

**ALLOCATION TRADEOFFS AMONG CHAPARRAL SHRUB SEEDLINGS  
WITH DIFFERENT LIFE HISTORY TYPES (RHAMNACEAE)<sup>1</sup>**

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- *Premise of the Study:* California chaparral shrub species have different life history types: Nonsprouters (NS) are killed by fire and persist through a fire-stimulated seed bank; facultative sprouters (FS) reestablish by a combination of vegetative sprouting and seeding; and obligate sprouters (OS) reestablish exclusively by sprouting. Nonsprouters and FS establish seedlings in open-canopy postfire environments, whereas OS establish seedlings between fires in the shady understory. We hypothesized that allocation differences among seedlings of postfire sprouters and nonsprouters and regeneration niche differences would lead to contrasting patterns in biomass accumulation (NS > FS > OS, in sun; OS > FS > NS, in shade).
- *Methods:* Seedlings of three species from each life history type were grown in sun and 75% shade. We measured net carbon assimilation and biomass accumulation after one year.
- *Key Results:* Biomass accumulation was similar in the sun except FS>OS. In the shade, NS had lower biomass than FS and OS. Assimilation rates, nitrogen relations, and allocation differences could not fully explain biomass accumulation differences. Instead, biomass accumulation was inversely related to water-stress tolerance and shade tolerance. Additionally, OS and FS differed in root/shoot allocation even though both are sprouters.
- *Conclusions:* Seedling growth and carbon assimilation rates were divergent among three life history types and were consistent with differences in tolerance to water stress and shade or sun regeneration niches, but not tradeoffs in sprouting-related allocation differences per se.

**Key words:** allocation; *Ceanothus*; drought; fire; growth; life history; photosynthesis; *Rhamnus*; sprouting.

The five Mediterranean-type climate regions of the world are “hotspots” of vascular plant diversity and are of special conservation concern (Cowling et al., 1996; Myers et al., 2000). In four of these regions (California, South Africa, Southwestern Australia, and the Mediterranean Basin), fire has been an important disturbance that has influenced biodiversity patterns and the evolution of plants (Bond and Midgley, 2003; Keeley et al., 2012). Plants in these regions have different life history types that are frequently defined by how plants respond to crown fire disturbance (Keeley et al., 2012). Understanding the functional role of each life history type is key to wise management and conservation, particularly in the face of climate change (Bond and Midgley, 2001; Coca and Pausas, 2009).

Different life history types include nonsprouters (NS; also called obligate seeders) that are killed by fire and only reestablish through seed germination cued by heat, smoke, or char. Facultative sprouters (FS; also called facultative seeders) regenerate by a combination of resprouting from a lignotuber and through a dormant seed bank cued to germinate by fire. Obligate sprouters (OS) regenerate after fire exclusively by resprouting from a lignotuber because their seeds are killed by fire.

Importantly, seedlings of these different life history types diverge in the environmental conditions where they commonly and most successfully recruit (i.e., their “regeneration niche”; Grubb, 1977). Nonsprouters recruit in open and arid microsites, which can be particularly stressful during the protracted summer rainless season in Mediterranean-type climate regions (Saruwatari and Davis, 1989; Thomas and Davis, 1989). Facultative sprouters recruit in open postfire microsites but are often most successful in the partial shade of resprouts and moist microsites (Frazer and Davis, 1988; Thomas and Davis, 1989; Pratt et al., 2008). Obligate sprouters recruit seedlings not after fire but instead during fire-free intervals in the deep shade of a chaparral understory (Keeley, 1992a; Pratt et al., 2008; Keeley et al., 2012).

In many plant lineages, sprouting is the ancestral condition and the loss of sprouting is a derived character (however, see Bond and Midgley, 2003). Along with the loss of sprouting comes a shift in life history type that is linked to a suite of reproductive and physiological traits (Ackerly, 2004; Paula and Pausas, 2006, 2011; Pratt et al., 2007; Hernández et al., 2011). Indeed, it appears that different life history types represent different functional types. A key difference between the life history types that forms the basis of hypotheses about their functional divergence is the cost associated with resprouting for FS and OS species (Bellingham and Sparrow, 2000; Knox and Clarke, 2005). Resprouting requires storing belowground reserves to support postfire shoot growth, as well as construction and maintenance of a lignotuber and buds (Bell and Pate, 1996; Vesik and Westoby, 2004). Resources allocated to storage and

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lignotuber growth for sprouting could alternatively be invested in more productive assets such as leaves or photosynthetic biochemistry that would increase whole-plant carbon gain. At the adult stage of development, sprouting costs may manifest as reduced growth and stature, and reduced seed production for sprouters (Fulton and Carpenter, 1979; Midgley, 1996). For many sprouting species, the production of a lignotuber and buds begins during the first year of development, as does the storage of carbohydrates (Verdaguer and Ojeda, 2002, 2005; Schwilk and Ackerly, 2005). Thus, all else being equal, sprouters should have reduced aboveground and overall growth at the seedling stage, compared with NS species. Reduced vegetative growth in resprouters compared with NS has often been found among seedlings in Southwest Australia (Pate et al., 1990), the Mediterranean Basin (Verdú, 2000), and South Africa fynbos (Bond and van Wilgen, 1996), whereas studies in California chaparral have failed to find a clear tradeoff between growth and sprouting ability (Thomas and Davis, 1989; Schwilk and Ackerly, 2005; Pugnaire et al., 2006). In some cases, overall biomass of life history types does not differ, but resprouters are found to allocate more biomass to roots than to shoots (Bell and Pate, 1996; Knox and Clarke, 2005; Pugnaire et al., 2006).

Besides carbon allocation differences among life history types, there are other factors that may affect growth, survival, and reproduction tradeoffs. For one, allocation of resources to stress tolerance may be under strong selection because of its influence on seedling survival (Cook, 1979; Pratt et al., 2008). As with allocation of reserves to enable resprouting, allocation of resources to stress tolerance (e.g., stress proteins and denser tissues) may compete with growth and reproduction. Another hypothesis suggests that sprouter reproduction is affected by genetic load (i.e., accumulation of somatic mutations over a long life span; Lamont and Wiens, 2003; Wiens and Slaton, 2012). The accumulation of somatic mutations leads to a higher abortion rate in sprouters than NS, and this reduces the reproductive investment because the ovules are aborted before they are filled with nutrient rich endosperm. This mechanism affecting reproductive allocation may be important at the adult stage, but it is not a factor that will affect growth at the seedling stage when plants are prereproductive. Other studies have found that NS species reach reproductive maturity more quickly than sprouters, and it has been suggested that this early investment in reproduction competes with growth (Knox and Clarke, 2005; Schwilk and Ackerly, 2005).

Understanding of growth tradeoffs between different life history types is incomplete, and the present study was designed to examine two tradeoffs that have yet to be fully addressed. Studies comparing growth tradeoffs between sprouters and non-sprouters have most often compared FS to NS (Knox and Clarke, 2005; Schwilk and Ackerly, 2005; Pugnaire et al., 2006); thus, controlled studies that explicitly examine NS, FS, and OS separately are lacking. We hypothesized that tradeoffs may manifest differently for the little-studied OS life history type, because of its contrasting regeneration niche and life history characteristics, such as its generally greater longevity compared with FS and NS. An additional gap in knowledge is the lack of a mechanistic understanding of potential growth differences among different life history types. Such information may be particularly important for understanding how different life history types may respond to climate change (Clarke et al., 2010). An analysis of this kind requires a controlled study replicated across the different life history types that includes measurements of a range of the functional traits (gas exchange and allocation) that determine growth.

We made detailed physiological measurements and growth analyses comparing NS, FS, and OS in a common environment, using taxa from the same lineage (Rhamnaceae) that all occur in the Santa Monica Mountains of southern California. Treatments replicated the regeneration niche of NS and FS (open canopy) and the OS (shady understory). We predicted that, in full sun, the life history types will fall along a continuum of biomass accumulation (above- and belowground) such that NS>FS>OS. In a shade treatment, consistent with typical microsite recruitment of OS seedlings, we predicted that the order would reverse such that growth will follow OS>FS>NS. We also predicted that relative allocation of biomass to roots would follow OS>FS>NS. Obligate sprouters in the Rhamnaceae have not been reported to form nitrogen-fixing symbioses; however, NS and FS in the genus *Ceanothus* nodulate and the nodule biomass was analyzed as part of growth analyses. Previously published results have established differential tolerance of water stress across life history types (Jacobsen et al., 2007; Pratt et al., 2007, 2008, 2010). These previous results, combined with those of the present study, allowed us to test for possible tradeoffs between seedling growth and traits that confer stress tolerance.

## MATERIALS AND METHODS

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., 2007). For full growing information, see Pratt et al. (2008); for seed mass and plant height data, see Pratt et al. (2007). In brief, seeds were germinated and seedlings were grown in a common garden in a complete randomized block design with a full sun and shade treatment (25% of full sun). Seedlings received natural precipitation and were grown in custom designed large containers (1.2 m tall and 250 mm wide; Blue-X Enterprises, Elk Grove, California, USA) filled with stream-washed natural soils from a pristine watershed on campus at Pepperdine University, Malibu, California. 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. (2007).

