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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Influence of summer marine fog and low cloud stratus on water relations of evergreen woody shrubs (*Arctostaphylos*: Ericaceae) in the chaparral of central California

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Abstract Mediterranean-type climate (MTC) regions around the world are notable for cool, wet winters and hot, dry summers. A dominant vegetation type in all five MTC regions is evergreen, sclerophyllous shrubland, called chaparral in California. The extreme summer dry season in California is moderated by a persistent low-elevation layer of marine fog and cloud cover along the margin of the Pacific coast. We tested whether late dry season water potentials (Ψ_{min}) of chaparral shrubs, such as *Arctostaphylos* species in central California, are influenced by this coast-to-interior climate gradient. Lowland coastal (maritime) shrubs were found to have significantly less negative Ψ_{min} than upland interior shrubs (interior), and stable isotope (δ^{13}C) values exhibited greater water use efficiency in the interior. Post-fire resprouter shrubs (resprouters) had significantly less negative Ψ_{min} than co-occurring obligate seeder shrubs (seeders) in interior and transitional chaparral, possibly because resprouters have deeper root systems with better access to subsurface water than shallow-rooted seeders. Unexpectedly, maritime resprouters and seeders did not differ significantly in their Ψ_{min}, possibly reflecting more favorable water availability for shrubs influenced by the summer marine layer. Microclimate and soil data also suggest that maritime habitats have more favorable water availability than the interior. While maritime seeders constitute the majority of local *Arctostaphylos* endemics, they exhibited significantly greater vulnerability to xylem cavitation than interior seeders. Because rare seeders in maritime chaparral are more vulnerable to xylem cavitation than interior seeders, the potential breakdown of the summer marine layer along the coast is of potential conservation concern.

Keywords Mediterranean-type climate · Maritime chaparral · Stable isotopes · Water potential · Marine layer

Introduction

Mediterranean-type climate (MTC) regions occur on five different continents and are characterized by hot, dry summers and mild, wet winters (Keeley et al. 2012). These climate conditions support high species diversity and exceptional local endemism (Myers et al. 2000), particularly in evergreen, sclerophyllous shrublands that are a dominant component of MTC ecosystems (Cowling et al. 1996). In cismontane California, chaparral is one example of evergreen, sclerophyll-dominated shrubland that is widespread and abundant (Schimper 1903; Cooper 1922). Chaparral has been studied extensively; however, this research has focused on the MTC region in southern California (Keeley 2000; Keeley and Davis 2007) where chaparral has been presumed to be most diverse (Cooper 1922; Eppling and Lewis 1942). Chaparral habitats during the summer months typically experience low soil volumetric water content (VWC) with high vapor pressure deficits (VPD) and high negative atmospheric water potentials (Ψ_{atm}), creating extreme end-of-the-dry season negative midday water potentials (Ψ_{min}) in

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evergreen plants (Bhaskar and Ackerly 2006). End-of-the-dry season water potentials are highly correlated to Ψ_{crit}, the critical water potential at which xylem resistance to embolism breaks down, leading to vascular cavitation, plant morbidity and potential mortality (Davis et al. 1999; Pockman and Sperry 2000; Bhaskar et al. 2007). Xylem resistance to cavitation is also highly correlated to the distribution of species in deserts and chaparral, and Ψ_{crit} is presumed to be an adaptive evolutionary trait (Pockman and Sperry 2000; Maherali et al. 2004; Ackerly 2004; Bhaskar and Ackerly 2006; Bhaskar et al. 2007).

Approximately 90 % of chaparral stands in California occur on coastal and interior uplands between 500 and 2,000 m a.s.l. (Keeley and Davis 2007), whereas lowland coastal chaparral (0–500 m a.s.l.) occurs patchily within a narrow coastal zone over several hundred kilometers from Mendocino County to Santa Barbara County, on several California Channel Islands and from San Diego County to northern Baja California. This lowland coastal chaparral ('maritime chaparral' sensu Griffin 1978) constitutes less than 5 % of chaparral in California (Keeley and Davis 2007). Maritime chaparral, however, is known for its disproportionate level of woody shrub endemism and diversity (Cody 1986; Keeley 1992; Sawyer et al. 2009). Although the summer marine layer is thought to be a possible reason for this phenomenon (Stebbins and Major 1965), the possible ecophysiological link between maritime chaparral diversity and summer dry season climate factors has not been previously investigated.

The influence of the summer maritime layer creates a gradient in ambient temperature and moisture conditions that extends from the coast to the interior, as well as from coastal lowlands to coastal uplands. High mountain ridges paralleling the coast (sometimes dissected by canyons or topographic gaps) generally block the fog, restricting it principally to coastal localities. Consequently, a steep coast-to-interior climate gradient is created by this dynamic marine layer (Johnstone and Dawson 2010). The summer marine layer has been a prominent feature in California for at least 16,600 years (Anderson et al. 2008), and it has likely existed during previous times for much longer because it is primarily driven by coastal upwelling (Millar 2012), which has occurred along the California coast since the late Pliocene (Jacobs et al. 2004).

Several recent studies have documented the influence of the summer marine layer on vegetation in the coastal zone of California. For example, in sites adjacent to maritime chaparral, coast redwood (*Sequoia sempervirens*) and understory species have been found to rely on fog drip or foliar water uptake to maintain xylem function during the summer months (Dawson 1998; Burgess and Dawson 2004; Limm et al. 2009). Disjunct populations of Bishop pine (*Pinus muricata*) on Santa Cruz Island in southern California also depend on water subsidies from fog drip; however, fog and cloud shading also improve the water status of these pines by lowering the VPD and reducing transpiration demand (Fischer et al. 2009). A similar growth response to fog has been demonstrated in Torrey pine (*Pinus torreyana*) (Williams et al. 2008).

One chaparral genus that is widespread in chaparral throughout the Central West Region (Baldwin et al. 2012; Fig. 1) and that exhibits high species diversity in maritime chaparral is *Arctostaphylos* (Ericaceae). In particular, local endemism in *Arctostaphylos* is concentrated along the central California coast (Vasey and Parker 2008; Sawyer et al. 2009; Parker et al. 2012). *Arctostaphylos* is characterized by two different post-fire life history strategies: facultative seeders resprout after wildfire events yet depend on fire stimulation for seed regeneration (resprouters), whereas obligate seeders are killed by wildfire and recruit only by fire-stimulated seed (seeders) (Keeley 2000; Keeley and Davis 2007; Keeley et al. 2012). While *Arctostaphylos* species are representative of demographic trade-offs characterized by these fire-type life histories (Keeley and Zedler 1978; Kelly and Parker 1990), *Arctostaphylos* life histories may also diverge in ecophysiological characteristics, as has been found in *Ceanothus* (Jacobsen et al. 2007; Pratt et al. 2010). Physiological trade-offs are predicted to influence water status because compared to resprouters, seeders have more shallow roots (Cooper 1922; Hellmers et al. 1955; Kummerow et al. 1977) and they also obtain nutrients and water more effectively in shallow soils (Paula and Pausas 2011).

