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Linkage between water stress tolerance and life history type in seedlings of nine chaparral species (Rhamnaceae)

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Summary

1. Chaparral shrub species along the southwest coast of North America survive wildfire by three different life history types: non-sprouters (*NS*) are killed by fire and only re-establish through germination of fire-stimulated seeds; facultative sprouters (*FS*) re-establish by a combination of vegetative sprouting and seed germination; and obligate sprouters (*OS*) only re-establish by vegetative sprouting because their seeds do not survive fire.

2. Post-fire seedlings of *NS* and *FS* re-establish in open canopy gaps, whereas *OS* seedlings primarily recruit in deep shade during fire-free intervals.

3. It was hypothesized that these life history differences, compared within the same family, Rhamnaceae, would result in differential seedling resistance to water stress such that $NS > FS > OS$.

4. Seedlings were grown in large pots in a common garden under treatments of sun, shade, irrigation and water stress. Mortality and physiology of seedlings were monitored for about 1 year.

5. In response to the water stress treatment in full sun, life history types were not different in their dry season predawn water potentials, which were extremely negative (< –9 MPa). Water potential of water-stressed shade grown plants were also not different, but were less negative than the sun treatment during the dry season (about –6 MPa).

6. For plants grown in full sun under water stress, *NS* exhibited 23% mortality, *FS* 60% and *OS* 35% mortality, while irrigated controls had greatly reduced mortality across all life histories. Among shade grown plants under water stress, *NS* exhibited 30% mortality, *FS* 20% and *OS* 1% mortality. This pattern of differential mortality was the same for irrigated plants indicating that water stress was not the cause of mortality in the shade.

7. Greater stem and root resistance to water stress induced cavitation were strongly correlated with lower percent mortality during the summer dry season suggesting a link between these traits and fitness.

8. *Synthesis*. This study finds a link between life history type and water stress tolerance. Consistent with open canopy specialization, *NS* survived best in full sun. The *FS* and *OS* life history type had better survival in the shade. The *OS* was unexpectedly versatile, surviving well in the sun and shade. The evolutionary history of the life history types is discussed as an important factor in linking water stress tolerance and life history.

Key-words: cavitation, *Ceanothus*, drought, fire, *Rhamnus*, sprouting, water potential, xylem

Introduction

Understanding how plant species of a similar life-form and phenology coexist is a crucial question in ecology (Silvertown 2004). Grubb (1977) suggested that such coexistence can be facilitated by differences in seedling requirements, or differences in what he called the 'regeneration niche'. This concept helps explain the coexistence of apparently similar plant species in the adult stage of growth, particularly in the biodiverse regions of the globe (Davis 1991). One example of such regions are the fire prone Mediterranean-type climate regions of the world located in California, the Mediterranean basin, the Cape Floristic Region of South Africa and south-western Australia. Much of these regions are dominated by evergreen

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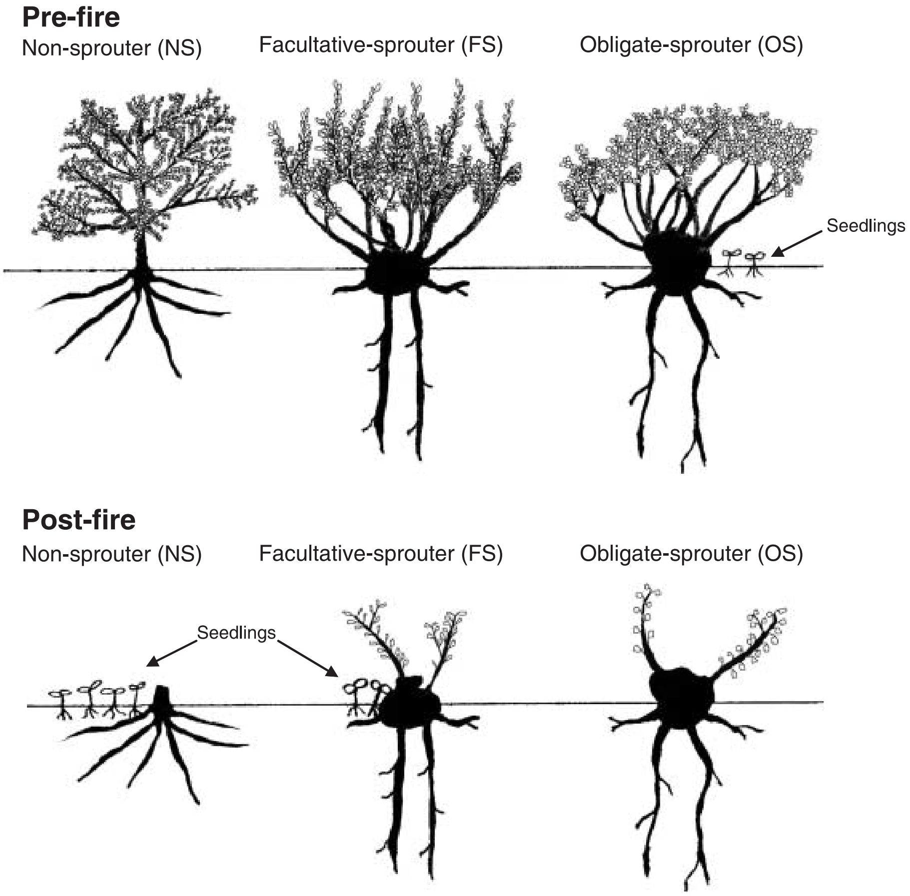

Fig. 1. Life history types of chaparral species based on how they regenerate following fire. Non-sprouters (*NS*) are killed by fire and recruit new seedlings in open gaps in the post-fire environment. Facultative sprouters (*FS*) recruit new seedlings in partial shade post-fire and burned shrubs resprout from a lignotuber. Seeds of obligate sprouters (*OS*) are killed by fire and burned shrubs resprout from a lignotuber. Seedlings of *OS* species recruit in the understorey of mature chaparral stands.

sclerophyllous shrub species that appear very similar in the adult stage of growth (Lamont & Bergl 1991). How these similar species coexist is of great interest for both basic and applied reasons (Cowling *et al.* 1996).

In southern California chaparral communities, differences in the regeneration niche can be extreme. For many species, regeneration is intimately linked to disturbance in the form of stand replacing fires (Fig. 1). Three classes of seedling recruitment are recognized. Non-sprouters (*NS* or obligate seeders) only recruit from fire-stimulated seed post-fire and undergo no post-fire vegetative sprouting. The opposite extreme to this is obligate sprouters (*OS*) that rarely recruit seedlings post-fire and undergo post-fire vegetative sprouting, often from a lignotuber. Intermediate between these two extremes are species that regenerate by a combination of seedling recruitment and vegetative sprouting (facultative sprouters [*FS*] or facultative seeders). Species that differ in their post-fire regeneration mode are also divergent in numerous other morphological traits (Keeley 2000; Ackerly 2004; Pausas *et al.* 2006; Pratt *et al.* 2007b).

The regeneration niche with respect to seedling establishment for the *NS* life history type is characterized by an open canopy and exposed environment following fire (Fig. 1). This is a stressful environment in southern California where seedlings are exposed to the summer rainless period, which is typically 6–9 months in duration, and desiccating temperatures in excess of 45 °C near the bare soil surface (Frazer & Davis 1988). The *OS* species recruit seedlings during fire-free intervals, typically in available microsites in the moist litter layer of the shaded understorey of a mature chaparral canopy (Fig. 1; Keeley 1992). The *FS* species have a regeneration niche similar to that of the *NS* species. However, *FS* species are able to persist by resprouting following fire, which mitigates the need for high recruitment success (Bond & Midgley 2001). Mortality among *FS* seedlings in arid microsites is typically high, and moister microsites are often important for successful recruitment of these species (Thomas & Davis 1989; Meentemeyer & Moody 2002).

A previous study showed that life history type in chaparral species from the same taxonomic group (Rhamnaceae) was linked to water stress tolerance in the adult growth stage (Pratt *et al.* 2007b). The hypothesis tested in this previous study was that differences in adult water stress tolerance would be coupled to life history types due to differences in regeneration niche among the *NS*, *OS* and *FS* life history types. The study showed that *NS* displayed greater water stress tolerance than both *FS* and *OS* life history types, and that *FS* and *OS* life history types were not different. This conclusion was based on analysis of adult stem and root cavitation resistance and also a hydraulic model of cavitation that included the rhizosphere (Sperry *et al.* 1998).

