COMPETITION, SEED LIMITATION, DISTURBANCE, AND REESTABLISHMENT OF CALIFORNIA NATIVE ANNUAL FORBS

Eric W. Seabloom,[1] Elizabeth T. Borer,[2] Virginia L. Boucher,[2,3] Rebecca S. Burton,[1,4] Kathryn L. Cottingham,[1,5] Lloyd Goldwasser,[2,6] Wendy K. Gram,[1,7] Bruce E. Kendall,[1,8] and Fiorenza Micheli[1,9]

[1]*National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara,
California 93101-5504 USA*
[2]*Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106 USA*

Abstract. Invasion by exotic species is a major threat to global diversity. The invasion of native perennial grasslands in California by annual species from the southern Mediterranean region is one of the most dramatic invasions worldwide. As a result of this invasion, native species are often restricted to low-fertility, marginal habitat. An understanding of the mechanisms that prevent the recolonization of the more fertile sites by native species is critical to determining the prospects for conservation and restoration of the native flora. We present the results of a five-year experiment in which we used seeding, burning, and mowing treatments to investigate the mechanisms that constrain native annuals to the marginal habitat of a Californian serpentine grassland. The abundance and richness of native species declined with increasing soil fertility, and there was no effect of burning or mowing on native abundance or richness in the absence of seeding. We found that native annual forbs were strongly seed limited; a single seeding increased abundance of native forbs even in the presence of high densities of exotic species, and this effect was generally discernable after four years. These results suggest that current levels of dominance by exotic species are not simply the result of direct competitive interactions, and that seeding of native species is necessary and may be sufficient to create viable populations of native annual species in areas that are currently dominated by exotic species.

Key words: California grasslands; community; competition; disturbance; environmental gradients; exotic species; fire; invasion; microsite limitation; restoration; seed limitation; serpentine.

INTRODUCTION

Invasion by exotic species is one of the major threats to global diversity (Mooney et al. 1986, Drake et al. 1989, Mills et al. 1994, Hobbs and Humphries 1995, Lodge et al. 1998), and exotic species currently constitute a major component of many regional floras. For example, about 20% of California's vascular-plant taxa are exotic species (Stein et al. 2000). In heavily invaded landscapes, native species are often restricted to small,

refugial populations in marginal habitat (McNaughton 1968, Mooney et al. 1986, Murphy and Ehrlich 1989, Harrison 1997, 1999*a, b*). This spatial isolation raises further issues for management and restoration of native communities. These populations may be particularly susceptible to extinction, because inbreeding depression and stochastic events (Lande 1993, Mills and Smouse 1994, Brown et al. 1996) can exacerbate the effect of the original invasion.

Here, we present the results of a study designed to isolate the mechanisms that have led to the exclusion of a suite of native annual forbs from a heavily invaded grassland in southern California, USA. The invasion of California grasslands is one of the most dramatic invasions worldwide (Baker 1978, Mooney et al. 1986, Armstrong and Huenneke 1992). Nearly all of the original 9.2×10^6 ha of the grasslands in California are currently dominated by annual grasses and forbs introduced from the Mediterranean region (Heady 1977, Baker 1978, Jackson 1985, D'Antonio and Vitousek 1992). As a result, many native species have been extirpated from more fertile sites and are restricted to patches of low-fertility, serpentine-derived soils (''hummocks''), which the exotic species are generally not able to invade (Murphy and Ehrlich 1989, Huenneke et al. 1990, Harrison 1997, 1999*a, b*). The soils

on these outcrops are characterized by low calcium to magnesium ratios and high concentrations of toxic heavy metals (Walker 1954, Proctor 1971, Proctor and Woodell 1975, Brooks 1987). In addition, these soils are usually shallow, rocky, and nutrient poor (Huenneke et al. 1990; Gram et al., *in press*).

As is the case elsewhere, a major restoration and conservation challenge for California grasslands is to develop management plans to (1) stop the continued spread of the exotic species into the native refugia, and (2) increase the regional abundance of the threatened species. With regard to the first goal, it is clear that tolerance of low nutrient conditions (Huenneke et al. 1990, Harrison 1999*b*) and drought (Heady 1956*a, b*, 1958, Pitt and Heady 1978, Hobbs and Mooney 1991) are critical elements in maintaining native dominance on serpentine hummocks. However, few studies have examined the ability of native species to reinvade the more fertile sites that are currently dominated by exotic species, which would facilitate the second goal.

In this study, we used a field experiment to investigate the mechanisms that prevent the reinvasion of the more fertile matrix habitat by native forbs, an under-studied component of the California grassland flora. In California, most of the grassland-restoration research focuses on developing techniques to establish a dense stand of perennial grasses (Stromberg and Griffin 1996, Stromberg and Kephart 1996), despite the historical importance of the forb component in the native California grassland community (Wester 1981, Hamilton 1997, Schiffman 2000). This focus on perennial grasses is partially pragmatic; it is much easier to manage a grassland to exclude all annual species through the use of burning and herbicide, because perennial and annual species have such different life histories (Stromberg and Kephart 1996). In addition, rangeland managers are becoming interested in perennial grass restoration, because it may improve summer grazing and increase nutrient retention (Menke 1989, Adams et al. 1999).

The focus on perennial grasses also stems from a debate about the original nature of the California grassland communities; these systems were already dominated by invasive exotics by the middle of the 19th century, early enough that it is difficult to reconstruct their original character (Heady 1977, Wester 1981, Hamilton 1997). The most common view of California grasslands is based on the examination of relict stands and suggests that the community was dominated by perennial bunchgrasses (Clements 1934). However, more recent research suggests that the pre-European grasslands were not dense stands of perennial grasses, but rather a complex mosaic of perennial grasses, annual forbs, and shrubs (Wester 1981, Hamilton 1997). If native annuals were the dominant species in these systems due to the continual perturbation of the soil by animals and the vagaries of the climate (as suggested by Schiffman 2000), the establishment of dense stands

of perennial grasses would not constitute a successful restoration of the community.

While most empirical research on invasions has focused on exotic species invading largely native communities (D'Antonio and Vitousek 1992, Robinson et al. 1995, Stohlgren et al. 1999, Levine 2000, Smith and Knapp 2001; but see Tilman 1997), it is interesting to note that the procedures for determining the probability of successful reintroduction of a native species into a system dominated by exotic species are conceptually similar to determining the probability of an exotic species invading a native community. Both scenarios involve finding the conditions under which population growth rates are positive for low population densities (Macarthur and Levins 1967, Gurney and Nisbet 1998). We apply invasion theory to restoration ecology in order to understand the mechanisms that could promote the reestablishment of native forbs in extant stands of exotic annual grasses.

The practicality of restoring a native community depends directly on the mechanisms by which the exotics competitively exclude the native flora. Turnbull et al. (2000) point out that seed-addition experiments can help to distinguish the relative importance of seed limitation, microsite limitation, and environmental heterogeneity in determining community composition. The California grassland system is well suited to seed-addition studies because many species are annual, the growing season is short and synchronized by the onset of winter rains, and there is not a persistent seed bank (Bartolome 1979). For these reasons, community composition is closely linked to each seasonal recruitment event and can change more rapidly than in communities dominated by long-lived perennial species.

We begin by proposing three mechanisms by which exotic annual grasses persist as the numerically dominant species in California grasslands: (1) seed limitation, (2) microsite limitation, and (3) spatial and temporal heterogeneity.

Hypothesis 1: The native forbs are seed limited, such that the dominance of exotic species depends on their higher rates of seed production and delivery

Prediction.—Addition of seed of native species will increase the abundance of seeded species, because there are empty microsites available for colonization.

Justification.—If competitive abilities are similar across all species, then the outcome of each recruitment event depends, in part, on the abundance of recruits of each species (Chesson and Warner 1981, Fagerstrom and Westoby 1997), and the ultimate composition of the community depends on the production and delivery of seed. In this case, the addition of seeds can lead to a long-term increase in the abundance of the seeded species (Tilman 1997). However, competitive hierarchies may vary along abiotic gradients, such that seed additions may in-

crease populations only in specific cases (e.g., after a burn or in a low fertility site).

Implications.—In this case, the success of a restoration can be increased through seeding of the native species. This mechanism also suggests that manipulation of the abiotic environment will not be sufficient to ensure the success of a restoration if the native flora is not reintroduced to the site in sufficient density.

Hypothesis 2: The native forbs are microsite limited, such that exotic species exclude native species during establishment and growth

Prediction.—Addition of seeds of native species will not increase the abundance of the seeded species in the presence of exotic species, because there are more than enough recruits of the competitively dominant exotic species to fill the available microsites. In addition, we may expect removal of vegetation via burning or mowing to temporarily increase native abundance *in the absence of seed additions* (Shoulders 1994, Pollak and Kan 1998, Hatch et al. 1999, Meyer and Schiffman 1999) due to the concomitant increase in bare ground.

Justification.—If there is a surplus of potential recruits, then the competitive dominant will always win in competitive interactions acting during establishment and growth, making community composition independent of the recruitment pool. There are many cases in which species composition is determined by competitive hierarchies and the availability of microsites (e.g., bare ground) (Burke and Grime 1996, Turnbull et al. 2000, Suding and Goldberg 2001). For example, in their review of 40 seed-addition studies, Turnbull et al. (2000) found that in about 50% of cases the addition of seed did not alter the abundance of the seeded species. *H*2 is a plausible and widely accepted mechanism to explain the current dominance by annual exotics in California grasslands, because although the exotic species were not actively seeded, they spread rapidly through the landscape (Heady 1977).

Implications.—If an invasive species is the competitive dominant, then the mere presence of this species prevents the reestablishment of the native flora. This is an example of a stable invasion window created by the removal of a geographic barrier to competitively dominant species (Johnstone 1986). To the degree that dominance of exotic species is independent of seed availability, the reestablishment of the native flora will depend on the eradication of the exotic species and continued quarantine of the restored area, two difficult and costly ventures (Hobbs and Humphries 1995, Lodge et al. 1998). In this case, successful long-term reestablishment of native species is unlikely (Heady 1977).

Hypothesis 3: Environmental heterogeneity mediates competition for microsites during establishment and growth

Prediction.—In the absence of seed additions, the abundance of native species should change with natural abiotic heterogeneity (e.g., soil fertility and year-to-year changes in precipitation).

