Is there a cost to resprouting?
Seedling growth rate and drought tolerance in sprouting and nonsprouting Ceanothus (Rhamnaceae)[1]

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Many woody plant species that depend upon fire-cued seed germination lack the ability to resprout. As the ability to resprout is widely assumed to be the ancestral condition in most plant groups, the failure to sprout is an evolutionary derived trait. Models for the evolutionary loss of sprouting assume a trade-off between seedling success and vegetative resprouting ability of adults. Such models require higher seedling success rates in nonsprouters than in sprouters. On the other hand, there seem to be few *a priori* reasons why a strong sprouter might not also have highly competitive post-fire seedlings. To test the hypothesis that nonsprouting plants have higher growth rates and/or drought survival, we grew seedlings of *Ceanothus tomentosus* from sprouting and nonsprouting populations in a common garden experiment. Each of these *C. tomentosus* populations was paired with a sympatric *Ceanothus* species that differed in resprouting ability. Sprouters exhibited greater allocation to root carbohydrate storage than did nonsprouters, but overall relative growth rates did not differ. Nonsprouters had earlier onset of flowering. These results provide mixed support for models of a sprouting/nonsprouting allocation trade-off.

Key words: allocation; carbon storage; fire; iteroparity; nonsprouters; sprouters.

Some woody species that are dependent upon fire to cue seed germination have apparently lost the ability to resprout following fire. The ability to resprout is widely assumed to be the ancestral condition in most plant groups, whereas loss of ability to resprout is the derived condition (Wells, 1969; Bond and Midgley, 2003). The loss of resprouting represents a significant demographic cost, as adults are killed by fire. Theoretical models for the evolution of nonsprouting (analogous to the evolution of semelparity from iteroparity) require some demographic advantage to offset this cost (Charnov and Shaffer, 1973; Bond and van Wilgen, 1996). The relative fitness of a resprouting life history has been modelled as a trade-off between sexual and vegetative allocation (Keeley and Zedler, 1977; Hilbert, 1987; Bellingham, 2000), and has often been assumed to reflect a cost associated with allocation of resources to storage (Bond and Midgley, 2001).

The hypothesized allocation cost associated with investing in resprouting structures could manifest at different points in the plant's life cycle. Studies in Australia have found greater root starch storage in sprouter adults than in nonsprouters, but higher growth rates among nonsprouters (Pate et al., 1990; Bell and Pate, 1996; Bell and Ojeda, 1999; Bell, 2001). The evidence for fecundity differences, however, is mixed. Some studies have found either no fecundity differences or greater yearly fecundity for sprouters: e.g., South African *Erica* (Bell and Ojeda, 1999), Australian *Banksia* and *Leucospermum* (Lamont, 1985; Zammit and Westoby, 1987), and California *Arctostaphylos* (Keeley, 1977; Keeley and Zedler, 1977; Kelly and

Parker, 1990) and *Ceanothus* (S. Davis, Pepperdine University, personal communication). Other studies, however, have found allocation differences, suggesting a fecundity trade-off with higher fecundity in nonsprouters: e.g., *Ceanothus* (Keeley, 1977; Carpenter and Recher, 1979) and *Hakea* (Enright and Goldblum, 1999).

The lack of a clear tradeoff between resprouting ability and fecundity has prompted some researches to investigate seedling survival differences between sprouters and nonsprouters. Empirical evidence of greater seedling drought survival among nonsprouters (Frazer and Davis, 1988; Thomas and Davis, 1989; Pratt et al., 1997; Williams et al., 1997) suggests that a sprouter vs. nonsprouter trade-off may result from differential seedling competitive ability, especially during drought. Allocation tradeoffs could lead to competitive differences between seedlings of sprouters and nonsprouters only if allocation differences appear early in ontogeny. Although the field studies cited earlier suggest a differential seedling growth and survivorship between sprouters and nonsprouters, it is difficult to explain why a seedling from a sprouter species should necessarily be a poorer performer, especially if the resprouter seedling begins allocating resources to underground carbohydrate storage only after the difficult establishment stage is accomplished.