Because cavitation resistance represents only one aspect of water stress tolerance (Tyree *et al.* 2002), and because the study by Pratt *et al.* (2007b) was done on plants at the adult stage of development, the present study was undertaken to extend the analysis to seedlings in a common garden under controlled conditions. Much field work has been done on post-fire demography of seedlings of *NS* and *FS* life history types (Keeley & Zedler 1978; Mills 1986; Frazer & Davis 1988; Thomas & Davis 1989; Saruwatari & Davis 1989); however, data are lacking for *OS* species. It is not possible to conduct a natural field experiment with seedlings from all three of these life history types because seedlings of only two of the life history types are present post-fire, *NS* and *FS*. Seedlings of the three life history types never occur together *in situ* because seeds of *NS* and *FS* are refractory and require a fire cue to germinate, whereas seeds of *OS* are short lived and intolerant of fire. Moreover, it is not possible to plant seedlings out in the field post-fire within an OS environment of deep shade because the closed canopy has been removed by fire. Thus, in order to test our hypothesis it was necessary to conduct a manipulative experiment in a common garden where both water stress and shading could be rigidly controlled.

Water stress tolerance was examined in terms of whole plant survival through the use of a manipulative water stress treatment. Water stress tolerance may change ontogenetically, and since the hypothesis that life history type is linked to water stress tolerance within the regeneration niche, it was crucial to assess water stress tolerance at the seedling stage of development. To this end, seedlings of nine species of chaparral shrubs within the family Rhamnaceae, all native to the Santa Monica Mountains of southern California, were grown in a common garden in large pots. Among these nine species, three were *NS* and three were *FS*, both in the genus *Ceanothus*, and three were *OS* in the genus *Rhamnus*. 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). Cavitation resistance was measured on stems and roots, and seedlings were exposed to an experimental water stress treatment and their mortality assessed. We also included a shade and sun treatment, to simulate the regeneration niche environment of the *OS* life history type, and the *FS* and *NS*, respectively (Fig. 1). We hypothesized that seedling water stress tolerance would be linked to life history type such that *NS* > *FS* > *OS*. We also predicted this pattern to hold in the shade, but that the mortality due to water stress would be reduced compared to full sun.

Methods

STUDY SITES AND PLANTS

Seeds were collected from naturally occurring populations of nine shrub species in the family Rhamnaceae (Table 1; Hickman 1993) at three sites in the Santa Monica Mountains in Los Angeles County, California (described in Pratt *et al.* 2007b). Seeds collected from *Ceanothus leucodermis* in the Santa Monica Mountains had been bored into by a seed predator, thus we obtained seeds for this species from a population near Lake Hemet in the San Jacinto Mountains in Riverside County, California.

To stimulate germination, seeds for *Ceanothus* spp. were boiled for 1-min and then transferred to a beaker of aerated deionised water for 24 h. *Rhamnus* spp. were not boiled, but were soaked in aerated water for 24 h. Seeds were plated onto autoclaved Petri plates containing germination paper (Anchor Paper Company, St Paul, MN) using sterile techniques in November 2002 through January 2003. In March and April 2003 germinated seedlings were transferred to small tree pots (D16 Deeppots, Stuewe and Sons Inc., Corvalis, OR) and grown in a greenhouse. Seedlings were kept well watered and were fertilized (Scott's Turf Builder, Scotts, Marysville, OH) to approximate the nutrient rich post-fire environment (Christensen & Muller 1975).

In August 2003 we transferred about 1500 seedlings to custom crafted large pots (1.2-m tall and 250-mm wide; Blue-X Enterprises Inc., Elk Grove, CA) on campus at Pepperdine University, Malibu, CA, USA. The climate in the study area is Mediterranean-type with hot and dry summers and cool wet winters and is described in Pratt *et al.* (2007b). Uniform native soil was collected from a debris basin at the base of Marie Canyon, a natural chaparral watershed on the campus of Pepperdine University, Malibu, CA, USA. The soil was loamy sand in texture as analyzed by the hydrometer method (Utah State University, Analytical Laboratories, Logan, UT).

The pots were placed in a common garden in a complete randomized block design with two treatments, namely water stress and a shade treatment (25% of full sun) and appropriate controls. Seedlings in the water stress treatment (in both the sun and shade) received only natural precipitation as described below, and control plants were given supplemental irrigation to keep their water potential in a range they commonly exhibit under field conditions during the wet winter months. Plants in some blocks were harvested for physiological measurements and others were tracked for water status and mortality.

WATER STATUS AND MORTALITY

Leaf water potential (ψ_w) was measured approximately monthly beginning in April 2004 until April 2005 using pressure chambers (Model 1001, PMS Instruments, Corvalis, OR; 3000 Series, Soil Moisture Equipment Inc., Goleta, CA) at predawn and midday (between 12:30 and 13:00 h). The summer dry season in 2004 saw no or only trace rainfall from 3 March until 21 October. The 2003–2004 annual rainfall total, measured from July to July, 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 April 2005, about 895 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 leaves of six different individuals for treatments and three individuals for irrigated controls from each species. Leaves were removed from plants, bagged, placed on ice and transported to a climate controlled laboratory in ≤ 20 min, where they were rapidly measured with a pressure chamber.

Beginning in July 2004, seedlings began showing signs of stress in the form of leaf yellowing, branch dieback and mortality. We scored seedling mortality beginning at this time and tracked mortality monthly through the dry season of 2004. Mortality was determined

Table 1. Species studied, abbreviations, cavitation resistance (ψ_{90}), minimum water potential (ψ_{min}) and percentage seedling mortality during an experimental drought

						Irrigated		Non-irrigated	
Life history and species	Abbreviations	Stem ψ_{90} (MPa)	Root ψ_{90} (MPa)	Sun ψ_{min} (MPa)	Shade ψ_{min} (MPa)	Sun mortality (%)	Shade mortality (%)	Sun mortality (%)	Shade mortality (%)
Non-sprouter average		-11.14^{A}	-8.94^{A*}	-8.47^{A}	-5.24^{A*}	0^{A}	28^{A}	23.1^{A*}	27.9^{A}
Subgenus *Cerastes*		(0.12)	(0.60)	(0.68)	(0.68)	(0)	(4.0)	(4.0)	(5.0)
Ceanothus megacarpus Nutt.	*Cm*	-11.07^{ab}	-7.79^{ab*}	-9.62^{ac}	-6.46^{a*}	0^{a}	32.0^{a}	27.2^{ab*}	21.6^{a}
		(0.52)	(0.91)	(0.90)	(1.20)	(0)	(18.2)	(15.1)	(13.2)
C. crassifolius Torrey	*Ccr*	-10.98^{ab}	-9.17^{b}	-8.57^{ac}	-4.09^{a*}	0^{a}	32.0^{a}	15.1b*	37.8^{a}
		(0.57)	(0.80)	(0.68)	(0.51)	(0)	(18.2)	(12.1)	(15.6)
C. cuneatus (Hook.) Nutt.	*Ccu*	-11.39^{a}	-9.86^{b}	-7.24^{ab}	-5.17^{a*}	0^{a}	20.0^{a}	27.2^{ab*}	24.3^{a}
		(0.37)	(1.35)	(0.84)	(0.69)	(0)	(15.6)	(15.1)	(13.8)
Facultative sprouter average		-7.58^{B}	-6.23^{B}	-7.48^{A}	-5.79^{A}	1.6^{A}	8.0^{B}	59.5^{B*}	18.9^{A}
Subgenus *Ceanothus*		(0.20)	(0.75)	(0.33)	(0.98)	(0)	(8.0)	(5.0)	(6.7)
C. spinosus Nutt.	*Cs*	-7.42^{bc}	-4.81^{a*}	-7.88^{abc}	-7.57^{a}	0^{a}	0^{b}	54.5^{cd*}	27.0^{a*}
		(0.67)	(0.97)	(1.26)	(1.74)	(0)	(0)	(16.9)	(14.3)
C. oliganthus Nutt.†	*Co*	-7.98^{abc}	-6.47^{ab}	-7.75^{abc}	-4.17^{a*}	5^{a}	24.0^{a}	69.6^{d*}	24.3^{a}
		(0.61)	(0.94)	(0.76)	(1.24)	(9.8)	(16.7)	(15.6)	(13.8)
C. leucodermis E. Greene	*Cl*	-7.34^{bc}	-7.40^{ab}	-6.82^{ab}	-5.65^{a}	0^{a}	0^{b}	54.5^{cd*}	5.4^{b}
		(0.51)	(0.53)	(0.74)	(0.79)	(0)	(0)	(16.9)	(7.2)
Obligate sprouter average		-7.85^{B}	-5.85^{B}	-9.56^{A}	-4.65^{A*}	0^{A}	0^{B}	35.3^{A*}	0.9^{B}
		(1.41)	(0.58)	(1.67)	(0.20)	(0)	(0)	(5.3)	(0.9)
Rhamnus ilicifolia Kellog	*Ri*	-8.79^{ab}	-6.94^{ab}	-10.98^{a}	-4.93^{a*}	0^{a}	0^{b}	45.4^{acd*}	0.0^{b}
		(0.59)	(0.81)	(0.41)	(0.78)	(0)	(0)	(17.0)	(0.0)
R. californica Eschsch	*Rca*	-5.07^{c}	-4.95^{a}	-6.23^{b}	-4.25^{a*}	0^{a}	0^{b}	33.3^{abc*}	2.7^{b}
		(0.50)	(0.67)	(0.79)	(0.57)	(0)	(0)	(16.0)	(5.2)
R. crocea Nutt.	*Rcr*	-9.70^{ab}	-6.35^{ab*}	-11.48^{c}	-4.77^{a*}	0^{a}	0^{b}	27.2^{ab*}	0.0^{b}
		(0.86)	(0.87)	(0.90)	(0.45)	(0)	(0)	(15.1)	(0.0)