In the study reported here, we investigated the late dry season water status (Ψ_{min}) of the chaparral shrubs of genus *Arctostaphylos* arrayed along a coast-to-interior summer marine layer gradient. We hypothesized that (1) the Ψ_{min} of *Arctostaphylos* shrubs will be less negative along the coast than in the interior, and that this relationship will persist despite the latitudinal effect of greater precipitation in the north versus the south; (2) the Ψ_{min} of seeders will be more negative than that of resprouters which coexist in the same microsites; (3) water use efficiency (WUE; δ^{13}C) of *Arctostaphylos* shrubs will be lower along the coast (more negative) than in the interior (less negative); (4) xylem vulnerability to cavitation will be greater (less negative P_{50} values) for the coastal *Arctostaphylos* shrubs than for interior *Arctostaphylos* shrubs (more negative P_{50} values). Regional differences between coastal and interior summer dry season climates have been broadly illustrated elsewhere (e.g., Johnstone and Dawson 2010), indicating that the coast is cooler and moister than the interior. However, we also measured local microclimate variables at a subset of our study sites to more fully characterize abiotic conditions associated with the summer marine layer climate gradient and to help interpret ecophysiological conditions of shrubs inhabiting these sites. Soil factors known to

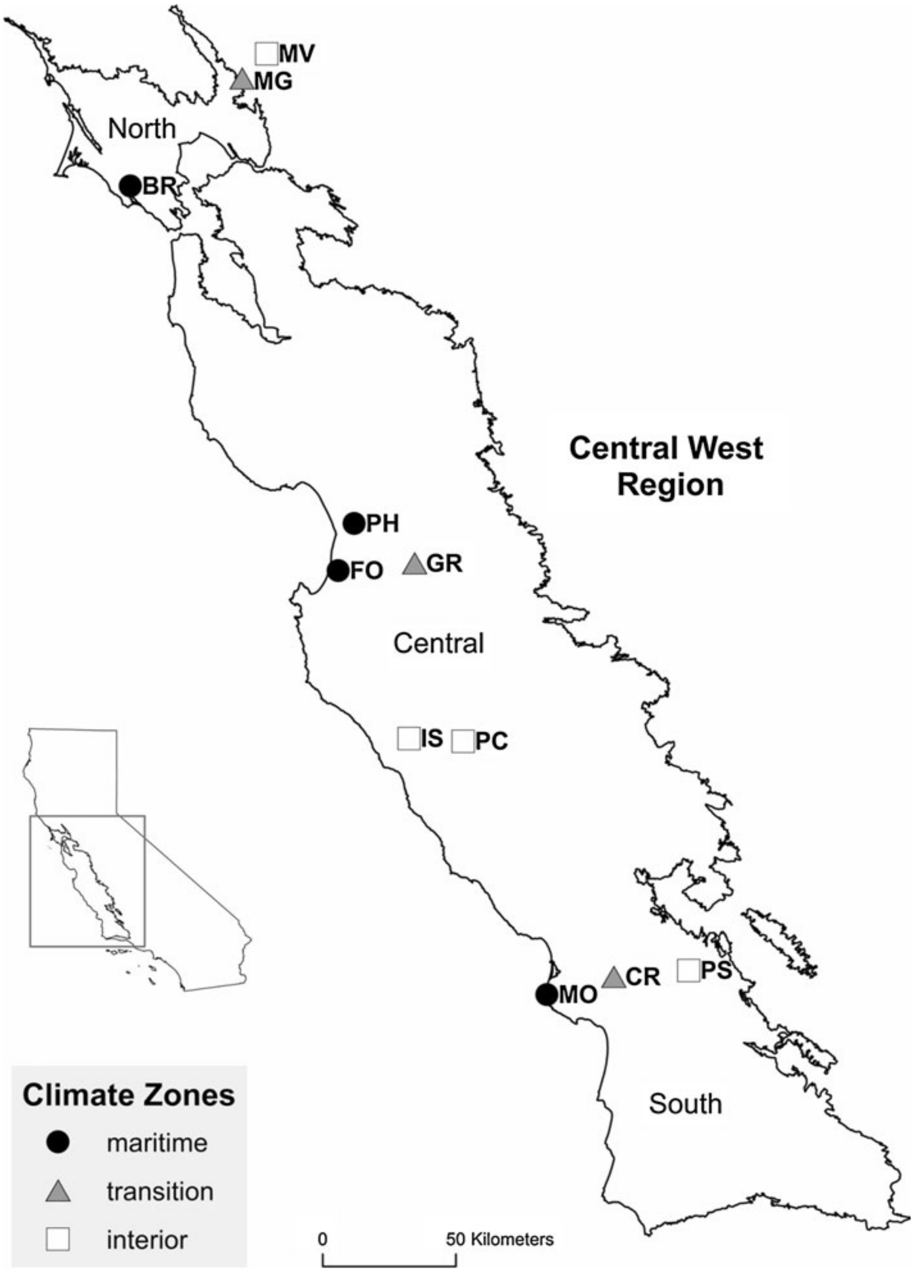

Fig. 1 Distribution of sampling sites in the Central West Region of California along a climate zone gradient (maritime, transition, interior). North subregion: *BR* Bolinas Ridge, *MG* Mount George, *MV* Mount Vaca; central subregion: *FO* Fort Ord, *PH* Pajaro Hills, *GR* Gabilan Ranch, *IS* Indians Station, *PC* Pine Canyon; south subregion: *MO* Montana de Oro, *CR* Cuesta Ridge, *PS* Pozo Summit. See Electronic Supplementary Material Table S1 for details of each study site

influence water-holding capacity [texture and organic matter (OM)], soil series, geological substrates and ecosystem types (dominant vegetation cover) were also identified for each site, and average daily and late dry season VWC values were compared among sites.

Materials and methods

Field sites

Sites were selected based on several criteria, including position along the coast-to-interior summer marine layer gradient, accessibility, security and presence of two or more species of *Arctostaphylos* with different life histories. Chaparral stands within sites were chosen based on visual similarity to adjacent stands and ease of access. Microsites within stands were randomly selected wherever two or more *Arctostaphylos* species were growing close enough together to be potentially sharing the same root zone (within 3 m from stem-base to stem-base) and where these microsites were ≥ 5 m distant from one another. Microsites within chaparral stands were variable in terms of slope, aspect and position relative to ridges and ravines.

In 2007, four study sites were established in the central subregion (Fig. 1), including two maritime, one transition and one interior [Electronic Supplementary Material (ESM) Table S1]. The two maritime sites were selected to contrast chaparral located at a low-elevation site near the ocean under persistent cloud shading by the summer marine layer to that located at a site farther from the ocean and higher in elevation which experiences frequent direct interception of summer marine cloud cover. The transition site was selected to test whether the coast-to-interior influence of the summer marine layer represents a gradient with an intermediate influence on *Arctostaphylos* shrub water relations. During June 2008, the central interior site (IS; ESM Table S1) burned in a wildfire. A new comparable interior site (PC; ESM Table S1) was established in August 2008.

