Effect of Seed Source, Topsoil Removal, and Plant Neighbor Removal on Restoring California Coastal Prairies

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Abstract

Grasslands are hot spots of biodiversity but are now widely threatened by changes in patterns of disturbances, such as grazing and fire regimes, exotic species invasions, and cultivation. The goal of this experiment was to find the most appropriate combination of treatments to reintroduce *Danthonia californica*, a formerly dominant perennial bunchgrass, into degraded California coastal prairies. *Danthonia californica* was sown from seed and transplanted at two sites and at two grazing intensities (grazed/ungrazed) in a multifactorial experiment testing the effects of (1) local versus nonlocal seed sources; (2) topsoil removal; and (3) reduction of plant neighbors. Seed emergence was very low, suggesting that transplanting may be a better option to reintroduce *D. californica*. Although transplants grown from nonlocal seeds survived better initially at both sites, transplants from local seeds had higher survival after 1.5 year at one site. This suggests that short-term plant establishment studies may be misleading. Topsoil removal greatly enhanced transplant survival, and neighbor removal primarily increased transplant growth. Our results suggest that removing topsoil prior to transplanting seedlings grown from local seeds is the most promising method to reintroduce *D. californica*. However, the benefits of removing topsoil to provide safe sites for plant establishment should be weighed carefully against potential negative effects on the native seed bank and microbial communities on a site-specific basis.

Key words: competition, *Danthonia californica*, exotic annual species, grazing, nitrogen reduction, weeding.

Introduction

Grasslands were once widespread, species-rich ecosystems, representing more than 25% of the vegetation cover of the world (Henwood 1998) and approximately 25% of California's natural vegetation (Barbour & Major 1977). Both globally (Jacobs et al. 1999) and in California (Heady et al. 1988), primary grassland cover has drastically decreased due to development, agricultural intensification, and altered disturbance regimes (Hoekstra et al. 2005); the remaining primary grasslands are fragmented and degraded. This loss and degradation of grasslands has significant impacts on the conservation of biodiversity, particularly in California where primary grasslands are important habitats for wildlife and hot spots of plant diversity (Stromberg et al. 2001).

California grasslands evolved with a number of disturbances, including intentional high-frequency burning by Native Americans, seasonal grazing by native ungulates, soil disturbance and grazing by burrowing mammals, and periodic drought stress (Heady et al. 1988). In the late eighteenth century, after European settlement, year-round, intensive cattle grazing was introduced along with numerous exotic forage grasses, and fire intervals increased. These systems are now dominated by annual exotic grasses and forbs of Mediterranean origin (Heady et al. 1988; Stromberg et al. 2001; Hayes & Holl 2003*a*, 2003*b*). Some of these ecosystems have been affected not only by changes in disturbance regimes but also by cultivation and/or native N-fixing plant invasion (Maron & Jefferies 1999), both of which lead to soil nitrogen enrichment. Such areas support even fewer native species than those that have never been cultivated or invaded (Stromberg & Griffin 1996; Hamilton et al. 2002).

California coastal prairies, which have received much less study than inland California grasslands, have been sufficiently affected by humans that their recovery is extremely slow (Hamilton et al. 2002) or even unlikely (Stromberg & Griffin 1996), and will require human

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intervention. The restoration of coastal prairies may require a combination of treatments on varying time scales because these areas evolved with several endogenous disturbances and because single-management strategies, including reintroducing fire or grazing (Bartolome & Gemmill 1981; Dyer & Rice 1997; Hatch et al. 1999), sowing native plant seeds (Wilson & Gerry 1995), or reducing soil N (Corbin & D'Antonio 2004), have not been demonstrated to be successful methods by themselves (for review, see Corbin et al. 2004).

When ecosystems have been severely degraded, Whisenant et al. (1995) proposed that restoration be initiated by enhancing soil and microenvironmental conditions and by reintroducing some species to improve habitats. We propose the reintroduction of California oatgrass (*Danthonia californica*) to degraded coastal prairies as a first step in restoring the habitat. Although little is known about the composition and cover of these herbaceous ecosystems before degradation, it is likely that original coastal prairies had a greater cover of native perennial grasses, such as *D. californica* or California hairgrass (*Deschampsia cespitosa*) on the coast and Purple needlegrass (*Nassella pulchra*) further inland. Most studies have focused on restoring *N. pulchra*, although a number of authors have noted the need for information on other perennial grass species (Hatch et al. 1999; Hayes & Holl 2003*a*).

