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Source: *Ecological Applications*, Vol. 15, No. 5 (Oct., 2005), pp. 1570-1580

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/4543464>

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## INVASIBILITY OF ROADLESS GRASSLANDS: AN EXPERIMENTAL STUDY OF YELLOW STARHISTLE

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**Abstract.** Roadless habitats are commonly found to be less invaded than habitats near roads, but few studies have tested whether this pattern is due to propagule limitation or to greater invasion resistance of roadless sites. We examined reasons for the lower frequency and cover of yellow starthistle (*Centaurea solstitialis*) in grassland sites >1000 m vs. 10 m from roads in an inland California, USA, foothill landscape. During winter 2001 and 2002, we planted 100 *Centaurea* seeds in 64 pairs of 30 × 30 cm plots (uncleared and cleared of aboveground plant material) at sites stratified by distance from roads (10 m and >1000 m), soil type (nonserpentine and serpentine), and aspect (cool, warm, and neutral slopes). In nonserpentine grasslands, *Centaurea* survival was greater in uncleared (but not cleared) near (10 m) plots than in distant (>1000 m) plots. These findings suggest that the effect of distance from roads on survival corresponds with higher aboveground biotic resistance in distant sites than in near sites. *Centaurea* biomass was greater in near than in distant plots (both uncleared and cleared) on nonserpentine soil, suggesting that either abiotic resistance or belowground biotic resistance could limit its growth in distant sites. These distance effects were no longer significant in models that included two biotic covariates: native grass cover (which was higher in distant sites and negatively correlated with *Centaurea* performance) and bare ground (which was lower in distant sites and positively correlated with *Centaurea* performance). On serpentine soil, there was no effect of road proximity on the performance of planted *Centaurea*. Our results suggest that *Centaurea* seeds can germinate in nonserpentine and serpentine grasslands regardless of distance from roads. Beyond the seedling stage, however, biotic resistance associated with higher native grass cover and lower levels of disturbance may inhibit *Centaurea* invasion of nonserpentine grassland sites that are distant from roads.

**Key words:** California, USA; *Centaurea solstitialis*; disturbance and invasibility; exotic plant invasion; grasslands; invasibility; noxious weeds; resistance to invasion; road effects on invasibility; serpentine.

### INTRODUCTION

Propagule supply is believed to be an important control on the rate and extent of invasion (Rejmanek 1989), and at small to moderate spatial scales, seed addition experiments have shown the importance of propagule limitation in determining invasion patterns (Bergelson et al. 1993, Burke and Grime 1996, Tilman 1997). Likewise, at the landscape scale, many studies have shown that sites distant from roads are less invaded than sites near roads (e.g., Frenkel 1970, Taylor and Davilla 1986, Tyser and Worley 1992, Gelbard and Belnap 2003, Gelbard and Harrison 2003). However, while the latter pattern is usually interpreted to mean that roads are sources of invasive propagules and that invasions are propagule-limited, such correlative studies leave open the possibility of confounding effects. Habitats distant from roads may be less invaded because they are abi-

otically harsher (e.g., rocky or infertile soils), biotically more resistant (e.g., higher native species abundance), or less disturbed than sites near roads. It is critical to understand whether propagule limitation or environmental variation (or both) is responsible for landscape-level invasion patterns, since these mechanisms have very different implications for predicting and managing invasions.

In a previous study, we found that even after controlling statistically for such potentially confounding factors as soil fertility, aspect, climate, and livestock grazing, grasslands >1000 m from roads still contained significantly more native grass species and fewer exotic forb species than grasslands 100 m or 10 m from roads. Noxious weeds that have been spreading in recent years (e.g., *Centaurea solstitialis* and *Aegilops triuncialis*) tended to show distance effects, while older invaders such as *Bromus*, *Avena*, and *Erodium* species did not (Gelbard and Harrison 2003). These results suggested that the effect of distance corresponded to exotic propagule limitation rather than environmental heterogeneity. However, experimental testing of this conclusion is warranted because of its critical practical implica-

Manuscript received 7 November 2003; revised 28 October 2004; accepted 6 December 2004; final version received 31 January 2005. Corresponding Editor: D. J. Mladenoff.

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tions. If roadless grasslands are less invaded only because of their isolation, then they are vulnerable to invasion if seeds are introduced. If they are less invaded because of abiotic resistance, they should remain resistant except to new invaders that are adapted to their physical conditions. If they are protected by biotic resistance, it is critical to protect the vegetation and soil characteristics that confer this resistance.

A prime candidate to test these ideas is yellow starthistle (*Centaurea solstitialis*), because it has yet to invade most roadless grasslands (Gelbard and Harrison 2003). This species was probably first introduced into California and Washington, USA, in the mid-1800s as a contaminant in alfalfa seed and spread along roads and other rights of way and throughout grasslands by vehicles, livestock, streams, wildlife, and wind (Roche and Roche 1988, Gerlach et al. 1998, Sheley and Petroff 1999, Roche and Thill 2001). Its spread appears to have intensified since the 1960s (Gerlach et al. 1998). It germinates in the fall, grows a deep taproot while maintaining a small basal rosette, bolts in late May through the senescing canopy of annual grasses, and flowers during summer (Roche et al. 1994, Sheley and Petroff 1999). It is intolerant of shade and prefers deep, fertile soils (Roche et al. 1994). *Centaurea* is abundant near roads (Roche and Roche 1988, Benefield et al. 1999, Gelbard and Harrison 2003), but has spread rapidly into adjacent grasslands, especially where vegetation and soils are disturbed (Roche and Roche 1988, Gerlach et al. 1998, Sheley and Petroff 1999, Roche and Thill 2001).

In addition to roads and disturbances, environmental variables are important influences on the spread of *Centaurea* (Roche et al. 1994, Sheley and Petroff 1999, LeJeune and Seastedt 2001). Infertile soils are an important refuge for native Californian grassland species from *Centaurea* invasion, the best-known example being serpentine soil, characterized by a low Ca:Mg ratio and low macronutrient (N and P) levels (Harrison 1999, Gelbard and Harrison 2003). In experimental studies, richer soils generally favor *Centaurea* species over native competitors (Herron et al. 2001). *Centaurea* is also known to be more prevalent in microhabitats characterized by high exposure, including warm, south-facing aspects (Roche et al. 1994, Sheley and Petroff 1999). Its success is lower in shallow rocky soils (Roche et al. 1994) and in sites with high richness or cover of perennial grass (Berube and Myers 1982, Roche et al. 1994, Sheley and Petroff 1999, DiTomaso 2000, Enloe et al. 2000) or other deep-rooted late-season species (Dukes 2001, 2002). Conversely, sites dominated by shallow-rooted exotic annual plants may be especially vulnerable to *Centaurea* invasion (Gerlach et al. 1998, Dyer and Rice 1999). It remains unclear how soil type, aspect, disturbance, and abundance of deep-rooted native species may interact with distance from roads to influence the ability of *Centaurea* to invade.

