

Effects of experimental soil disturbance on revegetation by natives and exotics in coastal Californian meadows

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Summary

1. Disturbance is widely believed to facilitate invasions by exotic plants, but is also important for the persistence of many native species. Here, I report the results of a series of field experiments designed to investigate the effects of soil disturbance on natives and aliens in Californian grassland vegetation. I also compare the effects of different types of soil disturbance to establish whether some favour aliens to a greater degree than others.

2. In two experiments, conducted at different locations, three types of soil disturbance (excavation, burial and simulated gopher mounds) were created, and their revegetation was compared with changes in undisturbed control plots over the next three years. A third experiment was used to provide data on the effects of soil disturbance on soil temperature, moisture and KCl-extractable nitrogen.

3. Disturbance affected both soil temperature and chemistry. Buried plots contained the most KCl-extractable nitrogen, and were also the warmest. Effects on soil moisture were relatively small.

4. Initially, most disturbances greatly reduced the numerical abundance both of groups dominated by natives (perennial graminoids and bulbs) and of groups dominated by aliens (annual graminoids). Disturbance also reduced maximal (summer) species richness, but in some cases increased the fraction of richness contributed by natives.

5. In subsequent years, richness rebounded as natives and exotics re-invaded. Native bulbs and perennial graminoids were slow to recover; instead, most disturbances increasingly became numerically dominated by exotic annual grasses, accentuating the effects of a multi-year drought.

6. The differing effects of experimental disturbances on aliens and natives can best be explained by considering relationships between sources of propagules, life histories and geographical origins.

7. Some types of disturbance were less damaging to native-dominated groups than others, but most ultimately favoured exotics. Consequently, it may be difficult to develop management strategies that preserve the diversity of disturbance-dependent natives while still excluding weedy aliens.

Key-words: biological invasions, colonization, grasses, introductions.

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Introduction

Understanding the conditions which promote the invasion and persistence of non-native species has proven to be a difficult challenge (Crawley 1987; Pimm 1987; Lodge 1993). One of the few generalizations

which have emerged is the empirical rule that biological invasions are frequently facilitated by disturbance (e.g. Elton 1958; Groves & Burdon 1986; Mooney & Drake 1986; Crawley 1987; Drake *et al.* 1989; Pimm 1991; Hobbs & Huenneke 1992; Huston 1994; but see Simberloff 1989). This would seem to suggest an alternative to difficult and costly programmes intended to control naturalized invaders: rates of invasion might be minimized if disturbance rates were reduced by such methods as fire

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suppression, flood control or the reduction of grazing pressure. The problem with this alternative is that natural disturbance often plays an important role in structuring native-dominated ecosystems (Grubb 1977; White 1979; Sousa 1984; Pickett & White 1985; Hobbs & Huenneke 1992; Huston 1994). Intertidal boulder-fields (Sousa 1979), grasslands (Platt 1975; Collins & Glenn 1988), and temperate and tropical forests (Connell 1978; Platt & Strong 1989) are among the many ecosystems believed to owe much of their biodiversity to their disturbance regimes. Perhaps a solution to this dilemma might be to suppress only those disturbances that primarily benefit exotics – but do all disturbances have similar net effects in this regard, or do some types of disturbance tip the balance in favour of native species?

This paper is one of a series (Kotanan 1994a,b, 1995, 1996, 1997) in which I consider the effects of soil disturbance on the plant communities of a set of Californian meadows. As is true of most Californian grasslands (Heady 1988; Heady *et al.* 1988; Sims 1988; Heady *et al.* 1992), these meadows have been altered profoundly by the invasion of Eurasian annual grasses. Currently, their vegetation is a mixture of native and exotic species, making them ideal for investigations into factors affecting the relative success of these two groups. In the past, most studies of the effects of disturbance on invaders have been speculative or correlative, rather than experimental (e.g. Mooney & Drake 1986; Drake *et al.* 1989; Hobbs & Huenneke 1992; but see Burke & Grime 1996). In contrast, I report here the results of two experiments designed to address this issue, with special emphasis on two related questions.

1. Does soil disturbance encourage exotics at the expense of native species?
2. Are all soil disturbances equivalent, or do different types of disturbance have significantly different effects on revegetation?

I am particularly concerned with the graminoids (Gramineae, Cyperaceae, Juncaceae) that structure the vegetation of my study sites. As is typically the case for Californian grasslands, most of the locally occurring alien graminoids are annuals, while most natives are perennials, suggesting that natives and aliens may respond very differently to the same disturbances. Similar considerations should apply to many other systems in which native perennial vegetation is threatened by weedy annual invaders.

Site description

This study was conducted at the Northern California Coast Range Preserve* (NCCRP) of the University of California (123°37'W, 39°45'N, about 240 km north of San Francisco). The principal study sites were the White House Meadow and the South Meadow,

which are openings in *Pseudotsuga menziesii* (Douglas Fir) – *Sequoia sempervirens* (Redwood) forest that are believed to have existed before the arrival of the first homesteaders in the 1880s (Johnson 1979). Both meadows were subsequently grazed by livestock and/or cultivated, but intensive agriculture ended by the 1930s (Johnson 1979).

Originally, both meadows were probably occupied by perennial-dominated coastal prairie, rather than the valley grassland typical of more arid inland areas of California (Heady 1988; Heady *et al.* 1988; Sims 1988; Heady *et al.* 1992). Today, the White House meadow is dominated both visually and in terms of biomass by native perennial graminoids, primarily the bunchgrass *Danthonia californica*, but such alien annual grasses as *Aira caryophyllea*, *Bromus hordeaceus*, *Briza minor*, *Vulpia bromoides* and *Vulpia myuros* are numerically much more abundant. In contrast, the South Meadow retains native perennial vegetation near its edges, while the remainder of its area is dominated by alien annuals including the species listed above, *Bromus diandrus* and *Bromus tectorum*. Few locally occurring annual graminoids are natives (Appendix 1). Native perennial 'bulbs' are common in both meadows (technically most are corms, primarily of *Dichelostemma*, *Brodiaea* and *Triteleia* spp.) and numerous native and alien dicots also occur. Apart from a few dicots, most species flower by the beginning of the annual drought in June. Additional information on the vegetation of these meadows may be found in Kotanan (1994a, 1995) and Appendix 1.

Although native to the Old World, pigs *Sus scrofa* L. are common as feral animals throughout much of California (Barrett 1978; Wood & Barrett 1979; Mayer & Brisbin 1991; Barrett 1993), and may have occurred at the NCCRP for more than a century (Johnson 1979). Pigs dominate the local regime of soil disturbance: on average, between 1990 and 1993, pigs annually grubbed more than 7% of the area of five major meadows at the NCCRP, displacing soil and removing or burying vegetation on spatial scales ranging from a few cm² to many m² (Kotanan 1995). These meadows are also disturbed to a lesser extent (<1% year⁻¹) by a variety of native burrowing animals, primarily pocket gophers *Thomomys bottae* Eydoux & Gervais and moles *Scapanus latimanus* Bachman (Kotanan 1995). These animal-created soil disturbances were used as the rationale for the experiments described below.