Data shown are means with SE in parentheses ($N = 6$–9). For mortality data 95% confidence limits are in parentheses ($N = 25$–37 counts). Within a column, means followed by the same letter are not different (lower case letters for species means and uppercase for life history type means) and those with unique letters are different. Asterisks in the root ψ_{90}, shade ψ_{min}, and non-irrigated mortality columns denote differences between stem and root ψ_{90}, sun and shade ψ_{min}, and non-irrigated and irrigated mortality, respectively ($P < 0.05$ for species and $P < 0.10$ for life history type averages). Predawn and midday ψ_{min} were pooled for comparisons.

†*Ceanothus oliganthus* var. *oliganthus* does not form a lignotuber or resprout following fire at our study sites (Pratt *et al.* 2007b).

by leaf coloration and brittleness of tissue, that is, if plants had no green leaves and stems were brittle when bent they were scored as dead. We continued to sample mortality through the winter of 2005 and assessed if any individuals that were previously deemed to be dead had resprouted following the alleviation of water stress.

HYDRAULIC CONDUCTIVITY AND CAVITATION RESISTANCE

Hydraulic conductivity (K_h; kg m MPa^{-1} s^{-1}) was measured under a low pressure head (*c.* 4 kPa) using de-gassed acid solution (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, OH) at the distal end. The solution passing through the stem was collected on the balance connected to a 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. Xylem specific conductivity (K_s) was calculated by dividing the maximum conductivity (see below) by the stem or root transverse xylem area.

Vulnerability to cavitation was estimated by constructing ‘vulnerability curves’. These curves depict the loss of K_h for main stems and roots over a range of xylem water potentials (ψ_x) generated using a centrifuge following the methods of Alder *et al.* (1997). Main stems were removed from six to nine individuals, bagged, placed on ice and brought to the laboratory where they were analyzed the same day. Roots were collected from the same individuals by carefully cutting open pots and sieving the soil away from the roots. Roots were also analyzed the same day. Because the seedlings were relatively small the main stems contained numerous side branches that impeded measurements. To prepare seedlings for measurements, side branches were removed three days prior to measurements using pruning shears repeatedly sterilized in 80% ethanol, and scars where branches were cut were sealed with pruning seal (Tree Pruning Sealer, The Tanglefoot Company, Grand Rapids, MI). Measurements were made during the winter rainy season, November 2004 through February 2005. Although all of our seedlings were the same age, due to differences in growth rate, stem and root diameters varied. Stems ranged from 3.6 to 9 mm and roots ranged from 1.3 to 7.6 mm. Most stems were about 5 mm in diameter and most roots were 3.5 mm in diameter. Stems and roots were recut to 0.27 m under water for the non-sprouting species to avoid xylem air entry and to 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 (< –10 MPa) required to fully embolize the stems and roots of these species (Pratt *et al.* 2007b). The diameter of the smaller rotor only generates pressures down to –10 MPa with the centrifuge we used (RC5G Plus, Sorvall, Kendro Laboratory Products, Asheville, NC). Following recutting, 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}), that is, 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 organ. The ψ_x at 90% loss in hydraulic conductivity (ψ_{90}) was used to compare among stems and roots. There were two different shapes to the vulnerability curves, concave (all stems and some roots) and convex (most roots). The ψ_{90} was calculated for concave shaped curves with a second order polynomial because it yielded a high r^2 (Fig. 5). For convex shaped curves, ψ_{90} was analyzed by fitting the PLC with a Weibull model.

$$\text{PLC} = 100(1 - e^{-(\psi_x/b)^{\wedge}c})$$

where *b* and *c* are curve fitting parameters. This model provided a better fit at high PLC, largely because it is a cumulative distribution model and it was well suited to fit the convex shaped root vulnerability curves (Neufeld *et al.* 1992). We did not use the Weibull model for concave shaped curves because it yielded a poor fit. We chose to use ψ_{90} over the more commonly used ψ_{50} because we were interested in using ψ_{90} to predict seedling mortality under severe water stress. Under the levels of water stress in this study both stems and roots were more than 50% embolized and were still alive and apparently healthy. Mortality did not occur until much higher levels of embolism were reached. In addition, we corrected for cavitation fatigue (Hacke et al. 2001). To do this, we calculated PLC using the K_h measured following the initial centrifuge spin at ≥ –0.5 MPa in place of K_{max} for species consistently showing fatigue, that is, high loss of K_h (PLC ≥ 20%) following a –0.5 MPa stress treatment. 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 resistance to cavitation.

STATISTICS

For cavitation resistance (ψ_{90}), differences among treatments were analyzed using ANOVA (SAS v.9.1, SAS Institute Inc., Cary, NC). The terms in the model included the fixed factors of organ (stem and root) and life history type (*NS*, *FS* and *OS*), and the interaction. Species was input as a random factor nested within life history type, and the final term was the interaction between organ and species nested within life history type. Life history type differences were analyzed as pre-planned comparisons using species nested in life history type as the error term (SAS, CONTRAST statement). Comparisons between life history type within stems or roots was also preplanned and was analyzed as contrasts using species nested in life history type as the error term. Differences between roots and stems were analyzed using organ times species nested within life history type as the error term with a Tukey's adjustment to control for the type I family error rate (SAS, LSMEANS statement). Because the design was unbalanced, a Satterthwaite correction was used (Potvin 2001). Comparison of seasonal minimum ψ_w was analyzed the same as ψ_{90} except instead of an organ term, a sun shade term was used to compare the sun vs. shade treatments. Comparisons of K_s and percentage loss of hydraulic conductivity at ψ_{min} were analyzed nonparametrically using Mood's median test because the data set contained some zeros, and could not be transformed to normality (MINITAB v.14.12, Minitab Inc., State College, PA). Differences for mortality data were analyzed using χ^2 analyses (MINITAB v.14.12). Data were transformed (arcsine for percentages and log otherwise) as necessary to satisfy assumptions of statistical models. When comparing treatments, differences were considered significantly different at $\alpha \leq 0.05$. If the *P*-value exceeded α we report treatments as similar or not different. For differences across life history types we adjusted α to 0.10 to avoid committing type II errors on account of small sample size ($N = 3$).

Results

For facultative sprouting species grown in full sunlight without any supplemental irrigation, mortality abruptly began in July and continued to increase until rain fell by 16 October 2004 (Fig. 2c). For *NS* and *OS* life history types mortality did not begin until August and increased until rain fell (Fig. 2a,e). Control plants receiving supplemental irrigation showed mortality levels not different from zero for the duration of the study (Table 1; Fig. 2a,c,e).

Mortality in full sun was greatest among non-irrigated *FS* species with greater than 50% of all individuals of *FS* species perishing (Table 1; Fig. 2c). Mortality was the lowest for the *NS* life history type, but mortality was not significantly different between *NS* and *OS* life history types (Table 1; Fig. 2). Sprouting species did show some resprouting from lignotubers after whole shoot dieback, and this can be seen as a decrease in apparent mortality for *C. spinosus* (Fig. 2c) and *Rhamnus crocea* (Fig. 2e).

For non-irrigated plants grown in a shade treatment, mortality was delayed until August and continued to increase until rain fell by 16 October 2004 (Fig. 2b,d,f). The only exception was for *NS* species, which showed continued mortality through the rainy season (Fig. 2b). Mortality for the non-irrigated *OS* species was not different from zero (Fig. 2f).

For shade plants, the irrigated treatment plant mortality was generally not different from non-irrigated shade plants as illustrated among *NS* and *OS* species (Table 1; Fig. 2b). The same was true for *FS* species, except for *C. spinosus*, which had lower mortality for irrigated plants compared to non-irrigated plants (Table 1).

