



Revegetation following soil disturbance and invasion in a Californian meadow: a 10-year history of recovery

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Abstract

Disturbance is necessary for the regeneration of many native plant species, but can also facilitate biological invasions. As a result, disturbance can play complex roles in vulnerable habitats such as remnant Californian perennial grasslands. To investigate these conflicts, plots in a northern Californian coastal grassland were experimentally disturbed in the winter of 1990–1991; these plots differed in the area and intensity (depth) of the soil disturbance applied. When these plots were revisited after 10 growing seasons, patterns of revegetation differed significantly from those observed early in recolonization (0–3 years). At the earlier samplings, exotic annual grasses rapidly increased in most disturbance types. After 10 years, these exotic annuals had retreated from the depth experiment, which had recovered to a vegetation dominated by native perennials in all but the most severely disturbed plots. In contrast, although differences between control and disturbed plots also disappeared in the area experiment, the average abundance of aliens did not decline substantially relative to 1993 levels, especially in larger disturbances. Nonetheless, populations of aliens remained small compared to the peak populations in the depth experiment, probably reflecting wetter soils at the site used for the area experiment. These results differ from those of other recent studies of soil disturbance in coastal Californian ecosystems, which indicate disturbance may result in the permanent replacement of native perennial vegetation by dense populations of exotic annual grasses. This difference may reflect the high resilience of northern coastal grasslands as well as the scale of disturbances considered by different studies.

Introduction

Invasions by exotic plants represent one of the most serious threats to the conservation and restoration of natural communities (US Congress 1993; Vitousek et al. 1996; Mack et al. 2000). Disturbance often tends to facilitate these invasions (Hobbs and Huenneke 1992; Mack et al. 2000; Sakai et al. 2001; Byers 2002); however, the effects of disturbance in natural systems are complex. First, many native species also depend on disturbance for recruitment opportunities or the suppression of competitors (Hobbs and Huenneke 1992). Second, the effects of a disturbance depend on such characteristics as its size and intensity, and the

manner in which these interact with the physical and biological environment (Sousa 1984; Pickett and White 1985; O'Neill et al. 1986). Finally, it has long been known that the consequences of disturbance typically are transient. As a result, frequent disturbance may result in one outcome, while infrequent disturbance may produce an entirely different community (e.g., Huston 1994); conversely, the results of a study may depend upon its duration.

Californian grasslands provide examples of systems which have been dramatically altered by invasions of alien plants. Populations of exotic Mediterranean annual grasses have increased to such an extent that they have widely replaced native perennial grasses,

in what surely is one of the most spectacular biological invasions worldwide, while efforts to restore native species have proven difficult (Heady 1988; Sims 1988; Heady et al. 1992). These annual invaders may benefit more from some types of disturbance than do co-occurring natives. For example, grazing and trampling by livestock may have contributed to the original replacement of native grasslands (Mack 1989). Similarly, communities dominated by Mediterranean annual grasses may establish and persist for years or decades following soil disturbance by cultivation (Stromberg and Griffin 1996) or construction (Zink et al. 1995; Stylinski and Allen 1999). However, some Californian grasslands have proven more resilient than others. In particular, wetter north coastal grasslands have resisted invasion by Mediterranean annuals more successfully than relatively arid central grasslands (Heady et al. 1988, 1992); the risks associated with disturbance and prospects for restoration may differ correspondingly between these habitats and more vulnerable grasslands.

In this paper, I focus on the effects of soil disturbance on exotic plants in a coastal Californian grassland. In previous publications (Kotani 1995, 1996, 1997a,b), I showed that a variety of experimental soil disturbances generally resulted in a rapid (1–3 years) increase in alien annual grasses at the expense of native perennials. Here I report the results of resampling after 10 years of recolonization. In contrast with other recent studies, I demonstrate that soil disturbance did not lead to the persistent replacement of perennial natives with alien annual grasses. I suggest that this discrepancy may reflect a tendency of moister Californian grasslands to be less vulnerable to invasion, possibly coupled with the effects of disturbance scale.

Materials and methods

This study was conducted at the University of California's Angelo Coast Range Reserve (123°37' W, 39°45' N), in coastal Mendocino county about 240 km north of San Francisco. This site is dominated by *Pseudotsuga menziesii* (Douglas Fir)–*Sequoia sempervirens* (Redwood) forest, but meadows occur as a series of small (2–8 ha) semi-natural openings along the valley of the Eel River. Most of these meadows are dominated both visually and in terms of biomass by the large native perennial grass, *Danthonia californica*, with smaller amounts of other native perennials such

