

Habitat patchiness promotes invasion by alien grasses on serpentine soil

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Abstract

Serpentine soils are considerably less invaded by alien species than nonserpentine soils in California's North Coast Ranges. However, alien species are significantly more prevalent on small patches of serpentine (< 5 ha) than in the interiors (> 100 m from edges) of very large ones (> 1 km²). We studied reasons for this pattern, focusing on the Mediterranean annual grasses *Avena fatua* L. and *Bromus hordeaceus* L. Using field transects, we found that both *Avena* and *Bromus* were more common at the edges of large patches than in large-patch interiors, even though soils from edges were not significantly different from soils in interiors. Using a growth experiment, we found that soils from small patches did not support better growth of either grass than soils from large-patch interiors. We conclude that the observed pattern is probably caused by small patches and large-patch edges receiving a higher flow of propagules from the nonserpentine matrix, and not by differences in habitat suitability. In both species, populations from small serpentine patches outperformed nonserpentine populations when grown on small-patch soil. This suggests that small serpentine patches may promote the evolution of serpentine-tolerant ecotypes of these alien grasses. © 2001 Elsevier Science Ltd. All rights reserved.

1. Introduction

Plant communities lie on a continuum from heavily invaded to relatively free from exotics. Reasons for this variation are not fully understood, although important correlates of invasion include disturbance, low diversity, and a high influx of alien propagules (Crawley, 1989; Hobbs, 1989; Parker and Reichard, 1998). Little attention has been given to landscape factors, such as the spatial juxtaposition of different habitats among which organisms may disperse. Yet a landscape approach may be especially appropriate in invasion ecology, since adjacent communities may differ sharply in their abundances of alien species, and since rates of propagule arrival may be a significant contributor to invadedness (Crawley, 1989). Landscape structure may also influence the ability of invading species to adapt to novel environments (Holt and Gaines, 1992; Holt and Gomulkiwicz, 1997). In this study we examined the consequences of landscape structure for invasion and

local adaptation by two Mediterranean grasses, *Avena fatua* L. and *Bromus hordeaceus* L., on outcrops of serpentine soil in the North Coast Ranges of California.

Although California's lowland grasslands have been taken over almost completely by Mediterranean grasses such as *Avena*, *Bromus* and *Lolium* spp, a native-dominated flora is still found on serpentine or ultramafic soils. Serpentine is a tectonically derived rock found in faulting zones throughout the world, which forms soils rich in magnesium and iron and poor in calcium and primary nutrients. For these reasons serpentines are much less invaded than nonserpentine soils, and provide a significant refuge for native California grasses and forbs (Kruckeberg, 1984; Huenneke et al., 1990). However, small patches of serpentine may be an exception. In a regional survey of plant diversity on serpentine, Harrison (1999) found that 24 small (< 5 ha) outcrops of serpentine supported an average of 6.0 ± 3.9 (SD) alien species each, in contrast to 1.3 ± 1.8 alien species on 24 equal-sized sampling plots in the interiors (> 100 m from edges) of large (> 1 km²) serpentine outcrops. In this study, we used experiments and observational evidence to attempt to explain this difference.

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At least two non-exclusive hypotheses might explain why small serpentine patches are more heavily invaded than large serpentine patches. First, the pattern might be a biological edge effect, in the sense that small patches and the edges of large patches might receive a high influx of alien propagules from the surrounding nonserpentine matrix. Second, the pattern might be a physical edge effect, in the sense that small patches and large-patch edges might have more favorable soil properties for alien species than do large-patch interiors. In either case, aliens such as *A. fatua* and *B. hordeaceus* (hereafter referred to as *Avena* and *Bromus*, respectively) should be just as prevalent at the edges of large serpentine outcrops as they are in the centers of small patches. In the second case, there should also be differences in soil quality between the edges of large patches and their interiors, and there should be differences in the growth and reproduction of alien grasses between small patches and the interiors of large ones. To test these hypotheses, we sampled 50-m transects on the edges of large outcrops, in which we measured the abundances of *Avena* and *Bromus*, and analyzed soil variables (Ca^{2+} , Mg^{2+} , NO_3^- , and soil texture). We compared these results with the same variables measured in small patches and large patch interiors by Harrison (1999). We also experimentally compared the growth and reproduction of *Avena* and *Bromus* on soil from small patches and large patch interiors.

Finally, we examined the role of small serpentine patches in promoting formation of serpentine-tolerant ecotypes of alien grasses. Whatever the reason for the greater prevalence of aliens on small patches, these patches may promote the adaptive evolution of ecotypes that can invade serpentine. Some recent theory suggests that landscape heterogeneity can play an important role in niche evolution (Holt and Gaines, 1992; Holt and Gomulkiewicz, 1997). Under this theory, adaptation to novel “sink” habitats is generally disfavored, but is most likely to occur when dispersal is passive and occurs at a reasonably high rate, as would be the case for plants dispersing into small patches of serpentine. In the experiment just described, we used *Avena* and *Bromus* seeds collected either from small serpentine patches or from nonserpentine sites. In addition to small- and large-patch soil, we used nonserpentine soil (Yolo Loam) as a third soil treatment. We asked whether alien grasses grown from seeds from small serpentine patches performed relatively better on serpentine soil, compared to those grasses grown from seed collected from nonserpentine habitats.