We tested topsoil removal as a restoration technique to reduce both competition from the exotic seed bank and soil nitrogen (Peeters & Janssens 1998; Marrs 2002; Wilson 2002). Indeed, the restoration of ecosystems invaded by annual exotic grasses and forbs without reducing exotic cover often has limited success (Corbin et al. 2004). Removing the soil surface seed bank may be expected to reduce competition because most of the exotic species in California grasslands are annuals. Reduced soil N in the establishment phase, while diminishing all plant growth, should favor slower growing native species that are adapted to low nutrient conditions as compared with faster growing exotics (Huenneke et al. 1990; Corbin et al. 2004). Other methods aiming at reducing soil nutrients, such as mowing and removing the cut biomass (Maron & Jefferies 2001) or carbon amendment (sawdust, sucrose, starch, cellulose: Wilson & Gerry 1995; Reever Morghan & Seastedt 1999; Alpert & Maron 2000; Török et al. 2000; Corbin & D'Antonio 2004), have shown limited positive effects on native species richness or biomass (Wilson 2002; Corbin et al. 2004). Moreover, topsoil removal has been shown to provide habitat for the endangered Ohlone Tiger Beetle (*Cicindela ohlone*), which is only found in coastal prairie (Knisley & Arnold 2004), but may also alter hydrology, soil texture, and microbial communities.

We propose an additional treatment, neighbor removal (mainly exotic annuals), to reduce exotic plants because reducing the seed bank may not be sufficient to overcome the competitive advantage of exotic annuals. Previous studies have shown that weeding (Dyer & Rice 1997) and late winter application of broad-leaved herbicide (Stromberg & Kephart 1996) early in the restoration can reduce exotic cover. A variety of other approaches have been proposed to reduce exotic cover and provide native seeds with suitable safe sites to germinate, including burning (Menke 1992; Dyer et al. 1996), or combining summer burning and intensive short-duration grazing or mowing in early spring (Menke 1992; Stromberg & Kephart 1996). Although these approaches frequently reduce cover of exotic species (Corbin et al. 2004), some studies show that they have limited value for prairie restoration (Dyer et al. 1996; Hatch et al. 1999), and prescribed burn permits can be hard to obtain (Edwards 1992) due to air quality and fire risk concerns (ARB 2002).

A major question facing restorationists is how locally seeds should be collected (McKay et al. 2005). This is a particularly important question for grass seeds because they have high genetic variation (Knapp & Rice 1996; Wilson 2002). It is commonly proposed to use local propagules because other ecotypes may be genetically unsuited to the local context and because commercial ecotypes may reduce local genetic biodiversity (Knapp & Rice 1994). However, local propagules are often hard to obtain. Few field studies on grassland species have tested the home-field advantage hypothesis (Wilson 2002), although it has been demonstrated in some species (e.g., Deerweed [*Lotus scoparius*] in California coastal sage scrub, Montalvo & Ellstrand 2000).

The goal of this experiment was to test the efficacy of various combinations of two levels of these treatments to enhance emergence of sown seeds (seedlings) and survival and growth of planted seedlings (transplants) of *D. californica*. Treatments included two seed sources (local or nonlocal), topsoil removal (topsoil removal or intact topsoil), and two neighbor removal intensities (neighbor removal or neighbors intact). We tested all combinations of the levels of these treatments at two sites and for two grazing intensities (moderately grazed or ungrazed) because grazing has showed mixed effects on native and exotic coastal prairie vegetation cover (Hatch et al. 1999; Hayes & Holl 2003*a*; Corbin et al. 2004).

Methods

Site Description

We conducted experiments at two coastal prairies in central California near Santa Cruz: Elkhorn (near Elkhorn Slough, South of Watsonville, lat 36°52′4.3″N, long 121°44′23.8″W, 7 km from the coast) and UCSC (on the University of California Santa Cruz campus, lat 36°59′5.5″N long 122°3′0.9″W, 3 km from the coast). Coastal prairies are found at less than 1,000-m elevation and within the area influenced by coastal fog (Heady et al. 1988). At both sites, the vegetation is dominated by annual European grasses (69% cover at Elkhorn and 63% cover at UCSC), such as Brome (*Bromus* spp.), Barley (*Hordeum* spp.), Italian ryegrass (*Lolium multiflorum*) and *Vulpia* spp.,

