

Peter M. Kotanen

**Revegetation following soil disturbance in a California meadow:
the role of propagule supply**

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Abstract Revegetation following a disturbance event initially should be constrained by the abundance and types of propagules available at the disturbed site. I tested this idea by conducting two experiments in which I created artificial soil disturbances by excavating or burying pre-existing grassland vegetation. In the first experiment, I varied disturbance intensity (depth), to investigate the consequences for revegetation when numbers of surviving propagules (dormant seeds and bulbs) were altered. In the second experiment, I varied the timing of disturbance, to investigate the consequences when disturbed sites experienced differing exposures to seasonal patterns of clonal growth and seed dispersal. I sampled these experiments from 1991 to 1993, and have interpreted their results using measurements of the seed bank, the bulb bank, and the seed rain. In the first (depth) experiment, bulbs declined in abundance with burial depth and were scarcer in deeper excavations. In contrast, numbers of annual graminoids initially showed no trends with respect to disturbance depth. These results reflect the depth distributions of the seed and bulb banks. Since bulbs occur deeply in the soil, progressively deeper disturbances left fewer survivors. Similarly, perennial graminoids could grow through the shallowest burials. In contrast, since the annual-graminoid-dominated seed bank is concentrated near the soil surface, disturbance depth mattered less to these species: any disturbance removing the surface layer was equally destructive. In the second (timing) experiment, more annual graminoids initially occurred in older plots. This result reflects seasonal patterns of seed production: plots exposed to more of the

annual-graminoid-dominated seed rain supported higher densities of annual graminoids as a result. In subsequent years, the vegetation of most plots in both experiments was increasingly dominated by annual graminoids, again as a consequence of their great abundance in the seed rain. These results indicate that interactions between soil disturbances and sources of propagules play an important role in controlling early stages of succession in newly created gaps. They also suggest that disturbance may play different roles in communities characterized by species with different reproductive strategies. Understanding sources of colonists will improve our ability to predict the effects of disturbance.

Key words Disturbance · Grasslands · Seed bank · Seed rain · Succession

Introduction

Natural disturbance plays an important role in structuring many biological communities. Gaps created by such disturbances as fires, storms, and the activities of burrowing animals can alter species' abundances, modify the physical environment, and create opportunities for regeneration, with strong consequences for community composition and biological diversity (White 1979; Sousa 1984; Pickett and White 1985; Hobbs and Huenneke 1992; Huston 1994). Such gaps may be recolonized from two demographic sources: survivors and immigrants to the disturbed site. For higher plants, the developmental state of these colonists also may vary: colonists may be seeds or vegetatively-produced ramets. Together, demographic source and developmental state define four pools of propagules: surviving ramets, the seed bank, encroaching ramets, and dispersing seeds. Theory predicts that at least the early stages of revegetation should be influenced by the ways in which disturbance interacts with these pools (Connell and Slatyer 1977; Denslow 1985). For example, since few ramets or buried seeds may survive a severe disturbance, revegetation should largely de-

P.M. Kotanen¹
Department of Integrative Biology,
University of California,
Berkeley, CA 94720, USA

Present address:

¹ Department of Botany,
Erindale College, University of Toronto,
3359 Mississauga Road N., Mississauga,
DN L5L 1C6, Canada
e-mail: pkotanen@credit.crin.utoronto.ca

pend upon immigrants, and succession should be protracted (Connell and Slatyer 1977; Thompson 1992). In contrast, a milder disturbance may allow the survival of both ramets and seeds. To the extent that these survivors represent the pre-disturbance vegetation, recovery should be rapid and direct (Connell and Slatyer 1977; Thompson 1992).

Small disturbance-created gaps in grasslands and old-fields have proven a particularly tractable model for studies concerned with the importance of propagule supply. Some of these studies have emphasized the role played by dispersing seeds (Platt 1975; Platt and Weis 1977; Gross and Werner 1982; Hobbs and Mooney 1985; Peart 1989a, b; Bergelson et al. 1993; Bullock et al. 1994, 1995); others have emphasized the importance of clonal encroachment (Rabinowitz and Rapp 1985; Rapp and Rabinowitz 1985; Goldberg and Gross 1988; Coffin and Lauenroth 1989; Arnthórsdóttir 1994; Bullock et al. 1995) or the seed bank (Gross 1980; Gross and Werner 1982; Marks and Mohler 1985; Lavorel et al. 1994). This paper addresses the roles played in revegetation by all three locally important propagule pools: the seed bank, the seed rain, and surviving ramets; I also discuss the limited role played by clonal encroachment. My principal question is whether the manner in which a disturbance interacts with these supplies of potential colonists affects revegetation.

While some researchers have investigated the role of propagule supply in revegetation by directly manipulating specific pools of propagules (e.g., by removing seeds and/or rhizomes: Marks and Mohler 1985; Rapp and Rabinowitz 1985), I adopted an alternative, indirect approach. Two experiments were conducted in which I created soil disturbances of various types, designed to interact in different ways with different propagule pools. In the first experiment, the depth of disturbance was varied. Since seeds, bulbs, and other ramets tend to be concentrated near the soil surface (Harper 1977; Fenner 1985, 1992; Leck et al. 1989), these pools of propagules were expected to be scarcer in deeper disturbances, allowing me to ask how revegetation was affected as they became less available. In the second experiment, the timing of disturbance was varied. Since clonal growth and seed production are highly seasonal in California grasslands (Bartolome 1989; Chiariello 1989; Young and Evans 1989), the importance of these sources of propagules was expected to differ among disturbances created at different times, allowing me to describe how variation in these pools influenced revegetation. In combination with measurements of the seed rain and the seed and bulb banks, the results of these two experiments demonstrate the role that propagules play in the early stages of succession in newly created gaps.

