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Authors: Power, Paula J., Stanley, Thomas, Cowan, Clark, and Roberts, James R.

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NATIVE PLANT RECOVERY IN STUDY PLOTS AFTER FENNEL (*FOENICULUM VULGARE*) CONTROL ON SANTA CRUZ ISLAND

Paula J. Power[1,3], Thomas Stanley[2], Clark Cowan[1], and James R. Roberts[1]

ABSTRACT.—Santa Cruz Island is the largest of the California Channel Islands and supports a diverse and unique flora which includes 9 federally listed species. Sheep, cattle, and pigs, introduced to the island in the mid-1800s, disturbed the soil, browsed native vegetation, and facilitated the spread of exotic invasive plants. Recent removal of introduced herbivores on the island led to the release of invasive fennel (*Foeniculum vulgare*), which expanded to become the dominant vegetation in some areas and has impeded the recovery of some native plant communities. In 2007, Channel Islands National Park initiated a program to control fennel using triclopyr on the eastern 10% of the island. We established replicate paired plots (seeded and nonseeded) at Scorpion Anchorage and Smugglers Cove, where notably dense fennel infestations (>10% cover) occurred, to evaluate the effectiveness of native seed augmentation following fennel removal. Five years after fennel removal, vegetative cover increased as litter and bare ground cover decreased significantly ($P < 0.0001$) on both plot types. Vegetation cover of both native and other (nonfennel) exotic species increased at Scorpion Anchorage in both seeded and nonseeded plots. At Smugglers Cove, exotic cover decreased significantly ($P = 0.0001$) as native cover comprised of *Eriogonum arborescens* and *Leptosyne gigantea* increased significantly ($P < 0.0001$) in seeded plots only. Nonseeded plots at Smugglers Cove were dominated by exotic annual grasses, primarily *Avena barbata.* The data indicate that seeding with appropriate native seed is a critical step in restoration following fennel control in areas where the native seed bank is depauperate.

RESUMEN.—La Isla Santa Cruz es la más grande de las Islas del Canal de California y mantiene una flora diversa y única, que incluye nueve especies enlistadas por el gobierno federal. Ovejas, ganado y cerdos que fueron introducidos en la isla a mitad del siglo diecinueve perturbaron el terreno, modificaron la vegetación nativa y facilitaron la extensión de plantas invasoras exóticas. La reciente eliminación de los herbívoros introducidos en la isla se dispersó el hinojo invasor (*Foeniculum vulgare*), que se expandió hasta convertirse en la vegetación dominante en ciertas áreas y ha impedido la recuperación de algunas comunidades de plantas nativas. En el 2007, el Parque Nacional de las Islas del Canal inició un programa para controlar el hinojo usando triclopir en el 10% del este de la isla. Establecimos réplicas de terrenos pareados (sembrados vs. no sembrados) en Scorpion Anchorage y Smugglers Cove, donde se encontraban plagas de hinojo notablemente densas (>10% de cobertura), para evaluar la efectividad del aumento de las semillas nativas tras la eliminación del hinojo. Cinco años después de la eliminación del hinojo, la cubierta vegetal aumentó mientras que los desechos y la cubierta de tierra desnuda se vieron reducidos significativamente en ambos tipos de terrenos ($P < 0.0001$). La cubierta de vegetación, tanto de las especies nativas como de otras especies exóticas (no hinojo), aumentó en Scorpion en ambos terrenos sembrados y sin sembrar. En Smugglers, la cubierta exótica disminuyó significativamente ($P = 0.0001$) mientras que la cubierta nativa, comprendida por *Eriogonum arborescens* y *Leptosyne gigantea* aumentó de manera importante ($P < 0.0001$) sólo en terrenos sembrados. Los terrenos no sembrados de Smugglers estaban dominados por hierbas anuales exóticas, principalmente *Avena barbata*. Los datos indican que sembrar con semillas autóctonas apropiadas es un paso crítico en la restauración que sigue al control del hinojo en áreas donde los bancos de semillas nativas están empobrecidos.

Much of coastal California experienced exotic plant invasions following European contact which resulted in a conversion of ecosystems dominated by native perennial grass and annual and perennial dicot species to ecosystems dominated by Eurasian annual grasses and forbs (Mack 1989). Because invasive plant species are known to outcompete native plants in recovering ecosystems, reduce biodiversity, and alter ecosystem function (Wilcove et al. 1998, Bossard et al. 2000, Pimentel et al. 2000), many studies have examined the mechanisms by which exotic annuals prevail over native perennial species in California's grasslands. Levine et al. (2003) suggested that the ability of exotic species to establish and spread is related to their ability to competitively suppress resident species. On the other hand, Corbin and D'Antonio (2004) found evidence that native perennial grasses

[1]Channel Islands National Park, 1901 Spinnaker Dr., Ventura, CA 93001.
[2]United States Geological Survey, Fort Collins Science Center, 2150 Centre Ave. Bldg. C, Fort Collins, CO 80526.
[3]E-mail: paula_power@nps.gov

are strongly competitive once established and that disturbance such as agriculture, grazing, and severe drought were likely important factors in shifts in community composition in California. Seabloom et al. (2003) found that exotic annual grasses were competitively superior only with repeated disturbance and that recruitment limitation of native perennials was a factor favoring the dominance of exotic annual species in Santa Ynez Valley, California.

Restoration efforts often focus on shifting community composition from exotic dominance to native dominance by controlling exotic species while native vegetation recovers after past disturbance. Often controlling exotic species is a disturbance itself and favors the resident exotics. For instance, treating one invasive species without augmenting the native plant community is often followed by reinvasion or establishment of a novel invader (Kettenring and Adams 2011). Also, a depauperate native seed bank may contribute to the success of exotics following control actions (Seabloom et al. 2003). In this study, we examined the benefits of seed augmentation to native plant recovery after removal of dominant exotic fennel and resistance by natives to novel invaders.

