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Effect of seed predation on seed bank size and seedling recruitment of bush lupine (*Lupinus arboreus*)

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Abstract Whether seed consumers affect plant establishment is an important unresolved question in plant population biology. Seed consumption is ubiquitous; at issue is whether seedling recruitment is limited by safe-sites or seeds. If most seeds inhabit sites unsuitable for germination, post-dispersal seed consumption primarily removes seeds that would otherwise never contribute to the population and granivory has minimal impacts on plant abundance. Alternatively, if most seeds ultimately germinate before they lose viability, there is greater potential for seed consumption to affect plant recruitment. Of the many studies on seed consumption, few ask how seed loss affects seedling recruitment for species with long-lived seed banks. We examined post-dispersal seed predation and seedling emergence in bush lupine (*Lupinus arboreus*), a woody leguminous shrub of coastal grasslands and dunes in California. We followed the fate of seeds in paired experimental seed plots that were either protected or exposed to rodent granivores in grassland and dune habitats. Significantly more seeds were removed by rodents in dunes than grasslands. In dunes, where rodent granivory was greatest (65% and 86% of seeds removed from plots by rodents in two successive years), there is a sparse seed bank (6.6 seeds m^{-2}), and granivory significantly reduced seedling emergence (in the same two years, 18% and 19.4% fewer seedlings emerged from exposed versus protected plots), suggesting seed rather than safe-site limited seedling recruitment. In contrast, rodents removed an average of 6% and 56% of seeds from grassland plots during the same two years, and the grassland seed bank is 43-fold

that of the dunes (288 seeds m^{-2}). Even high seed consumption in the second year of the study only marginally influenced recruitment because seeds that escaped predation remained dormant. Burial of seeds in both habitats significantly reduced the percentage of seeds removed by rodents. Results suggest that granivores exert strong but habitat-dependent effects on lupine seed survival and seedling emergence.

Key words Bush lupine · Granivory · Seed bank dynamics · Seedling recruitment

Introduction

How much seed consumers influence plant population dynamics is an important unresolved question in plant population ecology. Seed-eating organisms are ubiquitous, and seed loss can be quite high (Louda 1989; Crawley 1992; Hulme 1993). Granivores thus have the potential to exert strong effects on plant populations by altering patterns of plant establishment. However, for plants that produce dormant seeds that persist in long-lived seed banks, the population effects of seed consumption can be difficult to detect. Although we know recruitment out of seed banks can significantly alter plant population growth, age structure, persistence, and overall dynamics (Mertz 1971, Templeton and Levin 1979; Chesson 1983; MacDonald and Watkinson 1981; Venable and Brown 1988; Kalisz and McPeck 1993), we seldom understand the biotic and abiotic factors that influence seed demography. Especially lacking are data on spatiotemporal variation in the strength of factors that affect seedling recruitment. These data are critical to understanding the population dynamics of plants with long-lived seeds (Horvitz and Schemske 1994).

Whether seed consumers actually limit plant establishment is increasingly debated (Andersen 1989; Crawley 1989; 1990, 1992; Louda 1994; Louda and Potvin 1995), and controversy centers on whether plant populations are seed or safe-site limited. If plant popu-

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lations are safe-site limited, seedling recruitment is set by the number of sites available for successful seedling establishment and not by seed density. Most seeds inhabit sites unsuitable for germination; granivores mainly remove those seeds that otherwise never contribute to the population and therefore granivory has minimal effects of future plant recruitment. Alternatively, if populations are seed-limited, the magnitude of recruitment is set by seed abundance. In this case, granivore-driven reduction in seed density can lead to lower seedling recruitment. Whether limitations on seedling recruitment ultimately affect adult plant density depends on the extent to which there is compensatory density dependent seedling survival. If density dependence is strong enough, even gains in seedling establishment may not be reflected in adult plant density.

Few of the many studies that document high seed consumption examine how seed loss affects seedling or adult plant recruitment. The classic example of strong granivore effects on plant establishment comes from deserts, where granivory on large-seeded annual plants alters plant community structure (Inouye et al. 1980; Brown et al. 1986; Brown and Heske 1990). Results from short-term exclusion of rodents from grasslands are mixed (Borchert and Jain 1978; Reader 1993), and in some quarters there is the notion that "seed limitation may be the exception rather than the rule" (Crowley 1992).

Here we examine how seed predation affects seed bank size and seedling emergence of bush lupine (*Lupinus arboreus* Sims; Fabaceae), a perennial shrub native to southern and central California coastal grasslands and dunes. We explore whether seedling recruitment and seed bank size are influenced by three important factors that affect seed demography: (1) post-dispersal seed predation, (2) seed viability, and (3) seed dormancy.