Materials and methods

DISTURBANCE EXPERIMENTS

This paper principally reports the results of a pair of field experiments designed to test the same hypotheses at two different locations (the White House and South Meadows). In each, 72 plots were established in a c. 10 × 10 m grid, separated from one another by

Table 1. Dates on which the principal disturbance experiments were sampled. The White House Meadow (WHM) experiment was established on 22–23 December 1990; the South Meadow (SM) experiment was established on 13–14 January 1991

Year	Groups sampled	WHM experiment	SM experiment
1991	Bulbs	6–7 April	19–21 April
	Graminoids & dicots	3–5 July	23–25 July
1992	Bulbs	13–14 March	28 March–2 April
	Graminoids & dicots	15–22 July	23–28 July
1993	Bulbs	21 March–3 April	9–10 April
	Graminoids & dicots	8–9 July	9–10 July

c. 50 cm of undisturbed ground. Plots were square, measuring 25 × 25 cm; these dimensions were representative of the grain of disturbance within a pig-damaged area. Both experiments were established during the winter of 1990–91 (Table 1), in phase with the annual peak of pig and gopher disturbance (Kotanen 1995).

In each experiment, 18 plots were assigned randomly to each of four treatments: excavation, burial, simulated gopher mounds and controls. In the first two treatments, plots were excavated to a depth of 9 cm and the excavated earth was used to bury a further 18 plots, in rough imitation of the excavation and burial of vegetation that pigs create while grubbing (Kotanen 1994b, 1995). The depth chosen was within the range measured for nearby pig-created excavations (min = 3 cm, max = 13 cm, mean = 7.0 cm, $n = 86$). The remaining plots were either left undisturbed as controls or were buried to a depth of several cm with earth collected from nearby gopher and (occasionally) mole tailings, imitating the appearance of gopher mounds. Quantitative characteristics of similar experimental disturbances, including their timing, intensity and areal extent, have been addressed elsewhere (Kotanen 1994a, 1996, 1997); briefly, they may delay succession, but rarely influence its general direction.

At each sampling, shoots were counted in a square 10 cm × 10 cm quadrat centred in each plot, leaving an 7.5 cm unsampled buffer zone within each plot's perimeter (clonal encroachment is generally unimportant to revegetation at this location: Kotanen 1994a, 1996, 1997). This procedure acknowledges the modular nature of plant construction (Harper 1977), approximates revegetation in the sense of space occupancy, and avoids the problem of identifying individuals in a complex sward. Shoots were counted only if living and/or reproductive at the time of sampling, and only if rooted within the sampling quadrat. Results have been reported as shoots per cm².

Each experiment was sampled twice annually for 3 years (Table 1). Graminoids and dicots were counted in July, after most species had flowered but while their shoots were still in place. Bulbs were sampled in March or April; because of their flimsy leaves and

spring ephemeral phenology, few of their shoots were still identifiable by the principal summer sampling. This scheme may have missed a few scarce spring ephemerals (mostly dicots), but most other annuals (including the graminoids) remained conspicuous and identifiable in experimental plots until late in the summer. Sampling was extremely labour-intensive, and consequently the sampling of the two experiments was staggered rather than simultaneous.

For analyses of community composition, species were combined into four 'functional' or 'propagule' groups (e.g. McIntyre, Lavorel & Tremont 1995) on the basis of life history and morphology: annual graminoids (AG), perennial graminoids (PG), bulbs and dicots. The proportion of graminoid shoots contributed by annuals, $AG/(AG + PG)$, was calculated for each plot for which $(AG + PG) > 0$. These groups were used because they simplify analysis while capturing important characteristics of Californian grasslands, particularly the degree to which the system as a whole may be considered an annual grassland. Species richness and the fraction of species contributed by aliens were also determined at the July samplings; this reflects the annual maximum in species richness, but underestimates the occurrence of bulbs.

Since variances differed very strongly and irregularly among experimental treatments, multiple comparisons robust to inhomogeneous variances were used throughout. For each variable at each sampling, experimental treatments were compared in a pairwise fashion using a family of Welch's *t*-test for unequal variances with Satterthwaite's adjusted degrees of freedom, corrected for the number of comparisons per family by the Dunn–Sidak method (Sokal & Rohlf 1981; Day & Quinn 1989). Proportions were subjected to an angular transformation prior to analysis (Sokal & Rohlf 1981). Data from the two experiments were analysed separately because of differences in sites and timing.

PHYSICAL DATA

To allow the destructive collection of data on some of the physical effects of disturbance without disrupting the principal experiments, a separate set of soil dis-

turbances was created in December 1991, about 100 m from the primary White House Meadow experiment. Twelve plots were excavated and 12 buried, with 12 undisturbed controls, in a manner identical to the construction of the primary experiments; simulated gopher mounds were omitted for reasons of economy. The temperature of the top 1 cm of soil was measured on six sunny afternoons between May 1992 and April 1993, using a Barnant 115 Thermocouple Thermometer (The Barnant Company, Barrington, Illinois, USA). As well, on four occasions (December, February, April and June), one 100-mm deep × 18-mm diameter soil core was removed from each control plot and every other disturbed plot. Moist core samples were returned to the laboratory, where 20–30 g of soil from each sample was weighed, shaken with 75 mL of 2N KCl for 45 min, and filtered. The filtrate was analysed for NO₃ (including NO₂) and NH₄ with a Lachat autoanalyser, using standard colorimetric techniques (Keeney & Nelson 1982). The remainder of each core was weighed before and after drying for 24 h at 60°C, so that soil water content could be determined gravimetrically. These methods provide information on the amount of water and KCl-extractable inorganic nitrogen present in the soil during the initial stages of revegetation, but do not necessarily reflect the availability of nitrogen or rates of mineralization (Binkley & Hart 1989; Binkley & Vitousek 1991).

Results

THE LOCAL VEGETATION

The above-ground vegetation of most experimental plots (Appendix 1) was dominated in spring by bulbs (4 spp., primarily *Dichelostemma capitatum*), and in summer by graminoids (12 spp.); dicots (*c.* 26 spp.) were comparatively very scarce (Figs 1 & 2). Overall, annuals were not disproportionately likely to be exotics (Table 2; $P = 0.18$: Fisher's Exact Test). However, all annual graminoids other than *Juncus bufonius* and *Vulpia microstachys* were aliens, while the only perennial graminoid detected at the principal samplings

Table 2. Numbers of species occurring in the principal disturbance experiments, classified according to life history and geographical origin. Data are derived from Appendix 1. *Lotus* spp., *Madia* spp., *Nemophila* spp. and *Trifolium* spp. each have been assumed to include a single native species, while *Galium* has been assumed to include one native and one alien species; this underestimates the true number of native annuals

Group	Introduced	Native	Total
Annual	13	15	28
Biennial or perennial	3	11	14
Total	16	26	42

(*Danthonia californica*) was a native. Graminoids structure the vegetation of these meadows; although bulbs were often as abundant, their contribution to above-ground vegetation was very ephemeral. Consequently, changes in numbers of graminoids are of special importance.