Seedling growth was assessed as absolute biomass ( $n = 6$  for each species and treatment). Very young seedlings of approximately the same size were planted into the large pots in August 2003. Seedlings were kept hydrated to facilitate establishment, after which they received only natural rainfall beginning fall 2003. The 2003–2004 annual rainfall total, measured from July to July, was 235 mm, below the 128-yr mean of 379 mm (Thornton, 2005). Seedlings were harvested beginning on 16 June 2004, and harvests continued until 22 October 2004. At the time that biomass measurements started, the predawn  $\Psi_w$  was below the turgor loss point for most plants in full sun and the plants had ceased growing (Pratt et al., 2008). Thus, the varied times of harvest had little impact on biomass accumulation over time for full sun plants because they had all stopped growing by the time the harvest began, and as evergreens, little to no leaf abscission occurred. Plants in the shade treatment did not lose turgor until later than those in the full sun treatment (~September 2004). After they had lost turgor and had stopped growing, the shade plants were harvested (beginning 15 September 2004). To further test for harvest time effects on growth, harvested biomass was correlated with time, and no relationship was found for shade or sun plants. This indicates that most of the growth for plants had occurred before biomass measurements commenced.

Plants were harvested by cutting them from their pots and carefully sieving away soil using a 2-mm-mesh screen. This careful excavation allowed us to capture much of the biomass, including fine roots. A sample of leaves was set aside and their area was measured (Li-3100, Li-Cor Corporation, Lincoln, Nebraska, USA) before they were dried at 60°C to a constant mass. All plant material was oven dried for >7 d and then weighed on an analytical balance. Roots, shoots, leaves, and nodules (for  $N_2$  fixing species) were measured separately. The ratio of leaf area to dry mass was used to calculate whole-plant leaf area from leaf dry mass. These procedures allowed us to analyze root/shoot ratio (root dry mass/shoot dry mass; g/g), leaf weight ratio (LWR; leaf mass divided by total dry mass; g/g), and leaf area ratio (LAR; leaf area divided by plant dry mass; m<sup>2</sup>/g) (Hunt, 1978).

Xylem density (minus bark and pith) of stems and roots was measured by taking the dry mass of a shoot or root segment about 5 mm long and dividing by the

TABLE 1. Species studied, abbreviations, and growth and structural characteristics including leaf weight ratio (LWR), leaf area ratio (LAR), and specific leaf area (SLA) for seedlings grown in sun and shade treatments.

Life history and species	Abbreviations	Sun root/shoot ratio	Shade root/shoot ratio	Sun LWR (g/g)	Shade LWR (g/g)	Sun LAR (mm <sup>2</sup> /g)	Shade LAR (mm <sup>2</sup> /g)	Sun SLA (mm <sup>2</sup> /g)	Shade SLA (mm <sup>2</sup> /g)	Sun xylem density (kg/m <sup>3</sup> )	Shade xylem density (kg/m <sup>3</sup> )
<b>Nonsprouter mean</b>	<b>NS</b>	<b>0.77<sup>A</sup></b> (0.08)	<b>0.44<sup>A**</sup></b> (0.05)	<b>0.26<sup>A</sup></b> (0.01)	<b>0.38<sup>A*</sup></b> (0.04)	<b>1.19<sup>A</sup></b> (0.06)	<b>2.50<sup>A***</sup></b> (0.21)	<b>4.58<sup>A</sup></b> (0.17)	<b>6.66<sup>A*</sup></b> (0.52)	<b>603<sup>A</sup></b> (13)	<b>545<sup>A***</sup></b> (13)
Subgenus <i>Cerastes</i>											
<i>Ceanothus megacarpus</i> Nutt.	<i>Cm</i>	0.71 <sup>a</sup> (0.09)	0.38 <sup>ab***</sup> (0.06)	0.24 <sup>ab</sup> (0.01)	0.30 <sup>bc*</sup> (0.03)	1.19 <sup>ab</sup> (0.05)	2.13 <sup>a***</sup> (0.26)	4.86 <sup>a</sup> (0.21)	7.01 <sup>ac</sup> (0.67)	622 <sup>ab</sup> (13)	568 <sup>ab**</sup> (13)
<i>C. crassifolius</i> Torrey	<i>Ccr</i>	0.94 <sup>a</sup> (0.24)	0.24 <sup>***</sup> (0.03)	0.25 <sup>ab</sup> (0.02)	0.44 <sup>***</sup> (0.04)	1.08 <sup>a</sup> (0.11)	2.52 <sup>ab***</sup> (0.25)	4.25 <sup>a</sup> (0.21)	5.62 <sup>a</sup> (0.47)	579 <sup>a</sup> (14)	523 <sup>a***</sup> (18)
<i>C. cuneatus</i> (Hook.) Nutt.	<i>Ccu</i>	0.67 <sup>a</sup> (0.07)	0.30 <sup>ab***</sup> (0.03)	0.28 <sup>a</sup> (0.03)	0.39 <sup>ab**</sup> (0.03)	1.30 <sup>ab</sup> (0.15)	2.87 <sup>ab**</sup> (0.24)	4.63 <sup>a</sup> (0.38)	7.35 <sup>abcd*</sup> (0.33)	611 <sup>ab</sup> (11)	545 <sup>ab***</sup> (14)
<b>Facultative sprouter mean</b>	<b>FS</b>	<b>0.84<sup>A</sup></b> (0.09)	<b>0.31<sup>A*</sup></b> (0.04)	<b>0.19<sup>A</sup></b> (0.00)	<b>0.23<sup>B</sup></b> (0.04)	<b>1.64<sup>A</sup></b> (0.19)	<b>2.88<sup>A***</sup></b> (0.38)	<b>8.25<sup>B</sup></b> (1.07)	<b>12.30<sup>B**</sup></b> (0.99)	<b>602<sup>A</sup></b> (17)	<b>553<sup>A***</sup></b> (12)
Subgenus <i>Ceanothus</i>											
<i>C. spinosus</i> Nutt.	<i>Cs</i>	0.75 <sup>a</sup> (0.07)	0.37 <sup>ab***</sup> (0.07)	0.20 <sup>ab</sup> (0.02)	0.15 <sup>c</sup> (0.02)	1.32 <sup>ab</sup> (0.14)	2.15 <sup>a**</sup> (0.36)	6.41 <sup>ab</sup> (0.45)	13.79 <sup>b***</sup> (2.74)	609 <sup>ab</sup> (9)	543 <sup>ab***</sup> (11)
<i>C. oliganthus</i> Nutt. §	<i>Co</i>	0.74 <sup>a</sup> (0.06)	0.41 <sup>abc**</sup> (0.02)	0.19 <sup>ab</sup> (0.01)	0.27 <sup>**</sup> (0.02)	1.61 <sup>ab</sup> (0.12)	3.48 <sup>**</sup> (0.31)	8.23 <sup>bc</sup> (0.48)	12.71 <sup>b**</sup> (0.83)	628 <sup>ab</sup> (8)	577 <sup>**</sup> (8)
<i>C. leucodermis</i> E. Greene	<i>Cl</i>	1.03 <sup>bc</sup> (0.13)	0.55 <sup>bc***</sup> (0.06)	0.19 <sup>ab</sup> (0.01)	0.28 <sup>**</sup> (0.01)	1.99 <sup>b</sup> (0.15)	3.00 <sup>ab***</sup> (0.10)	10.12 <sup>b</sup> (0.58)	10.41 <sup>bc</sup> (0.20)	570 <sup>a</sup> (12)	539 <sup>ab**</sup> (12)
<b>Obligate sprouter mean</b>	<b>OS</b>	<b>1.70<sup>b</sup></b> (0.30)	<b>0.89<sup>b*</sup></b> (0.14)	<b>0.17<sup>A</sup></b> (0.00)	<b>0.24<sup>B</sup></b> (0.02)	<b>1.24<sup>A</sup></b> (0.06)	<b>2.44<sup>A***</sup></b> (0.08)	<b>7.30<sup>B</sup></b> (0.99)	<b>10.33<sup>B*</sup></b> (1.16)	<b>686<sup>A</sup></b> (32)	<b>658<sup>B</sup></b> (31)
<i>Rhamnus ilicifolia</i> Kellogg	<i>Ri</i>	1.20 <sup>ab</sup> (0.10)	0.70 <sup>cd**</sup> (0.09)	0.22 <sup>ab</sup> (0.01)	0.28 <sup>c</sup> (0.02)	1.23 <sup>ab</sup> (0.10)	2.28 <sup>a***</sup> (0.21)	5.39 <sup>ac</sup> (0.85)	8.16 <sup>b***</sup> (0.77)	673 <sup>b</sup> (13)	654 <sup>cd</sup> (17)
<i>R. californica</i> Eschsch	<i>Rca</i>	2.24 <sup>b</sup> (0.28)	1.17 <sup>de*</sup> (0.03)	0.15 <sup>b</sup> (0.01)	0.20 <sup>**</sup> (0.00)	1.35 <sup>ab</sup> (0.10)	2.49 <sup>ab***</sup> (0.09)	8.77 <sup>bc</sup> (1.29)	10.68 <sup>bc</sup> (1.23)	634 <sup>b</sup> (10)	606 <sup>c</sup> (12)
<i>R. crocea</i> Nutt.	<i>Rcr</i>	1.64 <sup>bc</sup> (0.19)	0.80 <sup>de***</sup> (0.08)	0.14 <sup>b</sup> (0.01)	0.20 <sup>**</sup> (0.00)	1.13 <sup>a</sup> (0.10)	2.54 <sup>ab***</sup> (0.10)	7.75 <sup>ab</sup> (1.09)	12.16 <sup>cd**</sup> (1.68)	746 <sup>c</sup> (15)	714 <sup>d</sup> (8)

Notes: Data are means, with standard error in parentheses. Within a column, means followed by the same letter are not different, whereas those with unique letters are different, with lowercase letters for species comparisons and capital letters for life history type comparisons. Asterisks in the shade columns denote instances in which species or life history types differed between sun and shade treatments (\* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ).

saturated volume obtained by submerging water-saturated segments underwater on an analytical balance. Specific leaf area (SLA) was measured on fully expanded leaves by measuring leaf area (Li-3100, Li-Cor Corporation, Lincoln, Nebraska, USA) divided by the dry mass obtained by drying the leaves in a drying oven for  $\geq 2$  d at  $60^\circ\text{C}$  and measuring the dry mass using an analytical balance.