Justification.—Temporal or spatial heterogeneity in the environment (e.g., the ratio of limiting nutrients) may promote coexistence, even under the case of strict competitive hierarchies (Chesson and Warner 1981, Tilman 1982). If the competitive hierarchy varies along an abiotic gradient, we may expect the relative abundance of different taxa to vary along that gradient or in response to interannual environmental changes, even in the absence of seed additions. Previous studies in California serpentine grasslands indicate that native species are more successful than exotic invaders in nutrient-poor sites (Huenneke et al. 1990) and in years of below average rainfall (Hobbs and Mooney 1991).

Implications.—Under *H*3, successful restoration of native species is primarily dependent on reestablishment of appropriate abiotic conditions. If the dominance hierarchy is dependent on an abiotic factor that can be manipulated to favor the native component of the community (e.g., burning frequency, hydrology, or nutrient availability), then reestablishment of native species will be much more likely under *H*3 than under *H*2. Furthermore, *H*3 implies that natural colonization will be sufficient to ensure the successful restoration of a native community once abiotic conditions are manipulated.

We report results of an experiment to evaluate plant community dynamics in response to three factors: proximity to native-dominated hummocks (1 m or 10 m), the application of three levels of vegetation removal (Control, Mowing, or Burning), and seeding of two native annual forbs, *Plantago erecta* (Plantaginaceae) and *Lasthenia californica* (Asteraceae). We use the results of our seed-addition experiments to distinguish between the three mechanisms (*H*1, *H*2, *H*3) by which exotic annual grasses may maintain their numerical dominance in California grasslands. Finally, we discuss the implications of our findings for long-term success of restoration of the native annual forb populations in California grasslands.

METHODS

Study site

Our study was conducted on the 2364-ha University of California Sedgwick Reserve, which lies ~50 km northeast of Santa Barbara, California, USA. The experiments were conducted in the upper portion of the reserve (~730 m in elevation) on a south-facing slope. The site was grazed more or less continuously from at least the late 1800s until cattle were removed in 1996. The soils are largely serpentine in origin and the landscape is dominated by a series of distinct rocky outcrops or "hummocks" surrounded by exotic-dominated grasslands or "matrix." The soils on these hummocks are shallow and infertile, with low cation ex-

TABLE 1. Results of principal components analysis of nine soil metrics and standing crop at the end of the five-year experiment investigating the constraint on native annuals in a California serpentine grassland.

| | Eigenvector | |
| | PC1 | PC2 |
Variable	(Cation Axis)	(Fertility Axis)
Biomass (g/m^2)	−0.145	0.539
Percent organic matter	−0.265	0.397
Phosphorus (ppm)	−0.369	0.072
Calcium (mol/kg)	0.376	0.171
Magnesium (mol/kg)	0.363	−0.100
Percent clay	0.391	0.053
Nitrogen (mg N/kg soil)	0.104	0.496
Percent sand	−0.379	−0.159
Cation exchange capacity	0.430	0.024
pH	0.080	0.482

Notes: PCI accounts for 51.6% of variance in the ten variables, and PC2 accounts for 28.9% of variance. Each variable represents the composite of six 1-m^2 plots. The eigenvectors indicate the strength of the relationship between the source variables and the composite PCA axis: the larger the absolute value of the eigenvalue, the greater the contribution of that variable to the axis. Soil elements are expressed as parts per million parts of soil.

change capacity and high sand content, and the hummock plant community is dominated by native annual forbs (e.g., *Lasthenia californica*, *Plantago erecta*, *Gilia achilleifolia*, and *Coreopsis bigelovii*) and legumes (*Astragalus gambelianus*, *Lotus strigosus*, *Lotus wrangelianus*, and *Trifolium albopurpurea*). The soils in the surrounding matrix are deeper and more fertile, with higher concentrations of N, organic matter, and clay, and the plant community is dominated by exotic annual grasses (e.g., *Avena barbata*, *Bromus hordeaceus*, and *B. madritensis*) and forbs (e.g., *Lactuca serriola*, *Erodium cicutarium*, and *Medicago polymorpha*). Gram et al. (*in press*) provide detailed descriptions of how plant composition and soil characteristics vary along the hummock to matrix gradient.

Experimental design

The experiment used a fully randomized block design with four replicate blocks and three fully crossed treatments within each block: (1) distance from hummock boundary (1 m or 10 m; hereafter referred to as 1-m and 10-m plots), (2) vegetation removal (Control, Mowed, or Mowed and Burned), and (3) seeding of native forbs (Control or Seeded). The experimental unit

was a single 1-m^2 plot. The four replicate blocks were distributed across three separate hummocks (mean area = 3018 m^2); two blocks were at opposite ends of a single 6626-m^2 hummock. Within each of the eight unique combinations of distance and block (4 blocks × 2 distances), six 1-m^2 plots were arrayed in a line perpendicular to the hummock edge (two levels of seeding × three levels of vegetation removal) for a total of 48 plots.

Each spring from 1997 through 2001, we sampled the vegetation in each individual plot during the period of peak biomass, which occurs in the late spring. We used two sampling strategies: (1) direct counts of all stems of each native species within each plot, and (2) pinframe sampling to estimate the percent cover of all species (native and exotic), litter, bare ground, and rock. Each pinframe sample consisted of 36 vertical wires arrayed in a 10-cm grid in the center of each plot. We recorded the identity of all species that touched a wire.

We collected the first set of plant composition data in 1997, prior to any experimental manipulations. Following the sample collections in 1997 and 1998, we used hand shears to cut all vegetation in the plots assigned to the Mowed and Mowed-and-Burned treatments. This plant material was removed for the Mowing-only treatment and burned in situ for the Mowing-and-Burning treatment.

After applying the Mowing and Burning treatments in 1997, we added the seed of two native annual forbs that are common on the adjacent hummocks: *Plantago erecta* (Plantaginaceae) and *Lasthenia californica* (Asteraceae). These forbs are diminutive plants that, at our study site, reach a maximum height of ~10 cm and have their highest densities near the edges of hummocks (Gram et al., *in press*). We added an equal volume of dried seed of each species to each plot (~20 mL). We estimated the number of germinable seeds added to each plot by calculating the maximum seeding effect in 1998 after accounting for between-year change in abundance in the control plots (130.7 seeds/m^2 for *P. erecta* and 33.7 seeds/m^2 for *L. californica*).

Abiotic variables as covariates

In addition to sampling community composition, we collected soil chemistry and plant biomass data as abiotic covariates. In the fall of 1998, we collected a 20 cm deep soil core from the edge of each 1-m^2 plot. We

TABLE 2. ANOVA comparing the level of two principal components used as covariates across four blocks (hummocks) and two distances from the hummock edge (1 m and 10 m).

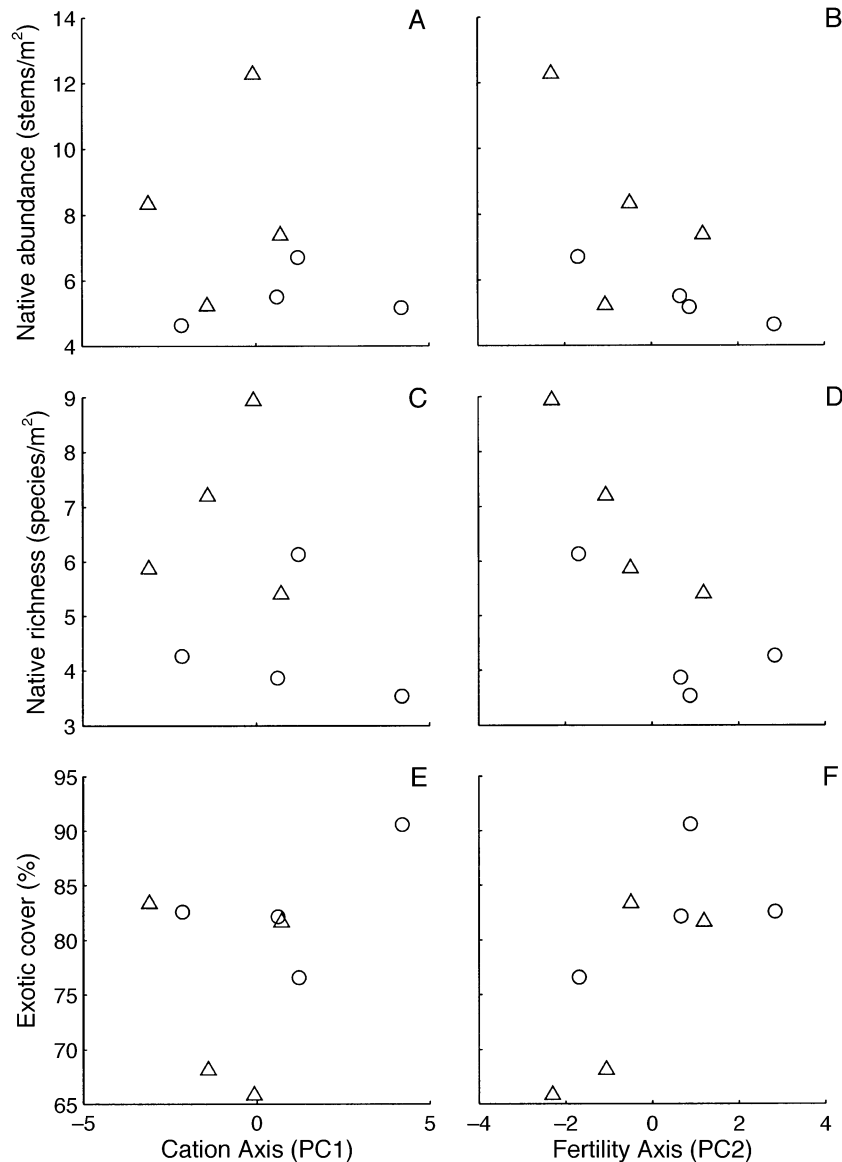| Source	df	PC1 (Cation Axis) ss	F	P	PC2 (Fertility Axis) ss	F	P
Block	3	22.100	3.370	0.173	11.690	2.380	0.248
Distance	1	7.489	3.420	0.161	3.587	2.190	0.236
Error	3	6.562			4.919		
Total	7	36.151			20.197		

FIG. 1. (A and B) Native abundance shows no relation to cation concentration ($r = -0.14$, $P = 0.596$) or fertility ($r = -0.647$, $P = 0.083$). (C and D) Native richness shows no relation to cation concentration ($r = -0.335$, $P = 0.417$) and declines with fertility ($r = -0.805$, $P = 0.016$). (E and F) Exotic species cover is unaffected by cation concentration ($r = 0.339$, $P = 0.412$) but tends to increase with fertility ($r = 0.704$, $P = 0.051$). The ordinates are two principal components (Cation Axis and Fertility Axis), which account for 80.5% of the original variability in the 10 original covariates. Data represent the mean across five years of plots that are either (triangles) 1 m or (circles) 10 m from the edge of a rocky serpentine outcrop.

combined the six cores from each of the eight block × distance combinations into a single sample. All soil samples were analyzed by A and L Western Agricultural Laboratories (Modesto, California, USA) for nitrogen, phosphorous (Weak Bray method), magnesium, calcium (soil elements expressed as parts per million parts of soil), soil pH, cation exchange capacity ($mol_c/$ 100 g), percent sand, percent silt, percent clay, and percent organic matter. At peak biomass in 2001, we clipped all aboveground vegetation from three regu-

larly spaced strips (10 × 100 cm) from each of the eight block × distance combinations. The three subsamples were combined and dried at 70°C until they reached constant mass and were weighed to the nearest 0.01 g.