REVEGETATION OF THE DISTURBANCE EXPERIMENTS

Functional group approaches can be misleading, since they demand the pooling of numerous species. In this study, however, the use of such groups allowed the detection of very similar responses in both of the principal experiments despite differences in their vegetation, location, timing of sampling and rates of re-disturbance by burrowing mammals. As might be expected, the groups dominated by a few similar species (perennial graminoids, bulbs) performed more consistently than more heterogeneous groups (annual graminoids, dicots). Atypically behaving annual graminoids are discussed below; dicots were too scarce to allow the identification of species-specific responses.

In both experiments, summer species richness and the abundance of most functional groups were initially reduced by most types of disturbance (Figs 1–3; Tables 3 & 4). The recovery of different groups varied markedly (Figs 1 & 2). Bulbs and perennial graminoids tended to recover slowly, if at all, remaining less common in most disturbances than in controls (the absence of significant differences among treatments for bulbs in the South Meadow in 1993 is probably an artefact of reduced statistical power – because of poor weather, only half the usual number of plots was sampled on this date). Dicots responded erratically, fluctuating in numbers and differing in behaviour between the two experiments. Annual graminoids also behaved dynamically, rapidly increasing in all treatments, and often equalling or exceeding the densities observed in control plots.

Multiple comparisons indicated that different disturbances had significantly different effects (Figs 1–4). For example, species richness was slower to recover in buried and gopher mound plots than in excavations (Fig. 3). Bulbs suffered worst in excavated and buried plots, but performed well in gopher mound plots, where their numbers often approached or equalled those observed in controls (Figs 1 & 2). In contrast, perennial graminoids fared poorly in all disturbance treatments, but were often more numerous in excavations than in burials (Figs 1 & 2). Patterns were more complex for dicots. In the South Meadow, dicots tended to do worst in buried and gopher tailing plots, while in the White House Meadow these trends were different or even (in 1992) reversed (Figs 1 & 2). Initially, annual graminoids also differed in behaviour between the two meadows: in 1991, numbers in excavated plots in the White House Meadow were significantly greater than numbers in controls, while in

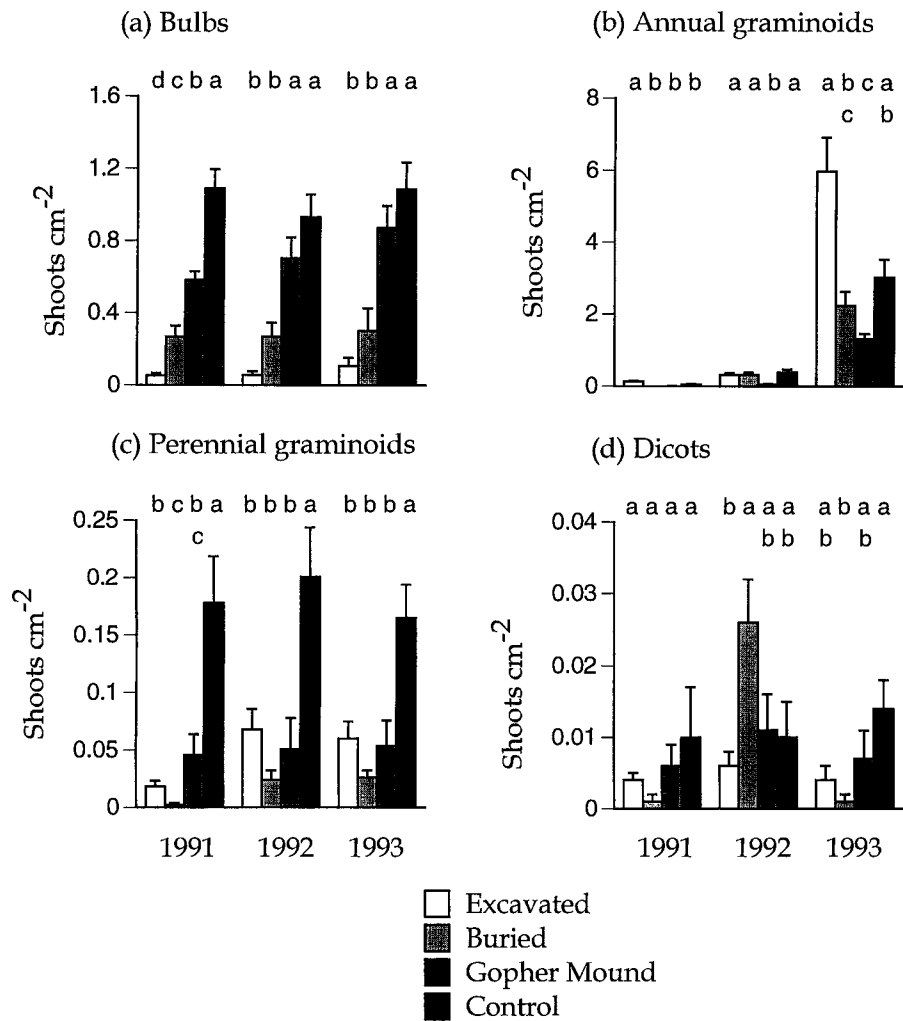


Fig. 1. Results of the White House Meadow experiment. Data represent mean (+SEM) numbers of shoots cm^{-2} produced by bulbs, annual graminoids, perennial graminoids and dicots. Sample size = 17 or 18 in all cases. Bulbs were sampled 3–4 months earlier than the other groups (Table 1) because of their spring ephemeral phenology. In each year, treatments not differing significantly from one another ($P > 0.05$) are designated with the same letter (multiple comparison tests; see Methods).

the South Meadow, annual graminoids were significantly reduced by all disturbance treatments (Figs 1 & 2). In subsequent years, however, annual graminoids increased in all treatments of both experiments, until by 1993, their abundance in both locations exhibited similar rankings (excavations > controls, burials > gopher mounds) and patterns of significance (excavations > other disturbance treatments and \geq controls).

The fraction of summer species richness contributed by aliens initially differed among treatments at both sites. In 1991, the flora of excavations contained a smaller proportion of aliens than did controls in both meadows (Fig. 3); as well, gopher mounds in the White House Meadow and burials in the South Meadow also contained a smaller proportion of aliens than their respective controls. These changes reflected both the loss of aliens (annual graminoids and dicots) and increases in natives (dicots, *Juncus bufonius* and *Vulpia microstachys*) (Tables 3 & 4). Most of these between-treatment differences rapidly disappeared as the

experimental disturbances were re-colonized (Tables 3 & 4); no differences were detected by 1993 (Fig. 3).