We conducted a field experiment to explore mechanisms responsible for the pattern that we observed previously, of lower frequency and cover of *Centaurea* at sites >1000 m than at those 10 m from roads (Gelbard and Harrison 2003). During 2001 and 2002, we planted *Centaurea* into plots uncleared vs. cleared of aboveground plant material in sites near to and distant from roads on different soil types (nonserpentine and serpentine) and aspects (cool vs. warm vs. flat slopes); we measured germination, survival, and biomass of the resulting plants. We used this experiment to test three nonexclusive explanations for the observed pattern. (1) Aboveground biotic resistance: This would be indicated by better performance of experimental *Centaurea* in near than in distant uncleared (but not cleared) plots. (2) Abiotic resistance or belowground biotic resistance: These would be indicated by better performance of experimental *Centaurea* in near than in distant cleared (as well as uncleared) plots. (3) Propagule limitation: This would be indicated by a lack of significantly better *Centaurea* performance in near than in distant uncleared or cleared plots. We also tested for the main effects on *Centaurea* performance of soil, aspect, and year and their interactions with each other and with distance from roads.

To further examine the sources of possible resistance, we analyzed our experimental results using a series of covariates representing abiotic factors (e.g., soil rockiness, fertility), biotic factors (e.g., native grass and forb cover), and disturbance (e.g., cover by bare ground). If, for example, *Centaurea* performance was better in near than in distant cleared plots, but the inclusion of soil rockiness as a covariate removed the significance of the distance effect, we would interpret this to mean that abiotic resistance explains (or contributes to) the distance effect. In the same example, if the inclusion of native species cover as a covariate removed the significance of the distance effect, we would interpret this to indicate belowground biotic resistance as the cause of the distance effect. If *Centaurea* performance were better in near than in distant uncleared (but not cleared) plots and the inclusion of native species cover removed the significance of the distance effect, this would indicate aboveground biotic resistance.

## METHODS

### *Site description*

The 130 000-ha study region consists of portions of the Putah and Cache Creek watersheds in California's inner North Coast Range (Napa, Lake, and Colusa Counties, USA; Fig. 1). The climate is Mediterranean, with hot, dry summers and cool, moist winters. This region's geology, soils, and vegetation are diverse (Smith and Broderson 1989, Hickman 1993, Harrison 1999). Soils derived from sandstone and shale tend to be fertile, well-drained silt loams that support vege-

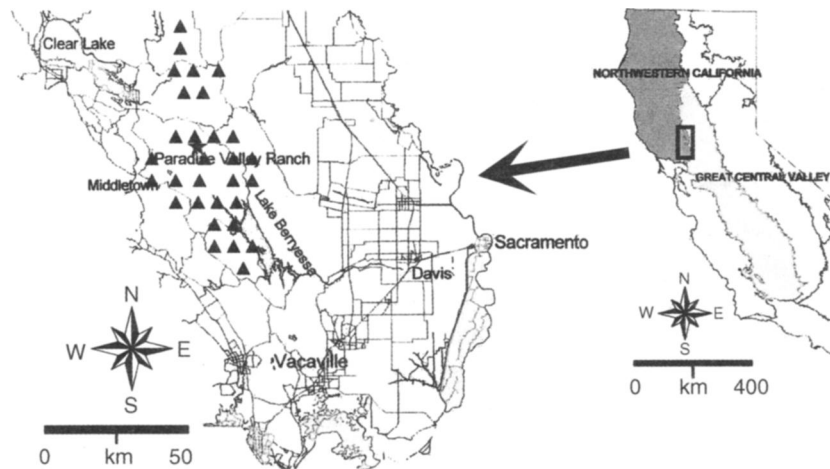


FIG. 1. Study area and landscape design within the inner north Coast Range of Napa, Lake, and Colusa Counties, California, USA, centered at  $\sim 38^{\circ}45' \text{ N}/122^{\circ}15' \text{ W}$ . Each triangle indicates the approximate location of a study site or a cluster of sites.

tation dominated by exotic annual grasses and forbs. Serpentine soils include well-drained gravelly loams and clays that contain high levels of Fe and Mg and low levels of Ca and primary nutrients (N, P), characteristics that support a flora that includes many fewer exotic species than natives (Harrison 1999). (See also Gelbard and Harrison [2003] for further site details.)

#### Site selection protocol

To identify suitable study sites, we acquired geographic information system (GIS) data detailing roads, topography, and soils within the study region and used ARC/INFO 7.1 and ARCVIEW 3.1 (Environmental Systems Research Institute, Redlands, California, USA) to create a regional-scale map of grasslands located 0–10 m and >1000 m from roads. (See Gelbard and Harrison [2003] for details of GIS analyses.) We acquired permission to access sites from private landowners and ground-truthed the GIS-created maps of roadless and roaded grasslands to identify suitable sampling sites, excluding sites that landowners indicated had been tilled or logged in the past. Once we identified candidate sites, we created a landscape-scale sampling design (Fig. 1) in which we stratified study sites by distance from roads, soil type (nonserpentine and serpentine), and aspect (cool slopes, aspect of  $330^{\circ}$ – $90^{\circ}$  and  $>10^{\circ}$  inclination; warm slopes,  $180^{\circ}$ – $270^{\circ}$  and  $>10^{\circ}$  inclination; and neutral slopes, all others, but  $<10^{\circ}$  inclination). For each candidate site >1000 m from roads, we located environmentally comparable sites (e.g., similar slope steepness and degree of rockiness and disturbance) on different aspects. We then visited grasslands approximately 10 m from paved roads (beyond the influence of roadside disturbance) to locate sites that were comparable to the roadless sites to form matching blocks of near and distant sites on different aspects and soil types. All actual distances for near sites were within the range 5–15 m; all sites

were >500 m apart to ensure independence of observations. We repeated this process until we had at least four replicates of each distance  $\times$  soil type  $\times$  aspect stratum. Total sample size was 33 nonserpentine and 31 serpentine sites. Of the nonserpentine sites, there were 14 near and 19 distant sites, and of the serpentine sites, there were 14 near and 17 distant sites.

