LIFE HISTORY TYPE AND WATER STRESS TOLERANCE IN NINE CALIFORNIA CHAPARRAL SPECIES (RHAMNACEAE)

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Abstract. Chaparral species of California, USA, exhibit three life history types in response to fire: non-sprouters (NS), facultative sprouters (FS), and obligate sprouters (OS). Adult non-sprouters are killed by fire; thus populations reestablish only through fire-stimulated seed germination and seedling recruitment. Facultative sprouters reestablish by both vegetative sprouting and seed germination. Obligate sprouters reestablish only by vegetative sprouting and do not recruit seedlings post-fire. Previous data suggest that post-fire NS and FS seedlings reestablish as open-canopy gap specialists, whereas OS seedlings primarily reestablish in deep shade during fire-free intervals. Their non-refractory seeds are killed by fire. We hypothesized that these differences in life history, compared within the same taxonomic group, would result in a range of relative resistance to water stress such that NS > FS > OS. To test our hypothesis, we estimated resistance to water stress using resistance to xylem cavitation (the water potential at 50% loss in hydraulic conductivity; Ψ_{50}) for stems and roots in nine species of the family Rhamnaceae: *Ceanothus megacarpus*, *C. crassifolius*, and *C. cuneatus* (NS); *C. spinosus*, *C. oliganthus*, and *C. leucodermis* (FS); and *Rhamnus ilicifolia*, *R. crocea*, and *R. californica* (OS). Stems of NS species displayed greater resistance to cavitation ($\Psi_{50} = -8.38 \pm 0.47$ MPa) compared to both the FS ($\Psi_{50} = -5.07 \pm 0.55$ MPa) and OS species ($\Psi_{50} = -5.99 \pm 0.38$ MPa), whereas FS and OS species were not different. For roots, the general pattern was the same, but roots were generally less cavitation resistant than stems. A hydraulic model predicted that water uptake in OS species was limited by extensive cavitation in vulnerable root xylem, consistent with a reliance on deep soil water. Water uptake in cavitation-resistant NS species was most limited by soil hydraulic resistance, consistent with maximizing extraction of shallow soil water. These results suggest a link between life history and water stress tolerance in chaparral.

Key words: *cavitation; Ceanothus; drought; fire; non-sprouting; sprouting; water potential; Rhamnus; xylem.*

INTRODUCTION

Understanding how the broad range of plant life history and physiological traits are integrated is a chief goal in the study of ecology and evolution. The biodiverse Mediterranean-climate regions have provided a model system for understanding the ecological and evolutionary consequences of life history variation among fire-recruiting plants (Ojeda et al. 2005, Keeley et al. 2006). Due to the summer rainless period in these regions, they have also been valuable for studying the physiology, ecology, and evolution of water stress resistance among evergreen woody perennials, especially in the California chaparral (Poole and Miller 1975, Saruwatari and Davis 1989, Thomas and Davis 1989, Kolb and Davis 1994, Jarbeau et al. 1995, Davis et al. 1998, 2002, Ackerly 2004, Jacobsen et al. 2005, 2007).

There is broad evidence for a correspondence between some chaparral life history types and traits commonly associated with water stress resistance (Cooper 1922, Barnes 1979, Ackerly 2004); however, a full understanding of water stress resistance and life history type is lacking. The purpose of the present study was to examine the relationship among three contrasting life history types and water stress resistance in nine species of chaparral shrubs with special reference to maintaining xylem water transport during water stress.

The fire-prone Mediterranean-type climate regions of the world are found in California, USA; the Mediterranean basin; the Cape Floristic Region of South Africa; and southwestern Australia. Generally, the evergreen sclerophyllous shrubs that naturally occur in these regions are able to rapidly regenerate following fire. The means of recovery among California chaparral species represents a continuum where, at one extreme, non-sprouters (NS or obligate seeders) only recruit seedlings from seed and undergo no vegetative sprouting. The opposite extreme of this are obligate sprouters

(OS) that exclusively undergo vegetative sprouting post-fire with no seedling recruitment. Intermediate between these two extremes are species that regenerate by a combination of sprouting and seedling recruits (facultative sprouters [FS] or facultative seeders). We use the term facultative sprouter here to mean that a species can regenerate by sprouting and seeding, whereas some authors prefer to use facultative seeders in the sense that post-fire seeding is optional (Keeley 2000).

Among chaparral in California, woody shrub species with different regeneration strategies are divergent in many of their life history traits. Non-sprouting and FS species are reproductively adapted to recruit seedlings and expand their populations in the post-fire environment, whereas OS species require long fire-free intervals for seedling recruitment and population expansion (Lloret and Zedler 1991, Keeley 1992a). Non-sprouters and FS produce seeds that generally are not animal dispersed, fall near the parent plant, and form a dormant seed bank that requires a fire cue to break dormancy (Keeley 1991, 1992b). Following fire, sites for colonization are extensive, and germinating seedlings are well positioned to exploit these available sites. Obligate sprouters produce seeds that are widely dispersed by vertebrates (often by birds), and the short-lived seeds do not form a dormant bank (Keeley 1994). Germination occurs with ample moisture, and the high temperatures during fire are usually lethal to their seeds. Post-fire, seedlings are absent or extremely rare and populations are maintained by sprouting from underground root structures. The OS species recruit seedlings during fire-free intervals, typically in available microsites in the litter layer of the shaded understory of a mature chaparral canopy (Keeley 1992a). With some exceptions, this pattern of recruitment leads to a patchy distribution across the landscape, whereas disturbance-dependent recruiters often form dense stands of approximately same-aged cohorts.

In addition to life history traits, adaptation to exploit the post-fire environment involves physiological and morphological adjustments relating to water stress during the long summer rainless season characteristic of Mediterranean-type climates (Parker 1984, Keeley 1998, Cowling et al. 2005). For example, in California, NS species in the genus *Ceanothus* (subgenus *Cerastes*) have small sclerophyllous leaves with stomatal crypts, and thick cuticles that are widely cited as adaptations to water stress (Cooper 1922, McMinn 1942, Nobs 1963). In addition, the stems of NS *Ceanothus* species are highly resistant to water stress induced cavitation compared to other woody species (Davis et al. 1999, Maherali et al. 2004, Jacobsen et al. 2007). The high degree of water stress tolerance in NS species reflects their specialization for recruitment and persistence in xeric microsites in the exposed post-fire environment (Frazer and Davis 1988, Thomas and Davis 1989, Odion and Davis 2000). Selection for water stress tolerance is further enhanced by density dependent intraspecific

competition for water that leads to stand thinning 5–15 years following fire (Schlesinger and Gill 1980).

In contrast to the NS species, FS species in the genus *Ceanothus* (subgenus *Ceanothus*) and OS taxa are not as morphologically and physiologically adapted to tolerate water stress. These species typically have less sclerophyllous (higher specific leaf area) leaves lacking stomatal crypts, and lower resistance to water stress-induced cavitation of stems than co-occurring NS species (Barnes 1979, Davis et al. 1999, Jacobsen et al. 2007). The relatively low resistance to water stress for FS species has demographic consequences with higher post-fire seedling mortality compared to NS species (Keeley and Zedler 1978, Frazer and Davis 1988, Thomas and Davis 1989). These physiological and demographic differences correspond with local species distributions with FS species occurring more commonly on more mesic north-facing slopes and NS species occurring on the most xeric sites (Odion and Davis 2000, Meentemeyer et al. 2001). It is likely that OS species that recruit in the shade are the least tolerant of water stress. Like the FS species, OS species tend to be distributed in more mesic environments (Meentemeyer et al. 2001). At present, it is difficult to precisely know how the water stress tolerance of OS species compares to NS and FS life history types due to a lack of ecophysiological data for the OS life history type.

In the present study, we hypothesized that differences in water stress tolerance are coupled to life history type in response to wildfire such that the degree of water stress tolerance is NS > FS > OS. This idea is consistent with morphological and water stress tolerance data for stems and leaves of NS and FS species (Barnes 1979, Davis et al. 1999). The present study expands on previous work to include the OS life history type (see also Jacobsen et al. 2007). Further, the role of roots and soil in water stress tolerance has not been previously addressed among the different life history types, even though several studies have shown the roots to be more vulnerable to water stress than stems (Sperry and Ikeda 1997, Hacke et al. 2000). We hypothesized that the patterns for roots and soil would parallel the patterns found in stems. The link between life history and physiology is broadly important to understanding the ecology and evolution of woody perennials in the biodiverse Mediterranean-type ecosystems (Ackerly 2004, Ojeda et al. 2005).