Because of the high level of correlation among the various soil and biomass covariates, we used Principal Components Analysis (PCA) to reduce the dimensionality of the data. The first two principal components accounted for 80.5% of the variance in the ten original

ERIC W. SEABLOOM ET AL.

TABLE 3. Results of a MANOVAR testing for overall community-level response (Levels) to vegetation removal at two distances from a serpentine hummock.

Source	df	Native richness		Native abundance		Bare ground		Litter		Exotic cover	
		ss	P	ss	P	ss	P	ss	P	ss	P
PC1	1	0.005	0.898	15.702	0.595	0.276	**0.002**	0.147	**0.020**	0.069	0.123
PC2	1	0.001	0.959	43.599	0.380	0.175	**0.008**	0.163	**0.015**	0.020	0.393
Block	3	3.176	**0.037**	252.354	0.239	0.615	**0.001**	0.217	**0.048**	0.257	0.051
Distance (D)	1	0.879	0.098	94.940	0.203	0.477	**0.000**	0.261	**0.004**	0.119	**0.050**
Removal (R)	2	0.028	0.950	16.076	0.860	0.008	0.808	0.251	**0.014**	0.021	0.671
D × R	2	0.122	0.805	15.459	0.865	0.293	**0.005**	0.163	**0.047**	0.005	0.903
Error	13	3.605		687.148		0.231		0.271		0.330	

Notes: Values show the main effects of block, distance from hummock (1 m or 10 m), and vegetation removal (Control, Mowed, and Burned) on native richness (species/m^2), native abundance (stems/m^2), and percent cover of bare ground, litter, and exotic species. Results show the overall response across five years. Two principal components are included as covariates in the analyses: PC1 (Cation Axis) and PC2 (Fertility Axis). Values of P significant at the 0.05 level are shown in bold.

variables (Table 1). The first axis (PC1) was positively correlated with four variables related to soil cation concentration (Ca, Mg, cation exchange capacity, and percent clay) and negatively correlated with P. The second axis (PC2) was positively correlated with three measures related to soil fertility (standing crop, N, and percent organic matter), as well as pH. We refer to PC1 as the Cation Axis and PC2 as the Fertility Axis. Neither the Cation nor Fertility Axis was significantly related to block or distance from the hummock. However, block accounted for ~60% of the variability in each axis (Table 2), indicating that the abiotic variables vary strongly across the study site, but are similar among distance categories. We used these two axes as covariates in the statistical analyses (see *Methods: Statistical analysis*), though their inclusion did not affect the overall conclusions of the analyses.

We have only a single collection of soil and biomass data for each of the eight block × distance combinations. Thus, the covariates are statistically confounded with block and distance. For this reason, there are cases when neither covariate is statistically significant in models containing block and distance, yet there is a clear relationship between the covariate and the response variable. In general, removing the block effect from these models caused the covariates to become strongly significant, suggesting the importance of across-site abiotic gradients.

Statistical analysis

We used multivariate analysis of variance with repeated measures (MANOVAR) to test for effects of our treatments within and among years (Potvin et al. 1990, von Ende 1993). We follow the protocol described by von Ende (1993) for testing three hypotheses using the MANOVAR approach: levels, flatness, and parallelism. The levels hypothesis tests whether treatment means vary when averaged across years (e.g., does exotic cover differ in burned and unburned plots?). The flatness hypothesis tests whether there are significant changes over time when responses are averaged across treat-

ments (e.g., does exotic species cover change during the course of the experiment?). The parallelism hypothesis tests whether among-year changes in means differ among groups (e.g., does the change in exotic cover over time differ in burned and unburned plots?). A lack of parallelism is indicated by the presence of significant treatment by year interactions. In addition to the overall test for parallelism, we present the results of a series of contrasts that compare differences among all pairs of adjacent years for tests that have significant treatment by year interactions using the PROFILE transformation in SAS (SAS Institute, Cary North Carolina, USA). These contrasts indicate the source of year by treatment interactions.

Within the MANOVAR framework, there is a choice of tests for the time and time × treatment effects; we report results for Wilks' λ, but note that results were qualitatively similar for Pillai's Trace and the Hotelling-Lawley Trace. We used a square-root transformation on all count variables to stabilize the variance. All analyses were conducted in SAS (SAS Institute, Cary, North Carolina, USA).

Separate analyses were conducted for population vs. community response variables. We examined only the effect of distance and removal treatments on the five community-level variables: native richness (species/m^2), native abundance (stems/m^2), and percent cover of bare ground, litter, and exotic species. Exotic species abundance was measured as cover rather than stem counts because of the difficulty in distinguishing individual grass genets. We included only plots that did not have seed added in these analyses because we wanted to examine the effects of distance and vegetation removal on the community in the absence of seeding native species. The experimental seeding treatment may have masked the background changes in abundance in response to the other treatments. In contrast, we included all plots when determining the effect of distance, removal, and seeding on the two population-level variables: the abundance of the seeded native forbs, *P. erecta* and *L. californica*.
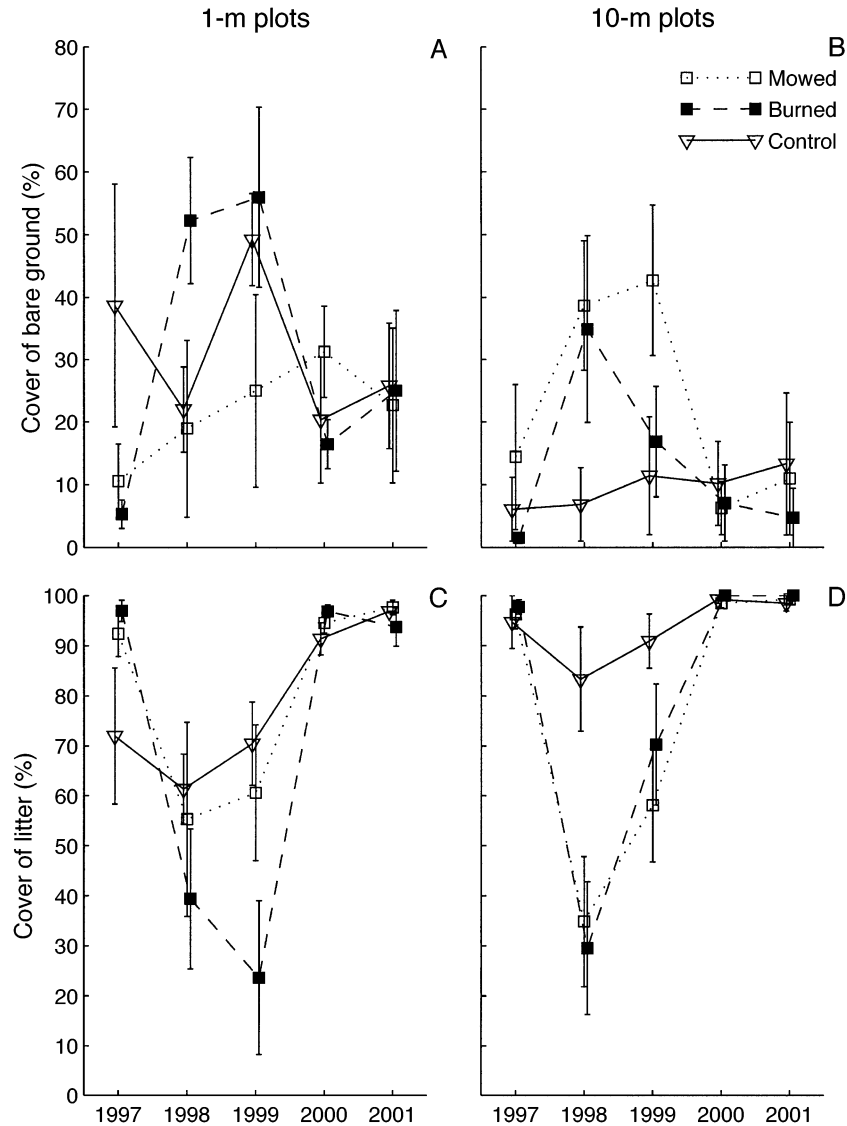
FIG. 2. Burning and mowing had no effect on (A and B) cover of bare ground and (C and D) litter in plots that were 1 m from the edge of a rocky outcrop (A and C) and they had transient effects in samples taken 10 m from the outcrop edge (B and D). The 10-m plots that were mowed or burned had more bare ground (B) and less litter (D) than did control plots in the years immediately following mowing and burning. These vegetation removal treatments were applied after the plots were sampled in 1997 and 1998. Error bars indicate ±1 SEM.

RESULTS

Community-level responses in the absence of seeding

Native richness and percent cover of exotic species were related to the abiotic covariates summarized by the Fertility Axis but not the Cation Axis (Fig. 1). However, as noted in the methods, these relationships were not significant in models that included block and distance effects (Table 3). Native richness and abundance tended to decline with increasing fertility (Fig. 1B, D). Soil fertility (PC2) affected native abundance only in the plots close to the hummocks: native abundance was always low in the 10-m plots, but declined

with increasing fertility in the 1-m plots (Fig. 1B). In contrast, exotic cover tended to increase with fertility regardless of distance (Fig. 1F).

The community response of natives was generally different from that of exotics, litter, and bare ground. Percent cover of bare ground, litter, and exotic species changed with distance from hummocks, but native richness and native abundance were constant (Table 3). Cover of bare ground was higher near the hummocks, whereas litter and exotic species were more prevalent in the 10-m plots (Table 3, Fig. 2). Vegetation removal (i.e., burning and mowing) only had a significant effect on cover of litter (Table 3), though this effect was tran-

TABLE 4. Results of a MANOVAR testing for Flatness and Parallelism in the community-level response to vegetation removal at two distances from a serpentine hummock.