Santa Cruz Island, the largest island within Channel Islands National Park, is home to 8 endemic plant species (Schoenherr et al. 1999) and 16 vegetation communities (Junak et al. 1995). In many areas, the native plant communities of coastal bluff scrub, coastal sage scrub, and grasslands were disturbed by agriculture, introduced sheep (*Ovis aries*), pigs (*Sus scrofa*), cattle (*Bos primigenius*), and a suite of exotic plant species. Exotic plants now comprise 26% of the island flora (Junak et al. 1995). Furthermore, decades of overgrazing significantly reduced woody vegetation in coastal scrub and chaparral communities and, in many areas, artificially maintained grasslands composed, in large part, of exotic annual grasses (Junak et al. 1995). Introduced ungulates have since been removed from Santa Cruz Island, largely benefiting native vegetation (Cohen et al. 2009). However, an unintended consequence of exotic animal removal was the rapid expansion of exotic fennel (*Foeniculum vulgare;* Dash and Gliessman 1994, Brenton and Klinger 1994, 2002).

Fennel, an erect perennial herb native to the Mediterranean area, was introduced to Santa Cruz Island in the late 1800s (Junak et al. 1995). Common in coastal bluff scrub, coastal sage scrub, chaparral, and riparian plant communities at lower elevations, fennel is particularly aggressive in abandoned agricultural fields and grazed areas (Beatty 1991). Fennel forms a leafy green rosette in the spring and fibrous, persistent reproductive stalks growing to 2–2.5 m during summer months, dwarfing grasses, native shrubs, and forbs in the understory. Fennel is a prolific seed producer, but it is unknown how long seeds remain viable in the soil. In response to fennel invasions on Santa Cruz Island and in mainland areas, a number of studies examined fennel control methods, including manual removal, chemical treatment, and prescribed fire (Bean and Russo 1988, Dash and Gliessman 1994, Klinger and Messer 2001, Brenton and Klinger 2002, Erskine-Ogden and Rejmanek 2005). The National Park Service in collaboration with The Nature Conservancy, which owns 76% of Santa Cruz Island, began a program in 2007 to control fennel using a 2% concentration of triclopyr in target areas along roads and trails island-wide. The work presented here focuses on restoration efforts on 85 ha on the eastern 10% of Santa Cruz Island, where we took a comprehensive and long-term approach to habitat restoration. Our approach included controlling fennel, augmenting resident native plants, and establishing long-term monitoring plots to track native plant recovery, fennel reestablishment from the seed bank, and establishment of novel invaders.

SITE DESCRIPTION

Santa Cruz Island is characterized by long, warm summers and mild, cool winters. Rainfall occurs primarily during winter months, averaging approximately 48 cm of precipitation per year. A blanket of fog commonly moves over the island during early summer months, contributing moisture to the hydrologic cycle (Fischer et al. 2009, Carbone at al. 2013).

Native plant communities, severely degraded by past land management practices, show signs of recovery across east Santa Cruz Island. However, fennel and nonnative annual grasses dominate many coastal bluff scrub, coastal sage scrub, chaparral, and grassland

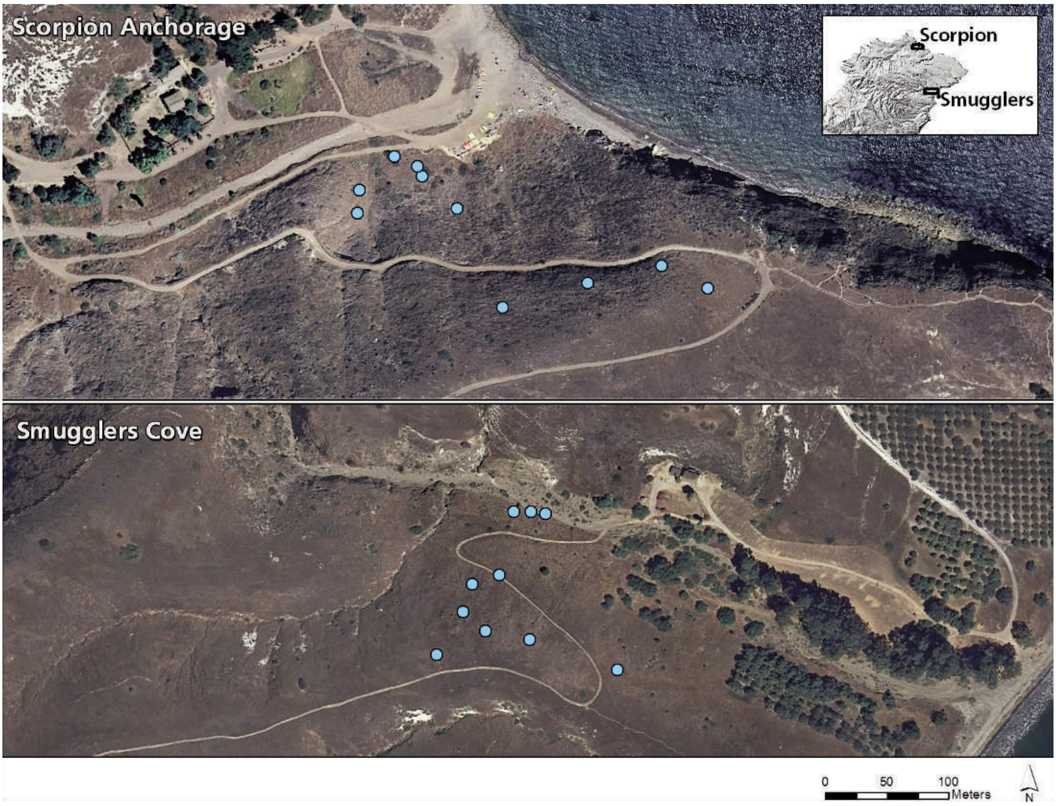

Fig. 1. Study areas in Scorpion Anchorage and Smugglers Cove, Santa Cruz Island, California. Dots indicate locations of fennel plot pairs. Inset shows location of sites on east Santa Cruz Island.

communities across much of the island (Cohen et al. 2009).