Net carbon assimilation ( $A_{\text{net}}$ ;  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) was measured on fully expanded outer canopy leaves during the wet season from 2 November 2004 to 26 April 2005 (one leaf per individual and  $n = 5$  for each of nine species and two treatments). Measurements were made over a range of photosynthetic photon flux densities to generate light response curves for each species. An Li-6400 gas exchange system was used for these measurements (Li-Cor, Lincoln, Nebraska, USA). Light intensities (90% red and 10% blue light emitting diodes in a Li-Cor fluorescence cuvette attachment) included 2000, 1000, 500, 250, 100, 50, 25, and zero  $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ . Cuvette conditions were set to and maintained at 375 ppm  $\text{CO}_2$ , a temperature of about  $22^\circ\text{C}$ , and a leaf to air vapor pressure deficit of 1–3 kPa. Analyses began in the morning hours ( $\sim 0900$  hours) and the light level first used in the cuvette was  $500 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ . To ensure that the photosynthetic reactions were properly induced, special attention was paid to the stability of this first value, which often took  $>20$  min to achieve full stability. Light levels were then increased to  $2000 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$  and then decreased incrementally to zero. Each light level was run for about twenty minutes to achieve full acclimation. In cases where plants had their stomata closed, the plant water status was measured to verify they were under water stress and measurements were made on a more hydrated individual instead. Along with  $A_{\text{net}}$ , stomatal conductance ( $g_s$ ;  $\text{mol m}^{-2} \text{ s}^{-1}$ ) was measured and instantaneous water use efficiency (WUE; maximum  $A_{\text{net}}/g_s$ ) was calculated. Nitrogen content of sampled leaves (g N/g dry leaf tissue) was analyzed by combustion (TruSpec C/N, Leco Corporation, St. Joseph, Michigan, USA) at Utah State University Analytical Laboratory. These values were multiplied by specific leaf area (SLA;  $\text{m}^2/\text{g}$  dry leaf tissue) to express them as leaf N content/leaf area. Photosynthetic nitrogen use efficiency was calculated by multiplying maximum  $A_{\text{net}}$  by leaf area/N content (N expressed on a molar basis;  $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ N s}^{-1}$ ). Quantum efficiency was calculated as the slope of the linear portion of the light response curve. The electron transport rate (ETR), at  $2000 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ , of leaves was calculated from PSII chlorophyll fluorescence measurements as  $\text{ETR} = [(F_m' - F_s)/F_m'] \times 2000 \times \alpha \times 0.5$ , where  $F_m'$  is the maximum fluorescence following a saturating pulse,  $F_s$  is the steady state fluorescence,  $\alpha$  is the leaf absorptance, and 0.5 accounts for the excitation of electrons twice, once in PSII and once in PSI. Leaf absorptance was measured using a spectroradiometer (model SE590, Optronic Laboratories, Orlando, Florida, USA) and an integrating sphere (model 1800-12, Li-Cor, Lincoln, Nebraska, USA). The light compensation point was taken as the light level at which the  $A_{\text{net}}$  value was zero. The dark respiration rate was taken as the stable  $A_{\text{net}}$  value in complete darkness.

Differences among treatments were analyzed using analysis of variance (ANOVA) in JMP version 9.0.0 (SAS Institute, Cary, North Carolina, USA). The terms in all the models included life history type (NS, FS, and OS), sun and shade (referred to as treatment), species as a random factor nested within life history type, and all possible interactions. Time of sampling was also analyzed as a covariate but was not found to be significant. A restricted maximum likelihood (REML) method was used for fitting the mixed ANOVA model. Life history type differences were analyzed as preplanned comparisons using species nested in life history type as the error term. Differences among species employed a Tukey's correction to control the experiment-wise Type 1 error rate. It was not a chief objective to analyze species differences, but comparisons are shown, and we caution that because of the large numbers of comparisons and Tukey's corrections, these comparisons have an inflated Type 2 error rate. Xylem density of stems and roots was not different, so they were pooled for analyses. Data were transformed as necessary to satisfy assumptions of statistical models. Data for nodule dry mass were non-normal, so comparisons were made using Mann-Whitney  $U$  tests in Minitab version 16.1 (Minitab, State College, Pennsylvania, USA). To control Type 1 error,  $P$  values were Bonferroni adjusted (Rice, 1990). Tests for association were conducted with Pearson correlation analyses (Minitab). A principal component analysis was used to simply describe relationships among traits and life history types because the number of traits examined ( $n = 14$ ) was large compared with the number of sampled species ( $n = 9$ ).

## RESULTS

Seedling life history types differed in biomass accumulation (hereafter "growth"; Fig. 1, Table 2). The FS life history type had the greatest overall growth, and the NS and OS life history

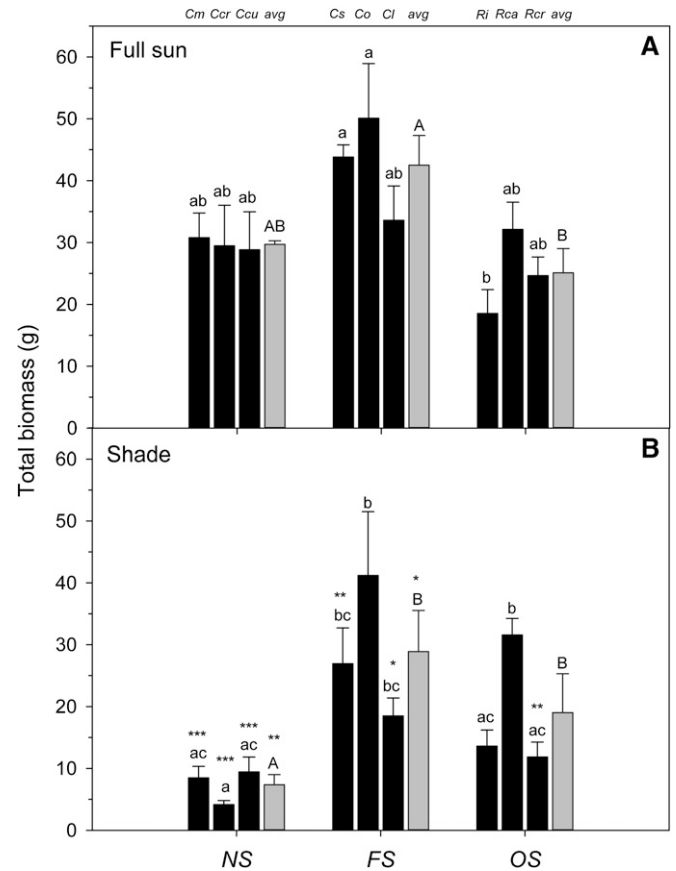


Fig. 1. Seedling biomass grown in full sun and shade (25% of full sun). Data are means  $\pm 1$  SE ( $n = 6$ ) for species (filled bars) and life history type (gray bars). Species abbreviations are above bars in panel A. Bars within each panel labeled with unique letters (lowercase for species means and uppercase for life history type means) are different, and asterisks in panel B denote differences between sun and shade (\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ).

types were not different (Fig. 1, Table 2). The differences were statistically significant for only the main effects contrasts between NS and FS (Table 2). Growth was generally reduced by the shade treatment (Fig. 1, Table 2), and there was a significant life history type  $\times$  treatment interaction (Table 2), indicating that life history types responded differently to the shade treatment. Within the sun treatment, the FS had greater growth than the OS (Fig. 1A), and the NS and FS did not differ significantly ( $F_{1,7.93} = 2.94$ ,  $P = 0.124$ ). In the shade treatment, the NS had the lowest growth and the FS and OS were not different (Fig. 1B). The interaction between life history type and treatment arose in part because both the NS and FS had lower growth in the shade, whereas sun and shade growth were not different in the OS (Fig. 1). In addition, NS growth was reduced by the shade treatment to a greater degree than for the other two life history types (Fig. 1).