During the 2009 dry season, we expanded the water potential analysis to include data collection from shrubs along coast-to-interior gradients 165 km north and 180 km south of the central study sites (Fig. 1; ESM Table S1). Study sites along these gradients were chosen using the same criteria as described above.

Microclimate

At the five central sites, we recorded temperature, relative humidity, short wave radiation, leaf wetness, and shallow (10 cm) soil moisture at 30-min intervals using HOBO Micro Station data loggers (Onset Corp, Cape Cod, MA). HOBO sensors are equipped with a 12-bit temperature RH smart sensor, a silicon (solar radiation) pyranometer, and a leaf wetness smart sensor. We also utilized 10-cm Decagon ECH$_2$O soil moisture probes that were calibrated for each soil type (Decagon Devices, Pullman, WA). This generated slope and intercept parameters that were used to calculate VWC data as a percentage of soil volume for each electroconductivity reading. For each pair of temperature and relative humidity data, we calculated estimates of VPD and Ψ_{atm}. Estimated VPD was calculated as the difference between saturated vapor pressure (e_s) and actual vapor pressure (e_a) where $e_s = 0.6108 \times \exp\,[T \times 17.27/(T + 237.3)]$ and $e_a = e_s \times (RH/100)$; the Ψ_{atm} values were calculated as $[(RT)/V_w]\,[\ln(RH/100)]$, where R is the universal gas constant, T is the temperature (K), V_w the partial molal volume of water and RH is the relative humidity.

Soil analyses

At each of ten study sites after June 2008 (ESM Tables S1 and S3) and based on a random sample point, we established a 20 × 50-m plot that was subsequently divided into ten 10 × 10-m subplots; a single A horizon soil sample (approx. 10 cm deep) was collected at the center of each subplot. Percentage cover of dominant shrubs in each subplot was estimated to provide information about the ecosystem type associated with the soil samples, and the estimates were averaged for the whole plot (0.1 ha). Soil samples were pooled into labeled plastic bags and returned to the laboratory for processing. Air-dried samples were lightly crushed, sieved to ≤ 2.0 mm and analyzed (Brookside Labs, New Knoxville, OH). A soil texture analysis was conducted, including percentage fractions of sand, silt and clay as well as percentage organic matter (OM).

Soil VWC was estimated at the end of the dry season in 2009 by collecting two soil samples from the top 10 cm of the A horizon soil in each microsite below the canopy of adjacent *Arctostaphylos* shrubs ($n = 20$ per site). These were placed in tightly sealed jars and kept cold until returned to the lab. Gravimetric analysis was used to calculate the volumetric water content (%) of each soil sample. Soil series and parent substrate were determined for each site, locating spatial coordinates on ‘SoilWeb—an online soil survey browser’ (http://casoilresource.lawr.ucdavis.edu/).

Plant water potential analyses

At all study sites, *Arctostaphylos* seeder and resprouter shrub species sharing the same microsites were tagged. Predawn and midday water potential readings were obtained for each *Arctostaphylos* shrub. A total of ten microsites with two or three coexisting species of *Arctostaphylos* shrubs were sampled per site. Each chaparral stand had at least one seeder and one resprouter shrub. If three species were present, they included a resprouter and two seeder species, and in all but one case the two seeder species were from different clades of *Arctostaphylos* (Boykin et al. 2005; Wahlert et al. 2009; ESM Table S2). Predawn and midday water potentials were sampled for each shrub from each site for three successive years at the end of the wet season (late March through mid April) and the end of the dry season (late August through mid September). For each sample, branches were excised using freshly sharpened hand pruners, sealed in a labeled plastic bag and then placed on ice in the dark until measured using a Scholander-type pressure chamber (PMS Instrument Co., Albany, OR). Total time from collection to the final measurement of 20–30 samples was generally within 1.5 h.

Water use efficiency

We used δ^{13}C values to compare the integrated WUE for different *Arctostaphylos* shrub species’ leaves (Farquhar et al. 1989; Dawson et al. 2002). We collected ten first-year leaves from each *Arctostaphylos* shrub that received predawn and midday water potential measurements during the dry season of 2009 from all ten localities ($n = 240$), placed them in labeled, sealed plastic bags, put them on ice for return to the laboratory and then dried them for 24 h at 40 °C. Dried leaf samples were analyzed for stable isotopes of $\delta^{13}C$ at the Center for Stable Isotope Biogeochemistry, University of California, Berkeley, CA. Dried leaves were ground to a fine 200-mesh powder using a ball grinder and analyzed for carbon (C) content (% dry weight) and C stable isotope ratios via elemental analyzer/continuous flow isotope ratio mass spectrometry using a CHNOS Elemental Analyzer (vario ISOTOPE cube; Elementar, Hanau, Germany) coupled with an IsoPrime100 IRMS (Isoprime, Cheadle, UK). The isotope ratio is expressed in "per mill" notation, where the isotopic composition of a material relative to that of a standard on a per mill deviation basis is given by $\delta\ ^{13}C = (R_{sample}/R_{standard}-1) \times 1{,}000$, where R is the molecular ratio of heavy to light isotope forms. The standard for carbon is V-PDB. The reference material NIST SMR 1547, peach leaves, was used as a calibration standard. External precision for C isotope analyses was 0.08 ‰.

Xylem vulnerability to vascular cavitation

In 2008, we randomly collected stem segments ($n = 6$) from nine populations of *Arctostaphylos* shrub species at four central sites for xylem vulnerability analysis (ESM Table S2), placed them in labeled plastic bags on ice and transported them to California State University, Bakersfield. Xylem vulnerability values for sample stems were determined according to methods outlined in Jacobsen et al. (2005). In brief, stems were connected to a tubing system and flushed with water for 1 h at 100 kPa, and the maximum hydraulic conductivity (K_{hmax}) was measured gravimetrically (Sperry et al. 1988) using an analytical balance (CP124S; Sartorius, Goettingen, Germany). Following the determination of K_{hmax}, stems were spun in a centrifuge (Sorvall RC-5B refrigerated super speed centrifuge or RC-5C; Thermo Fisher Scientific, Waltham, MA) using a small custom-built rotor (Alder et al. 1997). Vulnerability to cavitation curves were constructed by plotting the water potential (generated using the centrifuge) versus the percentage loss of conductivity (PLC). For each stem, curves were fit with a second-order polynomial model (Jacobsen et al. 2007). Percentage loss of conductivity values 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 because conduits that were previously embolized or damaged may become conductive following flushing, resulting in an elevated K_{hmax} (Hacke et al. 2000; Sperry and Hacke 2002; Maherali et al. 2004). Correction for cavitation is performed using K_h following a relatively mild pressure (greater than −0.5 MPa) that embolizes these non-functional conduits while leaving functional conduits intact, thus yielding a more realistic K_{hmax}. Corrected curves were then used to predict the water potential at 50 % loss in hydraulic conductivity (P_{50}) for each stem, and these values were averaged to obtain a species mean.