To test our hypotheses, we sampled nine species of chaparral shrubs within the family Rhamnaceae. Among these nine species, three are NS and three are FS, both in the genus *Ceanothus*, and three are OS in the genus *Rhamnus*. Each of three study sites included one of each of the three life history types to help control for site differences (Table 1). All nine species are woody evergreen shrubs, thus controlling for any life history trait or functional trait differences associated with life form (Vesk et al. 2004, Keeley et al. 2006). Water stress tolerance arises from a suite of morphological and

TABLE 1.   Study sites, life history types, and abbreviations for *Ceanothus* and *Rhamnus* species.

Life history and species	Abbreviations	Site	Elevation (m)	Date of last burn	Soil texture sand : silt : clay (%)†
NS subgenus *Cerastes*‡					
Ceanothus megacarpus Nutt.	Cm	1	60	1985	71:16:14
C. crassifolius Torrey	Ccr	2	150	1993§	62:32:16
C. cuneatus (Hook.) Nutt.	Ccu	3	335	1993	62:27:12
FS subgenus *Ceanothus*					
Ceanothus spinosus Nutt.	Cs	1	60	1985	64:21:15
C. oliganthus Nutt.‖	Co	2	150	1996	76:17:8
C. leucodermis E. Greene	Cl	3	335	1993	61:24:15
OS					
Rhamnus ilicifolia Kellog	Ri	1	60	1985	71:17:12
R. californica Eschsch	Rca	2	150	1996	54:34:12
R. crocea Kellog	Rcr	3¶	250	1996	74:16:10

Note: Abbreviations are: NS, non-sprouter; FS, facultative sprouter; and OS, obligate sprouter.
† All soil textures correspond to the sandy loam class.
‡ The NS and FS species are divided into well-supported monophyletic subgenera (McMinn 1942, Hardig et al. 2000, Richardson et al. 2000).
§ A large fire burned much of site 2 in 1996, but the sampled stand of *C. crassifolius* did not burn in 1996.
‖ *Ceanothus oliganthus* var. *oliganthus* occurs and was sampled at both sites 2 and 3. It does not form a lignotuber or resprout following fire.
¶ The population of *R. crocea* that we sampled was 3.2 km west of site 3.

physiological traits that include stomatal response to water deficits, turgor loss point in cells, and the sustained ability of xylem to transport water as water potential (Ψ_x) declines. Here, we focused on the ability of nine species of Rhamnaceae to sustain their transport of water to evergreen leaves in the face of increasing water stress, i.e., resistance of stem and root xylem to water stress induced cavitation. For chaparral, cavitation resistance is a more reliable predictor of water stress tolerance than the turgor loss point (Saruwatari and Davis 1989, Thomas and Davis 1989, Davis et al. 1998, 1999), and a study conducted in parallel with this one examined stomatal response to water stress in the species studied here (Watson 2006). We measured cavitation resistance of stems and roots, and seasonal changes in branchlet Ψ_x to assess water stress tolerance in these species. Using these results in conjunction with soil texture data, we employed a hydraulic model to predict the Ψ_x limiting water uptake by xylem cavitation and soil drying for each species (Sperry et al. 1998). Here we focused on adults, but cavitation resistance may change ontogenetically, and to evaluate this, a parallel study to this one examined cavitation resistance in seedlings for these same nine species (R. B. Pratt, *unpublished data*).

METHODS

Study sites and plants

Naturally occurring populations of nine species of shrubs in the family Rhamnaceae (Hickman 1993) were sampled at three sites in the Santa Monica Mountains in Los Angeles County, California, USA (Table 1). We chose to examine relatively closely related species from similar environments to help control for taxonomic and environmental effects on water stress tolerance and life history traits.

The climate in the area of study is Mediterranean-type. To provide an approximation to the climate at our field sites, we report long-term precipitation and temperature data collected at the Los Angeles Civic Center, which is located 47 km west of our study areas and at ~100 m elevation (Thornton 2005). The mean annual rainfall from 1877 to 2004 was 379 mm with 88% of the rain falling between the months of November through April. The mean annual temperature was 18.9°C, and the hottest month was August with a mean maximum temperature of 28.4°C averaged between 1914 and 2001.

The first site was located on the campus of Pepperdine University near the Pacific Ocean (34°2′4″ N, 118°42′0″ W) and contained *Ceanothus megacarpus*, *C. spinosus*, and *R. ilicifolia*. A second site, 6 km inland from the coast near Tapia State Park at 34°5′0″ N, 118°42′2″ W (described in Langan et al. 1997), contained *C. crassifolius*, *C. oliganthus* var. *oliganthus*, and *R. californica*. A third inland study site, ~7 km from the coast near Stunt Ranch Preserve (34°5′8″ N, 118°39′2″ W) contained *C. cuneatus* and *C. leucodermis*. The closest population of *R. crocea* that we could locate and sample was actually 3.2 km from this site (34°5′8″ N, 118°41′0″ W). The soil texture in the shallow layers (0.15–0.2 m) at all sites was the sandy loam class (Table 1). Site elevation, date of last fire, and soil texture are summarized in Table 1. A large fire burned much of sites 2 and 3 in 1996, but as is common with chaparral fires, some patches do not burn and the sampled stand of *C. crassifolius* was part of a patch that did not burn in 1996 (Table 1).

Life history type is not phylogenetically independent in the present study since the species within each of the three life history types are in three monophyletic clades (Table 1). We caution that the correlation of life history

type and clade membership may generate spurious associations between life history type and functional traits (see *Discussion*).

Plant traits

The plant traits of height, specific leaf area, and seed mass were measured for each species generally following the recommendations of Westoby (1998). For plant height, we sampled 12 plants of each species. Measurements were taken from the soil surface at the plant base to the tallest foliated branch in the crown. Although these plants were not all the same age (see time since last burned in Table 1), all of the plants were reproductively mature and were annually gaining height very slowly as is typical of mature chaparral shrubs. The height values are representative for these species growing at their respective microsites in the Santa Monica Mountains.

The specific leaf area (SLA; mm^2/mg) was estimated for current-year, fully expanded leaves growing in full sun (however, *R. californica* leaves could only be found in partial sun). The leaf area of 10 leaves per individual from $N = 6$ individuals was measured with a leaf area meter (Li-3100, LI-COR, Lincoln, Nebraska, USA). Leaves were dried for 5 d at 70°C and massed on an analytical balance (AE163, Mettler-Toledo, Columbus, Ohio, USA).

Seed mass (mg) was measured for 100 seeds selected randomly from a bag containing seeds from numerous individuals. The sampled seeds were collected from our sampled populations in the Santa Monica Mountains with the exception of *C. leucodermis*, which came from a population near Lake Hemet in Garner Valley in Southern California, Riverside County. These seeds were purchased from S and S Seeds (Carpinteria, California, USA) because the seeds we collected from our local population of *C. leucodermis* were preyed upon (they had small holes bored into them) and were nonviable. Seed mass was measured on an analytical balance in an air-conditioned laboratory. Because of differential permeability of seed coats to water, seeds were not oven dried, but were instead measured under the same laboratory conditions.

Seasonal water status

Branchlet water potential (Ψ_x) was measured for naturally occurring populations of our nine sampled species at each study site using a pressure chamber (Model 1001, PMS Instruments, Corvalis, Oregon, USA) at predawn and midday (between 12:30 and 13:00 hours) in the summer dry season (7–9 September 2004). Measurements were repeated during the winter rainy season (25 February–2 March 2005). The summer dry season in 2004 saw no or only trace rainfall from 3 March until 21 October. The 2003–2004 annual rainfall total was 235 mm, which is well below the 128-year mean of 379 mm (Thornton 2005). In contrast, the 2004–2005 annual rainfall was the second highest in 128 years, and at the time we made our measurements in February and March 2005, 837 mm of rain had fallen in Malibu, which was well above the 128-year mean for Los Angeles at this time of year (277 mm; Thornton 2005).