We chose 2 locations on east Santa Cruz Island for this study based on the occurrence of sizable, dense fennel stands; the potential for community recovery of coastal bluff scrub in both locations; and similarities in slope, aspect, and distance from the coast (Fig. 1). Coastal bluff scrub is found on coastal slopes around the island's perimeter and on steep canyon walls and outcrops. Common native species include *Eriogonum arborescens* (endemic), *Eriogonum grande* var. *grande* (endemic), *Leptosyne gigantea, Eriophyllum staechadifolium,* and *Rhus integrifolia,* although dominant species vary with slope, exposure, geologic substrate, and location (Junak et al. 1995).

In both sites, exotics (other than fennel) included the annual grass *Bromus diandrus,* with *Avena barbata* and *Lolium multiflorum* occurring occasionally. Native species observed beneath the fennel canopy included *Pseudognaphalium californicum* (annual), *Galium angustifolium* (perennial), and *Rhus integrifolia* (perennial) at Scorpion Anchorage (Scorpion); and *Amsinckia menziesii* var. *intermedia* (annual), *Deinandra fasciculata* (annual), *Lupinus succulentus* (annual), and *Stipa pulchra* (perennial) at Smugglers Cove (Smugglers). The sites differed with respect to geologic substrate, soil type, and soil characteristics (Table 1). Soil found at Scorpion, known as the Santa Cruz Island rock outcrop–Spinnaker–Topdeck complex, is derived from Santa Cruz Island volcanic rock and is somewhat excessively drained with very low available water capacity (about 2.5 cm). Soil at Smugglers, known as the Windage–Ballast complex, is developed from uplifted marine deposits derived from clayey shale (Monterey Formation) and is well drained with high available water capacity (about 22.86 cm; USDA–NRCS 2007).

TABLE 1. Site and soil characteristics found at study sites at Scorpion Anchorage and Smugglers Cove on Santa Cruz Island, California.

Feature	Scorpion Anchorage	Smugglers Cove
Soil	Rock outcrop–Spinnaker–Topdeck complex	Windage–Ballast complex
Slope (n = 20)	26.2°	21.7°
Aspect	North	North
Parental material	Volcanic breccia, andesite, or basalt and residuum weathered from volcanic breccia, andesite, or basalt	Uplifted marine deposits derived from clayey shale and limestone or calcareous shale
Depth to restrictive feature	15–45 cm to lithic bedrock; 20–45 cm to paralithic bedrock	>200 cm
Drainage class	Somewhat excessively drained	Well drained
Available water capacity	Very low (about 2.5 cm)	High (about 22.5 cm)

METHODS

Our strategy for recovering native coastal bluff scrub on east Santa Cruz Island focused on fennel control and native plant augmentation via seed broadcast. To evaluate this strategy, we established long-term monitoring plots specifically designed to track native plant recovery, fennel reestablishment from the seed bank, and establishment of novel invaders. Using GIS, we generated random point locations in 2 areas dominated by fennel (>10% cover; Cohen et al. 2009) to establish monitoring plots (Fig. 1). One area was located at Scorpion (1.02 ha) and the second area was located at Smugglers (2.03 ha). A paired-plot design was selected to control for variability within each site and to evaluate experimental (seeded) and control (nonseeded) treatments. There were 20 paired plots, for a total of 40 plots. Each plot was 1 m^2 with a 0.5-m buffer around the entire plot to reduce edge effect from plot manipulation and the effect of shading by nearby vegetation. Each experimental and control plot (plot pair) was oriented on a north–south axis with 1-m spacing between the 2 plots. The designation of seeded or nonseeded plot was determined by a coin toss.

In 2008, all fennel plants at Scorpion and Smugglers were treated. Reproductive fennel stalks were first cut and removed to better access the leafy rosettes, then plants were treated with 2% triclopyr. Paired plots were established and an initial condition assessment in each plot was conducted. To estimate fennel ensity in 2008, we recorded the number of treated fennel plants in each plot. We recorded percent cover of bare ground, litter, native vegetation, and exotic vegetation. Treated, dead fennel stumps and stalks were included in the litter category. Fennel seedlings which emerged from the seed bank in subsequent years were treated using 1% triclopyr after monitoring data were collected.

We selected *Artemisia californica, Leptosyne gigantea, Eriogonum arborescens,* and *E. grande* var. *grande* for seed broadcast because they were commonly occurring, recovering coastal bluff scrub species observed in Scorpion and Smugglers watersheds and not federally listed species or species of special concern. Before seeds were broadcast into the seeded plot, existing exotic vegetation in experimental and control plots was clipped as close to the soil surface as possible and litter was raked away. This action increased the likelihood that the target seeds would have good soil contact and light availability and thus have a higher likelihood of germination and eventual seedling success (Packard and Mutel 1992). Any resident native vegetation was not clipped or removed.

All native seed for this work was collected on Santa Cruz Island during 2007–2008 and stored in plastic totes in a constant temperature environment (22 °C). The source location and date collected were recorded for each lot of seeds. Seed mixes were placed by seed weight (seed + chaff) into packets 2 weeks prior to broadcasting. We calculated the number of seeds to be broadcast into each 1-m^2 plot to be a minimum of 1076 per species (see Valentine 1977). We determined the number of seed per species by weight per 100 seeds. Because we did not test for pure live seed, we increased the number of seeds broadcast to

TABLE 2. Precipitation recorded from a remote automated weather station located in the central valley on Santa Cruz Island, California.

Year	Precipitation (cm)
2008	54.58
2009	22.56
2010	71.65
2011	44.15
2012	33.96
2013	10.67

account for this uncertainty. The weight of seed packets were as follows: *E. arborescens* 115 g, *E. grande* var *grande* 26.5 g, *L. gigantea* 16.5 g, and *A. californica* 47.5 g. We broadcast seeds after the first rains at Smugglers on 16–17 November 2008 and at Scorpion on 10 December 2008 to increase the likelihood of high soil moisture during the critical period following seed germination. Both seeded and nonseeded plots were gently raked by hand after seed was broadcast.

In spring 2009–2013, we recorded the number of seedlings of the 4 native species broadcast, number of fennel seedlings, and percent cover of exotic species, native species, litter, and bare ground. In addition, all exotic and native species found growing in plots were identified and their presence was noted. No *A. californica* seedlings were observed in any plots during any years; therefore, this species was dropped from further analyses and discussion.