Data analysis

Microclimate data at study sites were analyzed for the dry season of 2009. Average maximum daily temperature (T_{max}), percentage leaf wetness, VPD, Ψ_{atm} and soil VWC were calculated for each month of the dry season and for the entire dry season for each study site. Mean and standard errors (SE) were calculated using JMP ver. 8.0 software (SAS Institute, Cary, SC). Vapor pressure deficits, Ψ_{atm} and VWC data were log transformed, and leaf wetness data were square-root transformed to meet the requirements of normality. Pearson's product–moment correlations were calculated among all four variables, and simple linear regressions were performed with square root leaf wetness as the dependent variable and log VPD, log Ψ_{atm} and T_{max} as independent variables.

Mean and standard errors for field-collected soil VWC were calculated. All VWC values from each study site were pooled into dry season climate zones and analyzed by one-way analysis of variance (ANOVA). We used a non-parametric Wilcoxon/Kruskal–Wallis rank sum test to test for a significant difference between climate zones. For the water potential analysis, we analyzed 3 years of predawn and midday Ψ data from both wet and dry seasons using a linear mixed model (SPSS ver. 19; SPSS, Chicago, IL) that is robust to deviations from normal assumptions (West et al. 2007; Bolker et al. 2009). We eliminated a third seeder species from one of the maritime study sites so that we could compare equal numbers of seeder and resprouter pairs from the same phylogenetic clade (ESM Table S2) across all five study sites. We used microsite as subject and life history, season and year as repeated effects. Fixed factors were zone, season, year and life history. The random factor was microsite. We computed different variance–covariance matrices for repeated effects and random effects. We utilized −2 log likelihood ratios to choose the best fitting model. Preliminary analysis revealed that the wet season-dependent variables were mildly different but that these were more a reflection of variable wet season precipitation rather than dry season marine layer effects. Accordingly, we dropped 'season' from the model and used only late dry season predawn and midday water potential values as dependent variables. We found that late dry season predawn water potentials were less negative than midday water potentials and predawn water potentials were highly correlated to midday water potentials in the

3-year study ($r = 0.90$, $P < 0.0001$) and the 2009 regional study ($r = 0.93$, $P < 0.0001$). Consequently, we focused on the late dry season midday water potentials (Ψ_{min}).

Late dry season 2009 midday water potential (Ψ_{min}) and δ^{13}C data were analyzed using a linear mixed model as dependent variables with microsite as subject, life history as a repeated effect, climate zone and life history as fixed effects and microsite as a random effect. As in the central study site temporal analysis, the model used pairs of seeders and resprouters at each study site rather than including the four sites with three species (one resprouter and two seeders). Again, we chose to pair seeder and resprouter species within the same clade (ESM Table S2). Consequently, we examined ten localities and 200 individual shrubs ($n = 20$ per study site, ten seeder and resprouter pairs per microsite) including four maritime study sites, three transition study sites, and three interior study sites (Fig. 1; ESM Table S1). Microsite differences between seeders and resprouters at each site for Ψ_{min} and δ^{13}C were evaluated by calculating estimated marginal means of the fixed effects and their interactions using Bonferoni post-hoc tests. We then ran a similar model using subregion as a fixed effect rather than climate zone.

To assess comparative xylem vulnerability to vascular cavitation of seeder and resprouter species located in different summer marine layer climate zones, we conducted one-way ANOVA examining differences between P_{50} values of all seeder and resprouter taxa in the central subregion. P_{50} values were found to meet the assumptions of normality. Maritime seeders and the seeders from transition and interior study sites (grouped as interior seeders) were significantly different. By contrast, P_{50} values of resprouters were intermediate between those of maritime and interior seeders regardless of position along the coast-to-interior summer marine layer gradient. Accordingly, we grouped the three maritime seeder taxa, the three resprouter taxa and the two interior seeder taxa and ran a second one-way ANOVA with P_{50} values as the dependent variable. We also plotted vulnerability curves for these three groups.

Results

Microclimate

During the summer dry season there were substantial differences between microclimate factors in chaparral patches occupying coastal lowlands in contrast to those occupying interior uplands. Average daily percentage leaf wetness, a factor known to be associated with fog condensation (Burgess and Dawson 2004), was much greater for the two maritime localities than for the transition and interior localities (Fig. 2d). Average daily T_{max} was consistent with these leaf wetness differences (Fig. 2a). Mirroring the leaf wetness differences, VPD and Ψ_{atm} were strongly correlated ($r = 0.99$, $P < 0.0001$) (Fig. 2b). Square-root transformed leaf wetness values, as the dependent variable, were found to be strongly correlated with log VPD, log Ψ_{atm} and T_{max} ($r^2 = 0.88$, 0.89, 0.76, respectively; all $P < 0.0001$) as separate dependent variables.

Soil analyses

Average daily VWC values of shallow soils during the dry season were more complex than the microclimate data (Fig. 2c). Of the two maritime study sites, Pajaro Hills (PH) had about threefold higher average daily soil VWC values than Fort Ord (FO). The two more interior study sites demonstrated a predictable pattern of decline in average daily soil VWC as the dry season advanced during June, July and August, while the average daily soil VWC at the two maritime study sites remained relatively stable and actually increased at Fort Ord in July and at Pajaro Hills in August. During these two months, virtually no rainfall was recorded at meteorological stations near these two sites (total precipitation at Castroville, Corralitos and North Salinas was 0.0, 1.01 and 0.0 mm, respectively) (California Irrigation Management Information System, http://wwwcimis.water.ca.gov/cimis/data.jsp).

Late dry season soil VWC values (Fig. 3) were consistent with the average daily soil VWC values (Fig. 2c). They were significantly greater at maritime study sites, reduced at transition study sites and lowest at interior study sites; much greater VWC variability occurred at maritime sites than in the interior. Mean VWC values were 7.2 ± 0.54, 4.0 ± 0.28 and 0.8 ± 0.10 % at the maritime, transition and interior study sites, respectively ($\chi^2 = 72.4$, $P < 0.0001$). VWC variability at the maritime study sites appeared to be partially associated with soil differences, particularly with percentage OM and the total fraction of sand (ESM Table S3). Neither substrates nor soil series are the same in any of the sites, yet they all tend to be rapidly draining and/or shallow (National Cooperative Soil Survey, accessed through SoilWeb).

Ecosystem types were all chaparral vegetation dominated by various combinations of manzanita (*Arctostaphylos* spp.), chamise (*Adenostoma fasciculatum*) and ceanothus (*Ceanothus* spp.). Each chaparral stand was classified by the dominant cover of these three genera in descending order (ESM Table S3). Manzanitas dominated at maritime study sites whereas chamise was more prominent in interior study sites. Transition study sites were more evenly mixed. Ceanothus was a relatively minor component in chaparral stands that were sampled (which, by design, focused on manzanita species).