and by annual European forbs (15% cover at Elkhorn and 26% cover at UCSC), such as Plantain (*Plantago lanceolata*) and storksbill (*Erodium* spp.) (Hayes & Holl 2003*b*). There are also patches of native perennial grasses: 9% cover at Elkhorn and 2% cover at UCSC. Both sites have slopes of less than 10% facing South and sandy loam soil greater than 1 m deep (pH 4.9; sand 60%; silt 28%; clay 17%; see Hayes & Holl 2003*b* for details). Pre-European vegetation is not known, and cattle have grazed the sites at least since the beginning of the nineteenth century. Elkhorn was partly cultivated before 1931, when the first aerial photograph was taken, and has been grazed since the 1950s. Hay was cultivated at UCSC from at least the early 1940s and possibly prior to this time. Cultivation ceased between 1957 and 1962. This site has been grazed with variable intensity since then, except for a few year abandonment in the early 1990s (Hayes & Holl 2003*b*).

We compiled weather data (precipitation, air and soil temperature, relative humidity, evapotranspiration, and duration of summer drought and of drought after the first rain in autumn) from the closest (<5 km) weather station to each site (CDWR 2005). Mean annual air temperature was approximately 13.5°C at both sites. Elkhorn received less rainfall over the study period from January 2002 to June 2004 (901 mm) than UCSC (1,314 mm), with the majority of precipitation falling between November and March. During the experiment, both sites received relatively less rainfall and had higher evapotranspiration than during the 20 previous years in average.

In 2004, we collected 24 soil samples at both sites, 12 inside and 12 outside the exclosure, half with topsoil removal and half with intact topsoil. Each sample consisted of three 10-cm-diameter, 2-cm-deep soil cores on four 1.5 × 1.5–m plots; soil was analyzed for total Kjeldahl N at the Laboratory of Ecology of Louvain, Belgium (Baize 2000), and a one-way analysis of variance (ANOVA) was run on the data.

Main Experimental Design

At each site, a 52 × 52–m cattle exclosure was installed in fall 1998 (Hayes & Holl 2003*b*). The areas outside the exclosure were grazed and inside the exclosure were mowed twice a year, once in spring and once in fall, until the start of the current study in 2002. This did not induce differences in community composition between the plots inside and outside the exclosure (Hayes & Holl 2003*b*).

We randomly allocated 12 plots inside (ungrazed) and 12 plots outside (grazed) the exclosure (see Fig. 1 for details). In each plot, we experimentally manipulated seed sources, topsoil, and plant interactions in a split–split plot design. Grazed plots were located in an area similar in size adjacent to the exclosure. During the experiment, cattle grazed Elkhorn at a stocking rate of six animals/ha for approximately four days at 45- to 60-day intervals from December to June and UCSC at a stocking rate of three animals/ha continuously from March to May.

Two seed sources were tested: local seeds collected in June 2002 in the hills around Santa Cruz, 40 km from Elkhorn and 15 km from UCSC, and seeds purchased from S&S Seeds, Inc. (Carpinteria, CA, U.S.A.), grown from source populations located at Fern Ridge Reservoir near Eugene, Oregon, and harvested in summer 2002, as