#### Field data collection

We obtained *Centaurea* seeds (gathered from the study region) from the University of California Weed Science Program (Davis, California, USA) and planted them in early January 2001 and 2002. Within each 10 m and >1000 m site, we randomly selected a point to locate two  $30 \times 30$  cm ( $0.09\text{-m}^2$ ) plots and marked that point with rebar for permanent identification; we avoided microsites that contained preexisting *Centaurea* seedlings. We clipped one plot to ground level and cleared live and dead aboveground plant material, leaving only bare soil and bases of bunchgrass clumps. To minimize the possibility that year 2 results could be confounded by a residual effect of year 1 *Centaurea* seed additions, we set up plots in a four-square checkerboard with the rebar in the center and planted seeds into the bottom two plots in 2001 and top two plots in 2002. In each uncleared and cleared plot, we planted 100 *Centaurea* seeds (equivalent to  $1111$  seeds/ $\text{m}^2$ ). During April 2001 and 2002, we counted the number of seedlings per plot. We also recorded the identities of all native and exotic species in the plots. Species definitions followed Hickman (1993). During mid-to-late June, we counted the number of adult plants, calculating survival as the proportion of adult plants present in June to seedlings present in April. We recorded the presence of all late-season native and exotic species in plots, clipped all *Centaurea* plants at ground level during early flowering to prevent contamination of the area, oven-dried each sample, and measured above-



ground biomass per plot, with separate measurements for (1) biomass of the entire uncleared plot, as an indicator of productivity, and (2) biomass of *Centaurea* alone.

To ask what other environmental variables correspond with *Centaurea* seed germination, survival, and biomass, we measured site characteristics, plant species richness and cover per square meter, and soil chemistry and texture in plant communities (sites) immediately surrounding plots. Between late March and June, 2001 and 2002, we sampled five 1-m<sup>2</sup> quadrats along a 40-m transect at each of the 64 sites. Within each site, we randomly selected a point to begin vegetation sampling (without any prior knowledge of plant species at that point), marked the Universal Transverse Mercator coordinates of the site with a global positioning system (GPS), and recorded slope steepness, aspect, and topographic position. From the central sampling point, we established the transect in a random direction and placed 1-m<sup>2</sup> quadrats at 10-m intervals along this transect. Within each 1-m<sup>2</sup> quadrat, we recorded percent cover by rock, gravel, and soil, and we recorded the percent cover of litter on top of the soil and bare ground. We then recorded the identities of all native and exotic grass and forb species within the quadrat and estimated the total percent cover by native vs. exotic grass, forb, perennial, and annual species.

We estimated the areal extent of quadrats (percentage) covered by disturbance indicators such as bare ground, rodent mounds, wildlife tracks and scat, and livestock hoof prints and dung. Measurements of the cover and presence of soil surface disturbances such as rodent mounds and livestock hoof prints have been used in other studies to indicate the presence or intensity of these disturbances (e.g., Harper et al. 1965, Holechek et al. 1998, Stohlgren et al. 2001).

Soil samples were analyzed at A & L Western Agricultural Laboratories (Modesto, California, USA) for organic matter content (as a percentage), phosphorous (as parts per million), exchangeable Ca, Mg, and K (as millimoles of charge per 100 g), cation exchange capacity (CEC), and particle size. Remaining soils in each sample were passed through a 60-mesh sieve and analyzed at the Soil Analytic Laboratory of the Division of Agriculture and Natural Resources, University of California at Davis for total N and C.

Precipitation varied considerably between the two study seasons. Total October–March rainfall was 597 mm in 2001 (26% below average) and 804 mm in 2002 (0.3% above average). Mean October–March temperature was 11.6°C in 2001 (10% above average) and 12.4°C in 2002 (19% above average).

#### Statistical analyses

We conducted statistical analyses using JMP 4.0 (SAS Institute 2000). We transformed percentage values by arcsine square root and log-transformed *Centaurea* biomass, and throughout the course of analyses,

we tested for deviations from the assumptions of each test. To confirm (for the study years) our previous observation of greater *Centaurea* abundance in 10 m than in >1000 m sites (Gelbard and Harrison 2003), we conducted repeated-measures analyses of variance (ANOVAs), with year as the repeated measure. Dependent variables included *Centaurea* frequency and cover per square meter, and independent variables included distance class, soil type, aspect, year, and the second- and third-order interactions of these variables.

To test whether there was a significant effect of distance from roads, clearing, soil type, aspect, and year on *Centaurea* (1) seed germination, (2) survival, and (3) biomass per plot, we performed repeated-measures ANOVAs. Dependent variables included the above measures of *Centaurea* abundance. Independent variables included distance class, clearing, soil type, aspect, year, and the second- and third-order interactions of these variables. For analyses on survival, we excluded plots that did not contain seedlings (83 of 256 plots over 2 yr) and for analyses on biomass, we excluded plots that did not contain adult plants (149 of 256 plots over 2 yr, including 43 of 132 on nonserpentine soils and 106 of 124 on serpentine soils). Since an insufficient number of serpentine plots contained adult plants for us to be able to test for differences in biomass, we conducted this analysis on nonserpentine only. Where we found a significant distance × clearing or distance × soil interaction effect, we used ANOVAs to identify significant differences between near and distant sites within each plot type or soil type. Where we found a significant distance, clearing, soil, or year × aspect interaction, we used the Tukey's honestly significant difference (hsd) multiple-range test to determine which pairs of means were significantly ( $P < 0.05$ ) different.

To ask whether 10-m and >1000-m sites differed in site characteristics, we used MANOVA. Independent variables included distance class, soil type, aspect, and all second-order interactions. Dependent variables included slope steepness, radiation load (Buffo et al. 1972), biomass, soil organic matter, total N, P, Ca, Mg, Ca:Mg ratio, CEC, soil texture, plant height, and cover (as percentages) by rock and gravel, bare ground, litter, and livestock- and wildlife-related disturbances. To ask whether near and distant plots and sites differed in plant community composition, we repeated the above MANOVA, but conducted separate tests for each year, with dependent variables including (1) numbers of native (grass, forb, perennial, and annual) species/0.09-m<sup>2</sup> plot, and (2) in grasslands surrounding plots (sites), (a) cover by native and exotic grass and forb species and percentage of native species per square meter, (b) numbers of native and exotic grass and forb species per square meter, and (c) numbers of native perennial and annual species per square meter. Where we found a significant distance × soil interaction, we used ANOVAs (repeated measures where appropriate) to iden-

tify significant differences between near and distant sites within each soil type.