Unlike fire-surviving sprouters, which invest in thick bark or underground storage organs, nonsprouters depend completely upon seedling regeneration following fire. There is reason to believe that competitive differences among chaparral species might result from different seedling growth rates and/or drought tolerance. Shallow-rooted seedlings are especially vulnerable to water stress during the summer drought (Kummerow et al., 1981; Poole et al., 1981; Williams et al., 1997; Davis et al., 1998), and selective pressures may be greater during the first summer drought after wildfire than at any other stage (Keeley and Keeley, 1977; Frazer and Davis, 1988; Williams et al., 1997). Some evidence suggests that species within the genus *Ceanothus* exhibit consistent differences in xylem vulnerability; species in the exclusively nonsprouting clade,

TABLE 1.   California collection sites for all populations of *Ceanothus* species. Seeds were collected from 10–30 mothers per site. Annual precipitation estimates from Daymet (Thornton et al., 1997, http://www.daymet.org) are shown with ±1 SD.

Site	Sprouter	Nonsprouter	County	Location	Mean annual precip (cm)
Northern	*C. tomentosus*	*C. cuneatus*	Mariposa	37°40.719′ N, 119°59.227′ W	94.0 ± 41.1
Southern	*C. leucodermis*	*C. tomentosus*	San Diego	33°25.360′ N, 117°05.061′ W	40.6 ± 17.3

subgenus *Cerastes*, have shallower roots and more resistant xylem than do members of subgenus *Ceanothus* (Davis et al., 1999).

Because direct evidence of a trade-off between seed production and resprouting ability is mixed, we investigate the possibility that early seedling drought tolerance may provide a sprouter/nonsprouter demographic trade-off. The extensive field studies of Pate et al. (1990, 1991), Bell and Pate (1996), and Bell and Ojeda (1999) have revealed striking differences between sprouter and nonsprouter root : shoot allocation. Differences among study site environmental conditions, however, can confound field comparisons of sprouters and nonsprouters from different locations. To our knowledge, only one study has compared sprouter and nonsprouter growth in a common garden; Jaks (1984) compared a single species each from two different genera. No study has investigated the relationship between resprouting, growth rate, and drought tolerance in chaparral plants in a controlled garden experiment, nor has any study attempted an experimental design with both environmental and phylogenetic controls.

One difficulty with cross-species comparisons is finding closely related taxa that differ in the trait of interest. The chaparral genus *Ceanothus* contains both resprouting and nonsprouting species, and many chaparral communities have more than one species of *Ceanothus*. Sprouter–nonsprouter pairs within a community have been used for comparisons in ecological studies (e.g., Keeley, 1977; Davis et al., 1998). Such comparisons, however, are weakened by the phylogenetic distance between the resprouting and nonsprouting species—a species pair usually contains members of two distinct clades within the genus. These two well-supported clades (Hardig et al., 2000) have consistent morphological differences as well as differences in resprouting ability: subgenus *Cerastes* is comprised of only nonsprouting species, and subgenus *Ceanothus* contains mostly resprouting species and several nonsprouters (McMinn, 1939).

In our study, we compare growth rates and non-structural carbohydrate storage of sprouting and nonsprouting *Ceanothus* taxa during the first summer drought following germination, controlling for both source environment and phylogeny. Although our study was not designed to test for fecundity tradeoffs, we also measured time to first flowering as a rough estimate of early reproductive effort. *Ceanothus tomentosus* C. Parry is an excellent study organism for investigating the relationship between seedling traits and resprouting ability because the species includes both sprouting and nonsprouting populations. Northern California populations resprout (D. Schwilk, personal observation; McMinn, 1939), whereas disjunct southern California populations are nonsprouters (J. Keeley, USGS Sequoia Kings Canyon National Park, personal communication; D. Schwilk, personal observation). This study compared seedlings from both populations grown in a common garden. The paired population approach provides a phylogenetic control to this experiment. However, because several

hundred miles separate these populations, it would be useful to have a community or environment control as well. To control for different native environments, the experiment included additional *Ceanothus* species; collected at each of the *C. tomentosus* collection sites, with contrasting sprouting behavior. A nonsprouting *Ceanothus* species was collected from the northern California site, and a resprouting species was collected from the southern California site (Table 1).

