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EFFECTS OF SOIL RESOURCES ON PLANT INVASION AND COMMUNITY STRUCTURE IN CALIFORNIAN SERPENTINE GRASSLAND[1]

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Abstract. Non-native annual grasses dominate most Californian mediterranean-climate grasslands today. However, native Californian grassland flora persists in grasslands on serpentine-derived soils. We manipulated soil nutrient resources to explore the links between nutrient availability, plant productivity, and the relative abundances of native and non-native species in serpentine grassland. Factorial combinations of nitrogen, phosphorus, and other components of a nutritionally complete formula were added to field plots over two growing seasons.

Fertilization with nitrogen and phosphorus increased biomass of the resident vegetation substantially in the first season, and within two years allowed the invasion and dominance of non-native annual grasses in patches originally dominated by native annual forbs. Species richness declined with fertilization, as the increased biomass production by invaders suppressed some native forbs. Increased macronutrient availability can increase production on serpentine-derived soil, even when other serpentine characteristics (such as low Ca/Mg ratios and high heavy-metal concentrations) have not been mitigated. Observed changes in community structure and composition demonstrate that the invasibility of plant communities may be directly influenced by nutrient availability, independent of physical disturbance.

Key words: California; community structure; grassland community; invasion; native vs. non-native species; nutrient additions; serpentine grassland; serpentine soils; soil nutrients.

INTRODUCTION

Introductions of species, whether deliberate or accidental, to intact communities provide ecologists with the opportunity to test their understanding of population and community ecology (Mack 1985, Vitousek 1986). Invasive species, those plants or animals capable of establishing themselves in relatively undisturbed natural communities, have recently been the subject of a major international review program (Drake et al., *in press*, Mooney and Drake 1986). The focus in these synthesis efforts has been on the determinants of success for a potential invader, and of vulnerability to invasion for an ecosystem or community. There has been less attention devoted to the insights to be gained when community structure is altered by the addition of a new component. To what extent are the composition and relative abundances of species regulated in a plant community, and what is the community-wide response when a new species enters?

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The mediterranean-climate annual grassland of California is ideal for investigations of the relationship between soil resources, plant community structure, and ecosystem processes (Huenneke and Mooney 1989). Native grassland vegetation in California's Central Valley and coastal regions consists of perennial bunchgrasses with diverse annual and perennial forbs (Heady 1977, Bartolome et al. 1986), with annual grasses apparently common in at least the drier portions of the Central Valley (Wester 1981). Today, although much of the Central Valley grassland has been displaced by intensive agriculture, annual grassland remains common in the coast ranges (Huenneke 1989).

Although grasslands persist, the native flora of California's grasslands has experienced one of the world's most dramatic episodes of ecological invasions (Mooney et al. 1986a). After settlement by the Spanish, many annual grasses and forbs native to Eurasia and the Mediterranean basin spread rapidly through California, and quickly became dominant in most Californian grasslands (Burcham 1957, Baker 1989). Today Californian annual grassland is overwhelmingly dominated by these invaders (such as members of the genera *Avena, Bromus, Erodium,* and *Hordeum*). These species constitute a stable, permanent annual vegetation in California (Heady 1977), in contrast to the successional or ruderal nature of the same species assemblages in their native Mediterranean ranges (Jackson 1985).

Native Californian grassland species do persist, either in remnant ungrazed stands, as ruderals in frequently disturbed areas, or in other sites where the invasive annuals have not become dominant. Chief among these refuges for the native flora are grasslands on serpentine-derived substrates. Serpentine-derived soils are known to be inimical to plant growth and productivity. They are frequently rocky and well drained, often contain high levels of toxic heavy metals, are characterized by extremely low Ca/Mg ratios, and often exhibit low levels of plant-available macronutrients such as N and P (Walker 1954, Proctor 1971, Proctor and Woodell 1975). In California, as elsewhere, there are many serpentine endemics (Kruckeberg 1984, Brooks 1987). Most non-native grassland species do not become dominant in serpentine grasslands, and native grassland species (including many formerly found in nonserpentine grasslands) persist as the dominants on these isolated patches. Productivity is low on serpentine grassland, and plant densities are high (Hobbs and Mooney 1985). The short life-spans and small size of the dominant species make serpentine grassland particularly amenable to experimental manipulations.

We chose annual grassland on serpentine-derived soils in the San Francisco Bay area, California, as the site for field manipulations of soil nutrient resources and measurements of plant community responses. We established permanent plots within a serpentine grassland and have applied nitrogen, phosphorus, and other essential plant nutrients in a factorial design to those plots since winter 1984, while making no attempt to mitigate other serpentine features. Here we describe the response of the diverse grassland community to the first two years of nutrient additions. We focus on plant community response—that is, productivity, species richness and composition, and relative abundance of native and non-native species—to the addition of plant nutrients.

METHODS

Study site

The study site was a level grassland-covered ridge (elevation ≈300 m) on a 3000-ha serpentine outcrop in Santa Clara County, California (37°15' N, 121°45' W). The serpentine-derived soil is of the Montara series (fine-loamy, serpentinic, thermic, lithic Haploxerolls). At the initiation of the study, native forbs appeared to dominate the ridgetop. Patches (5–20 m² in area) dominated by non-native annual grasses, primarily *Lolium multiflorum,* were scattered throughout native forb vegetation.

Although no burrowing activity was noted in the area at the start of the study, pocket gophers (*Thomomys umbrinus* or *T. bottae*) colonized the site during spring 1985. A few experimental plots were disturbed by gophers in April 1985, and several more by the following spring. Only Grass plots were invaded by gophers. There was no apparent discrimination among nutrient treatments by the gophers (in contrast to that reported by Tilman 1983 and Hobbs et al. 1988). Biomass and soil samples in 1986 were taken only from undisturbed (non-mound) areas, so results were apparently unaffected by aboveground gopher activity.

Climate

The central Coast Range of California, including the study area ≈27 km south of the city of San Jose, experiences the summer-dry, winter-wet mediterranean climate typical of California. During the two years of study mean monthly temperatures at the nearest weather station (San Jose, elevation 20 m) fluctuated near the long-term means (Fig. 1), although the second winter of study (1985–1986) was consistently warmer than normal. The first autumn and the second winter of study had unusually high precipitation totals (>450 mm precipitation in October 1985–April 1986).

Experimental design and fertilization

In late autumn 1984, an experimental area of the ridge (≈1.5 ha) was fenced to exclude grazing by cattle. The fenced area was divided into five contiguous blocks of 400 m² (excluding a 10 m wide buffer zone along the fenced boundary); the experimental design, as described below, was replicated within each of the five blocks. Experimental units were rectangular permanent plots, 2 m × 4 m, established in December 1984. Within each block eight plots were established within patches of native vegetation dominated by annual forbs (Forb plots), and eight plots within patches dominated by non-native annual grasses (Grass plots). Identification of vegetation patch type was based on the presence of standing dead material from the previous growing season, and on identification of new germinants. Plots were located to avoid large surface rocks (to minimize variation in area available for plant growth) and to avoid cattle dung remaining from pre-fencing grazing (to minimize heterogeneity in soil resources). After all plots (80 total) had been established, treatments were assigned randomly within blocks and vegetation type.