Water potential (ψ_w) for non-irrigated plants growing in full sun and shade began to decline in April, and did not stop declining until the onset of fall rains in October (Fig. 3), whereas irrigated controls remained hydrated during this time (Fig. 3). The seasonal minimum predawn water potential (ψ_{min}) was relatively low for all species (Table 1) and did not differ

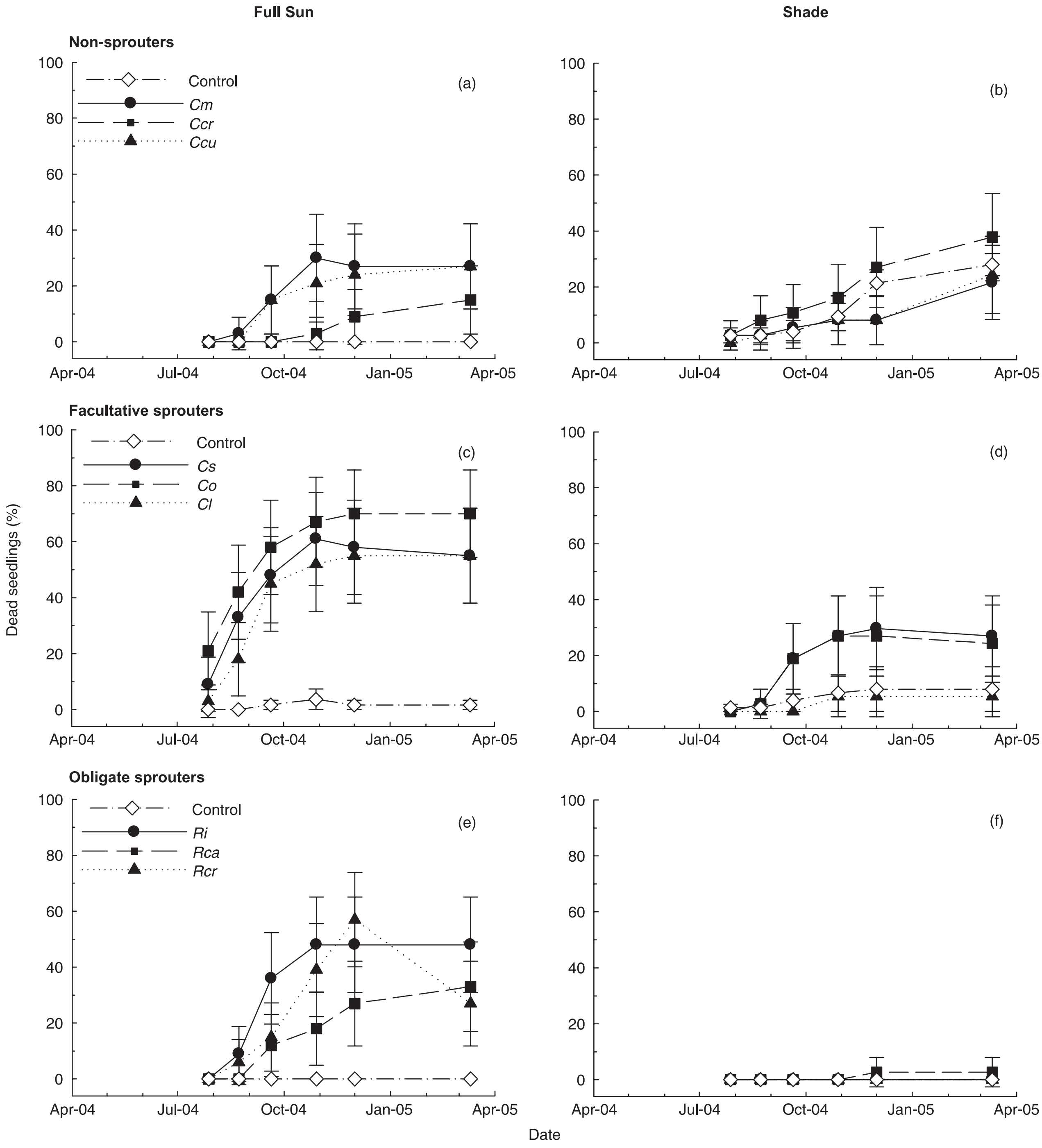

Fig. 2. Percent mortality of seedlings grown in full sun and shade in a common garden for nine species representing three different life histories (see Fig. 1 and Table 1 for abbreviations). Measurements were made during the natural rainless period which lasted from 1 March 2004 through 16–20 October 2004 when 60.8 mm of rain fell at our site. Mortality measurements began when plants first showed mortality (July 2004) and continued into the 2005 rainy season. Non-irrigated plants received natural rainfall, whereas irrigated control plants were watered to keep them hydrated. Data represent counts of number dead from the total sampled (N = 19 and 33 for irrigated and non-irrigated sun plants, respectively, and N = 25 and 37 for irrigated and non-irrigated shade plants, respectively), and bars are 95% confidence intervals for non-irrigated. For clarity, and because the values were similar across species, the irrigated controls are averaged across the three sampled species within each life history type.

among the three life history types. The shade $\psi_{\min}$ for non-irrigated plants was generally not as low as the sun treated plants (Table 1).

The difference between predawn and midday ψ_w was about 1 MPa for all life history types (Fig. 4). The result was consistent from the spring moist season through the driest sampling period (Fig. 4 regression slopes are not different within life history types). The *OS R. californica* stood out as exhibiting a different response. For this species, the difference between predawn and midday ψ_w was < 1 MPa and the difference declined seasonally, until during the driest part of the year they converged (Fig. 4c).

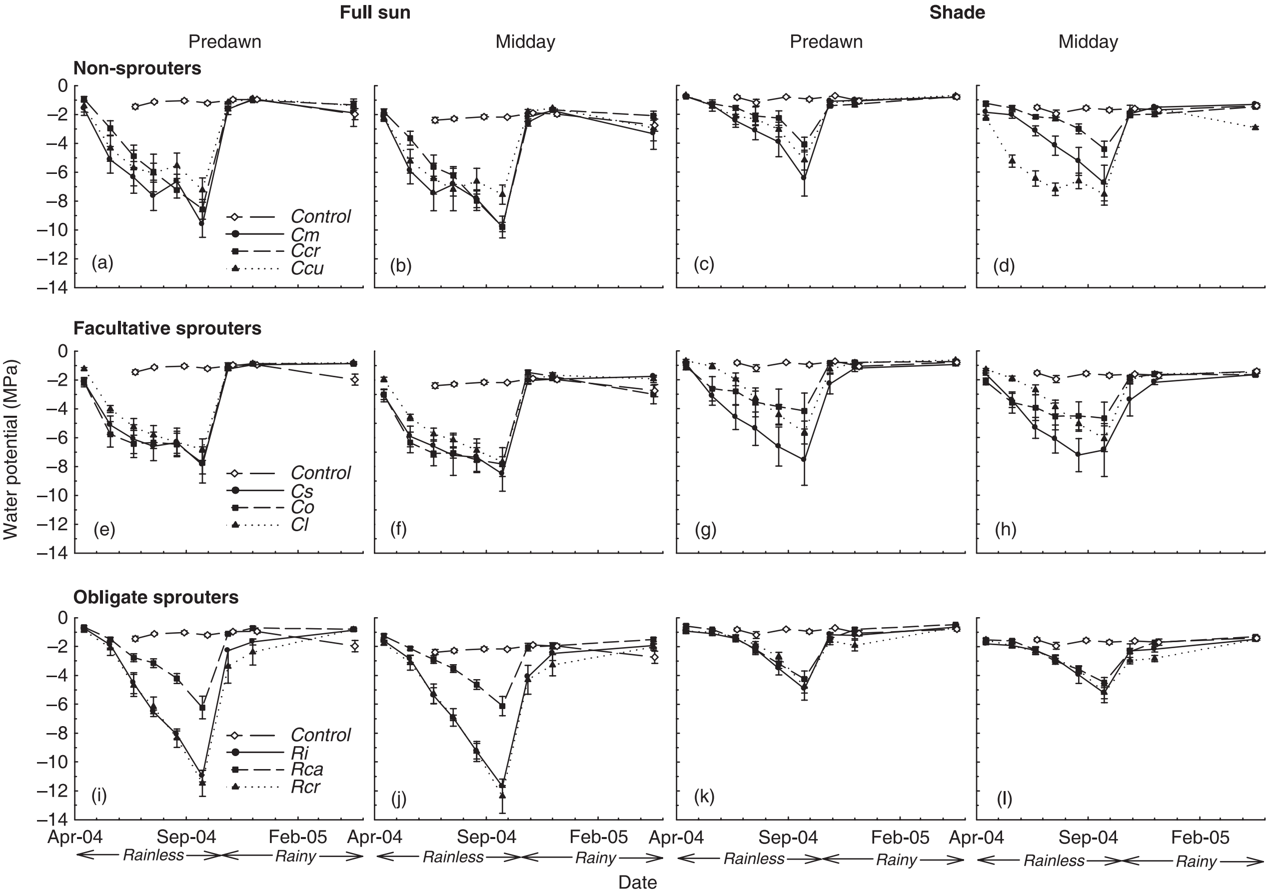

Fig. 3. Leaf water potential at predawn (a, c, e, g, i and k) and midday (b, d, f, h, j and l) for non-irrigated and irrigated seedlings representing three different life history types grown in full sun and shade in a common garden (see Table 1 for species abbreviations and Fig. 2 for treatments). Irrigated plants were not measured until June 2004 when non-irrigated plants began to dehydrate. Data represent means ($N = 6 \pm 1$ SE for non-irrigated and $N = 3 \pm 1$ SE for irrigated). For clarity, and because the values were similar across species, the irrigated controls are averaged across the three sampled species within each life history type.

