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Abiotic stress, competition, and the distribution of the native annual grass *Vulpia microstachys* in a mosaic environment

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Abstract We analyzed how abiotic stress and competition interact to control the abundance and performance of the native annual grass *Vulpia microstachys* (Londard and Gould; Poaceae) in a heterogeneous environment. At our study site, *V. microstachys* grows in nonserpentine grasslands dominated by tall invasive grasses, serpentine meadows dominated by short native forbs, and rocky serpentine slopes with a sparse native herb cover. We hypothesized that these three intermixed habitats acted as a gradient of increasing abiotic stress and decreasing aboveground competition, respectively. We further expected that the abundance and performance of *V. microstachys* would be highest in serpentine meadows, where neither aboveground competition nor abiotic stress were maximal. Soil and biotic variables showed roughly the expected patterns, but *V. microstachys* did not show the predicted peak in the middle of the gradient. Emergence, seedling survival, and abundance of *V. microstachys* were highest, and growth and seed production of survivors were lowest, on rocky serpentine slopes. Field experiments revealed that removal of competitors enhanced all demographic parameters, but only in the more productive habitats. An interaction between seed source and habitat, affecting emergence and survival, indicated ecotypic adaptation to the rocky serpentine slope habitat. We conclude that individual variation caused by local adaptation and phenotypic plasticity allows *V. microstachys* to survive in widely different habitats, none of which are optimal, resulting in considerable variation in demography.

Keywords Annual grass · Competition · Ecotypes · Plasticity · Serpentine

Introduction

Distributions of species along gradients in the environment, such as soil fertility, moisture availability, and salinity gradients, are classically thought to represent intermediate optima in the strength of biotic and abiotic limiting factors. Connell (1961) proposed that distributions might generally be limited by abiotic factors at the more stressful end of a physical gradient, and by competition or predation at the less stressful end. The related idea that plant community structure is governed by interspecific tradeoffs between stress tolerance and competitive ability is a feature of many ecological theories (e.g., Grime 1979; Keddy 1989; Brooker and Callaghan 1998). In support of these views, numerous empirical studies have shown that the strength and direction of interactions among plant species may vary systematically across abiotic gradients (e.g., Bertness and Hacker 1994; Callaway and King 1996; Callaway et al. 1996; Tielborger and Kadmon 2000; Pugnaire and Luque 2001). Yet the fact that some species are broadly distributed across stress gradients suggests there may be a large role for within-species variation in the ability to tolerate abiotic versus biotic limiting factors. In particular, both ecotypic adaptation and phenotypic plasticity may complicate the simple notion of species distributions as unimodal peaks along stress and competition gradients.

Ecotypic adaptation to abiotic stresses such as heavy metals and salinity has been shown in numerous studies (e.g., Antonovics et al. 1971; Cook et al. 1972; Hickey and McNeilly 1975). Local adaptation to the competitive environment is also possible, although this has been much less investigated (Rice and Mack 1991). Both these forms of local adaptation imply that a species may undergo divergent selection along an environmental gradient, so that neither its abundance nor its growth and reproductive performance necessarily shows a unimodal pattern. Likewise, numerous studies demonstrate that plants may show either “tolerance plasticity”, i.e., the ability to grow and reproduce at reduced size in unfavorable conditions, or “compensatory plasticity”, i.e., the

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ability to alter allocation so as to perform equally well in alternative conditions (Morrisset and Boutin 1984; Taylor and Aarssen 1988).

Serpentine soils offer an excellent setting for examining the interplay of abiotic stress, interspecific competition, local adaptation and phenotypic plasticity. These soils have high levels of exchangeable Mg and low levels of Ca; they are usually deficient in primary nutrients, and often have high amounts of Fe and nickel (Kruckeberg 1984). The vegetation on serpentine is characteristically sparse and stunted compared with that of surrounding nonserpentine soils; in some parts of the world, such as California, the flora includes a substantial number of species that are endemic to serpentine (Kruckeberg 1984). However, serpentine endemics can typically grow on nonserpentine soil if they are freed from interspecific competition (Walker 1954; Kruckeberg 1954; Rice 1989), implying these species are poor competitors yet good stress tolerators. The majority of the invasive annual grasses that now dominate the lowland grasslands of California are sparse or absent on serpentine (Turitzin 1982; Kruckeberg 1984; Huenneke et al. 1990).

