

Effects of gap area and shape on recolonization by grassland plants with differing reproductive strategies

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Abstract: Species with poor dispersal ability initially should be slower to colonize larger or rounder gaps than smaller or less circular gaps. Conversely, dispersive and seed-banking species should be less sensitive than poor dispersers to gap size and shape, and less confined near the edges of a gap. I tested these ideas with a 3-year experiment in which I monitored the revegetation of gaps in grassland vegetation. Initially, species reproducing largely by clonal growth (bulbs and perennial graminoids) were the most sensitive to gap size and (to a lesser extent) shape, reaching their greatest abundances in small and (or) rectangular openings. Species relying on seed dispersal (annual grasses) also tended to do best in smaller plots, but were less concentrated near the edges of the plots. Species relying on seed dormancy (dicots and *Juncus bufonius*) were least sensitive to plot size, shape, and distance from an edge. In subsequent years, these patterns often were obscured or reversed, reflecting continuing seed immigration and environmental and competitive conditions within gaps. These results indicate that species respond to gap size and shape in ways consistent with their reproductive biologies, and suggest that the importance of the dimensions of gaps may vary among plant communities.

Key words: disturbance, gap shape, gap size, grasslands, revegetation, succession.

Résumé : Les espèces ayant une faible capacité de dispersion au départ devraient coloniser plus lentement les grands espaces libres et plutôt circulaires, que les surfaces plus petites ou moins circulaires. Réciproquement, les espèces à forte dispersion et à banques importantes devraient être moins sensibles que les espèces à faible dispersion eu égard à la grandeur et à la forme des espaces libres, et moins confinées au pourtour de ceux-ci. L'auteur a vérifié cette hypothèse au cours d'une expérience de 3 ans dans laquelle il a suivi la revégétation des espaces libres dans une végétation de prairie. Au départ, les espèces qui se dispersent surtout par croissance clonale (bulbes et graminoides pérennes) sont les plus sensibles à la dimension des ouvertures et (à un moindre degré) à leur forme, atteignant leur plus grandes abondances dans les ouvertures petites et (ou) rectilignes. Les espèces qui dépendent de la dispersion par des graines (herbacées annuelles) ont également tendance à mieux réussir dans les ouvertures plus petites, mais sont moins concentrées aux pourtours de celles-ci. Les espèces faisant appel à la dormance des graines (dicotylées ainsi que le *Juncus bufonius*) sont moins sensibles à la dimension et à la forme des parcelles, et moins limitées à la proximité du pourtour. Au cours des années subséquentes, ces patrons sont fréquemment effacés ou renversés, ce qui indique une immigration continue des graines et un changement des conditions environnementales et de compétition à l'intérieur des parcelles. Ces résultats indiquent que les espèces réagissent à la dimension et à la forme des ouvertures de façon congruente avec la biologie de leurs reproductions, et suggère que l'importance de la dimension des ouvertures pourrait varier selon les communautés végétales.

Mots clés : perturbation, forme des ouvertures, dimension des ouvertures, prairie, revégétation, succession.
[Traduit par la rédaction]

Introduction

Disturbance-created gaps are important to the diversity and structure of many biological communities (White 1979; Sousa 1984a; Pickett and White 1985; Hobbs and Huenneke 1992). Gaps provide opportunities for regeneration, afford habitat for species that are competitively inferior or have environmental requirements not met in undisturbed areas, and add

spatial heterogeneity to otherwise homogeneous landscapes. Intertidal boulder fields (Sousa 1979a, 1979b, 1980), grasslands (Platt 1975; Collins and Glenn 1988), and forests (Connell 1978; Hartshorn 1980; Platt and Strong 1989) are among the many systems that owe much of their character to their regimes of gap creation and closure.

The revegetation of a newly created gap initially should be influenced by the size and shape of the gap (Sousa 1984a; Pickett and White 1985). Since most of the area of a small gap is close to an edge, such a gap should be recolonized rapidly by clonal ingrowth and by the short-range dispersal of propagules from immediately adjacent vegetation. In contrast, revegetation of larger gaps should be slower and more strongly dominated by species with good seed dispersal ability, while poor dispersers remained confined near the edges of the gap (Connell and Slatyer 1977; Miller 1982; Sousa

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1984a). Similarly, compared with gaps of other shapes, circular gaps should be colonized more slowly and less by clonal ingrowth and short-range dispersal, since circles have the minimal perimeter to area ratio and the maximal proportion of surface distant from any edge (Miller 1982; Sousa 1984a, 1985). These arguments also imply that the importance of gap size and shape may depend, in part, on the reproductive strategy of the species under consideration: species dependent on clonal encroachment should be affected more strongly by gap size and shape and the distance from the nearest edge than species with better dispersal ability or capable of surviving disturbance.