To ask whether any significant effects of distance from roads seen in the repeated measures ANOVAs were due to distance vs. environmental differences between near and distant sites not accounted for by ANOVAs (e.g., slope steepness, soil fertility, rockiness, disturbances), we conducted repeated-measures analyses of covariance (ANCOVAs). Before conducting each test, we ensured that the covariate did not violate the assumption of homogeneity of slopes between distance classes. Dependent variables included *Centaurea* survival and biomass, and independent variables included distance class and one environmental covariate per test with covariates including native grass, forb, perennial, and annual richness per 0.09-m<sup>2</sup> plot and per square meter in sites, slope, radiation load, P, percentage of sand, percentage of clay, relative plant height, and cover (as a percentage) by rock, litter, and bare ground.

To ask (1) what other environmental variables may correspond with *Centaurea* seed germination, survival, and biomass per plot and frequency and cover per site within each soil type, and (2) whether cover by bare ground was correlated with plant height and cover of wildlife- or livestock-related disturbances, we conducted correlation analyses. In all tests, we considered results with  $P < 0.05$  to be statistically significant and results with  $0.05 \leq P < 0.1$  to be marginally significant unless otherwise specified.

## RESULTS

### *Effects of distance from roads on yellow starthistle success*

The frequency and cover of *Centaurea* per square meter were greater in sites 10 m (near) than in those >1000 m (distant) from roads on both soil types (Fig. 2). In 30 × 30 cm (0.09-m<sup>2</sup>) plots at each site, distance from roads had no consistent effect on *Centaurea* seed germination, but showed significant effects on its survival and aboveground biomass (Table 1, Figs. 3–5). Seed germination was slightly greater in distant plots than in near plots in 2001, but the reverse was true in 2002; these effects were not significant within soil types (Table 1, Fig. 3). The effect of distance on survival depended on clearing and soil type (Table 1, Fig. 4). On nonserpentine soils, survival was greater in near plots than in distant uncleared plots only (Table 1, Fig. 4). *Centaurea* biomass was greater in near plots than in distant uncleared and cleared plots (Table 1, Fig. 5). On serpentine soils, there was no difference in *Centaurea* performance between near and distant plots, whether uncleared or cleared (Table 1, Figs. 3–5).

Uncleared plots 10 m and >1000 m from roads differed in numbers of native and exotic species per 0.09 m<sup>2</sup> in 2002 (whole-model MANOVA,  $P = 0.07$ ), including in marginally significant whole-model distance

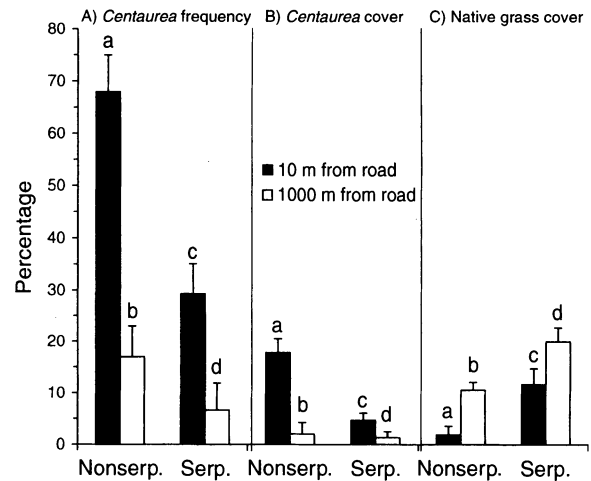


FIG. 2. (A) Frequency of *Centaurea* (percentage of total quadrats in which it occurs) and percent cover per square meter of (B) *Centaurea* and (C) native grass species in plant communities 10 m and >1000 m from roads in nonserpentine (Nonserp.) and serpentine (Serp.) grasslands ( $n = 64$ ). Cover values reflect means per square meter as measured in June 2001 and 2002 at sites containing 0.09-m<sup>2</sup> plots. Error bars indicate +SE. Different letters (a vs. b for nonserpentine, c vs. d for serpentine) indicate significant differences ( $P < 0.05$ ) between distance classes within each soil type, as indicated by repeated-measures ANOVA.

× soil ( $P = 0.10$ ) and significant distance × soil × aspect ( $P = 0.03$ ) interaction effects (Table 2). On nonserpentine soils, uncleared distant plots contained greater numbers of native grass and native perennial species per 0.09 m<sup>2</sup> than uncleared near-road plots (Table 2). In grasslands surrounding plots, sites 10 m and >1000 m from roads differed similarly in numbers of and cover by native species per square meter, and distant sites contained significantly lower cover by exotic and exotic forb species (Table 2). Sites 10 m and >1000 m from roads also differed in site characteristics and disturbances (whole-model MANOVA,  $P < 0.0001$ ), including in a significant ( $P = 0.02$ ) whole-model distance × soil type interaction (Table 3).

The effects of distance on survival and biomass in nonserpentine plots were no longer significant in ANCOVAs with native grass cover as a covariate. Native grass cover was higher in distant than in near sites and was negatively correlated with survival in 2002 and with biomass in both years (Appendix A). The effect of distance on biomass was no longer significant in ANCOVAs with bare ground, native perennial richness, and native grass richness as covariates. Bare ground was lower and native perennial and grass richness was higher in distant than in near sites, and *Centaurea* biomass was negatively correlated with native perennial and grass richness (Appendix A), but significantly positively correlated with bare ground (Appendix B).

TABLE 1. Significance levels ( $P$ ) showing the effects of distance from roads, clearing, soil type, aspect, year, and interactions on *Centaurea* seed germination and survival for two years on nonserpentine and serpentine soils and for aboveground biomass on nonserpentine soils only.