In addition to being the first intraspecific test of resprouting behavior on growth rate, this experiment allows us to test resprouting behavior and site of origin as separate effects on allocation and relative growth rates. We address the question, Does the hypothesized trade-off between resprouting ability and seedling survival manifest as a difference in the relative growth rates of seedlings? If so, are such differences dependent upon water availability? We predict that sprouters should exhibit greater relative growth rates of roots and increased carbohydrate storage. As a result, nonsprouters should have higher above-ground growth rates and greater relative growth rates than sprouters.

MATERIALS AND METHODS

Seed collection—We identified two sites for seed collection based on the species-selection criteria in the introduction. At the northern California site, resprouter *C. tomentosus* grew alongside nonsprouter *C. cuneatus* (Hook.) Nutt. The southern site provided nonsprouter *C. tomentosus* and sprouter *C. leucodermis* E. Greene (Table 1). All except *C. cuneatus* are members of the subgenus *Ceanothus* clade. This design provides two sprouter–nonsprouter comparisons within subgenus *Ceanothus*; one between the two *C. tomentosus* populations and the other between the sympatric Southern California *C. tomentosus* and *C. leucodermis* populations. Seeds were collected during June–July 1999 from 10–30 parent plants per population at each site. Seeds were randomly assigned to treatments and harvest blocks while evenly representing all mother plants.

Experimental design—The main experiment took place on the Stanford University campus (37°25.9′ N, 122°11.0′ W), Stanford, California, during February–November 2000, with limited measurements through May 2002. The experimental design was a blocked array of 432 plants (4 populations × 3 water treatments × 12 replicates × 3 harvests). Seeds from the four populations of plants were subjected to a heat treatment (60 s submersion in boiling water) followed by a 2-mo cold treatment, then germinated in flats. There were no differences in germination rates among the populations. After 2 wk in the greenhouse, the plants were transplanted into growing containers, which consisted of upright sections of PVC pipe (95 cm long × 20 cm diameter) that were fitted with a PVC cap at the bottom. The cap contained 10–15 1-cm-diameter holes to allow drainage. The tubes were filled to within 1 cm of the top with a 3 : 1 mixture of topsoil and sand on top of 4 cm of coarse gravel. The soil column was mechanically compacted to prevent settling after planting.

Because the germination of our different populations was synchronized, the seedlings germinated later in the year than they would in the field. The water treatments allowed us to extend the spring rains artificially; we then extended the drought with rainouts. The plants were fertilized once soon after establishment in the PVC tubes with 600 mL of 20–20–20 (N-P-K) solution (100

ppm N). The water treatments were applied through a drip irrigation system with separate pressure regulators for each of three randomized blocks. Within each block, the three treatments were applied using pressure-compensating drip emitters of different capacities, such that the water applied per unit time in the high water treatment was twice that of the medium water treatment, which in turn was twice that of the low water treatment. A removable rainout system of clear greenhouse plastic over a wire frame (Tufflite IV, Armin Plastics, 18901 E. Railroad St., City Of Industry, California, USA) allowed us to prevent any ambient precipitation from reaching the experimental plants, but it was deployed only when rain threatened. Throughout the season, the water levels were adjusted in tandem in an attempt to keep the soil in the low water treatment as dry as possible without killing the plants. Plants were watered every day through May, then once a week, then once every 2 wk. Beginning in July, all watering ceased and the rainouts were used when necessary through the fall to impose a complete drought. The total water additions through the spring extension (20 April–30 June) were 5, 10, and 20 cm for the low, medium, and high water treatments, respectively.