Among those species that are found on both serpentine and nonserpentine soils, the incidence of ecotypic adaptation is high. Kruckeberg (1967) found evidence for serpentine ecotype formation in 13 of 21 species he tested. However, the genetic and physiological basis for adaptation to serpentine remains poorly understood. Also, relatively little is known about the existence of local adaptation to varying degrees of harshness within serpentine soil, caused, for example, by variation in soil depth, texture, and nutrient and metal content. Rajakaruna and Bohm (1999) found correlative evidence that the native annual *Lasthenia californica* (Asteraceae), growing on a range of serpentine and nonserpentine soils, consists of multiple races with varying levels of stress tolerance.

We experimentally analyzed biotic and abiotic factors affecting the abundance, growth and reproduction of the native annual grass *Vulpia microstachys*. This species is the only common annual among the native grasses of California's interior prairies (Jackson 1985). Its life-history attributes, including shallow roots, short stature, and a short and early flowering period, are more typical of native forbs than of the deeply rooted perennial bunchgrasses that once dominated the prairies of this region (Mooney et al. 1986). Although *V. microstachys* is somewhat similar in life history to the invasive Mediterranean annual grasses that now dominate the region (e.g., *Avena*, *Bromus* and *Lolium* spp.), it is smaller in stature, earlier in terms of phenological characteristics, and more tolerant of drought (Mooney et al. 1986; Armstrong and Huenneke 1992). In pot experiments, its growth on serpentine soils responded positively to nutrient (N and P) addition (Turitzin 1982). However, nutrient addition also enhances the relative dominance of the much taller invasive annual grasses, such as *Avena fatua*, that are *V. microstachys*' most significant competitors (Rice 1989).

At our study site in northern California, *V. microstachys* grows in nonserpentine grasslands dominated by tall invasive annual grasses, serpentine meadows dominated by short native forbs, and rocky serpentine outcrops with a sparse native herb cover. We treated these three habitats as a natural gradient of increasing abiotic stress and decreasing aboveground productivity and competition, respectively. We hypothesized that both the abundance and the individual performance of *V. microstachys* would be highest in the intermediate habitat, serpentine meadows, because in this habitat neither aboveground competition nor abiotic stress would be maximal. We tested this through field surveys and experiments in which *V. microstachys* was planted into cleared and uncleared plots in each habitat. We used a reciprocal design in which seeds from each habitat were planted into plots in each habitat, so that we could also study local adaptation to biotic and abiotic conditions in the three environments.

Materials and methods

Study System

The study was conducted at the Donald and Sylvia McLaughlin University of California Natural Reserve (Napa and Lake County, Calif.; 38°52'N, 122°25'W), approximately 120 km north of San Francisco. Elevations range from 370 to 945 m. Geologic substrates include ultramafic and mafic rocks of the Coast Range Ophiolite (serpentine, peridotite, gabbro and greenstone), sandstones and shales of the Mesozoic Great Valley Sequence, and Quaternary Clear Lake volcanics. The geology, soils and vegetation of the site are described by University of California – Davis, Natural Reserve System (2000; see also <http://nrs.ucop.edu/reserves/mclaughlin/naturalhis/NaturalHistory.htm>). Species diversity in serpentine and nonserpentine grasslands at the site has been studied by Harrison (1999) and Safford and Harrison (2001).

Nonserpentine grasslands occur on loams formed from sandstones, mudstones and shales (Maymen, Millsholm, Lodo, Bressa and Dibble soil series). These grasslands intergrade with blue oak (*Quercus douglassi*) savanna and woodland and are dominated by non-native, annual grasses (e.g., *Avena fatua*, *Avena barbata*, *Bromus hordeaceus*, *Lolium multiflorum*, *Taeniatherum caput-medusae*), mixed with native and non-native forbs. Serpentine meadows in this area occur on loams and clay loams formed from serpentine and related mafic to ultramafic parent materials (Henneke, Montara and Okiota soil series) and soils vary from deep clays to shallow rocky slopes. Serpentine grasslands support a mixture of native and non-native grasses, with a variety of native (some endemic) forbs. The non-native component is considerably lower than in nonserpentine grasslands (Harrison 1999; Safford and Harrison 2001).

Rocky serpentine slopes are open areas within a matrix of serpentine chaparral, found on skeletal soils of the Henneke series. Herbaceous cover is sparse, and there are numerous serpentine endemics (e.g., *Streptanthus breweri*, *Calystegia collina*). The most common grasses are the native perennials *Elymus elymoides* and *Melica* spp.; one of the few non-native grasses present is *Bromus madritensis*.

Vulpia microstachys (Nutt.) Benth. is a cleistogamous annual grass native to western North America (Lonard and Gould 1974; Hickman 1993). *V. microstachys* germinates in November to February, matures and flowers in April to May, and sets seed in May to July (Joffe 1990; Joffe et al. 1987).