Water potential was measured on branchlets of 6–10 different individuals from each species. Branchlets were removed from plants, bagged, placed on ice, and transported to Pepperdine University in ≤60 min, where they were rapidly processed in a climate-controlled laboratory with a pressure chamber. A previous study has shown that Ψ_x immediately sampled on branchlets in the field do not differ from those of bagged branchlets transported to the laboratory on ice for adult chaparral species (S. D. Davis, *unpublished data*).

Hydraulic conductivity and vulnerability to xylem cavitation

Hydraulic conductivity (K_h; $kg·m·MPa^{-1}·s^{-1}$) was measured by pushing de-gassed acid solution through stems at low pressure (~4 kPa; Sperry et al. 1988). The solution used was low pH (pH 2 HCl) and ultra-filtered (0.1-μm pore filter) to prevent clogging of stems (Sperry et al. 1988). Stems were mounted in a tubing apparatus connected to a low-pressure head at the basal end and a 0.1-mg resolution analytical balance (AE163, Mettler-Toledo, Columbus, Ohio, USA) at the distal end. The solution passing through the stem was collected on the balance connected to a laptop computer to record flux of the solution. The pressure head, stem length, and flux through the stem were used to calculate K_h after fluxes were corrected by measuring and subtracting the background flow in the tubing before and after stem flux was measured.

Vulnerability to cavitation was estimated as the loss of K_h for lateral stems and roots over a range of xylem water potentials generated using a centrifuge. Stems were removed from species at field sites, bagged, placed on ice, and refrigerated until sampled in the laboratory in ≤1 day. Collections were made during the winter rainy season (February) through fall (October) with most species being sampled in the spring and early summer months in 2003–2004, except for *C. crassifolius*, which was sampled in 1999, and *C. megacarpus*, *C. spinosus*, and *R. ilicifolia*, which were sampled in May through August of 2000. In the field, stems cut were ~1 m long and contained a 3–12 mm diameter segment (most were 7–8 mm) in a distal part of the cut stem. Roots were taken from depths between 0.1 and 0.8 m, their length upon removal was 0.2–1 m, and their diameter ranged from 3 to 12 mm (most were 7–8 mm). Stems and roots were recut under water to avoid xylem air entry to 0.27 m for the non-sprouting species and 0.14 m for all others. Longer stems and roots were used for non-sprouting species because a larger centrifuge rotor was needed to generate the high negative pressures (less than −10 MPa) needed to fully embolize the stems and roots of these species (Alder et al. 1997, Davis et al. 2002). The diameter of the smaller rotor only generates

−10 MPa with the centrifuge we used (RC5G Plus, Sorvall, Kendro Laboratory Products, Asheville, North Carolina, USA). Following trimming, stems and roots were mounted in the tubing apparatus to measure K_h and then flushed at 100 kPa with acid solution. The post-flushing K_h represented maximum K_h(K_{max}), i.e., K_h with no emboli in the xylem. Stems and roots were subjected to predetermined water potentials by repeatedly spinning them in a centrifuge (technique reviewed in Alder et al. 1997). Hydraulic conductivity was measured after each centrifuge/pressure treatment, and percentage loss of hydraulic conductivity (PLC) was calculated as $100 \times (1 - K_h/K_{max})$ for each sampled stem. The Ψ_x at 50% loss in hydraulic conductivity (Ψ_{50}) was used to compare the nine species. Some stems and roots showed cavitation fatigue varying between 5 to 50 PLC for stems and roots at $\Psi_x \geq -0.5$ MPa (Hacke et al. 2001). We corrected for this by calculating PLC using the K_h measured following the initial centrifuge spin at ≥ -0.5 MPa in place of K_{max}. Resistance to cavitation calculated this way is more accurate because xylem that cavitates at $\Psi_x \geq -0.5$ MPa is unlikely to be functional in situ among our sampled species, and uncorrected curves will tend to underestimate a species resistance to cavitation.

Modeling hydraulic limits

Vulnerability curves and seasonal measurements of Ψ_x were incorporated in a hydraulic model (Sperry et al. 1998) to predict how cavitation in roots and stems limited water uptake by each species. We used the model in its simplest form where the flow of water from bulk soil to leaf is represented by three hydraulic conductances in series: a rhizosphere conductance from bulk soil to root, a root xylem component, and a shoot xylem component. These conductances decline with water potential according to xylem vulnerability curves and soil properties. The model calculates the steady-state rate of water flow from bulk soil at one matric potential to the canopy at another, lower water potential. This calculation is repeated for a range of leaf water potentials to determine how steady-state flow rates decline with declining water status. This yields the minimum leaf water potential permitting steady-state water uptake (Ψ_{crit}). Any water potential below Ψ_{crit} results in hydraulic failure: a soil–leaf hydraulic conductance of zero. The Ψ_{crit} minus a measured midday Ψ_x provides an estimate of the safety margin from hydraulic failure. The model also gives the loss of hydraulic conductance in rhizosphere, root, and shoot components associated with any canopy Ψ_x.

The model requires several inputs, many of which were held constant across species because they did not influence the Ψ_{crit} and conductance outputs. All species were assigned the same maximum whole-plant transpiration rate and hydraulic conductance (saturated soil and no cavitation) with equal portions below and above ground. The absorbing root area was set to 10 times the

transpiring area, a high-end value for drought-adapted plants. This ratio can be as low as 1 in mesic plants, where the ability to extract water from drying soil is less critical (Sperry et al. 1998). The higher this ratio, the less the water uptake is limited by rhizosphere flow resistance and the more it is limited by xylem cavitation. When the xylem is limiting, the Ψ_{crit} falls to its minimum at the Ψ, causing complete cavitation (Sperry et al. 1998). Our high-end ratio of 10 was chosen to give conservative (extreme) estimates of Ψ_{crit} and maximum Ψ_x safety margins.

Species-specific inputs included the vulnerability curves of root and stem xylem for each species. These determined how abruptly the root and stem conductances declined with water potential. The analogous "vulnerability curve" for the rhizosphere conductance was estimated from soil texture data. Soil texture was sampled beneath 18 shrubs (3 spp. × 6 replicates) per site at 15–20 cm depth and analyzed for percentage of sand, silt, and clay content by the hydrometer method (Soil Analytical Laboratory, Logan, Utah, USA). Average percentages for each site (Table 1) were used to estimate how soil conductivity should decline with soil matric potential (Campbell 1985, Sperry et al. 1998).

The final species inputs were the 6–10 pairs of drought predawn and midday water potentials (each pair from a different plant). The predawn Ψ_x was used to set the bulk soil water potential, and the midday Ψ_x was used to calculate safety margins. Each pair yielded 6–10 estimates per species of Ψ_{crit}, safety margins, and conductance loss in the rhizosphere, root, and stem components under drought conditions.

Statistics

Stem and root diameter have been previously reported to correlate with cavitation resistance (Sperry and Ikeda 1997); however, in the present study no significant correlation was found between diameter and cavitation resistance. Therefore, we analyzed the vulnerability curve data pooled across stem and root diameters using separate analyses for stems and roots. Comparisons among species were analyzed using ANOVAs followed by Tukey's post hoc analyses (Minitab version 14.12, Minitab, State College, Pennsylvania, USA). Comparisons between roots and stems for each species were analyzed as preplanned contrasts. Life history type was analyzed in a mixed ANOVA model with life history type as a fixed effect and species as a random effect nested within life history type (Proc Mixed, SAS version 9.1, Cary, North Carolina, USA). Data were transformed as necessary to satisfy assumptions of statistical models. When comparing treatments, differences were considered significantly different at an $\alpha \leq 0.05$. If the P value exceeded α, we report treatments as similar or not different.

RESULTS

Throughout the results we discuss differences among NS, FS, and OS life history types. We point out here

TABLE 2. Plant height, specific leaf area, and seed mass for nine species and three different life history types.

