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SOIL HETEROGENEITY AND PLANT COMPETITION IN AN ANNUAL GRASSLAND

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Abstract. Variation in competitive ability due to variation in soil characteristics is one possible mechanism allowing the local coexistence of plant species. We measured soil water, depth, and nitrogen pools and fluxes in distinct patches of three serpentine grassland species to determine whether soil heterogeneity existed and was correlated with plant species abundance. Through experimental manipulation of species' abundances, we also examined the relative importance of inherent site characteristics vs. plant species' effects in generating heterogeneity in the measured soil characteristics; and measured species' competitive abilities in different patch types. The three common grassland annuals, *Calycadenia multiglandulosum, Plantago erecta,* and *Lasthenia californica,* were segregated with respect to the measured soil characteristics. Differences in soil water, soil depth, soil microbial nitrogen, and soil carbon to nitrogen ratio were due to inherent site characteristics, while differences in nitrate availability were strongly affected by the identity of the species currently growing in a soil patch. Furthermore, all species performed significantly better against one other species in the patch type where they are normally most abundant. These results demonstrate that species diversity within this grassland contributes to soil heterogeneity and suggest that soil heterogeneity could contribute to the coexistence of these species.

Key words: California grassland; Calycadenia multiglandulosum; Lasthenia californica; *plant coexistence and competition;* Plantago erecta; *soil characteristics; soil heterogeneity; species diversity.*

INTRODUCTION

Field experiments have established that moderate to strong competition between plants exists in a wide variety of natural communities (Connell 1983, Schoener 1983, Fowler 1986, Goldberg and Barton 1992, Gurevitch 1992). Numerous hypotheses address the question of how species' coexistence and diversity are maintained given strong competitive interactions, although relatively few experimental tests of these hypotheses have been conducted for coexisting plant species.

Hypotheses regarding coexistence can be divided roughly into three groups: (1) those emphasizing temporal (Bratton 1976, Gulmon et al. 1983) and/or spatial resource partitioning (Parrish and Bazzaz 1976, Yeaton et al. 1977, Marion et al. 1987, McKane et al. 1990 Gordon and Rice 1992); (2) those emphasizing competitive equivalence and extremely long times to competitive exclusion (Jackson and Buss 1975, Huston 1979, Aarssen 1983, Hubbell and Foster 1986); and (3) those emphasizing factors which interrupt the process of competitive exclusion in time or space (Huston 1979)—e.g., herbivory (Janzen 1970), gap formation (Grubb 1977, Pickett 1980, Schmida and Ellner 1984, Hobbs and Hobbs 1987, Lavorel et al. 1994), aggregation of conspecifics (Atkinson and Shorrocks 1981, Tilman and Pacala 1993), and periodic (Hutchinson 1961, Whittaker and Levin 1977, Rice and Menke 1985) or stochastic (Chesson and Warner 1981, Fagerström 1988) changes in environmental conditions. Except for aggregation processes, all of the hypotheses in this third group involve environmental complexity and organismal trade-offs in their abilities to respond to this complexity (Tilman and Pacala 1993).

If trade-offs exist in species' responses to physical factors, or in species' competitive abilities for two or more limiting resources, then spatial heterogeneity in physical factors or resources could also allow species' coexistence by favoring different species at different points in space (Whittaker and Levin 1977, Tilman 1982, 1988, Tilman and Pacala 1993). This hypothesis should apply particularly well to plant species, because spatial heterogeneity in soil factors and soil resources is a ubiquitous feature of natural environments and is present at virtually every spatial scale (Inouye et al. 1987, Gibson 1988, Robertson et al. 1988, Lechowicz and Bell 1991, Kelly and Canham 1992, Jackson and Caldwell 1993); and trade-offs in the ability to capture resources are unavoidable, due both to the essential nature of plant resources and their distribution above- and belowground (Tilman 1982, 1988). The objectives of this study were to determine whether this mechanism

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of plant species coexistence could be operating in a diverse annual grassland community.

Variation in plant species' performances with variation in soil characteristics should generate associations between particular species and particular soil factors. Associations between plant species and nitrogen supply rates (Pastor et al. 1984, Wedin and Tilman 1990, Vinton and Burke 1995), carbon mineralization rates and microbial biomass carbon (Vinton and Burke 1995), soil fertility (Inouye et al. 1987, McGraw and Chapin 1989), soil salinity and soil moisture (e.g., Brereton 1971, Mahall and Park 1976, Pennings and Callaway 1992), soil texture (Beals and Cope 1964), and soil pH and various mineral nutrients (Snaydon 1962) have been documented. Furthermore, competitive balance often changes with either experimentally imposed or between-habitat variation in resource levels (Pickett and Bazzaz 1976, Tilman 1987, McGraw and Chapin 1989, Huenneke et al. 1990, Tilman and Wedin 1991*a*, Wilson and Tilman 1995) or environmental factors (Snaydon 1971, Goldberg 1985). However, evidence for within-habitat variation in species' competitive abilities due to observed variation in microhabitat features is limited (Pennings and Callaway 1992, Frego and Carleton 1995*a*, *b*).

The serpentine grassland at the Jasper Ridge Biological Preserve in Stanford, California exhibits a patchy vegetation structure (Hobbs and Mooney 1985), suggesting that variation in species' competitive abilities with soil characteristics may be important to species' coexistence there. Both species removals (H. L. Reynolds, *unpublished data*) and nutrient additions (Hobbs et al. 1988, Huenneke et al. 1990) have shown that competitive interactions are important in this grassland. We measured soil characteristics in patches of each of three species from this grassland in order to determine whether soil heterogeneity existed and was correlated with plant species abundance. Within a series of patches, we also experimentally manipulated species densities in order to determine whether heterogeneity in measured soil characteristics was caused by inherent site differences or was due to plant species' effects; and to measure performance of the three species in competition as a function of patch type. Since water and nitrogen (N) have strong effects on plant species' growth in serpentine grassland (Turitzin 1982, Hobbs et al. 1988), we focused on those two resources. We explored several indicators of differences in soil nitrogen cycling between species and patch types, including nitrate collection on resin bags (an indicator of nitrate availability), microbial N pools, microbial uptake of ^{15}N-labeled ammonium, and soil C:N ratio (all indicators of the size and strength of the heterotrophic N sink). We also measured soil depth, because species in this system differ in rooting depths and consequently, in access to deep water supplies (Gulmon et al. 1983).

Methods

Site and experimental design

We conducted our study in annual grassland developed on serpentine soil at the Jasper Ridge Biological Preserve in Stanford, California, USA. This low-productivity grassland supports at least 30 species of mostly native annual forbs and grasses, interspersed with native perennial bunch grasses. Climate at the site is mediterranean, with a mean annual rainfall of 589 $\pm$ 246 mm (Jasper Ridge Biological Preserve records) and a summer drought. Germination of annuals is relatively synchronous with the onset of fall rains in October or November, and virtually no seed bank persists from year to year (Hobbs and Mooney 1985). Growth continues until May for early season annuals, and into August for late season annuals.

Study species were *Plantago erecta* and *Lasthenia californica*, two dominant forbs that complete their life cycles early in the growing season (May); and *Calycadenia multiglandulosum*, an abundant late season forb which flowers in July and August. Over a 10-yr period, the percentage of *Plantago* cover varied between 5 and 55% in this grassland, while that of *Lasthenia* varied between 2 and 40%, and the percentage of *Calycadenia* cover has ranged from 5 to 12% (Hobbs and Mooney 1995). Although early and late season annuals differ in phenology and partitioning of water resources (Gulmon et al. 1983), early season annuals reduce the growth of late season annuals at the seedling stage (H. L. Reynolds, *unpublished data*).

In May 1992, we identified patches ($<$0.01 m^2–10 m^2) dominated by each study species and flagged and staked forty 20 $\times$ 20 cm plots in each of these patch types, for a total of 120 plots. Adjacent plots were at least 0.5 m apart, and all 120 plots were scattered over an area of $\sim$1 ha. After seeds had ripened (in May for *Plantago* and *Lasthenia*, and in August for *Calycadenia*), plots were cleared of standing dead biomass and the soil surface was vacuumed to remove seeds. Seeds for the experiment were separated from the standing dead material, and the rest of the material was autoclaved at 121°C for 1 h to kill remaining seeds. After plots were seeded, the standing dead material originally collected from each plot was returned to it by distributing the litter evenly over the soil surface.