The experimental treatments were factorial additions of nitrogen (N), phosphorus (P), "Other" (O, a complete fertilizer minus N and P), and all combinations thereof, including a control (C) that received no nutrients. N was added as NH_4NO_3 (N at 10 $g \cdot m^{-2} \cdot yr^{-1}$); P was added as $NaH_2PO_4 \cdot H_2O$ (P at 10 $g \cdot m^{-2} \cdot yr^{-1}$). The "Other" treatment was a combination of $CaCl_2$ (26.5 $g \cdot m^{-2} \cdot yr^{-1}$), $MgSO_4 \cdot 7H_2O$ (23.4 $g \cdot m^{-2} \cdot yr^{-1}$), KCl (21.3 $g \cdot m^{-2} \cdot yr^{-1}$), $FeCl_3 \cdot 6H_2O$ (1.15 $g \cdot m^{-2} \cdot yr^{-1}$), H_3BO_3 (0.05 $g \cdot m^{-2} \cdot yr^{-1}$), $CuSO_4 \cdot 5H_2O$ (0.0114 $g \cdot m^{-2} \cdot yr^{-1}$), $MnCl_2 \cdot 4H_2O$ (0.165 $g \cdot m^{-2} \cdot yr^{-1}$), $ZnSO_4 \cdot 7H_2O$ (0.0283 $g \cdot m^{-2} \cdot yr^{-1}$), and $Na_2MoO_4 \cdot 2H_2O$ (0.018 $g \cdot m^{-2} \cdot yr^{-1}$). The composition of the Other treatment was proportional to the added N and P, according to a general nutritionally complete formula.

N and P were added to individual plots by hand in dry (powdered) form. In the first year (1984–1985 season), the major components of Other (Ca, Mg, and K) were also administered in dry form. The remaining components of Other were added in solution in 500 mL/m² of deionized water. Equal volumes of deionized water were sprinkled over those plots not receiving Other. In the second year Ca was added in the liquid fraction, rather than in powdered form.

In the first year the annual fertilizer supplement was supplied in three equal applications: late December (after germination was largely completed), early February, and early March 1985. In the second season there were two equal applications, in late December and in early February.

Soils analysis and description

In late February 1985 a single soil core (depth 4.0 cm, volume 42 cm³) was taken systematically from each of the 80 plots. Water content was determined gravimetrically, and bulk density (excluding particles >2 mm) calculated. Pool sizes of available NO_3-N and NH_4-N were determined by automated colorimetry following KCl extraction of field-wet soil (Keeney and Nelson 1982). Available PO_4-P was measured by automated colorimetry after $NaHCO_3$ extractions (pH 8.5) (Olsen and Sommers 1982).

In late March 1986 cores of diameter 5.1 cm were taken systematically from each plot in Blocks II–V (Block I was not sampled due to lack of time). Cores were taken with a copper pipe pushed to the maximum depth possible; the depth of cores provided an estimate of effective soil depth. If the depth of the first core in a plot was <20 cm, additional cores were taken until a minimum of 20 cm depth had been collected (minimum sample volume 390 cm³). After the soils were air dried, sieved (2 mm), and ground, samples were analyzed for total N, P, and carbon, and for pH. Total N and carbon were determined using an automated Dumas combustion procedure (NA 1500, Carlo-Erba Stumentazione, Milan, Italy). Total P was determined by persulfate/peroxide digestion followed by automated colorimetric analysis. Soil pH measurements were made using 5 g of soil in a 1:1 paste with 0.01 mol/L $CaCl_2$, stirred intermittently for 30 min (McLean 1982).

Harvesting

Biomass samples were taken in the plots in the last week of March in both years. In 1985 the annual forbs had reached peak biomass at this time, and most species were in flower or in fruit. Most annual grasses, however, were still actively growing, and had not yet produced inflorescences. Some perennial species were in flower, but many others had not yet begun flowering. In 1986, the last week in March came somewhat later, phenologically, and a greater proportion of the species had initiated flowering.

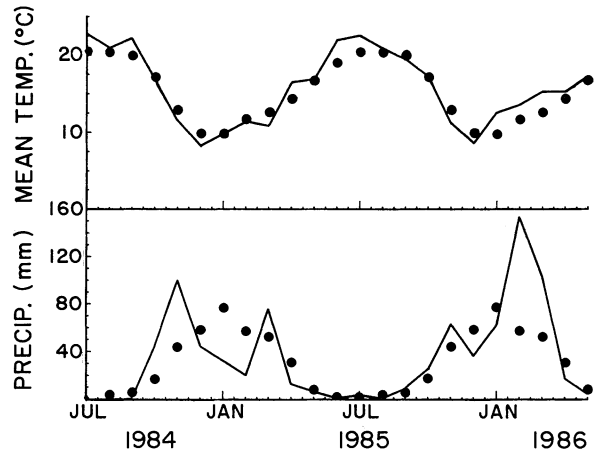In the biomass harvests, three circular subplots were

FIG. 1. Weather records for San Jose, California, during the study period. Plotted curve represents monthly records during the study period; single points indicate 30-yr mean monthly values. Top curve: mean monthly temperatures. Bottom curve: mean precipitation totals.

harvested from each plot by clipping all plants at the soil surface. In 1985 the subplots had a diameter of 10 cm (composite sample from each plot 78.5 cm²). In 1986, subplot diameters were increased to 12 cm (composite sample 113 cm²). Subplot locations were randomly selected, with the provisions that no two points were sampled from a single quarter of the plot, no samples were taken within 20 cm of the plot edge, and no samples in the second year were taken within 20 cm of a sample area from the previous season. The same locations were sampled in all 80 plots for a given year.

Aboveground biomass was sorted by species, dried at 60°C to constant mass, and weighed. Any standing dead plants or litter that appeared to date from previous seasons was omitted from the biomass sample. Species richness was estimated as the number of species found in the subsamples from each plot. These samples underestimate the true species richness and biomass of the plots in two ways: the subsamples inevitably missed some patchily distributed species within a plot, and the timing of harvest may have missed species that had already senesced. Species in serpentine grassland senescing early tend to be small in biomass (Mooney et al. 1986b).

Species were categorized as native or non-native, according to Munz and Keck (1968), and by growth form or species group. Native species included annual non-leguminous forbs, annual legumes, bulb or corm perennials, other perennial forbs, and perennial bunchgrasses. Non-native species included only annual grasses. *Vulpia microstachys* (=*Festuca microstachys* of Munz and Keck [1968]), the only native annual grass observed, could not be readily distinguished from the non-native *V. myuros* and was pooled with it. Except where noted, taxonomy follows that of Munz and Keck (1968).