Grasslands and oldfields have proven especially tractable for studies of small-scale gap dynamics (Platt 1975; Platt and Weis 1977; Gross 1980; Gross and Werner 1982; Hobbs and Mooney 1985; Marks and Mohler 1985; Rabinowitz and Rapp 1985; Rapp and Rabinowitz 1985; Belsky 1986a, 1986b, 1992; Goldberg and Gross 1988; Coffin and Lauenroth 1989; Peart 1989a, 1989b; Parish and Turkington 1990a, 1990b; Bergelson et al. 1993; Arnthórsdóttir 1994; Bullock et al. 1994, 1995; Lavorel et al. 1994; Aguilera and Lauenroth 1995; Burke and Grime 1996). In this paper, I discuss the results of an experiment in which I assessed the importance of gap size and shape for the early stages of recolonization by a variety of grassland plants. I found that plot area and shape were important, and that their effects were strongly dependent upon the dispersal and life history characteristics of the invading plants. Initially, largely clonal species tended to be more sensitive to plot area and shape and the distance from an edge than were dispersive species and seed bankers. Over time, these effects gradually were eclipsed by both seed immigration and within-plot processes. My results also suggest that the effects of gap area and shape may differ significantly among systems that differ floristically.

Methods

Study site

I conducted this study in the White House Meadow of the Angelo Preserve of the University of California (123°37'W, 39°45'N), about 240 km north of San Francisco. This meadow is one of a series of natural openings in Douglas-fir (*Pseudotsuga menziesii*²) – redwood (*Sequoia sempervirens*) forest. It probably once was occupied by perennial-dominated Coastal Prairie, but as is true of most Californian grasslands (Heady 1988; Heady et al. 1988, 1992; Sims 1988), it has been greatly altered by the invasion of Eurasian annual grasses. Currently, both the appearance and the biomass of this meadow are dominated by native perennial graminoids (here defined as Gramineae, Cyperaceae, and Juncaceae), primarily the bunchgrass *Danthonia californica*; however, annual grasses (mostly exotics) including *Aira caryophyllaea*, *Bromus hordeaceus*, *Briza minor*, and *Vulpia* spp. also are abundant. Native perennial Liliaceae and Amaryllidaceae (hereafter bulbs) are common, while numerous herbaceous dicots (forbs) occur infrequently. As a result of modern suppression methods, fire currently is unimportant at this location, but soil disturbances created by animals play a significant role in structuring the local vegetation (Kotanen 1994a, 1994b, 1995): between 1990 and 1993, more than 7% of the surface area of five major meadows at the Angelo Preserve annually was disturbed by feral pigs, *Sus scrofa*, pocket gophers, *Thomomys bottae*, and moles, *Scapanus latimanus* (Kotanen 1995). Additional infor-

Table 1. Dates on which the area × shape disturbance experiment was sampled.

Year	Event	Date
1991	Establishment	February 23 – March 9
	Sampling (bulbs)	—
	Sampling (graminoids + dicots)	June 12–14
1992	Sampling (bulbs)	February 29 – March 1
	Sampling (graminoids + dicots)	June 11–12
1993	Sampling (bulbs)	February 13–15
	Sampling (graminoids + dicots)	June 12–14

Note: Bulbs were not sampled in 1991.

mation on this site may be found in Johnson (1979) and Kotanen (1994a, 1994b, 1995).

Experimental methods

In February 1991, I created 45 plots, evenly spaced in an approximately 10 × 10 m grid. I left five plots undisturbed as controls, while I excavated the remaining plots to a depth of 9 cm (below the principal root and bulb zone), removing most pre-existing vegetation. Half of these gaps were circular, divided equally among four sizes. Each size represented a fourfold increase in area over the last (156, 625, 2500, and 10 000 cm²: treatments C1, C4, C16, C64). The remaining gaps were 1:4 rectangles, with areas again ranging in fourfold steps between 156 and 10 000 cm² (R1, R4, R16, R64). Plots were randomly allocated among treatments.

The principal data I collected were the numbers of living and (or) reproductive shoots rooted in a square 10 × 10 cm quadrat centred in each plot. The smallest rectangular plots were the only exception: since these measured only 6.25 × 25 cm, I instead examined a 100 cm² area of the floor of these plots. To investigate whether revegetation varied with respect to distance from the edge of a gap, I also sampled a 10 × 10 cm quadrat next to a random edge of the two largest sizes of plots. Each year, I performed the primary sampling in June (Table 1), after most species had flowered but while early spring annuals still were readily identifiable; however, I sampled bulbs 3–4 months earlier (Table 1) because their shoots withered and disappeared by June. I did not sample bulbs in 1991, since few remained visible by the initial sampling.

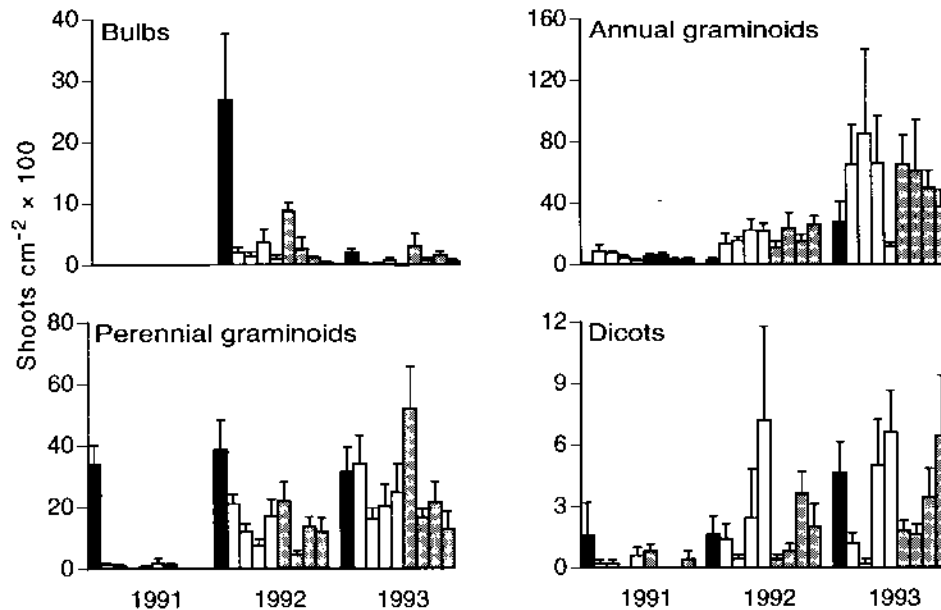
Counting shoots acknowledges the modular nature of plant construction and avoids the problem of identifying individuals in a complex sward, but does not necessarily reflect biomass. In particular, though local species of annual graminoids resemble one another in size, they are much smaller than perennial graminoids or bulbs: the dry mass of a shoot of *Danthonia* is more than 10 times that of a shoot of *Aira*.