Considering relative abundances rather than richness paints a somewhat different picture. As mentioned above, alien-dominated annual grasses rapidly colonized most disturbances, while native-dominated perennial bulbs and grasses enjoyed much smaller increases; as a result, the proportion of graminoids contributed by annuals generally ranked lowest in controls (Fig. 4). Some disturbances did benefit the few native annual graminoids occurring at this location. For example, in the White House Meadow, much of the initial success of annuals in excavated plots (Figs 1 & 4) was attributable to the prompt appearance of the native rush *Juncus bufonius* (Table 5). However, the importance of this species declined from 93% of annual graminoids in excavations to <1% as alien grasses (particularly *Aira*) increased in numbers (Table 5); consequently, changes in disturbed plots led to increasingly alien-dominated graminoid vegetation as time progressed (Fig. 4). In the South

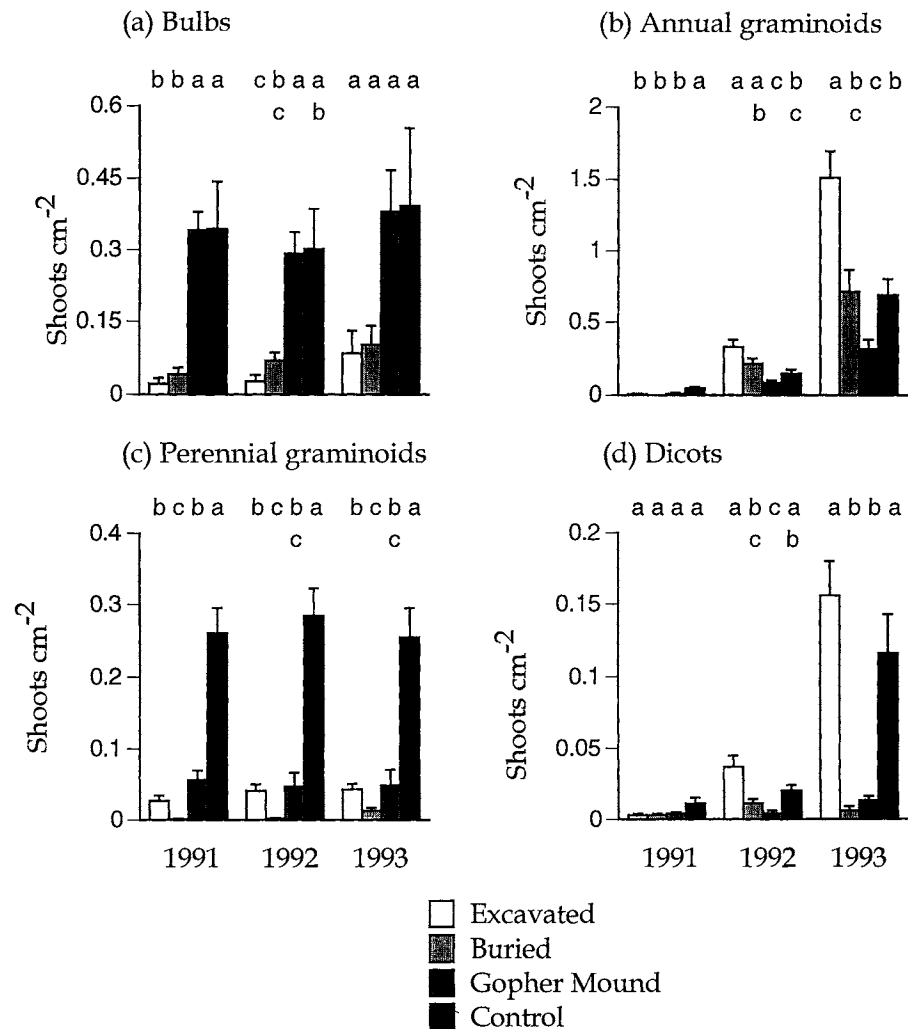


Fig. 2. Results of the South Meadow experiment. Data represent mean (+SEM) numbers of shoots cm^{-2} produced by bulbs, annual graminoids, perennial graminoids and dicots. Sample size = 18, except for bulbs in 1993, when poor weather restricted sampling to 8–10 plots per treatment. Other details are as in Fig. 1.

Meadow, *Juncus* was scarce, explaining the slower response of annual graminoids to excavation. However, many of the invading annuals were *Vulpia* spp., including the native *Vulpia microstachys* (Table 6). By the final sampling date, *Vulpia* contributed 67% of the annual graminoids observed in disturbed plots. Since *Vulpia* spp. are very difficult to distinguish in the field, this complicates efforts to estimate the proportion of annuals made up by aliens. However, even if all *Vulpia* spp. were assumed to be natives, disturbance would still have been responsible for reducing the relative importance of native perennials (Fig. 4).

Although moles and pocket gophers locally disturb $\ll 1\%$ of the ground surface per year (Kotanen 1995), 24 of the 72 White House Meadow plots (33%) were affected to some extent by these animals. In contrast, only one plot was disturbed in the South Meadow; the difference between experiments probably resulted from their chance positioning relative to active tunnel systems. In contrast with other studies (e.g. Hobbs & Mooney 1985, 1991), Kotanen (1996) found the

average effects of re-disturbance to be rather mild. This appears to be the case in these experiments as well: even though the South Meadow experiment suffered much less gopher damage than the White House Meadow experiment, both converged on very similar results (Figs 1–4).

PHYSICAL CHARACTERISTICS OF DISTURBED PLOTS

Soil temperatures differed strongly among treatments (Fig. 5). Controls were coolest, while buried plots were warmest; differences in mean temperatures ranged from 3 to 6°C in winter to as much as 20°C in summer, when soil temperatures commonly exceeded 50°C (maximum = 58°C) in buried plots.

Buried plots consistently contained more NH_4 than controls (Fig. 6). This result may reflect both increased rates of net mineralization (possibly reflecting the higher soil temperatures as well as disturbance *per se*), and decreased uptake by the reduced plant cover (Christensen 1985; Vitousek 1985). In contrast, exca-

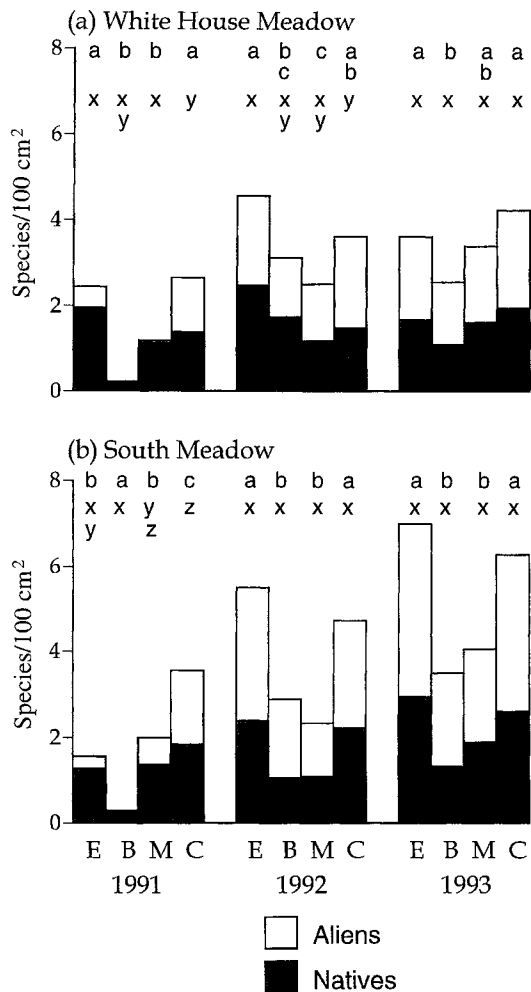


Fig. 3. Mean number of natives and aliens observed at the July sampling of each of the principal experiments (*Vulpia* and *Galium* were equally subdivided between these categories; see Appendix 1). The treatments are excavation (E), burial (B), gopher mound (M) and undisturbed controls (C). The letters above each treatment summarize two sets of multiple comparison tests (see Methods), one testing species richness (a,b,c) and one testing differences in the proportion of alien species (x,y,z). In each year, treatments sharing the same letter do not differ significantly ($P > 0.05$).