Life history and species	Plant height (m)†	SE	SLA (mm²/mg)‡	SE	Seed mass (mg)§
NS					
Cm	2.87[acf]	0.15	2.29[a]	0.17	16.86
Ccr	2.93[ac]	0.15	2.36[a]	0.10	5.18
Ccu	2.71[adf]	0.10	3.37[b]	0.18	5.30
FS					
Cs	3.05[ac]	0.22	6.18[c]	0.38	6.76
Co	4.72[b]	0.23	8.63[de]	0.47	6.21
Cl	3.54[c]	0.11	8.33[d]	0.26	7.12
OS					
Ri	2.03[def]	0.17	5.15[c]	0.34	12.65
Rcr	1.42[e]	0.10	7.86[d]	0.31	6.22
Rca	2.22[f]	0.10	11.45[e]	1.14	74.15

Notes: See Table 1 for abbreviations. Means followed by unique superscript letters are significantly different ($P < 0.05$).

† Mean height of plants in meters ($N = 12$).

‡ Specific leaf area (mm²/mg) of 10 leaves averaged for $N = 6$ individuals.

§ Mean seed mass (mg) per seed measured for 100 seeds taken randomly from a bag containing seeds from numerous individuals.

that each of the three life history types belong to monophyletic clades (Table 1; see *Discussion*).

The fundamental traits of plant height, specific leaf area, and seed mass are shown in Table 2. The OS species were generally shorter compared to NS and FS species. The shortest species was the OS *R. crocea*. The FS species were generally the tallest, and among them, *C. oliganthus* was taller than all other species. For specific leaf area (SLA), the NS species had the lowest values, reflecting their smaller and thicker leaves. The OS *R. californica* had the highest SLA. Seed mass was variable and no consistent pattern emerged across life history types. Of note, however, is that *R. californica* had seeds that were considerably larger than all other species.

Resistance to cavitation of stems and roots, estimated as the water potential at 50% loss in hydraulic conductivity (Ψ_{50}), differed across the life history types (Fig. 1). For stems, the pooled mean of Ψ_{50} for NS species was more negative than both FS and OS life histories, suggesting that the NS life history has the greatest resistance to water stress (Fig. 2A inset). Each of the three sampled NS species exhibited greater resistance to cavitation compared to the other six sampled species (Fig. 2A). None of the NS species were different from one another in their resistance to cavitation (Fig. 2A). The FS and OS life history types did not differ in their stem cavitation resistance (Fig. 2A inset). None of the FS and OS species differed in cavitation resistance, except for the OS *R. californica* (Fig. 2A). *Rhamnus californica* stood out as having the lowest resistance to cavitation among all nine of the sampled species (Fig. 2A).

Roots were similar to stems in the pattern of cavitation resistance among life history types (Fig. 1). As with stems, the pooled mean among the NS species was more negative than both FS and OS life history types, indicating that the NS life history type has the greatest root resistance to cavitation (Fig. 2B inset). However, there was some overlap in root Ψ_{50} between NS and an FS species: Two of the sampled NS species, *C. megacarpus* and *C. cuneatus*, displayed resistance to cavitation that was not different from the FS species *C. spinosus* (Fig. 2B). This overlap results from the high resistance to cavitation of roots for the FS *C. spinosus*, which had the highest resistance to cavitation among any of the FS and OS life history types (Fig. 2B). None of the FS and OS species were different from one another in their resistance to cavitation, except for *R. californica* and the aforementioned *C. spinosus* (Fig. 2B). As with the stems, roots of *R. californica* were the least cavitation resistant among all nine sampled species (Fig. 2B). In summary, cavitation resistance of roots and stems exhibited the same general pattern with NS species displaying the greatest resistance to cavitation, whereas FS and OS life history types were not different.

Roots were generally more susceptible to cavitation than stems (Figs. 1 and 2). The only exception to this pattern was for *C. spinosus*, whose stem and root Ψ_{50} were not different ($P \geq 0.05$). The other eight species had roots that were less resistant to cavitation compared to stems ($P \leq 0.05$).

Branchlet water potential (Ψ_x), measured at the end of the summer dry period, was most negative for NS species (Fig. 3A). This is illustrated by comparing the pooled mean among each life history type (Fig. 3A inset). Among all species, the NS *C. cuneatus* exhibited the most negative Ψ_x. The Ψ_x for NS species was generally more negative than the other species, with the exception that the NS *C. megacarpus* was not different from the OS *R. ilicifolia* (Fig. 3A). The FS and OS species were generally not different, except for the FS species *C. leucodermis* and the OS species *R. californica*, both of which had higher Ψ_x than all other species (Fig. 3A). As more negative values for Ψ_x indicate a greater degree of water stress, the results suggest that NS species generally experienced the greatest degree of water stress compared to the FS and OS species. The FS and OS species were similar in the degree of water stress they experienced during the dry season; however, two species, *C. leucodermis* and *R. californica*, avoided water stress (had a less negative Ψ_x) to a greater degree than the other species (Fig. 3A). At the end of the summer period, Ψ_x at predawn was not different than Ψ_x at midday, except for *R. crocea* whose Ψ_x at midday was more negative compared to predawn. This general lack of difference between predawn and midday suggests that plants (except for *R. crocea*) were restricting water loss and that transpiration was minimal.

The Ψ_x during the moist rainy season was not different for any of the three life history types (Fig. 3B inset). All species exhibited high Ψ_x values compared to the dry season indicating the alleviation of water stress by the winter rains. None of the species differed in their
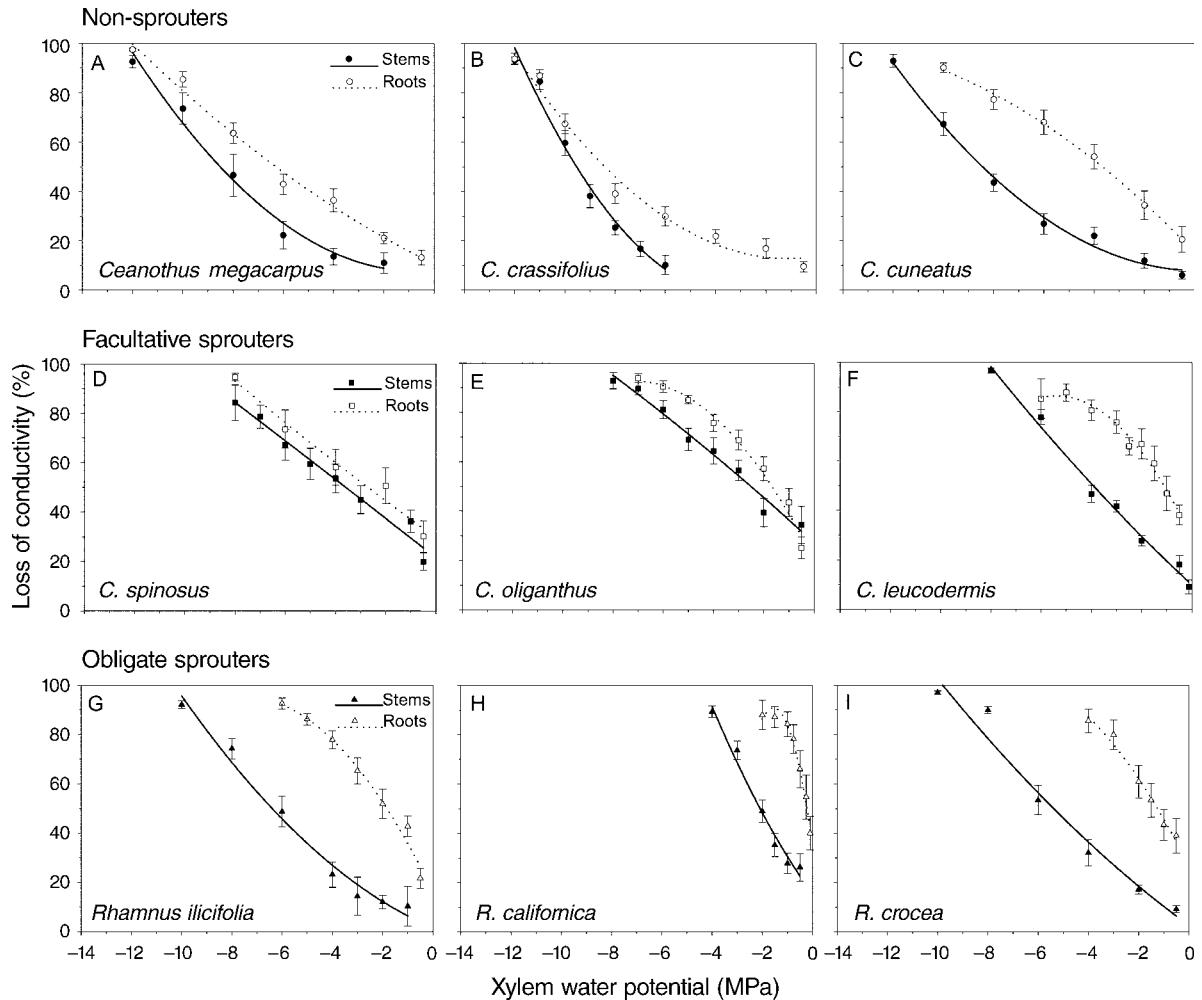
FIG. 1. Loss of hydraulic conductivity plotted as a function of xylem water potential of stems (solid symbols and lines) and roots (open symbols and dotted lines) for nine species representing three different life history types (see Table 1 for abbreviations). Data points are means ± SE ($N = 6$–12). Data were fitted with quadratic equations ($r^2 \geq 0.96$ and $P \leq 0.05$ for all plots).