Seed and bulb banks

To describe the component of revegetation *not* resulting from immigration, I assayed the seed and bulb banks using soil cores. At 2- to 3-month intervals over a 21-month period, I took 3.7 cm diameter cores from five random locations within the experiment, and then subdivided each 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. The sampling depth extended 1 cm deeper than the depth of the experimental plots, both because it is difficult to excavate a plot without somewhat disturbing and exposing the underlying soil, and because laboratory trials indicated that some local species (e.g., *Bromus* spp.) could successfully germinate despite burial beneath approximately 1 cm of soil. 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 cycle of 14 h light : 10 h

² Nomenclature follows Hickman (1993).

Fig. 1. Mean (\pm SEM) numbers of shoots produced by bulbs, annual graminoids, and perennial graminoids. From left to right, treatments are undisturbed controls (■), circular excavations (□) with areas of 156, 625, 2500, and 10 000 cm², and rectangular excavations (▨) of the same areas. Sample size was 45 plots on each date. Bulbs were not sampled in 1991.



dark and a daily temperature cycle averaging 25°C light : 10°C dark. I counted emergent seedlings after 2 months; examinations during waterings indicated that 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 have provided a reasonable estimate of this readily germinable component of the seed bank. 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 germination requirements (e.g., scarification, freezing) not available in the laboratory. Third, lab trials indicated that seeds of most of the species that dominate this system germinate readily, given sufficient moisture.

Seed dispersal

I constructed seed traps by placing disks of filter paper coated with the adhesive Tangle-trap (The Tanglefoot Company, Grand Rapids, Michigan) in the lower halves of 5 cm diameter Petri dishes, and covering each trap with 1-cm wire mesh to exclude rodents and birds. In April 1991, I permanently anchored 10 such traps to the ground surface at random locations within the experiment. At 1- to 2-month intervals 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.

Analysis of data

The functional group approach has proven useful in understanding the effects of disturbance on plant communities (McIntyre et al. 1995). In the present paper, I have taken an analogous approach, combining plants into four species groups united by similar life his-

tory (annual versus perennial), dispersal mode (seed versus vegetative), and morphology (graminoid versus forb). These groups are: (i) annual graminoids, (ii) perennial graminoids, (iii) perennial bulbs, and (iv) dicots. I used these groups because they simplified analysis while emphasizing reproductive and life history differences.

I used repeated-measures fixed effects ANOVAs to assess the effects of disturbance size and shape (Kirk 1982). Plot size and shape were considered fixed factors because they were deliberately selected; date was considered fixed because there is no reason to believe that the years of this experiment represented a random sample of Californian weather (Kirk 1982; Bennington and Thayne 1994). I did not include the undisturbed controls in these analyses, but I have presented their results for purposes of comparison; elsewhere, I have discussed other experiments designed to quantify differences between disturbed and undisturbed communities (Kotaniemi 1994a, 1995, 1997). To stabilize variances, I log-transformed all data before analysis (Cochran's C : $0.05 > p > 0.01$ for one ANOVA; $p > 0.05$ in the remainder).

Results

The colonizing flora

The vegetation of most plots was dominated by bulbs in spring, and by graminoids in summer (Fig. 1); the remainder of this paper will particularly emphasize these groups. Dicots (approximately 15 spp.) were comparatively scarce (Fig. 1). A single *Pseudotsuga* seedling was the only vascular plant observed that did not fall into any of the species groups used; this individual was omitted from all analyses.

All observed bulbs were *Dichelostemma capitatum* or (rarely) closely related species of *Brodiaea* and *Triteleia*, while all perennial graminoids sampled in disturbed plots were either *Danthonia californica* or (increasingly) *Luzula comosa* (Table 2). The most abundant annual graminoids in the principal (central) quadrats of disturbed plots were *Juncus bufonius* and *Aira caryophyllea*; *Briza minor*, *Vulpia*

Table 2. Graminoids occurring in disturbed plots (central quadrats only).