Effect	Seed germination ( $n = 256$ )	Survival ( $n = 173$ )	Aboveground biomass† ( $n = 89$ )
<b>Main</b>			
Distance from roads	0.98	0.47	<b>0.08</b>
Clearing	0.68	0.81	0.42
Soil type	< <b>0.0001</b>	0.37	<b>NA</b>
Aspect	<b>0.009</b>	0.76	0.70
Year	<b>0.02</b>	< <b>0.0001</b>	0.48
<b>Interaction</b>			
Distance × clearing	0.42	0.97	0.75
Distance × soil	0.88	0.74	NA
Distance × aspect	0.21	0.97	0.25
Distance × year	<b>0.05</b>	0.11	0.29
Clearing × soil	<b>0.02</b>	0.88	NA
Clearing × aspect	0.51	0.16	0.93
Clearing × year	<b>0.008</b>	0.61	0.47
Soil × aspect	0.30	0.73	NA
Soil × year	0.20	<b>0.03</b>	NA
Aspect × year	0.90	0.21	0.52
Distance × clearing × soil	0.86	<b>0.03</b>	NA
Distance × clearing × aspect	0.89	0.89	0.91
Distance × clearing × year	0.23	0.75	0.84
Distance × soil × aspect	0.96	<b>0.07</b>	NA
Distance × soil × year	0.54	0.59	NA
Distance × aspect × year	0.64	0.67	0.76
Clearing × soil × aspect	0.72	0.61	NA
Clearing × soil × year	<b>0.09</b>	0.48	NA
Clearing × aspect × year	0.69	<b>0.09</b>	0.53
Soil × aspect × year	0.86	0.61	NA

Notes:  $P$  values are from repeated-measures ANOVAs and included all the listed independent variables. Significant effects ( $P < 0.1$ ) are indicated in boldface type.

† NA indicates low sample size on serpentine plots; thus the analysis was conducted on nonserpentine plots only.

#### Soil type, aspect, disturbance, and other environmental correlates of *Centaurea* invasion

In addition to the effect of distance from roads, *Centaurea* seed germination and survival differed between uncleared and cleared plots, soil types, aspects, and years (Table 1, Figs. 3–4). Seed germination was significantly greater in cleared ( $17.0 \pm 2.0\%/0.09 \text{ m}^2$ ; mean  $\pm$  SE) than uncleared ( $4.7 \pm 2.0\%/0.09 \text{ m}^2$ ) plots on nonserpentine (ANOVA,  $P < 0.0001$ ), but not serpentine soils in 2001 (Fig. 3), and was greater in 2001 ( $8.5 \pm 1.0\%/0.09 \text{ m}^2$ ) than in 2002 ( $6.1 \pm 1.0\%/0.09 \text{ m}^2$ ; Table 1). It was greater (ANOVA,  $P < 0.0001$ ) on nonserpentine ( $13.9 \pm 1.6\%/0.09 \text{ m}^2$ ) than on serpentine ( $5.7 \pm 1.6\%/0.09 \text{ m}^2$ ) soils in cleared plots only (Table 1, Fig. 3) and was greater (Tukey's hsd multiple-range test,  $P < 0.05$ ) on neutral (flat) slopes ( $10 \pm 1.0\%/0.09 \text{ m}^2$ ) than on warm ( $6.8 \pm 1.0\%/0.09 \text{ m}^2$ ) or cool ( $5.4 \pm 1.0\%/0.09 \text{ m}^2$ ) slopes (Table 1).

*Centaurea* survival per 0.09-m<sup>2</sup> plot was significantly (ANOVA,  $P = 0.01$ ) greater in nonserpentine ( $38.3 \pm 4.5\%$ ) than serpentine ( $13.9 \pm 4.5\%$ ) plots in 2002, but not 2001 (Table 1) and was considerably greater in the year of average precipitation, 2002 ( $26.1 \pm 2.5\%$ ), than in the drought year of 2001 ( $3.6 \pm 2.5\%$ ;

Table 1). There was also a marginally significant interaction effect between distance, soil type, and aspect (Table 1). In nonserpentine plots only, survival was greater in near than in distant plots on cool ( $42.3 \pm 4.0\%$  vs.  $28.5 \pm 4.0\%$ ; ANOVA,  $P = 0.06$ ) and neutral ( $45.9 \pm 5.0\%$  vs.  $22.6 \pm 5.0\%$ ; ANOVA,  $P = 0.05$ ) slopes, but not on warm slopes ( $19.3 \pm 4.5\%$  vs.  $22.6 \pm 4.5\%$ ). In addition, there was a marginally significant interaction effect between clearing, aspect, and year (Table 1). In 2002, it was greater in cleared than in uncleared plots on cool slopes ( $78.7 \pm 14.5\%$  vs.  $33.5 \pm 11.5\%$ ;  $P = 0.05$ ), but in uncleared than in cleared plots on warm slopes ( $45.6 \pm 8.3\%$  vs.  $21.2 \pm 7.9\%$ ; ANOVA,  $P = 0.07$ ). *Centaurea* biomass did not differ between aspects or years (Table 1).

Within uncleared plots on each soil type, *Centaurea* seed germination, survival, and biomass per plot as well as its frequency and cover per site were significantly correlated with numerous environmental variables (Appendices A–C). *Centaurea* performance was positively correlated with radiation load, biomass, soil fertility, exotic richness, and cover by bare ground and negatively correlated with native richness and cover, especially that of native perennials and grasses; all but

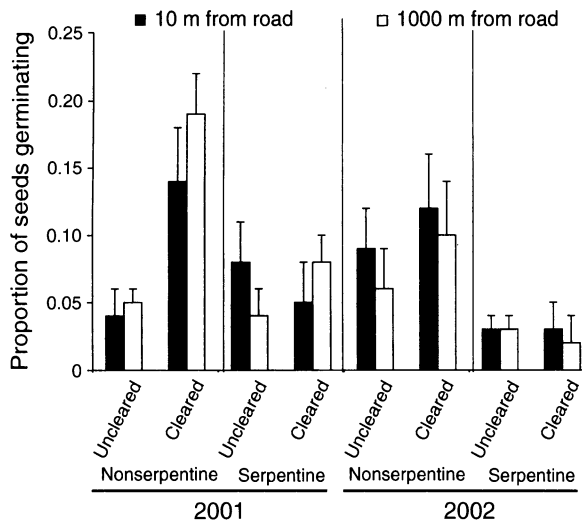


FIG. 3. Proportion of *Centaurea* seeds that germinated in 0.09-m<sup>2</sup> plots uncleared vs. cleared of aboveground vegetation and litter in sites 10 m and >1000 m from roads in nonserpentine and serpentine grasslands in 2001 and 2002 ( $n = 256$ ). Error bars indicate +SE. There were no significant differences ( $P < 0.05$ ) between distance classes within each soil type, as indicated by within-year ANOVAs; the overall significance of effect is indicated by repeated-measures ANOVA (Table 1).

one species of native grasses were perennial (Appendices A–C). Bare ground was strongly positively correlated with the cover of livestock-related disturbances ( $r = 0.69$ ,  $P < 0.0001$ ), but not wildlife-related disturbances, and was strongly negatively correlated with plant height ( $r = -0.45$ ,  $P < 0.005$ ).

