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Rodent seed predation and seedling recruitment in mesic grassland

Received: 2 March 1998 / Accepted: 28 September 1998

Abstract Seedling recruitment of two grasses (*Arrhenatherum elatius* and *Festuca rubra*) and two herbs (*Centaurea nigra* and *Rumex acetosa*) was measured in areas with and without rodents to which seeds of each species were sown at three seed densities (1000, 10,000 and 50,000 seeds m^{-2}) in two seasons (spring and autumn 1995). Seed removal was measured for 10-day periods and the fate of seedlings was followed for 15 months after sowing. The proportion of seed removed ranged from 6 to 85% and increased with increasing seed density for each species. Rodents had no effect on seedling emergence or survival in the spring sowing. In the autumn sowing, rodents reduced seedling emergence of all four species sown at 1000 and 10,000 seeds m^{-2} but had no impact at 50,000 seeds m^{-2} , presumably because of microsite limitation. We suggest the difference between spring and autumn arose because emergence was seed limited in autumn but microsite limited in spring; microsite availability was higher in autumn because a summer drought killed plants, reduced plant biomass and opened up the sward. Fifteen months after the autumn sowing, fewer *A. elatius* and *C. nigra* seedlings survived on plots exposed to rodents. This result reflected not only the reduced seedling emergence but also increased seedling mortality (seedling herbivory) in sites exposed to rodents. In contrast, *F. rubra* and *R. acetosa* showed density-dependent seedling survival which compensated for initial differences in seedling emergence, so that no effect of rodents remained after 15 months. The results suggest that rodent seed predation and seedling herbivory exert strong

effects on seedling recruitment of *A. elatius* and *C. nigra* when recruitment conditions are favourable (conditions that lead to high microsite availability) and may contribute to both species being maintained at low densities in the grassland. The results also demonstrate that highly significant impacts of rodent seed predation at the seedling emergence stage can disappear by the time of plant maturation.

Key words Seed density · Seedling emergence · Small mammal

Introduction

Post-dispersal seed predators have been shown to cause considerable seed loss in a wide variety of plant communities (Janzen 1971; Louda 1989; Crawley 1992). Thus, seed predators have the potential to exert a strong influence on plant populations by altering rates and patterns of plant recruitment (Crawley 1992). The best examples of this come from desert annual plant communities (Inouye et al. 1980; Davidson et al. 1984; Brown and Heske 1990), where there is a strong positive relationship between seed supply and plant recruitment. However, for populations of perennial plants there is often no relationship between the density of seed in the seed rain and the density of recruits into the population (Putwain et al. 1968; Peart 1989), and the impact of seed predators is less clear (Crawley 1992). If plant recruitment is limited by factors other than seed availability (e.g. by microsite availability or competition from established vegetation), then seed predators may simply kill seeds that would never have contributed to the population.

A number of authors have suggested that whether or not seed predators actually reduce plant recruitment may be related to seed density (Harper 1977; Anderson 1989; Crawley 1997). It is argued that there is a greater opportunity for subsequent density-dependent processes to compensate for seed losses (e.g. a shortage of mi-

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crossites, seedling competition) at high than at low seed densities. Consequently, seed predation might be expected to have a greater impact on seedling recruitment at low than at high seed densities (Crawley 1992). However, this may depend on how predator foraging behaviour is related to seed density. While some studies have found seed predation to be seed density independent (O'Dowd and Hay 1980; Webb and Willson 1985), some have found it to be inversely density dependent (i.e. predator satiation; Salisbury 1942) and others have found it to be directly density dependent (i.e. a lower proportion of seeds removed at low than high seed densities; Casper 1988; Hulme 1994a).

Here we describe an experiment on the effect of rodent seed predators on plant recruitment in a mesic grassland dominated by perennial herbaceous plant species. The work set out to address three related questions:

- (1) Is the rate of seed predation by rodents responsive to seed density?
- (2) Does seed predation by rodents reduce seedling establishment and adult plant density? Previous studies in perennial grasslands have shown that rodents can reduce seedling establishment (Reader and Buisson 1991; Reader 1993) but these studies have been too short-term to assess whether these reduced seedling densities persist to become reduced adult plant densities.
- (3) Is the effect that rodents have on plant recruitment related to seed density?