2. Methods

2.1. Study system and previous results

The study was conducted in Lake, Napa, and Sonoma Counties, CA, USA. Geology and soils of this area have

been mapped by Fox et al. (1973), Lambert and Kashiwagi (1978), and Wagner and Bortugno (1982). Flora and vegetation of this region are described by Kruckeberg (1984), Callizo (1992) and Sawyer and Keeler-Wolf (1995). Serpentine soils support chaparral dominated by leather oak (*Quercus durata*, Fagaceae), whiteleaf manzanita (*Arctostaphylos viscida*, Ericaceae), musk brush (*Ceanothus jepsoni* var. *albiflorus*, Rhamnaceae), silktassel bush (*Garrya congdonii*, Garryaceae), gray pine (*Pinus sabiniana*, Pinaceae), chamise (*Adenostoma fasciculatum*, Rosaceae), toyon (*Heteromeles arbutifolia*, Rosaceae), and bay laurel (*Umbellularia californica*, Lauraceae). Herbs occur sparsely on rocky slopes within the chaparral. Nonserpentine soils in this region are mainly derived from sedimentary rocks of the Franciscan formation. To the eastern (inland) side of the study area, the non-serpentine vegetation is predominantly blue oak (*Q. douglasii*) woodland; toward the west, coastal mixed evergreen forest with live oak (*Q. agrifolia*), Douglas fir (*Pseudotsuga menziesii*, Pinaceae), madrone (*Arbutus menziesii*, Ericaceae), bay laurel and other species.

In a previous study, Harrison (1997, 1999) sampled plant diversity on 24 small serpentine outcrops, 0.5–3 ha in area and isolated by > 1 km from any large area of serpentine (> 1 km²), and 24 equally-spaced sampling sites in the interiors (> 100 m from edge) of four large serpentine outcrops (approx. 6, 16, 30 and 55 km²). For native plant species restricted or nearly restricted to serpentine, the samples from small patches collectively included about the same number of species as the samples from large ones (equal regional diversity). However, the small patches had lower local richness (alpha diversity), balanced by higher differentiation in species composition (beta diversity). Another striking pattern was that for species not restricted to serpentine, including alien species, both local and regional diversity were considerably higher on small than large serpentine patches. Diversity patterns were also influenced by soil chemistry, slope, and distance inland (a proxy for climate), but these variables did not appear to explain the differences between small and large patches.

2.2. Study species

Among the alien species encountered in the above study, *Avena* and *Bromus* showed the strongest patterns of association with small serpentine patches. *Avena* was found on 15 of 24 small patches and 0 of 24 sites within large ones, while *Bromus* was found on 20 of 24 small patches and two of 24 sites within large ones. Both species are known to have existed in California for over 150 years (Mooney et al., 1986; Mack, 1989). Both species are good colonizers and are highly self-pollinating (Imam and Allard, 1965; Jain, 1969; Jain et al., 1970). Consistent with their inbreeding mating systems, most of the allozymic variation in both species is distributed

among populations, and within-population genetic variation is low (Jain and Marshall, 1967; Jain et al., 1970). Little is known about the degree to which either species forms ecotypes adapted to local environmental conditions. To our knowledge, differences between serpentine and nonserpentine populations have not been studied in *Avena*. Freitas and Mooney (1996) compared populations of *Bromus* from neighboring serpentine and sandstone soils, and found ecotypic differences in responses to water stress.

2.3. *Transects at the edges of large serpentine patches*

We sampled six sets of 50-m transects at the edges of each of four large serpentine patches, from 21 to 28 April 1997. We used the same large patches as in the earlier study (Harrison, 1999), with one exception. In the earlier study, half the small patches were located in the western (coast live oak forest) part of the region and half in the eastern (blue oak woodland) part, while only one large patch was in the western part and three were in the eastern part. To remedy this imbalance, in the present study we added a large patch in the western area and dropped one in the east. The new large patch, The Cedars, is located in western Sonoma Co., USA (36°36'N, 123°07'W). The other three are Sugarloaf Ridge (Sonoma Co.; 38°27'N, 122°31'W), Pope Canyon (Napa Co.; 38°39'N, 122°20'W), and Homestake Mine (Napa and Lake Co.; 38°52'N, 122°25'W).

At each of the four large patches, we used geologic maps and field reconnaissance to locate six separate sites where the boundary between serpentine and nonserpentine was distinct. For several reasons, the exact edges of large blocks of serpentine are often obscured. First, these edges often correspond to geologic faults, and streams and groundwater may follow these faults, so that riparian vegetation may separate the serpentine and nonserpentine habitats. Second, in some cases meadows on clayey soils composed of serpentine alluvium are found at the edges of large serpentine blocks, and these too separate serpentine chaparral from nonserpentine habitat. To best match the habitat transitions found at the edges of small serpentine patches, we chose locations where serpentine chaparral gave way to either blue oak woodland or coast live oak forest within a relatively short distance (usually <10 m). Our soil chemistry analyses later confirmed that we identified the edges of serpentine patches correctly. Within each large patch, the six transect sites we chose were separated by 100 m to 5 km from one another.