Year	Parameter	Dc	Lz	Jb	Ai [†]	Bz	Vu	Bh
1991	Mean	0.008 (0.002)	0.000 (0.000)	0.048 (0.007)	0.001 (0.000)	0.001 (0.000)	0.001 (0.000)	0.000 (0.000)
	Correlation	1.000**	0.000	0.995**	-0.176	0.034	0.336*	0.000
1992	Mean	0.096 (0.011)	0.042 (0.011)	0.149 (0.022)	0.010 (0.003)	0.011 (0.004)	0.008 (0.003)	0.008 (0.003)
	Correlation	0.657**	0.728**	0.934**	0.102	-0.136	0.174	0.363*
1993	Mean	0.121 (0.018)	0.128 (0.027)	0.167 (0.053)	0.264 (0.067)	0.080 (0.020)	0.028 (0.008)	0.014 (0.005)
	Correlation	0.517**	0.828**	0.750**	0.862**	-0.034	-0.070	0.148

Note: Data represent mean (SEM) number of shoots cm⁻². Also shown for each date are parametric part-whole correlations (*r*) (Sokal and Rohlf 1981) relating the abundance of each taxon to the total abundance of its respective species group (perennial or annual graminoids). Sample size was 40 plots on each date. Species codes are as follows: perennials: Dc, *Danthonia californica*; Lz, *Luzula comosa*; annuals: Jb, *Juncus bufonius*; Ai, *Aira caryophyllea*; Bz, *Briza minor*; Vu, *Vulpia* spp.; Bh, *Bromus hordeaceus*. *, *p* < 0.05; **, *p* < 0.01.

[†] Rarely may include seedlings of similar annual graminoids.

spp., and *Bromus hordeaceus* contributed the remainder (Table 2). However, the relative abundances of these species changed markedly over time. In particular, *Aira* rapidly increased from initial rarity to exceed *Juncus* both in abundance and in the strength of its correlation with annual graminoids as a whole (Table 2).

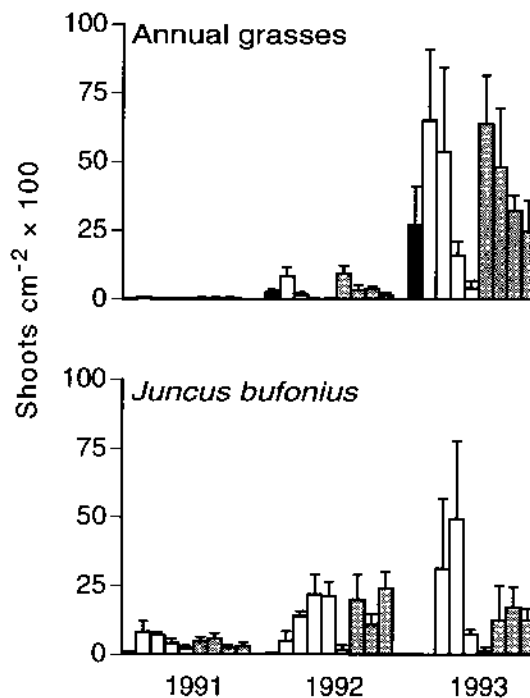
In contrast with other experiments at this location (Kotanen 1996, 1997), redisturbance by moles and pocket gophers was rare: only four plots (an R1, R4, R16, and a control) were so disturbed. These plots were not treated differently in the analyses, because (i) disturbance by fossorial animals is a natural, "background" process normally expected to interact with other disturbances at this location, (ii) the effects of such redisturbance generally are mild (Kotanen 1996), (iii) their exclusion did not substantially alter the results, and (iv) their treatment as a separate factor would have led to an excessively complicated design.

Effects of gap size and shape (central quadrats)

Gap shape had significant effects for only one group: bulbs were more common in rectangular gaps than in circular gaps (Fig. 1; Table 3). Gap size had significant overall effects on the density of bulbs, perennial graminoids, and dicots, but not on the density of annual graminoids (Table 3). Bulbs were consistently more common in smaller gaps than in the larger ones (Fig. 1; Table 3); however, for the remaining species groups, significant year × size interactions suggested that the results should be broken down by sampling date. These datewise analyses indicated that perennial graminoids were significantly affected by plot size in 1991 and 1992 (Dunn-Šidák corrected *p* < 0.05 on each date; smaller plots contained more shoots), but these effects were nonsignificant in 1993. Numbers of annual graminoids and dicots were significantly affected by plot size only in 1993 (*p* < 0.05), but these groups exhibited opposite trends: annual graminoids were more common in smaller plots, while dicots were more common in larger plots.

When annual graminoids were partitioned into *Juncus bufonius* and annual grasses per se, the results changed (Fig. 2; Table 4). In this case, overall tests detected a significant effect of plot size (for *Juncus*) and of both plot size and shape (for annual grasses), as well as significant interactions involving the year of sampling. When results were subdivided by year, significant effects of plot size (Dunn-Šidák corrected *p* < 0.05) were detected in 1992 and 1993 for both

Fig. 2. Mean (+ SEM) numbers of shoots produced by annual grasses and *Juncus bufonius* in controls (■), circular excavations (□), and rectangular excavations (▨). Order of treatments, sample sizes are as in Fig. 1.



Juncus and annual grasses. However, these two groups responded in opposite directions: *Juncus* was more common in larger plots, while annual grasses were more common in smaller plots (Fig. 2).