Traits related to allocation and structure (Tables 1 and 2), photosynthesis (Tables 3 and 4), nitrogen relations (Tables 5 and 6), and water use (Tables 7 and 8) were analyzed to better understand growth differences between life history types and with respect to light treatment. These traits are briefly assessed here and summarized in Figure 2.



TABLE 2. Main effect and interaction ANOVA output for growth-related parameters (see Table 1 and Fig. 1 for units, descriptive statistics, and abbreviations).

Source of variation	Growth		Root/shoot ratio		LWR		LAR		SLA		Xylem density	
	F	P	F	P	F	P	F	P	F	P	F	P
Life history	4.89 <sub>2,6</sub>	0.054	17.08 <sub>2,6</sub>	0.003	5.73 <sub>2,6</sub>	0.040	1.90 <sub>2,6</sub>	0.228	125.08 <sub>2,70.5</sub>	<0.001	7.49 <sub>2,5,9</sub>	0.023
Treatment	52.99 <sub>1,6</sub>	<0.001	181.11 <sub>1,6</sub>	<0.001	9.25 <sub>1,6</sub>	0.022	118.36 <sub>1,6</sub>	<0.001	146.04 <sub>1,62.3</sub>	<0.001	131.42 <sub>1,618</sub>	<0.001
Treatment × life history	9.06 <sub>2,6</sub>	0.015	1.78 <sub>2,6</sub>	0.247	0.66 <sub>2,6</sub>	0.548	0.32 <sub>2,6</sub>	0.733	1.82 <sub>2,62.3</sub>	0.169	9.14 <sub>2,6,12</sub>	0.014
Life history contrasts												
NS vs. FS	9.38 <sub>1,6</sub>	0.022	2.28 <sub>1,6</sub>	0.181	7.78 <sub>1,6</sub>	0.031	2.99 <sub>1,6</sub>	0.134	235.69 <sub>1,70.5</sub>	<0.001	0.05 <sub>1,5,9</sub>	0.815
NS vs. OS	0.95 <sub>1,6</sub>	0.365	31.87 <sub>1,6</sub>	0.001	9.35 <sub>1,6</sub>	0.022	0.00 <sub>1,6</sub>	0.940	120.33 <sub>1,70.5</sub>	<0.001	12.03 <sub>1,602</sub>	0.013
FS vs. OS	4.34 <sub>1,6</sub>	0.082	17.09 <sub>1,6</sub>	0.006	0.07 <sub>1,6</sub>	0.797	2.73 <sub>1,6</sub>	0.149	19.20 <sub>1,70.5</sub>	<0.001	10.43 <sub>1,5,9</sub>	0.018

Allocation and structural traits other than growth, differed among life history types for all traits except leaf area ratio (Table 2). The shade treatment significantly affected all measured traits in expected ways (e.g., lower root/shoot ratio, greater allocation to leaves, increased SLA, and lower xylem density; Tables 1 and 2). For one trait, xylem density, there was a significant life history × treatment interaction (Table 2) that was due to lower xylem density in the shade for NS and FS, whereas OS xylem density did not differ between sun and shade treatments (Table 1).

Photosynthetic traits were generally different among life history types for all traits except dark respiration ( $R_d$ ) and quantum efficiency (Tables 3 and 4). Compared to the OS, the NS and FS species generally had trait values indicative of species adapted to high light, such as higher values for carbon assimilation, ETR, light compensation, and absolute dark respiration. The shade treatment significantly reduced  $A_{net}$  on an area basis, ETR, the light compensation point, and  $R_d$  (Tables 3 and 4).

For traits related to nitrogen relations, life history types differed in the dry mass of nodules they produced, with the FS life history type producing more nodule biomass than the NS (Tables 5 and 6). The OS life history type does not form bacterial symbioses that result in root nodules, so they were not compared. For leaf nitrogen on a per area basis, the NS life history type was greater than the FS and OS (Tables 5 and 6). On a per mass basis and for  $P_{nuc}$ , the life history types did not differ (Tables 5 and 6). The shade treatment had the general effect of lowering the mass of nodules produced and the leaf nitrogen per unit leaf area, but did not affect leaf nitrogen per unit mass or  $P_{nuc}$  (Tables 5 and 6).

Among the nitrogen-fixing *Ceanothus* spp., nodule biomass was generally not associated with leaf-level nitrogen contents and  $A_{net}$ . Nodule biomass was not correlated with leaf-level nitrogen content or canopy nitrogen content (leaf-level nitrogen on an area and mass basis multiplied by canopy leaf area and leaf mass, respectively). The exception to this is that, in the shade treatment, nodule biomass was negatively associated with leaf-level nitrogen ( $r = -0.88$ ,  $P = 0.02$ ). Leaf-level nitrogen content was not correlated with  $A_{net}$  in the sun or shade. Total biomass was correlated with nodule mass, indicating that bigger plants produced more nodule mass (in sun:  $r = 0.97$  and  $P = 0.001$ ; in shade,  $r = 0.93$  and  $P = 0.007$ ). In addition, the mass of nodules produced in the sun was strongly correlated with the mass of nodules produced in the shade ( $r = 0.92$ ,  $P = 0.009$ ).

Water-relations traits of maximum  $g_s$  and WUE were not different among life history types (Tables 7 and 8). Shade did not have a significant effect on WUE; however, there was a significant life history type × sun/shade interaction that was a result of significantly lower WUE in the shade for the NS life history type compared with the sun, but the other life history types did not differ between shade and sun (Tables 7 and 8).

To summarize how the life history types differed with respect to growth and stress tolerance and to identify which traits were associated with growth, a principal component analysis was performed (Fig. 2). In full sun, growth was positively associated with  $A_{net}$  per unit mass, LAR, and mortality (Fig. 2A). The nine sampled species formed three clusters representing the three life history types (Fig. 2A). The FS life history type was associated most strongly and positively with growth and the aforementioned traits associated with growth (Fig. 2A). The NS were associated most strongly with traits reflecting resistance to water stress such as xylem cavitation resistance, low SLA, and low water-stress-induced mortality. In addition, the

TABLE 3. Gas exchange and light responses for seedlings grown in full sun and shade, including net carbon assimilation ( $A_{\text{net}}$ ) expressed on a per area and mass basis, electron transport rate (ETR), light compensation point (LCP) and leaf dark respiration ( $R_d$ ) (for description of data, see Table 1).