The transects were sampled in the same way as in the earlier study (Harrison, 1999) that compared large and small patches. At each location, extending 50 m from the edge into each habitat at right angles to the edge, we laid out a 5 m wide belt transect. We recorded the presence or absence of *Avena* and *Bromus* in the serpentine habitat. We also recorded the prevalence of the two

species in both habitats by counting flowering stems in a 1 × 1 m quadrat every 5 m. We collected four soil samples per transect, at -50, -10, +10 and +50 m from the edge, by scraping away the top 1 cm and collecting approx. 100 mg of rock-free soil. These soils were oven-dried, ground, and analyzed by the Division of Agriculture and Natural Resources Analytic Laboratory (University of California, Davis). Analyses included exchangeable Ca²⁺ and Mg²⁺ using ammonium acetate extraction and atomic absorption/emission spectrometry; NO₃-N, using KCl extraction and a diffusion-conductivity analyzer; and soil texture (% sand/silt/clay), using soil suspension and a hydrometer.

We used chi-squared tests to compare the prevalence of *Avena* and *Bromus* at the edges of large patches, as measured in this study, with their prevalence in large patch interiors and small patches as measured in the earlier study (Harrison, 1999). The earlier study used three 50 × 5 m transects per site. To make these data comparable with the present study, we used data from the first transect per site, yielding the following values: *Avena*, 0 of 24 large patch interiors and nine of 24 small patches; *Bromus*, one of 24 large patch interiors and 14 of 24 small patches. To see if grass abundances declined with increasing distance from the contact with nonserpentine, within the edges of large serpentine patches, we performed simple regressions of abundances on distance.

To verify that we had correctly identified serpentine edges, we performed a multivariate analysis of variance (MANOVA) on soil characteristics (Ca²⁺, Mg²⁺, NO₃-N, percent sand and percent silt), with soil type (serpentine or nonserpentine) as the independent variable. To determine whether soil conditions at the edges of the large patches varied with distance from the edge, we performed another MANOVA on the same soil characteristics, with distance (10 and 50 m from the edge) as the independent variable. To determine whether soils at large patch edges and/or small patches were in some way more favorable than soils in large patch interiors, we performed a third MANOVA on the same soil characteristics, in which the independent variable was location (large patch edge, large patch interior, or small patch; the category “edge” included data from both 10 and 50 m). This third analysis used soil data from Harrison (1999), collected in the identical way in large patch interiors and small patches. Following the MANOVAs, we performed selected ANOVAs on individual response variables.

2.4. *Growth experiment*

To determine whether soil conditions were more favorable for growth for *Avena* and *Bromus* on small serpentine patches compared with the interiors of large serpentine outcrops, we collected soil during May 1997 from the same 24 small and large patch sites sampled by

Harrison (1999). For each patch size treatment, soil from all 24 sites was mixed to minimize within-treatment variation. Subsamples from these serpentine soil mixtures were analyzed by A & L Western Agricultural Laboratories (Modesto, CA) for % organic matter, NO₃-N, K⁺, Ca²⁺, Mg²⁺, pH, and cation exchange capacity (C.E.C.). For the nonserpentine soil treatment, we used Yolo loam (a mixed, non-acid thermic Typic Xerochrept).

We collected seeds of *Avena* and *Bromus* from 17 of the 24 small patches, and from an equal number of nonserpentine sites within 1–5 km of each small patch, during 3–5 May 1997. Again, the material for each treatment was mixed to minimize within-treatment variation. From subsamples of the initial seed collection for both species, we determined average seed weights for both serpentine and nonserpentine populations.

On 11 November 1997, we planted seeds of each species from each of two populations (serpentine or nonserpentine) in each of the three soils (small patch, large patch, nonserpentine), with 10 replicates for each treatment combination. Five seeds were planted in each of 120 tubular (3.8 cm diameter × 21 cm depth) “containers” (Stuewe and Sons, Inc.) and kept outdoors in Davis, CA, USA. Two weeks later we thinned each pot to one individual, leaving the seedling closest to the center of the tube. The experiment was analyzed as a completely randomized factorial design with species, population (i.e. serpentine vs. nonserpentine), and soil type as fixed factors. The soil within the containers was kept near field capacity by frequent watering. During 10–23 May 1998 we harvested the mature plants just before seed dispersal, dried them, and measured above-ground dry weight, number of seeds, total seed weight, average seed weight, and root weight. The allocation to roots was calculated as root dry weight divided by the sum of shoot and root dry weights, and was arcsin square root transformed before analysis. Following a collective analysis using MANOVA, we performed “protected” ANOVAs on each of the response variables described above.