Source	df	Native richness		Native abundance		Bare ground		Dead cover		Exotic cover	
		λ	P	λ	P	λ	P	λ	P	λ	P
Year (Y)	4	0.421	0.051	0.767	0.576	0.271	**0.007**	0.069	**0.000**	0.113	**0.000**
Y × PC1	4	0.808	0.674	0.969	0.986	0.433	0.058	0.419	0.051	0.316	**0.014**
Y × PC2	4	0.698	0.417	0.886	0.858	0.377	**0.032**	0.303	**0.012**	0.239	**0.004**
Y × Block	12	0.242	0.158	0.432	0.619	0.128	**0.019**	0.172	0.053	0.240	0.154
Y × Distance (D)	4	0.811	0.682	0.952	0.970	0.442	0.064	0.444	0.065	0.323	**0.015**
Y × Removal (R)	4	0.695	0.842	0.771	0.936	0.338	0.137	0.146	**0.005**	0.391	0.220
Y × D × R	4	0.543	0.540	0.670	0.803	0.261	0.054	0.283	0.073	0.439	0.311

Notes: Values show the among-year effects of block, distance from hummock (1 m or 10 m), and vegetation removal (Control, Mowed, and Burned) on native richness (species/m^2), native abundance (stems/m^2), and percent cover of bare ground, litter, and exotic species. Two principal components are included in the analysis: PC1 (Cation Axis) and PC2 (Fertility Axis). Values of *P* significant at the 0.05 level are shown in bold.

sient (Fig. 2, Tables 4 and 5). There were significant interactions between the distance and removal treatments for both bare ground and litter, as well (Table 3). Mowing had only a weak and transient effect on the cover of litter and bare ground in the 1-m plots in 1998–1999, and burning had a stronger, though still transient, effect on these vegetation metrics (Fig. 2, Table 5). These treatment effects attenuated rapidly after the cessation of the treatments and were not detectable in 2000 (Fig. 2). Exotic cover changed among years (Table 4), but after correcting for post-hoc analysis, none of the individual year differences was significant (Table 5).

There were strong differences in the community among the sampling years (Fig. 3), which were closely related to the dramatic differences in timing and amount of rainfall (Fig. 4). For example, the cover of exotics tracked rainfall, dropping dramatically from 1998, the wettest year of the study, to 1999, the driest (Fig. 3C). This drop in exotic cover was greatest in the plots close to the hummocks, as indicated by the significant year by distance interactions (Table 4).

Response of seeded species

The responses of our target species (*L. californica* and *P. erecta*) to the environmental covariates were similar to those of total native abundance in the absence of seeding (Fig. 5, Table 6). In the 1-m plots, density of both species declined with increasing fertility (Fig. 5B, D), while in the 10-m plots, both species were consistently low in abundance. Both species were more abundant in the plots 1 m from the hummock than in the 10-m plots. There were no significant relationships between the background abundance of *L. californica* ($r = 0.389$, $P = 0.341$) and *P. erecta* ($r = -0.012$, $P = 0.979$) and the magnitude of the seeding effect, suggesting that seeding treatments succeeded in establishing populations in microsites not previously occupied by these species.

The seeding treatment increased the abundance of both species (Fig. 6B, D), but the effects were more complicated for *L. californica* than for *P. erecta* (Table 7). Only the main effect of seed addition and the seed × year interaction were significant for *P. erecta* (Tables

TABLE 5. Profile analysis using contrasts to compare the effects of distance from hummock (1 m or 10 m) and vegetation removal (Control, Mowed, and Burned) on percent cover of bare ground, litter, and exotic species in adjacent years.

Variable and treatment	1997 vs. 1998	1998 vs. 1999	1999 vs. 2000	2000 vs. 2001
Bare ground				
Year (Y) × Distance (D)	0.031	0.758	0.037	0.263
Y × Removal (R)	**0.010**	0.072	0.486	0.738
Y × D × R	0.431	0.459	**0.002**	0.375
Dead cover				
Y × D	0.104	0.357	0.172	0.453
Y × R	0.013	0.926	**0.011**	0.223
Y × D × R	0.746	0.203	0.087	0.172
Exotic cover				
Y × D	0.028	0.106	0.904	0.381
Y × R	0.023	0.160	0.120	0.294
Y × D × R	0.137	0.698	0.767	0.211

Notes: Significant tests indicate that among-year changes varied across treatment groups. Contrasts are based on the MANOVAR analysis shown in Tables 3 and 4. Boldface comparisons are significant using a Bonferroni adjustment for four repeated tests ($\alpha = 0.0125$).
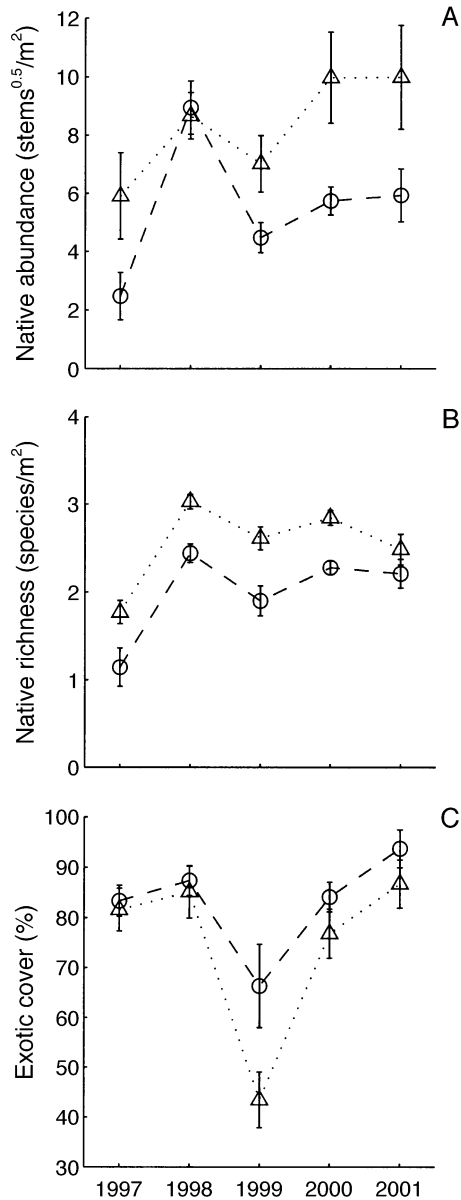
FIG. 3. (A) Native abundance and (B) richness were generally higher in plots 1 m from the edge of a rocky serpentine outcrop (triangles) than in those that are 10 m from the edge (circles). (C) Exotic species cover was lower in the 1-m plots. Exotic cover dropped in 1999, the year with lowest rainfall. Error bars indicate ±1 SEM.

6 and 7). The seed-addition treatment increased *P. erecta* abundance in all years and at both distances (Fig. 6C). Adding seed to the 10-m plots caused a persistent increase in the abundance of *P. erecta* to a level similar to that in unseeded 1-m plots. The interaction between seeding and year was caused by the dramatic density increase in seeded *P. erecta* plots in 1998 compared to the pretreatment plots in 1997 and unseeded plots in 1998 (Fig. 6, Table 8). The removal treatments had no detectable effect on *P. erecta* abundance across seeded

and unseeded plots (Fig. 7C, D, Table 6), and was invariant among years (Tables 7 and 8). The seeding effect for *P. erecta* was unrelated to the cover of exotics, bare ground, or native richness (Fig. 8B, D, F).

In contrast to *P. erecta*, many factors had significant effects on *L. californica* abundance and seeding performance (Table 6). In particular, this species was quite variable among years and treatments (Table 7). In unseeded plots, *L. californica* declined in density with distance from a hummock (Fig. 6B). Adding seeds of *L. californica* led to an initial increase in abundance in both 1-m and 10-m plots in all treatments (Figs. 6A and 7A, B). However, all *L. californica* populations declined in the 10-m plots, regardless of treatment, from a peak in 1998 (the highest rainfall year) through 2001 (Figs. 6A and 7B). The magnitude of the seeding effect for *L. californica* increased with the cover of bare ground and richness of the native community and declined with cover of exotic species (Fig. 8A, C, E).

DISCUSSION

We can strongly reject the hypothesis that competitive interactions acting alone during establishment and growth prevent the reestablishment of the native forbs in the matrix habitat (*H*2). In the absence of seeding, burning or mowing did not affect the richness or density of natives or cover of exotics. Instead, seed availability appears to constrain the recruitment of annual forbs into this exotic annual grassland (*H*1). All of our plots had >65% cover of exotic species, yet with a single addition of seed we were able to establish viable stands of native annual forbs in many plots. We found some evidence for an abiotically mediated competitive relationship (*H*3) in our examination of the effects of natural fertility gradients and year-to-year variability in precipitation. We found that native abundance and richness were higher in low fertility sites and at sites closer to the hummocks. While distance was not correlated strongly with fertility, it is likely that this difference is due to the shallower soils typical inside the hummock boundary (Gram et al., *in press*).