We conducted the study by sowing seeds of two perennial herbs (*Centaurea nigra* L. and *Rumex acetosa* L.) and two perennial grasses (*Arrhenatherum elatius* L. and *Festuca rubra* L.) into mature, undisturbed grassland that was protected from or exposed to rodents. We chose to work with these species because of their contrasting dynamics in the grassland at the experimental site (Nash's Field, Silwood Park). In experiments set up to investigate the interacting effects of herbivory, competitive release and soil nutrients, we have found that *A. elatius* and *C. nigra* are uncommon, while *F. rubra* and *R. acetosa* are among the most abundant species (M.J. Crawley and G.R., Edwards unpublished data). By studying species that vary in their local abundance within the grassland, we hoped to assess whether rodent seed predation and seed limitation contributed to the observed patterns of relative abundance. In particular, we hoped to assess whether rodent seed predation was an important factor leading to the general scarcity of *A. elatius* and *C. nigra*.

Materials and methods

Study site

The study was carried out during 1995 and 1996 in Nash's Field, Silwood Park (National Grid reference 41/944691), a species-poor grassland on acid, sandy soil with a long history of rabbit grazing

(National Vegetation Classification, MG7; Rodwell 1992). The grassland was dominated by the grasses *Agrostis capillaris* L., *F. rubra* and *Holcus mollis* L., and the herbs *Galium saxatile* L., *R. acetosa* and *R. acetosella* L. The vegetation cover was continuous except for a few molehills (<1% of the soil surface disturbed; G.R. Edwards, unpublished data), and these were avoided when quadrats were placed for the seed removal and seedling recruitment study. There was also a thick (2–3 cm) bryophyte layer, consisting mainly of *Rhytidiadelphus squarrosus* (Hedw. Warnst) and *Pseudoscleropodium purum* (Hedw. Fleisch). The experiment was conducted within a 35 × 20 m area that had been fenced with 3-cm square wire mesh to exclude rabbits in February 1995. The experimental area was bounded on two sides by a birch (*Betula pendula* Roth.) woodland and on the other two sides by grassland. The experimental site experiences an average annual rainfall of 653 mm with little seasonal pattern. Annual rainfall in both 1995 and 1996 was substantially below the long-term average and there was an extremely severe drought during spring and early summer of 1995. Nomenclature follows Stace (1995).

Rodent exclusion treatments

Rodents were excluded from parts of the grassland using cages made of 0.64-cm-square wire mesh. This mesh size has been shown to be highly effective in excluding rodents in previous studies (Hulme 1994a,b). The cages were 50 cm high, covered a 25 × 25 cm area, and were fastened to the ground using metal pins. The cages had a wire mesh roof to prevent rodents that climbed up the sides of the cage from entering it and consuming seed. The cages also excluded avian seed predators but did not exclude invertebrate seed predators like ants or carabid beetles. The rodent exposure treatment (cage control) used the same cages as the exclusion treatment except that 15 × 15 cm squares of wire mesh were cut out of two walls of the cage at ground level. Previous studies have shown that rodents enter through these holes and consume seed with no apparent reluctance (M.J. Crawley, unpublished data; R. Field, unpublished data). By using cage controls for the rodent access treatment, we were able to control for possible effects of the enclosure cage on microclimatic conditions, and hence to exclude direct, negative effects of the enclosure cage on seedling recruitment and growth.

Species and seed densities

Detailed studies of seed predation and seedling recruitment were carried out for four species (*A. elatius*, *C. nigra*, *F. rubra* and *R. acetosa*), chosen to represent a range of seed and seedling sizes (Table 1) and average population densities in Nash's Field (see Introduction). Four seed densities were used (no seed added, seed added at 1000, 10,000 and 50,000 seeds m⁻²). These seed densities encompass the normal range of localized seed rain in Nash's Field (G.R. Edwards and M.S. Heard, unpublished data).