Ψ_x except for *R. californica*, whose Ψ_x was lower than all other species (Fig. 3B). All species exhibited less negative predawn Ψ_x compared to midday Ψ_x except for *C. leucodermis*. The difference between predawn and midday Ψ_x during the moist season is presumably due to transpiration water losses in the morning. If this is true, then it suggests that *C. leucodermis* has lower *E* values or greater xylem transport efficiency compared to the other species.

Modeling predicted that NS species were least susceptible to hydraulic failure, i.e., had the most negative Ψ_{crit}, FS species were intermediate, and OS species had the least negative Ψ_{crit} (Fig. 4, compare *x*-axis values), consistent with their relative vulnerability to cavitation. Obligate-sprouters operated at much smaller safety margins from Ψ_{crit} during the dry season than NS species (Fig. 4).

The model predicted similar and substantial losses of whole-plant conductance during drought with an average of 77% ± 5% loss across all species. However, the distribution of conductance loss between soil, root, and shoot components differed substantially. This is best shown in terms of resistance (reciprocal conductance) because these components were in series and so their resistances are additive. In OS species between 55% and 84% of the predicted increase in whole plant resistance was caused by cavitation in the root xylem (Fig. 5A). By contrast, in the NS species between 75% and 84% of the resistance increase was in the rhizosphere or soil component (Fig. 5B). The FS species spanned the range between NS and OS species with *C. spinosus* predicted to have the greatest increase in resistance in the rhizoshere and *C. leucodermis* the greatest in the root xylem with *C. oliganthus* intermediate. Stem xylem was predicted to suffer little cavitation during drought, accounting for only 9% ± 1% of the increase in resistance across all species (analysis not shown).
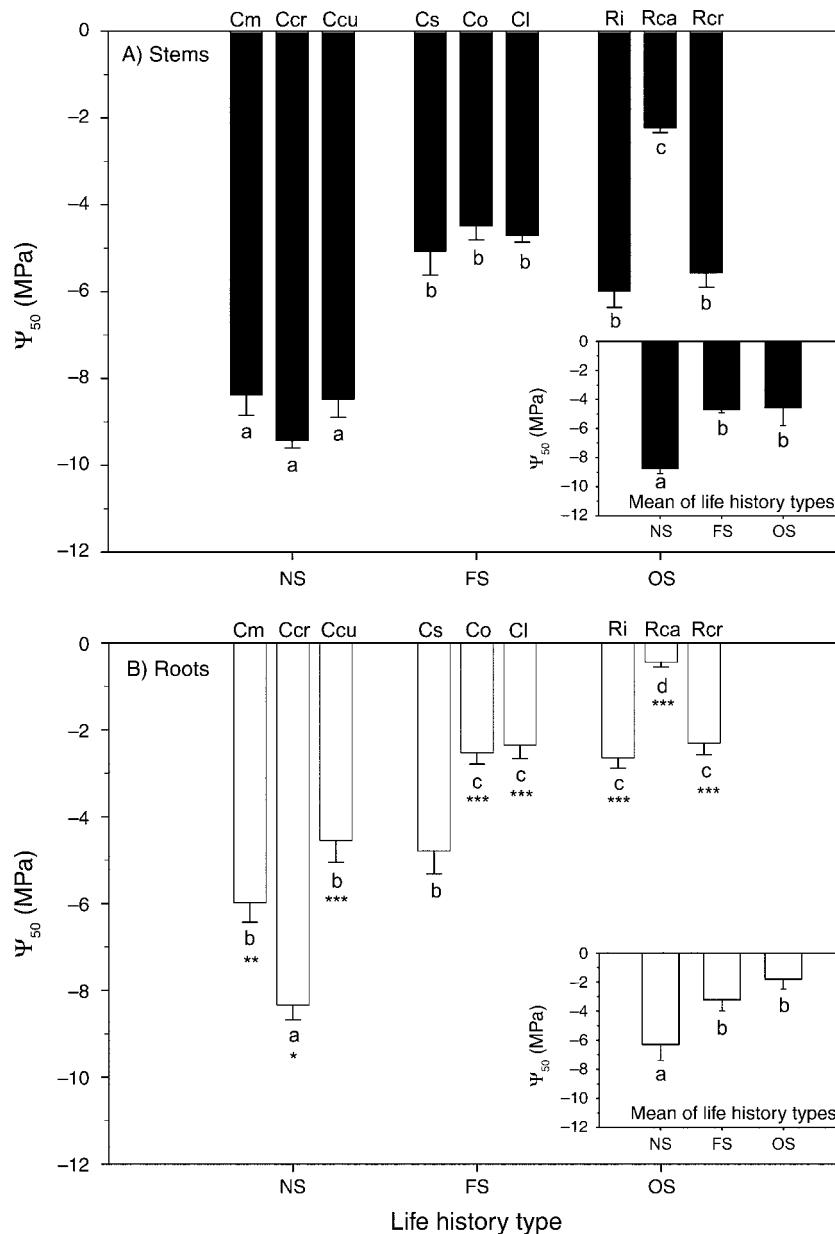
FIG. 2. The water potential at 50% loss of hydraulic conductivity (Ψ_{50}) of (A) stems and (B) roots for nine species representing three different life history types: non-sprouters (NS), facultative sprouters (FS), and obligate sprouters (OS) (see Table 1 for species abbreviations). Inset figures show the average Ψ_{50} across each life history type. Histogram bars show means, with error bars indicating SE ($N = 6$–12), and bars with unique letters are different from other bars (ANOVA; $P \leq 0.05$). Asterisks in panel B indicate differences between stems and roots (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$), and no asterisk indicates $P > 0.05$. For both insets, bars followed by a unique letter are significantly different ($P \leq 0.05$; ANOVA). Stem and roots were not different across life history types, reflecting low power to detect differences with $N = 3$.

The small safety margins in OS species (Fig. 4) were thus the result of considerable root cavitation (Fig. 5A). A few plants of *Rhamnus crocea* and *R. californica* were even predicted to be at their hydraulic limit with 100% cavitation in their root xylem. In the model, where there is only one soil–root–leaf flow path, complete cavitation in the roots terminates all water uptake. For the actual plant with multiple roots tapping soil at various matric potentials, this model result predicts that some fraction of these roots will be completely cavitated at the peak of drought in OS species.