Materials and methods

Study site

This study was conducted in the White House Meadow of the University of California's Northern California Coast Range (Angelo) Preserve (NCCRP) (123° 37' W, 39° 45' N). This meadow is one of a series of natural openings in a *Pseudotsuga menziesii* (Douglas fir) - *Sequoia sempervirens* (redwood) forest. Currently, it is dominated both visually and in terms of biomass by a native perennial grass, *Danthonia californica*, but as is true of many California grasslands (Heady 1988; Heady et al. 1988, 1992), this site has been greatly altered by the invasion of Eurasian annual grasses including *Aira caryophyllea*, *Bromus hordeaceus*, and *Briza minor*; *Juncus bufonius* (Juncaceae) and some *Vulpia* spp. (Gramineae) are the only native annual graminoids (grasses, rushes, or sedges). Native perennial Liliaceae and Amaryllidaceae (hereafter "bulbs") are abundant, while numerous herbaceous dicots (forbs) infrequently occur. Animal-created soil disturbance plays a major role in structuring the vegetation of these meadows (Kotanan 1994b, 1995). Between 1990 and 1993, more than 7% of the area of five major meadows at the NCCRP annually was disturbed by animals including feral pigs, *Sus scrofa*, pocket gophers, *Thomomys bottae*, and moles, *Scapanus latimanus* (Kotanan 1994b, 1995). Additional information on this site may be found in Johnson (1979) and Kotanan (1994a, b, 1995). Nomenclature follows Hickman (1993).

Disturbance experiments

Design

Two field experiments were established approximately 50 m apart in very similar vegetation. In each, square 25 cm × 25 cm plots, spaced 50 cm apart in a grid pattern, were created. These dimensions are roughly equivalent to the gap created by the death of a single bunchgrass, or to the disturbances created by gophers, moles, and (sometimes) feral pigs (Kotanan 1995).

I designed the first (depth) experiment to investigate the effects of the intensity (Sousa 1984) of disturbance. I created 72 plots in January 1991, during the annual peak of animal-created soil disturbance (Kotanan 1995), and divided them randomly into nine sets of eight plots. I left one of these sets undisturbed as controls. Each of the remaining eight sets I either excavated to a depth of 2, 4, 8, or 16 cm, or buried to a depth of 2, 4, 8, or 16 cm. The earth used to bury plots came from the excavations; soil (including propagules) from all depths of excavation was mixed together before being used. The depths used ranged from little more than litter removal to deeper than the main rooting zone.

I designed the second (timing) experiment to examine the effects of the timing of disturbance. In May, June, September, and December 1991, I excavated ten randomly chosen plots to a depth of 9 cm, and buried ten random plots to a similar depth beneath the excavated earth, as described above. A total of ten randomly-chosen plots were left undisturbed as controls. I did not completely sample this experiment until 1992, since all of 1991 was required for its establishment.

Sampling

For 3 years, I counted the living and/or reproductive shoots rooted within a square 10 cm × 10 cm quadrat centred in each plot. This procedure biased against the detection of clonal encroachment, but since all plots were the same size and shape, this bias should have been similar for all treatments. Counting shoots acknowledges the modular nature of plant construction and avoids the need for destructive sampling, but does not necessarily reflect biomass or numbers of genetic individuals. For example, the dry mass of a shoot of *Danthonia* ≈ 12× that of a shoot of *Aira*, and a clone of *Danthonia* may contain hundreds of shoots compared with < 10 for *Aira*.

Table 1 Dates on which the disturbance experiments were established and sampled

Year	Event	Depth experiment	Timing experiment
1991	Establishment	15–26 January	16 March–15 December
	Sampling (bulbs)	27–28 April	—
	Sampling (other groups)	22–24 August	17–19 June
1992	Sampling (bulbs)	17–19 April	1–10 May
	Sampling (other groups)	19–21 August	7–8 July
1993	Sampling (bulbs)	1–9 May	12–21 March
	Sampling (other groups)	21–24 August	20–23 June

I counted graminoids and dicots between mid-June and mid-August (Table 1), after practically all species had finished their annual growth and flowered, but while their shoots were still in place. Though I may have overlooked a few scarce spring ephemerals (mostly dicots), most other species remained easily identifiable at this time. However, it was necessary to sample bulbs between mid-March and early May; because of their spring ephemeral phenology, few of their shoots were identifiable by the principal summer sampling. Sampling dates differed from one year to the next, but in both experiments I always preserved this pre- and post-flowering sampling scheme. My sampling of the two experiments was staggered rather than simultaneous; consequently, I have treated each experiment as separate and independent.

Analysis

For most of the analyses presented in this paper, I combined species into four "propagule groups" united by life history, morphology, and dispersal mode (see McIntyre et al. 1995 for a similar approach). The groups I used were: (1) annual graminoids, (2) perennial graminoids, (3) bulbs, and (4) dicots. The use of these groups simplified analysis while reflecting characteristics important to California grasslands, particularly the degree to which a disturbance is annual-dominated vs. dominated by native perennials.

Repeated-measures ANOVAs produced very similar results to those reported here, but I did not adopt them for two reasons. First, repeated-measures tests revealed large treatment \times time interactions, indicating that results differed from one year to the next, and therefore suggesting that analyses should be done by sampling date (Kirk 1982). Second, it proved much more difficult to meet homogeneity of variance requirements (Cochran's *C* test: Kirk 1982) when combining several years' data (or several propagule groups) into a single analysis. To solve these problems, after a significant overall *F*-test I separately analyzed each year's data using Fisher's LSD multiple comparisons, adjusted for *a posteriori* use by the Dunn-Sidak method (Day and Quinn 1989). Since qualitatively different types of treatments (e.g., burial vs. excavation vs. controls) often had extremely different sample variances, I avoided comparisons of different types of disturbance to help in meeting homogeneity assumptions; elsewhere, I will discuss other experiments specifically designed to allow such comparisons. Instead, I divided each experiment into two independent families of comparisons (Kirk 1982), each including similar disturbances (excavations or burials) which differed only with respect to depth or timing; controls are presented primarily to provide "baseline" data. Square root transformations were best at controlling heterogeneity of variance and were used throughout, homogenizing variances for 34 of the 40 families of tests performed ($P > 0.01$; Cochran's *C* test). I have separately discussed the remaining tests in the RESULTS if a method robust to inhomogeneity of variance (Welch's *t*-tests for unequal variances implemented as *a posteriori* tests: Day and Quinn 1989) produced significantly different results.