Methods

Study site and species

All study sites were located on the 147-ha Bodega Marine Reserve (BMR), in central coastal California. BMR sits on Bodega Head, a narrow peninsula that borders the San Andreas fault zone. Bush lupine occupies two distinct habitat types at BMR (Fig. 1). Grasslands on BMR are underlain with light coarse sandy loam soil formed from the decomposed diorite granite of the Pacific Plate. In this habitat, bush lupine is a dominant plant where it forms dense stands (approximate density: 0.31 bushes m^{-2} with contiguous canopies). The interstitial spaces between lupine patches are occupied by a matrix of native and introduced grasses and forbs (Barbour et al. 1973). Grasslands abruptly give way to dunes where the Pacific Plate abuts the San Andreas fault zone. The dunes are characterized by extensive shifting and stabilized sand. Bush lupines there are less dense (approximate density: 0.01 bushes m^{-2}) than in grasslands; isolated lupines are scattered throughout the habitat. The dune community is dominated by the introduced beach grass, *Ammophila arenaria*. Other dominant plants of the dune community include coyote bush, (*Baccharis pilularis*) and dune heather, *Ericameria ericoides*.

We conducted experiments and censuses at three sites in the grasslands and two sites in the dunes habitat (Fig. 1). Each site was 1–2 ha in size, with a lupine density that appeared representative of

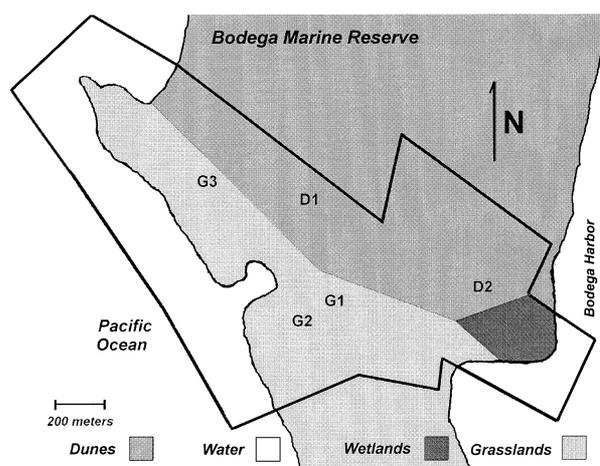


Fig. 1 Map of study area showing location of grassland and dune sites. Thick black line indicates boundary of Bodega Marine Reserve (BMR)

its habitat. Sites were separated by least 0.5 km (except for G1 and G2, which were separated by 200 m), and we treated each site as an independent replicate of habitat type. (Site G2 was previously referred to as "Upper Draw" by Strong et al. 1995).

Lupine seedling germination begins with the winter rains in late October and early November, peaks in late January and early February, and ceases with the end of the rainy season in April. Seedlings grow quickly and become large shrubs with canopies over 1 m in diameter by the time they first flower in their second spring. Relatively large seeds, weighing 0.015–0.07 g, are produced in leguminous pods which dehisce explosively in late July–August. The majority of seeds disperse within a few meters of their mother bush, but some seeds remain in opened dried pods that are retained on the bush until winter winds and rain dislodge them. Most lupine seeds have a "hard" seed coat (J.L. Maron, unpublished work), and as in most legumes, dormancy is physically enforced by a testa that prevents seeds from imbibing water (Hyde 1954; Rolston 1978). Dormancy may be broken by soil disturbance, oscillations in soil temperature, or other factors that scarify or crack the seed coat (Quinlivan 1961, 1966).

The primary consumer of dispersed lupine seeds at our site appears to be the deer mouse, *Peromyscus maniculatus* (Davidson 1975; E.L. Simms and J.L. Maron, unpublished work). These mice are common in both dune and grassland habitats, where they eat lupine seeds and nest under lupine shrubs, presumably for cover from avian predators (Barbour et al. 1973; Davidson 1975). Trapping studies at our sites indicate that *P. maniculatus* has a small home range size, (62–91 m^2 , E. Franklin, C. Lumas and R. Stein, unpublished work), which implies that different individuals inhabit each of our study sites. Short-term experiments indicate that predation on lupine seeds is greatest at night, when deer mice are active (E.L. Simms, J.L. Maron and J. Combs, unpublished work), and that mouse scat and tracks accompany the removal of lupine seeds from sand-filled dishes. The only other rodents present in both grasslands and dunes at our sites are voles (*Microtus californicus*), which generally feed on vegetative plant parts and are sparse in the dunes (Ostfeld 1985, 1992). Other short-term experiments indicate that the common granivorous birds at BMR (song sparrows, white-crowned sparrows, and house finches) avoid eating bush lupine seeds even while consuming intermingled palatable seeds from a commercial wild bird seed mix (E.L. Simms, unpublished work). Furthermore, in the present study, birds could not enter our experimental seed plots. Lupine seeds lack eliasomes and there are no seed-harvesting ants at our site.