Our results illustrate the importance of seed limitation in California grasslands: Simply exposing bare ground through mowing and burning did not increase the richness or abundance of native species. Seed limitation is probably the result of a combination of factors, including the lack of a persistent seed bank in California annual grasslands (Bartolome 1979), limited dispersal distances for many natives, and the long-term establishment of the exotics that dominate the system. We found no evidence that the seeding effect was related to the local abundance of the species in the control plots, which indicates that recruitment limitation imposes more constraints on species distributions than do environmental conditions (Turnbull et al. 2000). Recruitment from the regional species pool has been long recognized as a major factor controlling community
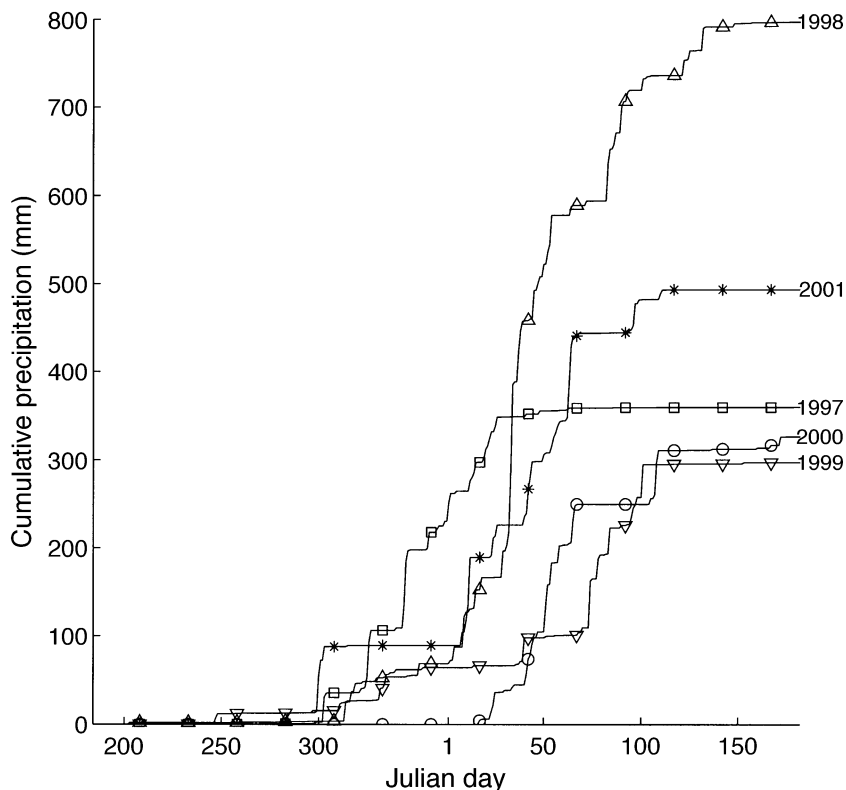
FIG. 4. Cumulative rainfall at Sedgwick Natural Reserve varies greatly in amount and timing. Each line represents the cumulative daily rainfall for a ''rain year,'' which begins in the middle of the Julian year (day 184, or 3 July). Each of the lines represents a single ''rain'' year spanning two calendar years (e.g., 1997 runs from Julian day 184 in 1996 to Julian day 183 in 1997).

composition (see reviews in Tilman 1997, Shurin 2000, Turnbull et al. 2000).

Turnbull et al. (2000) found that seed addition increased the abundance of species in about half of the 40 seed-addition experiments reviewed. Among the studies of arid grasslands cited in the study, ~40% were found to be seed limited, but unlike the California grassland described in our study, the majority were dominated by perennial species. In general, communities that are considered early successional showed more tendency to be seed limited (Turnbull et al. 2000). In the California grasslands, our study and others have shown that sites with sufficient water and nutrients tend to be dominated by exotic grasses (McNaughton 1968, Huenneke et al. 1990, Hobbs and Mooney 1991). But there is little evidence that cessation of disturbance, tilling, or grazing in these grasslands leads to succession or reestablishment of natives or perennials (Bartolome 1989, Stromberg and Griffin 1996, Leiva et al. 1997). The grasslands in our study may resemble early-successional communities without short-term prospects for change.

The seeded species differed in the degree of their seed limitation. *P. erecta* was strongly seed limited in all sites; seeding led to a consistent increase in density re-

gardless of the distance or removal treatments. In contrast, the success of seeding *L. californica* was the outcome of complex interactions between seed limitation and abiotic factors (e.g., site fertility and precipitation). Overall, seeding initially increased the abundance of *L. californica*, but this effect was strongest and most persistent in the shallow soils near hummocks.

Our results provide some evidence that variability in precipitation played a role in determining the outcome of competitive interactions between native forbs and exotic grasses (*H*3). The duration of our study incorporated a wide range of precipitation, including the 1997–1998 El Niño, which produced the single wettest month and the second wettest water year that the Central Coast region of California has experienced in over 100 years. Variability in precipitation was correlated with dramatic changes in the abundance of native and exotic species. High precipitation in 1998 increased the abundance of native species, while exotic cover dropped dramatically in the subsequent dry year. However, the time span of our data set is insufficient to discern general relationships between precipitation and community invasibility. McNaughton (1968) noted that moisture availability plays a key role in preventing exotic grasses from invading the shallow, sandy soils
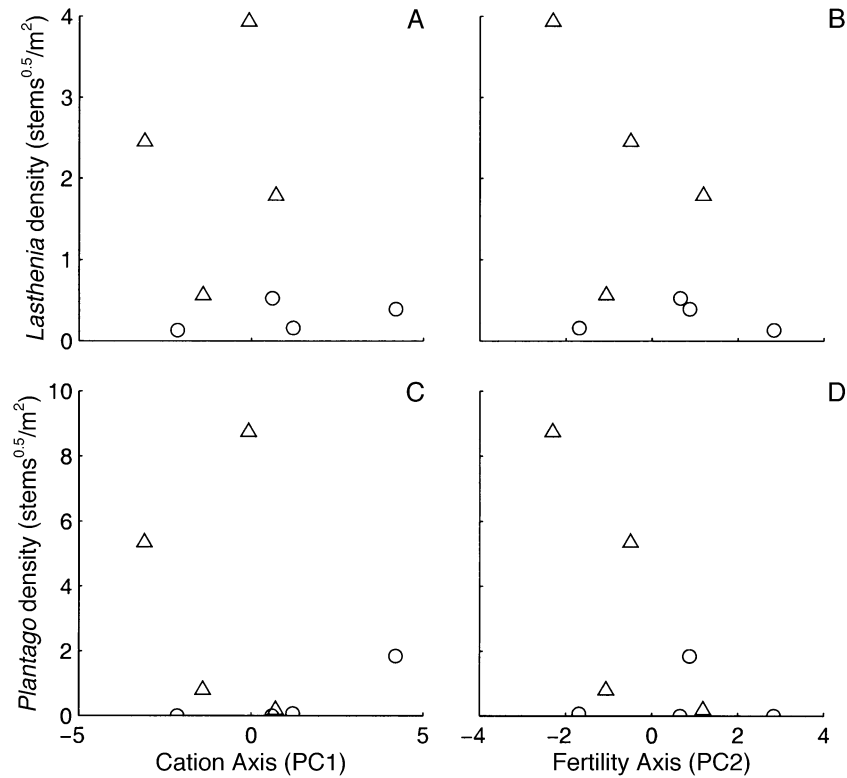
FIG. 5. (A and B) *Lasthenia californica* abundance is not affected by cation concentration ($r = -0.254$, $P = 0.543$) or fertility ($r = -0.490$, $P = 0.218$). (C and D) Likewise, *Plantago erecta* abundance is not affected by cation concentration ($r = -0.203$, $P = 0.630$) or fertility ($r = -0.571$, $P = 0.139$). The ordinates are two principal components (Cation Axis and Fertility Axis). Data represent the mean across five years of plots that are either (triangles) 1 m or (circles) 10 m from the edge of a rocky serpentine outcrop.

of serpentine hummocks, and, in their analysis of an 18-year data set, Pitt and Heady (1978) found that years with consistent rainfall favor grasses. Hobbs and Mooney (1991) also found that exotic annual grasses were better able to invade serpentine grasslands during years of high precipitation. We found that *L. californica* density increased dramatically in the 10-m plots during the highest rainfall year (1998). This finding is similar to the findings of Hobbs and Mooney for this species (1991).

TABLE 6. Results of a MANOVAR testing for overall abundance changes of two native, annual forbs (Levels) to seed addition and vegetation removal at two distances from a serpentine hummock.

Source	df	*Plantago erecta*			*Lasthenia californica*		
		ss	F	P	ss	F	P
PC1	1	1.632	0.020	0.885	101.697	5.440	**0.026**
PC2	1	1.924	0.020	0.876	82.914	4.430	**0.043**
Block	3	200.858	0.870	0.468	202.244	3.610	**0.023**
Distance (D)	1	131.677	1.700	0.201	252.351	13.490	**0.001**
Seed (S)	1	421.309	5.450	**0.026**	124.358	6.650	**0.015**
D × S	1	68.270	0.880	0.354	38.016	2.030	0.163
Removal (R)	2	103.501	0.670	0.519	50.894	1.360	0.271
D × R	2	35.086	0.230	0.798	15.121	0.400	0.671
S × R	2	37.027	0.240	0.788	12.956	0.350	0.710
Error	33	2550.743			819.322		

Notes: Values show the main effects of block, distance from hummock (1 m or 10 m), seed addition (Control or Seeded), and vegetation removal (Control, Mowed, and Burned) on abundance (stems/m²) of the two annual forbs added in the seed-addition treatment. Results represent the overall response across five years. Two principal components are included as covariates in the analyses: PC1 (Cation Axis) and PC2 (Fertility Axis). Values of *P* significant at the 0.05 level are shown in bold.
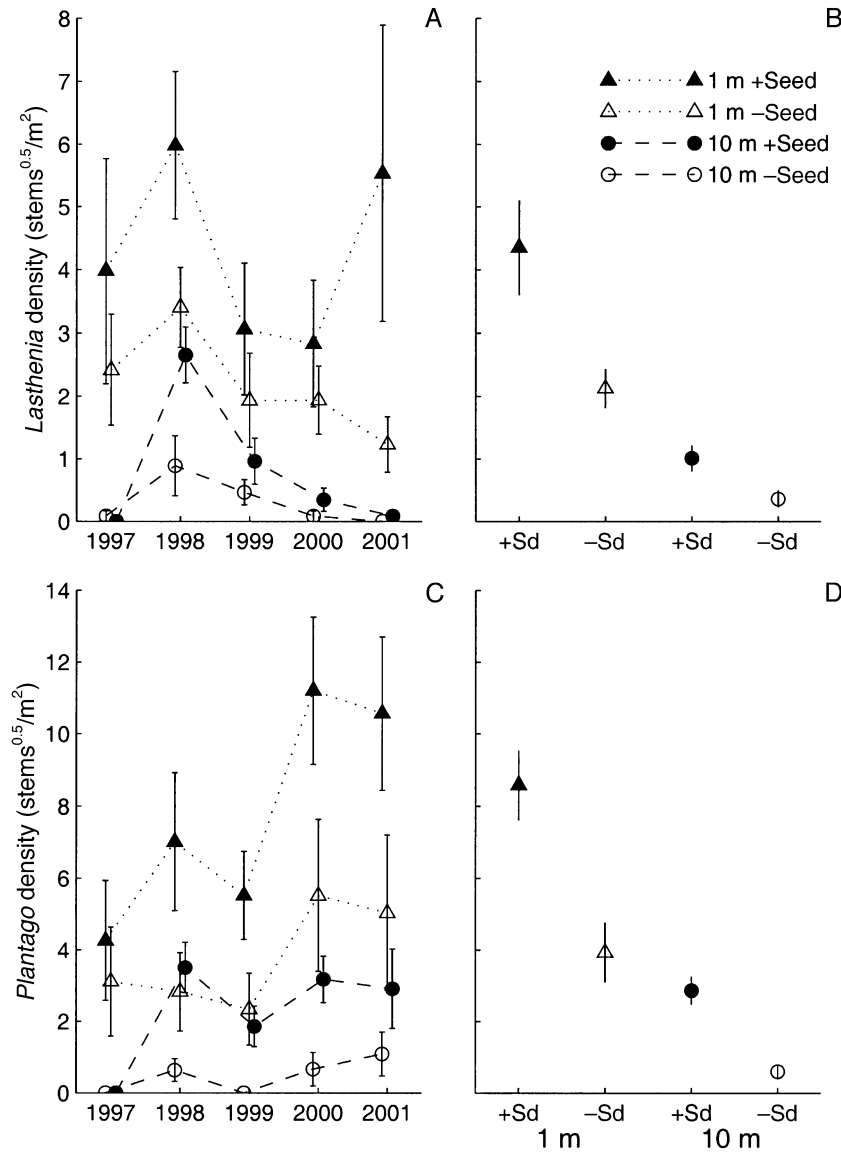
FIG. 6.   (A and B) *Lasthenia californica* and (C and D) *Plantago erecta* abundance is higher on plots that are 1 m from a rocky outcrop (triangles) than they are 10 m from the outcrop (circles). Adding seed of *L. californica* and *P. erecta* in 1997 (+Sd) initially increased their abundance in all treatments. This increase was maintained in subsequent years for *P. erecta* at 1 m or 10 m from the edge of a rocky serpentine outcrop and *L. californica* at 1 m from the hummock edge. No seed addition is represented by −Sd. Error bars indicate ±1 SEM.