3. Results

3.1. Transects

Avena was found at three of 24 large patch edges, intermediate between its prevalence in large patch interiors (0 of 24) and in small patches (nine of 24). Neither difference was significant ($\chi^2_{(1)} = 3$, $0.05 < P < 0.10$). *Bromus* was found at 15 of 24 large patch edges, significantly higher than its prevalence in large patch interiors [one of 24; ($\chi^2_{(1)} = 12.3$, $P < 0.001$)] but not significantly different than its prevalence in small patches (14 of 24; $\chi^2_{(1)} = 0.004$, $P > 0.10$).

Average abundances of both species were significantly higher on nonserpentine than on serpentine, and this effect was relatively stronger in *Avena* than *Bromus* (Table 1). On serpentine, the abundance of *Avena* did not change significantly with distance from the edge ($r = -0.5$; d.f. = 1,9; $P = 0.12$), while the abundance of *Bromus* decreased significantly with increasing distance from the edge ($r = -0.74$; d.f. = 1,9; $P = 0.009$). On nonserpentine, there were no trends in either species' abundance with distance ($P > 0.2$).

3.2. Soil analyses

Soil variables along the edge transects showed the expected differences between serpentine and nonserpentine (Table 2); the two soil types were highly different overall (MANOVA, Wilks' Lambda = 0.45, $F = 21.7$, d.f. = 5,90; $P < 0.001$), and subsequent analyses of variance showed that serpentine was significantly lower in calcium and higher in magnesium than nonserpentine ($P < 0.001$) and had significantly lower levels of nitrate ($P = 0.02$), a lower fraction of silt ($P = 0.001$), and a marginally higher fraction of sand ($P = 0.06$). Calcium and magnesium levels differed significantly between each pair of serpentine and nonserpentine sampling sites, including the pair of sites that were each 10 m from the edge (ANOVA with Bonferroni adjustment, P always < 0.02). However, there were no soil variables that differed significantly between the samples taken 10 m and 50 m from the edge (Table 2; MANOVA, Wilks' Lambda = 0.94, $F = 0.45$, d.f. = 6, 41; $P = 0.84$). This evidence confirms that the edges of serpentine patches were correctly identified in the field.

Levels of the soil variables differed overall among the three locations on serpentine, i.e. large patch edges (combining the samples from 10 and 50 m), large patch interiors, and small patches (MANOVA, Wilks' Lambda = 0.69, $F = 3.7$, d.f. = 10, 178, $P < 0.001$). However, examination of the mean values in Table 2 shows that for every variable, large patch edges and large patch interiors were more similar to one other than either one was to small patches. Subsequent univariate analyses of variance revealed that significant differences existed only between small patches and the edges and

Table 1

Average prevalences of *Avena* and *Bromus* (stems/m²; means and standard deviations) on transects at the edges of large serpentine patches. Effects of species, soil and their interaction are all significant at $P < 0.001$ in an analysis of variance (d.f. = 40,1,1,1)

<i>Avena fatua</i>	
Serpentine	0.3 (0.1)
Nonserpentine	9.9 (5.0)
<i>Bromus hordeaceus</i>	
Serpentine	6.0 (9.5)
Nonserpentine	56.7 (19.4)

Table 2

Soil characteristics (means and standard deviations). Analyses for soil samples collected along field transects in large and small patches. Large patch edges were sampled along transects at 10 and 50 m from the serpentine–nonserpentine contact. Small patches and large patch interiors were sampled by Harrison (1999)

	Large patch edges				Small patches	Large patch interiors
	Nonserpentine		Serpentine			
	–50	–10	10	50		
Ca ²⁺ (meq/100 g soil)	9.3 (2.7)	8.7 (4.5)	5.6 (3.7)	4.5 (3.0)	3.0 (2.7)	4.3 (3.0)
Mg ²⁺ (meq/100 g soil)	8.6 (6.8)	12.5 (8.5)	19.1 (7.9)	19.1 (8.6)	15.2 (6.1)	17.9 (5.2)
Nitrate (ppm)	10.4 (10.7)	11.8 (19.8)	5.2 (5.1)	5.2 (7.1)	8.7 (5.1)	4.9 (3.4)
% Sand	47.5 (17.0)	44.5 (18.0)	50.5 (13.6)	53.8 (14.1)	66.9 (11.1)	58.1 (7.9)
% Silt	40.2 (11.6)	39.1 (10.3)	34.0 (8.0)	31.9 (7.5)	23.4 (7.5)	29.1 (8.1)
% Clay	12.3 (6.7)	16.4 (10.5)	15.6 (7.0)	14.3 (8.0)	9.7 (5.7)	12.8 (4.3)

interiors of large patches. Small patches had coarser soil texture (i.e. higher percentage of sand, and correspondingly lower silt and clay; $P < 0.001$ and $P < 0.05$ for comparisons of % sand with edges and interiors respectively); and higher levels of nitrate ($P < 0.05$ for comparisons with edges and interiors, respectively). Thus, we found no evidence for soil-based edge effects.