Granivory experiment: a test of the effects of post-dispersal seed predation on seed loss and seedling emergence

To determine the fraction of lupine seeds that are eaten by mice, emerge as seedlings or remain dormant, we constructed paired experimental plots, from one of which mice were excluded. Each plot was established by removing a 30 cm × 30 cm × 15 cm deep block of soil from a haphazardly selected location beneath the outer edge of a lupine canopy. We lined the resulting pit with an open-topped woven wire box (mesh size = 0.636 cm × 0.636 cm), sieved the extracted soil through a 2-mm-mesh sieve to remove lupine seeds, and then returned it to the pit.

In August, we collected fully mature seeds from dried pods and added them to plots within 1–2 weeks after collection. We added 30 seeds to each plot, a density that lies within the natural range of the grassland lupine seed bank. Each plot received seeds from the shrub under which it was placed. In 1994 we placed all 30 seeds on the soil surface. In 1995 we divided each seed plot in two by burying a 30 cm × 15 cm piece of sheet metal down the center. On one side of the plot we placed 15 seeds on the soil surface and on the other side we buried 15 seeds by pushing them 2 cm into the soil. After adding the seeds, we covered the plots with senesced grasses and lupine litter. Mouse-exclusion plots were then covered with 32 cm × 32 cm × 2 cm tall mesh wire (mesh size = 0.636 cm × 0.636 cm) cages that were wired to the sides of the buried wire boxes to prevent entry by rodents.

To prevent seed rain into plots, in 1994 we constructed aluminum window-screen tents over each plot, and anchored them to the ground using metal stakes. In 1995 we used a slightly different design, creating open-sided tops out of woven wire (tops 50 cm × 50 cm × 7 cm tall; mesh size = 0.635) and covering these tops with aluminum window screen. Both types of tops allowed rodents to move under them.

In 1994 we placed nine pairs of plots under lupines at one dune site (D1), and six pairs of seed plots under lupines at a nearby grassland site (G1). In 1995, we placed six or seven pairs of seed plots at each of two separate dune sites (D1 and D2) and six to eight pairs of seed plots at each of three separate grassland sites (G1, G2, G3).

In both years, we censused plots for emerging seedlings every 2 weeks, starting after the first heavy rains in fall. At each census, we counted and removed all lupine seedlings that had emerged since the previous census. To determine whether protecting seeds from mice affected seedling emergence, we calculated the difference in seedling number between protected and exposed plots for each pair.

At the end of the germination season in late April, we sieved the soil from each plot to count the remaining lupine seeds. Relatively large lupine seeds are easy to separate from the sandy soil and we are confident that we were able to collect all seeds that were present in plots. Thus, in unprotected plots seeds unaccounted for in either the germination census or the final sieving were either removed by rodents or disappeared for other reasons. We assumed that for a given pair of plots, the caged and uncaged treatments had the same proportion of seeds missing for reasons other than granivory. Therefore, to estimate how many seeds were removed by mice, we subtracted the number of seeds and seedlings remaining in covered plots from the number of seeds and seedlings remaining in uncovered plots. If there were more seeds missing from the covered plot, then we assumed that there was no granivory in that pair of seed plots.

For analysis, we first examined if seed protection increased seed survival or seedling emergence. To do so, for each habitat we used a paired *t*-test to determine if mean seed and seedling numbers were different between exposed and protected seed plots. We used either a one-way ANOVA (for 1994–1995 data) or a nested one-way ANOVA (for 1995–1996 data; sites nested within habitat) to test for habitat differences in seed predation and seedling emergence. We used a *t*-test to examine interannual variation in seed predation. All analyses were performed using Systat (version 5.0 for Windows).

Seed bank density

To examine whether there were inter-habitat differences in seed bank size, we sampled lupine seed bank density at the outer canopy edge of mature lupines at the same sites we used for the granivory experiments. We sampled the seed bank at G1 and G2 and D1 and D2 in spring 1995 and at all three grassland and both dune sites in spring 1996. Within each site, we used a shovel to extract between six and eight 30 cm × 30 cm × 15 cm deep soil samples. Each sample was sieved, and all bush lupine seeds retained in the sieve were counted. We used a nested ANOVA (with sites nested within habitat type; Systat 5.0) to test whether there were significant differences between habitats in seed bank size.