Sampling of propagule pools

Dispersing seeds

I constructed seed traps by placing disks of filter paper coated with the adhesive Tangle-trap (The Tanglefoot Company, Grand

Rapids, Michigan, USA) in the lower halves of 5 cm \times 1 cm petri dishes, and covering each trap with 1-cm wire mesh to discourage rodents and birds. In April 1991, I permanently anchored ten such traps to the ground surface at random locations within each experiment. Every month for 20 months, I placed fresh filter paper in each trap. After approximately 2 weeks, I removed this paper and counted trapped seeds. Hobbs and Mooney (1985) found that seed losses from similar traps were negligible.

Soil seed and bulb banks

I sampled the seed and bulb banks at 2- to 3-month intervals over 21 months, using a 3.7 cm diameter soil corer. This diameter was ample even for the sampling of bulbs, since most bulbs were small (~5 mm), and since a partial or damaged bulb was counted only if its apex occurred in the sample. At each sampling, I collected cores from 5 random locations within each experiment, and then divided them into 2 cm thick slices. The depths I sampled were 0–2 cm (including seeds from the soil surface), 2–4 cm, 4–6 cm, and 8–10 cm. I removed roots and bulbs from each slice, which I then broke up and placed on a bed of sterile sand in a 5-cm pot. I incubated these pots with abundant water in a growth chamber with a day-night cycle of 14 h : 10 h and a daily temperature cycle averaging 25°C : 10°C. I counted emergent seedlings after 2 months; examinations during waterings indicated very few seedlings (< 1%) died before this final date.

I designed these methods to provide a standardized index of those seeds competent for rapid germination (Gross 1990), and therefore capable of immediately exploiting a new soil disturbance. Although different species can differ dramatically in their germination requirements (Harper 1977; Fenner 1985, 1992; Baskin and Baskin 1989), there are three reasons that these methods should provide a reasonable estimate of this readily germinable component of the seed bank, as of the date of sampling. First, the temperature regime fell within the limits expected in spring and fall (Johnson 1979), when most germination normally occurs in the field, while the light cycle corresponded to the beginning of May. Second, since the core samples were field-collected, the seeds they contained were pre-exposed to the germination stimuli (e.g., scarification, freezing) which had naturally occurred in the field by the collection date. Third, laboratory trials indicated that most of the species which dominate this system germinate readily, given sufficient moisture.

Results

Responses of vegetation to experimental disturbance

The recolonizing flora

In both disturbance experiments, the vegetation of most plots was dominated by bulbs in spring and by annual and perennial graminoids in summer (Figs. 1, 2). *Danthonia californica* was the only perennial graminoid detected in each experiment, but several species of annual graminoids were observed (Table 2). All bulbs probably were *Di-*

Fig. 1 Results of the disturbance depth experiment. Data represent mean (+SEM) number of shoots cm⁻²; n = 8 plots per treatment (E2-16 excavated to 2,4,8, or 16 cm; B2-16 buried to approximately these same depths; C undisturbed "controls"). Excavation or burial treatments which do not differ significantly from one another (P > 0.05; adjusted LSD test) are designated by the same letter (a-c for excavations; x-z for burials)

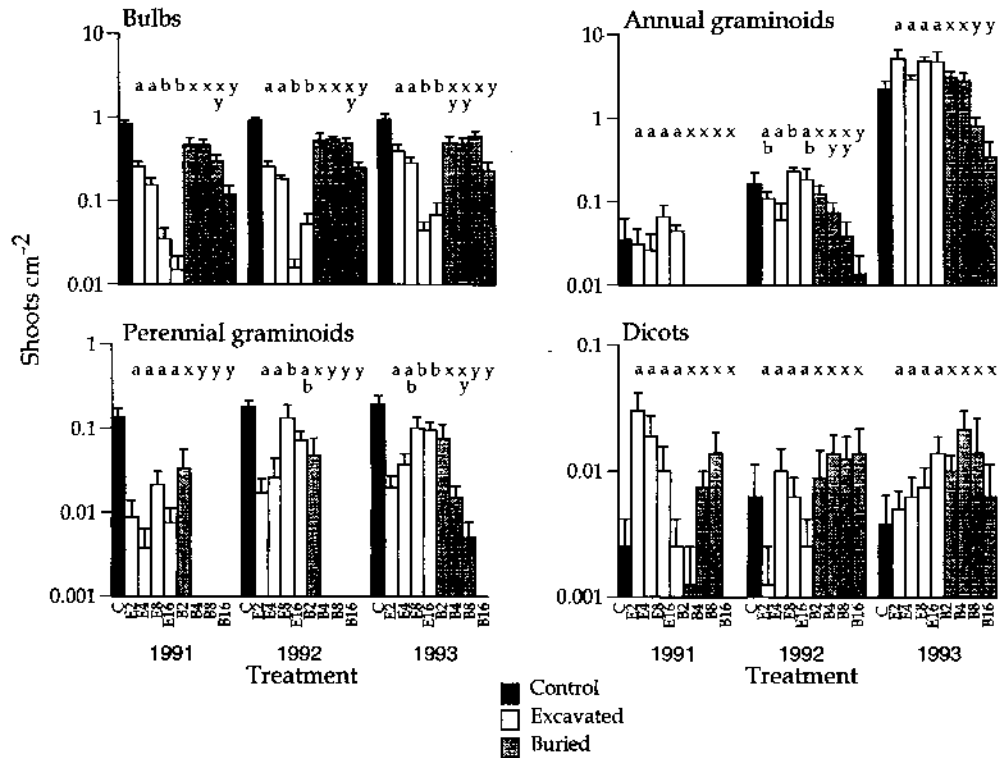
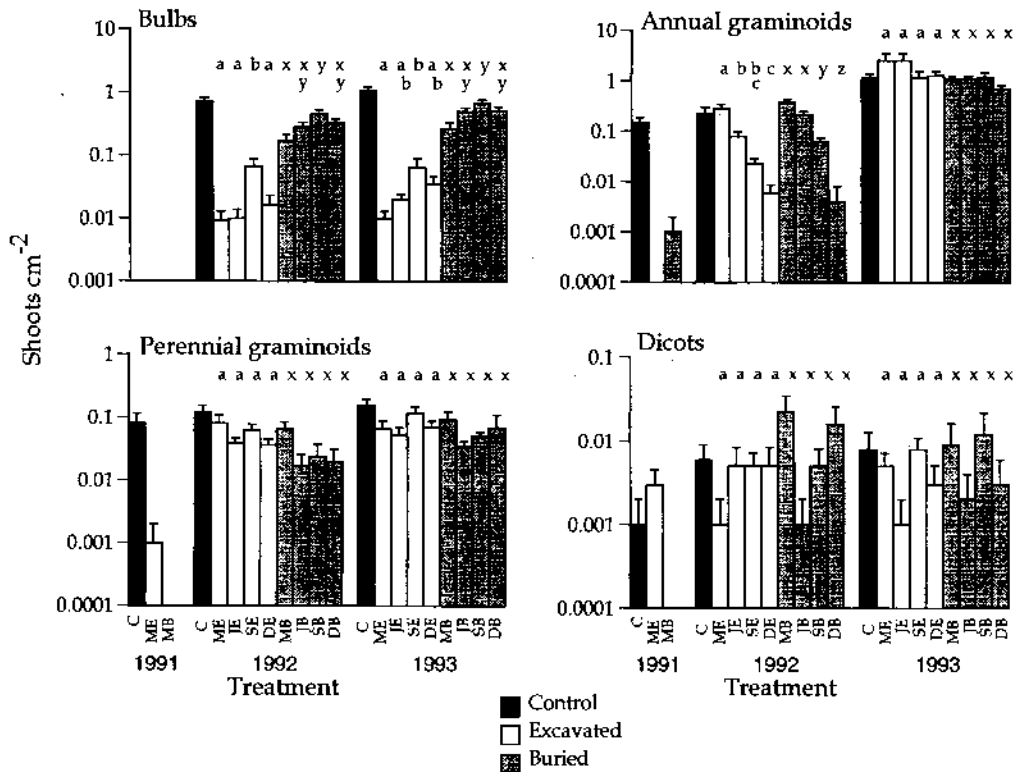