TABLE 1.   Extractable nutrients in treatment plots in spring 1985. Values presented are means of $n = 5$ measurements (from log-transformed data). Treatment notation is: C = control; N = nitrogen added; P = phosphorus added; O = "Other" nutrients added (a complete fertilizer minus N and P).

Treatment	NO_3-N	NH_4-N	PO_4-P
	Extractable soil nutrients (μg/g dry soil)		
Forb plots			
C	1.1	5.5	7.2
N	28.9	52.8	7.2
P	1.1	6.3	46.9
O	1.1	5.4	6.5
NP	7.0	23.7	52.2
NO	36.7	64.8	5.9
PO	1.0	5.5	43.5
NPO	11.8	32.4	53.5
Grass plots			
C	0.7	5.9	8.2
N	14.4	27.8	8.6
P	1.1	6.9	55.1
O	0.7	7.9	13.0
NP	6.4	28.6	53.9
NO	14.8	40.2	10.5
PO	1.0	6.8	71.7
NPO	18.6	35.1	54.8

In late April 1985, soil cores of diameter 5.4 cm and depth 20 cm were taken from each control, N, and NPO Grass plot (total of 15 samples). Samples were divided into 0–10 cm and 10–20 cm fractions, and live roots were extracted by wet sieving and weighed. Aboveground biomass was sampled from a small clipped area (diameter 10.1 cm, area 80.1 cm^2) above the core. These samples afforded an estimate of grass biomass produced later than the March harvest, as well as measures of root/shoot ratios in the three treatments.

Analysis of biomass and community structure

Biomass values (total biomass, and biomass contributions of each species group) were log-transformed and analyzed by three-way factorial analysis of variance (N, P, and O being the three factors). Vegetation types and years were analyzed separately. Community structure was contrasted among treatments by use of coefficients of community, dominance–diversity plots, and an index of dominance (the proportional contribution of biomass by the two most abundant species).

We measured similarity among the five replicates within a treatment in the Forb or Grass plots by calculating the coefficient of community, $CC = (2S_{ab})/(S_a + S_b)$, where S_a is the number of species in sample a and S_{ab} is the number of species in common between the two samples a and b. CC was calculated in this way for each pair of replicates within the control, nitrogen, and NPO treatments. The ten calculated coefficients for each treatment in each year were then averaged to give an overall estimate of similarity of composition

among replicates. CC values were also used to measure compositional similarity between Forb and Grass plots.

We investigated community structure responses to nutrient treatments from two perspectives. First, we used coefficients of community to assess the similarity of species composition among treatments. Second, dominance–diversity curves and an index of dominance were used to assess changes in patterns of relative abundances.

Species composition was compared among treatments with CC. All species found in the replicates of a treatment were pooled to give a treatment species list; then a single CC was calculated for each pair of treatments. By averaging the seven values of CC for a given treatment (one for each comparison with another treatment), one can estimate that treatment's similarity to all others (or conversely, its distinctiveness). The treatment with the lowest mean values of CC is the most distinct from all other treatments.

Dominance–diversity curves, or importance-value plots, rank the contributions of individual species to total community importance (Greig-Smith 1983). If increased levels of nutrient resources allow increasing dominance by vigorously growing species, with resulting suppression of other species, treatments with higher nutrient availability should demonstrate shorter, steeper dominance–diversity curves. Biomass values by species were summed across the five replicate plots, and divided by total biomass to yield individual species' percentage contribution to total biomass for a treatment. The percentage contributions (measures of a species' importance or dominance) were plotted on a log scale against species' rank. The resulting dominance–diversity curves approximated linear functions, and the slopes of the control and NPO regressions were compared statistically for Forb plots in both years.

RESULTS

Soil characteristics

Extractable levels of NO_3-N, NH_4-N, and PO_4-P after the first season reflected the fertilizer treatments. NO_3-N levels (in micrograms per gram) were consistently lower than NH_4-N levels (Table 1), in both Forb and Grass plots and across all treatments. Both NO_3-N and NH_4-N increased significantly with N applications. Factorial ANOVA showed significant interactions between N, P, and O additions for nitrate and ammonium N. PO_4-P increased directly with P applications; there were no detectable interactions with the other nutrients. The main effect of vegetation type (Forb vs. Grass plots) was nonsignificant for NO_3-N and NH_4-N; Grass plots had significantly higher PO_4-P than did Forb plots ($F_{1,64} = 11.53$, $P = .0012$).

The soil cores taken in spring 1986 provided estimates of soil depth in the plots. Mean soil depth (as indicated by depth of core) was greater in Grass plots than in Forb plots (33.1 cm vs. 14.3 cm; $t = -9.27$, P
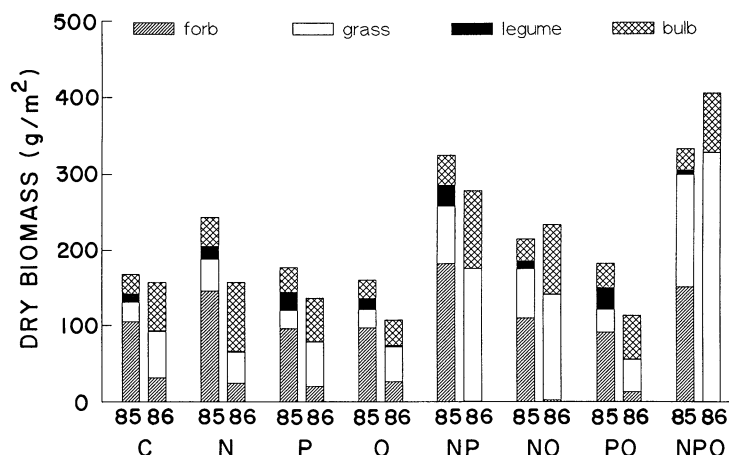
FIG. 2. Dry biomass for each species group, in Forb plots. Values plotted are means of five replicates (calculated from log-transformed data). In each pair of bars the left bar represents 1985 values, the right bar 1986 values. Treatment notation as in Table 1 legend.

< .0001). Soil bulk density was 0.99 ± 0.13 g/cm³ (X ± SD), and did not differ significantly between Forb and Grass plots ($t = 0.859$, 78 df, $P = .393$).