Plot centres versus edges

Most species groups initially tended to be at least as common near the edges of plots as at their centres, but this pattern often changed over time (Fig. 3); consequently, analyses were split by year. Perennial graminoids were more common near the edges of plots in 1991, as were bulbs in 1992, but were more common in the centres of plots by the following year (paired *t* tests; Dunn-Šidák *p* < 0.05). Dicots, annual graminoids, and annual grasses never differed significantly with respect to quadrat position, but *Juncus bufonius* was

Table 3. Effects of disturbance area and shape on the abundance of each species group.

Species group	Factor	df	MS	F
Bulbs	Shape	1	0.452	5.411*
	Size	3	0.405	4.847**
	Shape × size	3	0.230	2.751
	Plot (shape × size) [†]	32	0.084	
	Year	1	0.845	11.524**
	Year × shape	1	0.046	0.624
	Year × size	3	0.136	1.854
	Year × shape × size	3	0.077	1.043
	Year × plot (shape × size) [†]	32	0.073	
Perennial graminoids	Shape	1	0.043	0.394
	Size	3	0.713	6.540**
	Shape × size	3	0.140	1.285
	Plot (shape × size) [†]	32	0.109	
	Year	2	13.714	239.595***
	Year × shape	2	0.021	0.368
	Year × size	6	0.135	2.355*
	Year × shape × size	6	0.087	1.526
	Year × plot (shape × size) [†]	64	0.057	
Annual graminoids	Shape	1	<0.001	<0.001
	Size	3	0.154	0.806
	Shape × size	3	0.113	0.589
	Plot (shape × size) [†]	32	0.192	
	Year	2	8.186	110.351***
	Year × shape	2	0.106	1.424
	Year × size	6	0.356	4.796***
	Year × shape × size	6	0.020	0.274
	Year × plot (shape × size) [†]	64	0.0742	
Dicots	Shape	1	0.010	0.081
	Size	3	0.563	4.607**
	Shape × size	3	0.122	1.000
	Plot (shape × size) [†]	32	0.122	
	Year	2	1.634	27.425***
	Year × shape	2	0.004	0.068
	Year × size	6	0.149	2.496*
	Year × shape × size	6	0.123	2.061
	Year × plot (shape × size) [†]	64	0.060	

Note: Shown are the results of repeated-measures ANOVAs (SPF-pr.q fixed effects design; Kirk 1982). Data were log-transformed before analysis. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

[†]Error terms.

more common in the centres of plots in 1993 (paired t tests; Dunn-Šidák $p < 0.05$).

Soil seed and bulb banks

The size of the seed bank reached a maximum in late summer and a minimum in winter; numbers of bulbs were less variable (Fig. 4). Seedlings of at least eight species were observed (Table 5), but the active component of the seed bank was dominated numerically by annual graminoids (67% of all seedlings germinated); *Aira caryophyllea* alone contributed 44% of all seedlings, while *Juncus bufonius* contributed 22%. Dicots (three species) were very scarce, contributing only 2% of all seedlings. While bulbs were abundant (0.63/cm²), no seedlings of bulb-bearing species were detected.

Both bulbs and seeds declined rapidly in numbers with

depth (Table 5); as a result, the bias produced by not sampling the entire soil column was small. While bulbs, *Aira*, and *Juncus* were found in the deepest samples, 82% of the active seed bank and 89% of bulbs were located less than 4 cm from the soil surface (Table 5). Only *Juncus bufonius* was evenly distributed with respect to depth (48% deeper than 4 cm).

Seed dispersal

Seed dispersal was highly seasonal, with the total number of seeds trapped peaking from late May to June (Fig. 4). Seeds of eight species were trapped. Annual graminoids comprised 65% of the estimated total seed rain: *Aira caryophyllea* alone comprised 32%, while *Juncus bufonius* contributed 26%; *Bromus hordeaceus* and *Vulpia* spp. each contributed <5%. *Luzula subsemissilis* was the most common perennial grami-

Fig. 3. Mean (+ SEM) numbers of shoots at centres (■) and edges (□) of those plots ≥ 2500 cm² in area; *, a significant difference (Bonferroni $p < 0.05$). Sample size was 19–20 plots per bar. Bulbs were not sampled in 1991.