Table 1 Mean seed and seedling size (SE in parentheses) of the four species sown into grassland in spring and autumn 1995. Mean seed mass was calculated by weighing 100 individual seeds of each species. Mean seedling mass was calculated by weighing 40 seedlings of each species at 1 week of age. Seedlings were grown as individual plants in the glasshouse

Species	Seed mass (mg)	Seedling mass (mg fresh weight at 1 week)
<i>Arrhenatherum elatius</i>	2.19 (0.27)	14.61 (0.77)
<i>Centaurea nigra</i>	2.46 (0.18)	16.55 (1.41)
<i>Festuca rubra</i>	0.69 (0.51)	5.01 (0.23)
<i>Rumex acetosa</i>	0.79 (0.05)	10.31 (0.69)

Seed removal experiment

Seed removal from experimental patches of different seed densities was compared in sites protected from and exposed to rodents. The experiment was carried out twice: seeds were sown on 20 March 1995 (spring) and again on 20 September 1995 (autumn). Both experiments were conducted in the same experimental area and had the same experimental design. The treatments were a factorial combination of 2 rodent seed predation treatments (excluded, present) \times 3 seed densities (1000, 10,000 and 50,000 seeds m^{-2}), each replicated four times. A total of 96 Petri dishes, each 9 cm in diameter, were laid out at 2-m intervals in a 8×12 grid, and the treatments for the four species were randomly assigned to each location (3 seed densities \times 2 cages \times 4 replicates \times 4 species = 96 dishes). Each dish was carefully nestled into the bryophyte and litter layer and a cage was placed over the top. A plastic sheet was placed over the roof of each cage to protect the seeds from rain. Seeds were presented for 10 days within each dish on a surface of fine sand at rates approximately equivalent to 1000, 10,000 and 50,000 seeds m^{-2} (area dish = $6.36 \times 10^{-3} m^2$; 7, 64 and 318 seeds, respectively). The seeds and sand remaining in each dish were placed in a plastic bag and returned to the laboratory for counting. In this study, we considered removal from the dishes to be equivalent to predation, since most seeds are either consumed locally or placed in deep larder stores from which there is little successful establishment (Montgomery and Gurnell 1985). Any damaged seeds we encountered were classified as removed.

Seedling recruitment

Seedling recruitment from seeds sown at different seed densities was compared in sites protected from or exposed to rodents. The seedling recruitment experiment was conducted twice: seeds were sown on 2 April 1995 (spring) and again on 16 September 1995 (autumn). Both experiments were conducted in the same experimental area and had the same experimental design. A total of 128 quadrats, each measuring 25×25 cm, were laid out at 2-m intervals in a 8×16 grid and four replicates of the treatments were randomly allocated: 4 seed densities (0, 1000, 10,000 and 50,000 seeds m^{-2}) \times 2 rodent exclusion treatments \times 4 species \times 4 replicates = 128 plots. We used plots with no seeds added to measure the natural recruitment from the seed bank and seed rain. Seeds were sown by hand onto the vegetation in each quadrat and no attempt was made to force seeds to the soil surface or to bury seeds. For the spring sowing, cages were fixed into place immediately after sowing. For the autumn sowing, seeds were sown into cages that had been erected in late June. We erected cages approximately 2.5 months prior to sowing, before seed dispersal of most species in Nash's Field, allowing us to examine the effect of seed predation of the natural seed rain on seedling recruitment. The grid of quadrats used in the autumn-sowing experiment was different from that used in the spring-sowing experiment, being offset 1.5 m to the east.