#### DISCUSSION

The effects of distance from roads on the performance of experimental *Centaurea* differed depending on life stage, soil type, and disturbance. There was no difference in seed germination between near and distant plots on either soil type, indicating that *Centaurea* seeds can germinate and establish in grasslands regardless of distance from roads. However, *Centaurea* survival was higher in near than in distant uncleared (but not cleared) plots, indicating that aboveground biotic resistance may be responsible for inhibiting invasion in nonserpentine grasslands distant from roads. The biomass of surviving *Centaurea* was greater in near than in distant uncleared and cleared plots, indicating either abiotic or belowground biotic resistance. This effect was no longer significant in ANCOVAs with native perennial and grass abundance and bare ground cover as covariates, suggesting belowground biotic resistance. There was no effect of road proximity on *Centaurea* performance in serpentine plots, which suggests that its low abundance in roadless sites is due to propagule limitation rather than resistance. We speculate that if propagule limitation explains the effect of distance on *Centaurea* abundance on serpentine soils, it

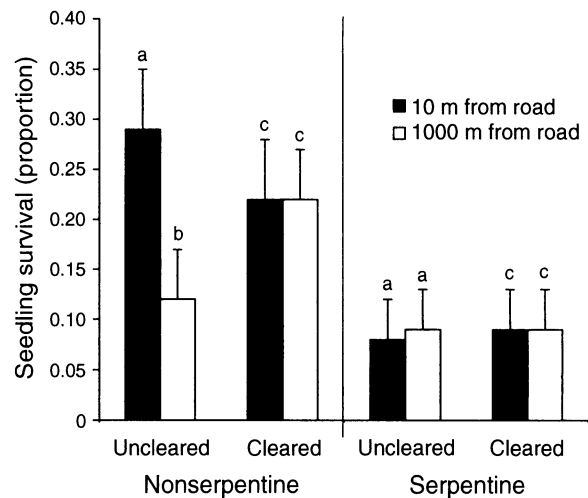


FIG. 4. Proportion of *Centaurea* seedlings that survived to adulthood in 0.09-m<sup>2</sup> plots uncleared vs. cleared of aboveground vegetation and litter in sites 10 m and >1000 m from roads in nonserpentine and serpentine grasslands for two years ( $n = 173$ ). Error bars indicate +SE. Different letters (a vs. b for uncleared plots; c vs. d for cleared plots [note that there are no significant differences for cleared plots, and hence no d's]) indicate significant differences ( $P < 0.05$ ) between distance classes within each soil type as indicated by within-year ANOVAs; the overall significance of effect is indicated by repeated-measures ANOVA (Table 1).

probably contributes to the effect of distance on nonserpentine soils.

A number of factors may explain the aboveground biotic resistance of roadless nonserpentine grasslands.

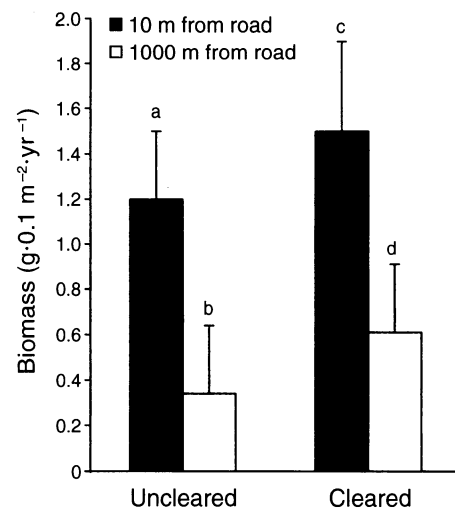


FIG. 5. Aboveground biomass of *Centaurea* during early flowering adulthood in 0.09-m<sup>2</sup> plots uncleared vs. cleared of aboveground vegetation and litter in sites 10 m and >1000 m from roads in nonserpentine grasslands for two years ( $n = 89$ ). Error bars indicate +SE. Different letters (a vs. b for uncleared plots; c vs. d for cleared plots) indicate significant differences ( $P < 0.05$ ) between distance classes as indicated by ANOVAs; the overall significance of effect is indicated by repeated-measures ANOVA (Table 1).



TABLE 2. Plant community composition (means ± SE) in (a) unclipped 0.09-m<sup>2</sup> *Centaurea* plots and (b) sites surrounding plots, showing variation between plots 10 m and >1000 m from roads within soil types over two consecutive years.

Variable	Nonserpentine		Serpentine	
	10 m	>1000 m	10 m	>1000 m
a) Composition of unclipped plots (per 0.09 m <sup>2</sup> )				
Native richness	2.5 ± 0.5	3.6 ± 0.4	7.9 ± 0.5	7.3 ± 0.4
Native grass richness	<b>0.1 ± 0.1</b>	<b>0.4 ± 0.1</b>	1.1 ± 0.1	1.0 ± 0.1
Native forb richness	2.4 ± 0.3	3.2 ± 0.3	6.8 ± 0.4	6.3 ± 0.4
Native perennial richness	<b>0.5 ± 0.2</b>	<b>1.1 ± 0.2</b>	2.0 ± 0.3	2.0 ± 0.3
Native annual richness	2.0 ± 0.4	2.5 ± 0.4	5.9 ± 0.4	5.3 ± 0.3
b) Composition of surrounding plant community (per square meter)				
Native cover (%)	<b>11.6 ± 2.6</b>	<b>27.3 ± 2.3</b>	50.2 ± 3.3	51.5 ± 2.9
Exotic cover (%)	<b>72.7 ± 3.4</b>	<b>60.7 ± 2.9</b>	29.7 ± 4.3	24.6 ± 3.8
Native grass cover (%)	<b>1.9 ± 1.8</b>	<b>10.6 ± 1.5</b>	<b>11.7 ± 3.1</b>	<b>20.0 ± 2.7</b>
Native forb cover (%)	<b>9.7 ± 2.2</b>	<b>16.7 ± 2.0</b>	38.5 ± 2.7	35.0 ± 2.4
Exotic grass cover (%)	27.6 ± 3.9	30.2 ± 3.3	23.7 ± 4.1	19.7 ± 3.5
Exotic forb cover (%)	<b>45.1 ± 4.2</b>	<b>29.9 ± 3.6</b>	6.0 ± 2.6	4.9 ± 2.2
Native grass richness	<b>0.3 ± 0.1</b>	<b>0.9 ± 0.1</b>	1.9 ± 0.2	2.0 ± 0.2
Native forb richness	<b>4.4 ± 0.6</b>	<b>6.0 ± 0.5</b>	11.0 ± 0.7	11.3 ± 0.6
Exotic grass richness	3.9 ± 0.2	3.5 ± 0.2	2.8 ± 0.3	2.8 ± 0.2
Exotic forb richness	<b>5.4 ± 0.3</b>	<b>4.1 ± 0.3</b>	1.1 ± 0.2	1.2 ± 0.2
Native perennial richness	<b>1.3 ± 0.3</b>	<b>2.6 ± 0.3</b>	4.4 ± 0.4	5.7 ± 0.4
Native annual richness	3.4 ± 0.5	4.3 ± 0.4	8.6 ± 0.7	8.6 ± 0.6