DISCUSSION

Our data support the hypothesis that non-sprouting (NS) species generally have greater resistance to water stress compared to both facultative and obligate
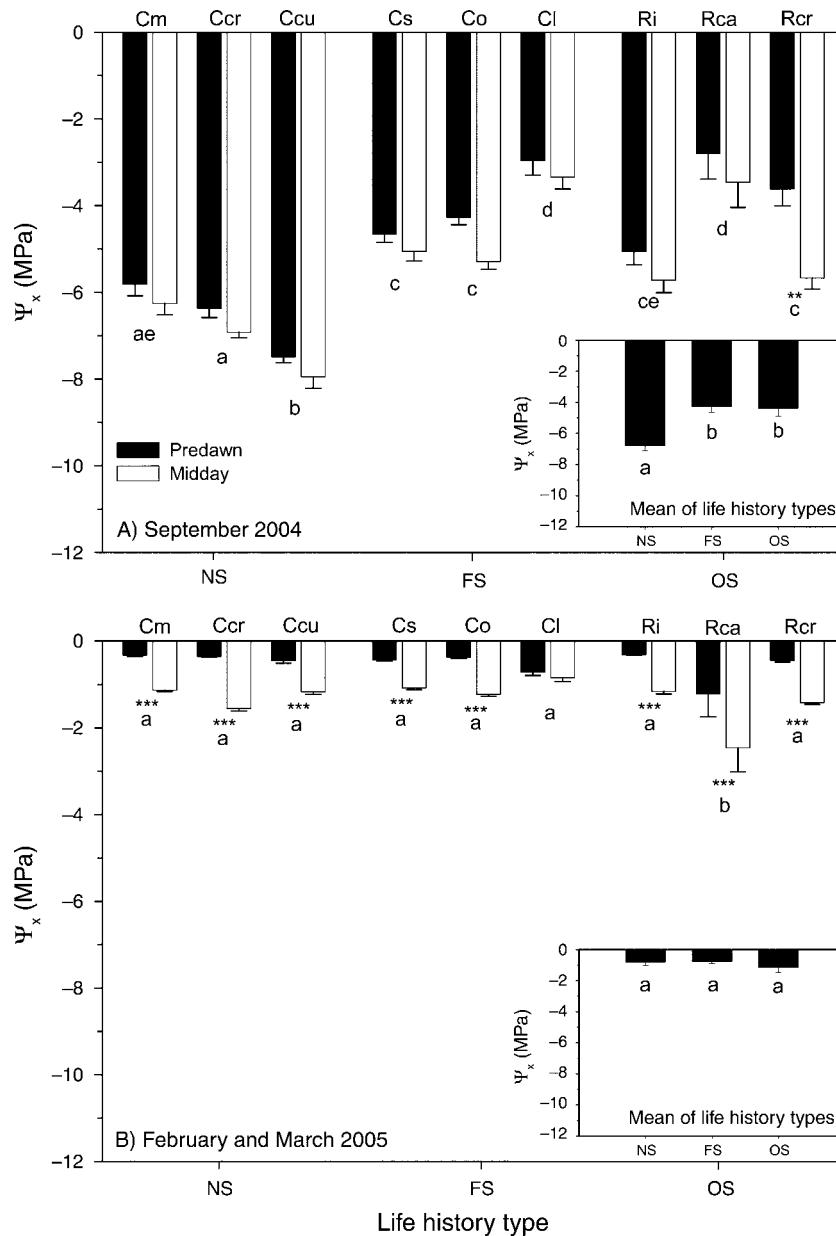
FIG. 3. Water potential (Ψ_x) at predawn (solid bars) and midday (open bars) shown for (A) the dry season (September 2004) and (B) the rainy season (February and March 2005) for nine chaparral species (see Table 1 for abbreviations). Histogram bars show means, with error bars indicating SE ($N = 6$–10), and predawn and midday bar pairs with unique letters are different from other bar pairs (ANOVA; $P \leq 0.05$). Asterisks below bars indicate differences between predawn and midday Ψ_x (** $P < 0.01$; *** $P < 0.001$), and no asterisk indicates $P > 0.05$. Life history type was analyzed separately from the data in the main panels (ANOVA). For both insets, bars followed by a unique letter are significantly different ($P \leq 0.05$).

sprouting species (FS and OS, respectively) as indicated by their greater resistance to cavitation of stems and roots, lower dry-season Ψ_x, and lower Ψ_{crit} values. In contrast to our initial hypothesis, however, FS and OS species did not consistently differ in their resistance to water stress-induced cavitation (Ψ_{50}). This indicates that NS *Ceanothus* spp. are more resistant to water stress than co-occurring FS congeners and OS confamilials. This is consistent with predictions for the NS life history

type, where adults are killed by fire and recruitment of seedlings typically occurs in the most arid and exposed microsites in the chaparral community leading to strong selection pressure for seedling water stress tolerance (Thomas and Davis 1989, Moreno and Oechel 1992, Odion and Davis 2000, Meentemeyer et al. 2001). These species are relatively long lived (healthy stands 100 years or older are not uncommon; Keeley 2000, Keeley et al. 2005) and undergo further selection for water stress
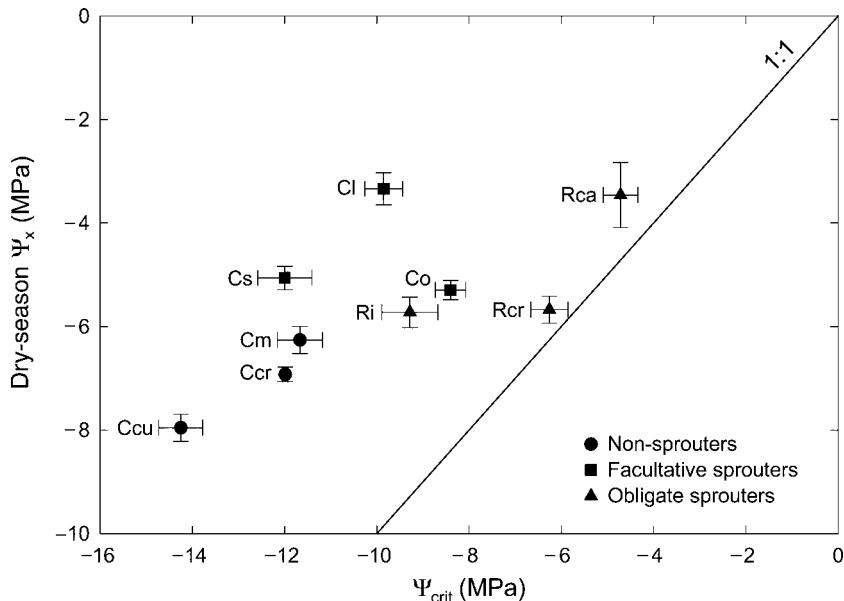
FIG. 4. Dry-season Ψ_x at midday plotted against the corresponding Ψ_{crit}, which is the least negative Ψ_x allowing water uptake without hydraulic failure. Safety margins between Ψ_x and Ψ_{crit} correspond to the vertical distance from the 1:1 line. Species abbreviations are given to the left of each datum point (see Table 1 for species abbreviations). Data points are means ± SE for 6–10 Ψ_x values per species.

tolerance as juveniles and adults. This occurs during a density-dependent thinning phase, where after 5–15 years dense stands thin partly due to competition for water (Schlesinger and Gill 1980, Schlesinger et al. 1982). In addition, due to their shallow rooting habit, periodic extreme drought events (such as occurred in 2001–2002) cause adult mortality for NS species, and this contrasts with deeper rooted sprouting species that suffer little to no mortality during such events (Horton and Kraebel 1955, Paddock 2006).

The OS *Rhamnus* spp. resprout following fire, whereas seedling recruitment is restricted to fire-free intervals and is facilitated by a well developed chaparral canopy (Keeley 1992*a*, Holmgren et al. 1997). Water is a major limiting factor for chaparral seedling recruitment, especially during the first summer rainless period after germination, when seedling roots are not fully developed. In the case of OS species that typically germinate below the canopy of adults, shade decreases seedling water stress and increases survival in the first year of growth compared to seedlings in full sun (R. B. Pratt, *unpublished data*). The OS species, which were predicted to be relatively vulnerable to water stress-induced cavitation, were actually rather resistant, with a Ψ_{50} of about −6 MPa. This is surprising given that recent meta-analyses incorporating NS, FS, and OS have shown that Mediterranean-type species exhibit a median Ψ_{50} of about −5 MPa (Maherali et al. 2004, Jacobsen et al. 2007). In addition, the Ψ_x for these two species underwent a considerable drop between the wet and dry season when it declined to about −6 MPa, a value similar to some of the shallow-rooted NS species (Fig.

3). Thus, the OS life history type is not characterized by intolerance of water stress at all stages of development. The crucial seedling establishment phase is facilitated by chaparral canopy shade and attendant reduced water stress, whereas the adult stage studied here is relatively tolerant of water stress. Higher water stress tolerance at the adult stage may be necessary for the successful transition from seedlings to saplings in that competition for soil moisture will be intensified due to increased canopy expansion and root extension into deeper soil horizons already occupied by the roots of older, established adults.