variations were relatively poor in NH_4 , probably because organic-rich surface layers had been removed. NO_3 varied inconsistently among treatments from one sampling to the next, but was scarce relative to NH_4 ; consequently, the overall abundance of KCl-extractable N mirrored the distribution of NH_4 . Differences in soil moisture among treatments were small and variable.

Discussion

EFFECTS OF DISTURBANCE

Many vegetation types are structured by recurring disturbances such as fires, storms and by the activities of burrowing animals (Sousa 1984; Pickett & White 1985; Platt & Strong 1989; Hobbs & Huenneke 1992).

The effects of such disturbances can be complex; as this study demonstrates, different disturbances can have distinctly different effects on the physical and chemical environment and the course of revegetation. Nonetheless, most experimental disturbances did have one thing in common: they produced increases in the numerical abundance of (primarily alien) annual graminoids at the expense of (native) perennial grasses and bulbs. Considering components of species richness instead of abundances, however, suggests a rather different answer: disturbance often produced a short-lived enhancement in the relative importance of natives. These perspectives are complementary, rather than contradictory, but the discrepancy between them suggests that such 'easy' monitoring techniques as the gathering of presence-absence data may be useful when the goal is to manage species richness *per se*, but misleading when the goal is to manage vegetation or habitat structure (Kotanen 1995).

Although excavation and burial had different effects on KCl-extractable N, the sharp reduction in plant cover associated with both types of disturbance suggests that, on a per-plant basis, increased amounts of N, water and physical space were available to the first colonists of all types of newly disturbed sites. Consequently, it is not surprising that most disturbances favoured annual graminoids, whose rapid growth allowed the exploitation of exposed soil before the arrival of potentially lethal mid-summer temperatures. Many other studies have also found that soil disturbance in old-fields and grasslands can create opportunities for the establishment of competitively inferior fugitives or weedy exotics (e.g. Platt 1975; Platt & Weis 1977; Hobbs & Mooney 1985; Martinsen, Cushman & Whitham 1990; Belsky 1992; Lavorel *et al.* 1994; McIntyre & Lavorel 1994; Kotanen 1995; McIntyre *et al.* 1995; Burke & Grime 1996). In contrast, the less dynamic response of perennial grasses and bulbs might be expected from their longer demographic turnover times (Connell & Sousa 1983). Soil disturbance represented an opportunity for alien annuals, but a lasting setback for native perennials, which showed very little recovery by the end of these experiments: it is clear that their recovery must require significantly longer than 3 years. Since disturbance by gophers and pigs is frequent at this location, much of the area of these meadows must be in a state of revegetation at any given time (Kotanen 1995).

DISTURBANCE AND PROPAGULE SUPPLY

The supply of propagules at a disturbed site can set limits on its revegetation (Kotanen 1994a, 1996, 1997): a favourable habitat is an opportunity lost unless propagules are available. For example, propagules of few local species occur deeply in the soil: >80% of the active seed bank is located <2 cm from the soil surface (Kotanen 1996). As a result, experimental disturbances usually removed the seed bank or smo-

Table 3. Results of the White House Meadow experiment. Data represent the mean number of species occurring per plot at the July sampling (Fig. 3), partitioned into the average number of species contributed by bulbs, annual graminoids, perennial graminoids and dicots; n = number of plots sampled. Because this sampling took place in summer, the occurrence of bulbs is underestimated

Year	Treatment	n	Bulbs	Annual graminoids		Perennial graminoids	Dicots		Total
				Alien	Native		Alien	Native	
1991	Excavated	18	0	0.500	1.000	0.667	0	0.278	2.444
	Buried	18	0	0.056	0	0.111	0	0.056	0.222
	Gopher mound	17	0.176	0.058	0.118	0.471	0	0.353	1.176
	Control	17	0.176	1.265	0.147	0.882	0	0.176	2.647
1992	Excavated	18	0	2.084	1.194	0.944	0	0.333	4.556
	Buried	18	0	1.389	0.333	0.556	0	0.833	3.111
	Gopher mound	18	0.111	1.333	0.167	0.556	0	0.333	2.500
	Control	18	0	2.137	0.139	1.000	0	0.333	3.611
1993	Excavated	18	0	1.833	0.556	1.000	0.111	0.111	3.611
	Buried	18	0.167	1.472	0.139	0.722	0	0.056	2.556
	Gopher mound	18	0.389	1.777	0.056	0.778	0	0.389	3.389
	Control	18	0.333	2.111	0	1.000	0.167	0.611	4.222

Table 4. Results of the South Meadow experiment. Data represent the mean number of species occurring per plot at the July sampling (Fig. 3). Other details are as in Table 3

Year	Treatment	n	Bulbs	Annual graminoids		Perennial graminoids	Dicots		Total
				Alien	Native		Alien	Native	
1991	Excavated	18	0.056	0.277	0.167	0.722	0	0.333	1.556
	Buried	18	0	0	0	0.056	0	0.222	0.278
	Gopher mound	18	0	0.528	0.250	0.833	0.111	0.278	2.000
	Control	18	0	1.500	0.389	1.000	0.222	0.445	3.556
1992	Excavated	18	0	2.777	0.556	0.889	0.333	0.945	5.500
	Buried	18	0	1.723	0.444	0.167	0.111	0.445	2.889
	Gopher mound	18	0	1.194	0.473	0.389	0.056	0.222	2.333
	Control	18	0	2.167	0.444	1.000	0.333	0.778	4.722
1993	Excavated	18	0	3.555	0.667	0.944	0.500	1.333	7.000
	Buried	18	0	2.056	0.500	0.556	0.111	0.278	3.500
	Gopher mound	18	0	2.028	0.528	0.667	0.139	0.694	4.056
	Control	18	0	3.167	0.500	1.000	0.500	1.111	6.278

thered it with seed-poor subsurface soil, initially reducing species richness. Thereafter, richness increased rapidly as a consequence of the abundant seed rain (4–8 seeds cm^{-2} year $^{-1}$; Kotanen 1996). This seed rain is strongly dominated (>85%) by alien annual grasses; 70–90% of seeds are produced by *Aira caryophylla* alone (Kotanen 1996). Consequently, the abundance of exotic grasses (and exotics in general) increased in step with richness. *Juncus bufonius* provides an informative exception to this picture. Despite its great rarity in undisturbed vegetation, this species is one of the very few at this location with a deeply distributed, abundant and persistent seed bank: it contributes 6% of the detectable seeds in the top 2 cm of soil, but 79% of seeds between 8 and 10 cm (Kotanen 1996). As a result, its seeds survived even in newly excavated plots, which they then were able to rapidly

colonize. *Juncus bufonius* appears to be an example of a fugitive in time: it disperses temporally, surviving in the seed bank until soil disturbance occurs.