Statistical Analyses

Based on the experimental design, we analyzed the percent cover and seedling number data as a split plot (i.e., paired plots) with repeated measures over years in a generalized linear mixed models framework (i.e., Proc GLIMMIX, SAS Institute, Inc. 2008). We considered location (Scorpion, Smugglers) to be a fixed effect, points to be a random effect nested within location, and treatment (nonseeded, seeded) to be a fixed effect. Years were treated as categorical variables in the analysis.

For the analysis of percent cover data, we first converted percentages to proportions then used an arcsine transformation to stabilize variances (Ott 1988). This step was necessary because much of the observed proportion data was near 0 or 1. For the seedling number data, we attempted to model the counts under the assumption the data were distributed as either Poisson or negative binomial. However, the large number of zeros encountered on some plots caused the analysis to fail because the optimization routine failed to converge. Consequently, instead of modeling counts directly, we computed the difference in the number of seedlings counted on paired plots (i.e., we subtracted the number of seedlings counted on nonseeded plots from the number counted on the paired seeded plots) and analyzed these data using a normal error distribution. For all analyses, we assumed the covariance structure on the repeated measures was first-order autoregressive, and we computed the denominator degrees of freedom (for F tests) using the Kenward and Roger (1997) adjustment.

We used F tests for overall tests of fixed effects with $\alpha = 0.05$ as the significance level. In cases where further investigation of the nature of the effects was desired, we used t tests on pairwise comparisons of the least-squares means generated under the analysis and $\alpha = 0.05$ as the significance level.

RESULTS

Fennel density prior to treatment in 2008 was 10.4 plants $\cdot$ m^{-2} and 7.3 plants $\cdot$ m^{-2} at Scorpion and Smugglers, respectively. After treating with 2% triclopyr, by early spring 2009 fennel density was reduced to 2.0 plants $\cdot$ m^{-2} and 0 plants $\cdot$ m^{-2} at Scorpion and Smugglers, respectively. A single follow-up treatment the following spring resulted in 100% effectiveness. Fennel seedlings that emerged from the seed bank in subsequent years were treated using 1% triclopyr after monitoring data were collected. By 2013, the number of fennel seedlings in all plots declined from 23.0 seedlings $\cdot$ m^{-2} in 2009 (which, with 22.56 cm precipitation, was a drought year) to <1 seedling $\cdot$ m^{-2} (Table 2). In spite of very wet years in 2010 and 2011, followed by an average rainfall year in 2012, the number of fennel seedlings observed declined over the study; and there were no significant main effects or interactions.

Percent Cover Data

Beginning in 2008 and ending in 2013, cover data were collected at the Scorpion and Smugglers locations for litter, bare ground, exotic vegetation, and native vegetation, except

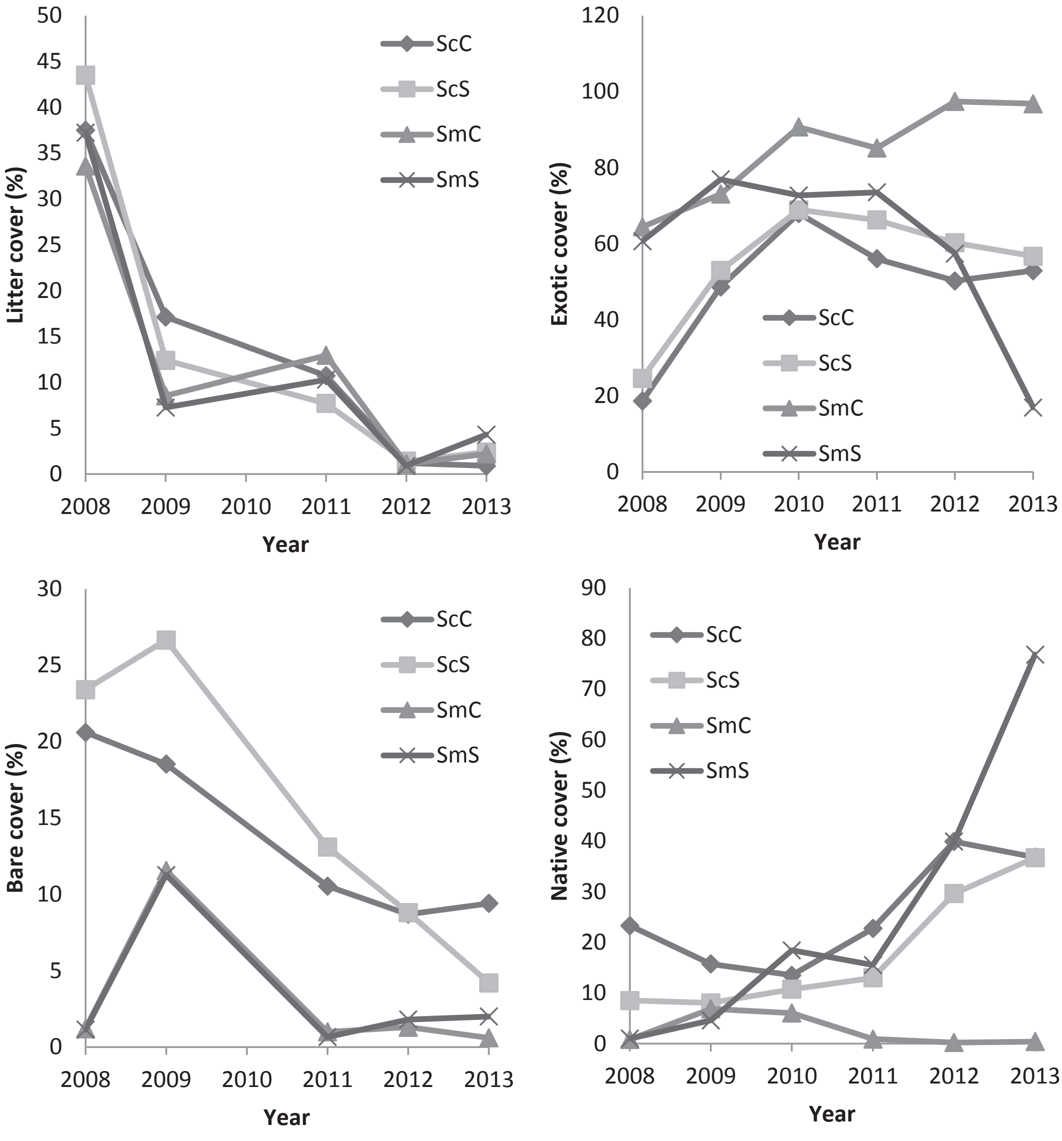

Fig. 2. Percent cover of litter, bare ground, exotic species, and native species in seeded and nonseeded plots at Scorpion and Smugglers on Santa Cruz Island, California. ScC = Scorpion control plots, ScS = Scorpion seeded plots, SmC = Smugglers control plots, SmS = Smugglers seeded plots.

in 2010 for litter and bare ground (Fig. 2). In general, analysis of these data found multiple main effects and interactions of importance (Table 3).