Life history and species	Sun $A_{\text{net}}$ max ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Shade $A_{\text{net}}$ max ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Sun $A_{\text{net}}$ max ( $\mu\text{mol g}^{-1} \text{s}^{-1}$ )	Shade $A_{\text{net}}$ max ( $\mu\text{mol g}^{-1} \text{s}^{-1}$ )	Sun ETR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Shade ETR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Sun LCP (quanta $\text{m}^{-2} \text{s}^{-1}$ )	Shade LCP (quanta $\text{m}^{-2} \text{s}^{-1}$ )	Sun $R_d$ ( $\mu\text{mol g}^{-1} \text{s}^{-1}$ )	Shade $R_d$ ( $\mu\text{mol g}^{-1} \text{s}^{-1}$ )
<b>Nonsprouter average</b>	<b>24.0<sup>A</sup></b> (5.2)	<b>16.3<sup>A</sup></b> (1.4)	<b>0.10<sup>AB</sup></b> (0.02)	<b>0.10<sup>A</sup></b> (0.01)	<b>206<sup>A</sup></b> (18)	<b>147<sup>A**</sup></b> (9)	<b>54.0<sup>A</sup></b> (22.8)	<b>15.2<sup>A**</sup></b> (3.0)	<b>-0.0095<sup>AB</sup></b> (0.0012)	<b>-0.0063<sup>A**</sup></b> (0.0014)
Subgenus <i>Cerastes</i>										
<i>Ceanothus megacarpus</i>	33.2 <sup>a</sup> (3.6)	13.5 <sup>ab***</sup> (2.9)	0.15 <sup>ab</sup> (0.01)	0.09 <sup>ab**</sup> (0.02)	236 <sup>a</sup> (10)	131 <sup>ab</sup> (16)	24.4 <sup>a</sup> (6.6)	15.6 <sup>a</sup> (6.2)	-0.0099 <sup>a</sup> (0.0014)	-0.0064 <sup>a</sup> (0.0019)
<i>C. crassifolius</i>	23.7 <sup>ab</sup> (2.6)	18.3 <sup>a</sup> (3.2)	0.10 <sup>ab</sup> (0.01)	0.10 <sup>a</sup> (0.02)	210 <sup>bc</sup> (15)	165 <sup>a</sup> (23)	38.8 <sup>a</sup> (5.2)	9.8 <sup>**</sup> (3.6)	-0.0072 <sup>a</sup> (0.0011)	-0.0037 <sup>a</sup> (0.0009)
<i>C. cuneatus</i>	15.0 <sup>b</sup> (5.2)	17.2 <sup>a</sup> (2.2)	0.06 <sup>a</sup> (0.01)	0.12 <sup>a*</sup> (0.01)	173 <sup>ab</sup> (23)	146 <sup>ab</sup> (15)	99.0 <sup>a</sup> (54.8)	20.2 <sup>ab**</sup> (5.8)	-0.0113 <sup>a</sup> (0.0031)	-0.0087 <sup>a</sup> (0.0015)
<b>Facultative sprouter average</b>	<b>18.2<sup>AB</sup></b> (0.5)	<b>13.2<sup>A</sup></b> (1.9)	<b>0.14<sup>A</sup></b> (0.01)	<b>0.15<sup>A</sup></b> (0.02)	<b>183<sup>A</sup></b> (4)	<b>120<sup>AB**</sup></b> (9)	<b>25.0<sup>A</sup></b> (1.6)	<b>13.5<sup>A**</sup></b> (3.7)	<b>-0.0108<sup>A</sup></b> (0.0013)	<b>-0.0098<sup>B</sup></b> (0.0008)
Subgenus <i>Ceanothus</i>										
<i>C. spinosus</i>	19.1 <sup>ab</sup> (3.5)	9.4 <sup>ab***</sup> (1.7)	0.13 <sup>ab</sup> (0.03)	0.11 <sup>a</sup> (0.01)	187 <sup>ab</sup> (13)	102 <sup>ab***</sup> (6)	21.7 <sup>a</sup> (6.3)	17.6 <sup>a</sup> (6.3)	-0.0081 <sup>a</sup> (0.0023)	-0.0092 <sup>a</sup> (0.0018)
<i>C. oliganthus</i>	18.4 <sup>ab</sup> (2.7)	14.1 <sup>a</sup> (1.6)	0.15 <sup>ab</sup> (0.02)	0.18 <sup>a</sup> (0.02)	187 <sup>ab</sup> (13)	127 <sup>ab**</sup> (7)	27.2 <sup>a</sup> (3.7)	6.1 <sup>ab**</sup> (2.9)	-0.0120 <sup>a</sup> (0.0029)	-0.0088 <sup>a</sup> (0.0020)
<i>C. leucodermis</i>	17.2 <sup>ab</sup> (1.2)	16.1 <sup>a</sup> (1.2)	0.17 <sup>b</sup> (0.01)	0.17 <sup>a</sup> (0.01)	177 <sup>ab</sup> (15)	132 <sup>ab**</sup> (7)	16.9 <sup>a</sup> (5.9)	26.3 <sup>a</sup> (5.3)	-0.0123 <sup>a</sup> (0.0016)	-0.0115 <sup>a</sup> (0.0025)
<b>Obligate sprouter average</b>	<b>13.1<sup>B</sup></b> (1.3)	<b>10.9<sup>A</sup></b> (1.6)	<b>0.09<sup>B</sup></b> (0.01)	<b>0.11<sup>A</sup></b> (0.01)	<b>141<sup>B</sup></b> (15)	<b>104<sup>B**</sup></b> (10)	<b>21.6<sup>A</sup></b> (6.0)	<b>4.5<sup>A***</sup></b> (1.9)	<b>-0.0070<sup>B</sup></b> (0.0003)	<b>-0.0059<sup>A</sup></b> (0.0008)
<i>Rhamnus ilicifolia</i>	14.7 <sup>b</sup> (1.8)	11.9 <sup>a</sup> (1.2)	0.08 <sup>ab</sup> (0.02)	0.10 <sup>a</sup> (0.01)	166 <sup>a</sup> (16)	116 <sup>ab</sup> (12)	30.8 <sup>a</sup> (9.7)	8.2 <sup>ab**</sup> (6.1)	-0.0076 <sup>a</sup> (0.0025)	-0.0055 <sup>a</sup> (0.0018)
<i>R. californica</i>	10.4 <sup>b</sup> (0.4)	7.6 <sup>a</sup> (0.8)	0.09 <sup>ab</sup> (0.01)	0.08 <sup>a</sup> (0.01)	112 <sup>b</sup> (15)	84 <sup>b</sup> (8)	10.2 <sup>a</sup> (3.5)	1.6 <sup>a</sup> (1.4)	-0.0064 <sup>a</sup> (0.0014)	-0.0047 <sup>a</sup> (0.0010)
<i>R. crocea</i>	13.9 <sup>b</sup> (1.8)	13.1 <sup>a</sup> (1.6)	0.11 <sup>ab</sup> (0.02)	0.14 <sup>a</sup> (0.02)	146 <sup>bc</sup> (22)	114 <sup>ab</sup> (9)	24.0 <sup>a</sup> (9.8)	3.6 <sup>ab**</sup> (2.3)	-0.0070 <sup>a</sup> (0.0012)	-0.0076 <sup>a</sup> (0.0006)

TABLE 4. Main effect and interaction ANOVA output for leaf light response parameters (for units and descriptive statistics, see Table 3).

Source of variation	$A_{\text{net area}}$		$A_{\text{net mass}}$		ETR		Light compensation Point		$R_d$		Quantum efficiency	
	F	P	F	P	F	P	F	P	F	P	F	P
Life history	<b>5.38</b> <sub>2,6</sub>	<b>0.045</b>	<b>4.89</b> <sub>2,6</sub>	<b>0.054</b>	<b>6.31</b> <sub>2,6</sub>	<b>0.034</b>	<b>5.07</b> <sub>2,6</sub>	<b>0.051</b>	3.41 <sub>2,6</sub>	0.102	1.56 <sub>2,6</sub>	0.284
Treatment	<b>5.19</b> <sub>1,6</sub>	<b>0.052</b>	0.21 <sub>1,6</sub>	0.662	<b>38.04</b> <sub>1,6</sub>	<b>&lt;0.001</b>	<b>40.16</b> <sub>1,6</sub>	<b>&lt;0.001</b>	<b>9.02</b> <sub>1,6</sub>	<b>0.023</b>	0.94 <sub>1,6</sub>	0.369
Treatment × life history	0.22 <sub>2,6</sub>	0.807	0.09 <sub>2,6</sub>	0.912	0.33 <sub>2,6</sub>	0.728	0.96 <sub>2,6</sub>	0.434	1.81 <sub>2,6</sub>	0.241	0.03 <sub>2,6</sub>	0.969
Life history contrasts												
NS vs. FS	2.42 <sub>1,6</sub>	0.170	<b>6.38</b> <sub>1,6</sub>	<b>0.044</b>	2.08 <sub>1,5.8</sub>	0.2	1.11 <sub>1,6</sub>	0.331	2.76 <sub>1,6</sub>	0.147	0.11 <sub>1,6</sub>	0.751
NS vs. OS	<b>10.76</b> <sub>1,6</sub>	<b>0.016</b>	0.11 <sub>1,6</sub>	0.747	<b>12.50</b> <sub>1,5.8</sub>	<b>0.012</b>	<b>9.81</b> <sub>1,6</sub>	<b>0.02</b>	0.83 <sub>1,6</sub>	0.395	2.78 <sub>1,6</sub>	0.145
FS vs. OS	2.96 <sub>0,1,6</sub>	0.135	<b>8.20</b> <sub>1,6</sub>	<b>0.028</b>	4.38 <sub>1,5.9</sub>	0.082	4.30 <sub>1,6</sub>	0.083	<b>6.64</b> <sub>1,6</sub>	<b>0.041</b>	1.79 <sub>1,6</sub>	0.229

NS were positively associated with LWR and whole plant leaf specific conductance (Fig. 2A). The OS life history type was positively associated with persistence traits such as a high root:shoot ratio, and xylem density, and low dark respiration rates (Fig. 2A). In the shade treatment, the relationships were much the same, except the shade reduced the mortality, thus the FS were not associated with mortality as they were in the sun. Moreover, the FS were positively associated with growth (Fig. 2B). Mortality was negatively associated with the OS life history type (Fig. 2B) reflecting the fact that they had virtually no mortality in the shade treatment. The NS species grew poorly in the shade and thus biomass was negatively associated with the NS life history type (Fig. 2B). Dark respiration also shifted somewhat in the shade with the FS life history type being negatively associated with it (i.e., the FS were associated with greater rates of  $R_d$ ; Fig. 2B). Seed mass and growth were largely uncoupled in sun and shade (Fig. 2).

## DISCUSSION

**Life history type differences**—Contrary to our predictions, the NS life history type did not accumulate greater biomass than the FS and OS life history types, both of which allocate resources to sprouting. This result is consistent with some other studies that fail to find a seedling growth advantage for NS compared with sprouting species (Knox and Clarke, 2005; Schwilk and Ackerly, 2005; Pugnaire et al., 2006); however, our results are different from these studies in other ways. For example, other studies have found that NS reach reproductive maturity more rapidly than FS (Knox and Clarke, 2005; Schwilk and Ackerly, 2005); however, during our study none of the species reached reproductive maturity, so allocation to reproduction was not a factor in our experiment. Additionally, it was clear that FS and OS were allocating resources to storage, as evidenced by their having well-developed small lignotubers. Moreover, a recent study of *C. tomentosus* seedlings in a common garden showed that total nonstructural carbohydrates were greater in FS races than in NS ones (Schwilk and Ackerly, 2005). We conclude that the NS use resources saved by not sprouting in ways that do not contribute to greater biomass accumulation and early reproduction in the critical first year of growth.