Seed viability and seedling emergence

During 1992–1996 we took advantage of a natural experiment to quantify germination from the natural grassland seed bank. In 1992 a large dense stand of lupine (approximately 40,000 bushes) at the G2 site produced seeds and then died en masse in late summer. There were no lupines uphill from the G2 site and lupine seeds are too heavy to be wind dispersed in the grassland. Thus, assuming no long-distance transport of seed by mammals, there was probably no subsequent seed input to this site until 1995, when a small proportion of the seedlings that emerged in 1994 flowered (there was no seedling recruitment at this site in 1993).

In late summers of 1993, 1994, 1995 and 1996 we estimated the size of the seed bank at G2 by counting the lupine seeds sieved from six to ten 30 cm × 30 cm × 15 cm deep soil samples obtained from randomly chosen locations. Seeds obtained from these samples were at least 2 years old, and seeds obtained in July 1995 and 1996 were 3 and 4 years old, respectively. In 1996 we avoided areas that received seed input during summer 1995 by sampling soil at least 10 m from the few lupine plants that produced seeds in 1995. Each year, all seeds removed from these samples were tested for viability. Seed viability was estimated by scarifying each seed with a razor to break the hard seed coat, surface-sterilizing the seeds in a 10% bleach solution for 10 min, and then soaking the seeds in fresh water for 1 h. All seeds imbibed after this treatment. Imbibed seeds were covered on both sides with wet germination paper and placed in covered plastic potting flats in a dark unheated room. The temperature of this room was ambient, and varied between *c.* 4 and 19°C. Thereafter, seeds were examined daily to determine whether germination had occurred.

To examine how dormancy and viability change with seed age, in August of both 1994 and 1995 we buried seeds in 13 cm × 10 cm fiberglass window screen bags. We placed 24 fully developed fresh seeds in each bag and sealed the bags closed with a soldering iron. We covered the bags on both sides with woven wire (mesh size = 0.635 cm) to protect them from fossorial mammals and buried them 5 cm beneath the soil surface under the outer edge of lupine canopies. Bags buried in a particular site contained seeds collected only from bushes growing in that habitat.

In 1994 we buried 6 bags in the G2 grassland site, 12 bags in the G1 grassland site, and 12 bags in the D1 dune site. In May 1995 we excavated half the bags from two of the sites (six from D1 and six from G1). Seeds in these bags had been buried for one germination season (1994–1995), but six bags at each site remained buried for two germination seasons (1994–1996). In 1995 we buried bags under six bushes at two dune sites (D1 and D2) and three grassland sites (G1, G2, and G3). In May 1996 we excavated all remaining bags, so the last bags were buried for only the second germination season (1995–1996). Immediately after excavation, bags were opened and all remaining seeds counted and tested for viability, as above. We used a Mann-Whitney test (Systat 5.0 for Windows) to compare percent seed viability between grassland and dune seeds.

In February of 1993, 1994 and 1995, we estimated seedling density at this site by counting the number of lupine seedlings in each of 30–48 randomly placed 1-m-diameter circles. In 1996 we estimated seedling density by counting the number of seedlings that emerged from six 4 m × 4 m permanent plots that were placed in

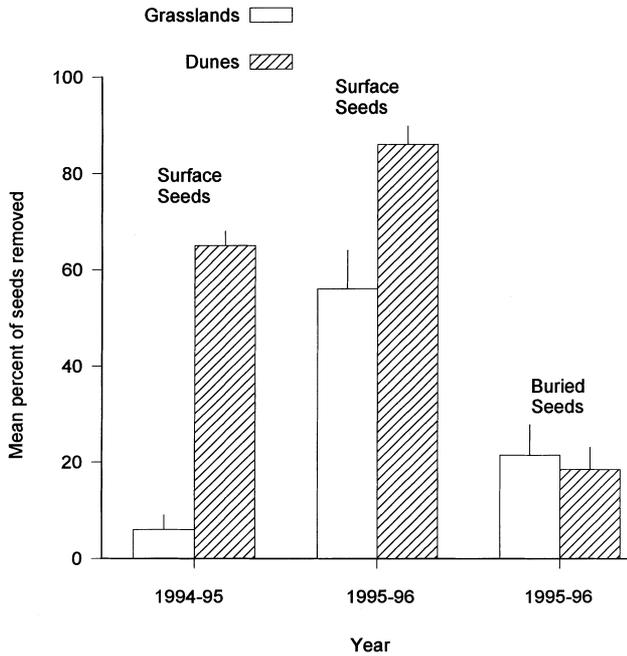


Fig. 2 Mean (± 1 SEM) percent of seeds removed from experimental seed plots exposed to mice. Seed plots placed within one grassland and dune site in 1994–1995 ($n = 6$ for grasslands $n = 9$ for dunes) and at three grassland sites and two dune sites in 1995–1996 ($n = 5$ –6 for grasslands, $n = 6$ –8 for dunes). See Methods for calculation of removal rates

randomly selected locations throughout the G2 as part of a separate study. To calculate the fraction of seeds that germinated, we divided seed density by seedling density. This is a conservative estimate of seed germination, since we only censused seedling density once, during the peak of germination, and some seedlings may have died before they were censused.