Fig. 2 Results of the disturbance timing experiment. Data represent mean (+SEM) number of shoots cm⁻²; n = 10 plots per treatment (EM-D excavated in March, June, or December; BM-D buried in these same months; C undisturbed "controls"). Excavation or burial treatments which do not differ significantly from one another (P > 0.05; adjusted LSD test) are designated by the same letter (a-c for excavations; x-z for burials). In 1991, only the treatments established before June were sampled, while bulbs were not counted because their shoots had withered before this first sampling; see Table 1



chelostemma capitatum and (rarely) closely-related species of *Brodiaea* and *Triteleia* (Hickman 1993; Kotanen 1995). Dicots (~ 16 species) were very scarce and never differed significantly among treatments (Figs. 1, 2); consequently, I have not emphasized dicots below.

Effects of disturbance depth

Perennial graminoids (= *Danthonia*) tended to be more common in deeper excavations and shallower burials (Fig. 1); in fact, they were absent from all burials deeper

Table 2 Mean (SEM) number of shoots cm^{-2} of annual graminoids in disturbed plots. Also shown are parametric part-whole correlations (Sokal and Rohlf 1981) between the abundance of each species and total abundance of annual graminoids at that sampling.

Experiment	Year	Parameter	Ai	Bh	Bd	Br	Bz	Vu	Jb
Depth	1991	Mean(SEM)	0.001 (0.001)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.020 (0.005)
		Correlation	0.096	0.000	0.000	0.000	0.124	0.092	0.993**
	1992	Mean(SEM)	0.077 (0.013)	0.009 (0.003)	0.000 (0.000)	0.000 (0.000)	0.002 (0.001)	0.008 (0.002)	0.010 (0.005)
		Correlation	0.900**	0.280*	0.000	0.000	0.122	0.157	0.261*
	1993	Mean(SEM)	3.134 (0.359)	0.006 (0.002)	0.000 (0.000)	0.000 (0.000)	0.007 (0.003)	0.006 (0.002)	0.004 (0.003)
		Correlation	1.000**	0.133	0.000	0.000	0.226	0.407**	0.013
Timing	1991	Mean(SEM)	0.000 (0.000)	0.001 (0.001)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
		Correlation	0.000	1.000**	0.000	0.000	0.000	0.000	0.000
	1992	Mean(SEM)	0.018 (0.005)	0.051 (0.011)	0.012 (0.003)	0.007 (0.004)	0.002 (0.000)	0.040 (0.010)	0.000 (0.000)
		Correlation	0.489**	0.822**	0.323**	0.237*	0.014	0.683**	-0.085
	1993	Mean(SEM)	0.822 (0.187)	0.277 (0.024)	0.029 (0.004)	0.002 (0.002)	0.045 (0.011)	0.305 (0.035)	0.000 (0.000)
		Correlation	0.971**	0.277*	-0.096	-0.026	0.290**	0.046	0.000

* $P < 0.05$, ** $P < 0.01$

than 2 cm in 1991 and 1992. Still, these results must be treated with caution, since I could not homogenize variances for perennial graminoids in buried plots, and since Welch's *t*-tests (see Methods) detected no significant differences with respect to burial depth. Surviving ramets of *Danthonia* often grew through plots buried to 2 cm, but practically all plants in excavations and more deeply buried plots were seedlings.

For annual graminoids, among-treatment differences primarily reflected the abundance of *Aira caryophylla*, *Vulpia* spp., and *Juncus bufonius* (Table 2). Buried plots initially were very barren, but annuals (99% *Aira*) began to invade in great numbers by the second (1992) sampling (Fig. 1; Table 2); thereafter, numbers of annual graminoids declined significantly with burial depth (Fig. 1). In contrast, annual graminoids tended to be more common in the deeper excavations in 1992, though not in 1993. Although practically absent from buried plots and controls ($<< 1\%$ of annual graminoid shoots), *Juncus bufonius* made up 94% of all annual graminoids in excavations in 1991. By 1992, however, *Juncus* was greatly outnumbered by *Aira*, which comprised 70% of the annual graminoids in excavations; this proportion rose above 98% by 1993. Annual graminoids (primarily *Aira*) greatly increased even in control plots during this study (Fig. 1).

Bulbs were abundant and were significantly affected by the depth of both excavation and burial (Fig. 1). Bulbs were most common in controls and declined in numbers as disturbance depth increased.