as the rush *Luzula comosa*, but they also contain large populations of small exotic annual grasses including *Aira caryophylla*, *Bromus hordeaceus*, and *Briza minor*. *Juncus bufonius* (Juncaceae) and some *Vulpia* spp. (Poaceae) are the only native annual graminoids (grasses, rushes, or sedges). Native perennial Liliaceae and Amaryllidaceae (geophytes or 'bulbs') are abundant, but only visible above-ground for a brief period in winter and spring. Numerous herbaceous dicots (forbs) occur infrequently. These meadows are regularly disturbed by non-native feral pigs (*Sus scrofa*), which severely damage patches of vegetation by grubbing for subterranean foods (Kotani 1995). Other sources of disturbance include native pocket gophers (*Thomomys bottae*) and moles (*Scapanus latimanus*) (Kotani 1995). Fire probably was once important, but has been suppressed for decades (Johnson 1979). Additional information on this study site may be found in Johnson (1979) and Kotani (1994, 1995). I use Hickman (1993) as my source for nomenclature and species' origins. Throughout, I use 'alien' and 'exotic' synonymously to mean plants introduced to California by human activity (Richardson et al. 2000). Most of the aliens at my study site are both naturalized and invasive, as defined by these authors.

In the winter of 1990–1991, I established a series of field experiments and surveys in *Danthonia*-dominated areas of five of the meadows occurring along the river corridor. Most ultimately were removed, or destroyed by pigs after their abandonment in 1993; however, two key experiments set about 50 m apart in one of the largest meadows, (the White House Meadow) still were available for sampling in 2000. Though these experiments are close together, previous results (Kotani 1995, 1996, 1997a, b) demonstrated most meadows at this site contain similar graminoid vegetation and share similar responses to soil disturbance.

I designed the first ('disturbance area') experiment to investigate the effects of disturbance size and shape on revegetation. I created 45 plots, separated by ~1 m; the proximity of these plots guaranteed that they experienced similar background conditions, including seed dispersal from nearby vegetation. I randomly assigned each plot to one of nine treatments: 1 : 4 rectangular excavations measuring 156, 625, 2500, and 10 000 cm² (widths = 6, 13, 25, and 50 cm), circular excavations of the same areas (diameters = 14, 28, 56, and 113 cm), and undisturbed controls. All excavations were ~8 cm in depth. I designed the second

('disturbance depth') experiment to investigate the effects of the disturbance intensity. I created 72 plots, spaced 50 cm apart in a grid pattern; again, this proximity facilitated comparisons among treatments. Plots were 25 cm × 25 cm squares, which I randomly assigned to nine treatments: excavation to a depth of 2, 4, 8, or 16 cm, burial to a depth of 2, 4, 8, or 16 cm, and undisturbed controls. The earth used to bury plots came from the excavations. An 8 cm depth of excavation or burial is comparable to the depth of soil disturbance by feral pigs (Kotanen 1995, 1996); a 625 cm² plot is comparable in size to a single gopher mound or bunchgrass clump, while a 1 m² plot is comparable to an isolated patch of pig-disturbed soil (Kotanen 1995, 1997a, b). These treatments almost completely removed the pre-existing vegetation: growing graminoids and dicots were nearly eliminated from all excavated plots, and could grow through only the shallowest burials, while seed banks of most species were also largely removed or buried (Kotanen 1996).

In June 2000, I repeated the sampling procedure I had employed for the first three summers after I established these experiments: I counted the living and/or reproductive shoots rooted within a 100 cm² area centered in the floor of each plot. For this paper, I have focussed my principal analyses on the two groups of plants which structure these meadows – alien annual and native perennial graminoids. Most dicots occurred at very low frequencies, while geophytes are not reliably detectable by mid-summer (Kotanen 1996, 1997a). I have retained the basic analysis scheme used in my original papers: after a significant overall *F*-test I separately analyzed each experiment's data using Fisher's LSD multiple comparisons, adjusted for *a posteriori* use by the Bonferroni/Dunn method. Data were log-transformed to meet ANOVA assumptions.

Results

Patterns of revegetation (2000)

For the disturbance depth experiment, all 72 plots were successfully located either by finding corner markers (49 plots) or by measurement relative to the locations of known plots (23 plots). Since this experiment had been carefully surveyed when first established, plots could be located by measurement to within a few centimeters; this guaranteed that the subplot sampled lay fully within the original plot boundaries. For the

disturbance area experiment, 35 of the 40 disturbed plots similarly were located by finding plot markers, while the positions of the five controls were estimated by measurement. Positions of these controls again were determined with high accuracy, and in any case are less critical than positions of disturbed plots, since they are simply samples of the surrounding undisturbed vegetation. The five missing plots were all the smallest disturbance size, which was significantly less likely to be rediscovered than other sizes of disturbed plots ($\chi^2 = 17.143$; *df* = 3; *P* < 0.001). The missing disturbed plots probably were not identifiable since they had been so completely recolonized; excluding these plots from analysis should make estimates of recolonization more conservative.