For litter cover, there was a significant year effect only (Table 3). Pairwise comparisons among years found 2008 differed from all other years, 2009 and 2011 differed from all other years but did not differ from each other, and 2012 and 2013 differed from all other years but did not differ from each other.

For bare ground, there were significant location, year, and location × year effects (Table 3). As indicated in Fig. 2, bare ground cover was greater at Scorpion than at Smugglers, and pairwise comparisons among years indicate bare ground increased between 2008 and 2009, decreased between 2009 and 2011, then remained stable from 2011 through 2013 (i.e., the means did not differ significantly). Fig. 2 suggests that different responses by location between 2008 and 2009

TABLE 3. *F* tests of fixed effects for percent cover (litter, bare ground, exotic vegetation, native vegetation), with main effects for location (loc: Scorpion, Smugglers), treatment (trt: control, seeded), and year (2008–2013) in study plots on Santa Cruz Island, California.

Effect	Num DF	Den DF	*F*	Pr > *F*
Litter				
loc	1	36.24	0.92	0.3437
trt	1	36.24	0	0.9803
loc * trt	1	36.24	0	0.9893
year	4	98.79	98.37	<0.0001
loc * year	4	98.79	1.9	0.1160
year * trt	4	98.79	0.97	0.4252
loc * year * trt	4	98.79	0.1	0.9808
Bare				
loc	1	18.14	5.47	0.0309
trt	1	29.2	0.03	0.8602
loc * trt	1	29.2	0	0.9474
year	4	129.8	18.83	<0.0001
loc * year	4	129.8	5.06	0.0008
year * trt	4	129.8	0.37	0.8310
loc * year * trt	4	129.8	0.78	0.5434
Exotic				
loc	1	18.8	11.92	0.0027
trt	1	19.33	2.85	0.1074
loc * trt	1	19.33	9.91	0.0052
year	5	137.5	16.97	<0.0001
loc * year	5	137.5	8.53	<0.0001
year * trt	5	137.5	6.97	<0.0001
loc * year * trt	5	137.5	5.49	0.0001
Native				
loc	1	18.98	2.41	0.1371
trt	1	18.88	3.35	0.0830
loc * trt	1	18.88	11.06	0.0036
year	5	149.1	16.05	<0.0001
loc * year	5	149.1	5.86	<0.0001
year * trt	5	149.1	10.37	<0.0001
loc * year * trt	5	149.1	4.91	0.0003

contributed to the significant location × year interaction.

All fixed effects for exotic cover, except treatment, were significant (Table 3). In general, exotic cover was greater at Smugglers than at Scorpion, though the seeded plots at Smugglers showed a steep drop from 2011 through 2013 that was not apparent in the control plots or any of the plots at Scorpion. This drop is likely responsible for the significant location × treatment, location × year, and location × year × treatment interactions. Pairwise comparisons among years indicate exotic cover in 2008 and 2013 differed from all other years but not from each other and 2010 differed from all other years except 2011. The years 2009, 2011, and 2012 did not differ from each other.

For native cover, location and treatment were not significant, but all other fixed effects were (Table 3). Pairwise comparisons among years indicate native cover in 2008 through 2011 did not differ; but in 2012 and 2013, native cover was significantly greater than in every other year, and 2013 was significantly greater than 2012. Figure 2 suggests that the differences in exotic cover from 2011 through 2013, where the Smugglers treatment and controls diverged and where the pattern of changes at Smugglers did not track the changes at Scorpion, were responsible for the significant location × treatment, location × year, year × treatment, and location × year × treatment interactions.

Seedling Count Data

Seedling count data for the native species *L. gigantea* (COGI), *E. arborescens* (ERAR), and *E. grande* var. *grande* (ERGR) were collected at the Scorpion and Smugglers locations beginning in 2009 and ending in 2013 (Table 4). Seedling count data for *F. vulgare*

TABLE 4. Seedling density (seedlings · m^{-2}) in seeded and nonseeded plots at Scorpion Anchorage and Smugglers Cove on Santa Cruz Island, California. n = 10; standard errors are in parentheses. FOVU = *Foeniculum vulgare,* COGI = *Leptosyne gigantea,* ERGR = *Eriogonum grande* var. *grande,* ERAR = *Eriogonum arborescens.*

Site	Plot	Species	2008	2009	2010	2011	2012	2013
Scorpion	Seeded	FOVU	10.4 (4.3)	33.2 (10.3)	7.6 (3.6)	0.4 (0.2)	0.2 (0.1)	0 (0)
		COGI		56.4 (27.4)	1.6 (0.8)	2.3 (1.8)	1.4 (0.8)	1.4 (0.9)
		ERGR		38.8 (11.0)	10.0 (6.6)	1.9 (1.6)	2.4 (1.5)	1.9 (1.5)
		ERAR		102.8 (33.4)	5.6 (3.6)	2.4 (1.3)	1.2 (0.8)	1.8 (1.1)
	Control	FOVU	2.8 (1.5)	41.6 (20.9)	22.8 (14.3)	0.7 (0.3)	0.4 (0.2)	0.5 (0.4)
		COGI		0	0	0	0	0
		ERGR		37.2 (24.9)	12.4 (7.2)	1.8 (0.9)	2.7 (1.8)	1.7 (1.0)
		ERAR		0	0	0	0.1 (0.1)	0
Smugglers	Seeded	FOVU	5.4 (2.9)	6.0 (1.7)	7.6 (2.0)	1.9 (0.6)	0.8 (0.4)	0.3 (0.2)
		COGI		50.4 (9.2)	17.3 (7.3)	4.8 (1.5)	4.5 (1.7)	3.4 (1.4)
		ERGR		10.4 (3.9)	0	0	0	0
		ERAR		121.6 (29.5)	19.1 (12.5)	3.7 (2.0)	3.5 (1.5)	2.7 (1.1)
	Control	FOVU	1.6 (0.9)	12.4 (7.4)	16.0 (4.3)	1.6 (1.0)	0.2 (0.1)	0 (0)
		COGI		0	0	0	0	0
		ERGR		0	0	0	0	0
		ERAR		0	0	0	0	0