Effects of disturbance timing

Perennial graminoids (= *Danthonia*) did not respond significantly to the timing of disturbance. In contrast, in

For the depth experiment, $n = 64$ plots on each date; for the timing experiment, $n = 20$ (in 1991) and 80 thereafter. *Ai* *Aira caryophylla*, *Bh* *Bromus hordaceus*, *Bd* *Bromus diandrus*, *Br* *Bromus* spp., *Bz* *Briza minor*, *Vu* *Vulpia* spp., *Jb* = *Juncus bufonius*

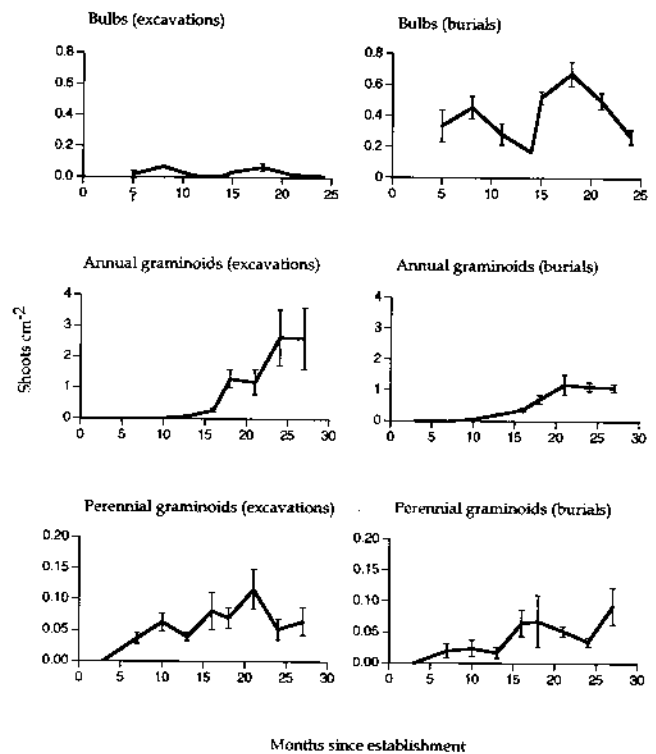


Fig. 3 Results of the disturbance timing experiment. The data of Fig. 2 have been re-plotted as shoots cm^{-2} (\pm SEM) in excavation and burial treatments vs. months since each treatment was established

both 1992 and 1993, plots disturbed early in 1991 (March) contained fewer bulbs than did later (September) disturbances (Fig. 2). Among-treatment differences in numbers of annual graminoids primarily reflected the abundance of *Aira caryophylla*, *Vulpia* spp., and *Bro*

Table 3 Cumulative number of experimental plots disturbed by burrowing mammals. Treatments are as in Figs. 1 and 2

Disturbance depth experiment			Disturbance timing experiment		
Treatment	Disturbed	Not disturbed	Treatment	Disturbed	Not disturbed
E2	1	7	EM	8	2
E4	2	6	EJ	6	4
E8	5	3	ES	8	2
E16	6	2	ED	8	2
B2	0	8	BM	2	8
B4	0	8	BJ	0	10
B8	2	6	BS	1	9
B16	0	8	BD	0	10
C	2	6	C	3	7
Total	18	54	Total	36	54

mus hordaceus; *Juncus bufonius* was scarce at this site (<< 1% of shoots) (Table 2). In 1992, annual graminoids were more common in plots which had been excavated early in the year (Fig. 2); though I could not homogenize variances for this family of tests, Welch's *t*-tests (see Methods) differed only by failing to separate excavations created in March from those created in June. As in the disturbance depth experiment, annual graminoids greatly increased even in controls by 1993 (Fig. 2).

Replotting these data against the time since disturbance indicates that not all the significant effects of timing can be explained simply by plots' ages (Fig. 3): while annual graminoids increased steadily in abundance with plot age, bulbs did not.

Re-disturbance of experimental plots

In both experiments, excavations were particularly prone to re-disturbance by pocket gophers and moles (Table 3). In the disturbance depth experiment, 14 of 32 excavated plots (44%) were re-disturbed by 1993, vs. only 4 of the remaining 40 plots (10%); these proportions differed significantly ($X^2 = 10.8, df = 1, P < 0.01$). Similarly, 30 of the 40 excavated plots (75%) in the disturbance timing experiment ultimately were affected, versus only 6 of the remaining 50 plots (12%); again, this difference was significant ($X^2 = 36.8, df = 1, P < 0.001$). Re-disturbance was not independent of the depth of excavation ($X^2 = 8.63, df = 3, P < 0.05$): deeper excavations suffered more than shallow ones. In contrast, the probability of re-disturbance did not depend on an excavation's timing ($X^2 = 1.60, df = 3, P > 0.50$).

While experimental plots could be buried completely, such severe effects were uncommon; much re-disturbance was confined to the margins of plots or to cracking of the soil surface. Consequently, the average effects of re-disturbance were mild, as indicated by factorial (re-disturbance × treatment) ANOVAs at the final (1993) samplings. For the timing experiment, annual graminoids were more common in undisturbed plots than in plots affected by burrowing animals ($F_{1,56} = 11.347, P < 0.01$). With this exception, no propagule group in either experiment was affected by re-disturbance ($P > 0.05$).

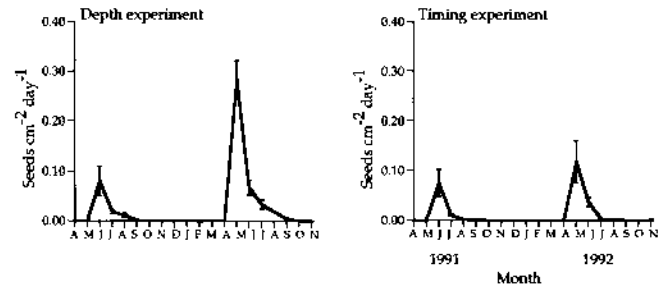


Fig. 4 Total flux of dispersing seeds. Data represent mean (\pm SEM) number of seeds captured $\text{cm}^{-2} \text{day}^{-1}$. Sample size = 7–10 5-cm seed traps for each date for each experiment; $n_{\text{total}} = 170$ samples for the depth experiment and 167 for the timing experiment

Propagule pools

Dispersing seeds

Dispersing seeds were abundant but highly seasonal, with the total number trapped peaking from late May to June (Fig. 4). Overall, 7.7 seeds $\text{cm}^{-2} \text{year}^{-1}$ fell in the depth experiment, while 3.7 seeds $\text{cm}^{-2} \text{year}^{-1}$ were captured in the timing experiment (averages calculated with months weighted equally). Comparable data are scarce, but Bartolome (1979) estimated that *Aira caryophyllea* alone produced 3.6 seeds $\text{cm}^{-2} \text{year}^{-1}$ at an annual grassland site in northern California, while *Vulpia* spp. produced as many as 12.3 seeds $\text{cm}^{-2} \text{year}^{-1}$.