Hobbs & Huenneke (1992) suggest that disturbance may often play a dual role, helping maintain disturbance-dependent natives while simultaneously facilitating invasions by exotics. This seems to be the case in this system: disturbance generally suppressed the dominant native perennials, but benefitted both alien annuals such as *Aira* and scarce native annuals including *Juncus bufonius* and a variety of dicots (Kotanen 1995). From a management perspective, this result seems discouraging: largely because of their prolific seed production, aliens prospered on the same disturbances occupied by native annuals, and soon came to dominate them numerically. Different disturbances had different effects on natives (especially

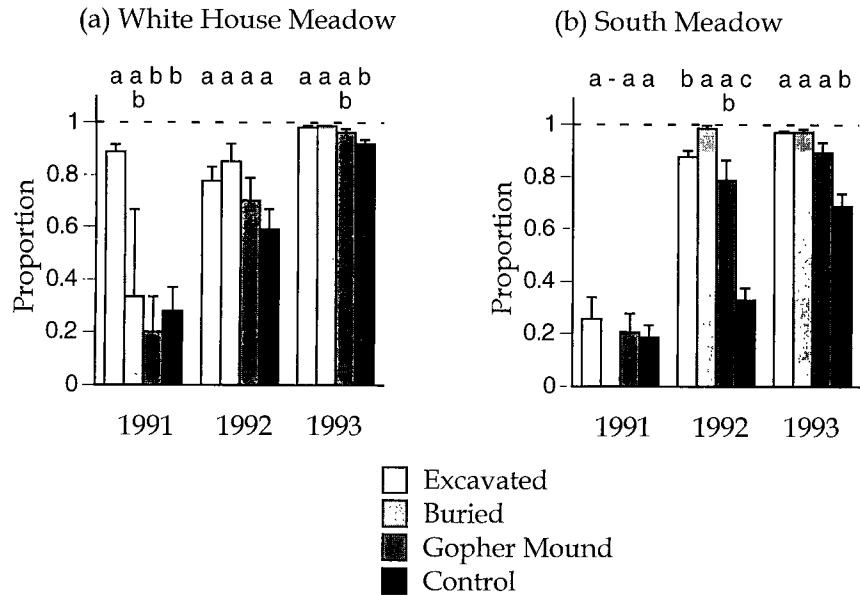


Fig. 4. The mean (+SEM) proportion of graminoid shoots produced by annuals in each of the principal experiments. Since undefined (0/0) values have been excluded, n increases from an average of 12 plots per treatment in 1991 to 17–18 plots per treatment in 1992 and 1993. Buried plots were the most likely to be excluded; in 1991, $n_{\text{buried}} = 3$ in the White House Meadow, while sample size in the South Meadow ($n_{\text{buried}} = 1$) was too small to allow the inclusion of this treatment in multiple comparison tests. With this exception, treatments not differing significantly from one another in each year ($P > 0.05$) are designated with the same letter.

Table 5. Results of the White House Meadow experiment. Mean (SEM) number of shoots of graminoids cm^{-2} , subdivided by species; n = number of plots sampled

Year/Treatment	n	<i>Danthonia californica</i>	<i>Juncus bufonius</i>	<i>Aira caryophylla</i>	<i>Bromus mollis</i>	<i>Vulpia</i> spp.	<i>Briza minor</i>
1991							
Excavation	18	0.018(0.005)	0.128(0.019)	0.007(0.004)	0	0	0.002(0.001)
Burial	18	0.002(0.002)	0	0	0.001(0.001)	0	0
Gopher mound	17	0.046(0.018)	0.006(0.004)	0	0.001(0.001)	0	0
Control	17	0.178(0.041)	0.004(0.003)	0.008(0.003)	0.034(0.017)	0.001(0.001)	0.002(0.001)
1992							
Excavation	18	0.068(0.018)	0.136(0.030)	0.151(0.034)	0.021(0.006)	0.006(0.002)	0.011(0.007)
Burial	18	0.024(0.008)	0.005(0.003)	0.252(0.068)	0.031(0.012)	0.028(0.020)	0
Gopher mound	18	0.051(0.027)	0.001(0.001)	0.044(0.010)	0.004(0.001)	0.005(0.004)	0.002(0.001)
Control	18	0.201(0.043)	0.001(0.001)	0.350(0.080)	0.034(0.011)	0.004(0.002)	0.003(0.001)
1993							
Excavation	18	0.060(0.015)	0.021(0.006)	5.916(0.947)	0.012(0.003)	0	0.027(0.013)
Burial	18	0.026(0.006)	0.001(0.001)	2.220(0.396)	0.004(0.002)	0.003(0.002)	0.001(0.001)
Gopher mound	18	0.054(0.022)	0.001(0.001)	1.283(0.153)	0.005(0.001)	0	0.013(0.007)
Control	18	0.165(0.029)	0	2.992(0.508)	0.008(0.002)	0	0.028(0.011)

perennials), and some were more favourable to alien grasses than others (e.g. excavations), but none was effective in preventing occupancy by exotics. These results suggest that aliens may rapidly overwhelm many management practices designed to benefit disturbance-dependent natives. Strategies designed to reduce the seed production of fecund exotics (e.g. fire, grazing; Menke 1992) may be necessary components of programmes that use disturbance as a tool for management or restoration.

REASONS FOR DIFFERENCES AMONG DISTURBANCES

The principal differences among experimental disturbances can be explained most simply by considering the effects of disturbance on the availability of propagules. For example, few bulbs or perennial graminoids grow deeply enough to escape being removed by an experimental excavation (Kotanen 1994a, 1996); consequently, these groups were scarce in most excavated plots. Bulbs were more abundant

Table 6. Results of the South Meadow experiment. Mean (SEM) number of shoots of graminoids cm⁻², subdivided by species; n = number of plots sampled