TABLE 5. F tests of fixed effects for differences in seedling count data for paired plots (i.e., count on seeded plot minus count on the paired control plot) for *Leptosyne gigantea* (COGI), *Eriogonum arborescens* (ERAR), *Eriogonum grande* var. *grande* (ERGR), and *Foeniculum vulgare* (FOVU), with main effects for location (loc: Scorpion, Smugglers) and year (2009–2013). Study plots were located on Santa Cruz Island, California.

Effect	Num DF	Den DF	F	Pr > F
COGI				
loc	1	12.3	0.23	0.6398
year	4	52	11.66	<0.0001
loc * year	4	52	0.44	0.7776
ERGR				
loc	1	12.1	0.05	0.8215
year	4	59.7	0.32	0.8640
loc * year	4	59.7	0.1	0.9826
ERAR				
loc	1	12	0.33	0.5741
year	4	55.6	25.02	<0.0001
loc * year	4	55.6	0.11	0.9771
FOVU				
loc	1	45	0.08	0.7773
year	5	98.2	1.94	0.0950
loc * year	5	98.2	0.15	0.9799

(FOVU) were collected at the Scorpion and Smugglers locations beginning in 2008 and ending in 2013 (Table 4). Analyses were performed on the difference data, where the differences were formed by subtracting the number of seedlings counted on control plots from the number of seedlings counted on the paired seeded plots.

For COGI and ERAR, there was a significant year effect only (Table 5). Pairwise comparisons among years found 2009 differed from all other years, but 2010 through 2013 did not differ among themselves. For ERGR, there were no significant main or interactive effects, though the general pattern observed mirrored that for COGI and ERAR (Table 5).

DISCUSSION

Fennel was successfully treated on the eastern 10% of Santa Cruz Island using 2% triclopyr on rosettes during spring 2008 and using 1% triclopyr as a follow-up treatment on fennel seedlings each spring from 2009 through 2013. Removing fennel disturbed the community and resulted in more light, more space, and presumably more available water and nutrients for resident natives and exotics to utilize.

Resident natives, new natives from seed broadcast, and exotics responded positively to disturbance from fennel removal. Exotic annual grasses responded quickly the first year after disturbance. *Avena barbata* and *Lolium multiflorum* shifted from occasional to common, and new invaders included *Brachypodium distachyon, Bromus madritensis* ssp. *madritensis,* and *Festuca myuros*—all annual grasses.

Natives were strongly competitive with exotics at both sites (year effects $P < 0.0001$) with treatment × location interaction ($P = 0.0036$). At Smugglers, exotic annual grasses responded quickly in both seeded and nonseeded plots during the first year following disturbance (Fig. 2). Native cover at Smugglers, composed almost entirely of *E. arborescens* and *L. gigantea* from seeding treatments, began to exert competitive pressure on exotic annual grasses at year 2 and 3, with strong competitive pressure during year 4 and 5. By the second year, established *E. arborscens* and *L. gigantea* were taller than the surrounding community, began to shade exotic annual grass seedlings, and by 2013, dominated plots in which they occurred (Fig. 2). In contrast, nonseeded plots at Smugglers were dominated by exotic annual grasses (99% cover; Fig. 2). These results indicate that *E. arborescens* and *L. gigantea* were absent from the seed bank; yet once established, they were strong competitors with exotic annual grasses. Evidently historical disturbances coupled with deep soils at Smugglers led to conditions that favored exotic species. Furthermore, repeated disturbance from grazing and competition with exotics led to a diminished seed bank and extreme limitation in native recruitment. Given the success of seeded *E. arborescens* and *L. gigantea* at Smugglers, dominance by fennel and exotic annual grasses in this location is partly the result of a depauperate native seed bank. Successful restoration at Smugglers will require seeding with native seed to replenish the seed bank and promote native recruitment.

At Scorpion, a similar pattern of early growth by exotic annual grasses followed by competitive pressure from native perennials occurred in seeded and nonseeded plots ($P = 0.0830$); however, in contrast to results observed at Smugglers, there was no significant difference between seeded and nonseeded plots at Scorpion. Native cover was composed of seeded species *E. arborescens* and *L. gigantea* (in seeded plots only) and *E. grande* var. *grande* (in seeded and nonseeded plots) and also of resident natives and 8 new native species (Tables 4, 6). These results indicate *E. grande* var. *grande* and other native species were present in the seed bank prior to fennel removal, and *E. arborescens* and *L. gigantea* were absent from the seed bank. Removing fennel resulted in conditions favorable for native species to grow and successfully compete with exotic grasses. In 2013, exotic cover was greater than native cover at Scorpion in seeded and nonseeded plots, but the trend in native cover between 2010 and 2013 was positive while the trend in exotic cover was negative. Future monitoring will reveal the outcome of the competitive interaction between natives and exotics at Scorpion.