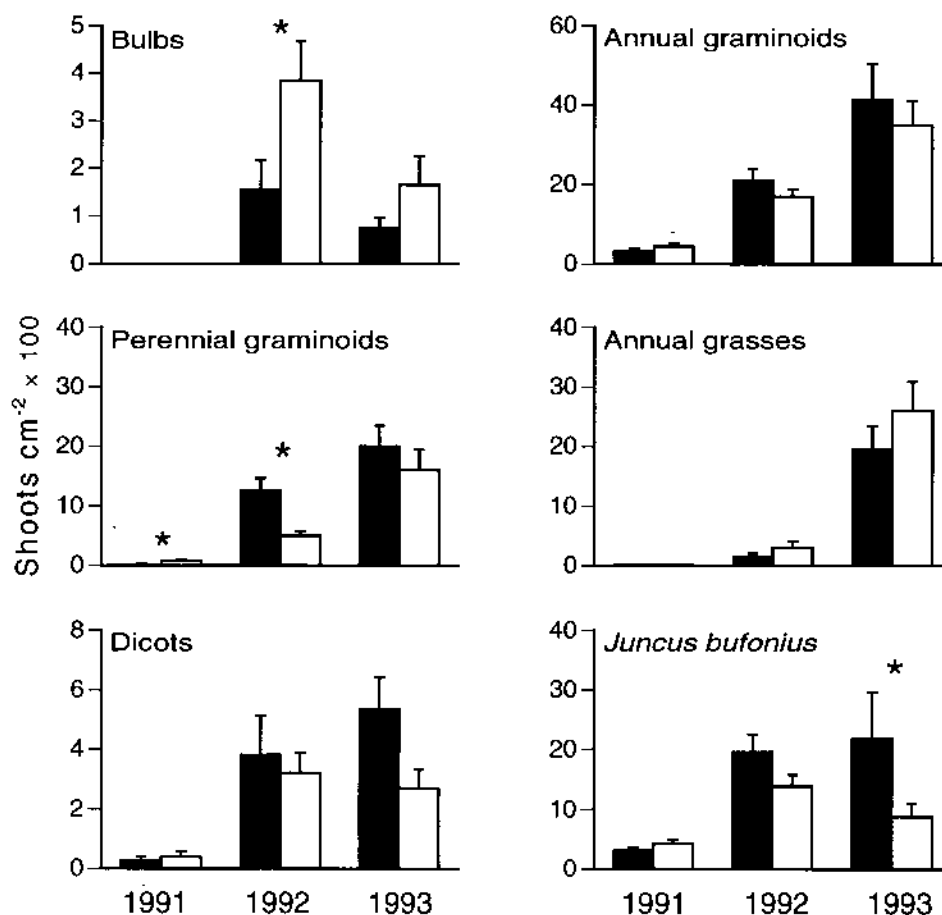


Table 4. Effects of disturbance area and shape on the abundance of *Juncus bufonius* and annual grasses.

Group	Factor	df	MS	F
<i>Juncus bufonius</i>	Shape	1	0.513	1.761
	Size	3	2.224	7.636***
	Shape \times size	3	0.216	0.742
	Plot (shape \times size) [†]	32	0.291	
	Year	2	1.235	11.804***
	Year \times shape	2	0.005	0.043
	Year \times size	6	1.035	9.892***
	Year \times shape \times size	6	0.126	1.205
	Year \times plot (shape \times size) [†]	64	0.105	
Annual grasses	Shape	1	1.133	8.094**
	Size	3	1.848	13.206***
	Shape \times size	3	0.188	1.344
	Plot (shape \times size) [†]	32	0.140	
	Year	2	16.986	225.253***
	Year \times shape	2	0.170	2.250
	Year \times size	6	0.359	4.760***
	Year \times shape \times size	6	0.087	1.149
	Year \times plot (shape \times size) [†]	64	0.075	

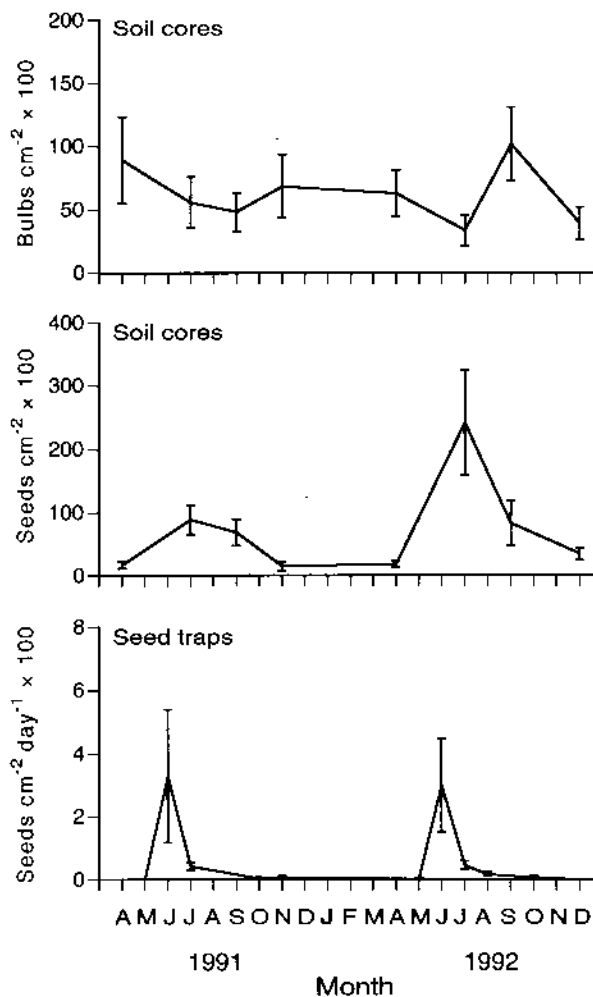
Note: Shown are the results of repeated-measures ANOVAs (SPF-pr.q fixed effects design; Kirk 1982). Data were log-transformed before analysis. **, $p < 0.01$; ***, $p < 0.001$.

[†] Error terms.

Table 5. Depth distribution of species represented in soil cores. Data represent mean (SEM) bulbs or seedlings cm^{-2} . Species codes for seedlings are as follows: perennials: Dc, *Danthonia californica*; Lz, *Luzula comosa*; annuals: Jb, *Juncus bufonius*; Ai, *Aira caryophyllaea*; Br, *Bromus* spp.; Dicots, all dicot seedlings. Sample size: $n = 39$ per cell.