At the start of the growing season in early November 1992, we set up five types of experimental treatments, each replicated eight times, in each of the three patch types. The treatments were (1) a low-density, low-competition control treatment seeded with the same species as that of the surrounding patch; (2) a high-density, intraspecific competition treatment also seeded with the same species as that of the surrounding patch; (3) two two-species interspecific competition treatments, each seeded with the same species as that of the surrounding patch type plus one of the other two study species; and (4) a ''patch conversion'' treatment seeded at high-

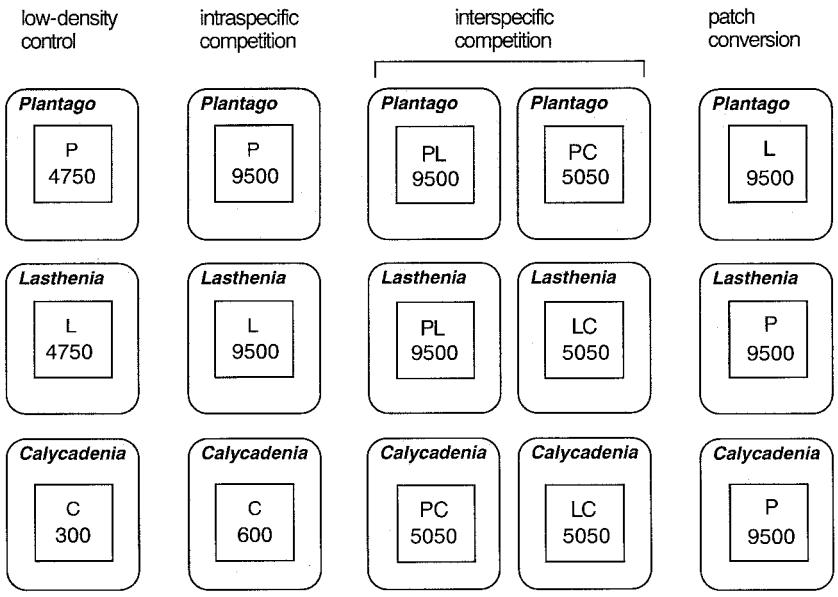

FIG. 1. Experimental design. Shaded areas represent patches of each species, as labeled; white squares represent experimental plots (not to scale). P, L, and C denote *Plantago erecta*, *Lasthenia californica*, and *Calycadenia multiglandulosum* monocultures; PL, PC, and LC denote two-way interspecific competition treatments. Total plot target densities (total no. plants/m^2) are presented underneath each experimental treatment.

density with a species different from that of the surrounding patch. This design allowed us to examine the relative effects of inherent patch characteristics vs. species' effects on measured soil characteristics (for each patch type, comparison of control and intraspecific plots with patch conversion plots). (Fig. 1). It also allowed us to examine intra- and interspecific competitive performances of these species in different patch types.

Low-density control plots were seeded to achieve target densities of half the minimum field density required for maximum yield (N. R. Chiariello, *personal communication*: 4750 plants/m^2 for *Plantago* and *Lasthenia*, and 300 plants/m^2 for *Calycadenia*), while target densities were twice as high for high-density plots (9500 plants/m^2 for *Plantago* and *Lasthenia*, and 600 plants/m^2 for *Calycadenia*). Target densities of *Lasthenia* and *Plantago* were approximate, as seeds were weighed out based on the average mass of 100 seeds.

Plots were overseeded based on 90% germination rates in bare soil for *Plantago*, and 40% germination rates in bare soil for *Lasthenia* and *Calycadenia* (N. R. Chiariello, *personal communication*). Before seeding, the soil surface in all plots was scraped lightly with a metal blade to loosen the surface soil and to uproot any germinating seedlings. Seeds were then sprinkled evenly over the plot and covered with the loosened surface soil, followed by the autoclaved litter originally collected from each plot. Seeds began germinating the first week of December, ~1 mo after natural vegetation. Additional seeds were added to plots where germination was sparse. Due to the presence of standing water, germination did not occur in some plots until the end of January. Because of poor *Calycadenia* germination, freshly germinated *Calycadenia* seedlings were transplanted into most *Calycadenia* plots at the end of January, resulting in exact target densities.

Plots were evaluated for their total numbers of seedlings in mid-February and weeded to target densities if necessary. Plots were also weeded of any species other than the target species. In addition, all vegetation in a 3-cm zone around each plot was removed in order to minimize the effects of vegetation surrounding each plot. Three-centimeter zones were deemed sufficiently wide given the diminutive stature (<10 cm for most species, Hobbs and Mooney 1985) and open canopy of serpentine grassland vegetation.

Soil and plant C and N measurements

To index N availability in control and experimental plots, mixed cation- (Dowex 50W-X8, H^+ form, 20–50 mesh) and anion-exchange (Dowex 1-X8, Cl^- form, 20–50 mesh) resin bags (Binkley 1984, Giblin et al. 1994) were placed 5 cm below the soil surface near the center of each plot in late November, using a 4-cm diameter vertical core. Resins were mixed in ~1:1 exchange capacity ratios (by volume), and ~17 g total resin was placed in each bag. Bags were made of nylon stockings tied off at each end. To flush excess H^+ from resins, bags were soaked in 4 mol/L NaCl for 40 h, then rinsed in deionized water until the pH of the rinse water approached that of the deionized water. Resin bags were recovered at the end of the growing season (the end of May for *Plantago* and *Lasthenia*, the end

of August for *Calycadenia*) and frozen until extraction. For the extraction, resins were removed from bags, rinsed with double deionized water to remove soil particles, and drained and leached with 100 ml 2 eq/L NaCl in 0.1 eq/L HCl, using Whatman GF/A glass microfiber filter paper presoaked in 0.1 eq/L HCl. Extracts were frozen until analysis. Extracts were analyzed for ammonium (NH_4^+) and nitrate (NO_3^-) using a Lachat autoanalyzer (Quik Chem Method No. 12-107062A, NH_4^+/12-107041B, NO_3^- and NO_2^-).

On a subset of our plots (low-density control and intraspecific competition *Plantago* and *Lasthenia* plots, as well as *Plantago* to *Lasthenia* and *Lasthenia* to *Plantago* conversion plots), we also measured plant and soil carbon (C), nitrogen (N), and microbial (chloroform-labile) N and ^{15}N. Plant and soil for these measurements was obtained from soil cores labelled with ^{15}N for concurrent measurements of plant $^{15}NH_4^+$ uptake (see *Methods: Plant performance*). Plant (root and shoot) and soil samples were ground and analyzed for C and N using mass spectroscopy. Microbial N and ^{15}N were measured using the chloroform-fumigation direct-extraction technique (Brookes et al. 1985). Two 5–15 g soil subsamples were extracted with 50 ml 0.5 mol/L K_2SO_4, one immediately, the other after exposure to $HCCl_3$ vapor for 24 h. The N in the extracts was converted to NH_4^+ by Kjeldahl digestion, and total NH_4^+ was determined colorimetrically. NH_4^+ in the digests was collected onto acidified filter disks using the NaOH diffusion procedure of Brooks et al. (1989), and ^{15}N content was determined by mass spectroscopy. Microbial N and ^{15}N were calculated as the difference in total N and ^{15}N between chloroform-fumigated and nonfumigated subsamples, divided by 0.54 to correct for extraction efficiency (Brookes et al. 1985).

To determine soil water, 1-cm diameter cores of maximum 30-cm depth (depth to subsoil was sometimes <30 cm) were taken from each plot in early April. Cores were placed in Zip-lock bags and refrigerated. The following day, coarse fragments (≥ 2 mm diameter) were removed from each core. The remaining soil was weighed, dried at 65°C for at least 72 h, and reweighed to determine soil water content. In addition, to obtain a time-integrated index of water availability (O'Leary 1988), we measured shoot $\delta^{13}C$ (see *Methods: Plant performance*).

Soil depth was measured in three quadrants of each plot with a 0.5-cm diameter sharpened steel rod inserted into the soil until it hit rock. If a rock was hit immediately an adjacent insertion point was tried (i.e., small surface rocks were not counted as subsoil). Average soil depth for each plot was calculated from these three measurements.