One of our main objectives was to evaluate growth and allocation for the OS life history type, for which studies are lacking. We found that they exhibit some significant differences from the FS and NS life history types that are consistent with differences in regeneration niches. For example, in full sun, the FS had greater biomass accumulation than the OS, even though both of these life history types sprout after fire and incur the costs associated with the sprouting habit. This is consistent with the FS regeneration niche being characterized by a more open canopy condition than that of the OS. Moreover, biomass accumulation of the OS was not significantly different between the sun and shade, indicating that the OS was better able to adjust to growing in the shade than the other two life history types. The biomass accumulation of NS was most strongly negatively affected by the shade treatment, which is consistent with a shade-avoiding open-canopy regeneration niche.

Some previous studies have found that sprouters allocate more biomass to roots than to shoots (Bell and Pate, 1996; Knox and Clarke, 2005; Pugnaire et al., 2006). We too find

TABLE 5. Nitrogen relations including photosynthetic nitrogen use efficiency ( $P_{\text{nut}}$ ) of seedlings grown in full sun and shade (for description of data, see Table 1).

Life history and species	Sun nodule dry mass (g)	Shade nodule dry mass (g)	Sun nitrogen (g/g) (%)	Shade nitrogen (g/g) (%)	Sun nitrogen per leaf area (g/m <sup>2</sup> )	Shade nitrogen per leaf area (g/m <sup>2</sup> )	Sun $P_{\text{nut}}$ ( $\mu\text{mol mol}^{-1} \text{s}^{-1}$ )	Shade $P_{\text{nut}}$ ( $\mu\text{mol mol}^{-1} \text{s}^{-1}$ )
<b>Nonsprouter average</b>	<b>0.79<sup>A</sup></b> (0.01)	<b>0.01<sup>A***</sup></b> (0.01)	<b>3.61<sup>A</sup></b> (0.82)	<b>3.94<sup>A</sup></b> (0.56)	<b>7.92<sup>A</sup></b> (1.71)	<b>5.93<sup>A</sup></b> (0.50)	<b>48.5<sup>A</sup></b> (15.2)	<b>39.9<sup>A</sup></b> (3.7)
Subgenus <i>Cerastes</i>								
<i>Ceanothus megacarpus</i>	0.78 <sup>bb</sup> (0.27)	0.00 <sup>***</sup> (0.00)	3.98 <sup>a</sup> (0.09)	3.65 <sup>a</sup> (0.17)	8.35 <sup>a</sup> (0.48)	5.36 <sup>ac***</sup> (0.47)	56.0 <sup>a</sup> (5.8)	36.3 <sup>a</sup> (8.4)
<i>C. crassifolius</i>	0.76 <sup>a</sup> (0.32)	0.00 <sup>***</sup> (0.00)	2.04 <sup>b</sup> (0.05)	3.14 <sup>ac***</sup> (0.49)	4.75 <sup>b</sup> (0.20)	5.50 <sup>ac</sup> (0.62)	70.3 <sup>ab</sup> (8.0)	47.4 <sup>a</sup> (9.0)
<i>C. cuneatus</i>	0.82 <sup>bb</sup> (0.29)	0.02 <sup>***</sup> (0.01)	4.81 <sup>c</sup> (0.11)	5.03 <sup>b</sup> (0.15)	10.65 <sup>a</sup> (0.80)	6.92 <sup>ac**</sup> (0.49)	19.1 <sup>a</sup> (5.3)	36.1 <sup>a</sup> (6.1)
<b>Facultative sprouter average</b>	<b>1.42<sup>b</sup></b> (0.23)	<b>0.29<sup>b***</sup></b> (0.03)	<b>2.85<sup>A</sup></b> (0.48)	<b>2.58<sup>A</sup></b> (0.49)	<b>3.84<sup>B</sup></b> (0.90)	<b>2.14<sup>B**</sup></b> (0.32)	<b>79.3<sup>A</sup></b> (19.6)	<b>92.0<sup>A</sup></b> (22.3)
Subgenus <i>Ceanothus</i>								
<i>C. spinosus</i>	1.64 <sup>c</sup> (0.22)	0.31 <sup>a***</sup> (0.16)	2.79 <sup>cd</sup> (0.11)	2.51 <sup>cd</sup> (0.25)	4.90 <sup>b</sup> (0.75)	2.01 <sup>bc***</sup> (0.33)	61.7 <sup>ab</sup> (19.0)	66.3 <sup>a</sup> (9.6)
<i>C. oliganthus</i>	1.69 <sup>bc</sup> (0.44)	0.33 <sup>a***</sup> (0.13)	3.72 <sup>a</sup> (0.12)	3.47 <sup>ac</sup> (0.13)	4.58 <sup>b</sup> (0.32)	2.75 <sup>bc***</sup> (0.10)	57.8 <sup>ac</sup> (11.0)	73.1 <sup>a</sup> (9.5)
<i>C. leucodermis</i>	0.95 <sup>ac</sup> (0.36)	0.21 <sup>a***</sup> (0.17)	2.05 <sup>bd</sup> (0.08)	1.76 <sup>d</sup> (0.07)	2.03 <sup>c</sup> (0.04)	1.65 <sup>bc</sup> (0.05)	118.5 <sup>b</sup> (9.5)	136.7 <sup>b</sup> (12.3)
<b>Obligate sprouter average</b>	<b>NA</b>	<b>NA</b>	<b>3.04<sup>A</sup></b> (0.52)	<b>2.80<sup>A</sup></b> (0.39)	<b>4.71<sup>AB</sup></b> (1.37)	<b>2.93<sup>B</sup></b> (0.22)	<b>51.6<sup>A</sup></b> (17.6)	<b>59.0<sup>A</sup></b> (12.1)
<i>Rhamnus ilicifolia</i>	NA	NA	3.70 <sup>b</sup> (0.26)	2.05 <sup>de***</sup> (0.28)	7.30 <sup>ab</sup> (0.73)	2.56 <sup>b***</sup> (0.34)	31.1 <sup>a</sup> (7.3)	72.0 <sup>ab</sup> (15.9)
<i>R. californica</i>	NA	NA	3.42 <sup>a</sup> (0.12)	3.36 <sup>ac</sup> (0.11)	4.15 <sup>bd</sup> (0.44)	3.33 <sup>c</sup> (0.42)	37.1 <sup>ac</sup> (4.8)	34.8 <sup>a</sup> (6.5)
<i>R. crocea</i>	NA	NA	1.99 <sup>b</sup> (0.35)	2.99 <sup>ac***</sup> (0.24)	2.65 <sup>cd</sup> (0.41)	2.89 <sup>bc</sup> (0.38)	86.7 <sup>bc</sup> (23.2)	70.3 <sup>a</sup> (14.6)



TABLE 6. Main effect and interaction ANOVA output for nitrogen related parameters (for units and descriptive statistics, see Table 5).

Source of variation	Nodule mass		Leaf nitrogen (g/g)		Leaf nitrogen (g/m <sup>2</sup> )		$P_{\text{nuc}}$	
	<i>Q</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Life history	<b>1049</b>	<b>0.002</b>	1.23 <sub>2,6</sub>	0.354	<b>7.02</b> <sub>2,6</sub>	<b>0.026</b>	2.25 <sub>2,6</sub>	0.185
Treatment	<b>1832</b>	<b>&lt;0.001</b>	0.04 <sub>1,6</sub>	0.843	<b>6.30</b> <sub>1,6</sub>	<b>0.045</b>	0.30 <sub>1,6</sub>	0.599
Treatment × life history	na	na	0.44 <sub>2,6</sub>	0.445	0.01 <sub>2,6</sub>	0.986	0.54 <sub>2,6</sub>	0.605
Life history contrasts								
NS vs. FS	na	na	2.72 <sub>1,6</sub>	0.188	<b>14.30</b> <sub>1,6</sub>	<b>0.009</b>	4.24 <sub>1,6</sub>	0.085
NS vs. OS	na	na	1.43 <sub>1,6</sub>	0.276	<b>7.79</b> <sub>1,6</sub>	<b>0.031</b>	0.33 <sub>1,6</sub>	0.585
FS vs. OS	na	na	0.08 <sub>1,6</sub>	0.785	0.55 <sub>1,6</sub>	0.484	2.20 <sub>1,6</sub>	0.188

this to be the case, but only for the OS life history type (i.e., the root/shoot ratio was similar between NS and FS, but was about 2× higher for the OS than for the other life history types in both sun and shade). Again, this is consistent with the OS regeneration niche, because the OS recruit in shade and likely grow slowly for many years as juveniles until a fire removes the canopy. Survival of this first fire is key and likely represents a critical bottle neck in the transition from the juvenile to the adult stage. Greater relative allocation to roots may be critical for the OS to be able to resprout after this first fire. Selection for the FS life history type to resprout after fire is strong, but the circumstances are different for FS, for at least three reasons. First, the FS recruit after fire and, thus, will generally have decades to develop an extensive root system, a lignotuber, and reserves before the next fire (the fire return interval in southern California is 50–100 yr; Keeley, 2006). By contrast, an OS species recruits during a long fire-free interval and, thus, the time between seedling recruitment and a fire will be shorter for OS species (Keeley, 1992b). The second difference is recruitment in the sun (FS) versus the shade (OS). The FS species will be

less light-limited than OS species, and this, coupled with the long interval of growth before the next fire, means that they will have more resources (time and carbon) to develop enough belowground reserves to sprout after fire. A third factor is that OS do not allocate resources to root nodule formation and the metabolic demands of nitrogen fixation as FS and NS do.