3.3. Growth experiment

Plant growth in the experiment was significantly affected by all main factors (species, population, soil type) and all two-way interactions between these factors (MANOVA; Table 3), so we performed a series of univariate protected ANOVAs on each of the response variables (Table 4). For the three major indicators of plant productivity (above-ground dry weight, total seed weight, and seed number per plant), there was a significant population (i.e. seed source) by soil type interaction (Table 4a–c). For both grass species combined, serpentine populations performed significantly better than the nonserpentine populations in the small patch serpentine soil (Fig. 1), mainly because of a decrease in performance by the latter. There was little difference between the source populations when they were grown in Yolo loam or large patch serpentine soil. In addition, there was a strong main effect of soil type on productivity because, regardless of species or population source, plants grown on Yolo loam had higher total biomass and greater reproductive output than plants grown on either type of serpentine soil (Fig. 1). Analyses of small patch and large patch soil mixtures used in the growth experiment (Table 5) indicate that the

Table 3

MANOVA of total seed number, total seed weight, aboveground dry weight, average seed weight, and root weight

	Wilks' Lambda	F	d.f.	P
Whole model	0.004	28.72	44	< 0.0001
Species	0.050	476.22	4	< 0.0001
Population	0.650	13.60	4	< 0.0001
Soil type	0.155	38.85	8	< 0.0001
Species × population	0.733	9.19	4	< 0.0001
Species × soil type	0.572	8.13	8	< 0.0001
Population × soil type	0.812	2.78	8	0.006
Species × population × soil type	0.910	1.22	8	0.289

small patch soil mixture had significantly lower Ca²⁺ levels, Ca²⁺/Mg²⁺ ratios, and C.E.C. (ANOVA; P always < 0.01) while Mg²⁺ levels were higher ($P < 0.01$). Soil texture was also coarser in the small patch soil mixture with significantly higher % sand and reduced silt (ANOVA; $P < 0.05$).

Seed number and average seed weight showed significant species by population interactions (Table 4c–d). Serpentine populations of *Avena* produced plants with more seeds but lower average seed mass than did nonserpentine populations, while seed parameters for *Bromus* did not differ significantly between populations (Fig. 2). Similar patterns in seed weight were found for the initial field collections. Weights of seeds from these initial collections (data not shown) showed a significant species by population interaction (ANOVA with d.f. = 76, 1; $P < 0.001$). Seed weight was not significantly different between populations of *Bromus*, while seeds were significantly smaller in serpentine compared to nonserpentine populations of *Avena*.

Relative dry weight allocation to roots was also dependent on the interactive effect of species and population (Table 4e). Serpentine populations of *Avena* allocated more to roots than nonserpentine populations, while populations

of *Bromus* did not differ significantly in allocation (Fig. 2). Mean proportional allocation to roots was significantly higher in large patch soil (0.34 ± 0.02) than in either small patch soil (0.29 ± 0.01) or nonserpentine soil (0.27 ± 0.02).

Table 4

Univariate analyses of the effects of species identity, population source and soil type on plant growth and reproduction

Source	d.f.	Sum of squares	F	P
(a) Total above ground dry weight per plant (ln transformed)				
<i>Total model R² (adjusted) = 0.75; N = 117</i>				
Species	1	0.3244	20.77	<0.0001
Population	1	0.0995	6.37	0.0131
Soil type	2	5.0057	160.23	<0.0001
Species×Pop	1	0.0034	0.22	0.6381
Species×Soil	2	0.0781	2.50	0.0868
Pop×Soil	2	0.1710	5.47	0.0055
Species×Pop×Soil	2	0.0334	1.07	0.3462
Error	105	1.6400		
(b) Total seed weight per plant (ln transformed)				
<i>Total model R² (adjusted) = 0.80; N = 116</i>				
Species	1	0.1337	28.73	<0.0001
Population	1	0.0260	5.58	0.020
Soil type	2	1.9901	213.78	<0.0001
Species×Pop	1	0.0069	1.48	0.225
Species×Soil	2	0.0186	2.00	0.139
Pop×Soil	2	0.0396	4.25	0.017
Species×Pop×Soil	2	0.0048	0.52	0.594
Error	104	0.4840		
(c) Seed number per plant (ln transformed)				
<i>Total model R² (adjusted) = 0.92; N = 117</i>				
Species	1	19.2016	942.57	<0.0001
Population	1	0.8394	41.20	<0.0001
Soil type	2	6.9009	169.37	<0.0001
Species×Pop	1	0.2408	11.82	0.001
Species×Soil	2	0.0251	0.61	0.541
Pop×Soil	2	0.2471	6.06	0.003
Species×Pop×Soil	2	0.0220	0.54	0.583
Error	105	2.1390		
(d) Average weight per seed				
<i>Total model R² (adjusted) = 0.78; N = 117</i>				
Species	1	0.1537	364.75	<0.0001
Population	1	0.0095	22.71	<0.0001
Soil type	2	0.0010	1.30	0.2765
Species×Pop	1	0.0117	27.89	<0.0001
Species×Soil	2	0.0010	1.18	0.3085
Pop×Soil	2	0.0012	1.43	0.2426
Species×Pop×Soil	2	0.0019	2.31	0.1036
Error	105	0.0442		
(e) Root allocation (arcsin sqrt transformed)				
<i>Total model R² (adjusted) = 0.18; N = 117</i>				
Species	1	0.0123	1.28	0.259
Population	1	0.0340	3.56	0.062
Soil type	2	0.1038	5.43	0.006
Species×Pop	1	0.0396	4.15	0.044
Species×Soil	2	0.0298	1.55	0.215
Pop×Soil	2	0.0080	0.42	0.658
Species×Pop×Soil	2	0.0027	0.14	0.864
Error	105	1.0032		