$^{15}NH_4^+$ uptake, shoot biomass, and survivorship

We measured in situ plant uptake rates of labelled NH_4^+, aboveground biomass, and survivorship in each experimental plot. We used NH_4^+ rather than NO_3^- in our uptake measurements, because NH_4^+ uptake potential is typically higher than NO_3^- uptake in these species (Jackson and Reynolds 1996), and because in situ plant NH_4^+ uptake is three to four times greater than NO_3^- uptake in similar California grasslands (Jackson et al. 1989). At the end of March 1993, after ~4 mo of growth, ammonium uptake rates were measured in all plots by injecting $^{15}NH_4^+$ into the soil within a 0.03-m diameter $\times$ 0.15-m deep area. Five uniformly spaced 1-mL aliquots of 0.96 mmol aqueous ^{15}N-NH_4SO_4 (99 atom percentage excess ^{15}N) were injected to a depth of 0.075 m. Twenty-four hours after labelling, all shoot material within the core was removed and dried at 65°C. Dried shoots were weighed, ground, and analyzed for ^{15}N enrichment, $\delta^{13}C$, and total C and N by mass spectrometry. $^{15}NH_4^+$ uptake was calculated as

$$\frac{(\text{mg shoot biomass per seed input}) \times (\text{shoot } [^{15}N])}{1 \text{ d}}$$

where shoot [^{15}N] (or enrichment) was calculated as

$$\frac{\%\ N_{\text{labelled shoots}} \times [(\text{atom } \%\ N)_{\text{labelled shoots}} - 0.3682]}{100}$$

and 0.3682 is the National Institute of Standards and Technology atom percentage ^{15}N of the reference material used (citrus leaves). Shoot biomass per core (and thus $^{15}NH_4^+$ uptake) was standardized by the total number of seeds sown per core (for *Calycadenia,* the number of seedlings transplanted per core) in order to compare results across density treatments for each species. (We feel that standardizing on a seed input basis is preferable to standardizing on a final number basis, since biomass per plant typically increases with decreases in plant density. This means that sufficiently large reductions in plant density [e.g., due to competition-related mortality] could result in inflated biomass per plant values compared to controls, even when total biomass in competition treatments is reduced compared to controls.)

A final harvest of aboveground tissue within each plot was made as senescence was occurring (the end of April 1993 for *Plantago* and *Lasthenia,* and the end of July 1993 for *Calycadenia*). To minimize edge effects, *Plantago* and *Lasthenia* biomass was harvested from a 10 $\times$ 10 cm area centered within each plot. In contrast, because of its relatively low density, *Calycadenia* biomass was harvested from the entire 20 $\times$ 20 cm plot area. Tissue was dried at 65°C for at least 48 h, and individuals harvested from each plot were counted and weighed by species. Shoot biomass and number of individuals were standardized by the number of seeds sown (for *Calycadenia,* the number of seedlings transplanted). We will refer to the latter variable as ''survivorship,'' but note that for *Plantago* and *Lasthenia* this variable includes the germination rate as well as mortality. Shoot biomass per plant was cal-

TABLE 1. Two-way treatment structure applied to soil water, shoot $\delta^{13}C$, and resin-bag nitrate data. μ_{ij}'s refer to cell means, where *i* indexes species and *j* indexes patch type. Note that μ_{11}, μ_{22}, and μ_{33} use both low-density control and intraspecific competition data (there were no differences between these treatments within species).

Species	Patch		
	1) *Plantago*	2) *Lasthenia*	3) *Calycadenia*
1) *Plantago*	μ_{11}	μ_{12}	μ_{13}
2) *Lasthenia*	μ_{21}	μ_{22}	⋯
3) *Calycadenia*	⋯	⋯	μ_{33}

culated as shoot biomass per harvested area (unstandardized) divided by the final number of plants per area.

Data analysis

Soil and plant C and N data.—We used ANOVA (MGLH, SYSTAT 5.2.1) to test for density effects between low-density control and intraspecific competition treatments of each species. In no case was density significant: therefore we lumped these treatments in subsequent analyses, doubling our sample size for those elements of the matrix. Also note that we transformed all data as necessary in order to meet the homogeneity of variance assumption for ANOVA (as assessed by Cochran's test [Winer et al. 1991]), but nontransformed data are presented in text and figures (mean ± 1 SE).

In order to examine the relative effects of species' vs. inherent patch characteristics on soil water, shoot $\delta^{13}C$, and resin bag N, we analyzed data from low-density control and intraspecific competition plots (lumped) and patch conversion plots using a missing cells factorial design (Table 1) (Milliken and Johnson 1984). We used SYSTAT's MGLH/Means Model with patch type and current species as main effects. Hypotheses of interest were tested with user-defined contrasts. As recommended by SYSTAT, post hoc comparisons on the least squares means were conducted using Fisher's LSD.

We were able to use two-way, fully factorial ANOVA to test for species' vs. patch effects on microbial N, microbial ^{15}N, plant and soil C:N, and total plant N, since these data were collected from a balanced subset of our experimental plots (low-density control and intraspecific competition *Plantago* and *Lasthenia* plots, as well as *Plantago* to *Lasthenia* and *Lasthenia* to *Plantago* conversion plots). Soil depth data were analyzed using one-way ANOVA with patch type as the main effect (clearly there would be no species' effects on soil depth in one growing season). Pair-wise comparisons for these one- and two-way ANOVAs were made using the Tukey-Kramer HSD (Bonferroni-protected) test. A correlation of midseason soil moisture with soil depth was made using SYSTAT's Corr/Pearson procedure.

$^{15}NH_4^+$ uptake, shoot biomass, and survivorship.—In order to examine the relative effects of competitor identity vs. patch type on performance of *Plantago* and *Lasthenia*, we used a missing cells factorial design on data from low-density control, intra- and interspecific competition, and patch conversion treatments (Table 2a, b). Hypotheses of interest were tested with user-defined contrasts. Post hoc comparisons on the least squares means were conducted using Fisher's LSD. Because plant growth is exponential (at least early on), additive effects of patch and competition on growth rate will result in multiplicative effects on plant biomass, and a factorial analysis would interpret such nonadditive effects as interactions (Wootton 1994). Therefore, biomass data for *Plantago* and *Lasthenia* were

TABLE 2. Two-way treatment structure applied to data on shoot biomass per seed sown (or per seedling transplanted), survivorship, shoot biomass per plant, and $^{15}NH_4^+$ uptake per seed (or seedling) sown for (a) *Plantago erecta,* (b) *Lasthenia californica,* and (c) *Calycadenia multiglandulosum.*

	Competitive milieu	Patch		
		1) *Plantago*	2) *Lasthenia*	3) *Calycadenia*
a) *Plantago erecta*	1) *Plantago,* low-density	μ_{11}	⋯	⋯
	2) *Plantago,* high-density	μ_{21}	μ_{22}	μ_{23}
	3) *Lasthenia,* high-density	μ_{31}	μ_{32}	⋯
	4) *Calycadenia,* high-density	μ_{41}	⋯	μ_{43}
b) *Lasthenia californica*	1) *Lasthenia,* low-density	⋯	μ_{12}	⋯
	2) *Lasthenia,* high-density	μ_{21}	μ_{22}	⋯
	3) *Plantago,* high-density	μ_{31}	μ_{32}	⋯
	4) *Calycadenia,* high-density	⋯	μ_{42}	μ_{43}
c) *Calycadenia multiglandulosum*	1) *Calycadenia,* low-density	⋯	⋯	μ_{13}
	2) *Calycadenia,* high-density	⋯	⋯	μ_{23}
	3) *Plantago,* high-density	μ_{31}	⋯	μ_{33}
	4) *Lasthenia,* high-density	⋯	μ_{42}	μ_{43}

Note: The μ_{ij}'s refer to cell means, where *i* indexes competitive milieu, and *j* indexes patch type.

TABLE 3. Results of means models for soil water, shoot $\delta^{13}C$, and nitrate (NO_3^-) accumulated on ion-exchange resin bags. NO_3^- data were natural-log transformed before analysis. See Fig. 2 for means and standard errors.