Based upon results during the rainy season for plants grown in full sun, resistance to cavitation (ψ_{90}) was greatest (ψ_{90} was most negative) for the *NS*, whereas the *FS* were not different from the *OS* (Table 1; Fig. 5; ANOVA for life history type $P = 0.02$). For stems, this pattern was general among species within each life history type, except for *R. californica*, which was more vulnerable to cavitation than the other *OS* species (Table 1). Although we had a shade treatment (25% of full sun), we sampled cavitation resistance for only three shade grown species and the data for the species that were sampled are not presented in the present paper.

Root ψ_{90} for the different life history types showed a similar pattern to stem ψ_{90} (Table 1). Root ψ_{90} for *NS* species was more negative that that of *FS* and *OS* species (Table 1; Fig. 5). Root ψ_{90} was less negative than stem ψ_{90} when compared across all species (ANOVA organ term $P \leq 0.001$), indicating that roots were generally more susceptible to cavitation. There were no interactions in the ANOVA analysis, either between life history type and organ (ANOVA $P = 0.63$), or between organ and species nested within life history type (ANOVA $P = 0.21$). When roots and stems were compared within life history type, only the *NS* species had stems that were more resistant to cavitation than roots (Table 1).

When cavitation resistance was analyzed on a relative basis, that is, a percentage of maximum K_h, roots stood out as being generally more susceptible to cavitation (Table 1; Fig. 5), especially at less negative ψ_w. However, when analyzed on an absolute basis (as declines in K_s), a different picture emerges (Fig. 5 insets). Because roots have greater K_s values to start with, they can suffer a steeper decline in conductivity and still remain as hydraulically efficient as stems (Fig. 5 insets; Fig. 6d). This is illustrated by comparing the K_s at ψ_{min}, which shows that root K_s is not different or significantly greater than stem K_s (Fig. 6b,d). Moreover, the shape of root vulnerability curves appears to be different from stems, which is likely important. Roots generally exhibit steep conductivity declines initially likely due to cavitation occurring in large diameter vessels, followed by a levelling off of conductivity where small but resistant vessels remain functional (a convex shape). Stems by contrast typically exhibited linear or concave shapes indicating the larger vessels were not as highly susceptible. The shape of the root curve resulted in roots maintaining positive K_s values at very low xylem ψ_w (Fig. 5), and a convergence of percentage loss of conductivity at relatively high conductivity losses, for example, > 90% (Figs 5 and 6a,c).

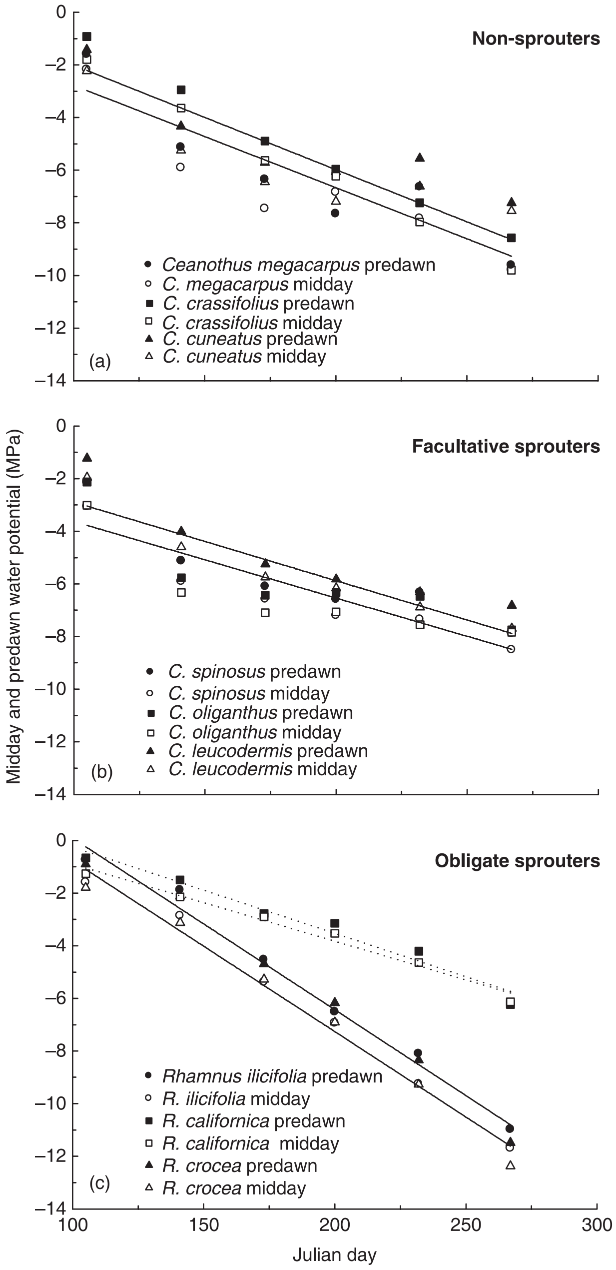

Fig. 4. Predawn and midday ψ_w plotted for the rainless period (March–mid October 2004). Linear regressions are fit through predawn and midday ψ_w pooled across species in a panel, except for the obligate sprouters, where *R. californica* is analyzed separately to illustrate its unique response (c). For all regressions $P < 0.001$ and $R^2 \geq 0.83$.

Life history types differed in the degree of cavitation in stems and roots at ψ_{min}. Stem percentage loss of conductivity was lowest for *NS* species, intermediate for *FS* species, and highest for OS species (Fig. 6a). For roots the pattern was the same, however, none of the life history types significantly differed in their root loss of conductivity at ψ_{min} (Fig. 6c). Expressing conductivity losses on an absolute basis (K_s) showed the same general pattern as percentage loss of conductivity, where stem K_s was greatest in *NS*, intermediate in *FS* and lowest in *OS* (Fig. 6b). Root K_s showed the same pattern as stems, except the only significant difference was that *NS* had greater K_s than *OS* and the *FS* was not significantly different from *NS* or *OS* (Fig. 6d).

The degree to which stems and roots cavitated was different across the life history types. *NS* had greater calculated percentage conductivity and K_s loss in their roots compared to their stems (Fig. 6), *FS* species lost a similar degree of conductivity (relative and absolute) in stems vs. roots, and *OS* species had greater losses of K_s in stems compared to roots (Fig. 6b,d).

Mortality in full sun was closely correlated to stem and root resistance to cavitation such that species with greater resistance to cavitation had lower percentages of mortality (Fig. 7).

Discussion

LIFE HISTORY TYPE AND WATER STRESS TOLERANCE

The hypothesis was tested that water stress tolerance is linked to life history type among *NS*, *FS* and *OS* taxa. Differences in the regeneration niche environment suggested that *NS* species would be the most resistant to water stress, *FS* would be intermediate, and *OS* would be least tolerant of water stress. Based on the mortality patterns in full sun, the *NS* was most resistant to water stress, the *OS* was intermediate and the *FS* was the least resistant to water stress. The irrigated controls in full sun had mortalities of about zero in all life history types suggesting that water stress was a chief causal factor. The pattern between the *FS* and *OS* life history types are the reverse of our prediction. This suggests that *OS* species, at the seedling stage, are more water stress tolerant than *FS* species, despite the fact that *OS* species recruit in shadier and presumably more mesic microsites. Soil moisture has been shown to be more favourable in the shady understorey beneath shrubs and trees in Mediterranean environments (Verdú & García-Fayos 1996), and in the present study water stress was mitigated in the shade compared to the full sun. It may be that competition for water between *OS* seedlings and the established adults requires *OS* species to develop higher water stress tolerance than previously assumed. We are unable to assess this because we conducted our experiment in a common garden with one individual per pot where seedlings were free from competition. We conducted our study in a common garden because the *NS*, *FS* and *OS* life history types do not all recruit seedlings post-fire in nature, thus the experiment is not possible *in situ*. As a first step to understanding how competition may be affecting water stress in the *OS* life history type it would be valuable to measure seasonal ψ_w for *OS* seedlings naturally occurring in the chaparral understorey. Studies of *OS* seedlings of oaks (*Quercus* spp.) have found that competition at high plant density increases water stress (Griffin 1973).