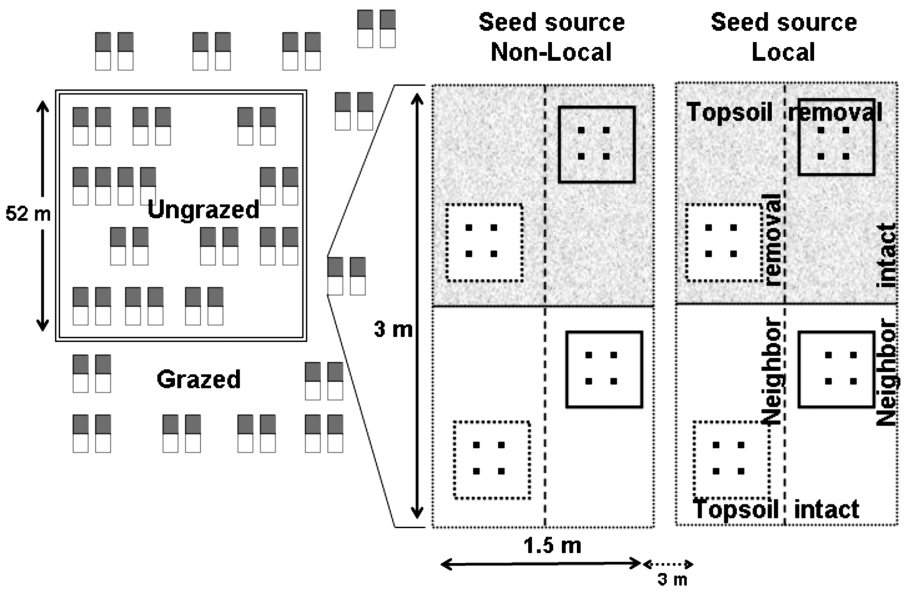

Figure 1. Experimental design layout. Each site had 12 paired 3 × 1.5 m–plots inside and outside the exclosure, with one plot from each pair allocated to one seed source (local, nonlocal). Each plot was split in two 1.5 × 1.5–m topsoil plots: topsoil intact (white) and topsoil removal (shaded). Each subplot was split in two 0.75 × 1.5–m neighbor subplots (separated by dashed line). Four transplanted plants are indicated with four large dots. Solid squares correspond to plant neighbor removal and dashed squares to intact neighbors. Only nonlocal seeds were sown at UCSC in the remaining space.

well. Seeds were stored dry at room temperature in paper bags until used.

We removed the topsoil layer (0–10 cm: litter layer and part of the Ah horizon) in one 1.5 × 1.5–m split plot in each plot in August 2002 by tilling and then scraping (Fig. 1). Topsoil removal also eliminated neighbors and the top layer of the seed bank. In January 2003, at transplanting, 25–35% of the ground cover was recolonized by plant species, and in March 2003 ground cover was greater than 70% on split plots with topsoil removal versus 90–100% on plots with intact topsoil.

To test the effect of plant neighbor interactions on seedlings and transplants, we allocated one half of each split plot to neighbor removal and we left neighbors intact in the other half (Fig. 1). Neighbor removal was performed by hand-pulling all small seedlings (native and exotic) and clipping all larger plants to the ground within a 25-cm-diameter area surrounding the four *Danthonia californica* transplants; we chose a 25-cm diameter because Davies et al. (1999) showed that some grassland plants responded to neighbor removal in areas greater than 15-cm diameter. We removed neighbors before sowing and transplanting, twice in spring 2003 and twice in winter 2003–2004.

Transplanting

In January 2003, we transplanted four *D. californica* plants into each of the 12 replicates (Fig. 1) of each seed source × topsoil × neighbor treatment (total of 1,536 transplants). These plants had been grown outdoors in individual containers for four months, watered as needed, and not fertilized. The four transplants were planted 50 cm apart to minimize interactions and were watered once when outplanted. Transplants that died within the first month were replaced.

Seeding Experimental Design

Using the same experimental design as in the main experiment described above, we seeded *D. californica* at UCSC only because there were patches of *D. californica* at Elkhorn that would have made it difficult to distinguish natural recruits from seedlings emerging from seeds we sowed. We only sowed purchased seeds because they are sorted through a machine to select seeds with embryos, whereas local seeds contained a sufficiently large number of seeds without embryos that we did not have enough apparently viable seeds for seeding experiments. In the nonlocal seed split plots, we sowed 25 purchased *D. californica* seeds, on 12 and 13 October 2002, before the first autumn rain, which occurred on 31 October 2002 (total of 2,400 seeds). Seeds were sown 6.25 cm apart in 5 × 5 seed grid, and pushed into the soil to a depth about equal to their size (Laude 1949).

Data Collection

We recorded seedling emergence by replacing grids on 12 and 13 December 2002, 6 and 7 January 2003, and 26 and 27 February 2003, 6, 10, and 17 weeks after the first rain. All seedlings (out of 25 seeds) recorded as emerged on any of the three sampling dates and alive at the last sample date were summed in each split plot to obtain the combined emergence and survival of the seedlings over 17 weeks. We monitored transplanted *D. californica* survival and growth over 1.5 years, which included one complete growth season and two grazing cycles. We measured survival in March 2003, June 2003, December 2003, and June 2004, after which we collected the aboveground and belowground biomass of all the transplants by sampling the same volume of soil around each plant. We washed the roots very carefully by holding them at the base of the stem, below the soil line. We dried the aboveground and belowground biomass at 70°C to a constant mass, weighed, and calculated an average biomass for each set of four transplants.