Seeds of 15 species were trapped, but annual graminoids comprised 97% of all seeds captured at each site (Table 4). *Aira caryophyllea* alone comprised 90% of the seeds captured in the depth experiment, and 70% of seeds in the timing experiment. Other annual grasses detected included *Bromus hordaceus*, *Vulpia* spp., *Briza minor*, and *Bromus diandrus*, but with the exception of *B. hordaceus* in the timing experiment (14%), none of these species ever exceeded 10% of the seeds captured. *Juncus bufonius* contributed 4.1% of seeds captured in the depth experiment, but no seeds in the timing experiment. More than 97% of the seeds of perennial graminoids had been produced by *Danthonia californica* (1.7% of all seeds). Seeds of dicots (~ 10 species) were trapped

Table 4 Seeds captured in sticky traps. Data represent mean (SEM) seeds captured $\text{cm}^{-2} \text{ day}^{-1} \times 100$; total sample sizes = 170 (depth experiment) and 167 (timing experiment). *Bulbs* all bulb-bearing species; *Dc* *Danthonia californica*, *Lz* *Luzula comosa* (pe-

rennial graminoids); *Bh* *Bromus hordaceus*, *Bd* *Bromus diandrus*, *Ai* *Aira caryophyllea*, *Vu* *Vulpia* spp., *Bz* *Briza minor*; *Jb* *Juncus bufonius* (annual graminoids); *Dicots* all dicots

Experiment	Bulbs	Dc	Lz	Bh	Bd	Ai	Vu	Bz	Jb	Dicots
Depth	0.006 (0.005)	0.034 (0.011)	0.002 (0.002)	0.010 (0.005)	0.000 (0.000)	2.646 (0.557)	0.046 (0.014)	0.012 (0.009)	0.128 (0.128)	0.051 (0.029)
Timing	0.000 (0.000)	0.032 (0.011)	0.000 (0.000)	0.205 (0.059)	0.007 (0.005)	1.045 (0.326)	0.139 (0.055)	0.043 (0.027)	0.000 (0.000)	0.004 (0.003)

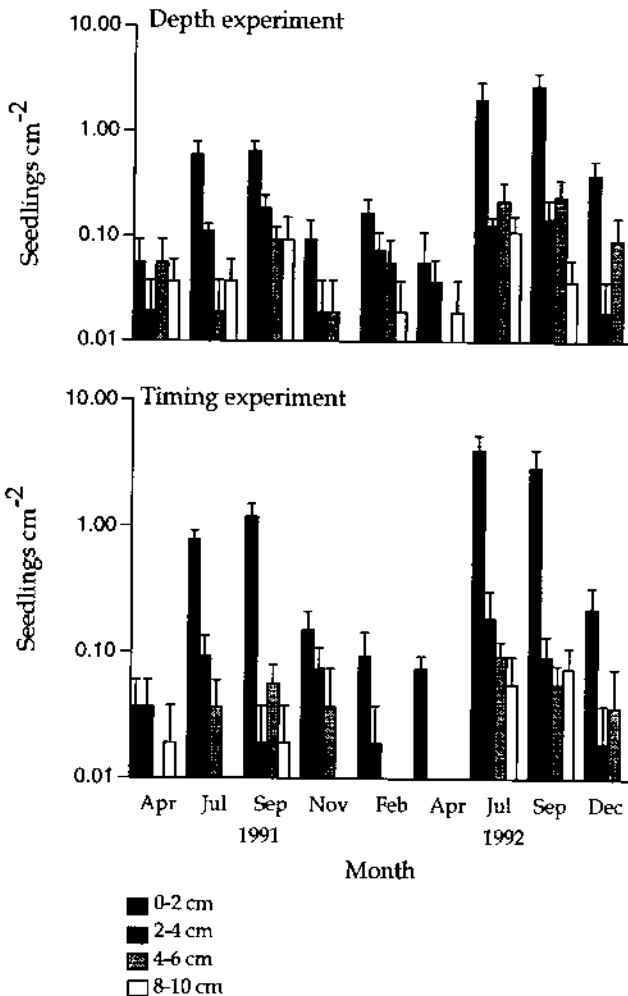


Fig. 5 Active seeds and bulbs cm^{-2} of soil surface. Data represent the mean (+ SEM) seedlings germinated or bulbs removed from 2-cm-thick soil samples. Five samples were taken from depths of 0–2, 2–4, 4–6, and 8–10 cm for each site and date; $n_{\text{total}} = 90$ cores or 360 core sections

in low numbers (1.3% of seeds), while seeds produced by bulbs were even scarcer (0.2% of seeds).

Soil seed and bulb banks

The active seed bank was most abundant in late summer and fall (Fig. 5). Means of 3.2 (depth experiment) to 4.4

(timing experiment) germinable seeds cm^{-2} occurred at the respectively most productive samplings. These numbers are within the range reported by Young and Evans (1989) for California annual grasslands, and slightly smaller than the numbers estimated for the total annual seed rain.

Twelve species were identified germinating from the soil cores. Perennial graminoids (95% *Danthonia californica*, 5% *Luzula subsessilis*) contributed 3.9% of seedlings. Dicots (~ 7 species) contributed 2.9%. Bulbs were abundant ($> 0.8 \text{ cm}^{-2}$), but no seedlings of bulb-bearing species were observed. Overall, the active component of the seed bank was dominated by annual graminoids: 93% of all seedlings (Table 5). In particular, *Aira caryophyllea* (possibly including some *Vulpia* spp.) accounted for 71% of all seedlings. *Juncus bufonius* contributed 19% of seedlings from the depth experiment, but only 1.8% of seedlings from the timing experiment

Numbers of seeds declined rapidly with depth. More than 80% of the active seed bank was located $< 2 \text{ cm}$ from the soil surface (Fig. 5, Table 5); consequently, the bias incurred by not sampling the entire soil profile should have been small. There were exceptions to this rule, however. In the depth experiment, where it was most abundant, *Juncus* was rather evenly distributed with respect to depth; consequently, its contribution to the seed bank increased from 6% of the seeds detected in the top 2 cm of soil to 79% of seeds between 8–10 cm (Table 5). *Aira* was found in nearly comparable numbers in some sub-surface samples, but was much more strongly concentrated near soil surface (Table 5). Bulbs also were concentrated near the soil surface, but declining numbers occurred to the deepest depths sampled (Table 5).