Notes: Results in boldface type indicate a significant difference (*P* < 0.1) between 10-m and >1000-m plots in year-specific MANOVAs and within a soil type, as indicated by repeated-measures ANOVA.

Distant sites contained higher numbers of and cover by native species and lower numbers of and cover by exotic species. They were also characterized by slightly higher litter cover and taller plant height, which can reduce ground light levels, and by lower cover by bare ground, which was strongly positively correlated with the cover of livestock-related disturbances, but not

wildlife-related disturbances, and strongly negatively correlated with plant height and native grass cover. The effect of distance on survival was no longer significant in the ANCOVA with native grass cover as a covariate. The effect of distance on biomass was no longer significant in the ANCOVA with native abundance and bare ground cover as covariates. These findings indi-

TABLE 3. Variation in site characteristics and disturbances (means ± SE) between sites 10 m and >1000 m from roads on nonserpentine and serpentine soils as indicated by MANOVA.

Variable	Nonserpentine		Serpentine	
	10 m	>1000 m	10 m	>1000 m
Physical factors				
Slope (degrees)*	<b>11.8 ± 1.2</b>	<b>13.5 ± 1.3</b>	<b>10.9 ± 1.0</b>	<b>13.4 ± 0.9</b>
Radiation (% total)*	<b>80.7 ± 2.0</b>	<b>77.8 ± 1.8</b>	<b>81.1 ± 1.7</b>	<b>78.1 ± 1.5</b>
Biomass (g·0.09 m <sup>-2</sup> ·yr <sup>-1</sup> )†‡	17.0 ± 1.7	17.3 ± 1.5	<b>16.3 ± 1.4</b>	<b>12.7 ± 1.2</b>
Soil organic matter (ppm)	5.1 ± 0.2	5.1 ± 0.2	4.6 ± 0.1	4.6 ± 0.1
Total N (ppm)	0.24 ± 0.01	0.25 ± 0.01	0.19 ± 0.01	0.21 ± 0.01
P (ppm)	14.9 ± 1.7	12.5 ± 1.5	6.8 ± 0.9	7.0 ± 0.8
Ca : Mg ratio	1.4 ± 0.2	1.6 ± 0.2	0.16 ± 0.01	0.19 ± 0.01
CEC (cmol <sub>c</sub> /kg)	17.6 ± 1.5	18.5 ± 1.3	25.4 ± 1.4	25.2 ± 1.3
Sand (%)	49.4 ± 3.6	50.3 ± 3.2	51.1 ± 3.1	49.6 ± 2.7
Silt (%)	26.3 ± 1.2	25.1 ± 1.0	21.0 ± 0.8	22.3 ± 0.7
Clay (%)	24.3 ± 3.2	24.6 ± 3.6	27.9 ± 2.3	28.1 ± 2.0
Rock and gravel (%)*	<b>4.3 ± 1.5</b>	<b>9.8 ± 1.3</b>	<b>30.3 ± 3.6</b>	<b>35.2 ± 3.2</b>
Litter (%)*	<b>56.4 ± 5.8</b>	<b>65.4 ± 5.1</b>	<b>34.5 ± 4.5</b>	<b>51.0 ± 4.3</b>
Disturbances				
Bare (%)†	<b>11.0 ± 1.8</b>	<b>7.7 ± 1.6</b>	20.1 ± 2.1	18.9 ± 1.8
Livestock (%)†‡	<b>20.1 ± 3.7</b>	<b>14.2 ± 3.3</b>	19.3 ± 3.4	23.8 ± 3.0
Wildlife (%)	2.7 ± 1.3	3.5 ± 1.1	1.1 ± 0.7	1.7 ± 0.6
Plant height (cm)*‡	<b>33.7 ± 2.2</b>	<b>44.4 ± 33.7</b>	34.0 ± 1.8	38.5 ± 1.6

Notes: Percentage (%) indicates cover values, except for soil texture. CEC is the cation exchange capacity. Results in boldface type indicate a significant difference (*P* < 0.1) between 10-m and >1000-m plots within a soil type, as indicated by ANOVA. Significance in MANOVA: † *P* < 0.1; \* *P* < 0.05. ‡ Distance × soil interaction.

cate that lower *Centaurea* survival and biomass in roadless nonserpentine grasslands is related to the higher native grass cover and lower levels of disturbances that create areas of bare soil, such as moderate to heavy livestock grazing. We acknowledge that factors we did not measure, such as the composition of the soil community, could have also contributed to the effects of distance on *Centaurea* performance.

All but one native grass species at our nonserpentine sites were perennial bunchgrasses, with *Nassella pulchra* and *Poa secunda* most abundant (Gelbard and Harrison 2003). Their negative relationship with *Centaurea* performance is consistent with previous observations that grasslands with a high prevalence of perennial grasses may resist *Centaurea* invasion, probably due to competition for deep soil moisture (Berube and Myers 1982, Jacobs and Sheley 1997, 1999, Olson and Wallander 1997, Dyer and Rice 1999, Sheley and Petroff 1999, Enloe et al. 2000, Dukes 2001, 2002). In addition, *Centaurea* biomass was positively correlated with cover by bare ground, providing evidence that disturbances that reduce plant cover and create areas of bare, disturbed soil may accelerate *Centaurea* invasions by increasing its growth and, probably as a result, its reproduction (Roche et al. 1994, Knops et al. 1995, Jacobs and Sheley 1999, Sheley and Petroff 1999, Dukes 2001, Hobbs 2001). Our results therefore indicate that where isolation of nonserpentine California grasslands from roads corresponds with high native grass cover and low levels of disturbance (Taylor and Davilla 1986, Halvorson 1992, Hamilton et al. 2002), it may confer both above- and belowground biotic resistance to *Centaurea* invasion.