Source†	Soil water (percentage of dry mass)				$\delta^{13}C$				NO_3^-(mg N/bag)			
	df	MS	*F*	*P*	df	MS	*F*	*P*	df	MS	*F*	*P*
Model	5	218.22	6.07	<0.01	5	12.94	9.13	<0.01	5	2.38	4.13	<0.01
Species	2	6.56	0.18	0.83	2	17.20	12.13	<0.01	2	3.28	5.7	0.01
Patch	2	337.38	9.39	<0.01	2	2.02	1.42	0.25	2	0.26	0.46	0.64
Species × Patch	1	58.88	1.64	0.21	1	6.76	4.77	0.03	1	2.18	3.79	0.06
Error	66	35.94			60	1.42			61	0.58		

† Null hypotheses (described with respect to cells in Table 1) were as follows: Species: $\mu_{13} = \mu_{33}$ and $\mu_{11} + \mu_{12} = \mu_{21} + \mu_{22}$; Patch: $\mu_{13} = \mu_{11}$ and $\mu_{12} + \mu_{22} = \mu_{11} + \mu_{21}$; Species × Patch: $\mu_{11} - \mu_{12} - \mu_{21} + \mu_{22} = 0$.

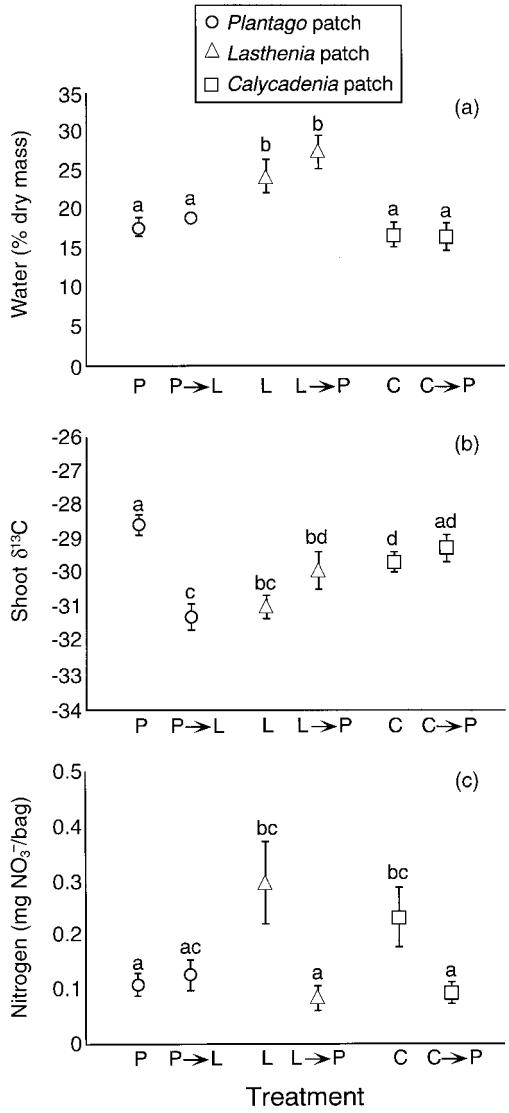

FIG. 2. (a) Soil water, (b) shoot $\delta^{13}C$, and (c) resin bag nitrate in *Plantago*, *Lasthenia*, and *Calycadenia* plots (P, L, and C: means of low-density control and intraspecific competition treatments) and patch conversion plots (P → L, L → P, and C → P). Significance ($P \leq 0.05$) of treatment differences is indicated by differing lowercase letters.

ln-transformed to avoid detecting interactions due solely to the exponential nature of plant growth. This resulted in slight violations of homogeneity of variance assumptions for *Lasthenia* shoot biomass per seed sown and $^{15}NH_4^+$ uptake per seed sown data.

The design for *Calycadenia* contained too many missing cells to use a missing cells factorial approach (Table 2c), so data from *Calycadenia* patches were analyzed using one-way ANOVA with competitive milieu as main effect. *T* tests were then used to compare interspecific competitive performance in *Lasthenia* and *Plantago* patches vs. in *Calycadenia* patches. Data were transformed as necessary to meet homogeneity of variance assumptions for ANOVA and the means model. Untransformed means (± 1 SE) are presented in all figures.

RESULTS

Soil, and plant C and N measurements

Soil depth and water.—Soil depth was significantly different among patch types, with soil in *Calycadenia* patches deepest, *Plantago* patches of intermediate depth, and *Lasthenia* patches shallowest (26.70 ± 2.65 cm, 17.16 ± 1.97 cm, 10.56 ± 0.90 cm, respectively; $P < 0.01$). There was also a strong effect of patch type on midseason soil water (Table 3). Soil water was significantly higher in *Lasthenia* control and *Lasthenia* intraspecific competition plots than in corresponding *Plantago* or *Calycadenia* plots (Fig. 2a). There was no effect of planting density (data not shown), nor of the identity of a species seeded into a plot (Table 3, Fig. 2a) on soil water. Thus, soil water was determined by inherent patch characteristics. Soil water was weakly and negatively correlated with soil depth (Pearson correlation coefficient = −0.29, $P = 0.02$).

Differences in water use efficiency among these species, as indicated by differences in shoot $\delta^{13}C$ values, provide support and a broader temporal context for the differences among patches in soil water that we observed at midseason (Table 3, Fig. 2b). Compared to *Plantago* patches, water use efficiency of *Plantago* shoots decreased (lower $\delta^{13}C$) in *Lasthenia* patches but not in *Calycadenia* patches. This greater water use per

unit of fixed carbon in *Lasthenia* patches is consistent with the wetter soil in these patches. *Lasthenia* grown in *Lasthenia* patches had more negative $\delta^{13}C$ values than either *Plantago* grown in *Plantago* patches or *Calycadenia* grown in *Calycadenia* patches, indicating lower water use efficiency in *Lasthenia* compared to *Plantago* and *Calycadenia.* This is consistent with a preference for wetter soil by *Lasthenia.* Water use efficiency of *Lasthenia* did not vary between patch types.

Soil ammonium and nitrate.—In contrast with soil water, nitrate accumulation on ion-exchange resin bags was strongly determined by species identity (Table 3). Seeding of plots with *Plantago* caused a decline in resin bag nitrate in *Lasthenia* and *Calycadenia* patches down to levels found in *Plantago* plots placed in *Plantago* patches (Fig. 2c). However, planting of *Lasthenia* in *Plantago* patches did not change the resin bag nitrate compared to *Plantago* planted in *Plantago* patches (Fig. 2c). These results suggest that *Plantago* reduces soil nitrate availability compared to *Lasthenia* and *Calycadenia,* and that this effect persists even when *Plantago* is no longer present. Again, there was no effect of density on nitrate accumulation (data not shown). Practically no ammonium was recovered from ion-exchange resin bags, so we excluded this variable from our analysis.

Microbial N and ^{15}N.—There was a significant patch-type effect on soil microbial N (Table 4), with *Lasthenia* patches supporting a larger microbial N pool than *Plantago* patches (Fig. 3a). Converting patches did not significantly affect microbial N, although microbial N in *Plantago* patches converted to *Lasthenia* was intermediate between (and not significantly different from either) *Plantago* and *Lasthenia* in their native patches. Consistent with an expanding microbial N pool in *Plantago* patches converted to *Lasthenia,* short-term microbial ^{15}N uptake was higher in this treatment than in unconverted *Plantago* patches (Figure 3b). However, patch differences in microbial N were not related to short-term microbial ^{15}N uptake: despite a larger microbial N pool in *Lasthenia* patches, short-term ^{15}N uptake in *Lasthenia* patches was similar to that in unconverted *Plantago* patches (Fig 3b). Thus, the larger microbial N pool in *Lasthenia* patches did not reflect a greater capacity for short-term immobilization of N.

Plant and soil N pools and C:N ratios.—Total plant N pools in *Lasthenia* and *Plantago* tended to be largest when these species were grown in their native patch type (Table 4, Fig. 3c), suggesting that both species performed best in their native patches. For both shoots and roots, C:N ratios were higher in *Plantago* compared to *Lasthenia* (Table 4, Fig. 4a, b). Additionally, C:N ratios of both shoots and roots were higher in *Plantago* patches compared to *Lasthenia* patches (Table 4, Fig. 4a, b), suggesting higher N availability in *Lasthenia* patches. Similarly, soil C:N values were lower in *Lasthenia* patches compared to *Plantago* patches (Table 4, Fig. 4c). Neither conversion of *Plantago* to *Lasthenia* nor of *Lasthenia* to *Plantago* altered soil C:N (Fig. 4c).