Using invasion theory to manage and restore native forbs in California grasslands

Theoretical and empirical research on invasions has focused on both the characteristics of communities vulnerable to invasion by exotic species and on the characteristics of successful invaders (e.g., Lodge 1993, Hobbs and Humphries 1995, Sax and Brown 2000). This work suggests that successful invaders are characterized by large native geographic ranges, broad physiological tolerances, high fecundity, rapid growth rates, and efficient dispersal mechanisms (Baker 1965, Forcella and Wod 1984, Bazzaz 1986, Moulton and

Pimm 1986, Crawley 1987, Burke and Grime 1996, Rejmanek and Richardson 1996). Characteristics of communities that make them susceptible to invasion include high levels of disturbance (Elton 1958, Frankell 1977, Fox and Fox 1986, Johnstone 1986, Hobbs and Atkins 1988, Robinson et al. 1995, Burke and Grime 1996, Case 1996, Suarez et al. 1998), bare ground (Burke and Grime 1996, Stohlgren et al. 1999), and eutrophication (Huenneke et al. 1990, Burke and Grime 1996). Communities that are geographically isolated (Elton 1958, Brown 1989) or have low densities of natural enemies or competitors (Elton 1958, Ricklefs

TABLE 7. Results of a MANOVAR testing for Flatness and Parallelism in the response of two annual forbs to seed addition and vegetation removal at two distances from a serpentine hummock.

Source	df	Plantago erecta			Lasthenia californica		
		λ	F	P	λ	F	P
Year (Y)	4	0.953	0.367	0.830	0.692	3.335	**0.023**
Y × PC1	4	0.806	1.800	0.155	0.699	3.231	**0.026**
Y × PC2	4	0.803	1.839	0.147	0.682	3.499	**0.019**
Y × Block	4	0.549	1.692	0.084	0.264	4.336	**0.000**
Y × Distance (D)	4	0.905	0.791	0.541	0.636	4.301	**0.007**
Y × Seed (S)	4	0.638	4.247	**0.008**	0.798	1.895	0.137
Y × D × S	4	0.963	0.291	0.882	0.876	1.058	0.394
Y × Removal (R)	4	0.785	0.963	0.473	0.405	4.291	**0.000**
Y × D × R	8	0.856	0.608	0.768	0.547	2.642	**0.015**
Y × S × R	8	0.913	0.348	0.943	0.735	1.250	0.287

Notes: Values show the among-year effects of distance from hummock (1 m or 10 m), seed addition (Control or Seeded), and vegetation removal (Control, Mowed, and Burned) on abundance of the two annual forbs added in the seed-addition treatment (stems/m^2). Two principal components are included as covariates in the analyses: PC1 (Cation Axis) and PC2 (Fertility Axis). Values of *P* significant at the 0.05 level are shown in bold.

and Cox 1972, Newsome and Noble 1986) may be relatively more subject to invasion, as well. Local species richness may affect the invasibility of communities, though the direction of the relationship is unclear; there is theoretical and empirical support for both a positive relationship (Robinson et al. 1995, Levine and D'Antonio 1999, Smith and Knapp 1999, Stohlgren et al. 1999) and a negative relationship (Elton 1958, Fox and Fox 1986, Case 1990, Tilman 1997, Knops et al. 1999, Stachowicz et al. 1999, Lyons and Schwartz 2001).

Most applications of invasion theory focus on understanding the mechanisms that determine the rate of spread of exotic species (see Hobbs and Humphries 1995), although invasion theory may also be applicable to the management and restoration of native species. Some characteristics of communities that make them more invasible (such as the richness of the local flora or the degree of geographical isolation during speciation) are inherent to the community and cannot be changed through management. Other factors that can increase invasibility of communities may be altered by human activity, and are thus good candidates for management. For example, management strategies may alter abiotic characteristics of a site, such as the availability of bare ground (Burke and Grime 1996, Turnbull et al. 2000) and soil fertility (Bakker and Berendse 1999). Alternately, management plans may be able to alter characteristics of the "reinvading" native community by introducing more species (Smith and Knapp 2001), increasing the number of introductions (Sax and Brown 2000), or increasing the seeding density (Turnbull et al. 2000). Restoration of native species requires

TABLE 8. Profile analysis using contrasts to compare the effects of distance from hummock (1 m or 10 m), seed addition (Control or Seeded), and vegetation removal (Control, Mowed, and Burned) on abundance (stems/m^2) of the two annual forbs added in the seed-addition treatment in adjacent years.

Variable and treatment	1997 vs. 1998	1998 vs. 1999	1999 vs. 2000	2000 vs. 2001
P. erecta				
Year (Y) × Distance (D)	0.781	0.790	0.349	0.364
Y × Seed (S)	**0.007**	0.387	0.166	0.939
Y × D × S	0.904	0.995	0.450	0.746
Y × Removal (R)	0.753	0.707	0.573	0.081
Y × D × R	0.957	0.955	0.739	0.123
Y × S × R	0.994	0.633	0.785	0.976
L. californica				
Y × D	**0.002**	0.624	0.935	0.460
Y × S	0.277	0.110	0.762	0.018
Y × D × S	0.434	0.870	1.000	0.073
Y × R	0.224	0.072	**<0.001**	0.091
Y × D × R	0.425	0.122	**0.004**	0.256
Y × S × R	0.166	0.543	0.790	0.188

Notes: Significant tests indicate that among year changes varied across treatment groups. Contrasts are based on the MANOVAR analysis from Tables 5 and 6. Boldface comparisons are significant using a Bonferroni adjustment for four repeated tests ($\alpha = 0.0125$).
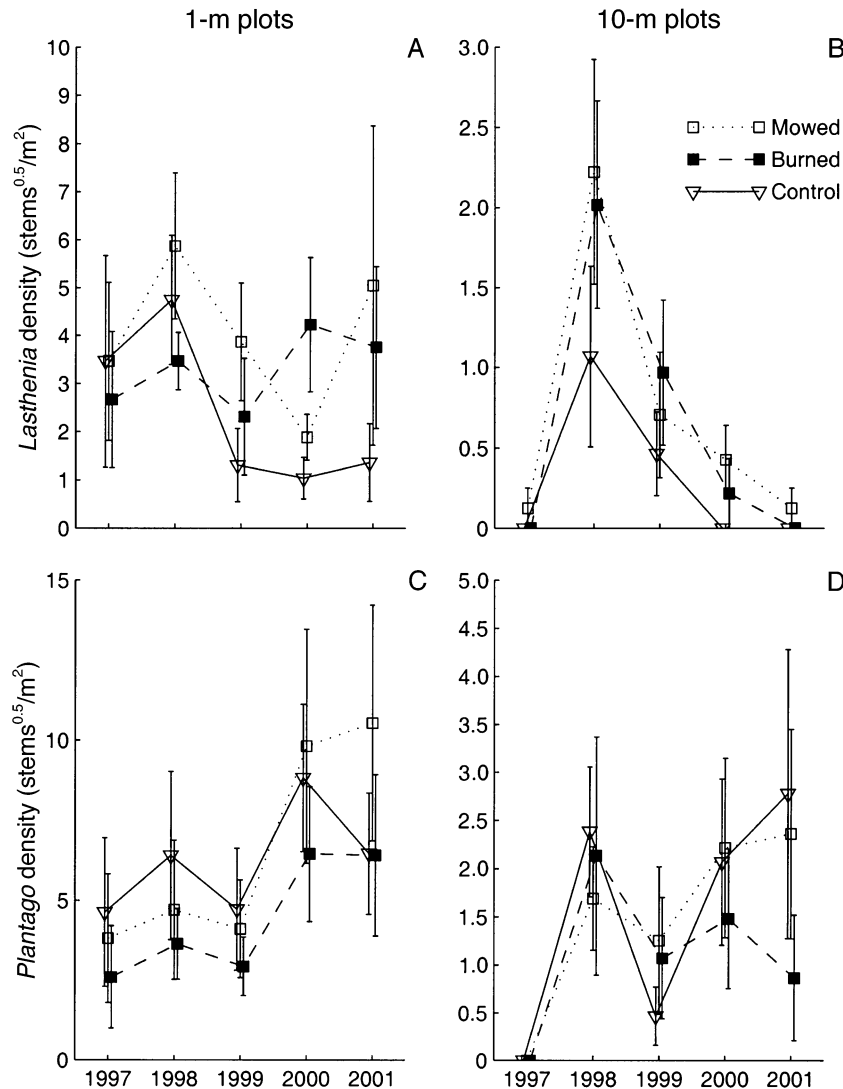
Fig. 7. Vegetation removal (i.e., mowing and burning) had no long-term effects on the abundance of *Lasthenia californica* in plots that were (A) 1 m or (B) 10 m from the edge of a rocky outcrop. The same was true for *Plantago erecta* in both (C) 1-m and (D) 10-m plots. The vegetation removal treatments were applied after the plots were sampled in 1997 and 1998. Error bars indicate ±1 SE. Note the different *y*-axes in the 1-m and 10-m plots for each species.

the same basic understanding of mechanisms that control the spread of exotic species. The key difference between these two scenarios is whether the goal is to manage a system to minimize the abundance of an exotic species or to maximize the rate of spread of a native species.