Depth (cm)	Bulbs	Dc	Lz	Jb	Ai	Br	Dicots	Total seeds
0–2	0.370 (0.056)	0.017 (0.009)	0.203 (0.044)	0.024 (0.009)	0.145 (0.045)	0.014 (0.006)	0.007 (0.005)	0.405 (0.082)
2–4	0.196 (0.030)	0.002 (0.002)	0.002 (0.002)	0.057 (0.011)	0.119 (0.095)	0.000 (0.000)	0.005 (0.003)	0.186 (0.094)
4–6	0.048 (0.016)	0.002 (0.002)	0.000 (0.000)	0.029 (0.008)	0.021 (0.009)	0.000 (0.000)	0.000 (0.000)	0.052 (0.012)
8–10	0.019 (0.013)	0.000 (0.000)	0.000 (0.000)	0.045 (0.010)	0.031 (0.018)	0.000 (0.000)	0.000 (0.000)	0.076 (0.020)

Fig. 4. Mean (+ SEM) seeds and bulbs detected in soil cores and seed traps. Sample size was 4–5 per date (soil cores) and 8–10 per date (seed traps).



noid (27% of the seed rain) followed by *Danthonia californica* (6%) and *Holcus lanatus* (<1%). Seeds of only one dicot (*Eremocarpus setigerus*) were captured (1% of the seed rain), while no seeds of bulb-bearing species were detected. *Danthonia* is likely to have been under-represented, since some of its seeds are produced by cleistogamous flowers and dispersed with disarticulating culms (Crampton 1974; Campbell et al. 1984) that are too large to enter a seed trap; the bias against most other species should have been small, since most produced small dispersules at heights well above the 1-cm rim of the traps.

Discussion

Gap size and shape

Studies from habitats as diverse as forests (Denslow 1980; Runkle 1982; Brokaw 1985; Platt and Strong 1989; Phillips and Shure 1990), the rocky intertidal (Paine and Levin 1981; Sousa 1984b), old fields (Davis and Cantlon 1969; Reader and Buck 1991), and grasslands (Coffin and Lauenroth 1989; Arnthórsdóttir 1994; Bullock et al. 1995; Burke and Grime 1996) have shown that the size of a gap may have important effects on succession. I also found gap area to have significant effects; gap shape was much less important. As expected, these results were not the same for all species groups. Initially, those groups dominated by species able to survive disturbance (deep seed bankers) or with abundant seed dispersal (annual grasses) were less sensitive to gap size, shape and (or) distance to the edges of plots than groups whose members relied wholly or partly on clonal ingrowth (perennial graminoids, bulbs). In subsequent years, these initial patterns often were obscured or even reversed, probably reflecting responses to environmental and competitive conditions within gaps.

There are several explanations for the relatively small effects of gap shape. First, while gap diameters varied 8-fold and gap areas varied 64-fold, perimeter length and perimeter to area ratio varied only 1.4-fold between rectangular and circular gaps of the same area. Second, while the distance from the centre of a gap to the nearest edge was smaller for a rectangular gap than for a circular gap of the same area, the distance to the furthest edge was increased. As a result, almost half (49.4%) of the perimeter of each rectangle was more remote from its centre than was true for the corresponding circular gap (thanks to M. Weis for pointing this out). These calculations suggest that the effects of gap shape may have been underestimated by measurements taken near the centres of gaps; edge versus centre contrasts may be more sensitive indicators of the importance of gap shape or perimeter.

Arrival of colonists

The strong initial effects of gap size and shape on the abundance of bulbs might be expected from the manner in which these species migrate into disturbed plots. The locally common bulbs produce a few seeds, and are practically absent from the seed rain (Kotanen 1994a, 1996), but produce large numbers of vegetative bulblets, in some cases at the ends of subterranean runners (Hickman 1993; Kotanen 1994a, 1995, 1996). As the walls of the experimental excavations crumbled, many such bulblets were transported into these plots along with the collapsing earth. Since this could move bulblets only

a few centimetres, bulbs were strongly sensitive to both gap size and shape, occurring most frequently near the edges of gaps and in smaller, less circular gaps.

The weaker effects of plot size and quadrat position on annual graminoids illustrate one of the problems of aggregating species into functional groups. Annual graminoids evidently comprised a heterogeneous category containing two subgroups with distinct reproductive strategies: grasses and *Juncus bufonius*. The local annual grasses have shallow seed banks; as a result, they were removed from plots during their initial excavation and recolonized primarily by seed immigration. In contrast, *Juncus bufonius* was common in the deeper fraction of the seed bank as well as in the seed rain. It did not depend on immigration from the surrounding undisturbed vegetation, where it is very scarce (Kotanen 1995). One consequence of this difference was that, while *Juncus* never was more common in smaller gaps or near edges, annual grasses declined in abundance with increasing plot size after the first sampling. Given that annual grasses rely much more heavily on the seed rain than does *Juncus*, there are two reasons to expect this pattern. First, small gaps have a larger perimeter:area ratio than large gaps, probably leading to higher per-unit-area rates of seed immigration (Sousa 1984a). Second, smaller gaps probably are more sheltered from wind by the surrounding vegetation, reducing surface air velocity. As a result, a seed produced inside a small gap or deposited by gravity or eddy currents into its protected air is unlikely to be subsequently removed (Chambers and MacMahon 1994; Vogel 1994).