Statistical Analyses

For survival and biomass data, we conducted ANOVA for split–split plot design on four separate models: one for each site × grazing treatment combination (R Statistical Computing version 2.0.1 2005). Seed source, topsoil removal, and neighbor removal were treated as categorical explanatory variables, with seed source as the whole-plot treatment, topsoil removal the first split plot, and neighbor removal the second split plot (Fig. 1). Only results of survival three months after transplanting (March 2003) and of survival and biomass 1.5 years after transplanting (June 2004) are presented here because analyses from other sampling dates were similar. Arcsine square root transformations were applied to survival data and log transformations to biomass measurements (Sokal & Rohlf 1998). Because grazing was not replicated within site, we could not evaluate grazing effects statistically. The number of seedlings that emerged in the field at UCSC was extremely low (<1%) although seed viability reached 96% (tetrazolium test). We thus could not carry out statistical analyses on emergence data.

Results

Soil Nitrogen

Overall, topsoil removal decreased soil N at both sites (topsoil removal: 0.21 ± 0.01 mg N/g of soil vs. intact topsoil: 0.25 ± 0.01 mg N/g of soil) although this effect was significant only on the Elkhorn grazed plots (topsoil removal: 0.23 ± 0.02 mg N/g of soil vs. intact topsoil: 0.31 ± 0.02 mg N/g of soil).

Survival Three Months after Transplanting

Topsoil removal increased three-month survival substantially in all grazed plots at UCSC (topsoil removal: 88.5% vs. intact topsoil: 72.9%; Table 1) and in intact neighbor plots

Table 1. ANOVA of treatment effects on survival of *D. californica* plants three months after transplanting in grazed and ungrazed areas at two sites.

	Elkhorn						*UCSC*					
	Grazed			*Ungrazed*			*Grazed*			*Ungrazed*		
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Replication	11			11			11			11		
Seed source	1	0.2	0.701	1	9.3	0.011	1	<0.1	1.000	1	15.3	0.002
Error (whole plot)	11			11			11			11		
Topsoil removal	1	0.2	0.651	1	1.3	0.267	1	8.5	0.008	1	1.0	0.319
Seed source × topsoil	1	1.9	0.182	1	0.2	0.630	1	0.4	0.532	1	0.6	0.463
Error (subplot)	22			22			22			22		
Neighbor removal	1	3.7	0.061	1	0.3	0.616	1	<0.1	0.889	1	0.1	0.817
Seed source × neighbor	1	0.1	0.803	1	<0.1	0.867	1	0.2	0.676	1	0.7	0.399
Topsoil × neighbor	1	4.4	0.042	1	<0.1	0.867	1	2.8	0.099	1	<0.1	0.939
Seed source × topsoil × neighbor	1	<0.1	0.933	1	0.7	0.404	1	0.7	0.404	1	1.0	0.319
Error (split subplot)	44			44			44			44		

that were grazed at Elkhorn (94.8% on topsoil removal × intact neighbors vs. 84.4% on intact topsoil × intact neighbors; Table 1).

Topsoil removal did not affect three-month survival in ungrazed areas (Table 1). In ungrazed areas, however, transplants grown from nonlocal seed survived slightly better than transplants grown from local seeds (Elkhorn: nonlocal seeds 99.5% vs. local seeds 95.31%; UCSC: nonlocal seeds 91.7% vs. local seeds 76.6%; Table 1). No other factors studied affected three-month survival (Table 1).

Survival 1.5 Years after Transplanting

Topsoil removal strongly increased *Danthonia californica* survival after 1.5 years whatever the site or grazing treatment (topsoil removed: 38.5% vs. topsoil intact: 12.1%; Table 2; Fig. 2). Neighbor removal significantly increased survival only at Elkhorn in both grazed (Table 2) and ungrazed areas (Table 2; Fig. 2) (neighbor removal: 42.7% vs. neighbor intact: 23.2%; Fig. 2). In the grazed area, once topsoil was removed, neighbor removal did not increase survival anymore (Table 2; Fig. 2).

After 1.5 year, seed source influenced survival only at Elkhorn, but contrary to earlier data, transplants grown from local seeds survived substantially better (Table 2; Fig. 2). On the grazed plots, survival of transplants grown from local seeds was 41.2% as compared with 25.5% for nonlocal seed; on the ungrazed plots, survival of transplants grown from local seeds × neighbor removal reached 55.2% versus 31.3% on nonlocal seeds × neighbor removal.