More than 5000 shoots were counted during the 2000 sampling. Both disturbed and control plots were dominated by mixtures of annual graminoids (57.8% of all shoots) and perennial graminoids (35.5% of all shoots); dicots (primarily native *Lotus* spp.) were rare (6.7% of all shoots). The only common perennial graminoid was the native *D. californica* (99.2% of perennial graminoid shoots in the depth experiment; 90.7% in the area experiment), though *L. comosa* (native), *Elymus glaucus* (native), and *Holcus lanatus* (exotic) did occur in and around experimental plots. *Luzula* may have been underestimated since it becomes more difficult to identify as the summer goes on, but again this should make estimates of revegetation by native perennials more conservative. *Holcus* contributed <2.5% of all perennial graminoid shoots in both experiments. *A. caryophyllea* (exotic) was the commonest annual graminoid in the area experiment (61.2% of annual graminoid shoots), but contributed only 8.9% of annual graminoid shoots in the depth experiment, where *B. hordeaceus* (exotic) was much more abundant (84.2%); this grass contributed 17.0% of annual graminoid shoots in the area experiment. The only native annual graminoids observed were some *Vulpia* spp. and *J. bufonius*. Both were scarce, respectively contributing <10% and <1% of annual graminoid shoots in both experiments.

The abundance of native perennial graminoids varied significantly among treatments in the disturbance depth experiment ($F_{8,63} = 5.15$, *P* < 0.001), although this effect tended to be pronounced only for the deeper burials, where their numbers were greatly reduced (Figure 1). Alien annual graminoids did not quite differ significantly among treatments in this experiment ($F_{8,63} = 2.01$, *P* = 0.06), though there was

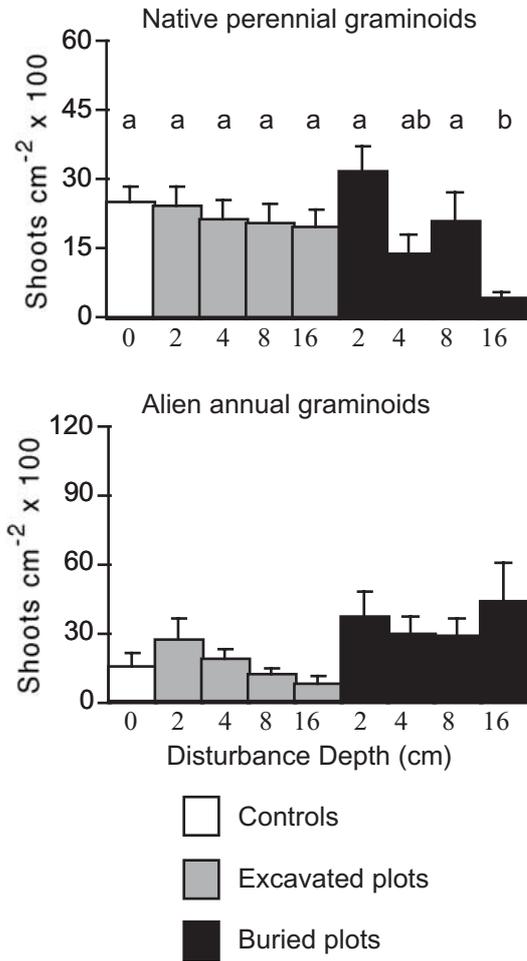


Figure 1. Results of the disturbance depth experiment. Data represent mean (+standard error) number of shoots per cm²; total sample size = 72 plots. Treatments are undisturbed controls and plots excavated or buried to 2, 4, 8, or 16 cm. For alien annuals, no significant differences were detected among treatments; for native perennials, treatments which do not differ significantly (Bonferroni/Dunn $P > 0.05$) are designated by the same letter.

a strong tendency for buried plots to support larger populations than other treatments (Figure 1). In contrast with these results, no differences were detected among treatments in the area experiment (alien annual graminoids: $F_{8,31} = 0.51$, $P = 0.84$; native perennial graminoids: $F_{8,31} = 0.92$, $P = 0.52$), though there was a tendency for larger disturbances to harbor denser populations of annuals (Figure 2). These analyses treat *Vulpia* as exotic, but patterns of significance were unchanged if this grass was instead treated as native. Alien perennial and native annual graminoids were too scarce to analyze statistically.