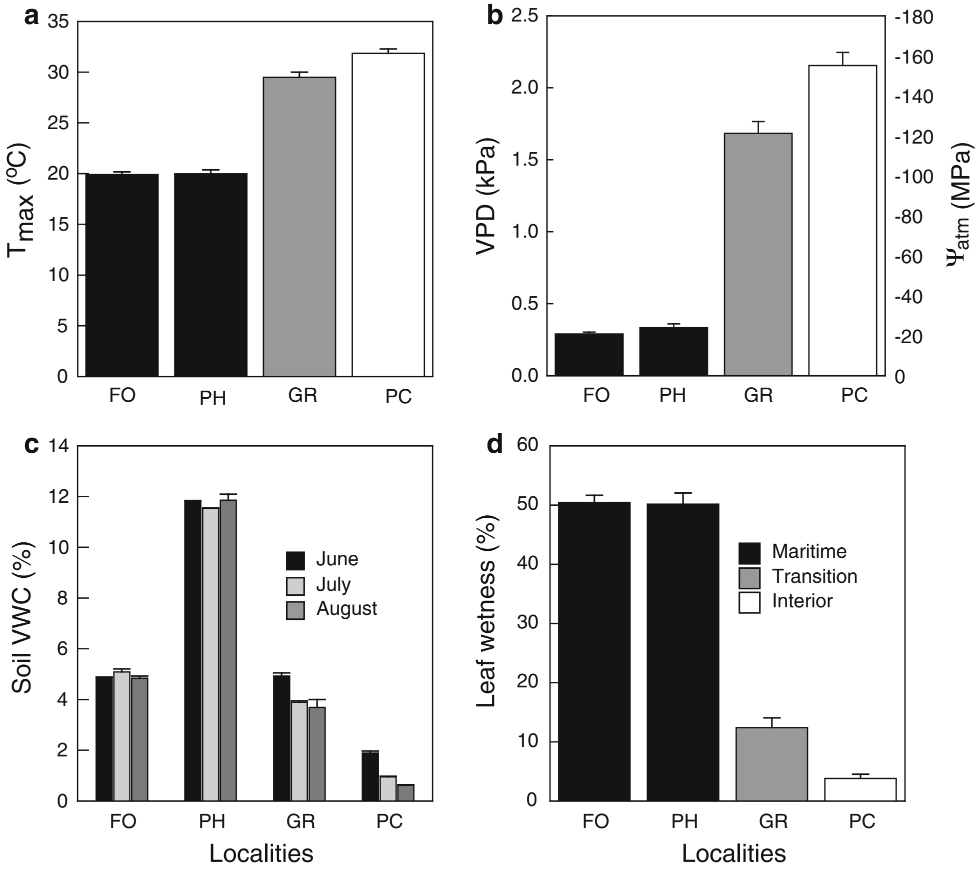

Fig. 2 Microclimate values for the dry season of 2009 at four central localities (1 May 2009–30 Sept 2009). See Fig. 1 legend for site codes. All data represent mean daily values ± standard error (SE), $n = 598$ except for soil volumetric water content (*VWC*) where $n = 368$ (01 June 2009–31 Aug 2009): **a** maximum daily temperature (T_{max}), **b** vapor pressure deficit (*VPD*) and atmospheric water potential (Ψ_{atm}), **c** June, July, and August VWC, **d** percentage leaf wetness

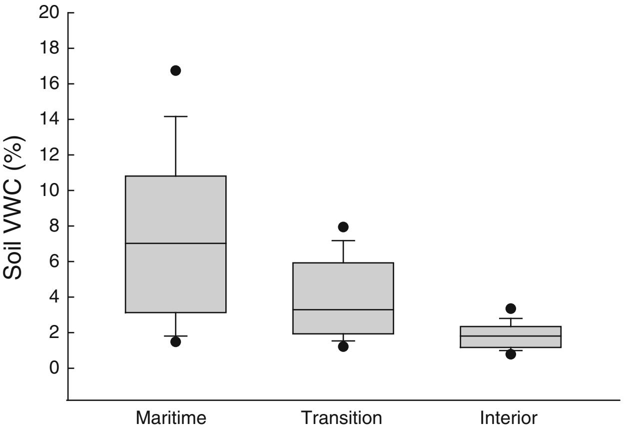

Fig. 3 Box plot of soil VWC in each summer dry season climate zone from maritime ($n = 80$), transition ($n = 60$) and interior sites ($n = 60$). Group values were significantly different based on a Wilcoxon/Kruskal–Wallis rank sum test ($\chi^2 = 72.4$, $P < 0.0001$). *Box plot* median value, *box outline* 25–75th percentiles, *whiskers* 5–95th percentiles, *dots* maximum–minimum values beyond the 5–95th percentiles

Plant water potential

The linear mixed model results for the 3-year study (Fig. 4a) demonstrated highly significant $\Psi_{\min}$ differences for *Arctostaphylos* shrubs in the three climate zones ($F_{2,41.4} = 141.7$, $P < 0.0001$), with the mean for maritime shrubs being the least negative (−3.45 ± 0.11 MPa), that for transition shrubs being intermediate (−4.63 ± 0.16 MPa), and that for interior shrubs being most negative (−6.39 ± 0.13 MPa). The mean of each of the three zones was also significantly different from each other ($P < 0.0001$). We found essentially the same results ($F_{2,97} = 170.0$, $P < 0.0001$) when $\Psi_{\min}$ values were compared among the three different climate zones for the 2009 dry season in all three subregions (Fig. 4b), with the mean for maritime shrubs being the least negative (−3.25 ± 0.12 MPa), that for transition shrubs being intermediate (−5.04 ± 0.14 MPa), and that for interior shrubs being the most negative (−6.72 ± 0.14 MPa). Life history traits ($F_{1,155.1} = 47.4$, $P < 0.0001$) and zone*life history trait interactions were also significantly different ($F_{2,155.1} = 16.5$, $P < 0.0001$) in the central 3-year study as well as the 2009 regional study ($F_{1,97} = 52.34$, $P < 0.0001$ for life history traits and $F_{1,97} = 10.88$, $P < 0.0001$ for zone*life history trait interactions). The $\Psi_{\min}$ 2009 results did not show any significant differences between seeders (−3.30 ± 0.13 MPa) and resprouters (−3.21 ± 0.15 MPa) in the maritime climate zone ($F_{1,97} = 0.38$), whereas there were highly significant differences ($F_{1,97} = 36.28$, $P < 0.0001$) between seeders (−5.54 ± 0.16 MPa) and