Biomass

Overall, neighbor removal greatly increased the biomass of transplants whatever the site or grazing treatment (e.g., at Elkhorn in the grazed area; neighbor removal: 1.18 g vs. neighbor intact: 0.11 g; Table 3; Fig. 3). Topsoil removal slightly increased the biomass of transplants (Table 3; Fig. 3). Seed source had a minimal effect on biomass of surviving transplants (e.g., at Elkhorn in the grazed area; local: 0.78 g vs. nonlocal: 0.52 g; Table 3; Fig. 3).

Discussion

Our results indicated that topsoil removal served to maximize *Danthonia californica* transplant survival and to slightly increase their biomass. Topsoil removal simultaneously manipulates available nutrients and biotic relations through the reduction of both the large exotic annual seed bank and the sparse perennial aboveground vegetation. The decrease in soil N may not have played a large role in our study. The fact that topsoil removal had no negative effect on *D. californica* biomass suggests that low N availability did not affect *D. californica* either because it is adapted to low nutrient availability or because our topsoil removal treatment did not remove enough N. The direct effects of available N, N dynamics, and other nutrient availability, as well as the effects of changes in hydrology, on both establishment and perennial/annual species interactions should be further investigated to understand the effects of topsoil manipulation.

In addition, topsoil removal had a slight positive effect on *D. californica* biomass, suggesting that topsoil removal mainly contributed to *D. californica* establishment by decreasing competition. This was consistent with the effect of neighbor removal, which also reduced competition, although topsoil removal was more efficient. The efficacy of topsoil removal versus an herbicide treatment (Stromberg & Kephart 1996), to lower the exotic seed bank prior to planting, should be compared, including the potential negative/positive impacts of both these restoration techniques on soil microbial communities, soil texture, and other native grasses and forbs.

Danthonia californica transplants on subplots with intact topsoil and neighbors survived three months after planting, but they grew little aboveground or belowground

Table 2. ANOVA of treatment effects on survival of *D. californica* plants 1.5 years after transplanting in grazed and ungrazed areas at two sites.

	Elkhorn						*UCSC*					
	Grazed			*Ungrazed*			*Grazed*			*Ungrazed*		
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Replication	11			11			11			11		
Seed source	1	8.8	0.013	1	8.7	0.013	1	0.9	0.368	1	<0.1	0.905
Error (whole plot)	11			11			11			11		
Topsoil removal	1	22.1	<0.001	1	66.7	<0.001	1	16.3	<0.001	1	30.7	<0.001
Seed source × topsoil	1	0.1	0.797	1	0.3	0.567	1	1.1	0.307	1	0.2	0.674
Error (subplot)	22			22			22			22		
Neighbor removal	1	11.9	0.001	1	23.5	<0.001	1	0.4	0.542	1	<0.1	1.000
Seed source × neighbor	1	0.1	0.792	1	6.5	0.014	1	2.4	0.131	1	0.6	0.462
Topsoil × neighbor	1	7.0	0.011	1	0.6	0.432	1	3.4	0.072	1	4.2	0.047
Seed source × topsoil × neighbor	1	4.5	0.040	1	0.2	0.662	1	1.5	0.225	1	1.7	0.201
Error (split subplot)	44			44			44			44		

biomass before summer and may not have been able to withstand summer drought. Past research concurred that perennial grasses cannot survive dry conditions when grown with exotic annual grasses because annuals outcompete perennials for light and perennials are thus unable to develop sufficient root biomass before summer to use deep soil moisture (Bartolome 1981; Dyer & Rice 1997, 1999). Hamilton et al. (1999) suggested that exotics and native perennial grasses compete for water at all stages. Therefore, in our study, when the annual seed bank, the main potential source of competition, was not reduced, neighbor removal has a positive effect on *D. californica* survival. The small scale at which this project was carried out, and particularly the modest size of areas from which neighbors and topsoil were removed, did not prevent exotic annuals from rapidly recolonizing inwards from edges. Neighbor removal may thus be useful when topsoil has been removed but when there is no grazing to reduce annual biomass. If the project was carried out on a larger scale, surrounding exotic annual seeds would likely recolonize the area more slowly and neighbor removal may thus not be necessary.