Survey of natural populations

To assess natural patterns in the abundance and performance of *V. microstachys*, we established 60 transects in the spring of 1998

and 1999. We identified five blocks containing adjacent nonserpentine grassland, serpentine meadow, and rocky serpentine slope habitat. In each block, we established four 50-m transects in each habitat. The location of each transect was randomly selected after stratification of the site into four sections, with a distance between transects of >100 m. We placed five 1×0.4-m quadrats at 10-m intervals along each transect.

Within each quadrat, we recorded total plant cover, cover and identity of invasive exotic plants, cover of *V. microstachys* and cover of bare areas or rock, using Daubenmire cover classes (Bonham 1989). To measure aboveground biomass, a 0.5×0.2-m quadrat was randomly located within the larger quadrat and live and dead material was clipped and collected. At each transect we recorded slope, aspect, and noted three categories of incidence (low, medium, high) for gopher mounds and grazing. We collected soils by scraping off the top 2 cm to remove litter, and gathering 100 g soil at ≤20 cm depth from each quadrat. Soil samples were analyzed at A and L Western Agricultural Laboratories (Modesto, Calif.). Analyses included organic matter (% OM); available P (Bray-P); K (K), Ca and Mg (Ca, Mg) using ammonium acetate extraction and absorption/emission spectrometry; pH, and cation exchange capacity (CEC). Ca and Mg were analyzed as the log-transformed Ca/Mg ratio.

We analyzed the soil data with respect to habitat using multivariate ANOVA (MANOVA) for a blocked design. We then used Scheffe's *F*-test to examine differences between each pair of habitats. We analyzed the effect of habitat on biomass using ANOVA for a blocked design, first power-transforming biomass to improve its normality (Hinz and Eagles 1976). We again used Scheffe's *F*-test to analyze differences between each pair of habitats. Scheffe's *F*-test (1959) was chosen as it is a relatively conservative multiple comparison test, controlling for maximum experiment-wise error rate for all sets of contrasts (Steele et al. 1997). For total, invasive and *Vulpia* cover, data were non-normal even after transformation, so we used the nonparametric Kruskal-Wallis' test to examine the effect of habitat on these variables.

To assess growth and seed production, we randomly selected ten plants in each of 50 transects in spring 1998. We used the same five blocks as for the 1998 cover and biomass data, and again randomly selected transects at sites >100 m apart. For the serpentine meadow and rocky serpentine habitats, we were able to sample at four independent locations in each block. For nonserpentine grassland, we were restricted to two independent sampling localities per block, due to the sparsity of *V. microstachys*. For each *V. microstachys* specimen, we measured height (defined as total height of all tillers), biomass, seed number, and average seed weight. We also measured the height of two randomly selected neighbors for each specimen, to ensure that we were not oversampling taller, more apparent *V. microstachys* specimens (our data revealed no such sampling bias).

Using MANOVA for a blocked design, we analyzed height, seed number, seed weight, and power-transformed biomass with respect to habitat type. Protected ANOVAs were then used to analyze the significance of habitat for each independent variable, and multiple comparisons were made using Scheffe's *F*-test.

Field experiment

To disentangle the roles of abiotic factors, competition and ecotypic differentiation, we conducted a field experiment with habitat, clearing, and seed source as the treatments. We used a split-split plot design, again using five blocks that each contained adjacent areas (plots) of the three habitats. Within each of these plots, we stratified and randomly chose three 1.5×1-m subplots >100 m apart. Within each subplot, the 0.5×1-m areas at either end were randomly assigned to cleared and uncleared treatments, with the middle area as a buffer zone. Within each 0.5×1-m area we randomly assigned one-third (0.33×0.5 m) to each of the three seed-source treatments.

In each area designated for the cleared treatment, we first clipped all plants to within 2 cm of the ground and then sprayed

with glyphosate (Roundup; 96%; Monsanto), between 15 and 24 December 1998. We planted *V. microstachys* in the 45 experimental plots between 30 December and 8 January 1999. The seeds were harvested from 200 maternal plants for each habitat, using the plants collected in the 1998 survey; we pooled seeds within each source habitat to create a representative sample. For each treatment combination, we planted 12 seeds, equally spaced across the 0.33 m×0.5 m area. To identify planted seeds, each seed was surrounded by two toothpicks or straightpins.

Every 10 days, we recorded number of emerging and surviving plants, plant height, number of tillers, and days to flowering. For cleared treatments, we continually removed all germinating plants excluding the focal *V. microstachys*. At each monitoring date we noted evidence of herbivory and/or disturbance. At maturity, surviving plants were harvested and we recorded dry aboveground biomass, number of tillers, height of tillers, seed set, and seed weight on a per plant basis.