*Centaurea* seed germination and survival, but not its biomass, were increased by clearing a 30 × 30 cm area of aboveground vegetation and litter, suggesting that this treatment is effective at reducing biotic resistance for its early but not its late life stages. During its early stages, when plants use shallow soil moisture, clearing aboveground plant material may reduce aboveground biotic resistance by increasing availability of space, light, and moisture for germinating seeds and established seedlings, especially on cool slopes where light is limited. The increase in radiation caused by clearing may increase soil temperature, resulting in changes to soil biota that increase mineralization and N availability, reducing resistance because increased N favors *Centaurea* species (Herron et al. 2001, LeJeune and Seastedt 2001). However, during later stages of *Centaurea* development, when plants use deep soil moisture, clearing aboveground plant material may fail to decrease biotic resistance because it does not reduce competition from the deep roots of native bunchgrasses. We cannot eliminate the additional possibility that slight differences in abiotic conditions between near and distant sites may have contributed to the effects of distance on *Centaurea* biomass.

The prevalence of native grass but not forb species negated significant effects of distance on *Centaurea* performance and was negatively correlated with *Centaurea* survival, biomass, frequency, and cover. This is similar to previous observations of relationships between *Centaurea* species and different plant life-forms (Kedzie-Webb et al. 2001). These results indicate that inverse relationships between invasibility and native abundance (e.g., Elton 1958, Knops et al. 1995, Tilman 1997, Levine and D'Antonio 1999, Anderson and Inouye 2001, Dukes 2002) may differ depending on plant life-form. California's native bunchgrasses and *Centaurea* are both late-season species that use deep soil moisture, while most native and exotic annual grasses and forbs complete their life cycles earlier in the spring and use shallow soil moisture (Gerlach et al. 1998, Dyer and Rice 1999). Similarly, plots dominated by established monocultures of the native perennial grass *Nassella pulchra* along with the late-season annual forbs *Hemizonia congesta* and *Lessingia hololeuca* (Dukes 2002) and the exotic perennial bunchgrasses *Agropyron intermedium* (Enloe et al. 2000) and *Agropyron desertorum* (Berube and Myers 1982) have resisted *Centaurea* invasion. Plant communities may be most resistant to invasion where they contain a high abundance of native species with similar life history characteristics to introduced exotics (Roche et al. 1994, Enloe et al. 2000, Dukes 2001, 2002).

Conversely, plant communities may be least resistant to invasion where they contain low abundance of species with similar life history characteristics to introduced exotics (Gerlach et al. 1998). *Centaurea* performed best at sites near roads, which were considerably more dominated by shallow-rooted exotic annuals than were distant sites and contained few native perennial grasses. This aspect of our results is suggestive of the hypothesis proposed by Simberloff and Von Holle (1999) that invasions may generate positive feedbacks, such that invasions render sites increasingly vulnerable to further invasions.

#### CONCLUSIONS AND IMPLICATIONS FOR CONSERVATION

This study provides a novel extension of what Mack (1996) called the best method for predicting the fate of plant invaders: experimental sowings beyond the invader's current range, with manipulations of field conditions. While the distant sites used in this study were within the broad geographic range of *Centaurea*, they were at the edge of its distribution at the within-landscape scale. We found previously that roadless grasslands are a scarce habitat that provides a significant refuge for native Californian species on nonserpentine soils (Gelbard and Harrison 2003). Here we have shown that the effect of distance from roads corresponds with greater biotic resistance of roadless than roaded grasslands, apparently associated with higher native grass cover and isolation from human distur-

bances. In light of our findings, grasslands distant from roads should be prioritized for conservation and carefully managed to maintain the characteristics that confer their resistance to invasion.

Examination of *Centaurea* performance at both local and landscape scales were crucial parts of this study. For example, our findings indicate that the low abundance of *Centaurea* at our distant sites may result from different factors on nonserpentine vs. serpentine soils. Propagule limitation is still implicated as a reason for the lack of invasion of distant serpentine sites and a probable contributor to the same effect on nonserpentine sites. Our conclusions would have differed had we not established plots over a sufficiently large area to include both soil types. Conversely, use of small plots allowed us to carefully examine under what physical, biotic, and disturbance conditions *Centaurea* would be most likely to invade roadless grasslands if propagules should be introduced. We conclude that roadless grasslands could become just as invaded by *Centaurea* as are roadsides, if seeds are introduced into habitats that have lost their native bunchgrasses or in which management conditions favor annual over perennial species (Mack 1989, Sheley and Petroff 1999, DiTomaso 2000, Hobbs 2001).

#### ACKNOWLEDGMENTS

We are grateful to Joe Callizo for plant identification and Kevin Rice, Jim Quinn, David Mladenoff, and three anonymous reviewers for helpful comments on this manuscript; Steve Enloe for providing *Centaurea* seeds; Joshua Viers for GIS assistance; Neil Willets for statistical advice; and the Land Trust of Napa County's Wantrup Wildlife Sanctuary for hospitality. For access to sites, we thank the individuals who represent the Blue Ridge-Berryessa Conservation Partnership, the UC Natural Reserve System, US Bureau of Land Management Knoxville and Cache Resource Districts, and the US Bureau of Reclamation Berryessa Recreation Area. Financial support was provided by NSF DEB 99-03421 and the UC Davis Biological Invasions IGERT.

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#### APPENDIX A

A table presenting correlations between *Centaurea* seed germination, seedling survival, and aboveground biomass per 0.09 m<sup>2</sup> and the richness and cover of native species within (a) 0.09-m<sup>2</sup> uncleared plots and (b) 1-m<sup>2</sup> quadrats in nonserpentine and serpentine sites surrounding plots is available in ESA's Electronic Data Archive: *Ecological Archives* A015-045-A1.

#### APPENDIX B

A table presenting correlations between physical, productivity (biomass), and disturbance variables and *Centaurea* seed germination, seedling survival, and aboveground biomass per 0.09-m<sup>2</sup> uncleared plots on nonserpentine and serpentine soils for two years is available in ESA's Electronic Data Archive: *Ecological Archives* A015-045-A2.

#### APPENDIX C

A table presenting correlations between selected environmental variables and (a) *Centaurea* percent cover per square meter, (b) *Centaurea* frequency per square meter, (c) native grass percent cover per square meter, and (d) native grass richness per square meter on nonserpentine soils for two years is available in ESA's Electronic Data Archive: *Ecological Archives* A015-045-A3.