Physiological differences among life history types in the sun and shade treatments were consistent with their regeneration niches. Consistent with open-canopy recruiting, electron transport rates in PSII were highest for the NS, intermediate for the FS, and lowest for the shade-recruiting OS. Shade tolerance of OS species was reflected in the lower rates of dark respiration and lower light compensation points for them than for the FS and NS life history types. Moreover, the lack of root nodules and nitrogen-fixing symbionts in the OS may have helped their carbon and energy budget, especially in the shade. Both the NS and FS form root nodules with Actinobacteria in the genus *Frankia*, and the shade treatment greatly reduced the nodule formation of these species, which suggests a carbon cost associated with the nodules. Other studies have also found a reduction

TABLE 7. Stomatal conductance ( $g_s$ ) and water use efficiency (WUE) for seedlings grown in full sun and shade (for description of data, see Table 1).

Life history and species	Sun $g_s$ max (mol m <sup>-2</sup> s <sup>-1</sup> )	Shade $g_s$ max (mol m <sup>-2</sup> s <sup>-1</sup> )	Sun WUE (μmol CO <sub>2</sub> mol H <sub>2</sub> O <sup>-1</sup> )	Shade WUE (μmol CO <sub>2</sub> mol H <sub>2</sub> O <sup>-1</sup> )
<b>Nonsprouter average</b>	<b>0.215<sup>A</sup></b> ( <b>0.040</b> )	<b>0.251<sup>A</sup></b> ( <b>0.033</b> )	<b>126<sup>A</sup></b> ( <b>16</b> )	<b>70<sup>A***</sup></b> ( <b>10</b> )
Subgenus <i>Cerastes</i>				
<i>Ceanothus megacarpus</i>	0.257 <sup>a</sup> (0.059)	0.316 <sup>a</sup> (0.086)	151 <sup>a</sup> (29)	49 <sup>a***</sup> (9)
<i>C. crassifolius</i>	0.254 <sup>a</sup> (0.037)	0.228 <sup>ab</sup> (0.037)	94 <sup>ab</sup> (4)	80 <sup>ab</sup> (6)
<i>C. cuneatus</i>	0.133 <sup>a</sup> (0.057)	0.209 <sup>ab</sup> (0.021)	134 <sup>a</sup> (26)	81 <sup>ab***</sup> (4)
<b>Facultative sprouter average</b>	<b>0.192<sup>A</sup></b> ( <b>0.009</b> )	<b>0.155<sup>B</sup></b> ( <b>0.029</b> )	<b>100<sup>A</sup></b> ( <b>1</b> )	<b>88<sup>A</sup></b> ( <b>4</b> )
Subgenus <i>Ceanothus</i>				
<i>C. spinosus</i>	0.207 <sup>a</sup> (0.045)	0.097 <sup>b</sup> (0.015)	104 <sup>ab</sup> (8)	97 <sup>ab</sup> (7)
<i>C. oliganthus</i>	0.194 <sup>a</sup> (0.038)	0.176 <sup>ab</sup> (0.027)	98 <sup>ab</sup> (5)	82 <sup>ab</sup> (4)
<i>C. leucodermis</i>	0.175 <sup>a</sup> (0.020)	0.191 <sup>ab</sup> (0.008)	99 <sup>ab</sup> (5)	83 <sup>ab</sup> (5)
<b>Obligate sprouter average</b>	<b>0.167<sup>A</sup></b> ( <b>0.026</b> )	<b>0.126<sup>B</sup></b> ( <b>0.026</b> )	<b>81<sup>A</sup></b> ( <b>8</b> )	<b>95<sup>A</sup></b> ( <b>10</b> )
<i>Rhamnus ilicifolia</i>	0.196 <sup>a</sup> (0.014)	0.142 <sup>a</sup> (0.012)	74 <sup>b</sup> (5)	85 <sup>ab</sup> (8)
<i>R. californica</i>	0.113 <sup>a</sup> (0.019)	0.074 <sup>b</sup> (0.017)	98 <sup>ab</sup> (11)	116 <sup>b</sup> (14)
<i>R. crocea</i>	0.191 <sup>a</sup> (0.019)	0.163 <sup>a</sup> (0.026)	72 <sup>b</sup> (4)	83 <sup>ab</sup> (9)

TABLE 8. Main effect and interaction ANOVA output for water-relationships-related parameters (for units and descriptive statistics, see Table 7).

Source of variation	$g_s$		WUE	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Life history	1.94 <sub>2,6</sub>	0.224	0.43 <sub>2,6</sub>	0.665
Treatment	0.74 <sub>1,6</sub>	0.420	4.09 <sub>1,6</sub>	0.089
Treatment × life history	2.28 <sub>2,6</sub>	0.181	<b>4.92<sub>2,6</sub></b>	<b>0.054</b>
Life history contrasts				
NS vs. FS	1.64 <sub>1,6</sub>	0.247	0.22 <sub>1,6</sub>	0.626
NS vs. OS	3.75 <sub>1,6</sub>	0.101	0.21 <sub>1,6</sub>	0.657
FS vs. OS	0.43 <sub>1,6</sub>	0.53	0.874 <sub>1,6</sub>	0.386

in nodule production when resources are limited (Burmeister and Van Auken, 1989; Pratt et al., 1997).

**Traits associated with growth and allocation differences**—It remains to be explained how FS species are able to allocate resources to storage while also achieving levels of biomass accumulation similar to those of NS species in the sun, and greater biomass in the shade. Ways in which the FS life history type could overcome the burden of carbon allocation to storage are by greater carbon assimilation rates, lower respiration rates, and/or allocation adjustments geared toward carbon acquisition or cheaper tissues; however, none of these alternatives fully explains our data. On the one hand, at the leaf level, there were some clear advantages for the FS. They had the greatest  $A_{net}$  on a per mass basis, suggesting the greatest carbon return per leaf carbon investment compared with the other life history types. In addition, SLA was greater for the FS, which indicates lower carbon investment per unit leaf area than in the NS. On the other hand, these leaf-level advantages did not lead to clear advantages at the whole-plant level. Although the  $A_{net}$  per mass rate was greater for the FS than for the NS (about 30% greater), the LWR was greatest for the NS (about 30% greater than the FS), which indicates that the NS were producing more photosynthetic leaf mass per unit of plant biomass, which would compensate for lower leaf-level rates. Moreover, LAR, an estimate of the photosynthesizing to respiring tissue (Hunt, 1978), was not different among life history types, and  $A_{net}$  per unit area was not different between the FS and NS. Root/shoot ratios were not different between FS and NS, and neither were  $R_d$  of leaves or xylem density. Thus, allocation patterns, photosynthetic traits, and tissue investments do not fully explain growth patterns.

We suggest that differences in stress tolerance and the costs associated with achieving greater levels of stress tolerance explain the observed differences in growth. The FS achieve greater levels of biomass production by allocating fewer resources to stress tolerance, as indicated by the negative association between stress tolerance traits and biomass accumulation. This analysis used data from two previous studies that analyzed mortality and water relations of seedlings grown in the same common garden used in the present study (Pratt et al., 2008, 2010). Adults and seedlings of the NS life history type are more water-stress-resistant and -tolerant than the FS, in the form of greater xylem cavitation resistance and greater survival of highly negative water potentials during a dehydration experiment (Pratt et al., 2007, 2008). Species that inhabit more stressful environments generally have lower growth rates than species from more productive environments (Grime, 1979; Chapin et al., 1993). For instance, there could be metabolic costs associated with osmotic adjustment, photoprotection, scavenging free

radicals, and production of dehydrin and heat shock proteins. In keeping with this principle, although NS and FS life history types co-occur, the two life history types tend to segregate into different niches, with the NS typically occupying more arid, and thus high-stress, microsites (Ackerly, 2004). Presumably, these costs are constitutive and not very plastic, as suggested by the poor growth of NS in the shade.

A previous study postulated a tradeoff between water stress resistance and carbon gain between NS and resprouters (FS and OS), with NS having greater water stress resistance (lower SLA and greater water use efficiency) than sprouters (Paula and Pausas, 2006). Our results do not support this tradeoff, in that NS simultaneously have greater water-stress resistance and greater or comparable carbon assimilation rates (see also Hernández et al., 2011).

We predicted that the NS would outgrow the OS, yet the two did not differ in growth. Moreover, the assimilation and allocation data point to some clear advantages for the NS over the OS. For example, the NS had greater  $A_{net}$  per unit area than the OS. The LAR did not differ between the two life history types, so this combination of traits might be expected to translate into greater growth for the NS. We suggest that differential stress tolerance and costs associated with bacterial symbiosis may explain why these two life history types did not differ in growth. The NS had greater survival following a water stress treatment in full sun than the OS (Pratt et al., 2008), and achieving a greater level of survival may require resources that would otherwise support growth. Another possibility is that costs associated with making and maintaining root nodules reduced growth in NS *Ceanothus* spp., whereas the OS *Rhamnus* spp. did not bear this cost because they do not nodulate.