Topsoil removal is a resource-intensive restoration project that has been carried out elsewhere: in Europe,

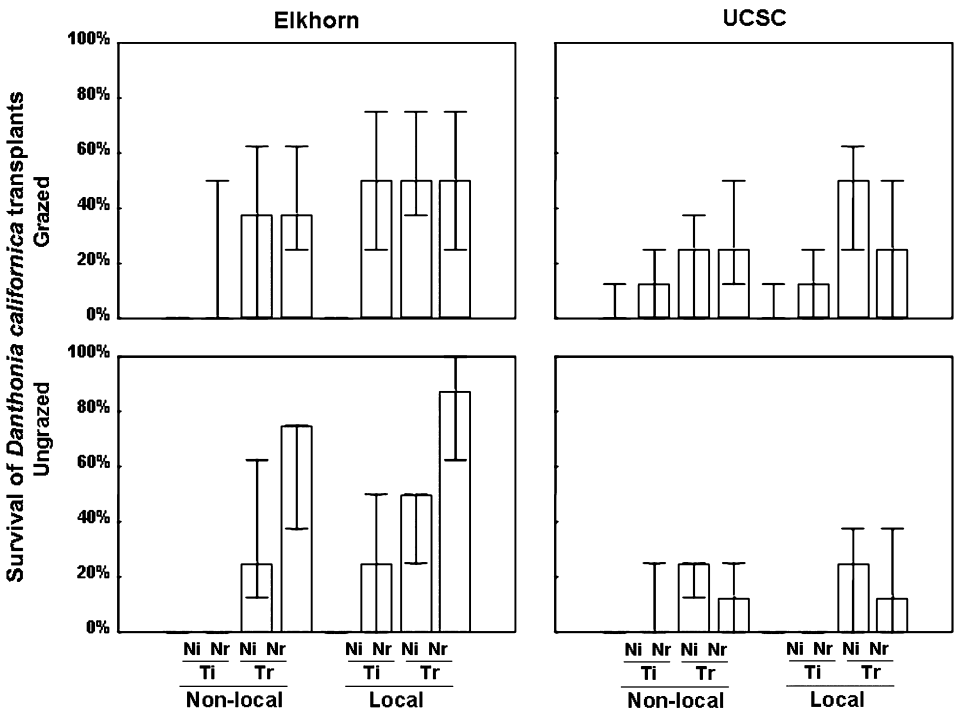

Figure 2. Survival of *D. californica* transplants after 1.5 years (see Table 2 for ANOVA results). Ti = topsoil intact, Tr = topsoil removal, Ni = neighbors intact, Nr = neighbor removal. Values are medians ± quartiles.

Table 3. ANOVA of treatment effects on biomass of *D. californica* plants 1.5 years after transplanting in grazed and ungrazed areas at two sites.

	Elkhorn						*UCSC*					
	Grazed			*Ungrazed*			*Grazed*			*Ungrazed*		
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Replication	11			11			11			11		
Seed source	1	6.1	0.031	1	4.2	0.065	1	<0.1	0.869	1	0.4	0.520
Error (whole plot)	11			11			11			11		
Topsoil removal	1	5.1	0.034	1	35.5	<0.001	1	4.8	0.040	1	16.8	<0.001
Seed source × topsoil	1	1.0	0.336	1	1.6	0.227	1	0.1	0.728	1	0.5	0.474
Error (subplot)	22			22			22			22		
Neighbor removal	1	65.8	<0.001	1	67.6	<0.001	1	32.7	<0.001	1	9.1	0.004
Seed source × neighbor	1	3.3	0.075	1	3.0	0.092	1	<0.1	0.934	1	0.3	0.601
Topsoil × neighbor	1	<0.1	0.872	1	7.1	0.011	1	0.1	0.732	1	0.3	0.595
Seed source × topsoil × neighbor	1	3.3	0.077	1	3.5	0.069	1	0.6	0.461	1	4.9	0.033
Error (split subplot)	44			44			44			44		

topsoil is removed from areas covering between 2 and 30 ha for published work only (Verhagen et al. 2001; Grootjans et al. 2002). Once removed, topsoil can be sold and this income used toward restoration (Marrs 1985, 2002). As topsoil removal is an intensive restoration technique, it should be considered carefully, in highly degraded prairies and only after testing the seed bank for native seeds (Grootjans et al. 2002; Marrs 2002). Another alternative for large-scale projects would be to remove topsoil in patches instead of throughout a site or in combination with other methods for reducing rapid reinvasion of exotic seeds, such as herbiciding or carefully timed mowing.