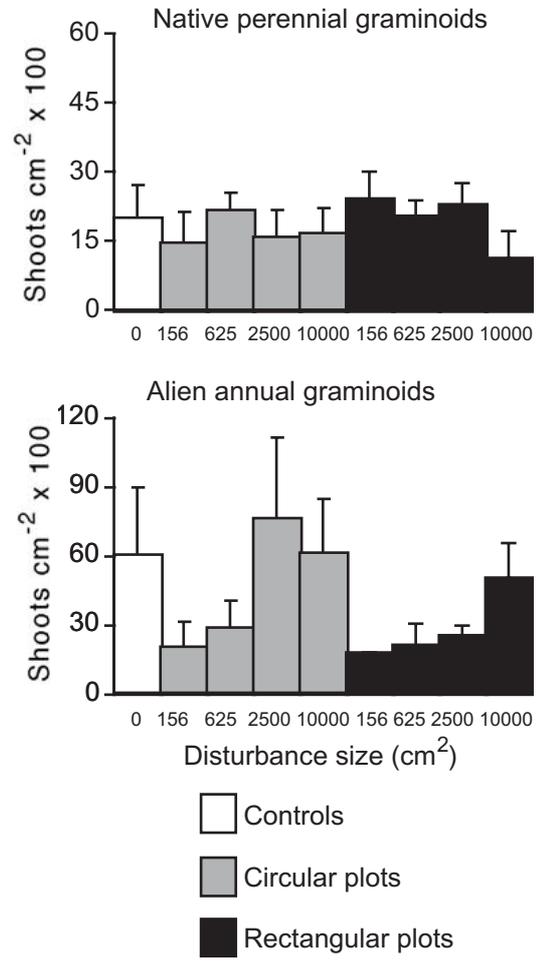


Figure 2. Results of the disturbance area experiment. Data represent mean (+standard error) number of shoots per cm²; total sample size = 40 plots. Treatments are undisturbed controls and circular or rectangular excavations with areas of 156, 625, 2500, and 10000 cm². No significant differences were detected among treatments.

Comparison with previous results (1991–1993)

Substantial changes had occurred in the vegetation of these plots since 1991–1993 (Figures 3 and 4; Table 1; Kotanen 1996, 1997a). Initially, both excavation and burial greatly reduced populations of native perennial graminoids (100% *D. californica* in the depth experiment, but with *L. comosa* gradually increasing to a 49% : 51% *Luzula*–*Danthonia* mix by 1993 in the area experiment). These plants were slow to recover, and by 1993 still were scarcer in most disturbances than in control plots (Figures 3 and 4). By this date, numbers of perennial graminoids tended to increase with

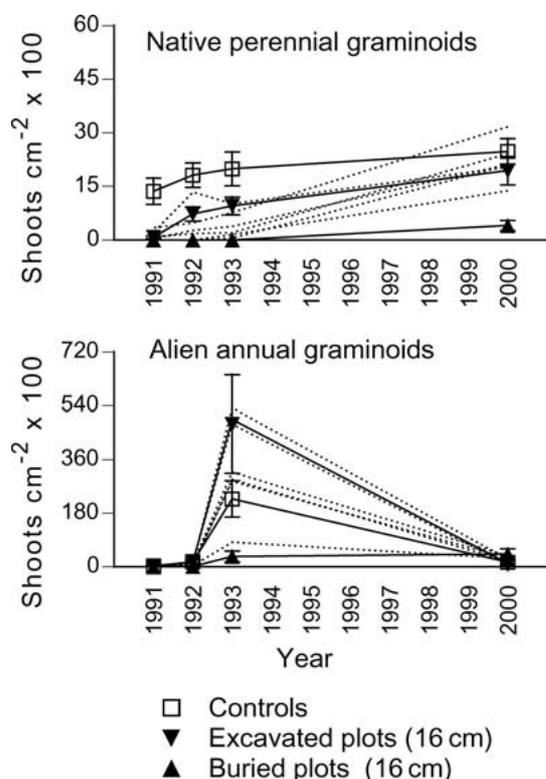


Figure 3. Long-term trends in the disturbance depth experiment. Data represent mean number of shoots per cm^2 . Treatments are undisturbed controls and plots excavated or buried to 2, 4, 8, or 16 cm. Sample trajectories (mean \pm standard error) are shown for controls and for the most extreme disturbance treatments (16 cm excavations and 16 cm burials); other treatments are indicated with dotted lines. Data for 1991–1993 are derived from Kotanen (1996); data were not collected between 1993 and 2000.

depth in excavated plots, but they still were absent from all but the shallowest burials (Kotanen 1996); these patterns of colonization probably reflect the trapping of dispersing seeds by excavations and the ability of buried plants to grow through sufficiently shallow layers of soil (Kotanen 1996). The only alien perennial detected in these experiments by 1993, *H. lanatus*, was very rare ($\ll 1\%$ of perennial graminoid shoots). Burial of experimental plots also initially reduced populations of annuals, particularly in the more deeply buried treatments (Kotanen 1996), and by 1993 the abundance of alien annual graminoids in buried plots remained comparable to or less than numbers in controls (Figures 3 and 4). In contrast, annuals rebounded very rapidly in excavations (Kotanen 1996, 1997a), and by 1993 alien annual graminoids dominated most excavation treatments (Figures 3 and 4). Much of this rapid increase was attributable to the