Analysis of variance indicated no differences among treatments in pH in March 1986, but slight differences between Forb and Grass plots (Forb, mean pH = 6.35; Grass, mean pH = 6.44; $F_{1,42} = 4.16$, $P = .048$). Neither vegetation type, treatment, nor their interaction had significant effects on total carbon or total nitrogen (ANOVA), suggesting that the post-fertilization increases in extractable N were small relative to pools of organic N. Total carbon averaged 2.17% (95% confidence interval 2.09–2.26), and total nitrogen averaged 0.21% (95% CI 0.20–0.22). Carbon/nitrogen ratios, however, did vary slightly between vegetation types (ANOVA, $F_{1,48} = 5.16$, $P = .03$): 10.3 (95% CI 10.1–10.6) in Forb plots and 10.7 (95% CI 10.5–11.0) in Grass plots. Total phosphorus was more variable; both treatment ($F_{7,47} = 4.896$, $P = .0003$) and vegetation type ($F_{1,47} = 10.17$, $P = .0025$) were significant main effects in the ANOVA. There was no significant interaction between treatment and vegetation. Total P averaged 0.032% in Forb plots and 0.028% in Grass plots.

Biomass responses

Total biomass.—Total aboveground biomass in the control Forb plots was low relative to that in most North American grasslands (Lieth and Whittaker 1975), averaging <200 g/m², but in N-fertilized plots biomass was comparable to that of more fertile mesic grasslands. In both years total aboveground production was greater in plots that received applications of N, especially in combination with P and O, in the Forb plots (Fig. 2). In the first year only the main effects of N and of P were significant (Table 2); in the second year, however, N × P and N × O two-way interactions were also significant.

Biomass was greater in every treatment in the Grass plots than in the corresponding Forb plots (Figs. 2 and 3). In the first year of applications, total biomass was substantially, and significantly, greater in N-fertilized plots (Table 3). The second year's responses differed substantially from the first year's results; biomass production in the N-fertilized plots was lower than in the preceding year, and the factorial ANOVA found no significant effects of fertilization treatment. In plots not receiving N, biomass levels were comparable between years.

Biomass by species groups: Forb plots.—Species groups differed in their patterns of biomass across treatments. Both native forbs and non-native annual grasses were present as germinants in all experimental plots when fertilization began in the first year, although abundance differed between initially forb-dominated and grass-dominated plots. In the first year in Forb plots, the main effect of N additions had a significant (positive) effect on biomass of native annual (non-legume) forbs (Table 2, Fig. 2). Non-native annual grass biomass was also greater in N-fertilized plots. Annual grasses constituted 15% of total biomass in control plots, and 42% of the total in NPO plots. Biomass of other species groups (native legumes, bulb and corm species, and perennial grasses) did not respond to treatment in the first year, in part because some of these species were so sparse that the harvest regime did not adequately sample them.

In the second year, annual native forb biomass was lower in the fertilized plots than in the previous year, and significantly lower than in control plots (Fig. 2, Table 2). Native annual forb biomass was virtually zero in the NP and NPO treatments in 1986. Non-native annual grass biomass, particularly that of *Lolium multiflorum* and *Bromus mollis,* was significantly larger in N-fertilized plots than in control plots. Non-native annual grass biomass contributed 37% of total biomass in the control and 80% in the NPO treatment. Native
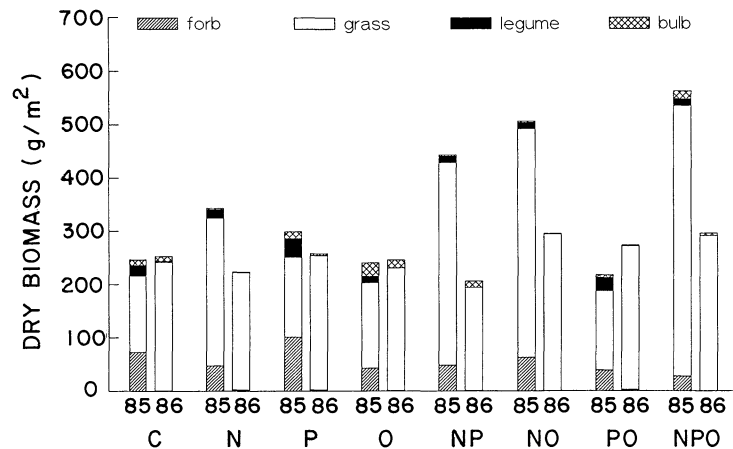
Fig. 3.   Dry biomass for each species group, in Grass plots. Values plotted are means of five replicates (calculated from log-transformed data). In each pair of bars the left bar represents 1985 values, the right bar 1986 values. Treatment notation as in Table 1 legend.

bulb and corm species biomass had a significant positive response to N and O, while native legume biomass was lower in all treatments than in the first year (significantly affected by N and P; Table 2, Fig. 2). Perennial grass biomass was still too low to be sampled effectively.

Biomass by species groups: Grass plots. — In the plots initially dominated by non-native annual grasses, first year responses were qualitatively similar to the second year of results in Forb plots: non-native annual grass biomass increased substantially, and native annual forbs declined in abundance (Table 3, Fig. 3). Main effects of N and of O were significant for non-native annual grasses. Native components contributed less than half of total biomass; native annual forbs persisted through the first year as a minority fraction in fertilized plots.

In the second year, non-native annual grass biomass mirrored the reduction of total biomass in the fertilized plots; there were no significant effects of fertilization treatment on the annual grasses (Table 3). Native bulb/corm species and perennial bunchgrasses made the only other measurable contribution to biomass in Grass plots, but these groups showed no significant treatment effects. In both years, fertilized Forb plots achieved total biomass equal to or greater than that in Grass plots. By the second year, relative abundances of species groups in the N-fertilized Forb plots closely resembled those in Grass plots (Figs. 2 and 3), with a predominance of non-native annual grasses.

Late spring grass biomass and root/shoot ratios. — The small cores sampled in late April 1985 from the control, N, and NPO Grass plots yielded aboveground biomass values of 300–1300 g/m² (Table 4), considerably higher than biomass samples from the previous month. The increase was nearly all due to an increase in annual grass biomass; forb biomass was lower than in the previous samples.

Belowground biomass in the top 20 cm in the April samples was considerably less than aboveground biomass (Table 4). The top 10 cm contained most of the root biomass. Mean root/shoot ratios were 0.57 in the control, 0.47 in the N, and 0.32 in the NPO treatments. However, between-block variability was so great that the differences among treatments in root/shoot ratios were not significant (Page's test for ordered alternatives, $P > .05$).

Species richness, species composition, and community structure

Species numbers. — In 1985 the mean species richness of samples from Forb plots was 12.3 (per 79-cm² sample). A one-way analysis of variance confirmed that the eight treatments did not differ significantly in species richness. Species richness in the Grass plots was lower (mean of 8.6 species/79 cm²), again with no significant differences among treatments (one-way ANOVA, $P = .068$).

In 1986 fewer total species were encountered in the samples taken; mean species richness could not be compared statistically between years, but because larger areas were sampled in 1986 than in the previous year, the decline in richness was striking. In the initially forb-dominated plots, mean species richness over all treatments was 9.5 (per 113-cm² sample); species number varied significantly with treatment (ANOVA, $P = .002$), with significantly lower values in the NP and NPO plots (6–7 species) than in the control (11 species; Dunnett's test of multiple comparisons against a control, $P < .01$ for both). Species richness in the Grass plots (overall mean of 5.1 species) was again lower than that in the Forb plots. Species richness varied among treatments (ANOVA, $P = .045$), with the NP, NO, and NPO treatments having the lowest mean species richness (3–4 species per 113-cm² sample relative to the control's 8).