Results

Granivory experiment, 1994–1995

In dunes, granivores significantly reduced seed density (paired t -test, $t = 3.24$, $P < 0.01$); on average, mice removed 65% (\pm SEM 3%) of seeds from plots. In grasslands, however, an average of only 6% (\pm SEM 3%) of seeds were removed from plots, a non-significant effect (Fig. 2; paired t -test, $t = 0$, $P = 1.0$).

Some seeds were missing for reasons other than predation. Although we do not know the fates of seeds missing from protected plots, they likely died while dormant or while germinating but prior to emergence. Disappearance from protected plots did not differ between habitats (t -test, $t = -1.22$, $P = 0.24$). An average of 29% and 14% of seeds disappeared from protected plots in dunes and grasslands, respectively. Moreover, there was no significant difference between habitats in the germination percentage of seeds in protected plots (Fig. 3; ANOVA, $F_{1,13} = 0.31$, $P = 0.58$).

In the dunes, protecting seeds from mice not only decreased seed loss, but also enhanced seedling emer-

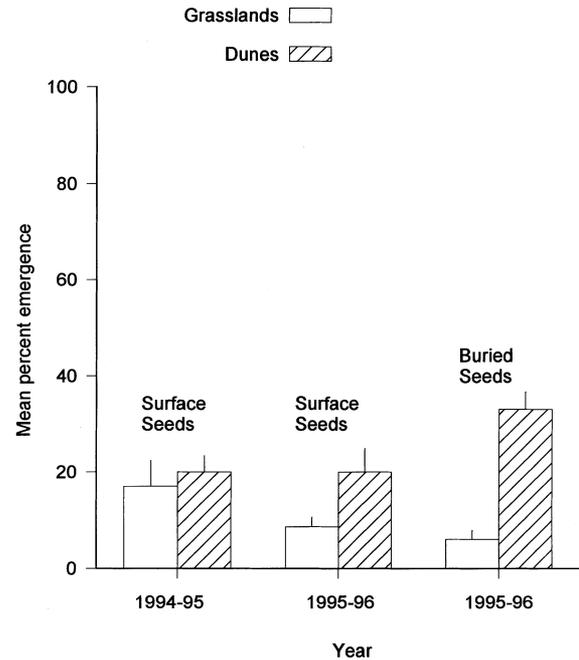


Fig. 3 Mean (± 1 SEM) percent of seeds that germinated and emerged from experimental seed plots protected from mouse granivory in 1994–1995 and 1995–1996. Seed plots placed within one grassland and dune site in 1994–1995 ($n = 6$ for grasslands, $n = 9$ for dunes) and at three grassland sites and two dune sites in 1995–1996 ($n = 5$ –6 for grasslands, $n = 6$ –8 for dunes)

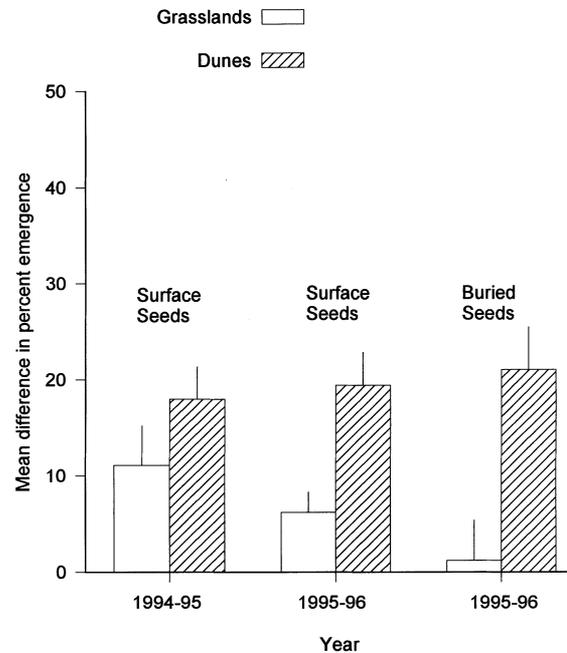


Fig. 4 Mean (± 1 SEM) difference in seedling emergence between pairs of protected and exposed experimental seed banks. Pairs of seed plots placed within one grassland and dune site in 1994–1995 ($n = 6$ for grasslands, $n = 9$ for dunes) and at three grassland sites and two dune sites in 1995–1996 ($n = 5$ –6 for grasslands, $n = 6$ –8 for dunes)

gence over that in exposed seed plots (Fig. 4; paired t -test, $n = 9$, $t = 3.123$, $P < 0.001$). In comparison, protection of seeds from mice in the grassland did not

affect seedling emergence (Fig. 4; paired *t*-test, $n = 6$, $t = 1.46$, $P = 0.2$).