Seeded *E. arborescens* and *L. gigantea* survived at both Smugglers and Scorpion while *E. grande* var. *grande* survived only at Scorpion. At Smugglers, *Eriogonum grande* var. *grande* germination (10.4 seedlings · m^{-2} in 2009) was followed by 100% mortality by 2010. Grasses are effective competitors for water and nutrients and can interrupt succession through competition for water with native perennials (D'Antonio and Vitousek 2003). The effective uptake of water and nutrients by grasses is likely the result of their dense, shallow root system (Philips 1963, Davis and Mooney 1985). The root systems of most woody species are deeper and less dense than those of grasses. Grasses may therefore be more effective as competitors against seedlings than saplings or adults of woody species or shrubs. Efficient water use may be the means by which exotic grasses outcompeted *E. grande* var. *grande* on soils at Smugglers. Alternatively, *E. grande* var. *grande* may be better adapted to volcanic soils found at Scorpion compared with shale-derived soils found at Smugglers. Additional studies are required to understand the mechanism for the mixed outcome of *E. grande* var. *grande* in this study.

It is common for a novel invader to appear following treatment of one exotic species (Kettenring and Adams 2011). In this study, invaders were exotic annual grasses which were not strong competitors with native

TABLE 6. Species present in study plots at Scorpion and Smugglers on Santa Cruz Island, Channel Islands National Park, California. Resident species were present in plots in 2008. Undetected species were present in 2008 but not in 2013, and Novel species were not present in 2008 but were observed in 2013. Sm:S = Smugglers, seeded; Sm:UnS = Smugglers, nonseeded; Sc:S = Scorpion, Seeded; Sc:UnS = Scorpion nonseeded. N = native, E = exotic.

Species	Resident	Undetected	Novel
Achillea millefolium (N)			Sc:S
Amsinckia menziesii var. *intermedia* (N)		Sm:UnS, Sm:S	
Avena barbata (E)	Sm:S, Sm:UnS; Sc:S, Sc:UnS		
Baccharis pilularis (N)	Sc:S	Sm:UnS	
Brachypodium distachyon (E)			Sm:S, Sm:UnS; Sc:S, Sc:UnS
Brassica nigra (E)	Sm:S, UnS		
Bromus carinatus (N)			Sc:S, UnS
Bromus hordeaceus (E)	Sc:S, UnS	Sm:S, UnS	
Bromus madritensis ssp. *madritensis* (E)			Sm:S, Sm:UnS; Sc:S, Sc:UnS
Brachypodium distachyon (E)	Sm:S, Sm:UnS; ScS, Sc:UnS		
Castilleja lanata ssp. *hololeuca* (N)			Sc:UnS
Centaurea melitensis	Sm:S	Sm:UnS	
Daucus pusillus (E)	Sm:S, Sm:UnS		Sc:UnS
Dichelostemma capitatum (N)			Sc:S
Deinandra fasciculata (N)		Sm:S, UnS	
Dudley spp. (N)		Sc:S	
Elymus triticoides (N)			Sc:S, UnS
Eriogonum arborescens (N)			Sm:S, Sc:S
Eriogonum grande var. *grande* (N)	Sc:S; UnS		
Eriophyllum confertiflorum (N)			Sc:UnS
Eriophyllum staechadifolium (N)			Sc:UnS
Festuca myuros (E)			Sc:S, UnS
Festuca perennis (E)	Sm:S, UnS		Sc:S, UnS
Foeniculum vulgare (E)	Sm:S, Sc:UnS	Sm:UnS, Sc:S	
Galium angustifolium (N)	Sc:S, UnS		
Hazardia detonsa (N)			Sm:S
Hordeum brachyantherum (N)			Sm:S, Sc:S, UnS
Hordeum marinum ssp. *gussoneanum* (E)		Sc:S, Sc:UnS	
Hordeum murinum (E)	Sm:S	Sm:UmS	Sc:UnS
Lactuca serriola (E)	Sc:UnS	Sm:UnS, Sc:S	
Leptosyne gigantea (N)			Sm:S, Sc:S
Lupinus succulentus (N)	Sm:S	Sm:UnS, Sc:UnS	
Medicago polymorpha (E)			Sm:S
Melica imperfecta (N)		Sc:UnS	Sc:S
Pseudognaphalium californicum (N)	Sc:S, Sc:UnS	Sm:S	
Rhus integrifolia (N)	Sc:UnS		Sc:S
Sonchus oleraceus (E)		Sm:UnS	
Sanicula arguta (N)		Sm:UnS	Sc:S, UnS
Stipa pulchra (N)	Sm:UnS	Sm:S, Sc:S, Sc:UnS	

perennials. Exotic perennials such as *Cardaria draba* and *Pennisetum clandestinum* may be stronger competitors and more difficult to control than exotic annual grasses. Further studies are needed to investigate the competitive outcome between native island perennials and exotic perennials.

Large- and small-scale disturbance alters successional forces and prolongs the period during which exotics and native species compete for resources (D'Antonio and Vitousek 2003). Due to the absence of burrowing animals such as pocket gophers and ground squirrels, Santa Cruz Island does not experience repeated, small-scale disturbances which favor exotic annual grasses (Dyer et al. 1996, Hamilton et al. 1999, Peart 1989, Seabloom et al. 2003). Island native perennials may have a level of protection from disturbance not shared by their mainland counterparts because of the absence of repeated, small-scale disturbances created by burrowing animals.

With the removal of the last exotic ungulate in 2006, island plant communities are recovering from repeated landscape-level disturbance created by decades of overgrazing. However, the island will likely be subjected to another large-scale disturbance—global climate change. Various models predict that changing climatic conditions in California will include a warmer and drier climate and greater frequency of extreme weather events (Cayan et al. 2008). With impending climate change, native plant communities may be especially vulnerable to disturbance and competition with exotic species. Further studies are needed to determine if native species can resist conversion to exotic dominance following repeated landscape-level disturbances such as more frequent and extreme drought, extreme temperatures, torrential rain, or reduced fog input. Removing stressors, reducing other human-caused disturbance, restoring native species dominance, and establishing a native seed bank are important steps toward conditions that favor native perennials that are confronted with landscape-level disturbance.

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LITERATURE CITED

BOSSARD, C.C., J.M. RANDALL, AND M.C. HOSHOVSKY, EDITORS. 2000. Invasive plants of California's wildlands. University of California Press, Berkeley, CA.