We analyzed the results for emergence and survival in a MANOVA for a split-split plot design, with habitat, clearing, and source as independent variables. We then used protected ANOVAs to examine individual effects on emergence and survival, and made multiple comparisons using Scheffe's *F*-test. We performed the same set of analyses on the seed number, height and biomass of surviving individuals on a per plant basis. Height and seed number were power-transformed (Hinz and Eagles 1976), and biomass was log-transformed.

Results

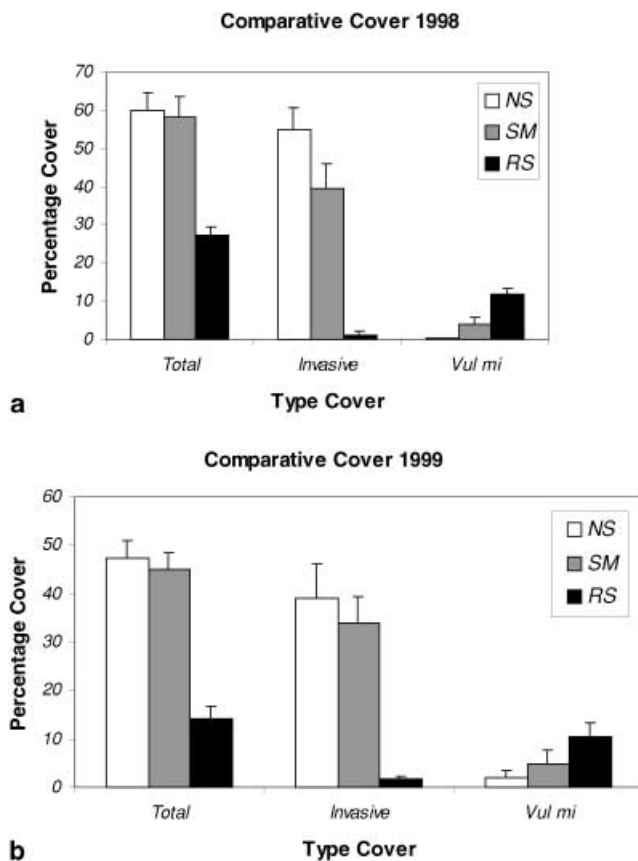
Survey

Soil attributes varied significantly among habitats (MANOVA, Wilks' lambda=15.03, $P<0.001$). OM, P, and Ca/Mg ratio were significantly higher and pH lower in nonserpentine grasslands than in serpentine meadows or rocky serpentine slopes; OM, K and CEC were higher in serpentine meadows and nonserpentine grasslands than in rocky serpentine slopes (Table 1; ANOVAs for overall differences, $P<0.01$; Scheffe's tests for pairwise differences, $P<0.05$).

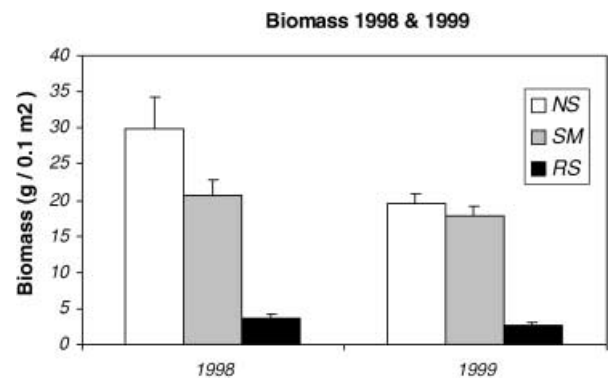
Total, invasive, and *Vulpia* cover varied significantly among the three habitats in both 1998 and 1999 (Kruskal-Wallis' tests, $P<0.01$; Fig. 1). In both years, total and invasive cover were significantly lower in rocky serpentine slope than serpentine meadow or nonserpentine grassland (Bonferroni-adjusted *t*-tests with overall $\alpha=0.05$, per comparison $\alpha=0.008$). Differences between serpentine meadow and nonserpentine grassland were significant (where $\alpha=0.05$) for invasive cover ($P=0.013$) and *V. microstachys* cover ($P=0.017$). In 1998, *V. microstachys* cover was significantly lower in nonserpentine grassland than in rocky serpentine slopes; in 1999, *V. microstachys* cover was significantly lower in nonserpentine grassland than in either rocky serpentine slopes or serpentine meadow (Fig. 1). Cover of *V. microstachys* was negatively correlated with total biomass, total cover and invasive cover, and positively correlated with the Ca/Mg ratio (Pearson's correlation coefficients=−0.83, −0.82, −0.91, 0.74 in 1998; −0.83, −0.63, −0.83, 0.66 in 1999). Total and invasive cover and biomass were negatively correlated with Ca/Mg (Pearson's correlation coefficients=0.68, 0.48, 0.62 in 1998; 0.55, 0.39, 0.48 in 1999).