Our definition of successful seedling recruitment is that a seedling must survive to at least 1 year of age or to flowering (if this occurs within 12 months of germination). Thus, seedlings are not necessarily recruits, and recruitment can be considered to be comprised of two stages: (1) germination and emergence followed by (2) seedling survival and growth (see also Cook 1980). We followed the fate of seedlings that emerged for 15-month periods after seeds were sown (until June 1996 for the spring sowing, and until December 1996 for the autumn sowing). Censuses were made every 2 weeks in the first 2 months after sowing and every 2 months after that. At each census, any new seedlings were tagged with a toothpick inserted into the soil nearby and their location marked on a map of the quadrat. Seedlings were recorded as either live or dead, with all missing seedlings recorded as dead. It was not possible to assign a cause of death to seedlings as most were extremely desiccated or missing completely. The

seedling identification key of Hanf (1983) and a seedling herbarium of all species present at the site (made by the authors) were used in seedling identification. Flowering stems of *A. elatius*, *F. rubra* and *R. acetosa*, and capitula of *C. nigra* were counted in all quadrats in late June 1996.

Statistical analysis

The effects of seed predation, seed density and the interaction of these effects on seed removal, seedling emergence, seedling survival and flowerhead production were analysed by analysis of deviance using the statistical package GLIM (NAG 1985). In all analyses, an appropriate error structure (Poisson or binomial) ensured that the residuals were constant and normally distributed. The proportion of seeds removed from Petri dishes, the proportion of sown seeds that emerged, and seedling survival were analysed using binomial errors, while the number of seedlings that emerged, the number of seedlings surviving, and flowerhead production were analysed using Poisson errors. Where Poisson or binomial models were over-dispersed, a scale parameter was estimated empirically and *F*-tests rather than χ^2 tests were used (Crawley 1993). Each species was analysed separately.

Results

Seed predation

Spring

For all four species, there was a significant effect of the interaction between rodent exclusion and seed density on the proportion of seeds removed from experimental patches in spring ($F_{2,18}$: *A. elatius* = 4.1, *C. nigra* = 4.8, *F. rubra* = 3.9, *R. acetosa* = 4.1, $P < 0.05$; Fig. 1a). The proportion removed increased with increasing seed density in patches to which the rodents had access, while the proportion removed from patches from which rodents were excluded was low (<21%) and did not change with seed density. We do not know what caused the seed loss inside the rodent exclusion cages, but possibilities include seed predation by invertebrates, raindrop splash and wind. We did not make any quantitative assessment of the rodent population, but wood mouse (*Apodemus sylvaticus*) and harvest mouse (*Micromys minutus*) were caught in Longworth traps at the site.

Autumn

The same trends for seed removal that occurred in the spring experiment occurred in the autumn experiment (significant rodent exclusion \times seed density interaction, $F_{2,18}$: *A. elatius* = 5.3, *C. nigra* = 5.2, *F. rubra* = 4.3, *R. acetosa* = 4.9, $P < 0.05$; Fig. 1b). When data from all species and both seasons were combined, we found no significant effect of season ($F_{1,144} = 0.52$, $P > 0.05$) or species ($F_{3,144} = 2.01$, $P > 0.05$) on the proportion removed.