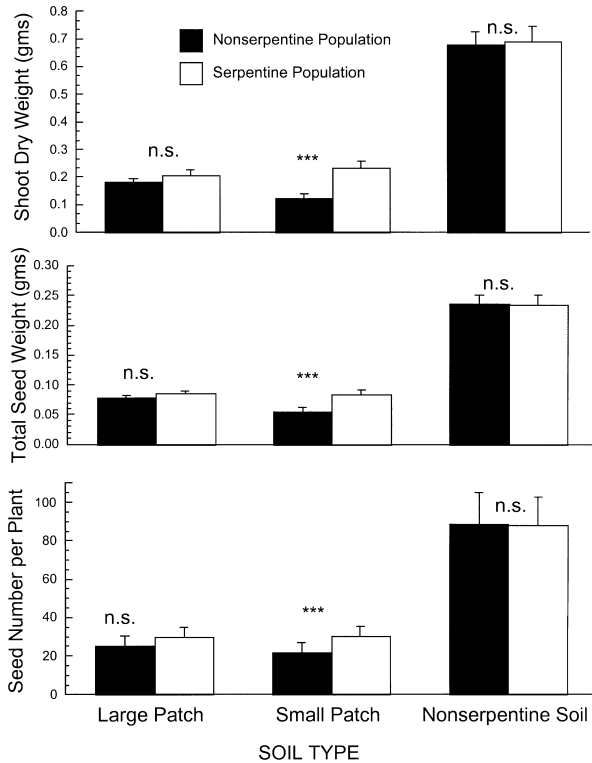


Fig. 1. Interactive effects of soil type and population source on plant performance in the annual grasses *Avena fatua* and *Bromus hordeaceus*. Because there were no significant differences between species in response (i.e., no significant three-way interaction), results were averaged across species. For linear contrasts between populations within each soil type, *** indicates a difference at $P < 0.001$ while n.s. indicates not significant at $P > 0.05$.

4. Discussion

Our transect results indicate that the greater prevalence of alien grasses on small than large serpentine patches is caused at least partly by an edge effect. This was especially clear for *Bromus*, which was just as common within 50 m of the edges of large patches as it was on small patches, and declined strongly in prevalence (i.e., stem density) on large patches as distance from the edge increased. For *Avena* the situation was less clear, since its occurrence at the edges of large patches was intermediate between its occurrence on small patches (moderate) and large patch interiors (absent), and since its prevalence on large patches did not decline significantly with distance from the edge. But the sparsity of *Avena* on serpentine in general gave these tests low statistical power. There may also be some additional factor, not identified here, that contributed to making *Avena* more abundant on small patches than large ones.

Edge effects could be caused either by physical differences in environmental suitability, or by higher rates of propagule arrival from the surrounding matrix. Our results provide little support for an explanation based on environmental suitability. Earlier soil analyses (Harrison,

Table 5
Soil characteristics (means and standard deviations) for large and small patch soil mixtures used in growth experiment

	Large patch soil mixture	Small patch soil mixture
Ca ²⁺ (meq/100 g soil)	5.2 (0.37)	1.8 (0.08)
Mg ²⁺ (meq/100 g soil)	24.3 (0.23)	13.4 (0.61)
Ca ²⁺ /Mg ²⁺ ratio	0.21 (0.02)	0.13 (0.001)
C.E.C	29.4 (0.85)	15.5 (0.71)
% Sand	57 (1.41)	70 (2.83)
% Silt	26 (1.41)	15 (2.83)
% Clay	17 (0.07)	15 (0.07)

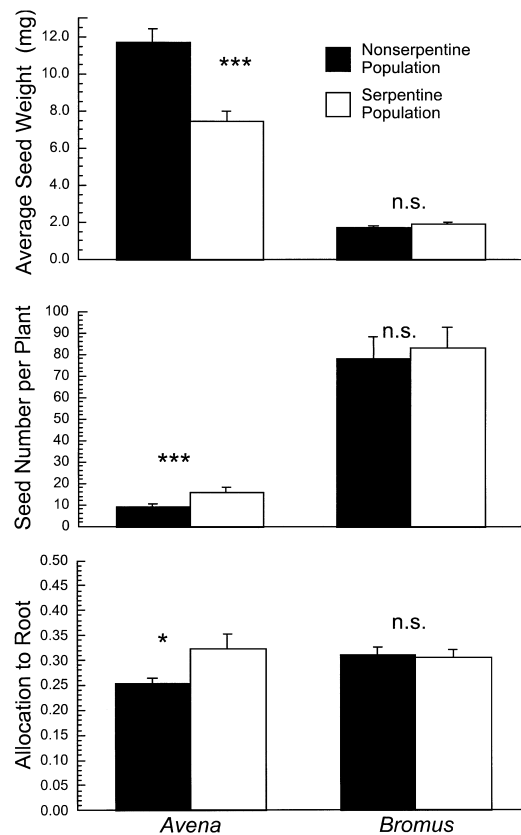


Fig. 2. Differences between *Avena fatua* and *Bromus hordeaceus* across all soil types in the effect of population source on seed characteristics and root allocation. For linear contrasts between populations within each species, *** indicates a difference at $P < 0.001$, * indicates a difference at $P < 0.05$, and n.s. indicates not significant at $P > 0.05$.