Table 1 Soil attributes of the sites. OM Organic matter, CEC cation exchange capacity

Habitat	Block	OM	P	K	Ca/Mg	pH	CEC
Serpentine	Blueridge	2.575	2.25	66.75	0.2	7.275	22.15
Serpentine	Researchhill	4	6.25	180.5	0.19	6.925	24.85
Serpentine	Slurryline	3.6	3.75	251.25	0.22	6.95	41
Serpentine	Sweeney	3.25	6.25	232	0.24	6.75	35.125
Serpentine	Tailingspond	2.9	2	218	0.18	7.15	34.075
Rocky slopes	Blueridge	1.675	1.5	38.5	0.31	7.475	15.9
Rocky slopes	Researchhill	2.8	5	59	0.16	7.3	13
Rocky slopes	Slurryline	1.975	4.75	71	0.13	7.15	16.95
Rocky slopes	Sweeney	2.025	3.25	52.5	0.12	7.025	13.85
Rocky slopes	Tailingspond	1.975	2	39.5	0.11	7.225	13.875
Nonserpentine	Blueridge	3.35	7.25	200.5	1.02	6.875	25.875
Nonserpentine	Researchhill	4.55	12.75	218.75	0.97	6.25	23.925
Nonserpentine	Slurryline	4.675	7.5	234.75	0.84	6.55	29.95
Nonserpentine	Sweeney	3.15	16.5	149.5	1.88	6.125	19.975
Nonserpentine	Tailingspond	4.225	11.25	175.5	0.98	6.05	16.825

**Fig. 1** Total, invasive, and *Vulpia microstachys* (Vul mi) cover in the three habitats, nonserpentine grasslands (NS), serpentine meadows (SM), and rocky slopes (RS), as surveyed in **a** 1998 and **b** 1999

Total biomass also varied significantly among habitats (ANOVA, $F=110.18$, $df=2$, $P<0.001$ for 1998; $F=105.8$, $df=2$, $P<0.001$ for 1999). Biomass was lower on rocky serpentine slopes than in serpentine meadows or nonserpentine grasslands in both years; serpentine meadow and nonserpentine grassland differed in biomass in 1998 but not 1999 (Scheffe's tests, $\alpha=0.05$; Fig. 2).

**Fig. 2** Total biomass (g) per 0.1 m² in the three habitats, NS, SM, and RS, as surveyed in 1998 and 1999. For abbreviations, see Fig. 1

Cover of *V. microstachys* was negatively correlated with biomass, total cover and invasive cover, and positively correlated with the Ca/Mg ratio (Pearson's correlation coefficients = -0.83, -0.82, -0.91, 0.74 in 1998; -0.83, -0.63, -0.83, 0.66 in 1999). Total and invasive cover and biomass were negatively correlated with Ca/Mg (Pearson's correlation coefficient = 0.68, 0.48, 0.62 in 1998; 0.55, 0.39, 0.48 in 1999).

