maynard

et al., 2004), suggesting this may be a consistent difference among these shrub communities. Additionally, desert shrubs may be accessing deeper soil moisture reserves which are fairly stable and recharge mainly during above-average precipitation years, as has been described for the Chihuahuan Desert (Snyder *et al.*, 2006).

During the dry season, Ψ_{wmin} was not different among the sites, suggesting that species at these sites are experiencing a common amount of water stress. The across-species mean Ψ_{wmin} was -4.6 MPa. This value is similar to the average Ψ_{wmin} reported for 26 chaparral species in years of average precipitation (Jacobsen *et al.*, 2007b), for 17 species from the winter rainfall region of South Africa (Jacobsen *et al.*, 2007b), and for six species from the Great Basin Desert (Hacke *et al.*, 2000). This suggests this Ψ_{wmin} may represent a common physiological limit of arid and semi-arid shrub communities. This is also consistent with a mean cavitation resistance (Ψ_{50}) of approx. -4 to -5 MPa which has been found across Mediterranean-type and Desert ecosystems (Hacke *et al.*, 2000; Maherali *et al.*, 2004; Jacobsen *et al.*, 2007b).

Minimum Ψ_w was correlated with Ψ_{50} with a 1 : 1 relationship between these traits for the chaparral species, as has been reported in previous studies (Hacke *et al.*, 2000; Jacobsen *et al.*, 2007b; Pratt *et al.*, 2007a); however, there was no correlation among these traits within the coastal sage scrub or Mojave Desert scrub. This suggests that these communities may vary considerably in the amount of water stress-induced embolism that they experience seasonally. While chaparral shrubs appear to reach *c.* 50% native embolism seasonally, it appears that shrubs in other arid systems may have alternative thresholds and may regularly reach significantly higher amounts of xylem embolism. For example, *Coleogyne ramosissima* in the Mojave Desert has a relatively high Ψ_{50} and yet reaches comparatively low Ψ_w in the field. Its native embolism is consistent with this pattern (during the dry season, shrubs are typically > 98% embolized; Jacobsen *et al.*, 2007c; A. L. Jacobsen, unpublished). Indeed, high seasonal amounts of embolism have been reported for species of the Sonoran Desert (Pockman & Sperry, 2000) and for the coastal sage (Hargrave *et al.*, 1994; Kolb & Davis, 1994). Thus, while Ψ_{wmin} and Ψ_{50} may be correlated in some communities, it does not appear that these traits are always correlated, and Ψ_{wmin} may not be a generally useful predictor of Ψ_{50} in arid and semi-arid communities, as has been suggested (Jacobsen *et al.*, 2007b).

Among these three communities, species displayed differential stomatal sensitivity to water stress, with the relationship between Ψ_w and g_s significantly varying among communities. Among coastal sage scrub species, g_s declined rapidly with declining Ψ_w , suggesting high stomatal sensitivity to water stress. Consistent with our predictions, the chaparral had a much shallower slope between g_s and Ψ_w when compared with the coastal sage scrub species. This implies that chaparral species, which have stem xylem that is more resistant to

cavitation, can tolerate greater declines in Ψ_w before limiting stomatal gas exchange.

In contrast to these first two communities, on average, species from the Mojave Desert scrub showed no change in g_s in response to changes in Ψ_w when data were pooled across species. This suggests that these species do not alter their stomatal conductance in response to water stress and that they may be using alternative strategies to limit water loss. However, it should be noted that while this is the general pattern across species, there are some species from the desert community that displayed rather sensitive stomatal responses. For instance, both *Coleogyne ramosissima* and *Larrea tridentata* displayed relatively steep declines in stomatal conductance with declining water potential (Fig. 5c; medium dashed line for *C. ramosissima* and dash-dot-dot line for *L. tridentata*).

While differences in stomatal sensitivity among communities may imply that species in these communities vary in their regulation of water balance (i.e. isohydric vs anisohydric), this is unlikely since species within these communities are not different in their Ψ_{wmin} . Instead, it appears that water status may be otherwise regulated in shrubs of the Mojave Desert. Many of the Mojave Desert scrub species may be reducing total leaf area rather than reducing water loss through individual leaves. Indeed, during the course of the present study, individuals of many desert species reduced their leaf area, although only one species (*L. andersonii*) is completely deciduous and lost all of its leaves. This pattern of leaf drop as a means of regulating whole-plant stomatal conductance appeared most pronounced in *Ambrosia dumosa*. In this species, stomatal conductance increased as water potential declined, largely as a result of reduced leaf area, which likely increased the water supply to individual leaves even though whole-plant water status was reduced (Fig. 5c solid line). Significant leaf drop during drought has been described previously in desert shrubs during the dry season (Smith *et al.*, 1995).

Consistent with the idea that species in these three communities are employing different suites of traits in response to water stress, species appear to be differentially adjusting leaf area to maintain similar dry-season K_1 and g_s in response differences in cavitation resistance and therefore seasonal embolism. Stomatal conductivity was correlated with K_1 when pooled across sites, with species with greater K_1 displaying greater g_{smin} and g_{smax} consistent with previously reported correlations between K_1 and g_s (Sperry, 2000; Santiago *et al.*, 2004). Additionally, dry season K_1 and g_{smin} were not different among sites, suggesting that perhaps there is a common minimum hydraulic flow which must be sustained in order to maintain evergreen leaves in arid and semi-arid environments. This is consistent with the greater amount of leaf drop observed in the coastal sage and Mojave Desert communities concomitant with their greater susceptibility to cavitation and presumably higher amounts of dry-season embolism. Coastal sage scrub species displayed significantly higher g_{smax} than the other two communities which may partially result from their

high stomatal sensitivity to changes in water status. Xylem specific conductivity was not correlated with most water relations and leaf traits, including Ψ_{50} , K_s , K_1 , and g_s ; however, across sites, Ψ_{wmax} and K_s were correlated.