1999) had shown that small patches had significantly higher nitrate and coarser soil texture than large patch interiors. However, this study showed that the soil characteristics of large patch edges, rather than resembling those of small patches, more closely resembled

those of large patch interiors; also, the soil characteristics of large patches did not differ significantly between 10 and 50 m from their edges. Yet despite their similarity in soil characteristics to large patch interiors, large patch edges had much more *Bromus* than interiors, in fact just as much as small patches.

The results of the plant growth experiment also did not support a role for environmental suitability. Neither *Avena* nor *Bromus* performed significantly better in any respect on the small patch soil mixture than on large patch soil. In fact, the reverse trend was evident in the population by soil type interactions involving seed number, total seed weight and shoot weight. For both species, these variables were higher in serpentine populations than nonserpentine populations, but only when the plants were grown on small patch soil. This indicates that small patch soil mixture was actually harsher in some way than the large patch soil mixture. In support of this conclusion, the soil analyses of the large and small patch mixtures indicated that the soil texture was coarser and that some soil chemistry parameters (e.g. C.E.C. and $\text{Ca}^{2+}/\text{Mg}^{2+}$ ratios) were significantly less favorable for plant growth in the small patch soil (Table 2). This trend for coarser soils and lower $\text{Ca}^{2+}/\text{Mg}^{2+}$ ratios in small patches compared to large patches was also found by Harrison (1999).

We conclude that the greater prevalence of the two alien grass species on small serpentine patches, compared with the interiors of large ones, is probably caused by higher rates of propagule arrival from the surrounding nonserpentine matrix. This is perhaps not a surprising conclusion, considering the enormous abundances of both *Bromus* and *Avena* in the nonserpentine grasslands in our study region (Table 1). In turn, the influx of alien grasses onto small serpentine patches appears to have interesting evolutionary consequences, as indicated by the results of our growth experiment. The significant population by species and population by soil interactions found in this experiment suggest that small patches may be acting as breeding grounds for serpentine-adapted ecotypes of alien grasses.

In both species, populations from small serpentine patches outperformed populations from nonserpentine soil when grown in soil from small serpentine patches. In addition, serpentine populations of *Avena* produced more but lighter seeds and allocated relatively more biomass to roots than did nonserpentine populations. These results indicate the existence of differentiated serpentine and nonserpentine ecotypes in *Avena* and *Bromus*. Although some studies have demonstrated the existence of serpentine ecotypes within native species (Kruckeberg, 1954; Proctor and Wooddell, 1975; Wild and Bradshaw, 1977; Westerburg and Saura, 1992), there has been little similar evidence for alien species (but see Freitas and Mooney, 1996). Selection for tolerance to extreme soils can occur rapidly (e.g. Jain and Bradshaw, 1966; Antonovics et al., 1971; Linhart and Grant, 1996),

and continual dispersal into small patches from the surrounding matrix could provide the necessary genetic variation. The inbreeding mating system of both grasses should help to promote differentiation by reducing gene flow. This is one of the first studies to support the idea that the spatial configuration of patches within a landscape influences the potential for adaptation to a novel environment (Holt and Gaines, 1992; Holt and Gomulkiewicz, 1997).

Rather than adaptation to serpentine per se, an alternative explanation for the better performance of the serpentine populations in the small patch soil might be overall greater vigor in plants capable of surviving on serpentine. Two results contradict this interpretation, however. First, the growth and reproduction of plants from the serpentine population was not significantly better across all soil types, as might be expected if these plants had higher overall robustness. Second, in the initial collections, seed weights were not higher in the serpentine populations; in fact in *Avena* the seed weights were lower for serpentine populations.

Our study illustrates several facets of invasion and conservation biology that deserve more attention. First, it shows that the prevalence of alien species within a given habitat type may be affected by the flow of propagules among habitats. Even harsh serpentine soils, with their strong abiotic resistance to invasion, are more likely to be invaded when they are juxtaposed with other habitats that supply an abundance of propagules. While this idea is a truism in landscape ecology, ours is one of relatively few studies to demonstrate it in a naturally patchy landscape. Second, our study also suggests that invasion dynamics can depend on the interaction of processes at ecological and evolutionary time scales. Dispersal limitation in ecological time appears to be the primary reason for the differences we observed in the degree of invasion on small and large serpentine patches. But the current pattern of distribution will change in the longer term, to the extent that the flow of propagules among habitats fosters serpentine-adapted ecotypes. It is possible that the refuges for native species provided by soils such as serpentine may be undermined by the process of evolutionary adaptation in heterogeneous landscapes.