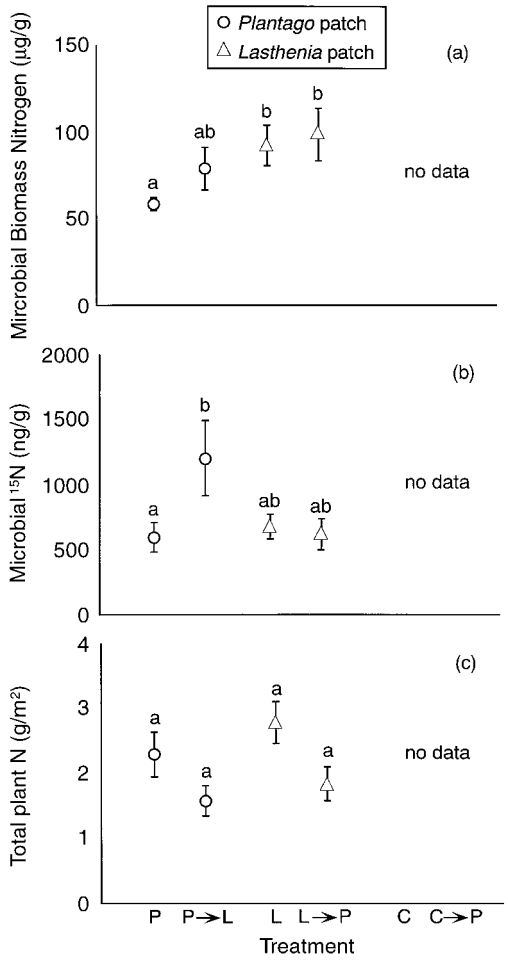

FIG. 3. (a) Microbial biomass nitrogen (μg/g dry soil), (b) microbial ^{15}N (ng/g dry soil), and (c) total plant N in *Plantago* and *Lasthenia* plots (P and L; means of low-density control and intraspecific competition treatments) and patch conversion plots (P → L and L → P). Significance ($P \leq 0.05$) of treatment differences is indicated by differing lowercase letters.

$^{15}NH_4^+$ uptake, shoot biomass, and survivorship

Plantago.—Shoot biomass per seed sown of *Plantago* was reduced when *Plantago* grew in *Lasthenia* patches compared to *Plantago* patches, regardless of competitive milieu (Table 5, Fig. 5a). The same trend was seen for *Plantago* grown in *Calycadenia* patches compared to *Plantago* patches (Fig. 5a). *Plantago* survivorship paralleled these results (Table 5, Fig. 5b), suggesting that reduced germination and/or increased mortality of *Plantago* grown in *Lasthenia* and *Calycadenia* patches compared to *Plantago* patches were responsible for observed reductions in shoot biomass per seed sown. *Plantago* appeared unaffected by competition in its own patch-type: per seed sown and per

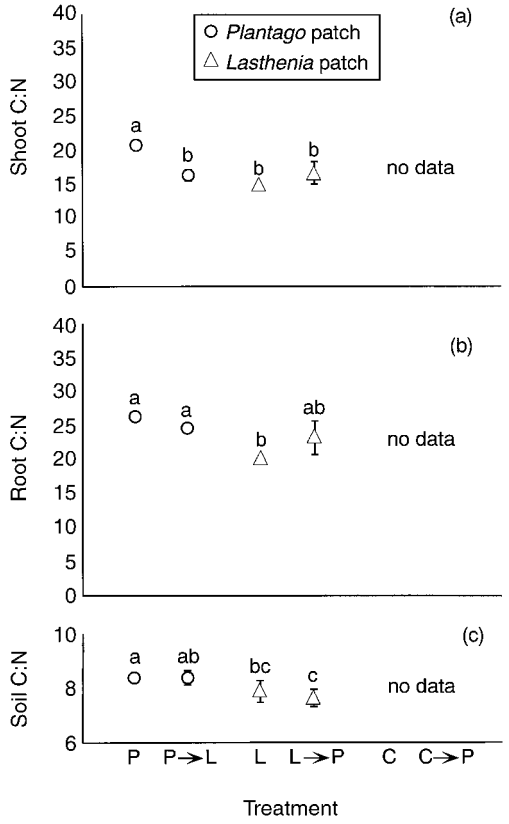

FIG. 4. C:N of (a) shoots, (b) roots, and (c) soil in *Plantago* and *Lasthenia* plots (P and L; means of low-density control and intraspecific competition treatments) and patch conversion plots (P → L and L → P). Significance ($P \leq 0.05$) of treatment differences is indicated by differing lowercase letters.

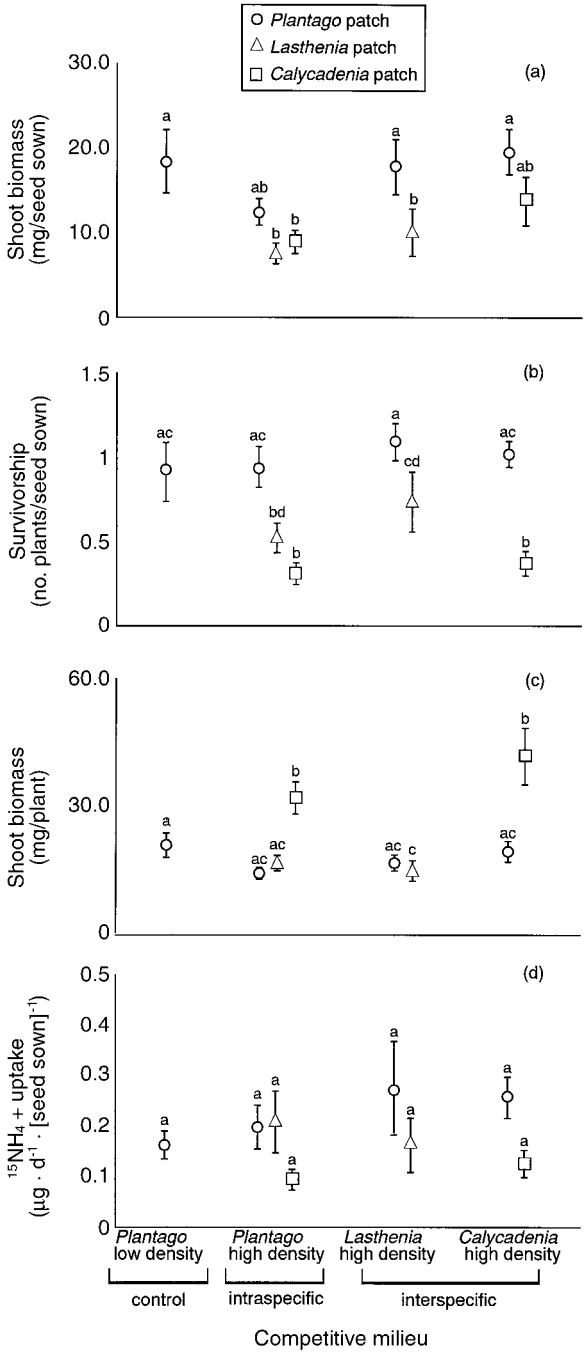

FIG. 5. Performance of *Plantago erecta* in low-density control, intraspecific competition, and interspecific competition treatments. (a) Shoot biomass per seed sown, (b) survivorship, (c) shoot biomass per plant, and (d) $^{15}NH_4^+$ uptake per seed sown. Significance ($P \leq 0.05$) of differences among all means within a graph is indicated by differing lowercase letters.

plant shoot biomass as well as survivorship of *Plantago* grown in *Plantago* patches were similar regardless of competitive milieu (Fig. 5a, b, c).

Shoot biomass per plant of *Plantago* was significantly higher in *Calycadenia* patches than either *Plantago* or *Lasthenia* patches (Fig. 5c), which is responsible for the significant main effect of patch on this variable when comparing intraspecific and interspecific competitive milieus in all patch types (Table 5). Biomass per plant is typically inversely related to planting density (Harper 1977), suggesting that observed reductions in final *Plantago* density in *Calycadenia* patches compared to *Plantago* patches occurred early enough in the growing season for survivors to take advantage of reduced demands on resources. There was no significant effect of density, patch type, or competing species on $^{15}NH_4^+$ uptake per seed sown of *Plantago* (Table 5, Fig. 5d).