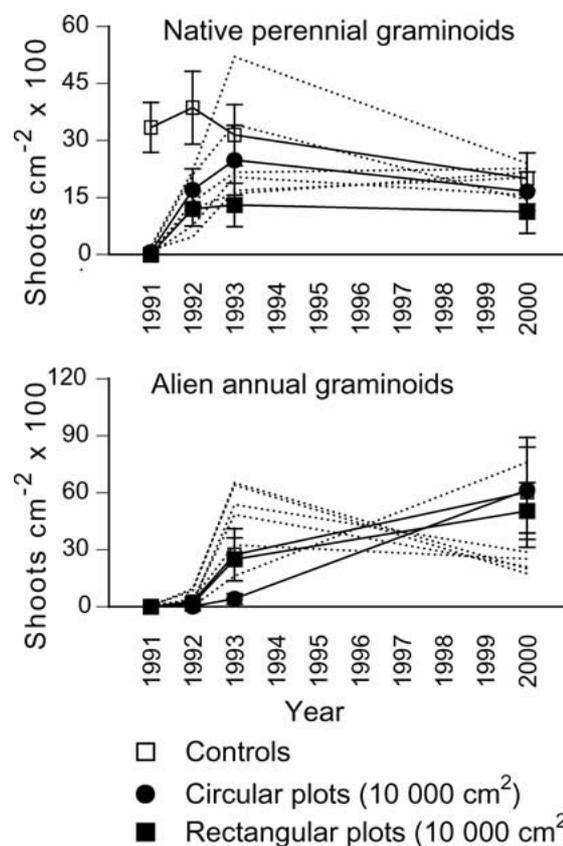


Figure 4. Long-term trends in the disturbance area experiment. Data represent mean number of shoots per cm^2 . Treatments are undisturbed controls and circular or rectangular excavations with areas of 156, 625, 2500, and 10000 cm^2 . Sample trajectories (mean \pm standard error) are shown for controls and for the most extreme disturbance treatments (10000 cm^2 circular plots and 10000 cm^2 square plots); other treatments are indicated with dotted lines. Data for 1991–1993 are derived from Kotanen (1997a); data were not collected between 1993 and 2000.

grass *A. caryophylla*, which became by far the most abundant alien annual graminoid in these experiments (Kotanen 1996, 1997a). *Aira* increased from a few stems per plot in 1991 to maxima in excess of 1000 stems per 100 cm^2 quadrat by 1993; populations of this grass increased even in control plots (Figure 5), probably in response to the severe drought California experienced from 1987 to 1992 (Kotanen 1996). Native annuals usually were scarce compared to alien annuals ($< 5\%$ of annual graminoid shoots). The commonest native annual graminoid, *J. bufonius*, increased from nearly undetectable levels in control plots to transiently becoming one of the most conspicuous early colonists in some excavation treatments, but this species generally remained scarce relative to

Table 1. Summary of the colonizing flora in each experiment. Numbers indicate mean (\pm standard error) number of shoots per 100 cm² for controls and disturbance treatments. Data for 1991–1993 are derived from Kotanen (1996, 1997a).

Experiment	Year	Treatments	Native perennial graminoids ^a	Alien perennial graminoids ^b	Native annual graminoids ^c	Alien annual graminoids ^d	Dicots
Depth	1991	Control ($n = 8$)	13.625 \pm 3.664	0.000 \pm 0.000	0.000 \pm 0.000	3.500 \pm 2.803	0.250 \pm 0.164
		Excavated ($n = 32$)	1.031 \pm 0.296	0.000 \pm 0.000	3.969 \pm 0.855	0.250 \pm 0.110	1.531 \pm 0.419
		Buried ($n = 32$)	0.844 \pm 0.586	0.000 \pm 0.000	0.000 \pm 0.000	0.000 \pm 0.000	0.562 \pm 0.190
	1992	Control ($n = 8$)	18.125 \pm 3.425	0.000 \pm 0.000	0.000 \pm 0.000	16.625 \pm 5.806	0.625 \pm 0.498
		Excavated ($n = 32$)	6.250 \pm 1.759	0.000 \pm 0.000	1.906 \pm 0.925	12.844 \pm 2.297	0.594 \pm 0.173
		Buried ($n = 32$)	1.188 \pm 0.787	0.000 \pm 0.000	0.062 \pm 0.043	6.250 \pm 1.327	1.219 \pm 0.310
	1993	Control ($n = 8$)	19.875 \pm 4.726	0.000 \pm 0.000	0.000 \pm 0.000	228.250 \pm 60.772	0.375 \pm 0.263
		Excavated ($n = 32$)	6.344 \pm 1.266	0.000 \pm 0.000	0.688 \pm 0.563	449.906 \pm 56.029	0.812 \pm 0.171
		Buried ($n = 32$)	2.406 \pm 1.038	0.000 \pm 0.000	0.031 \pm 0.031	180.625 \pm 31.331	1.281 \pm 0.400
2000	Control ($n = 8$)	24.750 \pm 3.589	0.000 \pm 0.000	0.000 \pm 0.000	15.500 \pm 5.281	5.500 \pm 2.087	
	Excavated ($n = 32$)	21.250 \pm 1.928	0.000 \pm 0.000	0.000 \pm 0.000	16.188 \pm 2.849	0.875 \pm 0.383	
	Buried ($n = 32$)	17.562 \pm 2.851	0.219 \pm 0.154	0.094 \pm 0.069	34.562 \pm 5.452	5.781 \pm 1.353	
Area	1991	Control ($n = 5$)	33.400 \pm 6.585	0.400 \pm 0.400	0.600 \pm 0.600	0.000 \pm 0.000	1.600 \pm 1.600
		Excavated ($n = 40$)	0.800 \pm 0.209	0.000 \pm 0.000	4.825 \pm 0.702	0.225 \pm 0.067	0.275 \pm 0.095
	1992	Control ($n = 5$)	38.600 \pm 9.563	0.000 \pm 0.000	0.400 \pm 0.400	2.600 \pm 0.927	1.600 \pm 0.927
		Excavated ($n = 40$)	13.750 \pm 1.541	0.000 \pm 0.000	14.900 \pm 2.155	3.600 \pm 0.779	2.300 \pm 0.715
	1993	Control ($n = 5$)	31.400 \pm 8.029	0.000 \pm 0.000	0.000 \pm 0.000	27.400 \pm 13.724	4.600 \pm 1.536
		Excavated ($n = 40$)	24.850 \pm 3.190	0.000 \pm 0.000	16.650 \pm 5.261	38.650 \pm 6.672	3.275 \pm 0.634
	2000	Control ($n = 5$)	20.000 \pm 6.723	0.200 \pm 0.200	0.000 \pm 0.000	60.200 \pm 28.918	3.800 \pm 2.200
		Excavated ($n = 35$)	18.000 \pm 1.783	0.686 \pm 0.312	0.114 \pm 0.114	40.257 \pm 7.080	3.486 \pm 0.805