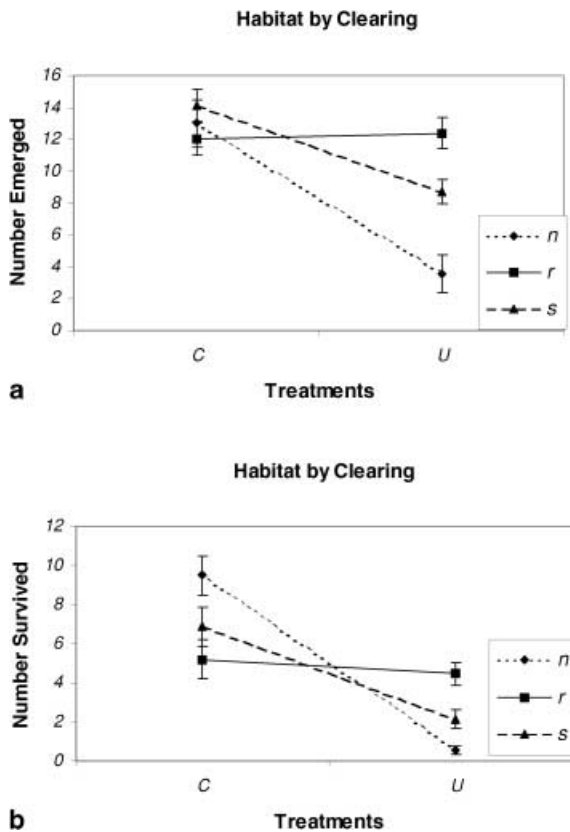
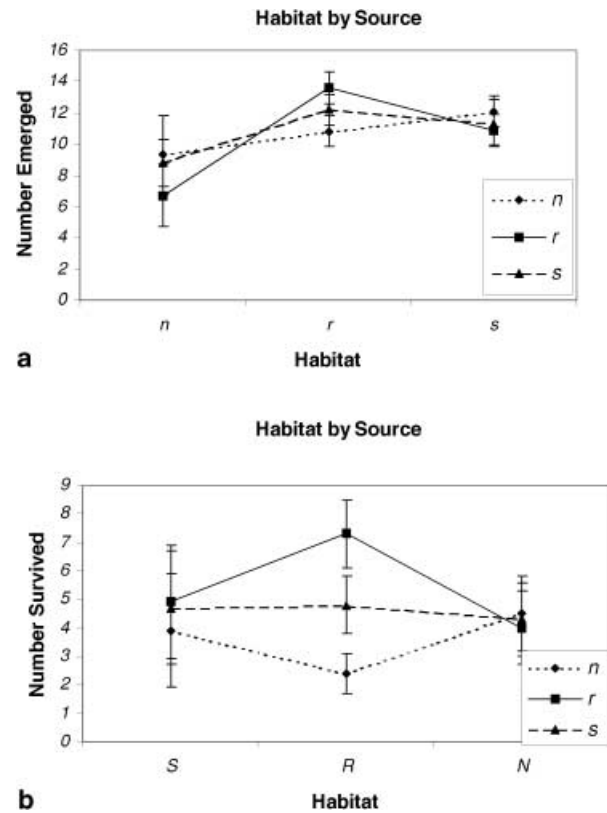
Total height, biomass and seed number of *V. microstachys* individuals varied among habitats (Table 2; MANOVA, $F=21.1$, $df=2$, $P<0.001$ for height; $F=7.1$, $df=2$, $P=0.02$ for seed number; $F=63.8$, $df=2$, $P<0.001$ for biomass). Total height was highest in serpentine meadows and lowest in rocky serpentine slopes, while seed number and biomass were highest in nonserpentine grassland and lowest in rocky serpentine slopes. Mean seed weights showed no significant differences among habitats.

Experiment

Emergence and survival of experimental plants varied significantly by block, habitat, clearing (i.e., cleared or

Table 2 Biomass, seed number and height of *Vulpia microstachys* among habitats

Habitat	Block location	Biomass (g)	Seed number	Height (cm)
Serpentine	Blueridge	0.14	27.8	37.7
Serpentine	Slurryline	0.11	36.3	39.0
Serpentine	Sweeney	0.09	29.7	31.0
Serpentine	Researchhill	0.09	25.6	24.9
Serpentine	Tailingspond	0.06	18.7	22.2
Rocky slopes	Blueridge	0.04	14.6	15.6
Rocky slopes	Slurryline	0.04	12.0	12.0
Rocky slopes	Sweeney	0.05	16.8	13.7
Rocky slopes	Researchhill	0.05	17.6	13.3
Rocky slopes	Tailingspond	0.03	10.5	9.3
Nonserpentine	Blueridge	0.14	41.4	37.6
Nonserpentine	Slurryline	0.10	20.8	25.7
Nonserpentine	Researchhill	0.10	25.0	23.1
Nonserpentine	Tailingspond	0.06	29.8	29.4

**Fig. 3** Effect of the habitat×clearing interaction on **a** emergence and **b** survival for experimental *V. microstachys*. Habitats are nonserpentine (*n*), serpentine meadows (*s*), and rocky slopes (*r*). Clearing treatments are cleared (*C*) and uncleared (*U*)**Fig. 4** Effect of the habitat×source interaction on **a** emergence and **b** survival for experimental *V. microstachys*. Habitats and seed sources are nonserpentine (*n*; *N*), serpentine meadows (*s*; *S*), and rocky slopes (*r*; *R*). For other abbreviations, see Fig. 3

uncleared treatment), seed source, source×habitat, block×habitat, habitat×clearing, and block×clearing×habitat (MANOVA, $P < 0.05$ for source and source×habitat, $P < 0.001$ for other variables). While clearing had no effect in rocky serpentine slopes, it significantly increased emergence and survival in both nonserpentine grasslands and serpentine meadows (Figs. 3, 4). Emergence and survival were lowest in uncleared nonserpentine grassland, and highest in cleared nonserpentine grassland (Figs. 3, 4). Emergence and survival of seeds from rocky serpentine

slopes were higher when these seeds were planted in that habitat than when they were planted in the other two habitats; likewise, when planted on rocky serpentine slopes, seeds from rocky serpentine slopes had higher emergence and survival rates than seeds from the other two habitats (Figs. 3, 4).