Lasthenia.—In contrast with *Plantago,* shoot biomass per seed sown of *Lasthenia* was reduced by both patch and competition effects (Table 6); and in particular, by the combination of competition with *Plantago* in *Plantago* patches (Fig. 6a). Survivorship of *Lasthenia* was also reduced under these conditions (Fig. 6b), although significance was marginal (Table 6). The decline in shoot biomass was accompanied by a decline in $^{15}NH_4^+$ uptake per seed sown (Table 6, Fig. 6d).

TABLE 4. Summary of two-way ANOVA results for microbial N, microbial ^{15}N uptake, total plant N, shoot and root C:N, and soil C:N ratio. See Figs. 3 and 4 for means and standard errors.

Dependent variable	Source	df	MS	*F*	*P*
Microbial N	Species	1	448	0.38	0.54
(μg N/g dry soil)	Patch	1	7302	6.11	0.02
	Species × Patch	1	2051	1.72	0.20
	Error	43	1195		
Microbial ^{15}N	Species	1	9670	3.72	0.06
(ng ^{15}N/g dry soil)	Patch	1	6257	2.40	0.13
	Species × Patch	1	5770	2.22	0.15
	Error	38	2603		
Total plant N	Species	1	0.13	0.10	0.76
(g N/m^2 ground area)	Patch	1	1.17	0.88	0.35
	Species × Patch	1	6.85	5.16	0.03
	Error	42	1.33		
Shoot C:N	Species	1	99.99	11.26	<0.01
	Patch	1	82.32	9.27	<0.01
	Species × Patch	1	14.28	1.61	0.21
	Error	41	8.88		
Root C:N	Species	1	59.03	6.11	0.02
	Patch	1	154.04	15.94	<0.01
	Species × Patch	1	4.18	0.43	0.51
	Error	42	9.66		
Soil C:N	Species	1	0.19	0.61	0.44
	Patch	1	4.03	13.32	<0.01
	Species × Patch	1	0.16	0.51	0.48
	Error	42	0.30		

$^{15}NH_4^+$ uptake per seed sown was also reduced for *Lasthenia* grown with *Calycadenia* in *Calycadenia* patches compared to *Lasthenia* grown in any competitive milieu in *Lasthenia* patches (Fig. 6d), even though *Calycadenia* had no effect on shoot biomass per seed sown or survivorship of *Lasthenia* (Fig. 6a, b, c).

Calycadenia.—There were no effects of competitive milieu on shoot biomass per seedling transplanted, survivorship, or shoot biomass per plant of *Calycadenia* grown in *Calycadenia* patches (Table 7, Fig. 7). However, shoot biomass per seedling transplanted of *Calycadenia* was reduced when *Calycadenia* grew with *Lasthenia* in *Lasthenia* patches compared to *Calycadenia* patches (*t* test, $P = 0.01$, Fig. 7a). This could be due to either a patch, a species, or a combined patch-species effect of *Lasthenia* on *Calycadenia,* but because our design did not include *Calycadenia* monocultures grown in *Lasthenia* patches, we cannot distinguish between these alternatives. Shoot biomass per plant of *Calycadenia* was similarly reduced when *Calycadenia* was grown with *Lasthenia* in *Lasthenia* patches (*t* test, $P = 0.01$, Fig. 7c), but neither survivorship (*t* test, $P = 0.70$) nor $^{15}NH_4^+$ uptake per seed sown (*t* test, $P = 0.56$) showed similar effects (Fig. 7b, d). Thus, *Calycadenia* growth, but not survivorship or nitrogen acquisition, appears to be reduced by patch or species–patch effects of *Lasthenia*. In contrast, there were no patch or species–patch effects of *Plantago* (all corresponding *t* test, *P* values were >0.05, Fig. 7).

DISCUSSION

Results of this study show that three common grassland annuals exhibited associations with soils of different nitrogen availability, depth and/or moisture content: *Calycadenia* was abundant in patches of deepest soil, *Plantago* in patches of intermediate depth and lowest soil nitrogen availability, and *Lasthenia* in the shallowest and wettest patches. Furthermore, in interspecific competition against one other species, shoot biomass (and variously, survivorship, shoot biomass per plant, or N acquisition) of all species was significantly greater when growing in their own compared to the other species' patch type. For *Plantago*, this appeared to be due strictly to a patch effect: shoot biomass per seed sown of *Plantago* in *Lasthenia* sites tended to be lower regardless of whether planted in intra- or interspecific competition. In contrast, *Lasthenia*'s lower shoot biomass per seed sown occurred only in competition with *Plantago* in *Plantago* sites. Our experiment was not designed to allow distinction between patch vs. species' effects of *Lasthenia* on *Calycadenia.*

In this serpentine grassland, soil microtopography appears to be the primary determinant of heterogeneity in soil water content. *Lasthenia* patches, with the highest soil water content of the three patch types examined, occurred in areas of slightly lower elevation than *Plantago* or *Calycadenia* patches, suggesting a simple physical determinant. These depressed areas where *Lasthenia* was dominant tended to collect standing water

TABLE 5. Results of means models for components of *Plantago erecta* biomass and $^{15}NH_4^+$ uptake. ''Comp'' refers to competitive milieu (high-density *Plantago erecta, Lasthenia californica,* or *Calycadenia multiglandulosum*).

	Shoot biomass (g/seed sown)				Survivorship (no. plants/seed sown)				Shoot biomass per plant (g/plant)				$^{15}NH_4^+$ uptake (mg $^{15}N_{shoot}\cdot d^{-1}\cdot$[seed sown]$^{-1}$)			
Source†	df	MS	*F*	*P*	df	MS	*F*	*P*	df	MS	*F*	*P*	df	MS	*F*	*P*
Model	7	1.24	3.18	0.01	7	0.75	6.93	<0.01	7	1.13	8.35	<0.01	7	0.92	1.33	0.26
Comp	3	0.68	1.74	0.19	3	0.14	1.31	0.28	3	0.32	2.36	0.10	···	···	···	···
Patch	2	2.18	5.58	0.01	2	1.81	16.58	<0.01	2	2.44	18.00	<0.01	···	···	···	···
Comp × Patch	2	0.07	0.19	0.83	2	0.01	0.06	0.94	2	0.08	0.59	0.56	···	···	···	···
Error	55	0.39			55	0.11			55	0.14			49	0.69		

Note: Biomass and uptake data were natural-log transformed before analysis. Null hypotheses were not explored in cases where the means model was not significant. See Fig. 5 for means and standard errors.

† Null hypotheses (described with respect to cells in Table 2a) were as follows: Comp, $\mu_{21} + \mu_{22} = \mu_{31} + \mu_{32}$ and $\mu_{21} + \mu_{23} = \mu_{41} + \mu_{43}$; Patch, $\mu_{21} + \mu_{31} = \mu_{22} + \mu_{32}$ and $\mu_{21} + \mu_{41} = \mu_{23} + \mu_{43}$; Comp × Patch, $\mu_{21} - \mu_{22} - \mu_{31} + \mu_{32} = 0$ and $\mu_{21} - \mu_{23} - \mu_{41} + \mu_{43} = 0$.

into February. Furthermore, converting plots from *Plantago* to *Lasthenia* did not increase soil water content, suggesting that differences in plant transpiration rates did not substantially contribute to differences in soil water content. *Lasthenia*'s positive association with soil water explains why *Lasthenia* is most abundant in wet years as well as in wet soil patches (Hobbs and Mooney 1991, 1995). Although not tested by this study, such interannual variation in soil water may also contribute to the coexistence of these species.

It is likely that *Calycadenia*'s association with deeper soil is linked to its deep root system, which can tap into sources of water (and perhaps nutrients) available at depth, a trait clearly important for a summer annual species (Mooney et al. 1986). *Lasthenia*'s greater abundance in shallower soil compared to *Plantago* may simply reflect different depth preferences, possibly because of some other factor correlated with soil depth. For example, soil water showed a weak negative correlation with soil depth in this study. Our results suggest that *Lasthenia* is competitively excluded from drier but deeper soil by *Plantago* (Fig. 6a).