TABLE 2. Results of factorial analyses of variance for dry biomass (total and by species groups) for Forb plots in 1985 and 1986. Main effects are Nitrogen (N), Phosphorus (P), and Other (O, complete fertilizer minus N and P) treatments. There is 1 df for each main effect and for each interaction term; for each analysis the residual df = 33.

	1985		1986	
Source of variation	SS	F-ratio	SS	F-ratio
		Total biomass		
N	2.207	31.96***	2.749	43.55***
P	.478	6.92*	.361	5.72*
O	.001	.01	.279	4.42*
N × P	.162	2.34	.528	8.36**
N × O	.003	.04	.314	4.97*
P × O	.040	.57	.014	.23
Residual:	2.279	(MS 0.069)	2.083	(MS 0.063)
		Annual non-legume forb biomass		
N	1.599	10.25**	61.168	32.40***
P	.091	.58	27.695	14.67***
O	.216	1.39	11.321	6.00*
N × P	.298	1.91	11.490	6.09*
N × O	.068	.43	5.704	3.02
P × O	.009	.06	.551	.29
Residual:	5.148	(MS 0.156)	62.296	(MS 1.888)
		Annual grass biomass		
N	11.138	17.64***	9.412	24.70***
P	1.456	2.307	2.950	7.74**
O	.990	1.57	.949	2.49
N × P	1.117	1.77	3.787	9.94**
N × O	.549	.87	3.786	9.94**
P × O	.189	.30	.249	.65
Residual:	20.840	(MS 0.632)	12.574	(MS 0.381)
		Legume biomass		
N	.914	.63	27.032	17.09***
P	1.235	.86	10.754	6.80*
O	1.363	.94	.092	.06
N × P	1.340	.93	7.166	4.53
N × O	3.734	2.59	.279	.18
P × O	.861	.60	.001	.00
Residual:	47.656	(MS 1.444)	52.202	(MS 1.582)
		Bulb/corm species biomass		
N	.190	.85	3.270	25.20***
P	.163	.72	.091	.70
O	.315	1.40	.565	4.36*
N × P	.206	.92	.158	1.22
N × O	.135	.60	.102	.79
P × O	.000	.00	.088	.68
Residual:	7.421	(MS 0.225)	4.281	(MS 0.130)
		Perennial grass biomass		
N	2.485	.62	2.788	.34
P	4.936	1.23	1.377	.17
O	4.778	1.19	3.831	.47
N × P	.979	.24	.160	.02
N × O	.028	.01	3.289	.40
P × O	4.018	1.00	3.495	.43
Residual:	132.532	(MS 4.016)	270.050	(MS 8.183)

* $.01 \leq P < .05$; ** $.001 \leq P < .01$; *** $P < .001$.

Within-treatment variability of composition.—Although a few dominants were found throughout most plots, the diverse serpentine grassland was characterized by a heterogeneity of subordinate or sparse species. In 1985 the coefficient of community for replicates within a Forb treatment averaged between 0.71 and 0.75. The average coefficient of community for the Grass plots in the same year ranged more widely, from 0.58 to 0.76 (Table 5).

We hypothesized that similarity among replicates within a treatment would become greater in the second year than in the first, as nutrient additions swamped the original variability among replicates. A statistical comparison is not strictly valid, because of the differences in sampling between years that could affect efficiency of sampling composition, but comparison of the similarity values (Table 5) shows that CC values decreased, if anything, in the second year (i.e., variability among replicates increased).

If nutrient applications were substantial enough to

TABLE 3.   Results of factorial analyses of variance for dry biomass (total and by species groups) for Grass plots in 1985 and 1986. Main effects are Nitrogen (N), Phosphorus (P), and Other (O, a complete fertilizer minus N and P) treatments. There is 1 df for each main effect and for each interaction term; for each analysis the residual df = 33.

Source of variation	1985		1986	
	SS	MS	SS	MS
Total biomass				
N	3.572	47.79***	.055	.27
P	.111	1.49	.002	.01
O	.000	.00	.000	.00
N × P	.040	.53	.026	.13
N × O	.489	6.54*	.003	.02
P × O	.082	1.10	.010	.05
Residual:	2.467	(MS 0.075)	6.725	(MS 0.204)
Annual non-legume forb biomass				
N	.845	1.86	14.871	2.61
P	.220	.48	.533	.09
O	1.958	4.30*	19.865	3.48
N × P	.644	1.41	1.331	.23
N × O	.958	2.10	17.800	3.12
P × O	1.035	2.27	.522	.09
Residual:	15.031	(MS 0.456)	188.351	(MS 5.71)
Annual grass biomass				
N	9.085	99.17***	.001	.00
P	.130	1.42	.002	.01
O	.438	4.79*	.331	.91
N × P	.161	1.76	.075	.21
N × O	.238	2.60	.286	.79
P × O	.045	.50	.035	.10
Residual:	3.023	(MS 0.092)	11.967	(MS 0.363)
Legume biomass				
N	2.397	3.10	15.216	14.36***
P	.552	.71	.816	.77
O	1.004	1.30	3.013	2.84
N × P	1.658	2.14	.224	.21
N × O	.155	.20	4.693	4.43*
P × O	.179	.23	.112	.11
Residual:	25.532	(MS 0.774)	34.971	(MS 1.060)
Bulb/corm species biomass				
N	15.380	3.04	2.353	.29
P	.056	.01	.089	.01
O	2.668	.53	.280	.03
N × P	5.907	1.17	33.062	4.04
N × O	2.968	.59	.016	.00
P × O	.120	.02	3.513	.43
Residual:	166.831	(MS 5.055)	270.090	(MS 8.185)
Perennial grass biomass				
N	2.412	.33	8.669	1.31
P	.023	.03	7.223	1.09
O	7.677	1.05	11.077	1.67
N × P	.071	.01	2.163	.33
N × O	1.512	.21	1.463	.22
P × O	.014	.00	3.758	.57
Residual:	242.393	(MS 7.345)	219.053	(MS 6.628)

* .01 ≤ P < .05; ** .001 ≤ P < .01; *** P < .001.

obscure the initial heterogeneity among plots, one might also predict that treatments receiving nutrients would be less variable than the control plots in a given year. However, CC values for the NPO plots were equal to or smaller in magnitude than the controls in three of the four year-by-vegetation type combinations. Only for the Grass plots in 1985 did the NPO plots have higher CC values than the controls (Table 5).