The specific mechanisms that constrain the spread of native species will determine the success of alternative management strategies. For example, if a community is microsite limited and the exotic species are inherently competitively dominant (H2), the primary goal must be extirpation and quarantine, because the mere presence of superior competitors will limit the potential abundance of native populations. Eradication and quarantine are often expensive and difficult (Zavaleta 2000, Zavaleta et

al. 2001). If the relative competitive dominance of an invasive exotic species is maintained through a change in the abiotic conditions (H3), careful site management may shift the competitive hierarchy to favor native species through control of nutrient inputs (Bakker and Berendse 1999, Tilman et al. 1999), burning, grazing, or mowing (Shoulders 1994, Pollak and Kan 1998, Hatch et al. 1999, Meyer and Schiffman 1999). The seed-limitation hypothesis (H1) offers the most hope for restoration, because it suggests that viable populations of native species can be introduced simply by seeding at sufficiently high densities.

Seed limitation is common in many plant communities (Turnbull et al. 2000), and its importance due to degraded seed banks and geographic isolation has been
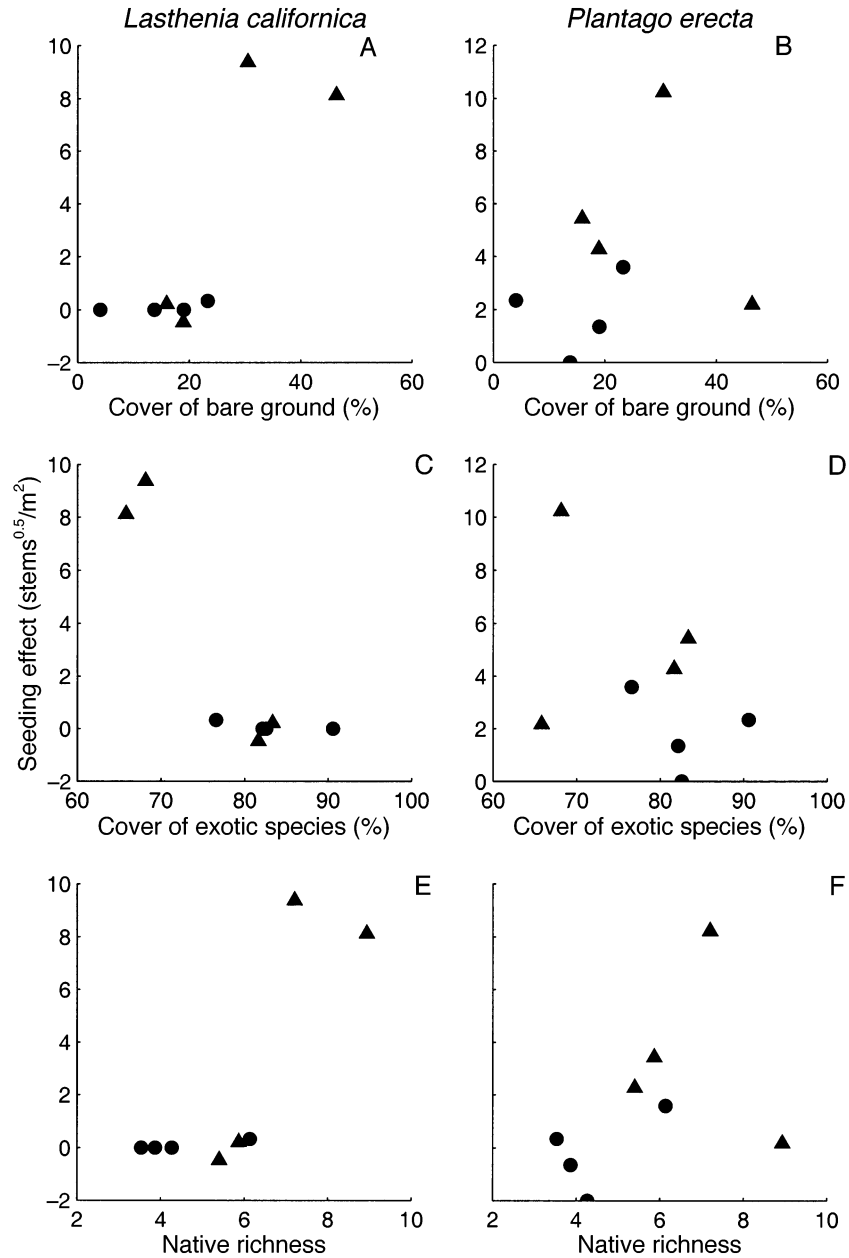
FIG. 8. The magnitude of the *Lasthenia californica* seeding effect (the difference between the control and seeded plots) is highest in plots with the highest cover of bare ground (A; $r = 0.801$, $P = 0.017$), the lowest cover of exotic species (C; $r = -0.881$, $P = 0.004$), and the highest native richness (E; $r = 0.803$, $P = 0.016$). The *Plantago erecta* seeding effect was unrelated to cover of bare ground (B; $r = 0.243$, $P = 0.561$), cover of exotic species (D; $r = -0.427$, $P = 0.291$), and native richness (F; $r = 0.437$, $P = 0.279$).

discussed in the restoration literature (Galatowitsch and van der Valk 1996, Bakker and Berendse 1999). However, many researchers in restoration ecology focus their attention solely on the restoration of abiotic conditions and rely on natural colonization to reestablish the native flora (Mitsch and Wilson 1996). While it is clear that the restoration of the abiotic environment is critical, the prevalence of seed limitation in plant communities suggests that simply altering abiotic conditions may not be sufficient to restore a native community within a reasonable time span.

For example, although the initial invasion of California grasslands by exotic annuals is attributed largely to a shift in abiotic conditions through heavy grazing and drought (Jackson 1985, D'Antonio and Vitousek 1992), these grasslands do not return to a native-dominated state even after decades without grazing (Bartolome 1989, Stromberg and Griffin 1996, Leiva et al.

1997). Similarly, degraded seed banks and geographic isolation can prevent the reestablishment of the native flora in wetland systems even after the previous abiotic conditions have been restored (Godwin 1923, Galatowitsch and van der Valk 1996, Bakker and Berendse 1999). If grazed communities possess multiple stable equilibria, as is suggested by many other studies, then grassland restoration may require more complicated measures than simply altering grazing or burning regimes (Noy-Meir 1975, Laycock 1991, Schwinning and Parsons 1999, Holmgren and Scheffer 2001).

We found that the level of seed limitation varied between species: *P. erecta* was strictly seed limited, while *L. californica* was seed limited in low fertility locations and microsite limited in high fertility areas. These results suggest that the ability of both species to dominate individual microsites is comparable to that of exotic annuals; however, seed limitation, combined with unfavorable local abiotic conditions for *L. californica*, hinders its ability to reenter the exotic-dominated grasslands. If dominance by exotic species is not simply the result of direct competitive interactions, seeding of native species may be sufficient to create viable populations of native annual species in areas currently dominated by exotic species.

Basic research into invasion theory and mechanisms of coexistence has been used to predict and control the spread of exotic species and conserve small populations (Hobbs and Humphries 1995, Shea et al. 1998, Shea and Chesson 2002). Here we have suggested ways in which these theories can provide a useful framework in which to develop management strategies for restoring native species to areas that are currently dominated by exotic species.

LITERATURE CITED

Adams, T. E., C. E. Vaughn, and P. B. Sands. 1999. Geographic races may exist among perennial grasses. California Agriculture **53**:33–38.

Armstrong, J. K. and L. F. Huenneke. 1992. Spatial and temporal variation in species composition in California grasslands: the interaction of drought and substratum. Pages 213–233 *in* A. J. Baker, M. J. Proctor, and R. D. Reeves, editors. The Vegetation of Ultramafic (Serpentine) Soils. First International Conference on Serpentine Ecology. Intercept Ltd., Andover, UK..

Baker, H. G. 1965. Characteristics and modes of origin of weeds. Pages 147–169 *in* H. G. Baker and G. L. Stebbins, editors. The genetics of colonizing species. Academic Press, New York, New York, USA.

Baker, H. G. 1978. Invasion and replacement in Californian and neotropical grasslands. Pages 368–384 *in* J. R. Wilson, editor. Plant relations in pastures. Commonwealth Scientific and Industrial Research Organization (CSIRO), East Melbourne, Australia.

Bakker, J. P., and F. Berendse. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology and Evolution **14**:63–64.

Bartolome, J. W. 1979. Germination and seedling establishment in California annual grasslands. Journal of Ecology **67**:273–281.

Bartolome, J. W. 1989. Local temporal and spatial structure. Pages 73–80 *in* L. F. Huenneke and H. A. Mooney, editors. Grassland structure and function: California annual grassland. Kluwer Academic, Dordrecht, The Netherlands.

Bazzaz, F. A. 1986. Life-histories of colonizing plants: some demographic, genetic, and physioloical features. Pages 259–276 *in* H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.

Brooks, R. R. 1987. Serpentine and its vegetation. Pages 32–47 *in* T. R. Dudley, editor. Ecology, Phytogeography and Physiology Series. Dioscorides Press, Portland, Oregon, USA.

Brown, J. H. 1989. Patterns, modes and extents of invasion by vertebrates. Pages 155–179 *in* J. A. Drake, H. A. Mooney, F. DiCastri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasion: a global perspective. John Wiley and Sons, NewYork, New York, USA.

Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics **27**: 597–623.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology **77**:776–790.

Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. Proceedings of the National Academy of Sciences of the United States of America **87**:9610–9614.

Case, T. J. 1996. Global patterns in the establishment and distribution of exotic birds. Biological Conservation **78**: 69–96.

Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes species coexistence in lottery competitive models. American Naturalist **117**:923–943.

Clements, F. E. 1934. The relict method in dynamic ecology. Journal of Ecology **22**:39–68.