Granivory experiment, 1995–1996

As in the previous year, granivory on unburied seeds significantly reduced seed density in dunes (ANOVA, $F_{1,24} = 523.3$, $P < 0.0001$). Unlike the previous year, granivores also reduced the density of unburied seeds in the grasslands (ANOVA, $F_{1,28} = 577.0$, $P < 0.0001$). Seed loss nevertheless remained significantly greater in dunes than grasslands (Fig. 2; ANOVA $F_{1,26} = 12.37$, $P < 0.002$), with an average of 86% (\pm SEM 3.8%, 2 sites) and 56% (\pm SEM 8%, 3 sites) of seeds removed from dune and grassland plots, respectively. Within dunes, the intensity of rodent granivory on surface seeds was not significantly different between years (*t*-test, $t = -1.64$, $P = 0.11$). In grasslands, however, surface seed loss was significantly lower in 1994–1995 than 1995–1996 (*t*-test, $t = 32$, $P = 0.004$).

Granivory also significantly reduced the density of buried seeds (ANOVA, $F_{1,24} = 6.7$, $P < 0.01$ for dunes, $F_{1,28} = 9.0$, $P < 0.006$ for grasslands), although burial reduced seed removal rates compared to surface seeds (Fig. 2; paired *t*-test, $n = 17$, $t = 3.4$, $P < 0.004$ for grassland and $n = 14$, $t = 11.2$, $P < 0.0001$ for dune sites). In contrast to surface seeds, predation on buried seeds did not differ between habitats (ANOVA; $F_{1,26} = 0.11$, $P = 0.75$). In dunes, an average of 19% (\pm SEM 4.5%) of buried seeds were lost to rodent predation, whereas in grasslands, an average of 21% (\pm SEM 6.3%) of buried seeds were taken by mice.

Seed loss from protected plots was significantly greater in grasslands than dunes (mean seed loss from covered plots = 22% \pm 2.2% in grasslands and 14% \pm 2.0% in dunes; ANOVA, $F_{1,26} = 7.9$, $P < 0.009$). Within each habitat, loss of seeds protected from granivory was not influenced by burial (paired *t*-test, $n = 14$, $t = 1.91$, $P = 0.38$ for dunes and $n = 17$, $t = 0$, $P = 1$ for grasslands), so that germination and seedling emergence were significantly greater in dunes than in grasslands, for both surface (ANOVA $F_{1,26} = 6.6$, $P < 0.017$) and buried (ANOVA, $F_{1,26} = 43.2$, $P < 0.001$) seeds (Fig. 3).

Protecting surface seeds significantly increased seedling recruitment in both habitats (Fig. 4; paired *t*-test, $n = 14$, $t = 2.8$ for dunes and $n = 17$, $t = 2.99$, $P < 0.009$ for grasslands). Although seed protection significantly increased seedling emergence from surface seeds in grasslands (by an average of 0.93 seedlings/plot, a 6% increase in recruitment), the magnitude of this effect was greater in dunes than grasslands (ANOVA, $F_{1,26} = 8.36$, $P < 0.008$). Moreover, protecting buried seeds significantly increased seedling emergence in dunes (paired *t*-test, $n = 14$, $t = 2.4$, $P < 0.002$) but not in grasslands (paired *t*-test, $n = 17$, $t = 2.59$, $P = 0.85$). Thus, although protecting dunes seeds from granivory significantly enhanced seedling recruitment, in grasslands the effect was slight.

Seed bank density

The natural density of lupine seeds in the soil was substantially higher in the grassland than the dune habitats in 1995 (ANOVA, $F_{1,23} = 8.25$, $P < 0.009$). Seed bank density averaged 275 (\pm SEM 128) and 254 (\pm SEM 44) seeds m^{-2} at the G2 and G3 grassland sites, respectively. In contrast, the seed bank near lupines in dunes was sparse, and averaged 7.3 (\pm SEM 3.6) and 42.2 (\pm SEM 15.4) seeds m^{-2} at the D1 and D2 sites, respectively. In 1996, there were again statistically significant differences in seed bank size between habitats (ANOVA, $F_{1,28} = 44.9$, $P < 0.009$), with the seed bank under bushes in three separate grassland lupine stands averaging 601 (G1), 194 (G2), 182 (G3) seeds m^{-2} while the seedbank under lupines at the two dune sites averaged 11.1 seeds m^{-2} .