^aDepth experiment: >99% *D. californica*, <1% other; Area experiment: 68% *D. californica*; 32% *L. comosa*.

^bBoth experiments: 100% *H. lanatus*.

^cBoth experiments: 100% *J. bufonius*.

^dDepth experiment: 92% *A. caryophyllea*, 8% other; Area experiment: 64% *A. caryophyllea*, 17% *B. minor*, 11% *B. hordeaceus*, 8% other.

Aira (Figure 5). There was a tendency for the abundance of both perennial and annual graminoids to decrease with increasing excavation size, but these trends were weak and generally non-significant, while plot shape had no significant consequences for either group (Kotanen 1997a).

Since 1993, continuing changes in the vegetation of experimental plots largely have erased the early differences among disturbance treatments. Densities of *Danthonia* in most treatments remained stable or increased, restoring numbers of native perennial graminoids in disturbed plots to the same range as the controls (Figures 3 and 4). In the depth experiment, the alien annual grasses which transiently dominated disturbed plots declined precipitously, restoring densities to much nearer the initial control values (Figure 3). Final values for both treatments and controls still remained higher than 1991 values, though the difference was small compared to 1993 densities (Figure 3). In contrast, alien annual grasses in the area experiment declined only slightly in most disturbance treatments, and increased in the largest disturbances (Figure 4). Alien annuals also increased in the control plots

(Figure 4), which may have been persistently invaded by colonists originating in the experimental disturbances. As a result, even though differences between controls and disturbance treatments disappeared by 2000, alien annual graminoids remained commoner in all treatments than in 1991 (Figure 4). Despite this poor recovery, densities of alien annual graminoids in this experiment consistently remained far below the high values observed in the depth experiment (Figures 3 and 4 – note the difference in scales); consequently, alien annuals in the area experiment never displaced native perennials.

Discussion

Did soil disturbance lead to persistent changes in dominance by native versus alien graminoids?

The early stages of recolonization of these experiments by grasses primarily depended upon the seed rain (Kotanen 1996). Surviving plants occurred in only the shallowest disturbance treatments (Kotanen 1996).

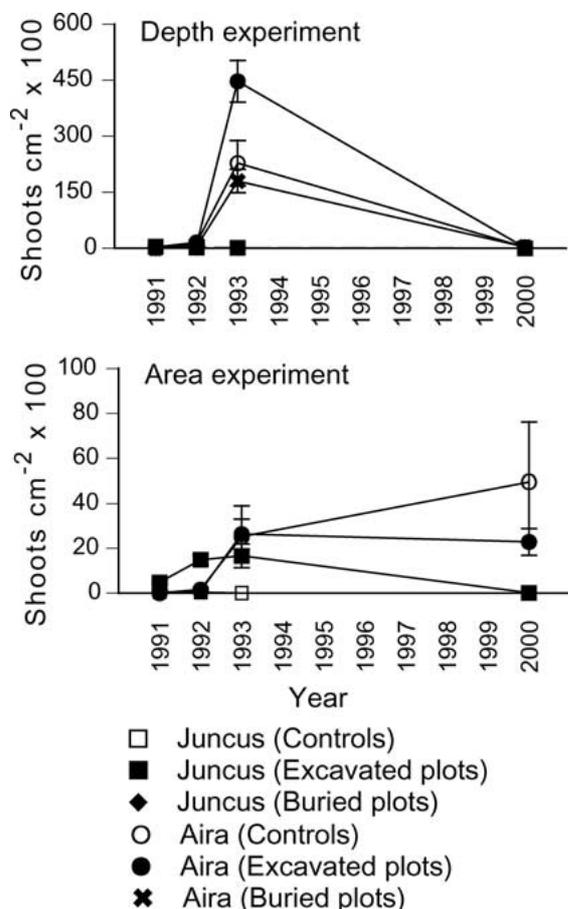


Figure 5. Changes in populations of the most abundant native (*J. bufonius*) and alien (*A. caryophyllea*) annual graminoids during these experiments. Data represent mean number of shoots per cm^2 (\pm standard error) in undisturbed control plots, excavations (all treatments pooled), and buried plots (all treatments pooled). Data for 1991–1993 are derived from Kotanen (1996, 1997a); data were not collected between 1993 and 2000. Single points along the x-axis may represent several treatments with similar values.