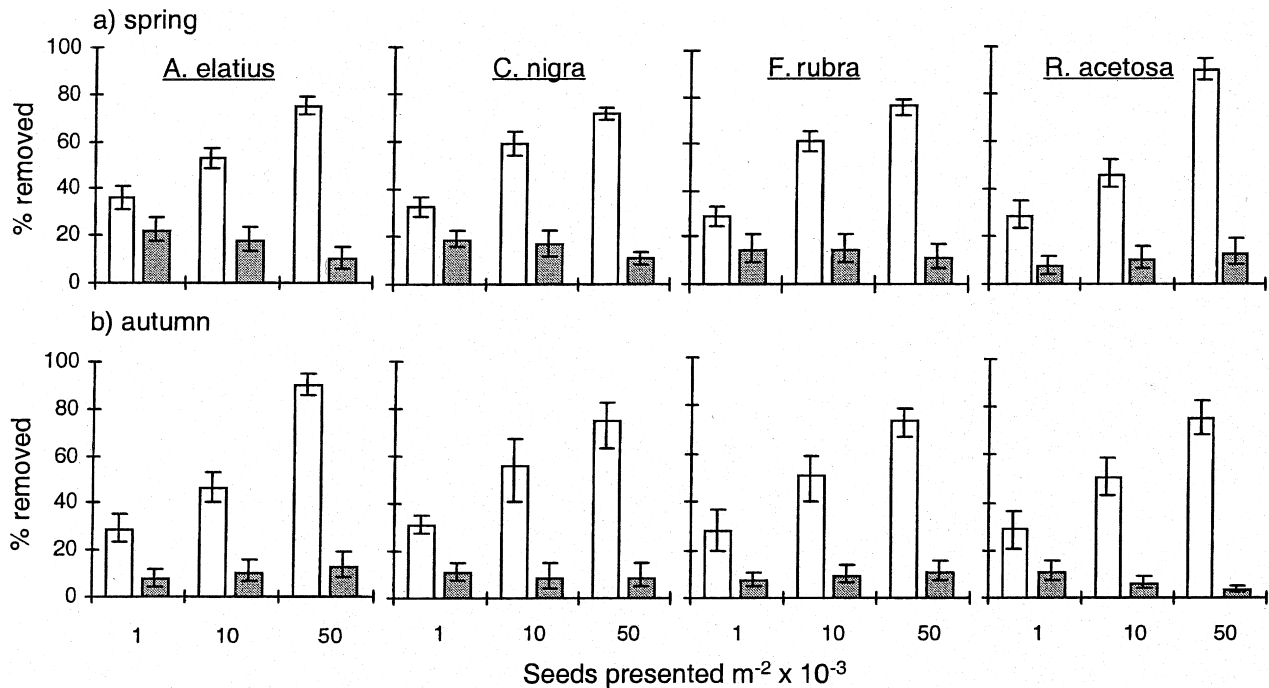


Fig. 1 Seed removal in spring (a) and autumn (b). The effect of rodent enclosure cages and the density of sown seeds on the mean percentage (\pm SE, $n = 4$, back-transformed from logits) of seeds removed from Petri dishes (open bars rodent exposed, closed bars rodent protected)

Seedling emergence and survival of sown species

Spring sowing

There was little seedling emergence of the sown species from the seed bank at the study site in spring 1995 (April–May); in the 32 plots to which no seeds were added (rodent access and rodent exclusion), we found only three seedlings of *R. acetosa*, two of *F. rubra* and none of *C. nigra* or *A. elatius*. Therefore, we restricted statistical analysis to the plots where seeds had been sown (24 plots for each species). There were no significant effects of seed density, rodent exclusion or any interaction between them on the total number of seedlings that emerged in spring 1995 (April–May) for any of the four sown species (Fig. 2a). For all four species, the proportion of sown seeds that emerged decreased with increasing seed density ($F_{2,18}$: *A. elatius* = 25.3, *C. nigra* = 30.6, *F. rubra* = 60.5, *R. acetosa* = 106.6, $P < 0.01$; Fig. 2b), but there was no significant effect of rodent exclusion nor any interaction (Fig. 2b). All of the seedlings that were tagged in spring 1995 died over the course of the extremely dry summer of 1995.

There was little emergence in autumn 1995 in quadrats sown with seeds in spring 1995 (i.e. seeds that had survived the summer). We observed only three seedlings of *C. nigra*, three of *R. acetosa*, three of *A. elatius* and five of *F. rubra*, and none of these seedlings survived until summer 1996. No seedlings of the sown species

emerged in spring 1996 in quadrats that had been sown with seeds in spring 1995.