Seedlings of all life history types experienced extremely low ψ_w consistent with the shallow root systems of seedlings, and previous results under natural field conditions for *NS* and *FS* (Saruwatari & Davis 1989; Thomas & Davis 1989). This suggests that seedlings did not have a mechanism for avoiding

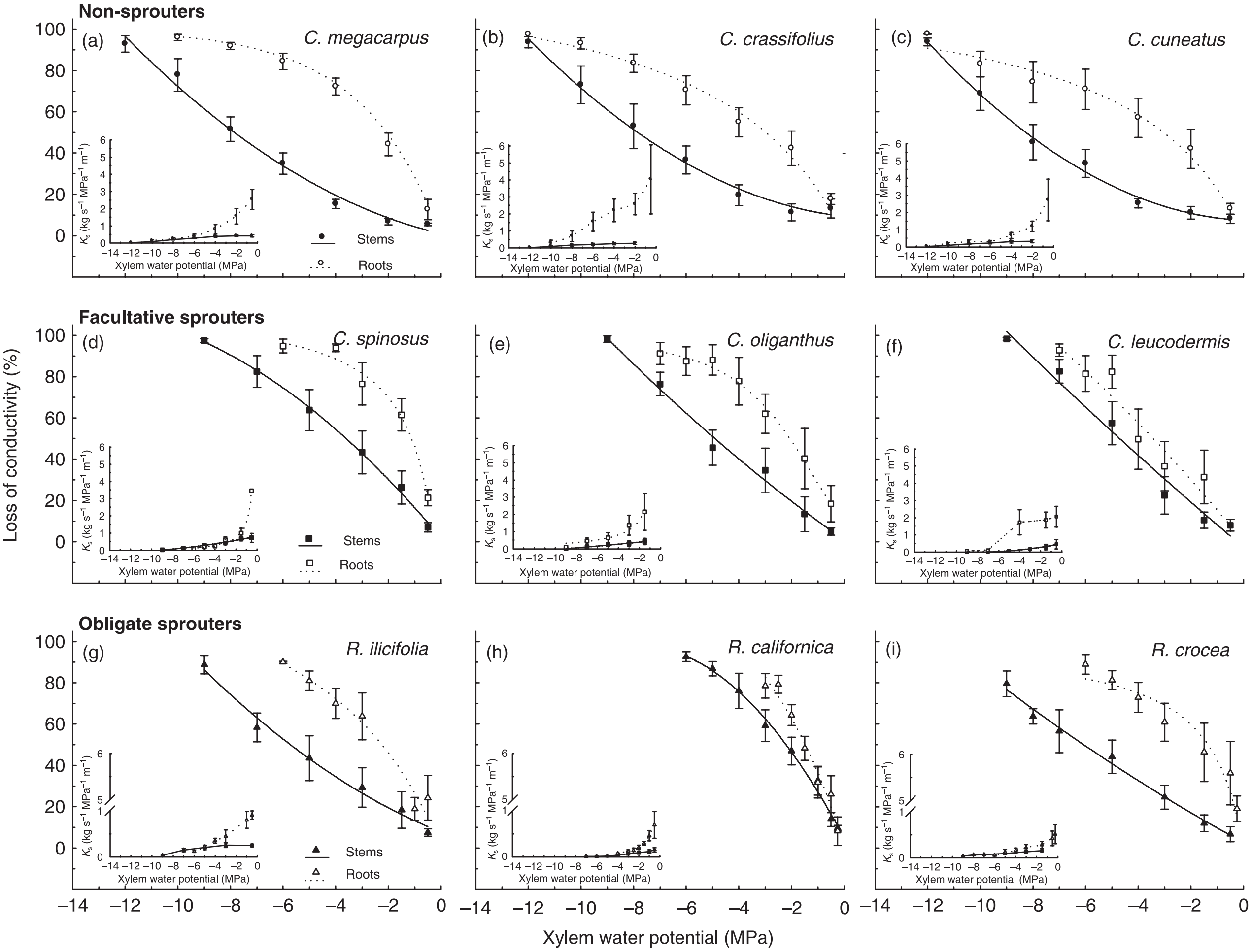

Fig. 5. Loss of hydraulic conductivity plotted as a function of xylem water potential of stems (closed symbols and solid lines) and roots (open symbols and dotted lines) for nine species representing three different life histories (see Table 1 for abbreviations). Insets depict loss of xylem specific hydraulic conductivity (K_s) as a function of water potential. Data points are means ± 1 SE (N = 6–9). Data for stems were fit with quadratic equations ($r^2 \geq 0.91$ and $P < 0.05$ for all plots), and roots were fit with Weibull and quadratic models depending on their shape (see Methods).

water stress, and instead were reliant on their ability to tolerate it. Predawn and midday ψ_w differed by about 1 MPa for all life history types from the wetter spring months through the dry fall months, with the exception of *R. californica* (discussed below). Barring significant capacitance in these seedlings, midday ψ_w will primarily be determined by stomatal conductance, the leaf to air vapour pressure deficit, the hydraulic conductivity of the soil and plant, and the soil ψ_w, all of which changed from the wet season to the dry season. There is no reason why the difference in predawn and midday ψ_w would be predicted to remain relatively constant. It is possible that the difference between predawn and midday ψ_w represents a regulated set point. Hickman (1970) measured seasonal changes in ψ_w for 44 species in southern Oregon, across a range of life-forms, and found that the majority of the species displayed a pattern similar to that shown in Fig. 4. It remains unclear as to why this pattern prevails in Mediterranean-type climates and why some species are exceptions, for example, *R. californica* (Fig. 4). However, our study suggests that this pattern persists in a common garden and an environment devoid of competition for soil moisture.

With respect to ψ_w there was one species that was exceptional. The *OS R. californica* maintained a more favourable water status than all other species and thus avoided the most intense water stress. Moreover, *R. californica* did not exhibit a consistent 1 MPa difference between predawn and midday ψ_w as found in the other species. Instead, the difference was generally < 0.5 MPa and this difference decreased as the dry season progressed (Fig. 4c). This suggests that *R. californica* is likely more conservative in its water use than the other species and that it became more conservative as its tissue desiccated. *Rhamnus californica* also stands out as being the least resistant to cavitation. Three traits that were likely important that allowed *R. californica* to minimize the degree of water stress were efficient stomatal closure (Watson 2006), water stress-induced crown dieback (Davis & Mooney 1986a; Pratt *et al.* 2007b), and an elevated root to shoot ratio compared to the other sampled species (Pratt, unpublished data). It is also interesting to note that recent molecular phylogenetic analyses have placed *R. californica* into the genus *Frangula* (Bolmgren & Oxelman 2004). This phylogenetic difference helps to explain why *R. californica* is consistently