We found inherent patch differences in microbial N pools and total soil carbon to nitrogen ratios, as well as species' effects on nitrate availability, findings that provide further evidence for microhabitat segregation of these species. Differences in availability of nitrate were due to the depression of nitrate availability by *Plantago* rather than to inherent site differences. Tilman and Wedin (1991*b*) found differences among perennial grasses in the levels to which they reduced extractable soil ammonium and nitrate, and related these findings to differences in root allocation and biomass. However, greater N uptake by *Plantago* does not explain the lower levels of soil nitrate associated with *Plantago* in our experiment. In fact, total plant N of *Plantago* grown in *Lasthenia* patches—where soil nitrate was reduced—tended to be lower than total plant N in *Lasthenia* control plots. Also, *Plantago* and *Lasthenia* control plots did not differ significantly in total plant N, even though resin bag nitrate was significantly lower in *Plantago* control plots. Thus, differences in plant N uptake cannot explain the low levels of soil nitrate associated with *Plantago* compared to *Lasthenia.*

Alternatively, *Plantago* may be associated with low soil nitrate levels because it depresses the activity of nitrifiers. The fact that resin bag nitrate in plots converted from *Plantago* to *Lasthenia* were intermediate between *Plantago* control plots and *Lasthenia* and *Calycadenia* control plots indicates a historical effect of *Plantago* on soil nitrate levels that cannot be explained

TABLE 6. Results of means models for components of *Lasthenia californica* biomass and $^{15}NH_4^+$ uptake. ''Comp'' refers to competitive milieu (high-density *Plantago erecta* or *Lasthenia californica*).

	Shoot biomass (g/seed sown)				Survivorship (no. plants/seed sown)				Shoot biomass per plant (g/plant)				$^{15}NH_4^+$ uptake (mg $^{15}N_{shoot}\cdot d^{-1}\cdot$[seed sown]$^{-1}$)			
Source†	df	MS	*F*	*P*	df	MS	*F*	*P*	df	MS	*F*	*P*	df	MS	*F*	*P*
Model	6	3.69	5.21	<0.01	6	0.05	1.95	0.09	6	1.00	2.40	0.04	6	5.09	5.63	<0.01
Comp	1	4.08	5.76	0.02	···	···	···	···	1	0.60	1.45	0.24	1	4.26	4.72	0.04
Patch	1	4.25	6.00	0.02	···	···	···	···	1	0.36	0.88	0.35	1	12.48	13.81	<0.01
Comp × Patch	1	5.68	8.02	0.01	···	···	···	···	1	0.53	1.28	0.26	1	2.39	2.64	0.11
Error	46	0.71			48	0.03			46	0.42			42	0.90		

Note: Biomass and uptake data were natural-log transformed before analysis. Null hypotheses were not explored in cases where the means model was not significant. See Fig. 6 for means and standard errors.

† Null hypotheses (described with respect to cells in Table 2b) were as follows: Comp, $\mu_{21} + \mu_{22} = \mu_{31} + \mu_{32}$; Patch, $\mu_{21} + \mu_{31} = \mu_{22} + \mu_{32}$; Comp × Patch, $\mu_{21} - \mu_{22} - \mu_{31} + \mu_{32} = 0$.

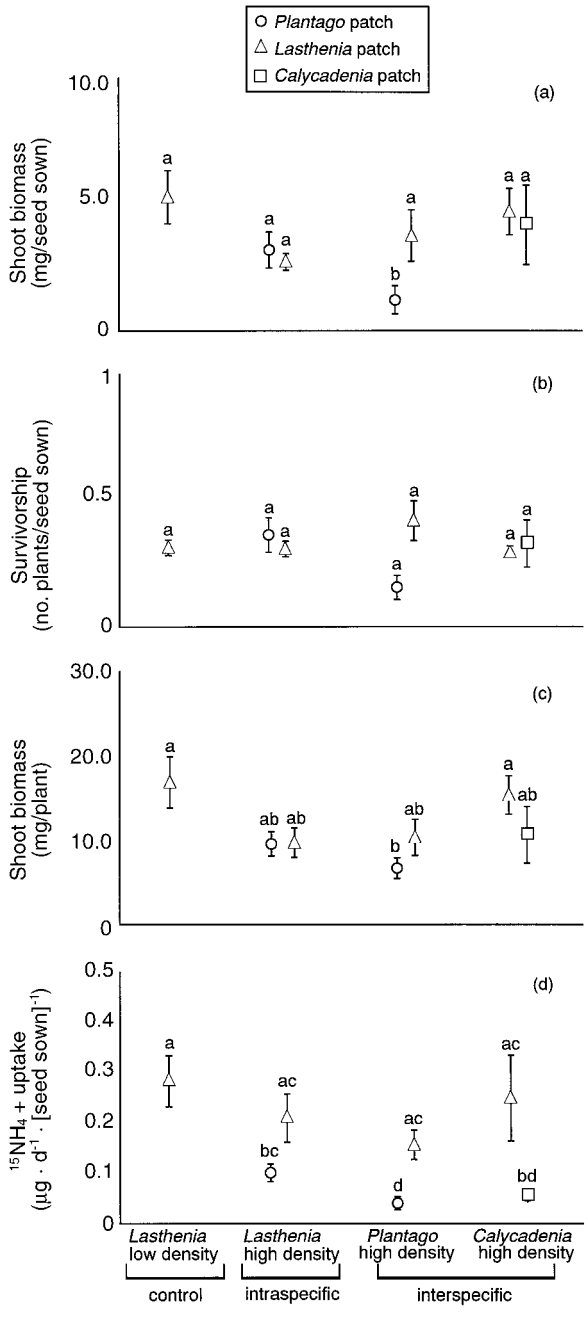

FIG. 6. Performance of *Lasthenia californica* in low-density control, intraspecific competition, and interspecific competition treatments. (a) Shoot biomass per seed sown, (b) survivorship, (c) shoot biomass per plant, and (d) $^{15}NH_4^+$ uptake per seed sown. Significance ($P \leq 0.05$) of differences among means within a graph is indicated by differing lowercase letters.

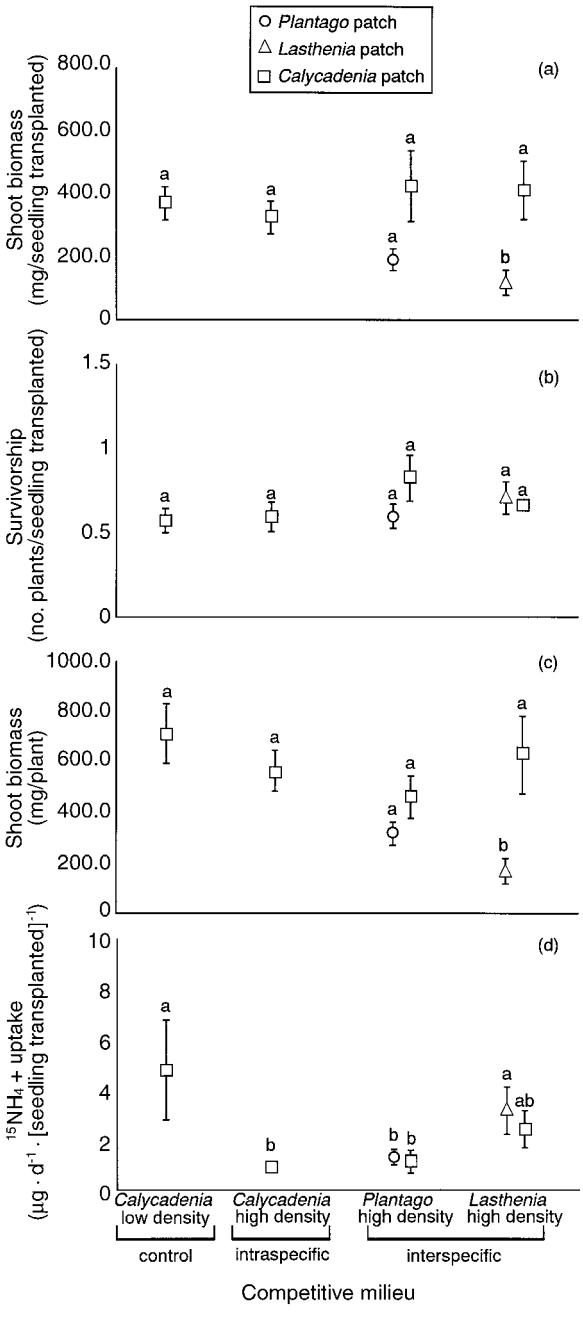

FIG. 7. Performance of *Calycadenia multiglandulosum* in low-density control, intraspecific competition, and interspecific competition treatments. (a) Shoot biomass per seedling transplanted, (b) survivorship, (c) shoot biomass per plant, and (d) $^{15}NH_4^+$ uptake per seedling transplanted. Significance ($P \leq 0.05$) of differences among means from *Calycadenia* patches, and within *Plantago* and *Lasthenia* competitive milieus is indicated by differing lowercase letters.