Year	Treatment	n	<i>Danthonia californica</i>	<i>Juncus bufonius</i>	<i>Aira caryophyllaea</i>	<i>Bromus mollis</i>	<i>Bromus diandrus</i>	<i>Bromus tectorum</i>	<i>Vulpia</i> spp.	<i>Briza minor</i>	<i>Gastridium ventricosum</i>
1991	Excavation	18	0.027(0.007)	0.001(0.001)	0.001(0.001)	0	0	0	0.001(0.001)	0.003(0.002)	0
	Burial	18	0.001(0.001)	0	0	0	0	0	0	0	0
	Gopher mound	18	0.056(0.014)	0.003(0.002)	0	0.001(0.001)	0.003(0.001)	0	0.002(0.001)	0.001(0.001)	0.001(0.001)
	Control	18	0.260(0.035)	0.001(0.001)	0.006(0.003)	0.007(0.003)	0.007(0.003)	0	0.023(0.007)	0.002(0.001)	0
1992	Excavation	18	0.041(0.009)	0.001(0.001)	0.068(0.020)	0.009(0.003)	0.003(0.002)	0	0.214(0.034)	0.036(0.014)	0
	Burial	18	0.002(0.001)	0	0.046(0.029)	0.005(0.003)	0	0.152(0.034)	0.004(0.002)	0.004(0.002)	0
	Gopher mound	18	0.047(0.020)	0.001(0.001)	0.009(0.004)	0.004(0.002)	0.001(0.001)	0	0.066(0.015)	0.001(0.001)	0
	Control	18	0.284(0.039)	0	0.022(0.007)	0.028(0.009)	0.003(0.001)	0	0.089(0.020)	0.006(0.003)	0
1993	Excavation	18	0.043(0.008)	0.006(0.004)	0.437(0.136)	0.033(0.008)	0.003(0.001)	0	0.793(0.112)	0.242(0.049)	0
	Burial	18	0.013(0.004)	0	0.023(0.007)	0.010(0.004)	0.001(0.001)	0	0.673(0.150)	0.008(0.003)	0
	Gopher mound	18	0.048(0.023)	0.001(0.001)	0.048(0.016)	0.007(0.002)	0.001(0.001)	0.009(0.009)	0.240(0.060)	0.007(0.003)	0
	Control	18	0.255(0.040)	0	0.151(0.038)	0.054(0.017)	0.006(0.002)	0	0.432(0.089)	0.048(0.016)	0

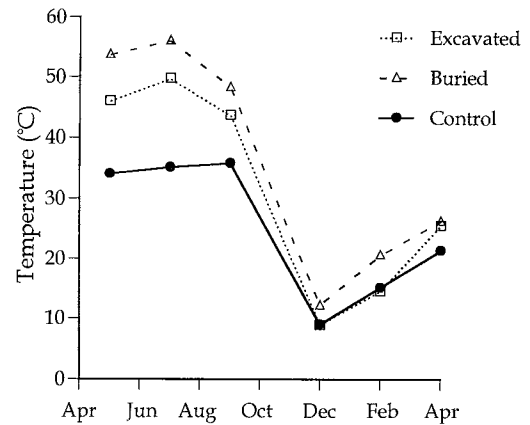


Fig. 5. Temperature (°C) of the top 1 cm of soil in experimental disturbance treatments (burial, excavation and undisturbed controls). Standard errors are too small to be shown at this scale. On each date, n = 12 plots per treatment.

in gopher/mole tailing plots (which they could grow through), and more abundant still in buried plots (in which many survived in the overturned soil), but perennial graminoids, which lack deeply buried perennating organs, were usually smothered or killed by these disturbances. Similarly, excavations developed especially high average densities of annual graminoids, probably both because they acted as pitfall traps for dispersing seeds and because they provided sheltered refuges from heat and drought. In contrast, buried plots never fully recovered their species richness, probably both because of their extreme temperatures and because seeds were easily removed from their surfaces by wind or rainfall. For slowly regenerating perennial groups, differences among treatments were persistent; for annuals, they were rapidly eliminated or reversed as seeds rained in from the surrounding vegetation.

Physical differences among treatments may also have contributed to patterns of revegetation, though their influence is less obvious than that of propagule supply. For example, burial produced a pulse of increased inorganic N, while excavation did not. In both cases, this probably translated to increased per-capita amounts of inorganic N, but these two types of increased nutrient availability (resource pulse vs. per-capita increase only) have the potential to affect different species in different ways (e.g. Miao & Bazzaz 1990; Miao, Bazzaz & Primack 1991). In particular, a pulse of increased resources may favour rapidly growing, disturbance-loving opportunists (e.g. annual grasses) more than a per-capita increase alone, leading initially to increased growth, seed production and re-seeding of disturbed plots. In contrast, slower-growing perennials may be less responsive to pulses of increased nutrients. This may be one reason that, after one year of recolonization, the (AG/AG + PG) ratio tended to be highest in buried plots.

TRENDS IN UNDISTURBED PLOTS

Californian grasslands vary strongly in composition from one year to the next, primarily in response to

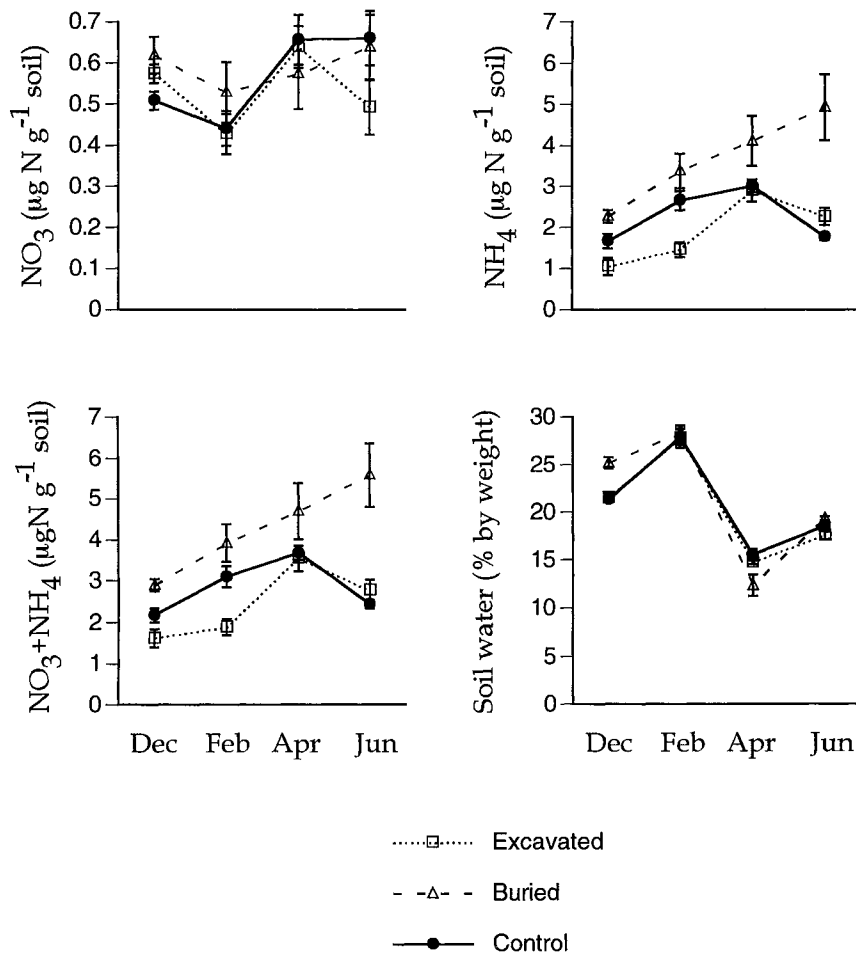


Fig. 6. Mean (+SEM) concentrations of KCl-extractable inorganic N and water in experimental disturbance treatments (excavation, burial and undisturbed controls). Nitrate (NO₃), ammonium (NH₄) and total extractable N (NO₃ + NH₄) are expressed as μg N g⁻¹ dry soil; soil water is expressed as percentage of soil fresh weight. On each date, n = 6 excavated plots, 6 buried plots, and 12 control plots.