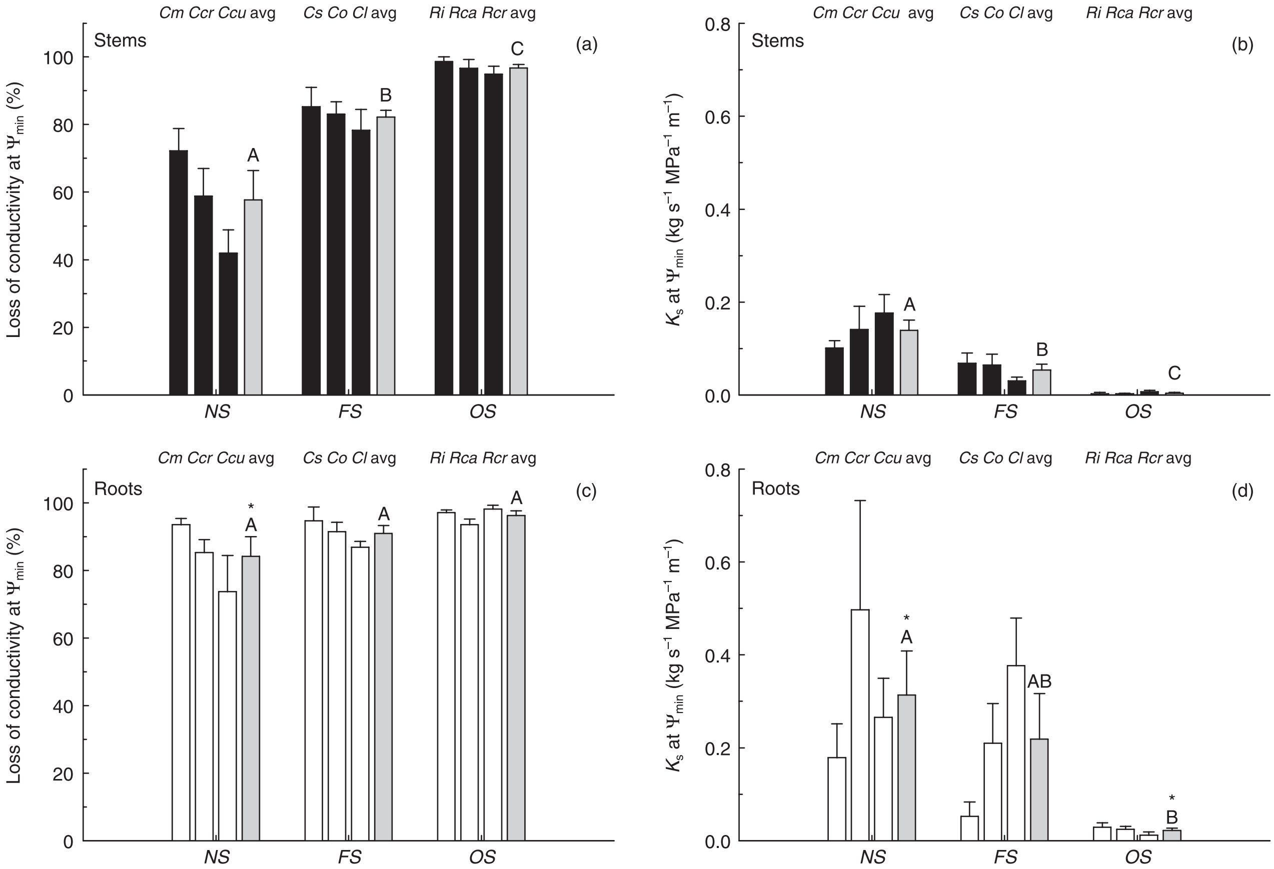

Fig. 6. Calculated percentage loss of conductivity and xylem specific conductivity at the predawn minimum ψ_w for plants in the full sun treatment. Data are for seedlings of nine species representing three different life history types (see Table 1 for abbreviations). Grey bars show the average (avg) ± 1 SE for each life history type ($N = 3$) and grey bars within a panel with unique upper case letters are significantly different ($P < 0.10$). Solid bars (a, b) and open bars (c, d) are species means ± 1 SE ($N = 6$–9). Asterisks in panel c and d indicate differences between stems and roots ($^*P \leq 0.05$; $^{**}P \leq 0.01$), and no asterisk indicates $P > 0.05$.

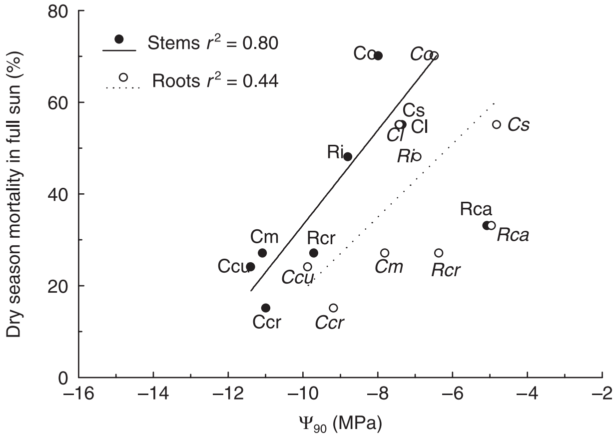

Fig. 7. Final mortality values for plants grown in full sun plotted against stem and root resistance to cavitation (ψ_{90}) for nine species (see Table 1 for abbreviations). Closed symbols and solid line are stems and open symbols and dotted line are roots. Species abbreviations for roots are in italics. Data points are means and error bars are omitted for clarity ($N = 6$–9 for ψ_{90}). Lines shown are for linear regressions for stems ($r^2 = 0.80$; $P < 0.01$) and roots ($r^2 = 0.44$; $P = 0.07$). *Rhamnus californica* is excluded from the regression analyses (see Discussion).

different with respect to its physiology compared to the other species examined (cf. Davis & Mooney 1986a,b).

Our chief conclusion is that life history type is linked to water stress tolerance and that the link can be understood in the context of regeneration niche differences; however, the shared evolutionary history of these monophyletic life history types (*NS* in the subgenus *Cerastes*, *FS* in the subgenus *Ceanothus* and *OS* in the genus *Rhamnus*, respectively; Table 1; Hardig *et al.* 2000) must also be considered for a full explanation of the connection between water stress and life history type. This will be examined below by considering the evolutionary history of the genus *Ceanothus* and the history of the chaparral environment as outlined by Axelrod (1989).

In the lineages studied, the sprouting trait is ancestral and the loss of sprouting is derived (Wells 1969). Molecular data date the split between the two lineages within *Ceanothus* to between 19 and 39 million years ago (Jeong *et al.* 1997), and this is corroborated by fossil evidence (Mason 1942). After their initial split, speciation in these lineages did not occur until more recently (Jeong *et al.* 1997; Richardson *et al.* 2004). Since the split of the two lineages, the climate in southern California has become generally more arid and gone from a summer wet to a summer dry Mediterranean type climate, and has seen an increase in fire frequency (Axelrod 1989). The change in environment, and the extinction of numerous taxa at this time would have created space that the *NS* life history type would be well suited to invade (Axelrod 1989). The chief advantages that the *NS* life history type would have over *FS* or *OS* life history types to exploit a changing environment are shorter generation times (determined by the fire return interval) and non-overlapping generations that would have facilitated adaptive change, and allowed them to invade and dominate expanding open and arid microsites (Wells 1969; Axelrod 1989). The picture that emerges is that the shared evolutionary history of the *NS Cerastes* lineage is important for understanding the present day link between the high degree of water stress tolerance and its specialization in an arid regeneration niche.

Consistent with the evolutionary history of *Ceanothus*, it was recently suggested that the evolutionary transition from an *FS* to an *NS* life history type did not lead to a short-term gain in water stress tolerance for *NS* taxa (Pratt *et al.* 2007b). This can be illustrated by considering *C. oliganthus* of the sprouting subgenus *Ceanothus*, which is a non-sprouter after fire in the Santa Monica Mountains (a fact that only became known after this study was initiated). Some races of species in the subgenus *Ceanothus* are *NS* life history types, and two commonly cited examples are *C. oliganthus* var. *oliganthus* and *C. tomentosus* var. *tomentosus* (Schwilk & Ackerly 2005; Fross & Wilken 2006). Other generally allopatric races (*C. oliganthus* var. *sorediatus* and *C. tomentosus* var. *olivaceous*) appear able to sprout (Schwilk & Ackerly 2005; Fross & Wilken 2006). The presence of sprouting and non-sprouting races suggests that the loss of sprouting in the subgenus *Ceanothus* is likely a relatively recent occurrence.

In the present study, we find that water stress tolerance of *C. oliganthus* is more similar to *FS* species even though it is functionally an *NS* life history type. A recent report for adults of the same species examined here came to the same conclusion (Pratt *et al.* 2007b). Also characteristic of *FS* species, the regeneration niche of *C. oliganthus* appears to be restricted to more mesic sites (Meentemeyer *et al.* 2001). It appears that the immediate short-term advantage gained by transitioning from an *FS* to an *NS* life history type is not heightened tolerance of water stress as found in the subgenus *Cerastes*, but instead an increase in competitive ability (Midgley 1996). Instead of allocating resources to storage, production and maintenance of a lignotuber, an *NS* in the subgenus *Ceanothus* allocates more to shoot elongation increasing the ability to compete for light in moist and shady microsites (Pratt *et al.* 2007b). Furthermore, there are likely other short-term advantages for evolving an *NS* type, such as improved reproductive efficiency (e.g. greater seed to ovule ratios; Lamont & Wiens 2003).