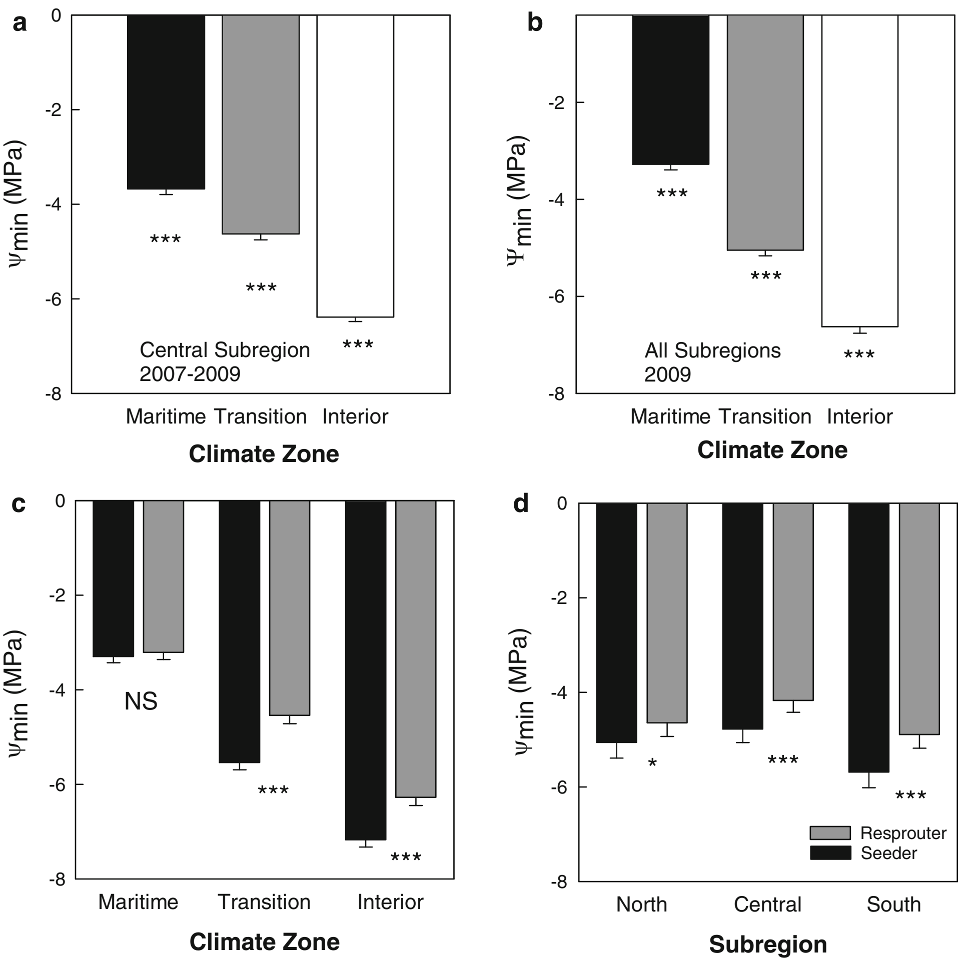

Fig. 4 Late dry season midday water potential ($\Psi_{\min}$); graphs represent mean ± SE. **a** Central sites over 3 successive years (2007–2009), by climate zone ($n = 290$), **b** all three subregions (north, central, south) in 2009, by climate zone ($n = 200$), **c** seeder ($n = 110$) and resprouter ($n = 90$) species, by climate zone, **d** seeder ($n = 130$) and resprouter ($n = 70$) species, by subregion. Differences between climate zone mean in **a** and **b** are significant at $***P < 0.0001$. Pairwise differences between seeder and resprouter mean in **c** and **d** are significant at $*P < 0.05$ or $***P < 0.0001$, or not significant (*NS*). Estimated marginal mean SE and contrasts were calculated by a linear mixed model (see text)

resprouters (−4.54 ± 0.18 MPa) in the transition zone and between seeders (−7.17 ± 0.16 MPa) and resprouters (−6.23 ± 0.18 MPa) in the interior zone ($F_{1,97} = 29.58$, $P < 0.0001$). We did not find significant differences among $\Psi_{\min}$ values for the three subregions (Fig. 4d); however, significant life history trait differences were found in all three subregions ($F_{1,97} = 36.46$, $P < 0.0001$).

Water use efficiency

The analysis of δ^{13}C values for the late dry season 2009 study revealed a highly significant climate zone effect ($F_{1,97} = 17.11$, $P < 0.0001$; Fig. 5). This effect is restricted to the interior shrubs (−26.47 ± 0.18 ‰) which differed significantly ($P < 0.0001$) from maritime shrubs (−27.79 ± 0.16 ‰) and transition shrubs (−27.62 ± 0.18 ‰). No significant life history or significant climate zone*life history trait interaction effects were found. Water potentials values and WUE (δ^{13}C) were significantly correlated ($r = -0.55$, $P < 0.0001$).

Xylem vulnerability to vascular cavitation

Xylem vulnerability values (Fig. 6a) for maritime seeders (−5.21 ± 0.21 MPa), resprouters (5.90 ± 0.18 MPa) and interior seeders (−7.21 ± 0.24 MPa) differed significantly ($F_{2,48} = 20.99$, $P < 0.0001$). The vulnerability curves (Fig. 6b) further illustrate the greater vulnerability to xylem cavitation by maritime seeders versus interior seeders, whereas the resprouters are more similar to the maritime seeders than the interior seeders.

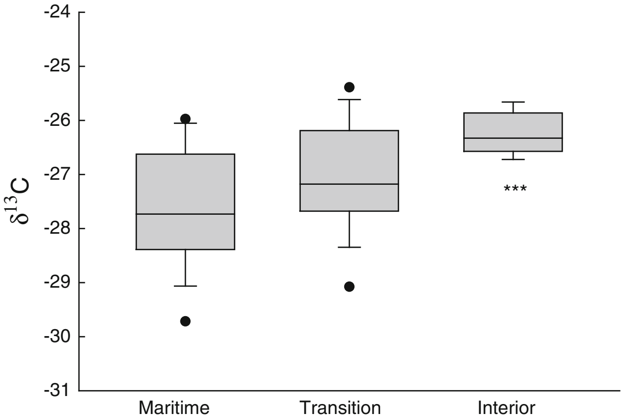

Fig. 5 Box plot of late dry season 2009 δ^{13}C values from shrubs sampled for midday water potential (Ψ_{min}) values by summer marine layer climate zone. Pairwise differences between mean reveal that only interior sites differed significantly (***$P < 0.0001$) from maritime and transition sites. *Box plot* Median value, *box outline* 25–75th percentiles, *whiskers* 5–95th percentiles, *dots* maximum–minimum values beyond the 5–95th percentiles