by direct effects of plant uptake. The higher soil C:N in *Plantago* compared to *Lasthenia* patches could indicate a stronger sink for N in the heterotrophic microbial biomass, and thus less N available for nitrifiers. As root material is an important substrate for microbial growth, the higher C:N ratio of roots in *Plantago* patches could also favor immobilization over nitrification, thereby reducing nitrate accumulation on the resin bags. Because soil and root C:N ratios were higher in

TABLE 7. Results of one-way ANOVAs for components of *Calycadenia multiglandulosum* biomass and $^{15}NH_4^+$ uptake. ''Comp'' refers to competitive milieu (last column of Table 2c: low-density *Calycadenia,* high-density *Calycadenia,* high-density *Plantago,* or high-density *Lasthenia*).

Dependent variable	Source	df	MS	*F*	*P*
Shoot biomass (g/seedling transplanted)	Comp	3	0.02	0.33	0.80
	Error	27	0.05		
Survivorship (no. plants/seedling transplanted)	Comp	3	0.03	1.15	0.35
	Error	27	0.07		
Shoot biomass per plant (g/plant)	Comp	3	0.10	1.00	0.41
	Error	27	0.10		
$^{15}NH_4^+$ uptake (mg $^{15}N_{shoot}\cdot d^{-1}\cdot$[seedling transplanted]$^{-1}$)	Comp	3	3.62	4.98	0.01
	Error	24	0.73		

Note: Density data were square-root transformed before analysis and uptake data were natural-log transformed before analysis to meet the homogeneity of variance assumption for ANOVA. See Fig. 7 for means and standard errors.

Plantago patches, it is unlikely that the larger microbial N pool in *Lasthenia* patches was related to a greater microbial demand for N (e.g., caused by a higher substrate C:N ratio). Rather, higher microbial N in *Lasthenia* patches may be partially due to greater N mobility in the wetter soils there.

There are several possible reasons for the surprising lack of ammonium recovered from resin bags. First, if ammonium is limiting and in high demand by plants and microbes, there may be little available to accumulate on resin bags, especially if resins are poorer competitors for ammonium than these organisms (Binkley 1984). Second, due to its charge, ammonium is a relatively immobile ion, such that resin bags are likely to be sampling only the small volume of soil around each bag. Finally, ammonium on bags may have been converted to nitrate via nitrification while the bags were still in the field.

In contrast with resin bag nitrate, differences in microbial N and soil C:N ratios between *Lasthenia* and *Plantago* patches were not affected by converting patches from *Lasthenia* to *Plantago* or vice versa. However, if these patches have persisted over many years, the higher C:N ratio of soil in *Plantago* patches may be related to the higher C:N ratio of *Plantago* tissue. Because the soil C and N pools are large and turn over fairly slowly, it is not surprising that the 1-yr manipulation of species' composition had no effect on soil C:N, even if differences in species' characteristics are the main determinant of soil C:N. Also, converting patches from *Plantago* to *Lasthenia* tended to increase microbial $^{15}NH_4^+$ uptake, demonstrating that species' identity may influence microbial N acquisition, at least in the short term. Greater microbial ^{15}N uptake in *Plantago* patches converted to *Lasthenia* may be due to a weaker plant N sink in these plots, as total plant N and ^{15}N uptake tended to be lower in *Plantago* patches converted to *Lasthenia* than in unconverted *Plantago* patches. Thus, although our conversion treatments altered neither the size of the microbial N pool nor soil C:N ratios, species' effects on microbial $^{15}NH_4^+$ uptake as well as differences among species in tissue C:N ratios suggest that species' characteristics may influence both these soil parameters.

The species and patch effects on soil water and N suggest possible mechanisms for the observed differences in species' competitive performances. The shallower, wetter (and frequently inundated) soil of *Lasthenia* patches may explain the lower survivorship of *Plantago* and the lower shoot biomass (per seed sown or per seedling transplanted) of *Plantago* and *Calycadenia* grown in *Lasthenia* patches. *Plantago*'s negative effect on soil nitrate availability may be linked to the reductions in shoot biomass per seed sown and N acquisition of *Lasthenia* when grown with *Plantago* in *Plantago* patches. Explicit tests of these mechanisms have yet to be conducted, however.

This study demonstrates that variation in competitive performance with patch type occurs in this grassland. However, none of the study species performed best against both of the other species when growing in their own patch type. For example, *Lasthenia* performed best in interspecific competition with *Plantago* when growing in *Lasthenia* vs. *Plantago* patches, but *Lasthenia*'s performance in *Calycadenia* patches was not significantly different from its performance in *Lasthenia* patches. Thus, while site-related differences in performance may be contributing to species coexistence in this grassland, other mechanisms of species coexistence must also operate. *Plantago* and *Lasthenia* both complete their growth and reproduction by the onset of the summer drought (May), but the more deeply rooted *Calycadenia* can continue growth into summer by virtue of its ability to tap into deep water supplies. This spatial and temporal habitat partitioning may be important to coexistence as well. Species competitive abilities may vary annually with rainfall. Hobbs and Mooney (1995) have shown that *Lasthenia* abundance is strongly correlated with rainfall levels in the previous year. Gopher activity is also likely to contribute to species coexistence in this grassland. Gopher mounds are often preferentially colonized by taller species, like *Ca-*

lycadenia (Hobbs and Mooney 1985, Hobbs and Hobbs 1987), and growth and seed production of plants growing on gopher mounds is generally higher than in undisturbed vegetation (Hobbs and Mooney 1985).

Few studies examine actual variation in the competitive ability of species in the field. Exceptions include studies of coexisting perennial grasses (Fowler 1990, Tilman and Wedin 1991*a*, Wilson and Tilman 1995). Fowler (1990) found differential responses of three grass species to three different types of microenvironments, ''tree'' (underneath *Juniperus ashei* canopies), ''grassy,'' and ''rocky.'' For two of the grasses, growth was reduced by the same amount compared to growth alone regardless of competitor and microenvironment; the other grass was not affected by competition with the other two species, regardless of microenvironment. She did, however, find that different species grew better in different sites, and concluded that this could contribute to coexistence. Tilman and Wedin (1991*a*) showed that the outcome of competition among four perennial grasses in planted arrays in the field was often predicted by their abilities to draw down extractable soil NO_3^- and NH_4^+. Wilson and Tilman (1995) found that competitive responses among eight old-field plant species varied with soil fertility treatment. Many studies have documented vegetation or species associations with soil characteristics at both within-habitat (e.g., Snaydon 1962, Brereton 1971, Turkington et al. 1977, Inouye et al. 1987, Weir and Wilson 1987, Wedin and Tilman 1990) and between-habitat or between vegetation-type scales (Goldberg 1982, 1985, McGraw and Chapin 1989, Schlesinger et al. 1989). These associations are suggestive of variation in species performances with soil characteristics. However, more studies that explicitly examine changes in intra- and interspecific competitive ability with site are required to determine whether this is an important mechanism of species coexistence, especially on local (within-habitat) scales. Tilman and Pacala (1993) suggest that numerous processes can contribute to local species coexistence, but in most habitats the specific processes most important for coexistence have not been identified. Achieving this formidable goal will require evaluation of the relative contributions of all plausible forces generating species coexistence in particular habitats to determine which are most important. This will likely require a combination of observational, experimental, and theoretical approaches.

In summary, each of three California serpentine grassland annuals was found to perform significantly better against one of the other study species in the patch type where they occur most abundantly, and this was correlated with inherent patch differences in soil moisture and depth and to differential species' effects on nitrogen availability. This suggests that variation in species' competitive abilities among microsites may be an important mechanism of species coexistence in this grassland.

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