We measured soil moisture in 48 growing tubes using time domain reflectometry (TDR; Topp et al., 1980). These measurements were made along a pair of vertically oriented stainless steel waveguides that extended to depths of 60 cm. We used preexisting calibration curves for sandstone soil (J. Dukes, personal communication; but see Field et al., 1997) to convert readings from a cable tester (Tektronix 1502C, Beaverton, Oregon, USA) to estimates of soil volumetric water content.

Nondestructive measurements—We took a suite of nondestructive measurements at three times during the season: 16–18 May (census 1), 19–20 June (census 2), and 10–11 August (census 3). Measurements included: basal stem diameter, length of the main stem, number of leaves on the main stem, number of leaves on other branches, and length and width of three mature leaves.

Harvests—Two harvests of 144 plants each were conducted at the beginning and end of the summer drought: 17–23 July (harvest 1) and 13–20 October (harvest 2). These harvests provided the biomass estimates for relative growth analysis. Predawn water potential of each plant was measured with a pressure bomb apparatus (Soilmoisture Equipment, Goleta, California, USA) before harvesting. Aboveground biomass was divided into separate categories: leaves, main stem, and auxiliary stems. The soil column was removed intact and separated into three depth sections: 0–30 cm, 30–60 cm, and 60–90 cm. Roots were separated from soil by washing. Root biomass was measured separately for each depth range.

The final 144 plants were allowed to grow until mid-November with no additional water. At this time, stem and root samples were collected from 36 plants for analysis of total nonstructural carbohydrates. Collected tissue was immediately frozen in liquid nitrogen, and carbohydrate content was analyzed according to da Silveira et al. (1978). After the collections for total nonstructural carbohydrates were completed, the rainouts were removed and the remaining plants were allowed to continue growing under natural rainfall.

Time to first flowering—The remaining 108 plants were allowed to grow under ambient rainfall through May 2002. As a coarse measure of early reproductive output, plants that flowered in the third growing season (spring 2002) were recorded. Due to poor pollination and high seed abortion rates, seed production was very low and was not measured

Analysis—Multiple regression of the census 1 measurements against the harvest 1 biomass measurements allowed us to estimate time $t = 0$ biomass for those plants not harvested until the second harvest. We produced a separate regression model for each population and for aboveground (stem) and belowground biomass, resulting in eight linear models with stem diameter and length having the strongest weight in all models (model slopes were not homogenous among species). These models were used only for predicting biomass and the time of harvest 1. Growth analysis was then carried out by comparing the measured harvest 2 data with the estimated biomass of these plants at the first harvest. Abscised leaves were impossible to collect in this
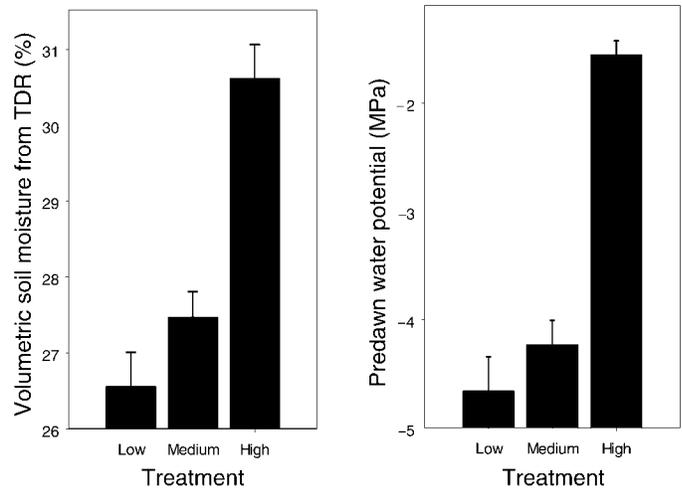

Fig. 1. Effects of treatment on soil water content (estimated using time domain reflectometry) and predawn water potential in *Ceanothus* at the first harvest (June 2000), averaged across all populations. Error bars indicate standard errors.

outdoor experiment. Therefore, the relative growth rate analysis uses total stem biomass in place of total above-ground biomass.