Our original prediction that OS species would be the most vulnerable to water stress was only supported by *R. californica*. *Rhamnus californica* was the most vulnerable to water stress among sampled species: The Ψ_{50} was −2.2 MPa, a value well above the −5.0 MPa mean for chaparral species (Jacobsen et al. 2007). *Rhamnus californica* is better suited to and has the highest affinity for shaded microsites among our sampled species. This is indicated by the high specific leaf area for this species compared to the other eight sampled species (Table 2) and its distribution in California (Cooper 1922, Davis and Mooney 1986) and the Santa Monica Mountains where adults are largely restricted to deep or partial shade (R. B. Pratt, *personal observation*). In addition, *R. californica* has seeds 5 to 10 times more massive than the other sampled species, giving it an advantage in avoiding hazards (including water and low-light stress) during recruitment (Baker 1972, Westoby et al. 1996). At field site two (Table 2), there are individual plants in partially exposed
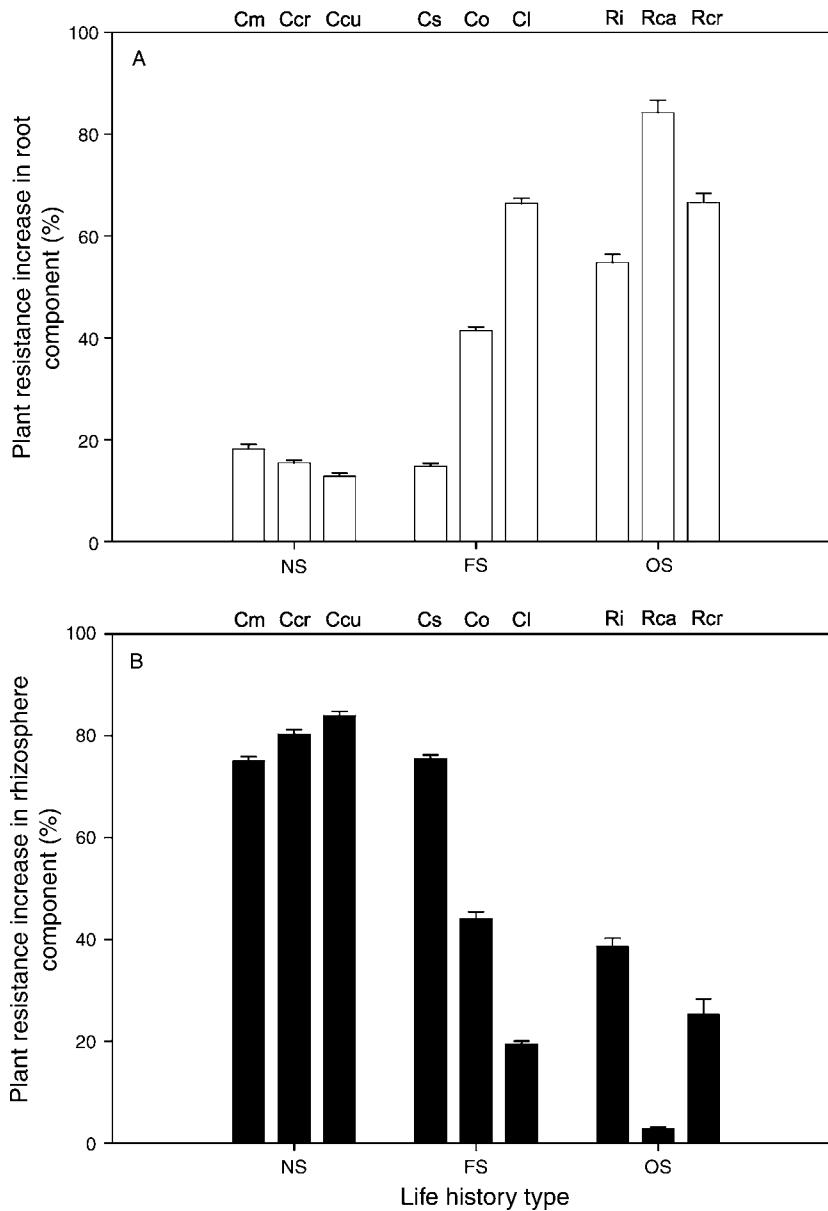
Fig. 5. The percentage of the modeled increase in whole-plant resistance during drought localized (A) to the root component because of cavitation and (B) to the rhizosphere component because of rhizosphere soil drying. Histogram bars show means + SE for 6–10 Ψ_x values per species (see Table 1 for species abbreviations).

microsites, and we have observed partial crown dieback concurrent with low water potential (Ψ_x) in these individuals (R. B. Pratt and S. D. Davis, *unpublished data*). This may be a case of water stress-induced dieback (Davis et al. 2002) as has been observed before for this species near San Francisco in northern California (Davis and Mooney 1986), suggesting that these plants are prone to severe stress in high light. Although such dieback can be extensive, these plants often survive by resprouting new branches. Thus, the water stress-coping strategy in *R. californica* at the adult stage is one where branches are periodically sacrificed to

preserve whole-plant survival and ensure future reproduction (Rood et al. 2000), a strategy incompatible with the NS life history type. The large seed and resprouting strategy employed by *R. californica* is successful as this species is among the most broadly distributed in the Mediterranean climate regions in California (Cooper 1922).

As with stems, and consistent with what we hypothesized, root resistance to cavitation was greater for NS species compared to the FS and OS species. This is consistent with the observation that NS species typically have shallower root systems compared to FS and OS

species (Hellmers et al. 1955, Kummerow et al. 1977, Thomas and Davis 1989). Shallower roots among the NS species were suggested here based on their lower predawn Ψ_x during the dry part of the season compared to both FS and OS species (Fig. 3A). Root resistance to cavitation is known to vary with soil texture (Sperry and Ikeda 1997), but this is unlikely a chief factor in the present study because sampled roots were in a similar sandy loam soil texture (Table 1). Having roots more resistant to cavitation especially benefits more shallowly rooted species by enabling them to maintain hydraulic function at lower Ψ_x and thus extract more water from drying soil (Sperry and Hacke 2002).

As with stems, roots for FS and OS species did not differ in their resistance to cavitation. The similarity in predawn Ψ_x during the dry season between FS and OS species suggests that they had similar rooting depths and were both more deeply rooted than the NS species (Fig. 3A). This observation relies on the assumption that Ψ_x at predawn approximates soil water potential in the rooting zone, and is consistent with the fact that all species except *R. crocea* had dry-season predawn and midday Ψ_x values that were not different. This suggests that transpiration (E) was likely minimal at the end of the dry season, and thus could not cause disequilibrium between plant and soil water potential (Donovan et al. 2003). One caveat here would be that if the plants were transpiring to a similar degree overnight and at midday they would have a similar Ψ_x and be in disequilibrium with the soil; however, previous studies have found that chaparral species tend to strongly restrict their water loss during the dry season, thus we think this is unlikely (Miller and Poole 1979). *Rhamnus crocea* likely had access to more soil moisture during the dry season due to the relative lack of competition for water, since the density of shrubs at the *R. crocea* site was lower there than at the other sites.

The root systems of the sampled FS and OS species were older than the root systems of NS individuals because sprouters survive multiple fires, whereas root systems of NS species are only as old as the last fire (Table 1). Presumably the older sprouting root systems have more time to develop extensive roots than the roots of younger non-sprouting species. The apparent similarity in rooting depth between the FS and OS species may put them in greater competition with each other at the adult stage of development, in contrast to the NS species, which are more shallowly rooted as adults.