Thus, species among these three sites are divergent in their functional traits related to available water resources. The pattern of water use displayed by the coastal sage scrub species is consistent with adaptation to utilize shallow temporarily available water (Schwinning & Ehleringer, 2001). Coastal sage scrub species tend to have shallow roots (Hellmers *et al.*, 1955) and display significantly higher wet seasonal g_s than species in the other two sites, and have high stomatal sensitivity to plant water status. By contrast, shrub species from the desert likely have deeper root systems (Gibbens & Lenz, 2001), low maximum stomatal conductivity, and low stomatal sensitivity to plant water status, consistent with a strategy of tapping mostly deeper soil moisture reserves (Schwinning & Ehleringer, 2001). Chaparral shrub species are a blend of these two extremes, with species exhibiting both deep and shallow rooting systems (Cooper, 1922; Hellmers *et al.*, 1955), intermediate stomatal sensitivity to water stress (Poole & Miller, 1975), and low maximum stomatal conductivity not significantly different from that of the Mojave Desert species. Recent work has shown that deep and shallow water-use strategies are linked with life history type in the chaparral (Pratt *et al.*, 2007b). These differential water-use strategies point to the importance of root structure and function in these water-limited communities, although root traits were not measured in the present study.

Species that are utilizing suites of traits that occur in overlapping areas between communities (see Fig. 7) tend to be those with broad ranges that occur across communities, suggesting there are certain suites of traits that may be successful in many communities. Additionally, variability in the suites of traits displayed by species within each community suggests that there are many different successful 'strategies' possible within a single community (Marks & Lechowicz, 2006). Such functional differences may be balanced by additional, unmeasured, functional traits.

Specific leaf area does not correlate well with plant functional traits among these arid shrub species. SLA was different among the sites, with the coastal sage scrub species having significantly higher SLA compared with the chaparral and Mojave Desert scrub. However, SLA was highly variable among species within a site, suggesting lack of convergence to a single SLA within these environments. Additionally, SLA was not correlated with water relations or leaf traits, including Ψ_{50} , Ψ_{wmax} , Ψ_{wmin} , K_s , K_1 , and g_s , and thus was not useful as a predictor of these physiological traits. SLA is likely correlated to other plant traits not included in the present study, such as leaf life span and photosynthetic capacity (Gulfás *et al.*, 2003; Ackerly, 2004; Poorter & Bongers, 2006), or may be responding to microsite differences in nutrient availability (Wright *et al.*, 2002).

The strong relationship between seasonal water potential and xylem density among data pooled across communities suggests that xylem density may indeed be a useful tool in categorizing plant functional strategies and plant functional variation both across broad regions and within communities (c.f. Ackerly, 2004; Preston *et al.*, 2006; Swenson & Enquist, 2007) and that these traits are likely biophysically constrained. Xylem density was strongly correlated with Ψ_{wmax} and Ψ_{wmin} across communities, with species having denser xylem displaying more negative Ψ_{wmax} and Ψ_{wmin} . Xylem density was also correlated with g_{smax} across communities such that species with denser xylem had lower maximum stomatal conductance. The range in xylem density among species within these communities is consistent with what has been reported for other shrub communities (Hacke *et al.*, 2000; Zanne *et al.*, 2006; Jacobsen *et al.*, 2007a), but is smaller than the ranges in xylem density reported for some communities of tropical, savanna, and temperate trees (Osunkoya *et al.*, 2007; Hao *et al.*, 2008). This difference is largely the result of the presence of more low-xylem-density species in these forests relative to arid and semi-arid shrub communities.

The Ψ_{wmin} that plants experienced was a better predictor of xylem traits than xylem cavitation resistance (Ψ_{50}). Additionally, xylem density was not predictive of xylem cavitation resistance (Ψ_{50}) within any of the three plant communities examined, contrary to what has been found in other studies (Hacke *et al.*, 2001; Jacobsen *et al.*, 2007b). This may be due to the 1 : 1 relationship between Ψ_{50} and Ψ_{wmin} found in these earlier studies. In the present study, where Ψ_{50} and Ψ_{wmin} are not correlated or are correlated in a relationship that is not 1 : 1, xylem density appears to be nonpredictive of cavitation resistance (Pratt & Black, 2006). This suggests that xylem density should not be used to predict cavitation resistance in communities unless the relationship between Ψ_{50} and Ψ_{wmin} has been determined. By contrast, the strong correlation between Ψ_{wmin} and xylem density suggests that these traits may be functionally related and predictive of one another. This is supported by previous studies that have found these traits to be related (Hacke *et al.*, 2000; Ackerly, 2004; Jacobsen *et al.*, 2007a,b). This relationship may be useful in the development of global plant functional trait models.

Arid shrub communities appear divergent in their adaptation to water stress, even though they experience similar amounts of water stress with a community-level average Ψ_{wmin} of approx. -4.6 MPa. The relationship among xylem functional traits, including Ψ_{wmin} , Ψ_{50} , K_s , and xylem density, appears to be community-specific and may be related to differential ability of species to tolerate or avoid high seasonal amounts of embolism. The relationship between g_s and Ψ_w also appears to be community-specific and may reflect differential water use by shrubs in these communities, perhaps in response to different rainfall predictability, soil moisture, precipitation, or soil nutrients among sites. Trait relationships that are community-specific in the present study may provide the basis for tests

of community convergence. It may be that shrub communities in some of the other Mediterranean-type climate regions worldwide display similar relationships to those found in the three communities sampled in the present study.

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