Our experimental design allowed analysis by three-way ANOVA with the factors resprouting behavior (two levels), site (two levels), and water treatment (three levels). To investigate covariance relationships within our data, we compared standardized major axis (SMA) slopes, calculated according to Warton and Weber (2002) using a likelihood ratio method. Homogeneity of slopes was determined by permutation testing using the (S)MAT software by Daniel S. Falster, David I. Warton, and Ian J. Wright (available at http://www.bio.mq.edu.au/ecology/SMATR). For homogeneous slopes, differences in elevation were tested by Model II ANCOVA (ANOVA after rotating x and y around the SMA).

RESULTS

Water treatments had significant effects on soil moisture as measured by TDR and on predawn water potential (Fig. 1), but no difference in water potential was found among populations. Across all populations, sprouters had higher final root shoot ratios than did nonsprouters. Sprouters and nonsprouters had homogenous slopes (SMA slope = 1.195, r^2 = 3.341). For a given total aboveground biomass, sprouters had greater root allocation (Fig. 2) indicated by significant differences in elevation (df = 1, F = 14.42, $P < 0.001$).

Estimation of harvest 1 biomass—Three nondestructive measurements were significant in all eight linear models created to estimate the initial biomass: basal stem diameter, stem length, and number of leaves on main stem. For each model, r^2 values ranged from 0.72 to 0.89 (Table 2).

Growth analysis—Site had a significant effect on initial biomass (the southern California populations had higher initial biomass, $P < 0.001$), but resprouting behavior had no effect. The final biomass of the southern California populations was also higher than that of the northern populations, but not significantly.

Relative growth rate was dependent on site and treatment (Table 3). Northern California plants had higher relative growth rates than did southern plants, and greater water availability resulted in higher relative growth rates (Fig. 3). Al-
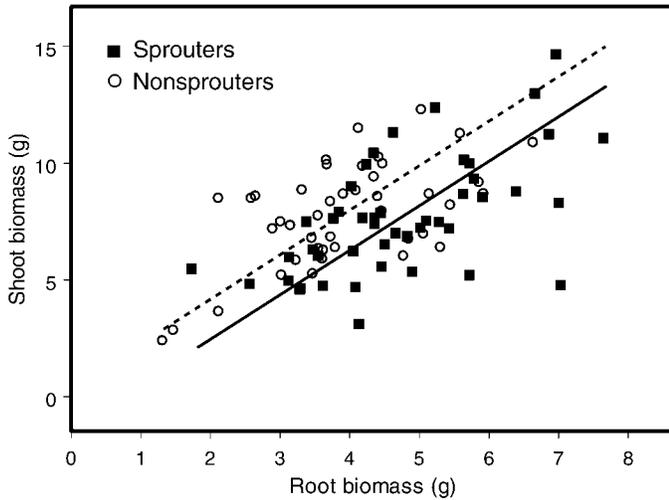
Fig. 2. Shoot vs. root biomass in *Ceanothus* for sprouters (closed squares) and nonsprouters (open circles). SMA slopes were homogeneous (slope = 1.907, r^2 = 3.34, 3.341). Lines show common slope relationship through group bivariate means. Model II ANCOVA showed a significant effect of resprouting behavior (df = 1, F = 14.42, $P < 0.001$).

though overall growth rates did not differ between sprouters and nonsprouters, sprouters showed a greater relative belowground growth rate for the same aboveground growth rate (Fig. 4). SMA slopes were homogeneous (slope = 1.118, sprouters r^2 = 0.064, nonsprouters r^2 = 0.82) and there was a significant effect of resprouting behavior, (df = 1, F = 6.45, P = 0.013).

Nonstructural carbohydrates—Resprouters stored more carbohydrates in root tissue than did nonsprouters. A three-way ANOVA revealed a significant effect of resprouting behavior on percentage nonstructural carbohydrates in roots (Table 4, Fig. 5). This effect showed an interaction with treatment: in medium and high water treatments, sprouters had significantly higher levels of nonstructural carbohydrates in their roots. No pattern to stem carbohydrate levels emerged.