Discussion

My results indicate that soil disturbances which differ spatially or temporally from one another may be recolonized by different propagule pools, leading to initially different successional trajectories. These trajectories may remain distinct when external sources of propagules are scarce, but are likely to converge rapidly when revegetation is dominated by a source of propagules largely external to the disturbed site (in this study, the seed rain). As a corollary, my results also suggest that disturbances

Table 5 Species represented in soil cores, subdivided by depth. Data represent mean (SEM) bulbs or seedlings cm⁻². Total sample size = 90 cores or 360 core sections; *n* = 45 per cell. *Dc* *Dan-*

thonia californica, *Lz* *Luzula comosa* (perennial graminoids); *Br* *Bromus* spp., *Ai* *Aira caryophyllea* (may include some *Vulpia* spp.), *Jb* *Juncus bufonius* (annual graminoids); *Dicots* all dicots

Experiment	Depth (cm)	Bulbs	Seedlings					
			Dc	Lz	Br	Ai	Jb	Dicots
Depth	0-2	0.467 (0.076)	0.025 (0.007)	0.002 (0.002)	0.023 (0.009)	0.641 (0.190)	0.048 (0.014)	0.017 (0.007)
	2-4	0.345 (0.058)	0.002 (0.002)	0.000 (0.000)	0.000 (0.000)	0.031 (0.009)	0.048 (0.013)	0.002 (0.002)
	4-6	0.079 (0.021)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.033 (0.016)	0.056 (0.015)	0.000 (0.000)
	8-10	0.008 (0.005)	0.002 (0.002)	0.000 (0.000)	0.000 (0.000)	0.004 (0.003)	0.031 (0.010)	0.002 (0.002)
Timing	0-2	0.566 (0.082)	0.048 (0.009)	0.002 (0.002)	0.256 (0.067)	0.728 (0.227)	0.004 (0.003)	0.023 (0.007)
	2-4	0.221 (0.036)	0.002 (0.002)	0.000 (0.000)	0.002 (0.002)	0.041 (0.016)	0.006 (0.003)	0.008 (0.004)
	4-6	0.035 (0.013)	0.000 (0.000)	0.000 (0.000)	0.002 (0.002)	0.017 (0.006)	0.010 (0.005)	0.006 (0.003)
	8-10	0.008 (0.008)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.014 (0.007)	0.000 (0.000)	0.004 (0.003)

may play different roles in plant communities dominated by different propagule groups.

To understand these conclusions, it is necessary to consider how sources of propagules interacted with different experimental disturbances. In this Discussion, I will first consider patterns of propagule availability, and then use these patterns to interpret the effects of my experimental disturbances. Although all pools of propagules contributed to revegetation in some degree, I will particularly emphasize those whose role each experiment was designed to investigate: surviving seeds and ramets in the case of the disturbance depth experiment, and immigrants in the case of the timing experiment.

Propagule pools

Sources of colonists

Clonal encroachment often is important in the revegetation of small grassland disturbances (Rapp and Rabinowitz 1985; Rabinowitz and Rapp 1985; Goldberg and Gross 1988; Coffin and Lauenroth 1989; Arnthórsdóttir 1994; Bullock et al. 1995). However, with the exception of some bulbs (Niehaus 1971), most common species at my study site either have a compact "bunchgrass" morphology (e.g., *Danthonia*) or are incapable of producing adventitious roots (most annual grasses and dicots). Consequently, clonal growth is important in revegetation at this location only at much smaller spatial or much longer temporal scales (Kotani 1994a). At the scales of my experiments, practically all colonists instead came from one of the other three propagule pools: the seed rain (including seeds produced by the colonists themselves), the seed bank, and surviving ramets.

Spatial and temporal patterns of propagule availability

These pools of propagules varied both spatially and temporally. For example, the seed rain reached a sharp summer peak, which was reflected in turn by the autumn peak in the seed bank. Mortality may have contributed to

the subsequent decline in soil seed populations, but most seed loss can be attributed to germination, which begins following the first winter rains. Such transient seed banks are typical of many grasslands (Roberts 1981; Rice 1989; Thompson 1992), including many California locations (Bartolome 1979; Young et al. 1981; Hobbs and Mooney 1985; Young and Evans 1989).

Short-lived seeds should tend to have a shallow distribution in the soil since they have little time to migrate vertically before they germinate or die. In this study, most seeds occurred at or near the soil surface, as Young et al. (1981) and Young and Evans (1989) also described for other California grasslands. In contrast to this general picture, the relatively uniform depth distribution of seeds of *Juncus bufonius* and its abundance in excavations despite its rarity in the surrounding undisturbed vegetation (Kotani 1995) both suggest that its seed bank includes a long-lived component, as reported by Grime et al. (1988). Bulbs, the only ramets which routinely survived disturbance, also extended deeply into the soil but decreased in numbers with depth; since bulbs of this group are capable of vertical migration through the soil (Niehaus 1971), these results again may indicate a short life expectancy.

Responses to experimental disturbance

Disturbance depth: the role of survivors

The intensity of disturbance should affect revegetation by influencing the number of surviving propagules (Connell and Slatyer 1977; Malanson 1984; Sousa 1984). I investigated this idea by experimentally varying disturbance depth. Although their effects usually were weak, burrowing animals further intensified experimental excavations (particularly the deeper ones) by burying vegetation with sub-surface soil and presumably, in the case of gophers, by eating bulbs and other plant material (Huntly and Inouye 1988). Excavations probably were especially prone to re-disturbance because they were more likely to intersect tunnel systems. This result is not an artifact, but instead reflects a real, repeatable interaction. Tilman

(1983) similarly found that pocket gophers (*Geomys bur-sarius*) preferentially invaded a subset of experimental treatments (high nitrogen treatments), in that study slowing succession.