Community structure.—For Forb plots in 1985, CC values were uniformly high for all treatment compar-isons (overall mean CC, 0.88; Table 6). By the second year, however, variability among treatments was great-er (lower CC values), and the values for NP and NPO treatments were lowest (i.e., the NP and NPO treat-ments were most distinct from all others in composi-tion). The Grass plots showed the same trends, with overall high CC values among treatments in the first year, and lower CC values in the second (NPO treat-ment again showed the lowest values; Table 6). *Lolium multiflorum* and *Bromus mollis* dominated the N-fer-

TABLE 4. Above- and belowground dry biomass in late April 1985 from control, N, and NPO Grass plots. $n = 5$ for all treatments. Values given are means (from log-transformed data) with ranges in parentheses.

Treat-ment*	Root biomass (g/m²)	Propor-tion of roots in top 10 cm	Shoot biomass (g/m²)
C	219 (161–346)	0.73	395 (322–528)
N	324 (233–386)	0.76	634 (391–1353)
NPO	288 (233–380)	0.83	887 (662–1061)

* Treatment symbols are: C = control; N = nitrogen addition; NPO = addition of nitrogen, phosphorus, and other nutrients (in sum, a complete fertilizer).

tilized Forb plots in 1986, making these plots similar in appearance to Grass plots. However, CC comparisons demonstrated no greater overall similarity between the Forb N and Grass Control treatments (CC = 0.343) than between Forb C and Grass C (0.344). The increased similarity in dominants was not reflected in any convergence of rarer species.

In the 1985 Forb plots, there was little difference among dominance–diversity curves for the control, N, and NPO treatments. A comparative regression analysis demonstrated no significant difference in slope between the C and NPO plots. However, by 1986 the curves differed more strongly among treatments in the Forb plots (Fig. 4), with the NPO curve substantially steeper than that for the control ($F = 74.3$, $P < .0001$). In addition to the changes in slope, comparison of the dominance–diversity curves also illustrates the differences among treatments in species richness (e.g., the lower species richness of the NPO plot relative to the control; Fig. 4).

If nutrient additions favor one or a few species, at the expense of others, then larger proportions of total community biomass would be contributed by the dominants. As an index of dominance, we calculated the sum of the relative biomass contributions of the two most abundant species within a plot. In 1985, the Forb control and NPO plots did not differ in dominance value (52% of total biomass contributed by the two most abundant species). By 1986, however, the treatments differed significantly ($t = -2.64$, $P = .03$); in the NPO plots the two most abundant species represented

TABLE 5. Mean coefficients of community (CC; means ± SD) for the 10 pairwise comparisons among the five replicate samples within each treatment, for control, N, and NPO treatments in 1985 and 1986.

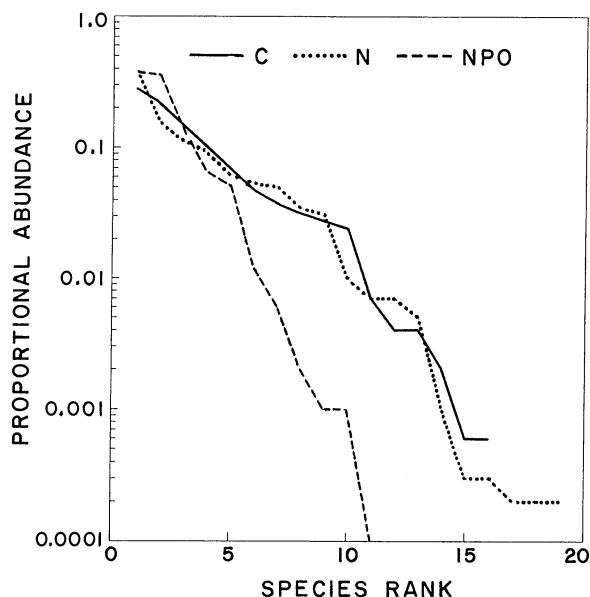| Treatment*	1985	1986
Forb control	0.75 ± 0.08	0.80 ± 0.06
Forb N	0.71 ± 0.07	0.67 ± 0.12
Forb NPO	0.73 ± 0.08	0.70 ± 0.10
Grass control	0.58 ± 0.12	0.58 ± 0.08
Grass N	0.76 ± 0.10	0.55 ± 0.09
Grass NPO	0.70 ± 0.08	0.62 ± 0.14

* Treatment symbols as in Table 4.

FIG. 4. Dominance–diversity plots for control, N, and NPO treatments in 1986 Forb plots. Vertical axis is proportion of total dry biomass contributed by a given species, plotted on a log scale; horizontal axis is species rank, from most abundant to least.

75% of total biomass. The Grass plots had higher overall dominance values (77% in 1985), and in both years dominance values were significantly greater in NPO than in control Grass plots (1985, $P = .01$; 1986, $P = .046$).

Single-species responses

The various species groups or growth forms responded differently to the nutrient applications. Each species group comprised several species, however; did species within a group differ in their response to fertilization? We made qualitative comparisons among species by plotting mean biomass values by treatment. In general, species responded to treatment in an individualistic manner. For example, in the 1985 Forb plots, two of the most abundant native annual forbs (*Evax sparsiflora* and *Lasthenia californica*) responded positively to N, NP, and NPO applications, while a third dom-

TABLE 6. Mean coefficients of community, calculated for each treatment with each of the seven other treatments. Treatment notation as in Table 1.

Treatment	Forb plots		Grass plots	
	1985	1986	1985	1986
C	0.889	0.738	0.729	0.663
N	0.879	0.740	0.711	0.619
P	0.883	0.748	0.716	0.588
O	0.886	0.727	0.731	0.656
NP	0.878	0.639	0.696	0.569
NO	0.856	0.705	0.771	0.586
PO	0.881	0.733	0.702	0.666
NPO	0.859	0.611	0.729	0.476