Autumn sowing

There was little seedling emergence of the sown species from the recent seed rain or the seed bank in autumn 1995 (September–November); in the 32 plots to which no seeds were added, we found four seedlings of *R. acetosa*, seven of *F. rubra*, one of *A. elatius* and none of *C. nigra*. Because seedlings were so scarce in the control plots, we restricted statistical analysis to the plots where seeds were added. For all four species, there was a significant interaction between rodent exclusion and seed density on the total number of seedlings that emerged in autumn 1995 ($F_{2,18}$: *A. elatius* = 4.9, *C. nigra* = 5.1, *F. rubra* = 3.7, *R. acetosa* = 15.5, $P < 0.05$; Fig. 3a). Seedling density increased with increasing seed density, and rodents reduced seedling densities at only 1000 and 10,000 seeds m^{-2} . The rodent exclusion \times seed density interaction was also significant when the proportion of the sown seeds that emerged was analysed ($F_{2,18}$: *A. elatius* = 5.1, *C. nigra* = 5.8, *F. rubra* = 3.9, *R. acetosa* = 18.4, $P < 0.05$; Fig. 3b). For all four species, the proportion that emerged decreased with increasing seed density. Rodents reduced the proportion at 1000 and 10,000 seeds m^{-2} , but not at 50,000 seeds m^{-2} . Few seedlings of the sown species emerged in spring 1996 (four of *C. nigra*, two of *R. acetosa*, three of *F. rubra* and one of *A. elatius*) or in autumn 1996 (one of *C. nigra*, two of *R. acetosa* and none of *A. elatius* and *F. rubra*) in quadrats sown with seeds in autumn 1995.

In contrast to the spring sowing, some of the seedlings that emerged in the autumn sowing did survive until the following year, although survival was low in

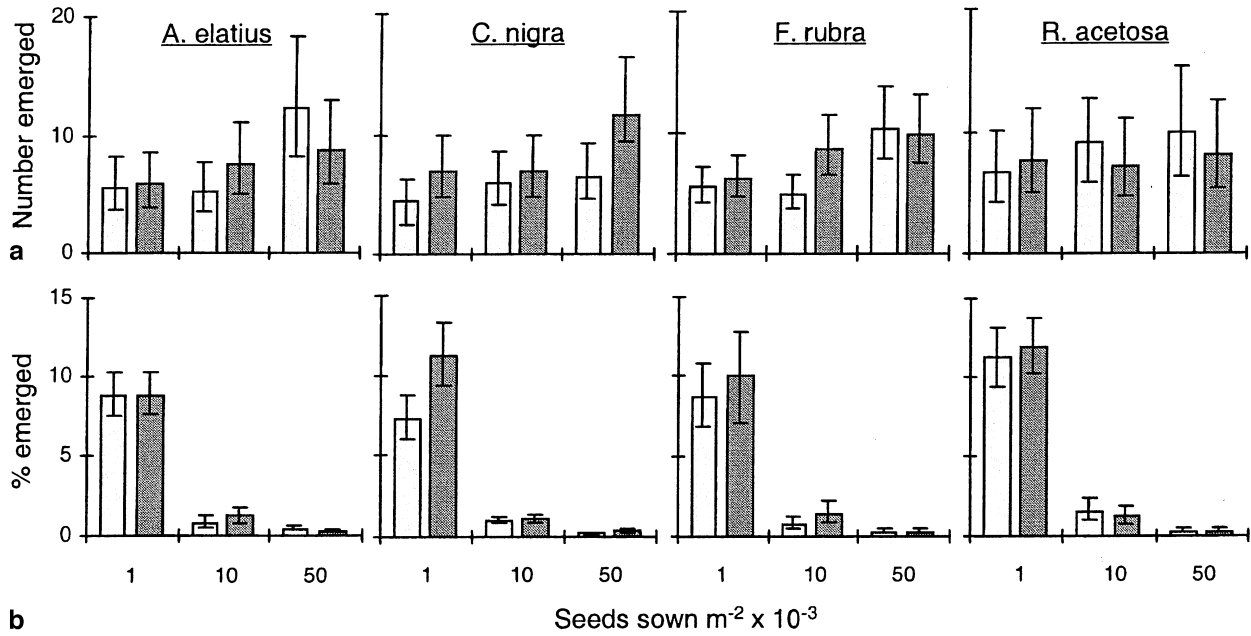
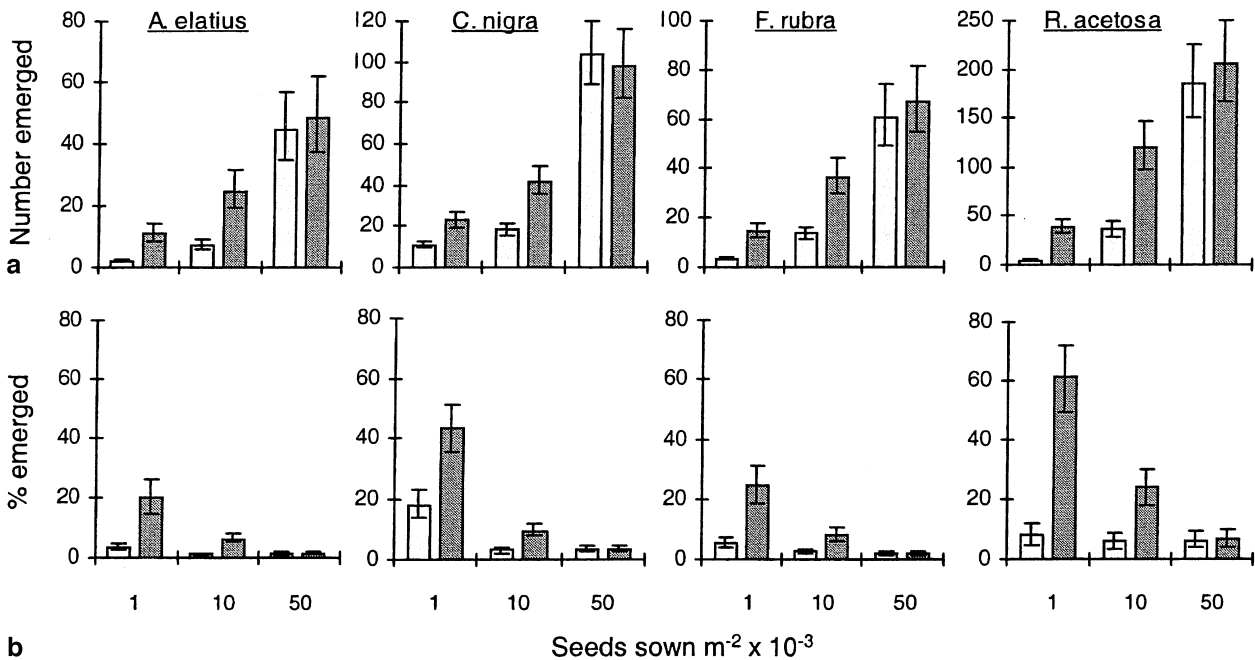