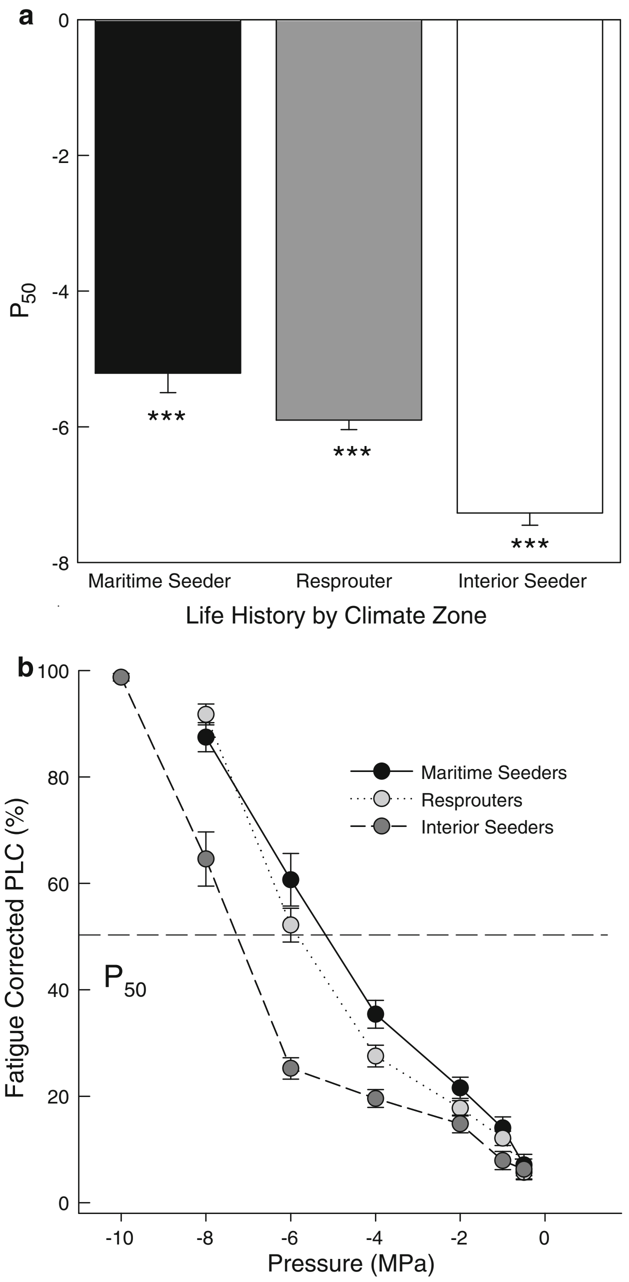

Fig. 6 Comparison of xylem vulnerability to cavitation (P_{50} pressure at which 50 % loss of xylem conductivity occurs) of maritime seeders ($n = 16$), resprouters ($n = 23$) and interior seeders ($n = 12$). **a** Mean ± SE and pairwise differences between three life history groups (***$P < 0.0001$). **b** Xylem vulnerability curves based on percentage loss of conductivity (*PLC*) for maritime seeders, resprouters and interior seeders; *dashed horizontal line* P_{50}

Discussion

A contemporary ecophysiological understanding of California chaparral (Miller et al. 1983; Davis et al. 1999; Keeley 2000; Dawson et al. 2002; Bhaskar and Ackerly 2006) would predict that chaparral habitats have very low soil moisture levels at the end of the dry season in the face of extreme transpiration demand and, accordingly, many evergreen shrubs will have extremely negative Ψ_{min} values, high WUE (less negative δ^{13}C values) and low vulnerability to vascular cavitation. Resprouter shrubs will have less negative Ψ_{min} values in the same chaparral stands as congeneric seeders, presumably because resprouters have deeper root systems (Davis et al. 1999; Pratt et al. 2010). Our findings are consistent with these expectations for *Arctostaphylos* shrubs in the interior chaparral. By contrast, in lowland coastal (maritime) chaparral, we found that *Arctostaphylos* shrubs have significantly less negative Ψ_{min} values and lower WUE and that post-fire obligate seeders (not resprouters) exhibit greater vulnerability to vascular cavitation (Figs. 4, 5, 6). Further, in maritime chaparral, seeders and resprouters sharing the same microsites did not exhibit significantly different Ψ_{min} values, supporting our hypothesis that these ecophysiological differences are associated with microclimate factors characteristic of the summer marine layer. We found that maritime chaparral habitats experience a greater average daily leaf wetting than interior chaparral, lower VPD, less negative Ψ_{atm} and relatively stable soil VWC over the course of the summer dry season (Fig. 2). Further, while late dry season VWC is on average much greater in maritime chaparral, it also appears to be variable, depending on characteristics associated with soil water-holding capacity (Fig. 3; ESM Table S3), whereas VWC is uniformly low in the interior regardless of soil conditions. These patterns are essentially coincident with the distribution and variability of summer fog and low cloud cover that seasonally dominates the California coast. In addition to reducing transpiration demand, summer fog and low cloud cover also potentially provide water subsidies through fog drip and foliar uptake (Dawson 1998; Limm et al. 2009); consequently, water availability in lowland coastal chaparral is likely to be greater than that in upland coastal chaparral (transition) or interior chaparral.

The ecophysiological differences we found between interior and coastal *Arctostaphylos* shrubs are consistent with other differences between maritime and interior chaparral. For example, maritime chaparral appears to have a longer fire return interval than interior chaparral (Odion and Tyler 2002; Anacker et al. 2011), and its distribution is more patchy and restricted to isolated edaphic islands (Sawyer et al. 2009). Chaparral communities in the interior are relatively less diverse and well adapted to withstand extreme seasonal drought conditions, while maritime chaparral species are numerous, less specialized for drought tolerance and characterized by local endemism (Cody 1986; Keeley 1992; Sawyer et al. 2009). Obligate seeder shrub diversity is greater than resprouter (facultative seeder) shrub diversity in most MTC regions (Table 3.4, p 69 in Keeley et al. 2012). As in California, however, high seeder shrub diversity has been particularly associated with more mesic MTC subregions in South Africa (Ojeda et al. 2005; Cowling et al. 2005) and southwestern Australia (Cowling et al. 2005). Consequently, in parts of MTC regions with more favorable water availability, high levels of post-fire obligate seeder shrub endemism may be a global phenomenon.

Although the contrast between interior and maritime chaparral is strong, this is not a bimodal system with a well-defined boundary because the summer marine layer creates a climatic gradient over a topographically heterogeneous landscape. This gradient is particularly complex because it has both horizontal and vertical components (Johnstone and Dawson 2010). In general, there is a transition zone of fog and low cloud cover influence between coastal lowlands below 500 m a.s.l. and coastal uplands above 500 m a.s.l. At higher elevations near the ocean (at approx. 1,000+ m a.s.l.), climate conditions become more interior-like, as is true the farther one travels inland at any elevation beyond the reach of the marine layer. As hypothesized, *Arctostaphylos* shrubs in transition zones tend to have Ψ_{min} values that are intermediate between those of the maritime and interior habitats (Fig. 4a, b). Although transition zone chaparral does not appear to be as rich in woody shrub species endemism as maritime chaparral (Vasey, unpublished data), it does host several rare *Arctostaphylos* species (Parker and Vasey 2004; Parker et al. 2012) and although the conservation priority for maritime chaparral is well recognized, this transition zone is also likely to be of significant conservation value (Stebbins and Major 1965).