1985 GRASS

—— Evax ---- Plantago ---Lasthenia

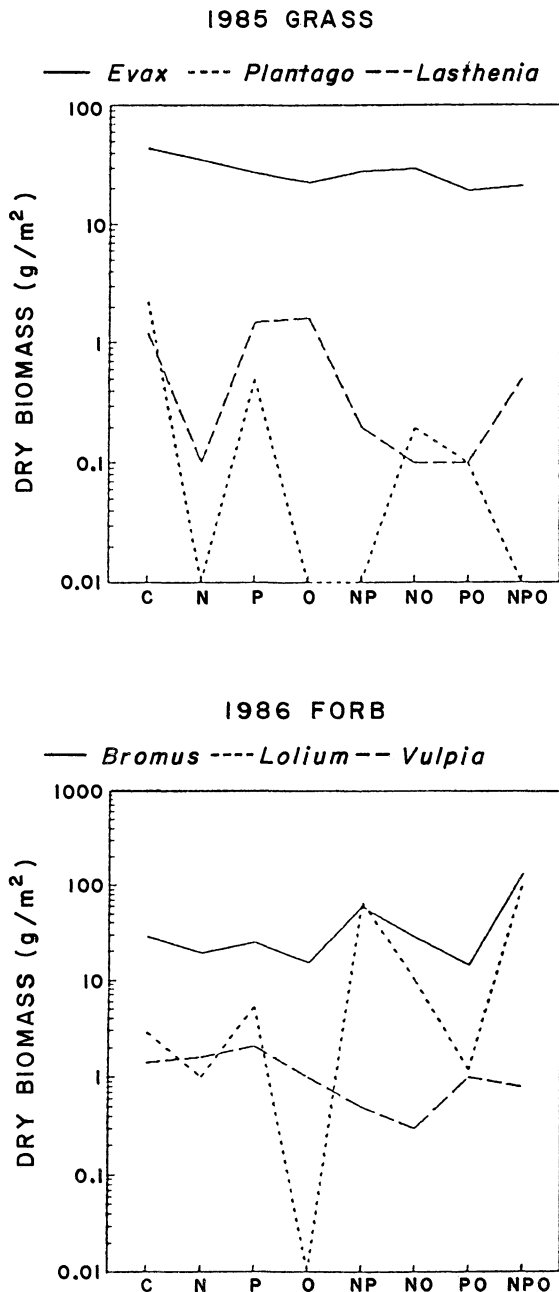## 1986 FORB

—— Bromus ----Lolium —— Vulpia

FIG. 5. Individual species' dry biomass values by treatment, in 1985 Grass plots (top) and 1986 Forb plots (bottom). Plotted values are means (on log scale; $n = 5$). Treatment notation is as in Table 1. Species abbreviated as: *Evax = Evax sparsiflora*; *Lasthenia = Lasthenia chrysostoma*; *Plantago = Plantago erecta*; *Bromus = Bromus mollis*; *Lolium = Lolium multiflorum*; *Vulpia = Vulpia microstachys/myuros*.

inant native, *Plantago erecta,* displayed instead a decrease in mean biomass in the NP and NPO plots. In the 1985 Grass plots, the same three species again differed in response: *Evax* varied little among treatments, while both *Plantago* and *Lasthenia* decreased in the N

and NP treatments (Fig. 5, top). There were differences in responses among the non-native annual grasses, as well. In the 1986 Forb plots, for example, *Bromus mollis* and *Vulpia microstachys/myuros* responded similarly (showing little response to treatment), while *Lolium multiflorum* displayed substantial positive response to NP and NPO additions, and a negative response to the O treatment (Fig. 5, bottom).

Correlations among biomass components

In general, biomass values for native annual forbs and legumes were negatively correlated within individual plots with non-native annual grass biomass, and with total biomass (Table 7). Native bulbs, however, were positively correlated with non-native annual grasses (at least in the 1986 Forb plots), indicating responses similar to those of the non-native annual grasses in those plots.

DISCUSSION AND CONCLUSIONS

Limits to productivity on serpentine-derived soils

Plant production on this serpentine-derived soil responded positively to macronutrient additions. Tissue nutrient concentrations of both N and P in *Plantago erecta* and *Bromus mollis* demonstrated that the added nutrients were in fact available for plant uptake (R. Koide, *personal observation*). After fertilization, biomass increased to levels typical of non-serpentine grassland, suggesting that low levels of plant-available N and P (rather than Ca deficiencies, heavy-metal toxicity, or other special features of serpentine) are a primary constraint to productivity on this site. Fertilization with NPK on other Californian serpentine soils has sometimes increased productivity (of crop species, native plants, and non-natives), but in other cases has elicited no response (e.g., Martin et al. 1953, Turitzin 1982). The extreme variability in chemistry among particular serpentine sites certainly precludes any single explanation for their low productivity (Walker 1954, Proctor and Woodell 1975, Kruckeberg 1984).

It is perhaps surprising that the native annual forbs were able to respond so vigorously to N and P additions in the first season, in the absence of abundant non-native grasses. Plants adapted to life in environments with low nutrient availability, such as serpentine soils, might well lack the capacity to increase growth rates opportunistically when nutrient levels are increased (Grime 1979, Chapin et al. 1986). However, most of these native species are not true serpentine endemics. Presumably the genetic constitution that allowed these species to range widely throughout California's grasslands (including non-serpentine sites) persists in today's serpentine populations.

An interesting idiosyncratic response to fertilization was displayed by *Lolium multiflorum,* one of the an-

TABLE 7. Correlations among dry biomass contributions of species groups.† $n = 40$ for all correlations. Values given are product-moment correlation coefficients, with significance level noted as follows: *, $0.01 \leq P < 0.05$; **, $0.001 \leq P < 0.01$; ***, $P < 0.001$.

Species group	1985 Forb plots					1985 Grass plots				
	Forb	Legume	Bulbs	Pgr	Total	Forb	Legume	Bulbs	Pgr	Total
Ann grass	.031	−.028	.019	−.151	.628***	−.341*	−.341*	−.294	−.001	.866***
Forb		.089	.135	−.003	.684***		.379*	.098	.133	.033
Legume			.169	.222	.242			.030	.361*	−.029
Bulbs				.111	.339*				.323*	−.128
Pgr					.093					.256

Species group	1986 Forb plots					1986 Grass plots				
	Forb	Legume	Bulbs	Pgr	Total	Forb	Legume	Bulbs	Pgr	Total
Ann grass	−.786***	−.555***	.450**	−.137	.830***	−.325*	−.124	.011	−.090	.859
Forb		.693***	−.391*	.134	−.761***		.164	−.133	−.002	−.069
Legume			−.448**	.053	−.652***			.345*	.180	−.196
Bulbs				−.167	.538***				.099	.037
Pgr					.196					.064

† Species groups are denoted as follows: Ann grass = non-native annual grass; Forb = native annual forbs; Legume = native annual legumes; Bulbs = native corm and bulb species; Pgr = native perennial grasses; Total = sum of all biomass per plot.

nual grasses that responded most vigorously to N and P additions. *Lolium* biomass declined strongly in the Forb O treatment (Fig. 5). These same treatments were among those where native species persisted best. We speculate that the native species, well adapted to serpentine's low Ca/Mg ratio, were able to utilize the Ca component of the O additions while not being harmed by added Mg. In contrast, a non-serpentine-adapted plant (such as an invader annual grass) might have been suppressed by the addition of Mg, and unable to respond to the simultaneous addition of Ca. In greenhouse studies, non-native annual grasses growing in serpentine soil are capable of responding positively to calcium (Koide et al. 1987).

Another conspicuous response to fertilization was the disappearance of legumes from nitrogen-supplemented plots. This effect parallels the well-known depression of legumes after fertilization, and the increase in grass productivity that often follows a good legume year in both annual and perennial grasslands (Jones and Woodmansee 1979, Lauenroth and Dodd 1979, Menke 1989).