The effect of resprouting on nonstructural carbohydrates was most pronounced in the comparison of the two *C. tomentosus* populations, indicating a significant difference despite a presumably recent divergence (Fig. 5). The significant difference between the southern populations indicates an effect within subgenus *Ceanothus* under common conditions. Because the site effect remains relatively constant at just under 1% (Fig. 5), the difference in carbohydrate levels between the two *C. tomentosus* populations indicates the influence of some other factor. The significant resprouting by treatment interac-

TABLE 2. The r^2 values for models to estimate biomass of *Ceanothus* species. Independent variables in the regression were stem diameter, stem length, and number of leaves on main stem. These models were used to estimate the initial biomass for the plants harvested at the second harvest.

Population	Root biomass	Stem biomass
C. tomentosus (North)	0.87	0.83
C. tomentosus (South)	0.84	0.80
C. cuneatus	0.89	0.72
C. leucodermis	0.80	0.81

TABLE 3. Effect of resprouting behavior (R), site (S), and water treatment (T) on aboveground (stem) and belowground relative growth rates (ln) of *Ceanothus* species.

Factor	Degrees of freedom	Mean square		Pr(F)	
		Root	Stem	Root	Stem
R	1	0.151	0.0007	0.241	0.956
S	1	0.717	0.901	0.0121	0.0457
T	2	2.092	2.99	0.0002	0.0016
R × S	1	0.110	0.022	0.316	0.751
R × T	2	0.109	0.070	0.606	0.854
S × T	2	0.234	0.139	0.344	0.731
R × S × T	2	0.438	0.409	0.18	0.161
Residual	132	0.108	0.0221		

tion term reveals that the effect of resprouting was strongest among the medium and high water treatment plants.

Reproductive output in third growing season—Significantly more nonsprouter than sprouter *C. tomentosus* flowered in spring of 2002 (*G* test, *G* = 6.3, *P* < 0.025, Table 5). The other two species displayed almost no second-year flowering. Southern *C. tomentosus* plants showed a slight trend to flower earlier in the season, but multiple censuses throughout the spring ensured that differences in within-season timing did not bias the enumeration of flowering individuals.

DISCUSSION

This study is the first to detect an effect of resprouting strategy on carbohydrate storage in an intraspecific comparison. Although this study did not reveal the hypothesized trade-off between resprouting ability and seedling growth rate, it did reveal several differences in relative allocation to roots and shoots between sprouters and nonsprouters (Fig. 2). These differences do not suggest any poorer seedling performance in the resprouting populations, however. Sprouters, in fact, had similar overall growth rates to nonsprouters, but had higher root carbohydrate levels.

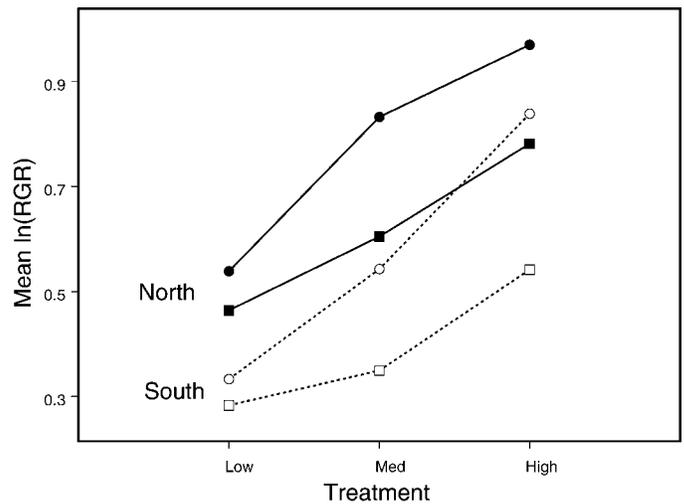The high chaparral seedling mortality documented during