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References

- Antonovics, J., Bradshaw, A.D., Turner, R.G., 1971. Heavy metal tolerance in plants. *Advances in Ecological Research* 7, 1–85.
- Callizo, J., 1992. Serpentine habitats for the rare plants of Lake, Napa and Yolo Counties, California. In: Baker, A.J.M., Proctor, J., Reeves, R.D. (Eds.), *The Vegetation of Ultramafic (Serpentine) Soils*. Intercept, Andover, pp. 35–51.
- Crawley, M.J., 1989. Chance and timing in biological invasions. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmanek, M., Williamson, M. (Eds.), *Biological Invasions: a Global Perspective*. Wiley, New York, pp. 407–423.
- Fox, K.F., Sims, J.D., Barlow, J.A., Helley, E.J., 1973. Preliminary Geologic Map of Eastern Sonoma and Western Napa Counties, CA. USGS, Denver CO.
- Freitas, H., Mooney, H., 1996. Effects of water stress and soil texture on the performance of two *Bromus hordeaceus* ecotypes from sandstone and serpentine soils. *Acta Oecologica* 17, 307–317.
- Harrison, S., 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. *Ecology* 78, 1898–1906.
- Harrison, S., 1999. Local and regional diversity in a patchy landscape: native, alien and endemic herbs on serpentine soils. *Ecology* 80, 70–80.
- Hobbs, R.J., 1989. The nature and effects of disturbance relative to invasions. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmanek, M., Williamson, M. (Eds.), *Biological Invasions: a Global Perspective*. Wiley, New York, pp. 389–405.
- Holt, R.D., Gaines, M.S., 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evolutionary Ecology* 6, 433–447.
- Holt, R.D., Gomulkiewicz, R., 1997. How does immigration influence local adaptation A reexamination of a familiar perspective? *American Naturalist* 149, 563–572.
- Huenneke, L., Hamburg, S., Koide, R., Mooney, H., Vitousek, P., 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71, 478–491.
- Imam, A.G., Allard, R.W., 1965. Populations studies in predominantly self-pollinated species. VI. Genetic variability between and within natural populations of wild oats from differing habitats in California. *Genetics* 51, 49–62.
- Jain, S.K., 1969. Comparative ecogenetics of *Avena fatua* and *A. barbata* occurring in central California. *Evolutionary Biology* 3, 73–118.
- Jain, S.K., Bradshaw, A.D., 1966. Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. *Heredity* 21, 407–441.
- Jain, S.K., Marshall, D.R., 1967. Populations studies in predominantly self-pollinated species. X. Variation in natural populations of *Avena fatua* and *A. barbata*. *American Naturalist* 101, 19–33.
- Jain, S.K., Marshall, D.R., Wu, K., 1970. Genetic variability in natural populations of softchess (*Bromus mollis* L.). *Evolution* 24, 649–659.
- Kruckeberg, A.R., 1954. The ecology of serpentine soils. III. Plant species in relation to serpentine soils. *Ecology* 35, 267–274.
- Kruckeberg, A.R., 1984. *California Serpentine: Flora, Vegetation, Geology, Soils and Management Problems*. University of California Press, Berkeley, CA.
- Lambert, G., Kashiwagi, J., 1978. *Soil Survey of Napa County, CA*. Soil Conservation Service, Washington, DC.
- Linhart, Y.B., Grant, M.C., 1996. Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* 27, 237–277.
- Mack, R.N., 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmanek, M., Williamson, M. (Eds.), *Biological Invasions: a Global Perspective*. Wiley, New York, pp. 155–179.
- Mooney, H.A., Hamburg, S.P., Drake, J.A., 1986. The invasions of plants and animals into California. In: Mooney, H.A., Drake, J.A. (Eds.), *Ecology of Biological Invasions of North America and Europe*. Springer, New York, pp. 250–272.
- Parker, I.M., Reichard, S.H., 1998. Critical issues in invasion biology for conservation science. In: Fiedler, P.L., Kareiva, P. (Eds.), *Conservation Biology for the Coming Decade*. Chapman & Hall, New York, pp. 283–305.
- Proctor, J., Wooddell, S.R.J., 1975. The ecology of serpentine soils. *Advances in Ecological Research* 9, 255–366.
- Sawyer, J.O., Keeler-Wolf, T., 1995. *A Manual of California Vegetation*. California Native Plant Society, Sacramento, CA.
- Wagner, D.L., Bortugno, E.J., 1982. *Geologic map of the Santa Rosa Quadrangle, California, 1:250,000*. State of California, Resources Agency, Sacramento, CA.
- Westerburg, A., Saura, A., 1992. The effect of serpentine on the population structure of *Silene dioica* (Caryophyllaceae). *Evolution* 46, 1537–1548.
- Wild, H., Bradshaw, A.D., 1977. The evolutionary effects of metalliferous and other anomalous soils in south-central Africa. *Evolution* 31, 282–293.