Vegetative ingrowth generally was ineffective, since most perennials at this site are bunchgrasses with very limited lateral expansion, and the annuals tiller rather than grow laterally (Kotanen 1997a). Finally, only a few non-grass species (such as *J. bufonius*) proved able to recolonize from persistent seed banks (Kotanen 1996, 1997a). The effects of disturbance consequently reflected the relative availability of dispersing seeds of different species; in particular, alien annual grasses soon overtook most other groups as a function of their overwhelming seed production (Kotanen 1996, 1997a). This effect may have been accentuated by the drought of 1987–1992, which probably favored

drought-tolerant annual grasses over native perennials in both disturbed and control plots (Kotanen 1996). Since all experimental plots experienced the same weather, drought alone cannot explain the differences observed among treatments or between treatments and controls; instead, disturbance apparently had the effect of amplifying climate-driven change (Kotanen 1996). As well, disturbed plots may have contributed invaders to the surrounding undisturbed grassland, but any effect was apparently transient (as for the depth experiment) or modest in size (as may be the case for the area experiment). It should be noted that Californian grasslands are well known for their interannual variability (Talbot et al. 1939; Heady 1958; Pitt and Heady 1978; Bartolome 1989; Hobbs and Mooney 1991); changes in control plots are to be expected in a long-term study.

I previously predicted that continuing immigration and the subsequent growth and reproduction of colonists would gradually reduce seed limitation, erasing both differences among disturbance treatments and differences between disturbances and the surrounding undisturbed vegetation (Kotanen 1997a). Ten years after disturbance, this appears to be the case, at least for the perennials: with a few exceptions, the native perennial graminoids (*Danthonia* and *Luzula*) which typically dominate undisturbed areas have established populations in disturbed plots which are comparable to controls, often at the expense of annuals. The principal exception is the deepest burial treatment; however, even these plots have substantially recovered relative to their condition in 1993.

These results also indicate that in spite of their initial success, exotic annual grasses failed to persistently replace native perennials within disturbed plots. In the depth experiment, despite reaching very high densities, the numbers of alien annuals in disturbed plots ultimately declined towards both control plots and their own original vegetation structure. In the area experiment, recovery was much less complete, but annuals never approached the dominance that was typical in the depth experiment. Thus, though disturbance did favor annual exotics (and some annual natives) in both experiments, the result was not a persistent annual-dominated grassland: either the dominance by annuals was transient, or the result was a mixed annual–perennial vegetation. In themselves, these are not surprising results: many studies of perennial grasslands and old fields have indicated that soil disturbance creates opportunities for the establishment of competitively-inferior fugitives or

weedy exotics, which gradually are replaced by more competitive perennials (e.g., Bazzaz 1968; Platt and Weis 1977; Armesto and Pickett 1985; Inouye et al. 1987; Tilman 1987; Huberty et al. 1998). The underlying processes leading to this replacement probably are shared in many grassland and old field systems. Nonetheless, Californian annual grasslands are not necessarily temporary successional stages, but can be a persistent feature of the landscape, and in many areas have stably replaced the pre-existing native vegetation (Heady 1988; Sims 1988; Heady et al. 1992); indeed, replacement of native vegetation by exotic annual grasses is a frequent trend worldwide (D'Antonio and Vitousek 1992). This is apparently not the case for the meadows in the present study, where alien-dominated annual vegetation was a temporary stage, if it occurred at all.

Conservatively, soil disturbances recurring at intervals longer than 10 years seem likely to allow recovery sufficient to permit the co-existence of native perennials with exotic annuals at this site, but more frequent disturbances may risk progressively changing vegetation structure. For example, less than 1% of the area of the meadows at this site is disturbed annually by moles and pocket gophers (Kotanen 1995), suggesting that these disturbances are unlikely to significantly alter the vegetation at this location. In contrast, I have estimated that grubbing by feral pigs annually disturbs 7% of the area of these meadows, reducing native perennial cover and creating habitat for both native and alien annuals (Kotanen 1995). Pigs probably grub some sites much more frequently (particularly seeps and damp areas) and avoid others, resulting in substantial variance around this mean estimate. Native perennials recently seem to be stable or increasing in most meadows at this location (pers. obs. 1990–2000), suggesting that average levels of pig damage currently lie below the limit required to shift vegetation toward a structure dominated by alien annuals; nonetheless, damage in favored sites may approach or exceed this threshold.