Seed viability and seedling emergence

At G2, 83% of dormant seeds at least 2 years old (out of 30 seeds dug from the soil in August 1994) were viable and 59% of those at least 3.75 years old (out of 119 dug from the soil in May 1996) were viable.

The majority of seeds buried in bags for 8 months remained dormant. An average of 51% (\pm SEM 8.2) and 41% (\pm SEM 2.5) of buried seeds remained dormant in grasslands and dunes, respectively, during 1994–1995 and an average of 74% (\pm SEM 4.6) and 51% (\pm SEM 0.6) of buried seeds remained dormant in grasslands and dunes, respectively, during 1995–1996. Dormancy declined with burial time. After 20 months of burial an average of 25% (\pm SEM 5.7) and 16% (\pm SEM 4.6) of seeds remained dormant in grasslands and dunes, respectively.

An average of 91% ($n = 6$ bags, mean number seeds/bag = 9.8) and 82% ($n = 7$ and 6 bags at the two dune sites, respectively; mean number seeds/bag = 13) of seed buried in dune habitats in 1994–1995 and 1995–1996 were viable. In grassland habitats, seed viability after 8 months of burial was 100% ($n = 6$ bags; mean number seeds/bag = 11.8) in 1994–1995 and 94% in 1995–1996 ($n = 6$ bags at each of three sites, mean number of seeds/bag = 14.5). In neither year was there a significant difference between habitats in seed viability (Mann-Whitney $U = 48$, $P = 0.18$ for 1994–1995, $U = 154$, $P = 0.18$ for 1995–1996).

The number of seeds that remained dormant declined with increasing duration of burial (Fig. 5), but their viability did not decline with time. Average viability of seeds buried in dunes and grasslands was 100% ($n = 5$ bags; mean number seeds/bag = 3.0) and 92% ($n = 6$ bags at each of two sites; mean number of seeds/bag = 10.6), respectively.

Average seedling density in grasslands was 0 ($n = 40$), 1.7 ($n = 30$) and 6.8 ($n = 48$) individuals m^{-2} in 1993, 1994, and 1995, respectively. Thus the percentage of

buried seeds that emerged during these years was 0, 0.67%, and 2.4%, respectively.

Discussion

We found substantial differences in the amount of predation on lupine seeds between nearby habitats. Seed predation in dunes was intense. Only 35% and 14% of seeds in experimental plots escaped predation in experiments replicated in two separate years. In contrast, seed predation was lower in grasslands; 94% and 44% of grassland seeds escaped predation during the same two years. Seed burial significantly reduced seed removal, and in both habitats only between 18.5% and 21.5% of buried seeds were removed by rodents. These results resemble those from many studies of granivory, in which seed predation can be high but extremely variable depending on microhabitat, habitat, and burial (reviews in Louda 1989; Crawley 1992; Hulme 1993).

For granivores to impose top-down effects on plant populations, seed consumption must inhibit seedling recruitment. If the number of safe-sites is low, high seed mortality may have little or no effect on seedling recruitment (Andersen 1989; Crawley 1992). We found habitat-specific effects of granivory on seedling recruitment. In dunes, where rodent granivory was greatest, there is a sparse seed bank and protecting seeds increased seedling emergence, suggesting seed rather than safe-site limited seedling recruitment. In contrast, our results suggest that grassland populations were safe-site limited. Even high seed consumption (in 1995–1996) only marginally influenced recruitment because seeds that escaped predation remained dormant.

Short-term data, however, may be inadequate for demonstrating that seed density does not limit grassland seedling recruitment. Dormant lupine seeds retain viability for long periods in the soil. We found that *L. arboreus* seeds buried in bags up to 20 months maintained 92–100% viability. Among seeds sampled from the natural seed bank that were a minimum of 46 months old, 59% were viable. Lupine germination out of the seed bank is notoriously episodic; across years, seedling density at G2 has ranged between 0.13 and 64 seedlings m^{-2} (Davidson 1975; J.L. Maron, unpublished work). Bursts of germination lead to the formation of dense even-aged stands. During these episodic events, seed density may limit recruitment. This, in fact, may be generally true for plants with similar recruitment dynamics. Episodic recruitment is common (Christensen 1985) and disturbance and recruitment are often coupled (Grubb 1988). Mass germination and high seedling emergence follow disturbance because it provides both the physiological cues that many seeds need to germinate and enhances seedling establishment by removing safe-site limits on recruitment. Fire, for example, removes above-ground vegetation that otherwise might inhibit germination or seedling survival (Christensen and Muller 1975). If germination-triggering disturbances

allow sufficiently high seedling establishment, seedling density may correlate with seed density, and plant populations may suffer “episodic seed limitation.” Chronic granivory can affect plant populations by limiting the number of seeds available to germinate during these episodes. Whether this occurs is unknown, but it is more likely to be important for species such as lupines, which have relatively large seeds and moderate-sized seed banks. We suggest that short-term observations may incorrectly lead to the conclusion that safe-site limitation of recruitment prevents granivory from affecting plant density.