Height, seed number and biomass of experimental plants were significantly affected by habitat, clearing and the habitat×clearing interaction (overall MANOVA, $P < 0.01$; individual ANOVAs, $P < 0.05$). The effect of

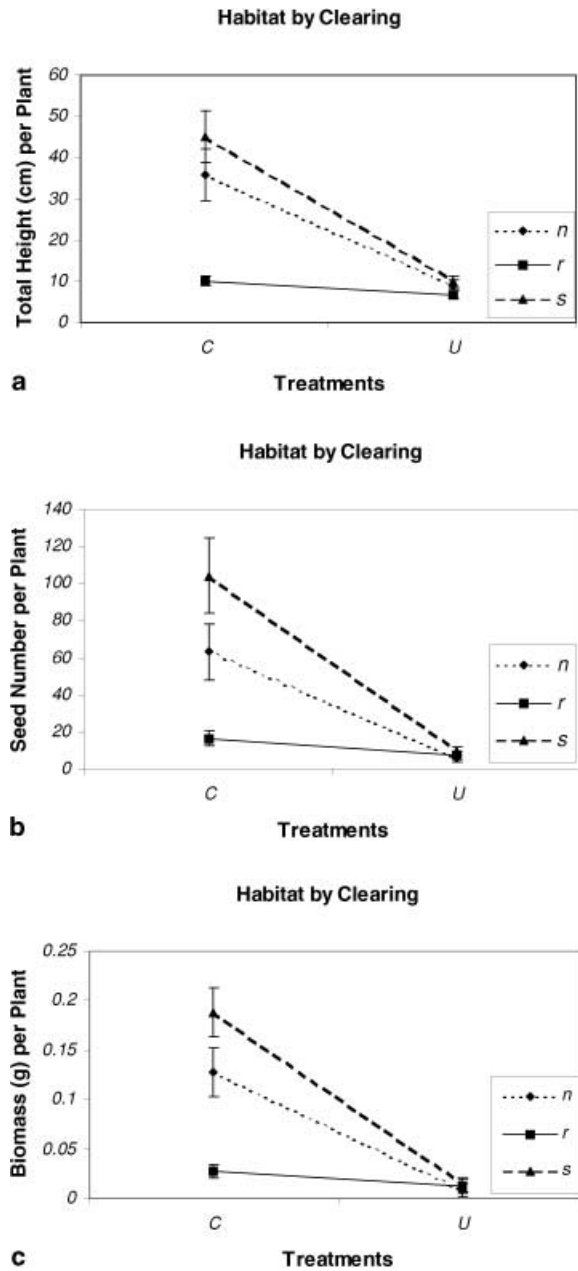


Fig. 5 Effect of the habitat \times clearing interaction on **a** total height (cm) per plant, **b** seed production per plant, and **c** total biomass (mg) per plant for experimental *V. microstachys*. Habitats are n, s, and r. Clearing treatments are C and U. For abbreviations, see Figs. 3 and 4

habitat \times clearing on height and seed number was similar to the effect of this interaction on growth and survival. Clearing had no effect on rocky serpentine slopes, but led to significantly greater height, biomass and seed number in nonserpentine grasslands and serpentine meadows (Fig. 5). In uncleared plots, growth and reproduction did not differ across habitats; in cleared plots they were highest in nonserpentine grassland and lowest on rocky serpentine slopes.

Discussion

As we expected, the harshness of the abiotic environment experienced by *V. microstachys* was lowest in nonserpentine grassland and highest on rocky serpentine slopes, while the effect of competitor removal followed the reverse pattern. Yet the abundance and individual performance of *V. microstachys* did not show the predicted peak in the supposedly intermediate habitat, serpentine meadow. Across the three habitats, *V. microstachys* showed considerable variation in demographic parameters, evidently caused by both ecotypic adaptation and phenotypic plasticity. None of the three habitats was optimal for emergence, survival, growth and reproduction. We discuss each of these issues in turn.