Crawley, M. J. 1987. What makes a community invasible? Pages 429–454 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonization, succession, and stability: the 26th Symposium of the British Ecological Society held jointly with the Linnean Society of London. Blackwell Scientific Publications, Oxford, UK.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics **23**: 63–87.

Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Regmanák, and M. Williamson, editors. 1989. Biological invasions: a global perspective. Wiley, Chichester, UK.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, UK.

Fagerstrom, T., and M. Westoby. 1997. Population dynamics in sessile organisms: some general results from three seemingly different theory-lineages. Oikos **80**:588–594.

Forcella, F., and J. T. Wod. 1984. Colonization potential of alien weeds are related to their 'native' distributions, implications for plant quarantine. Journal of the Australian Institute of Agricultural Science **50**:35–41.

Fox, M. D., and B. J. Fox. 1986. The suseptibility of natural communities to invasion. Pages 57–66 *in* J. J. Burdon and R. H. Groves, editors. Ecology of biological invasions. Cambridge University Press, Cambridge, UK.

Frankell, R. E. 1977. Ruderal vegetation along some Californian roadsides. University of California Publications in Geography **20**:1–63.

Galatowitsch, S. M., and A. G. van der Valk. 1996. The vegetation of restored and natural prairie wetlands. Ecological Applications **6**:102–112.

Godwin, H. 1923. Dispersal of pond flora. Journal of Ecology **11**:160–164.

Gram, W. K., E. T. Borer, K. L. Cottingham, E. W. Seabloom, V. Boucher, B. E. Kendall, L. Goldwasser, F. Micheli, and R. S. Burton. *In press*. Distribution of plants in a California serpentine grassland: Are rocky hummocks spatial refuges for native species? Plant Ecology.

Gurney, W. S. C., and R. M. Nisbet. 1998. Ecological dynamics. Oxford University Press, New York, New York, USA.

Hamilton, J. G. 1997. Changing perceptions of pre-European grasslands in California. Madroño **44**:311–333.

Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. Ecology **78**:1898–1906.

Harrison, S. 1999a. Local and regional diversity in a patchy landscape: native, alien, and endemic herbs on serpentine. Ecology **80**:70–80.

Harrison, S. 1999b. Native and alien species diversity at the local and regional scales in a grazed California grassland. Oecologia **121**:99–106.

Hatch, D. A., J. W. Bartolome, J. S. Fehmi, and D. S. Hillyard. 1999. Effects of burning and grazing on a coastal California grassland. Restoration Ecology **7**:376–381.

Heady, H. A. 1956a. Changes in a California annual plant community induce by manipulation of natural mulch. Journal of Range Management **37**:398–812.

Heady, H. F. 1956b. Evaluation and measurement of the California annual type. Journal of Range Management **9**:25–27.

Heady, H. F. 1958. Vegetational changes in the California annual type. Ecology **39**:402–415.

Heady, H. F. 1977. Valley grassland. Pages 491–514 *in* M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. John Wiley and Sons, New York, New York, USA.

Hobbs, R. J., and L. Atkins. 1988. Effects of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australia wheatbelt. Australian Journal of Ecology **13**:171–179.

Hobbs, R. J., and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. Conservation Biology **9**:761–770.

Hobbs, R. J., and H. A. Mooney. 1991. Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. Ecology **72**:59–68.

Holmgren, M., and M. Scheffer. 2001. El Niño as a window of opportunity for the restoration of degraded arid ecosystems. Ecosystems **4**:151–159.

Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology **71**:478–491.

Jackson, L. E. 1985. Ecological origins of California's Mediterranean grasses. Journal of Biogeography **12**:349–361.

Johnstone, I. M. 1986. Plant invasion windows: a time-based classification of invasion potential. Biological Reviews **61**:369–394.

Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecology Letters **2**:286–293.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist **142**:911–927.

Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a vewpoint. Journal of Range Management **44**:427–433.

Leiva, M. J., F. S. I. Chapini, and R. Fernandez Ales. 1997. Differences in species composition and diversity among Mediterranean grasslands with different history: the case of California and Spain. Ecography **20**:97–106.

Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science **288**:852–854.

Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos **87**:15–26.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8**:133–137.

Lodge, D. M., R. A. Stein, K. M. Brown, A. P. Covich, C. Bronmark, J. E. Garvey, and S. P. Klosiewski. 1998. Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. Australian Journal of Ecology **23**:53–67.

Lyons, K. G., and M. W. Schwartz. 2001. Rare species loss alters ecosystem function: invasion resistance. Ecology Letters **4**:358–365.

Macarthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist **101**:377–385.

McNaughton, S. J. 1968. Structure and function in California grasslands. Ecology **49**:962–972.

Menke, J. W. 1989. Management controls on productivity. Pages 173–200 *in* L. F. Huenneke and H. A. Mooney, editors. Grassland structure and function: California annual grassland. Kluwer Academic, Dordrecht, The Netherlands.

Meyer, M., and P. Schiffman. 1999. Fire season and mulch reduction in a California grassland: comparison of restoration strategies. Madroño **46**:25–37.

Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1994. Exotic species and the integrity of the Great Lakes: lessons from the past. BioScience **44**:666–676.

Mills, L. S., and P. E. Smouse. 1994. Demographic consequences of inbreeding in remnant populations. American Naturalist **144**:412–431.

Mitsch, W. J., and R. F. Wilson. 1996. Improving the success of wetland creation and restoration with know-how, time, and self-design. Ecological Applications **6**:77–83.

Mooney, H. A., S. P. Hamburg, and J. A. Drake. 1986. The invasions of plants and animals into California. Pages 250–272 *in* H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.

Moulton, M. P., and S. L. Pimm. 1986. Species introductions to Hawaii. Pages 231–249 *in* H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.

Murphy, D. D., and P. R. Ehrlich. 1989. Conservation of California's remnant native grasslands. Pages 201–212 *in* L. F. Huenneke and H. A. Mooney, editors. Grassland struc-

ture and function: California annual grassland. Kluwer Academic, Dordrecht, The Netherlands.

Newsome, A. E., and I. R. Noble. 1986. Ecological and physiological characteristics of invading species. Pages 1–20 *in* J. J. Burdon and R. H. Groves, editors. Ecology of biological invasions. Cambridge University Press, Cambridge, UK.

Noy-Meir, I. 1975. Stability of grazing systems: an application of predator-prey graphs. Journal of Ecology **63**:459–481.

Pitt, M. D., and H. F. Heady. 1978. Responses of annual vegetation to temperature and rainfall patterns in Northern California. Ecology **59**:336–350.

Pollak, O., and T. Kan. 1998. The use of prescribed fire to control invasive exotic weeds at Jepson Prairie Preserve. Pages 241–249 *in* C. W. Witham, E. T. Bauder, D. Belk, W. R. Ferren, Jr., and R. Ornduff, editors. Ecology, conservation, and management of vernal pool ecosystems. Proceedings of 1996 conference. California Native Plant Society, Sacramento, California, USA.

Potvin, C., M. J. Lechowicz, and S. Tardif. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. Ecology **71**:1389–1400.

Proctor, J. 1971. The plant ecology of serpentine. II. Plant response to serpentine soils. Journal of Ecology **59**:397–410.

Proctor, J., and S. R. J. Woodell. 1975. The ecology of serpentine soils. Advances in Ecological Research **9**:255–366.

Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77**:1655–1661.

Ricklefs, R. E., and G. W. Cox. 1972. Taxon cycle in the wet Indian avifauna. American Naturalist **106**:195–219.

Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. Ecology **76**:786–794.

Sax, D. F., and J. H. Brown. 2000. The paradox of invasion. Global Ecology and Biogeography **9**:363–371.

Schiffman, P. M. 2000. Mammal burrowing, erratic rainfall and the annual lifestyle in the California prairie: is it time for a paradigm shift? Pages 153–159 *in* J. E. Keeley, M. Baer-Keeley, and C. J. Fotheringham, editors. Second interface between ecology and land development in California. U.S. Geological Survey Open File Report 00-62.

Schwinning, S., and A. J. Parsons. 1999. The stability of grazing systems revisited: spatial models and the role of heterogeneity. Functional Ecology **13**:737–747.

Shea, K., P. Amarasekare, M. Mangel, J. Moore, W. W. Murdoch, E. Noonburg, A. Parma, M. A. Pascual, H. P. Possingham, C. Wilcox, and D. Yu. 1998. Management of populations in conservation, harvesting and control. Trends in Ecology and Evolution **13**:371–375.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution **17**:170–176.

Shoulders, C. L. 1994. Methods of restoring *Nassella pulchra* (purple needlegrass) at Jepson Prairie Preserve, Solano County, CA. Thesis. University of Wisconsin, Madison, Wisconsin, USA.

Shurin, J. B. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. Ecology **81**:3074–3086.

Smith, M. D., and A. K. Knapp. 1999. Exotic plant species in a C_4-dominated grassland: invasibility, disturbance, and community structure. Oecologia **120**:605–612.

Smith, M. D., and A. K. Knapp. 2001. Size of the local species pool determines invasibility of a C_4-dominated grassland. Oikos **92**:55–61.

Stachowicz, J. J., R. B. Whitlatch, and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. Science **286**:1577–1579.

Stein, B. A., L. S. Kutner, and J. S. Adams. 2000. Precious heritage: the status of biodiversity in the United States. Oxford University Press, Oxford, UK.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs **69**:25–46.

Stromberg, M. R., and J. R. Griffin. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. Ecological Applications **6**:1189–1211.

Stromberg, M. R., and P. Kephart. 1996. Restoring native grasses in California old fields. Restoration and Management Notes **14**:102–111.

Suarez, A. V., D. T. Bogler, and T. J. Case. 1998. Effects of fragmentation and invasion on native ant communities on coastal southern California. Ecology **79**:2041–2056.

Suding, K. N., and D. Goldberg. 2001. Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. Ecology **82**:2133–2149.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology **78**:81–92.

Tilman, E. A., D. Tilman, M. J. Crawley, and A. E. Johnston. 1999. Biological weed control via nutrient competition: potassium limitation of dandelions. Ecological Applications **9**:103–111.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos **88**:225–238.

von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113–137 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.

Walker, R. B. 1954. Factors affecting plant growth on serpentine soils. Ecology **35**:259–266.

Wester, L. 1981. Composition of native grasslands in the San Joaquin Valley, California. Madroño **28**:231–241.

Zavaleta, E. 2000. The economic value of controlling an invasive shrub. Ambio **29**:462–467.

Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology and Evolution **16**:454–459.