Nodule biomass was not correlated with leaf-level or canopy-level nitrogen content, which was predicted. One caveat to our analysis is that we did not measure nitrogen content of stems or roots. Nodule biomass was positively associated with plant biomass, which indicates that bigger plants produced more nodules. In addition, nodule mass for a species grown in the sun was correlated with nodule biomass in the shade, which indicates that nodule production was a species-specific response that did not interact with the shade treatment.

#### **Life history type tradeoffs: Beyond allocation to sprouting**

In many cases, NS life history types have evolved from a sprouting ancestor (Wells, 1969), and the factors that favor the evolution of NS from a sprouting ancestor are of great interest (Keeley and Zedler, 1978; Bond and Midgley, 2001; Ojeda et al., 2005). One hypothesis posits that a key advantage of NS is greater growth, height, and competitive ability made possible by the loss of sprouting (Midgley, 1996; Bellingham and Sparrow, 2000; Pratt et al., 2007). Some studies, including the present one, have not found support for this hypothesis (Knox and Clarke, 2005; Schwilk and Ackerly, 2005; Chew and Bonser, 2009). However, we cannot rule out that the initial evolutionary advantage for NS was greater competitive ability but that it was subsequently lost over the course of evolution (Pratt et al., 2007). This raises an important caveat to the present study: all the species within a given life history type are also from well-supported monophyletic clades (Burge et al., 2011). Thus, we cannot rule out phylogenetic effects on our analyses (also see discussion in Pratt et al., 2007).

Another hypothesis is that NS have more resources to allocate toward reproduction (Bond and van Wilgen, 1996). At the

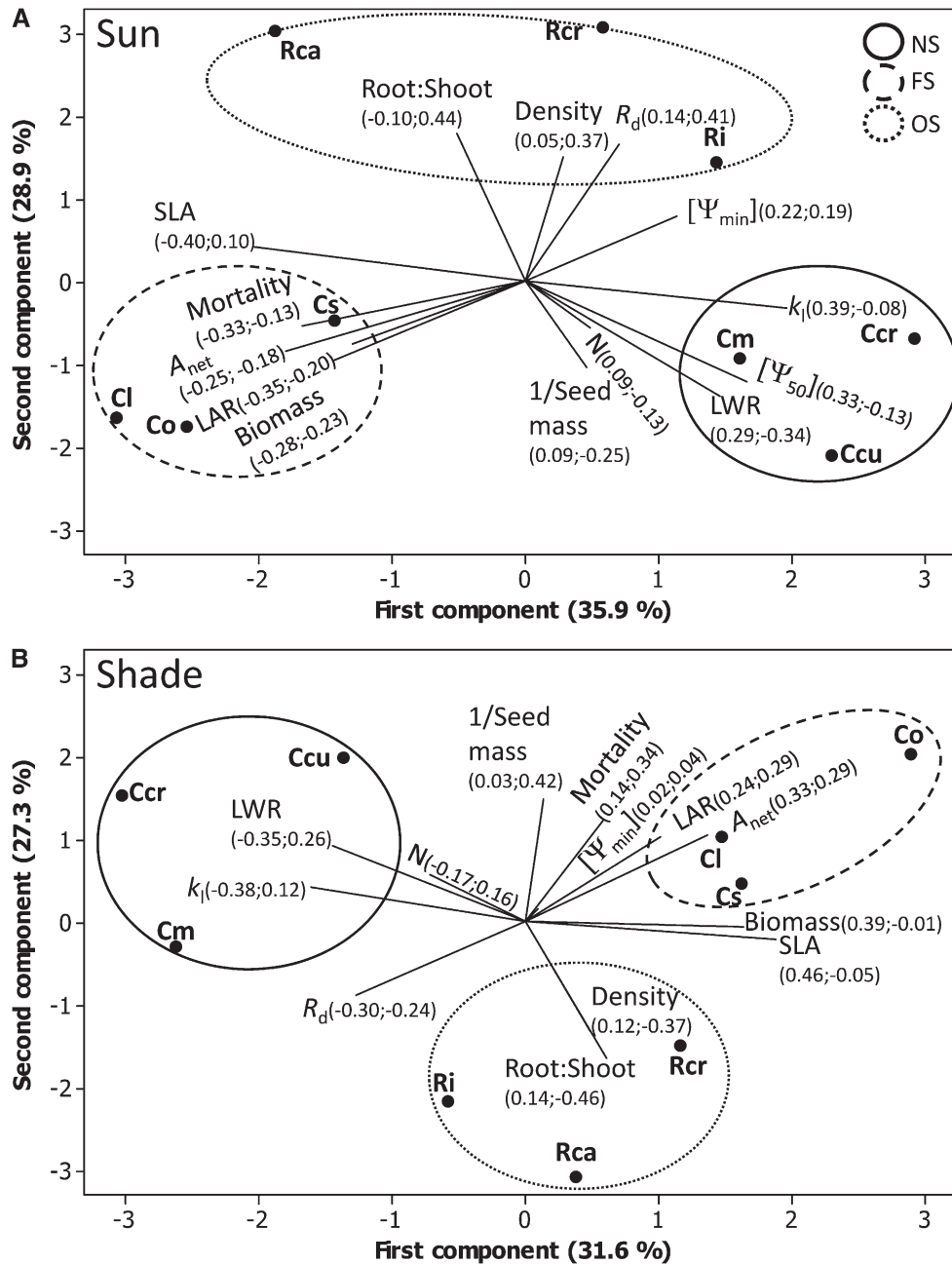


Fig. 2. Principal component analysis summary of traits related to biomass production and life history types (see Tables 1, 3, and 5 for abbreviations) grown in (A) full sun and (B) shade. Among the traits, assimilation and N (leaf nitrogen) are on a per mass basis,  $[\Psi_{50}]$  is the absolute value for water potential at 50% loss of hydraulic conductivity of stems and roots averaged (Pratt et al., 2008),  $[\Psi_{min}]$  is the absolute value for minimum water potential recorded during a water-stress treatment (Pratt et al., 2008),  $k_1$  is whole-plant hydraulic conductance (Pratt et al., 2010), “mortality” refers to percentage water-stress-induced mortality (Pratt et al., 2008), and “density” refers to xylem density. Closed symbols represent component scores for each species. To see the loadings for the different traits simultaneously with the scores for each species, the trait values were scaled. The values in parentheses are the unscaled principal component scores for each trait.

1-year-old seedling stage examined here, chaparral shrubs generally either do not flower or produce very few flowers. Schwilk and Ackerly (2005) found that NS mature earlier than FS; however, we did not find this to be the case and it seems unlikely that this trait would be general among NS chaparral species, because selection for it may be weak. Selection for early reproduction would be strong if the disturbance (fire) interval was short, but historically in southern California, chaparral fire is unlikely to

return in the first two decades following a fire (Keeley, 2006); however, this is changing as a result of anthropogenic ignitions. There could be selection for early maturation if fecundity declines with age, but this is not the case in chaparral, and very old stands generally produce robust seed crops (Keeley and Keeley, 1977; Zammit and Zedler, 1992; Luo et al., 2007). It is possible that reproduction differences among life history types manifest at a later stage of development; however, studies comparing

reproduction (typically seed production) of NS and FS chaparral shrubs have found mixed evidence for an NS reproductive advantage (Keeley, 2000). By contrast, this tradeoff appears to be at work in other Mediterranean-type ecosystems (see Bond and van Wilgen, 1996, and references therein). We hypothesize that selection in the chaparral may be more strongly driven by the inevitable and protracted summer rainless period and the need to tolerate the stresses this brings (Cowling et al., 2005). Thus, resources of NS are not necessarily allocated to growth or reproduction, and instead allocation of greater resources to achieving greater levels of stress tolerance may be a key factor in the evolution of the chaparral NS life history type. This model is consistent with a general tradeoff between adult longevity, exemplified by the OS, and seedling survival, which is key for NS.

Although the NS species and the FS species studied here are in the same genus and presently co-occur, they form two well-supported monophyletic clades that diverged ~13 mya (Burge et al., 2011). Since splitting, species in the clade that contains the NS taxa (subgenus *Cerastes*) have come to occupy generally more arid microsites (at least in foothill regions of southern California) and have evolved a suite of traits consistent with water-stress resistance such as low SLA, high xylem cavitation resistance to water stress, and stomatal crypts (Cooper, 1922; Davis et al., 1999; Meentemeyer and Moody, 2002; Pratt et al., 2007, 2008). By contrast, FS species in the subgenus *Ceanothus* have come to occupy more mesic sites and are less resistant to water stress (Ackerly et al., 2006; Jacobsen et al., 2007; Pratt et al., 2007, 2008). Such differences are important for understanding tradeoffs between different life history types, and the evolution of greater stress tolerance is likely a key trait that enhances seedling survival (Pratt et al., 2008) but that also comes at the cost of reduced growth.

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