Survey data indicated a general decrease in soil nutrients and OM in the predicted direction. Some soil variables were significantly different between nonserpentine grassland and serpentine meadow (OM, pH, Ca/Mg, P), while others were significantly different between serpentine meadow and rocky serpentine (OM, K). Biotic variables generally followed the opposite pattern, with total and invasive cover higher in nonserpentine grassland and serpentine meadow than on rocky serpentine slopes. Surprisingly, although serpentine meadow and nonserpentine grassland differed in their soil attributes, including their Ca/Mg ratio, we did not find strong differences in total or invasive cover between these two habitats; however, in 1998 there was a significant difference in both biomass and invasive cover in the expected direction.

Experimental results corroborated the survey data in demonstrating that the habitats varied in the intensity of abiotic and biotic factors. Height, biomass and seed number of experimental plants were significantly lower in rocky serpentine than in serpentine meadow and nonserpentine grassland, when averaged over clearing and source effects. However, there were significant positive effects of clearing, and a habitat \times clearing interaction, demonstrating that the effects of competition varied both among habitats and among life stages. Emergence was lower in serpentine meadow and nonserpentine grassland in the presence of competition, but was roughly equal across habitats when competition was absent. Growth and seed production did not vary among habitats in the presence of competition, but were highest in serpentine meadow and nonserpentine grassland when competition was absent. Survival was lowest in serpentine meadow and nonserpentine grassland in the presence of competition, yet highest in these habitats when competition was absent. Thus, it appeared that emergence was reduced by the presence of competitors in the higher-biomass environments, but was not affected by the soil variation among environments; growth, seed production and survival were affected by both competitors and soil. Our results agree well with earlier studies that demonstrate that competitive effects vary both among life stages and among habitats (e.g., Morris and Wood 1989, Bertness and Yeh 1994; Callaway et al. 1996).

Significant effects of seed source indicated that some of the observed phenotypic variation in *V. microstachys* among habitats could be genetically based. The lack of differences in seed weight among habitats argues against maternal effects. Emergence and survival were higher for seeds from rocky serpentine, grown in rocky serpentine, than for either the same seeds grown in another habitat or seeds from another habitat grown on rocky serpentine slopes. Growth and seed production, however, did not differ among seed source treatments, indicating that all variation among habitats in these parameters was the result of phenotypic plasticity. The phenotypic responses of *V. microstachys* to environmental variation appeared to exemplify "tolerance plasticity", i.e., the ability to grow and reproduce at reduced size under unfavorable conditions (Morrisset and Boutin 1984; Taylor and Aarssen 1988).

We were clearly incorrect in predicting that *V. microstachys* would grow best and be most abundant in the supposedly intermediate habitat, serpentine meadow. One flaw in this prediction was the expectation that serpentine meadows would be a substantially harsher environment than nonserpentine grasslands, which was not well supported by our data. A more basic missing element in our prediction was the recognition of individual variability and its demographic consequences. In the abiotically harsh habitat of rocky serpentine slopes, *V. microstachys* shows evidence of local adaptation that increases its ability to germinate and survive, as well as of phenotypic plasticity that enables it to reproduce at small size. These two forms of variation result in abundant populations of small individuals with few seeds. In the two richer habitats, serpentine meadow and nonserpentine grassland, competition strongly reduces emergence and survival, but phenotypic plasticity enables the few survivors to take advantage of the richer soils, leading to sparse populations of large individuals with many seeds. With such strikingly different demographic patterns, we may expect *V. microstachys* populations on varying soils to respond very differently to yearly weather variation (cf. Armstrong and Huenneke 1992) and other perturbations.

Our results reinforce the conclusions of earlier studies in several respects. We found the factors that affect abundance and performance to vary along environmental stress gradients (e.g., Connell 1961). We found more consistent effects of competitor removal on soils with higher nutrient levels and biomass (e.g., Grime 1979; Keddy 1989; Gurevitch 1990). We also found that local ecotypic adaptation is an important factor in allowing species to exist on a range of soils (e.g., Kruckeberg 1967, 1984). However, our results are also unique in several ways; for example, few previous authors have examined the relative contributions of ecotypic variation and phenotypic plasticity, acting at different life stages, in enabling plants to deal with varying levels of biotic versus abiotic stress. Also, although many studies have examined serpentine versus nonserpentine ecotypes, few have determined whether ecotypes form in response to

soil variation within serpentine (for one exception see Rajakaruna and Bohm 1999). More generally, 40 years after Connell's (1961) landmark study, there is still a need for studies that disentangle the abiotic and biotic, ecological and evolutionary factors that control species distributions; the results of such studies may well continue to overturn simple generalizations.

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