Increasing seedling establishment by protecting seeds from granivores may not increase adult density if density-dependent seedling survival is fully compensatory. Lupine seedling survival, however, is not strongly density dependent; manipulating seedling density over 3-fold had no significant effect on survival (J.L. Maron, unpublished work). Moreover, episodes of high recruitment lead to dense stands. Davidson (1975) commented that lupine populations appear to “pulsate” as disproportionately large age-classes move through a population’s age structure through time.

Given the higher rates of seed loss from granivory and germination in dunes compared to grasslands, it seems likely that differential seed loss contributes to the large habitat differences in seed bank size. Differences in seed rain between habitats may also play a role in seed bank size, however. Lupine cover is much greater in grasslands compared to dunes, and since bushes in the two habitats produce similar numbers of seeds (J.L. Maron and E.L. Simms, unpublished work), seed rain is probably also greater in grasslands.

Habitat differences in the intensity of rodent granivory might result from higher densities of *P. maniculatus* in dunes, greater per capita consumption of lupine seeds in dunes, or predator satiation in the grasslands. Mark and recapture studies of mice in late summer, when seed predation is intense, indicate similar relative densities in the two habitats (E.L. Simms and J.L. Maron, unpublished work). The cover provided by senesced annual grasses may reduce per capita seed consumption in grasslands relative to dunes, where seeds are dispersed onto bare sand. Other studies have similarly found that plant cover significantly reduces seed predation risk (Ashby 1967; Harvey and Meredith 1981; Mittelbach and Gross 1984; Webb and Willson 1985; Schupp 1988; Willson 1988; Holmes 1990; Hulme 1994; Myster and Pickett 1993; Reader 1993). Although deer mice lack cheek pouches, they do cache seeds (Howard and Evans 1961; Barbour et al. 1973; Tadlock and Klein 1979), which suggests that differential satiation is unlikely to be an important cause of habitat differences in granivory.

One potential shortcoming of our experiments is that we could not follow the demographic fate of seeds after they were removed from plots. Although we cannot rule out the possibility that seeds removed from plots were cached rather than eaten, other studies suggest that

caching may not significantly alter our conclusions. For example, in one study in Michigan, although mice began storing seeds in mid-October, much of the stored food was gone by the end of December, and by March it had all disappeared (Howard and Evans 1961). Furthermore, at nearby Point Reyes, California, Boyd (1991) found some caching of *Cakile maritima* seeds by *P. maniculatus*, but determined that the vast majority of seeds taken by mice were consumed or otherwise lost to the plant population.

Our results suggest that habitat differences in granivory play an important role in generating spatial patterning in both seed bank density and the mode by which seedling recruitment is limited. In the dune habitat, rodent consumption of relatively large lupine seeds has an effect analogous to that in desert systems, in which rodent granivory reduces the seed bank and thereby limits recruitment of large seeded annuals (Brown et al. 1986; Inouye et al. 1980; Brown and Heske 1990). Indeed, one of the desert plants most affected by long-term rodent exclusion is also a lupine; rodent exclusion produced an 8-fold increase in *Lupinus sparsiflorus* density (Brown et al. 1986). In contrast to the dune habitat, where *L. arboreus* recruitment is seed limited, short-term data imply that recruitment is safe-site limited in grasslands. Thus, our data suggest that a species can be limited by safe-sites in one habitat but seeds in another, even in the same year. Whether grassland lupine populations are ultimately seed limited remains an open question, however. While short-term studies such as this one can successfully identify seed limitation on recruitment, dormancy in the seed bank and episodic germination bouts dictate that long-term studies are necessary to rule out seed limitation in this species. We also agree with Eriksson and Ehrlén (1992), who argue that absence of evidence for seed limitation does not necessarily indicate that recruitment is safe-site limited.

Concern about whether seeds or safe-sites limit recruitment in plant populations is motivated by the larger question of whether consumers influence plant population dynamics. We propose that the most fruitful empirical approach to this question is long-term consumer exclusion experiments to determine directly how consumers influence plant population dynamics. Our results suggest, however, that the issue is not whether consumers affect plant populations, but under what circumstances. It appears likely that the world remains green (*sensu* Hairston et al. 1960) because consumers influence plant population dynamics in some situations but not others. If so, then future research should be directed toward determining the ecological factors underpinning spatial and temporal variation in the extent of consumer influence on plant populations.

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