Since the seed rain was negligible during winter, dispersal can have contributed little to the first year of revegetation (1991); instead, most of the initial colonists must have originated, as intended, as surviving ramets or dormant seeds. However, most species at this location had seeds and perennating organs concentrated close to the soil surface; consequently, they initially were equally reduced by any disturbance that removed or buried this critical surface layer, or mixed it with seed-poor subsurface soil. There were only three exceptions to this general picture. First, *Danthonia californica* was best at revegetating the shallowest burials because it was able to grow through them. Second, since bulbs also could grow through burials, and since actively-growing bulbs occurred deeply in the soil, declining numbers of bulbs survived in both excavations and burials as disturbance depth increased. Finally, since seeds of *Juncus bufonius* occurred evenly throughout the top 10 cm of soil, this species abundantly colonized excavations of all depths, explaining the initial success of annual graminoids in excavated plots. These results emphasize that the severity of a disturbance may differ for plants with different reproductive strategies.

In 1992 and 1993, bulbs remained scarcest in the most deeply-disturbed plots, and perennial graminoids remained scarcest on the deepest burials, maintaining the patterns established early in the experiment. Annual graminoids also developed a pattern of declining abundance on progressively deeper burials, probably because it was difficult for short-statured annuals to disperse seeds onto their raised surfaces: *Aira caryophylla*, the commonest species, generally was less than 25 cm tall. In contrast, the tendency in 1992 of both groups of graminoids to do better in deeper excavations may have reflected both propagule supply (if deeper excavations were more effective traps for dispersing seeds, including those produced within each plot) and environment (if deeper excavations provided moister, more sheltered microhabitats). For perennial graminoids this pattern persisted, but for annual graminoids, it was soon obscured by the annual-dominated seed rain; by the final sampling, no significant differences remained.

Few other studies have experimentally examined the effects of soil disturbance intensity in grasslands; however, Belsky (1986 a, b, 1992) provides some striking parallels. Working in another patchy, perennial-dominated, semi-arid grassland with a poorly-developed seed bank (the Serengeti), Belsky also found significant differences between the revegetation of soil disturbed to 1–2 cm and deeper (15 cm) disturbances. As in my experiments, vegetative regrowth (including regrowth by tuberous species) initially was most important in the shallower disturbances, while seedlings (presumed to be immigrants) were most common in more deeply-disturbed plots. Finally, Belsky also found recovery to be rapid: regrowth

and seed influx eliminated between-treatment differences within three years.

Disturbance timing: the role of immigrants

Which species initially invade a disturbed site should depend in part on the propagules available at the time when the disturbance occurs (Gross 1980; Sousa 1984, Underwood and Denley 1984; Denslow 1985). For example, Hobbs and Mooney (1985) found that the timing of gopher disturbance relative to seed dispersal significantly influenced revegetation in a California annual grassland. Perozzi and Bazzaz (1978), Busing and Clebsch (1983), Coffin and Lauenroth (1989), and Lavorel et al. (1994) provide other examples of revegetation depending on disturbance timing.

In my study, perennial graminoids probably were insensitive to the timing of disturbance both because surviving fragments always were available as colonists, and because the vegetative multiplication of colonizing ramets largely decoupled their numbers from external supplies of propagules. The contrasting tendency of older plots to support greater numbers of annual graminoids than younger plots can be explained by considering reproductive phenology. By 1992, plots created in March of 1991 had been exposed to a full season of seed influx, but June plots had been exposed to a truncated season, and September and December plots had yet to experience the annual peak of seed dispersal. The reduced abundance of annual graminoids in plots re-disturbed by burrowing animals probably was also a result of their briefer exposure to post-disturbance seed rain. The loss of between-treatment differences by 1993 occurred partly because all plots had experienced at least one season's seed production and dispersal by this date, overwhelming any differences among them; as well, since burrowing animals occurred equally in all types of excavation, they tended to homogenize the annual graminoid vegetation of these treatments.

In contrast with annual graminoids, the abundance of bulbs was not a simple consequence of the time elapsed since disturbance. The explanation may be that bulbs are less vulnerable to damage when dormant (in late summer and autumn) than when actively growing.

Trends in control plots

California grasslands vary strongly in composition from one year to the next, primarily in response to weather (Heady 1956, 1958; Pitt and Heady 1978; Bartolome 1989; Hobbs and Mooney 1991; Heady et al. 1992). Dry years should favour annual grasses relative to perennials, since the annuals tend to be more xerophytic (Bartolome et al. 1980; Heady et al. 1992), and also may reduce litter production to the benefit of litter-intolerants such as *Aira* (Heady 1956). I conducted my experiments near the end of a 6-year drought, which was associated with large

increases in some annual grasses (notably *Aira*) in both undisturbed controls and the surrounding meadow. Since all experimental plots experienced the same weather, drought alone cannot explain the differences observed among treatments: though small relative to interannual variation, these differences are significant. Instead, one important effect of disturbance may be to accelerate climatically-driven changes (Davis 1989). For example, Hobbs and Mooney (1991) found that the vegetation of gopher mounds was more sensitive to rainfall variation than was undisturbed annual grassland.

Community composition and the revegetation of disturbances

Recovery from disturbance may proceed very differently in communities with well-developed seed banks than in communities relying upon seed dispersal and clonal growth for regeneration (Denslow 1985; Leck et al. 1989; Thompson 1992). My results suggest that the role of characteristics of disturbance such as intensity and timing also may vary as a consequence of the propagule groups present in the local species pool. Armesto and Pickett (1985) provide one relevant example in which the intensity of above-ground biomass removal had different effects in two different old-field communities. In my own study, differences between the responses of deeply-distributed species (e.g., bulbs) and surface species (e.g., *Danthonia*, *Aira*) suggest that the depth of disturbance would have been more important had buried pools of propagules been better developed. Similarly, the effects of timing might have been less pronounced but more persistent had the seed rain been more modest. Understanding sources of colonists will improve our ability to predict the effects of disturbance, and to use disturbance as a tool for management, conservation, and restoration (Thompson 1992; Chambers and MacMahon 1994).

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