Interestingly, early survival of transplants grown from nonlocal seeds was slightly higher than that of transplants grown from local seeds for both sites. Ultimately, however, transplants grown from local seed survived better at one site, whereas there was no difference at the other site. Although the use of locally adapted seeds for this species could not be confirmed in this study, it may not be the case over its entire range. *Danthonia californica* is distributed throughout western Canada and the western United States; within California, it can be found in bioregions as varied as the North Coast, the Sierra Nevada Foothills, the High Sierra Nevada, the Central Coast, or San Francisco Bay (Hickman 1993). Although California-based

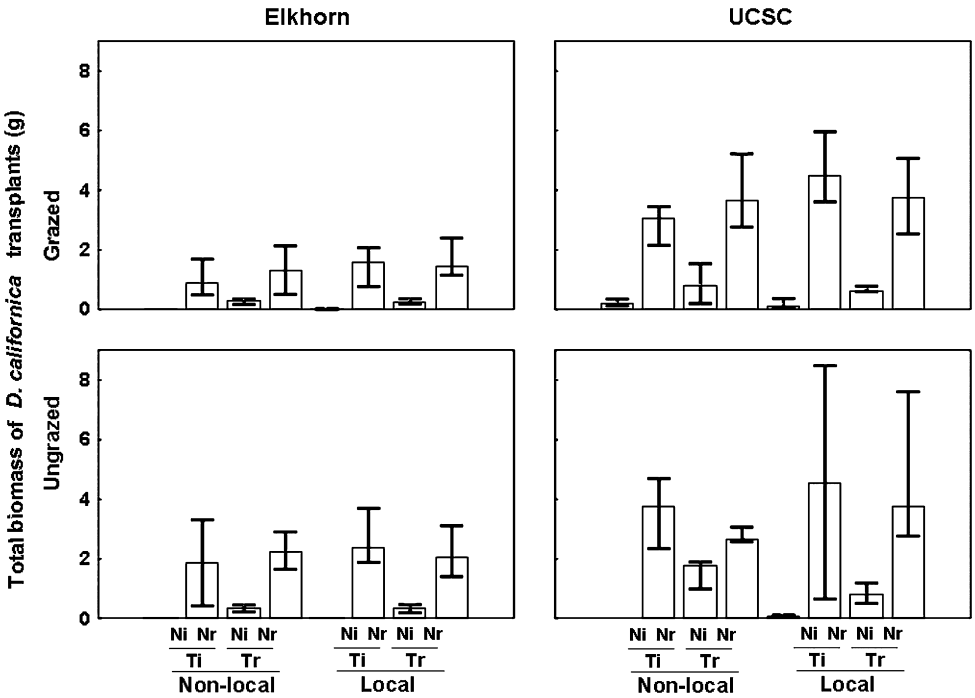

Figure 3. Biomass of *D. californica* transplants after 1.5 years (see Table 3 for ANOVA results). Ti = topsoil intact, Tr = topsoil removal, Ni = neighbors intact, Nr = neighbor removal. Values are medians ± quartiles.

seed companies often grow plants from California, seeds may be locally adapted at much smaller scales. *Nassella pulchra* has been shown to be locally adapted across a coastal to interior climatic gradient (Knapp & Dyer 1998). Our purchased seeds came from southern Oregon, a location with a generally less severe summer drought than the central coast of California. This result suggests that studies on plant establishment that are carried out on short periods may be misleading.

Seedling emergence in the field was very low, and seeding *D. californica* may not be the most appropriate restoration technique. Our results should be treated tentatively because we only have emergence data from one site and the year of the experiment was drier than average. Studies of other native perennial California grasses showed that they could be restored by seeding (Seabloom et al. 2003); even in cases with low establishment (<1%), some grass species, such as *N. pulchra* (Dyer et al. 1996), could be seeded in large quantity because they are affordable ($79/kg; Pacific Coast Seed 2005) to produce densities of surviving grasses similar to those achieved by more costly transplanting seedlings. However, ours was one of the few studies of reintroducing *D. californica*, which seemed to have much lower emergence than *N. pulchra* and for which seeds are much more expensive ($331/kg; Pacific Coast Seed 2005). Therefore, transplanting *D. californica* may be a better option, but additional work on the emergence requirements of this species is needed.

Implications for Practice

This study suggests that restoring *D. californica* to highly degraded California coastal prairie will be challenging. The ideal combination of treatments to plant *D. californica* is

- to remove topsoil from degraded prairies to provide a suitable establishment environment for *D. californica* seedlings
- to transplant *D. californica*
- to collect seeds locally because it may help to increase survival, although more field research is needed
- to remove neighbors to increase survival and ensure maximum growth, if necessary

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