Perennial graminoids were subject to some of the same factors affecting recolonization both by bulbs and by annual grasses. Most of the locally common species (e.g., *Danthonia californica*, *Luzula comosa*) possess a bunchgrass morphology in which new tillers are produced very close to the parent shoot, and therefore have a very limited ability to spread clonally into a disturbed site. Consequently, like bulbs, perennial graminoids initially were most common in small plots and near the edges of plots. However, like annual grasses, perennial graminoids (especially *Luzula*) do commonly occur in the seed rain, though rarely in the subsurface seed bank. Immigrating seeds may have contributed to the higher numbers of perennial graminoids in smaller plots (see above), but also allowed perennials to permanently establish away from the walls of plots, gradually obscuring the patterns initially produced by clonal encroachment.

The scarcity of dicots in the seed rain and their weak response to plot dimensions and quadrat position suggest that, like *Juncus*, many of these species also may have recruited from buried seed, but were not detected in soil cores because the correct germination cues were not provided. The local dicots include many legumes, euphorbs, and other hard-seeded species (Kotanen 1995) that may require complex germination stimuli (Harper 1977; Fenner 1985, 1992; Baskin and Baskin 1989).

Later events

Initially, the revegetation of disturbed plots is likely to have been strongly limited by a scarcity of propagules (Kotanen 1996). The fact that most observed patterns of recolonization were consistent with patterns in propagule supply suggests that, at least initially, physical differences among gaps were not strong enough to obscure immigration-driven patterns.

Over time, however, the space within a newly created opening is likely to become increasingly saturated both by the continuing influx of immigrants and by the growth and reproduction of successful colonists within the gaps themselves. As well, as plots revegetate, the establishment of plants in their interiors may protect them from surface air currents (Chambers and MacMahon 1994), aiding in the trapping and retention of dispersing seeds, and further accelerating revegetation. As a result, the revegetation of a gap gradually should become less strongly influenced by constraints on immigration and more strongly controlled by environmental conditions and within-plot processes, such as competition and local seed production.

Gaps differ physically from the surrounding vegetation (Kotanen 1997). Excavated plots tend to be warmer, especially in the summer, experience more frost heave in winter, are less shaded, and are more frequently flooded. As well, because plant populations are severely reduced during gap creation, excavations initially may contain greater per-capita pools of nitrogen and water. Some of these physical conditions probably are little influenced by gap size or shape (e.g., flooding, soil nitrogen), but others may be significantly affected by gaps' dimensions. As often is the case for forest gaps (e.g., Platt and Strong 1989), physical conditions in smaller and narrower excavations probably deviate less from the physical conditions of the surrounding vegetation. For example, smaller and less circular gaps are more completely shaded by the surrounding vegetation than are larger, rounder gaps, and consequently should also experience lower temperatures, higher humidity, and possibly less frost heave. Over time, both differences among gaps and differences between gaps and the surrounding vegetation should gradually diminish as revegetation proceeds.

Despite the short duration of this study, within-plot processes may explain why some groups gradually developed patterns of abundance opposite to those predicted from considerations of immigration alone. For example, dicots were more abundant in larger plots in 1993, and both *Juncus bufonius* and perennial graminoids tended to be more common in the centres of plots than at their edges. These patterns probably reflect a performance advantage: plants often grow better or have a higher expectation of setting seed in larger gaps, in part because they are more isolated from competition with the surrounding vegetation (e.g., Goldberg and Werner 1983; McConnaughay and Bazzaz 1987, 1990; but see Burke and Grime 1996 for a counter example).

Refuges versus gaps

Discussions of reserve design often assume that larger and more circular habitat patches are better for the conservation of biodiversity than the converse (Simberloff 1988); discussions of disturbance and patch dynamics (Connell and Slatyer 1977; Sousa 1984a; Pickett and White 1985) suggest that smaller and less circular gaps often should be more rapidly revegetated. These views are different sides of the same coin: conservation emphasizes the stability of populations, while rapid recolonization demands that rates of population change be maximized. Large, circular gaps may extend the persistence of populations of gap-dependent species, just as large, circular forest remnants may be best for the preservation of forest species. Conversely, small, rectangular gaps may be a better choice if the goal is to increase, rather than

decrease, successional rates and the immigration of near-edge species.

Floristic considerations

My results emphasize that the importance of gap size and shape depend upon the reproductive strategies occurring in the local flora. If clonally spreading species are abundant, as is the case in many perennial grasslands, the dimensions of gaps may strongly affect revegetation (e.g., Coffin and Lauenroth 1989; Arnthórsdóttir 1994; Bullock et al. 1995). In contrast, if seed banks, highly dispersive seeds, or survivors provide most of the colonists, then gap size and shape initially may be less important (e.g., Uhl et al. 1988; Coffin and Lauenroth 1989; Bullock et al. 1995). A corollary is that the effects of different disturbances may be similar in some systems but not in others. For example, gopher mounds (ca. 100 cm²) and disturbances created by feral pigs (often many square metres) might be expected to support differing vegetation in highly clonal perennial grasslands, but perhaps not in dispersal-dominated annual grasslands. Lessons learned in one system may apply only in communities with similar reproductive spectra. If so, then functional classifications of reproductively diverse natural communities may be essential to our ability to adequately predict the effects of disturbance (McIntyre et al. 1995).

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