weather (Talbot, Biswell & Hormay 1939; Heady 1956, 1958; Pitt & Heady 1978; Bartolome 1989; Hobbs & Mooney 1991). These changes are complex, but in general, dry, unproductive years should favour annual grasses relative to perennials, since the annuals tend to be more xerophytic (Bartolome, Stroud & Heady 1980; Heady *et al.* 1992), and at least in the case of *Aira*, litter-intolerant (Heady 1956; J. Bartolome, personal communication). The experiments described in the present paper were conducted near the end of a 6-year drought, which produced large increases in the numbers of prolific annual grasses (notably *Aira*) in undisturbed vegetation. Since all experimental plots experienced the same weather, drought alone cannot explain the differences among experimental treatments. Instead, one important effect of disturbance may be to accelerate climatically driven changes (Davis 1989); as an example, Hobbs & Mooney (1991) found that the vegetation of gopher mounds was more sensitive to rainfall variation than was undisturbed annual grassland. Still, the changes observed in controls were much larger than between-treatment differences. From the perspective of management, this

again is a discouraging result, since it suggests that the importance of aliens in Californian grasslands may often depend more strongly upon climate than upon managed disturbance regimes.

SPECIES COMPOSITION AND COMMUNITY HISTORY

Since many of the effects of disturbance can be explained by considering the life histories and dispersal strategies of the functional groups involved, this study should be relevant to other systems in which native perennials are threatened by invasive annuals, as is the case in many temperate grasslands (Mack 1989; D'Antonio & Vitousek 1992). A corollary is that whether disturbance benefits aliens more than natives may depend on the correlation between life history and geographical origin within the local species pool (Kotani 1995). If the important perennials in this system had been aliens while most of the annuals had been natives, disturbance might have reduced, rather than increased, dominance by exotics. Similarly, if

different species often respond differently to disturbance, then the effects of disturbance might be expected to vary from one assemblage to the next. Assemblages dominated by groups of species capable of rapidly invading disturbed areas (e.g. *Aira*) are likely to be resilient (*sensu* Pimm 1984), while assemblages dominated by less opportunistic species (e.g. *Danthonia*) are likely to suffer more lasting effects (Sousa 1980; Denslow 1985). A system's resilience should be influenced in turn by its history of disturbance (Denslow 1980, 1985; Hobbs & Huenneke 1992; McIntyre & Lavorel 1994). Species that respond slowly to disturbance are likely to be lost from frequently disturbed systems, especially if they lack seed banks or other means of long-term persistence. Instead, these systems may contain species that benefit from disturbance (e.g. *Aira*) or even require disturbance for persistence (e.g. *Juncus bufonius*) (Denslow 1980).

This site may have been buffered against experimental disturbance by a long history of grubbing by feral pigs. Feral pigs may have been present at the NCCRP for more than a century (Johnson 1979), while at current rates of grubbing, the half-life of an ungrubbed point would be only about 10 years (assuming grubbing was randomly distributed) (Kotani 1994a). Many studies have shown that pigs can strongly alter plant assemblages (e.g. Bratton 1974, 1975; Kotani 1994b, 1995). At the NCCRP, grubbing by pigs produces effects similar to those of experimental disturbance: in the short term, the relative contribution of natives to species richness increases, but in the long term, pigs probably create habitat for alien grasses at the expense of native perennials (Kotani 1994b, 1995). It seems reasonable to suspect that pigs may have played an important role in structuring the modern plant communities of these meadows. Repeated pig disturbance may long since have extirpated sensitive species, while increasing populations of weedy natives and aliens (particularly *Aira caryophyllea*). If so, this may now be a 'perturbation-resistant' assemblage, in which the effects of soil disturbance are small compared to areas of California where pigs are a more recent introduction. In other words, this location may be haunted by the Ghost of Pigs Past.

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Appendix 1

Vascular plant species which occurred (+) in each of the disturbance experiments. Also indicated are the life history and presumed geographical origin of each species. Nomenclature follows Hickman (1993); data are derived from the same source or by personal observation.

Species	Life history	Presumed origin	White House Meadow	South Meadow
(a) Graminoids				
<i>Aira caryophyllea</i>	Annual	Introduced	+	+
<i>Briza minor</i>	Annual	Introduced	+	+
<i>Bromus hordaceus</i>	Annual	Introduced	+	+
<i>Bromus diandrus</i>	Annual	Introduced		+
<i>Bromus tectorum</i>	Annual	Introduced		+
<i>Danthonia californica</i>	Perennial	Native	+	+
<i>Gastridium ventricosum</i>	Annual	Introduced		+
<i>Juncus bufonius</i>	Annual	Native	+	+
<i>Luzula comosa</i>	Perennial	Native		+
<i>Vulpia</i> spp.*	Annual	Various	+	+
(b) Herbs				
<i>Aphanes occidentalis</i>	Annual	Native		+
<i>Cerastium glomeratum</i>	Annual	Introduced	+	+
<i>Clarkia purpurea</i>	Annual	Native		+
<i>Dichelostemma capitatum</i> †	Perennial	Native	+	+
<i>Eremocarpus setigerus</i>	Annual	Native	+	+
<i>Erodium cicutarium</i>	Annual	Introduced		+
<i>Eschscholzia californica</i>	Perennial	Native	+	+
<i>Galium</i> spp.††	Annual	Various	+	+
<i>Githopsis specularoides</i>	Annual	Native	+	
<i>Hesperivax sparsiflora</i>	Annual	Native	+	
<i>Hypericum perforatum</i>	Perennial	Introduced	+	
<i>Hypochaeris glabra</i>	Annual	Introduced		+
<i>Lotus humistratus</i>	Annual	Native	+	
<i>Lotus</i> spp.	Annual	Native	+	+
<i>Lupinus bicolor</i>	Annual	Native	+	+
<i>Madia</i> spp.	Annual	Native		+
<i>Nemophila</i> spp.	Annual	Native		+
<i>Plantago lanceolata</i>	Perennial	Introduced		+
<i>Ranunculus uncinatus</i>	Perennial	Native		+
<i>Rumex acetosella</i>	Perennial	Introduced	+	+
<i>Sanicula bipinnatifida</i>	Perennial	Native		+
<i>Trichostema lanceolatum</i>	Annual	Native	+	+
<i>Trifolium dubium</i>	Annual	Introduced		+
<i>Trifolium</i> spp.	Annual	Native		+
(c) Woody plants				
<i>Acer macrophyllum</i> †††	Perennial	Native	+	

* Includes two alien and one native spp.

† Rarely includes one *Brodiaea* sp. and two *Triteleia* spp.

†† Includes at least one alien and one native species.

††† Seedling – died within a few months.