The hydraulic model results supported the conclusions about life history types discussed thus far in the *Discussion*, but also allowed us to assess safety margins from hydraulic failure and localize the limiting resistances to the rhizosphere, root xylem, or stem xylem. Model output indicated that in all species stem hydraulic resistance did not appreciably increase during the dry season, indicating stems were not limiting hydraulic conductivity consistent with a previous chaparral study (Kolb and Davis 1994). Increased hydraulic resistance

was restricted to the root xylem or the rhizosphere depending on life history class (Fig. 5). Because NS species exhibited a greater degree of cavitation resistance, they maintained a greater margin of safety from hydraulic failure, and hydraulic failure was predicted to first occur in the rhizosphere and not the xylem, which is consistent with a previous study for an NS chaparral species (Davis et al. 2002). The extreme cavitation resistance of both roots and stems in NS plants should allow them to extract the maximum amount of water from a limited volume of drying soil, and also to resume water uptake quickly after the onset of early seasonal rainfall. These results indicate that cavitation resistances in NS species are well suited for a shallow rooting habit. The OS species operated closest to their hydraulic limits (Ψ_{crit}) among the three regeneration strategies. Two OS species (*R. crocea* and *R. californica*) were predicted to show complete cavitation in at least a portion of their root systems. The localization of hydraulic failure to root xylem (Fig. 5) resulted from the generally greater susceptibility to cavitation of roots for the OS species. Although root cavitation may have lead to some dieback in the OS *R. californica* (see third paragraph in the *Discussion*), the other two OS species, *R. crocea* and *R. ilicifolia*, did not exhibit dieback during the course of our study. We hypothesize that exceptionally vulnerable root xylem may favor plant water status in deep-rooted species by disconnecting the plant from drying shallow soil layers. As long as there are enough roots tapped into deeper and wetter soil, sacrificing the shallow roots would increase rather than decrease the overall plant water status (Meinzer et al. 1999).

One FS species, *C. spinosus*, maximized its cavitation resistance in a similar fashion to the NS species in the sense that cavitation was predicted to occur in the rhizosphere before it occurred in the plant xylem. This species is largely restricted to arid coastal environments in southern California and a small percentage of seedlings survive the severe water stress post-fire (Thomas and Davis 1989).

The general hypothesis emerging from the modeling results is that plants with roots and stems of equal and extreme cavitation resistance will be shallow rooted and specialized for maximum water uptake from a limited and drying soil volume. Plants with root xylem that is much more vulnerable than stem xylem will be deep rooted or otherwise have phreatophytic tendencies, and specialized for drawing water from a deep and stable source during drought. In this sense, the OS–FS–NS life history categories are points on a continuum of water use specialization from deep to shallow soil, respectively.

For evergreen woody chaparral shrubs, categorizing species by regeneration response to fire has proven valuable as a predictor of post-fire early successional dynamics (Keeley et al. 2006) and suites of physiological traits (Ackerly 2004). However, it should be noted that such a classification scheme breaks down when applied across a broader range of life forms. For example,

woody NS species produce a single post-fire seedling cohort, whereas suffrutescent NS species reach reproductive maturity more rapidly and produce multiple seedling cohorts in the post-fire years (Keeley et al. 2006). In the present study, we restricted our analyses to a life form of evergreen woody shrubs, and caution must be taken when extrapolating results to a broader range of life forms.

In the present study, we chose to examine relatively closely related species from similar environments to help control for taxonomic and environmental effects on water stress tolerance and life history traits. However, this design led to sampling species whose life history type is not phylogenetically independent since the species within each of the three life history types (NS, FS, and OS) are each in three monophyletic clades (subgenus *Cerastes*, subgenus *Ceanothus*, and the genus *Rhamnus*, respectively; Table 1). The correspondence of life history type and clade may generate spurious associations between life history type and functional traits. If life history type is indeed linked to water stress tolerance in a phylogenetically independent fashion, we would expect to see results similar to those here across other distantly related taxa.

Among California chaparral taxa, the heath family (Ericaceae) provides one opportunity for a phylogenetically independent test of the results presented here. Some populations of the NS *Arctostaphylos glauca* in the San Jacinto Mountains of southern California have developed high stem resistance to water stress induced cavitation ($\Psi_{50} = -9$ MPa; Paddock 2006). Poole and Miller (1975) found low Ψ_x values (less than -6.5 MPa, which was the limit of their pressure chamber) in *A. glauca* that were comparable to the co-occurring NS *C. gregii* in southern California. At our study site 3, *A. glauca* co-occurs with the FS *A. glandulosa,* and during a severe drought in 2001–2002, the Ψ_x for *A. glauca* was -11.2 MPa compared to -6.2 MPa for *A. glandulosa,* suggesting greater water stress tolerance in *A. glauca* (Jacobsen et al. 2007). These data suggest that at least one chaparral NS in the family Ericaceae, *A. glauca*, has evolved high tolerance of water stress in support of a phylogenetically independent link between life history type and water stress tolerance.

For the evolution of the NS life history type, water stress tolerance may not have been the chief driving factor. For *Ceanothus*, the sprouting trait is ancestral and non-sprouting is derived (Wells 1969). The evolutionary transition from sprouting to non-sprouting likely did not lead to an immediate high degree of water stress tolerance for NS taxa. During the course of this study, we concluded that *C. oliganthus* of the sprouting subgenus *Ceanothus* at both our study sites 1 and 3 is a non-sprouter after fire, does not produce a lignotuber, and is single stemmed. Some races of species in the subgenus *Ceanothus* are non-sprouters, and the two most commonly cited are *C. oliganthus* var. *oliganthus* and *C. tomentosus* var. *tomentosus* (Schwilk and Ackerly

2005, Fross and Wilken 2006). Other largely or entirely allopatric races (*C. oliganthus* var. *sorediatus* and *C. tomentosus* var. *olivaceous*) are apparently able to sprout (Schwilk and Ackerly 2005, Fross and Wilken 2006). The loss of sprouting in the subgenus *Ceanothus* is likely a relatively recent occurrence as suggested by the existence of sprouting and non-sprouting races.

We find that water stress tolerance of *C. oliganthus* is similar to other FS species even though functionally it is a non-sprouter. In addition, also characteristic of FS species, *C. oliganthus* occupies more mesic sites. What then is the advantage for *C. oliganthus* to evolve the NS life history if it is not the achievement of high tolerance to water stress? A partial explanation to this question is that the loss of sprouting in *C. oliganthus* has increased its competitive ability (Midgley 1996). This has been achieved in at least three ways. First, *C. oliganthus* grows taller than the other sampled species (Table 2). At field site 3, *C. oliganthus* has grown taller than and shaded out many competitors that can be found dead in the understory (R. B. Pratt, *personal observation*). Second, *C. oliganthus* forms a dense even-aged cohort of individuals that recruit post-fire and persist as is common to the NS life history type. This high-density population coupled with the taller growth diminishes available microsites in the understory for shade-intolerant species. Last, *C. oliganthus* produces numerous large shallow roots (Hellmers et al. 1955; R. B. Pratt, *personal observation*) that likely make it a good competitor for first seasonal rain events. This rooting habit is consistent with the NS species, but contrasts to the other FS and OS species that typically have fewer shallow roots and a greater number of deep roots (Hellmers et al. 1955; R. B. Pratt, *personal observation*).

The NS life history type has to recruit new seedlings post-fire or the population declines and may go extinct (Zedler et al. 1983), thus species employing the NS strategy in southern California have to be tolerant of water stress (such as those *Ceanothus* spp. in the subgenus *Cerastes*) or they are restricted to more mesic microsites such as *C. oliganthus* in the present study. This pattern is similar in Mediterranean climate regions of South Africa where NS *Erica* spp. are more common in moister regions (Ojeda et al. 2005). Due to the relatively recent loss in sprouting in *C. oliganthus*, it may have not had time to evolve a greater degree of water stress and invade more arid microsites (Zedler 1994). However, the loss of sprouting in *C. oliganthus* may be the initial step towards the invasion of more arid microsites that are extensive post-fire, since the pace of adaptive change should be quicker for the NS life history type with its shorter generation times (Wells 1969). Non-sprouters are also freed from the costs of constructing and maintaining sprouting structures and they avoid gene flow with parental genotypes in the post-fire environment, both of which may facilitate adaptive change. Finally, recruiting dense cohorts of seedlings may lead to increased competition for water and density-dependent selection

for water stress tolerance presuming stands thin as documented for other NS species (Schlesinger et al. 1982). The dense stand of *C. oliganthus* at site 3 is 12 years old and is showing signs of thinning (R. B. Pratt and S. D. Davis, *personal observation*). This thinning process may be crucial in culling from the gene pool less competitive genotypes (higher root to shoot ratios or a greater density of deeper roots) and ones that are less tolerant of water stress.

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