Fig. 3. Mean aboveground (circles) and belowground (squares) relative growth rates (RGR, both as natural log) for *Ceanothus* in northern California (solid lines, closed symbols) and southern California (dashed lines, open symbols).
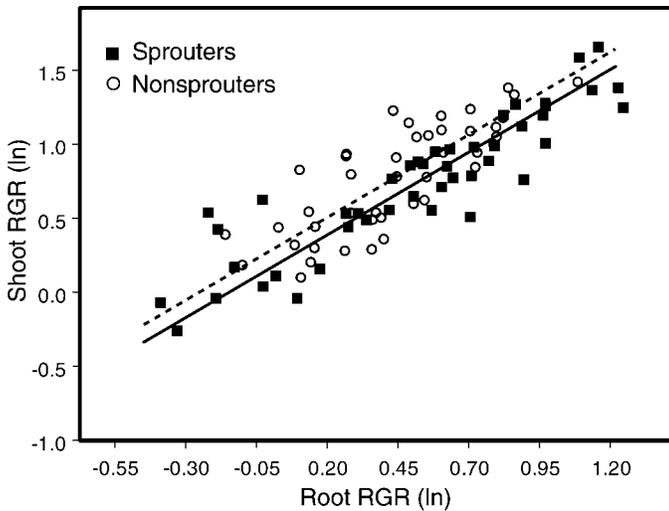
Fig. 4. Aboveground (shoot) vs. belowground relative growth rates (RGR, both as natural log) of sprouting and nonsprouting *Ceanothus*. SMA slopes are homogeneous (slope = 1.118, r^2 = 0.64, 0.82) and elevation of the relationships is significantly different (df = 1, F = 6.45, P = 0.013). Lines show common slope relationship through group bivariate means. Negative growth rates generally resulted from leaf loss and shoot dieback.
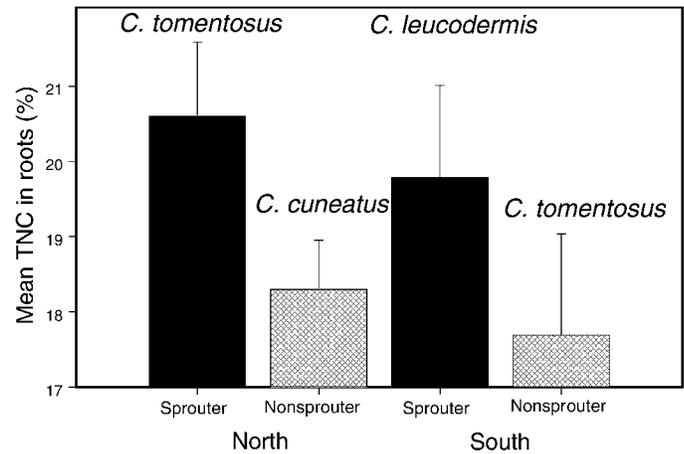

Fig. 5. Proportion of total non-structural carbohydrates in roots from four *Ceanothus* populations in northern and southern California. Error bars indicate standard errors.

the summer drought (Frazer and Davis, 1988; Davis et al., 1998) suggests that differences in first-season growth might explain a sprouter vs. nonsprouter trade-off. No such differences are evident from this study, however. Drought treatments in this study were not as severe as the drought experienced by seedlings under natural conditions: only the low water treatment plants reached predawn water potentials as negative as those measured in *Ceanothus* in nature (Davis et al., 1998, 1999, 2002), and mortality in the field is much higher than in our experiment. Additionally, growth rate as measured in this experiment may not be an adequate proxy for seedling survival and performance. Even if seedlings survive by tolerating drought with little growth, however, these shrubs' long-term survival depends upon sinking roots deep enough to sustain tolerable water potentials through subsequent droughts. Those seedlings with more extensive roots should be best positioned to take advantage of the winter rain when it arrives.