A major difficulty in evaluating the summer marine layer gradient is the lack of a standard methodology to measure fog and low cloud cover (Johnstone and Dawson 2010). Average daily summer dry season T_{max} has been used as a surrogate for this purpose (Johnstone and Dawson 2010). Our study tested average daily dry season VPD, Ψ_{atm} and T_{max}. While T_{max} works reasonably well as a fog surrogate, VPD and Ψ_{atm} appear to provide a better fog signal, primarily because they combine measurements of both relative humidity and temperature. High-elevation coastal uplands tend to have relatively low T_{max} values despite experiencing high VPD and more negative Ψ_{atm}. Although Ψ_{atm} and VPD are essentially equivalent (but differ by a factor of 10^3; i.e., kilopascal vs. megapascal; Fig. 2b), there are certain advantages to using Ψ_{atm} over VPD. One such advantage is that Ψ_{atm} directly measures atmospheric demand in megapascals, which is the same unit used to evaluate Ψ_{soil}, plant Ψ_{min} and P_{50}, thereby allowing the researcher to more intuitively appreciate the powerful transpiration demand placed on shrubs. For example, dry season Ψ_{atm} values were -159.6 ± 6.3 MPa for the interior site at Pine Canyon versus -23.0 ± 1.0 MPa for the maritime site at Fort Ord. Additionally, the calculation of VPD relies on the assumption that internal leaf temperature is equal to the ambient air temperature, whereas the calculation of Ψ_{atm} does not require this assumption. Nonetheless, empirical tests have found that internal leaf temperature generally is highly correlated to ambient temperature, especially for small leaves (Kahmen et al. 2011). Moreover, VPD is widely used in the literature as a critical measure of plant–atmosphere water relations, and a tight correlation between fog and VPD has been well documented (Burgess and Dawson 2004). Measuring Ψ_{atm} or VPD, ideally remotely, should provide better insight into the dynamics of the summer marine layer, including better information for defining the transition zone.

Water relations among *Arctostaphylos* shrubs (particularly Ψ_{min} values) along the summer marine layer gradient were found to be consistent both over 3 successive years and at a regional scale during 1 year. Because the California coast extends over 1,000 km, and there is evidence that summer marine fog and low cloud cover have existed at various times along the coast for millennia (Millar 2012), this coastal dry season climate gradient is most likely a powerful driver of ecological and evolutionary processes. The xylem vulnerability analysis (Fig. 6) suggests differentiation among *Arctostaphylos* species, with highly significant P_{50} differences between maritime zone seeders and interior (and transition) zone seeders, as we hypothesized based on their different Ψ_{min} values (Bhaskar and Ackerly 2006). Because xylem resistance to cavitation is likely to be a strongly selected adaptive character (Pockman and Sperry 2000; Maherali et al. 2004; Bhaskar and Ackerly 2006), the xylem vulnerability data suggest that maritime seeders evolved in a more moderate mesic environment than interior seeders, consistent with the more favorable dry season water availability conditions of coastal lowlands as revealed by lower average daily VPD values, less negative Ψ_{atm} and higher percentage of leaf wetness values (Fig. 2b, d). An alternative possibility not explored in this study is that xylem vulnerability to winter freezing is also a factor limiting the distribution of chaparral species in this region (Boorse et al. 1998), possibly in combination with drought sensitivity (Davis et al. 2002).

Average daily soil VWC is also higher during the dry season in maritime compared to interior chaparral (Davis 1981; Fig. 3). The results of our comparison of soil VWC data between Pajaro Hills and Fort Ord (Fig. 4c), however, indicate that soil factors (e.g. texture and percentage OM) can constitute an important influence on soil VWC levels, as is also illustrated by the field collected soil VWC (Fig. 3; ESM Table S3). Other local soil nutrient conditions, as well as factors such as fire regimes, are also key ecological and evolutionary drivers of diversity and species distribution in chaparral (Stebbins and Major 1965; Raven and Axelrod 1978; Keeley et al. 2012). Yet, while these other factors are well recognized in the literature, the regional importance of a water availability gradient associated with the summer marine layer has previously not been documented for this ecosystem. It is likely that all of these factors are important to structuring chaparral composition and adaptive traits throughout coastal California (Anacker et al. 2011; Keeley et al. 2012).

Because *Arctostaphylos* seeders are the most diverse group of species that occur in California maritime chaparral (Vasey and Parker 2008; Sawyer et al. 2009; Parker et al. 2012), the results of this study have potentially important conservation implications. If the summer marine layer declines over time, as some evidence suggests is already happening (Johnstone and Dawson 2010; but see Snyder et al. 2003 for a contrasting view), this climate shift may constitute an additional risk to obligate seeder coastal endemic species. In contrast, the P_{50} values of maritime and interior resprouters are rather similar, suggesting that water availability is not as critical a factor for adult resprouters as seeders in maritime habitats; this is also consistent with the less negative Ψ_{min} values of interior and transition resprouter species compared to seeders (Fig. 4c).

In summary, based on our study of ecophysiological variables in a diverse set of *Arctostaphylos* shrub species widespread in chaparral throughout central coastal California, maritime chaparral is distinct from interior chaparral in a number of important responses to water availability across a summer marine layer gradient. Like other MTC regions (Cowling et al. 2005), evidence indicates that the greatest overall woody plant species diversity and endemism in MTC shrublands is situated in more mesic, less extreme seasonal drought-prone areas. This is not to say that there is necessarily greater species diversity in chaparral stands at local scales in these areas (cf. Meentemeyer et al. 2001) but rather within the species pool at a more regional scale; i.e., higher beta diversity (Harrison et al. 2006). Further, this is not a bimodal condition, but rather there is a summer marine layer gradient conforming to coastal topographic heterogeneity and a transition zone along this gradient that is biologically meaningful and potentially of conservation concern. Conceptually, long-term climate conditions associated with the summer marine layer, represented best by VPD and Ψ_{atm} in our analysis, correlate strongly with ecophysiological characteristics of these *Arctostaphylos* species. The combined results of the Ψ_{min} and xylem vulnerability analyses suggest that certain local endemic *Arctostaphylos* seeders in maritime chaparral have P_{50} values substantially less negative than average Ψ_{min} values of interior seeders; i.e. their xylem vulnerability is substantially greater than minimum late dry season water potentials under field conditions in the interior. This suggests that these local endemics are vulnerable to a shift to more interior climate conditions if the summer marine layer breaks down. Given the uncertainty in future summer fog regimes (Snyder et al. 2003; Johnstone and Dawson 2010), future conservation planning for maritime chaparral species should take this possibility into consideration.

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