BEAN, C., AND M.J. RUSSO. 1988. The Nature Conservancy. Element stewardship abstract for *Foeniculum vulgare.* [Cited 21 July 2006]. Available from: http://tncweeds.ucdavis.edu/esadocs/foenvulg.htmo

BEATTY, S.W. 1991. The interaction of grazing, soil disturbance, and invasion success of fennel on Santa Cruz Island, CA. The Nature Conservancy, Santa Barbara, CA.

BRENTON, R.K., AND R.C. KLINGER. 1994. Modeling the expansion and control of fennel (*Foeniculum vulgare*) on the Channel Islands. Pages 497–504 *in* W.L. Halvorson and G.J. Maender, editors, The Fourth California Islands Symposium: update on the status of resources. Santa Barbara Museum of Natural History, Santa Barbara, CA.

______. 2002. Factors influencing the control of fennel (*Foeniculum vulgare* Miller) using triclopyr on Santa Cruz Island, California. USA. Natural Areas Journal 22(2):135–147.

CARBONE, M.S., A.P. WILLIAMS, A.R. AMBROSE, C.M. BOOT, E.S. BRADLEY, R.E. DAWSON, AND S.M. SCHAEFFER. 2013. Cloud shading and fog drip influence the metabolism of a coastal pine ecosystem. Global Change Biology 19:484–497.

CAYAN, D.R., E.P. MAURER, M.D. DETTINGER, M. TYREE, AND K. HAYHOE. 2008. Climate change scenarios for the California region. Climate Change 87:S21–S42.

COHEN, B., C. CORY, J. MENKE, AND A. HEPBURN. 2009. A spatial database of Santa Cruz Island vegetation. Pages 229–244 *in* C.C. Damiani and D.K. Garcelon, editors, Proceedings of the 7th California Islands Symposium. Institute for Wildlife Studies, Arcata, CA.

CORBIN, J.D., AND C.M. D'ANTONIO. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology 85: 1273–1283.

D'ANTONIO, C.M., AND P.M. VITOUSEK. 2003. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23(1992):63–87.

DASH, B.A., AND S.R. GLIESSMAN. 1994. Nonnative species eradication and native species enhancement: fennel in Santa Cruz Island. Pages 505–512 *in* W.L. Halvorson and G.J. Maender, editors, The Fourth California Islands Symposium: update on the status of resources. Santa Barbara Museum of Natural History, Santa Barbara, CA.

DAVIS, S.D., AND H.A. MOONEY. 1985. Comparative water relations of adjacent California shrub and grassland communities. Oecologia 66:522–529.

DYER, A.R., H.C. FOSSUM, AND J.W. MENKE. 1996. Emergence and survival of *Nassella pulchra* in a California grassland. Madroño 43:316–333.

ERSKINE-OGDEN, J.A., AND M. REJMANEK. 2005. Recovery of native plant communities after the control of a dominant invasive plant species. *Foeniculum vulgare:* implications for management. Biological Conservation 125:427–439.

FISCHER, D.T., C.J. STILL, AND A.P. WILLIAMS. 2009. Significance of summer fog and overcast for drought stress and ecological functioning of coastal California endemic plant species. Journal of Biogeography 36:783–799.

HAMILTON, J.G., C. HOLZAPFEL, AND B.E. MAHALL. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. Oecologia 121:518–526.

JUNAK, S., T. AYERS, R. SCOTT, D. WILKEN, AND D. YOUNG, EDITORS. 1995. A flora of Santa Cruz Island. Santa Barbara Botanical Garden, Santa Barbara, CA.

KENWARD, M.G., AND J.H. ROGER. 1997. Small sample inference for fixed effects from restricted maximum likelihood. Biometrics 53:983–997.

KETTENRING, K.M., AND C.R. ADAMS. 2011. Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. Journal of Applied Ecology 48:970–979.

KLINGER, R.C., AND I. MESSER. 2001. The interaction of prescribed burning and site characteristics on the diversity and composition of a grassland community on Santa Cruz Island, California. Pages 66–80 *in* K.E.M. Galley and T.P. Wilson, editors, Proceedings of the Invasive Species Workshop: the role of fire in the control and spread of invasive species. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, FL.

LEVINE, J.M., M. VILÁ, C.M. D'ANTONIO, J.S. DUKES, C. GRIGULIS, AND S. LAVOREL. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London Series B 270: 775–781.

MACK, R.N. 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. Pages 155–179 *in* J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson, editors, Biological invasions: a global perspective. John Wiley & Sons, New York, NY.

OTT, L. 1988. An introduction to statistical methods and data analysis. 3rd edition. PWS-KENT Publishing Company, Boston, MA.

PACKARD, S., AND C.F. MUTEL, EDITORS. 1992. The tallgrass restoration handbook for prairies, savannas, and woodlands. Island Press, Washington, DC.

PEART, D.R. 1989. Species interactions in a successional grassland. III. Effects of canopy gaps, gopher mounds and grazing on colonization. Journal of Ecology 77:267–289.

PHILIPS, W.S. 1963. Depth of roots in soil. Ecology 44: 424–429.

PIMENTEL, D., L. LACH, R. ZUNIGA, AND D. MORRISON. 2000. Environmental economic costs of nonindigenous species in the United States. BioScience 50:53–65.

SAS INSTITUTE, INC. 2008. SAS/STAT® 9.2 User's Guide. SAS Institute, Inc., Cary, NC.

SCHOENHERR, A.A., C.R. FELDMETH, AND M.J. EMERSON. 1999. Natural history of the islands of California. University of California Press. Berkeley, CA.

SEABLOOM, E.W., W.S. HARPOLE, O.J. REICHMAN, AND D. TILMAN. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences 100(23):13384–13389.

[USDA–NRCS] UNITED STATES DEPARTMENT OF AGRICULTURE–NATURAL RESOURCES CONSERVATION SERVICE. 2007. Soil survey of Channel Islands National Park, California. Available from: http://soils.usda.gov/survey/printed_surveys/.

VALENTINE, J.F. 1977. Range development and improvements. Brigham Young University Press, Provo, UT.

WILCOVE, D.S., D. ROTHSTEIN, J. DUBOW, A. PHILLIPS, AND E. LOSOS. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607–615.

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