Are results from this site typical of long-term studies elsewhere in coastal California?

The recovery of my experimental plots contrasts with results in other coastal Californian habitats, where recent studies have indicated that soil disturbance in both grasslands and shrublands tends to replace native perennials with persistent communities dominated by

exotic annual grasses. For example, Zink et al. (1995) studied a pipeline corridor constructed through grassland, coastal sage, and chaparral in southern California. They found that more than 10 years after disturbance, this corridor was dominated by exotic annuals (largely grasses); in contrast, surrounding undisturbed communities retained a high proportion of native cover. Similarly, Stylinski and Allen (1999) reported that southern California chaparral and coastal sage scrub disturbed by construction, excavation, tillage, and other forms of mechanical soil perturbation remained dominated by exotic annual grasses and herbs as much as 71 years after disturbance, again in contrast with the apparently stable surrounding shrubland. They interpreted this result as evidence that soil disturbance converted native shrublands to an alternative stable state. Finally, Stromberg and Griffin (1996) studied abandoned agricultural fields in central California. They found that previously cultivated fields were stably dominated by annuals (mostly exotics) more than 60 years after the cessation of agriculture, while native perennial relict grasslands continued to persist in uncultivated areas.

In contrast with these studies, removing the pre-existing native perennial vegetation from my plots increased the prominence of exotic annual grasses, but failed to create a stable annual-dominated vegetation even though the annuals involved are among the most widespread, abundant, and aggressive of California's biological invaders (Sims 1988; Heady et al. 1992). A possible explanation is that the small spatial scale of even my largest disturbances may have permitted much faster revegetation than was possible in the much larger agricultural fields and construction areas of other studies (Zink et al. 1995; Stromberg and Griffin 1996; Stylinski and Allen 1999). It is suggestive that alien annual grasses continued to increase in the largest plots in my area experiment, even though they declined in smaller plots, including those in the depth experiment; perhaps 1 m² is approaching the size at which a stable population becomes possible. Against this is the observation that although most meadows at this location (including the White House meadow) were cultivated by homesteaders between the 1880s and the 1920s (Johnson 1989) and periodically are redisturbed by feral pigs (Kotanen 1995), they retain large populations of native perennial graminoids (Kotanen 1995). This suggests that a larger spatial scale of soil disturbance need not result in permanent displacement of perennial natives at this location. This resilience itself may reflect a long history of occasional large-scale disturbances at

this site; examples include fire and possibly grizzlies before settlement, giving way to pigs and agriculture thereafter (Johnson 1989; Kotanen 1995).

Another possibility may be that *Danthonia*-dominated north coastal grasslands are intrinsically more resilient against invasions by Mediterranean annuals than are drier habitats such as Central Valley grasslands (Heady 1988; Sims 1988; Heady et al. 1992), central coastal bunchgrass vegetation (Bartolome and Gemmill 1981; Knops et al. 1995; Stromberg and Griffin 1996), interior grasslands (Mack 1986, 1989; D'Antonio and Vitousek 1992), or southern shrublands (Zink et al. 1995; Eliason and Allen 1997; Stylinski and Allen 1999). In favor of this hypothesis is the observation that native perennials in north coastal Californian grasslands often seem able to replace or co-exist with annual invaders which elsewhere have stably outcompeted native grasses (Heady et al. 1988, 1992). The reason may be that exotic annuals tend to be more xerophytic than native perennials (Bartolome et al. 1980; Heady et al. 1992). As a result, they gain more of a relative advantage in drier inland and southern regions than in the relatively wet northern California coast. This explanation also is consistent with the differences observed between my area and depth experiments. Though both were situated in the same meadow, the area experiment was in a much wetter site close to a small seasonal creek; perhaps this is why alien annuals performed less well than in the drier site used for the depth experiment. In northern coastal areas, a worse threat than annual grasses may be exotic perennial grasses such as *H. lanatus*, which seems to be increasing at the Angelo Coast Range Reserve (pers. obs. 1990–2000). Peart (1989) found recruitment by this grass in coastal California was increased by small soil disturbances, including pocket gopher mounds.

Implications

My results indicate that soil disturbances at the scale and frequency of gopher or mole burrowing are unlikely to result in the dominance of exotic annual grasses in northern coastal Californian grasslands. Instead, invasion of these disturbances is transient, as has been reported elsewhere in northern California (Hobbs and Mooney 1985, 1991). Even large soil disturbances such as those created by feral pigs may not lead to the loss of native perennial vegetation, as long as redisturbance is not too frequent. These results also

suggest that the restoration of damaged north coastal grasslands may be less difficult than studies at other locations imply, at least if perennial exotics can be controlled. Though disturbance often may be expected to favor invasions (Hobbs and Huenneke 1992; Byers 2002), characteristics of the disturbance, the local plant communities, and the site affected may determine whether these invaders permanently displace native species, or simply enjoy modest or temporary increases in their abundance.

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