In California there is only one other lineage (*Arctostaphylos*) of chaparral shrubs that contains both *FS* and *NS* life history types (Boykin *et al.* 2005). If the tendency for the *NS* life history type to invade arid microsites is general then we may expect to see the patterns observed in this study to be repeated for *Acrtostaphylos*. This analysis is underway, and there is some evidence for the evolution of a higher degree of water stress tolerance in *NS* in the California chaparral genus *Arctostaphylos* compared to *FS* congeners (Paddock III 2006; Pratt *et al.* 2007b; Vasey, *et al.*, unpublished data). In the Mediterranean type climate regions of South Africa, south-western Australia, and the Mediterranean basin there are numerous lineages that have both *NS* and *FS* life history types that are distantly related to those sampled here that could provide additional tests of these patterns.

LIFE HISTORY TYPE AND SHADE TOLERANCE

It has been hypothesized that there is a trade-off between shade tolerance and water stress tolerance, and that under shaded conditions water stress may be more intense (Smith & Huston 1989). However, as in other recent studies (Holmgren 2000; Sack & Grubb 2002; Hastwell & Facelli 2003; Sánchez-Gómez *et al.* 2006), we did not find evidence to support this prediction, and instead shaded plant water stress, grown without competition, was less intense compared to plants in full sun. Shade mitigated seedling water stress, and it mitigated mortality in a life-history type dependent fashion. Mortality in the shade was generally not linked to water stress since irrigated control mortality was generally not different from non-irrigated plants. Instead, shade mortality was due to other causes such as carbon starvation and biotic factors such a powdery mildew and aphids, which were more abundant in the shade compared to the sun (Pratt, personal observation, Roberts & Paul 2006).

Consistent with a shady regeneration niche, the *OS* life history type had almost no mortality in the shade (Fig. 1). The *FS* life history type had lower levels of mortality in the shade compared to the full sun consistent with some field studies that have found greater *FS* survival in the partial shade of resprouts (Frazer & Davis 1988; Thomas & Davis 1989). It appears that partial shade is an important part of the *FS* regeneration niche, assuming minimal competition. In contrast, the *NS* had levels of mortality in the shade not different from the full sun. Moreover, by the end of the experiment *NS* plants in the shade were small and susceptible to powdery mildew, scale insects, and aphids and appeared unlikely to survive longer term. This is consistent with their regeneration in open canopy post-fire microsites (Fig. 1; Frazer & Davis 1988; Thomas & Davis 1989).

XYLEM CAVITATION AND WATER STRESS TOLERANCE

Numerous traits confer water stress tolerance among vascular plants. One that appears to be important in evergreen shrubs is the ability to sustain xylem water transport to evergreen leaves (Davis *et al.* 1999; 2002; Williams *et al.* 1997; Tyree *et al.* 2002; Lopez *et al.* 2005). The *NS* species sampled in the present study displayed relatively high levels of cavitation resistance, and the *FS* and *OS* were close to average values when compared to other Mediterranean type climate shrubs (Maherali *et al.* 2004; Jacobsen *et al.* 2007b). Stem and root cavitation resistance were both strongly and positively correlated with greater seedling survival of water stress. This result suggests an important role for cavitation resistance in tolerating severe water stress at the seedling stage of development when water stress is generally unavoidable. Furthermore, it suggests a strong link between cavitation resistance and fitness.

These results for seedlings stand in contrast to a recent study of chaparral shrubs at the adult stage during an intense drought year. Paddock III (2006) found that mortality and dieback of adult chaparral shrubs was greatest among more cavitation resistant *NS* species of *Ceanothus* and *Arctostaphylos* compared to less resistant species. This pattern was attributed to the generally shallower roots for the *NS* species. At the adult stage of development high cavitation resistance is linked to shallow rooting depth (Sperry & Hacke 2002; Lopez *et al.* 2005; Pratt *et al.* 2007b) and development of low minimum ψ_w (Pratt *et al.* 2007a; Jacobsen *et al.* 2007b). There appears to be a limit to the water stress that an adult shallow rooted evergreen shrub can tolerate, and a strategy of avoiding extreme dehydration by way of a deep rooting habit appears to be safer during drought (Paddock III 2006). Adult resprouting species have the advantage over *NS* because their roots have more resources (often a lignotuber) and a greater time period over multiple resprouting events to generate a more extensive and deeper root system. In contrast, at the seedling stage, roots of all species have had little time to develop, and are therefore relatively shallow by the onset of the first summer dry season after germination (Frazer & Davis 1988; Thomas & Davis 1989), and thus cavitation resistance in seedlings is linked to lower rates of mortality, as observed in the present study.

These results have important implications for using cavitation resistance as a trait to predict drought tolerance. Although counterintuitive, adult evergreen plants in semiarid regions with greater resistance to cavitation may be more susceptible to mortality during a severe drought, and thus may be singled out as sensitive species. There appears to be a trade-off in semiarid environments: on the one hand, seedlings highly resistant to cavitation exhibit greater survival at the juvenile stage, whereas in the adult stage they are susceptible to mortality from extreme drought because of shallow root formation. The Mediterranean type climate regions around the globe have been experiencing severe droughts in recent years, as have other arid and semiarid regions, and this pattern is predicted to continue (e.g. Seager *et al.* 2007). Using cavitation resistance as index of adult sensitivity to such events may be helpful in identifying species of concern.

It is somewhat paradoxical that *NS* species appear to be the best fit to recruit and establish seedlings in dry microsites post-fire but in the adult stage, having established at dry microsites, these same *NS* may be most prone to drought-induced mortality. In the seedling stage, all competing species have shallow roots, but in the adult stage only *NS* retain shallow roots. Species that are *FS* and *OS* can hold moist microsites post-fire through repeated resprouting and avoid dry microsites, and they also avoid the *NS* level of drought-induced mortality by way of deep roots.

Rhamnus californica was exceptional among the sampled species in its response to the water stress treatment and was excluded from analyses correlating cavitation resistance and mortality. As already stated, *R. californica* was more conservative in its water use and avoided the most severe water stress and consequently had relatively high survival. Consistent with a water stress avoidance strategy, *R. californica* displayed the greatest stem and root susceptibility to cavitation. *Rhamnus californica* is known to commonly experience dieback as an adult (Davis & Mooney 1986a; Pratt *et al.* 2007b) and as a seedling, which was observed in this study. Thus, the strategy employed by *R. californica* is to suffer crown dieback during episodes of water stress, which reduces leaf area and mitigates water stress. Resprouting after dieback ensures individual survival, albeit at reduced productivity and loss in carbon investment. It appears that evergreen shrub xylem is not universally adapted to tolerate water stress, and that even among this growth form there are alternative strategies for coping with water stress (Jacobsen *et al.* 2007a). Presumably the more conservative strategy of *R. californica* leads to its competitive exclusion in more competitive chaparral stands, and its stunted understorey growth form in mixed chaparral (Davis & Mooney 1986a,b).

A previous study employing a modelling approach on adults of the same species studied here found that stems underwent little cavitation, and that cavitation primarily occurred in the roots for *OS* and *FS* species, and the rhizosphere for *NS* species (Davis *et al.* 2002; see also Pratt *et al.* 2007b). The results suggested that the life history types *OS*–*FS*–*NS* represent a continuum of specialization for using deep to shallow soil water, respectively. The results of the present study suggest that stems and roots underwent considerable cavitation in all life history types (Fig. 6). At the seedling stage of development when root systems are diminutive stem cavitation may be unavoidable.

Within a species, stems are generally found to be more resistant to cavitation than roots (Alder *et al.* 1996; Linton *et al.* 1998; Matzner *et al.* 2001; Martinez-Vilalta *et al.* 2002; however see Hukin *et al.* 2005). This appears not to be the case in the present study as roots generally maintained greater K_s at ψ_{min} than stems. This suggests that under severe water stress, stems were more hydraulically limiting than roots. This may partially explain why root ψ_{90} was not as strong a predictor of mortality as stem ψ_{90} (Fig. 7). The soil class used in the study was a loamy sand, and no doubt the rhizosphere would have also had low conductivity at ψ_{min} (Sperry *et al.* 1998).

Conclusion

The regeneration niche concept helps to explain the coexistence of apparently functionally similar chaparral taxa in a life history type dependent fashion. Different chaparral life history types exhibit clear regeneration niche differences that separate based on water stress and shade tolerance. For water stress tolerance *NS* > *OS* > *FS*, and for shade tolerance *OS* > *FS* > *NS*. The relatively high levels of water stress and high shade tolerance partially explains the success of the *OS* life history type through time (Valiente-Banuet *et al.* 2006), as well as their current success in mixed chaparral in California. Additional studies of water stress and shade tolerance in other Mediterranean type climate species will help to clarify the generality of the link between these forms of stress tolerance and life history type.

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