The substantial first-year increase of biomass in the NP and NPO plots, particularly in the Grass plots, resulted in a heavy accumulation of standing dead material. Dense annual grass litter decomposes slowly in this climate, especially if intact and upright, and such thatch has major effects on the emergence, success, and composition of autumn germinants (Heady 1956, Young and Evans 1989). In the NP and NPO Grass plots few individuals (chiefly of weedy species such as *Amsinckia intermedia*; L. F. Huenneke, *personal observation*) germinated in the second year, accounting for their compositional distinctiveness from the other Grass plots. A temporary increase in productivity in one year, caused by increased resource levels, may thus impinge on future productivity.

Invasibility of annual grassland ecosystem

Ecological invasions are often linked to resource enrichment arising from ecosystem disturbance (Mooney and Drake 1986), but data from plant invasions in natural ecosystems have been scarce. Reviews of plant invasions elsewhere (e.g., Australia: Bridgewater and Backshall 1981, Groves and Burdon 1986; Hawaii: Gerrish and Mueller-Dombois 1980) suggest greater invasibility of more fertile sites. However, most examples are confounded by physical site disturbance, which reduces competition due to native plants and creates opportunities for germination and establishment by weedy or invading species. Our results confirm that increased nutrient availability, without physical disturbance of soil or of native vegetation, can favor the invasion and success of non-native species in an ecosystem where natural levels of resource availability are low.

The success of non-native annual grasses occurred even in fertilized Forb plots, where abundant inputs of native annual forb seeds were not reflected in the species composition of vegetation in the following autumn (L. F. Huenneke, *unpublished manuscript* on seed rain). Hobbs et al. (1988) reported similar results from another serpentine site, where natives responded to NPK additions in the first year, but non-natives increased later. Why were native species so poorly represented in the second year, despite their substantial majority in the seed rain? Fertilization may affect (directly or indirectly) germination, establishment, growth rates, or competitive outcomes; each of these influences end-of-season biomass. Experimental manipulation and

detailed observation of individual life history stages will be necessary to distinguish among these alternatives.

Community structure and species richness

Simple nutrient additions were sufficient to alter completely the nature of the dominant grassland vegetation by the second year. Species richness declined significantly, and composition shifted substantially. In plots with abundant non-native annual grasses, the decline in species number resulted from the loss of native annual forbs and legumes. Decreased richness was accompanied by increased dominance of a few species (specifically non-native annual grasses), as reflected in steeper dominance–diversity curves and greater dominance values in fertilized Forb plots. All of these changes increased the similarity of fertilized Forb plots to Grass plots. However, variability among the numerous subordinate or low-abundance species appeared to obscure this convergence when assessed with coefficient of community values. We had expected large nutrient additions to obscure the initial heterogeneity among replicates, but species composition as reflected in CC values grew more variable within a treatment through time. However, NP and NPO plots were the most distinctive in composition, in both Forb and Grass plots. Community structure, then, is clearly related to nutrient resource availability.

The native serpentine grassland community is a diverse assemblage. What evidence is there for niche differentiation among species? Species groups or growth forms clearly differed in their response to nutrient resources (e.g., the different responses of native annual forbs and of native bulbs). However, are the various species within a growth form equivalent in their use of resources? The individualistic responses of species within a group (Fig. 5) suggest non-equivalence. Gulmon's (1979, Gulmon et al. 1983) work on sets of annual grasses and annual forbs from Californian grassland demonstrated significant differentiation in physiology and competitive ability within each growth form. The differentiation of responses to fertilization likely is attributable to such differences in competitive ability and in minimum resource requirements, rather than use of different resources.

Soil properties, disturbance, and natural heterogeneity

As the initially Forb-dominated plots responded to nutrient supplementation, they became more similar in composition and community structure to the Grass plots. Were the plots dominated initially by native annual forbs and by non-native annual grasses different in some significant respect, or is the patchiness of vegetation in this serpentine grassland a transient or stochastic phenomenon? The soil analyses found that Forb and Grass plots differed only slightly in extractable nutrient concentrations, total nitrogen and carbon, and

pH (although total P was greater in Forb plots). However, the greater effective depth of soil in Grass plots suggested that plants in those plots experience greater resource availability. A requirement by non-native annual grasses for higher resource availability would explain both their distribution on deeper soil and their positive response to the increased resource availability within fertilized Forb plots. Thus the serpentine plant community appears to contain at least two "guilds": one comprising many of the native annual forbs, with low competitive ability but capable of exploiting shallow or low-nutrient soil patches; the other made up of species (largely non-native annual grasses) requiring greater resource supplies, in the form of either deeper or higher-N soils.

Where total resource levels increased to a point high enough to support the invaders, many native annual forbs were suppressed or eliminated. Even in those plots originally dominated by non-native annual grasses, composition in the second year of fertilization was shifted to weedier species. Such results have important implications for the persistence of native vegetation in many low-nutrient habitats, as atmospheric deposition of nitrogen has in some cases become substantial enough to trigger similar changes in community structure (Heil et al. 1988).

The "responses" of various species or species groups to nutrient applications, of course, might actually be a response to the altered competitive environment (the growth response of competitors), rather than a direct response to altered nutrient levels. Correlations among biomass values for species groups were consistent with both hypotheses. If competition were occurring in these plots, the native annual forbs and legumes (small in stature) would presumably be most sensitive to the reduction of light availability by the vigorously responding non-native annual grasses. Although we did not test directly for resource competition, there is evidence of aboveground competition for light even in the sparse canopy of serpentine grassland (Turitzin 1978). Root biomass did increase somewhat with fertilization, but not to the same degree as did aboveground biomass; lower root/shoot ratios were found in the fertilized plots. Such a pattern conforms to Tilman's (1985, 1987) predictions that increased nutrient resources (notably nitrogen) result in increased competition for light among vigorously growing plants.

Both non-native annual grasses and native perennial grasses increased in abundance overall in the fenced experimental area (including control plots) by the second year, and native annual forbs declined. In the grazed areas outside the fenced site, however, native annual forbs remained an important constituent of initially Forb-dominated plots throughout the study (L. F. Huenneke, *unpublished manuscript*). Grazing may serve as a moderate-intensity disturbance in this system (Fox 1979, Huston 1979), with cattle removing grass biomass and thus allowing the persistence of native annual

forbs. Gopher disturbance may play an equivalent role in limiting grass performance and allowing recolonization by forbs (Hobbs and Mooney 1985, Hobbs et al. 1988), while directly altering physical, chemical, and mycorrhizal status in the soil (Koide and Mooney 1987, S. P. Hamburg, L. F. Huenneke, and R. Koide, *unpublished manuscript*). Similarly, the negative effect of voles on grass dominance can lead to increased forb abundance in the Mediterranean grasslands of Israel (Noy-Meir 1988). The implication is that the large size (and presumed competitive vigor) of annual grasses frequently allow them to exclude smaller forb species, unless grass biomass is severely limited, either by resource limitation or by frequent disturbance.

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