Differential storage of nonstructural carbohydrates in roots proved to be the most striking difference between sprouter and nonsprouter populations. This difference was significant among the two *C. tomentosus* populations, and the difference in carbohydrate storage between the two southern California populations, *C. leucodermis* and *C. tomentosus*, demonstrates

the same effect between co-occuring species in the same subgenus. Presumably, carbohydrate storage in roots provides the reserves necessary for resprouting after fire (Bowen and Pate, 1993). Greater starch storage in adults of resprouting species has been reported for Western Australian Proteaceae (Pate et al., 1990), Epacridaceae (Bell and Pate, 1996), and Restionaceae (Pate et al., 1991), and for South African *Erica* spp. (Bell and Ojeda, 1999). When such studies have investigated seedlings, significantly higher root carbohydrate storage has been found even in first-year seedlings of resprouting species (Pate et al., 1990; Bell and Pate, 1996). If sprouters maintain higher carbon allocation to roots, reduced above-ground investment should result. No difference in aboveground or total growth was detected in this study, however.

Although this study was not designed to test fecundity differences, the earlier onset of flowering in nonsprouter populations of *C. tomentosus* relative to sprouter populations (Table 5) suggests that nonsprouters may be allocating carbon to early reproduction rather than root carbohydrate storage. The net effect of these two allocation strategies may result in no difference in growth rates between sprouters and nonsprouters, yet still represent a sprouter vs. nonsprouter trade-off between sexual and vegetative reproduction.

Differential carbon allocation is not the only possible explanation for the evolutionary loss of resprouting. Wiens et al. (1989a, b) have suggested that long-lived plants may accumulate somatic mutations that manifest in greater seed abortion and perhaps reduced seedling fitness. Meney et al. (1997) found higher seed abortion rates among resprouting monocots, and recent work by Steve Davis and students (S. Davis, Pep-

TABLE 4. Effect of resprouting behavior (R), site (S), and water treatment (T) on total nonstructural carbohydrates in root tissue of *Ceanothus* species.

Factor	Degrees of freedom	Mean square	F-Value	Pr(F)
R	1	43.61	5.156	0.031
S	1	4.56	0.539	0.469
T	2	3.40	0.805	0.377
R × S	1	0.093	0.011	0.917
R × T	2	28.33	6.698	0.015
S × T	2	6.56	1.556	0.223
R × S × T	2	10.29	2.43	0.130
Residual	132	1.79	8.458	

TABLE 5. Number of *Ceanothus* plants in each population that flowered in the second season. Significantly more nonsprouter *C. tomentosus* individuals flowered than did plants from the sprouter population (*G* test, G = 6.3, P < 0.025).

	Sprouters		Nonsprouters	
	C. tomentosus	*C. leucodermis*	*C. tomentosus*	*C. cuneatus*
Flowering	5	0	15	1
Not flowering	16	26	10	25
Total alive in third season (of 27)	21	26	25	26

perdine University, personal communication) suggests that resprouting chaparral shrubs may have much higher rates of spontaneous seed abortion than the nonsprouting species. This difference is hypothesized to result from accumulated somatic mutations in the long-lived resprouters. Our own preliminary measurements of seed abortion in *C. tomentosus*, however, revealed no difference in abortion rates between the northern and southern populations, although the northern (resprouting) population had higher rates of predation by parasitic wasps (unpublished data).

Another possible nonallocation difference between sprouters and nonsprouters is that nonsprouters have on average shorter generation times and potentially increased rates of evolution. In a changing environment, lineages with short generation times may have an advantage (e.g., Schwilk and Kerr, 2002). Short generation time has been proposed as an explanation for the seemingly high rates of speciation in nonsprouting lineages (Wells, 1969), although recent investigation has found mixed support for this diversification hypothesis (Bond and Midgley, 2003). To what extent a changing environment might select for reduced generation time is unknown. Even during periods of rapid climate change, migration might buffer plants from experiencing severely changing selective pressures (Ackerly, 2003).

This experiment is the first to examine intraspecific variation in resprouting behavior. Although no differences in overall growth rate were detected, the results generally support the findings of previous interspecific studies, in which sprouters exhibit greater carbohydrate storage, and suggest a trade-off between sexual and vegetative reproduction.

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