Fig. 2 Seedling emergence for seeds sown in spring. The effect of rodent exclusion cages and the density of sown seeds on the mean number of seedlings (per 0.25×0.25 m, \pm SE, $n = 4$, back-transformed from logs) that emerged (a) and the mean percentage (\pm SE, $n = 4$, back-transformed from logits) of sown seeds that emerged (b) (open bars rodent exposed, closed bars rodent protected)

most cases (Fig. 4). However, it is noteworthy that not all of the statistically significant effects on seedling emergence persisted when the number of seedlings surviving in December (winter) 1996 was analysed (compare Figs. 3 and 4). For *A. elatius* and *C. nigra*, seedling density in December 1996 (irrespective of emergence date of seedlings) was greater on plots protected from rodents ($F_{1,18}$: *A. elatius* = 95.1, *C. nigra* = 62.0,

$P < 0.01$; Fig. 4a) and increased with increasing seed density ($F_{2,18}$: *A. elatius* = 42.7, *C. nigra* = 31.4, $P < 0.01$; Fig. 4a), but there was no significant interaction. Rodents reduced the proportion of seedlings that emerged in autumn 1995 that survived until December 1996 for *A. elatius* and *C. nigra* ($F_{1,18}$: *A. elatius* = 20.5, *C. nigra* = 34.5, $P < 0.01$, Fig. 4b; analysis includes only those seedlings that emerged in autumn 1995). For

Fig. 3 Seedling emergence for seeds sown in autumn. The effect of rodent exclusion cages and the density of sown seeds on the mean number of seedlings (per 0.25×0.25 m, \pm SE, $n = 4$, back-transformed from logs) that emerged (a) and the mean percentage (\pm SE, $n = 4$, back-transformed from logits) of sown seeds that emerged (b) (open bars rodent exposed, closed bars rodent protected)



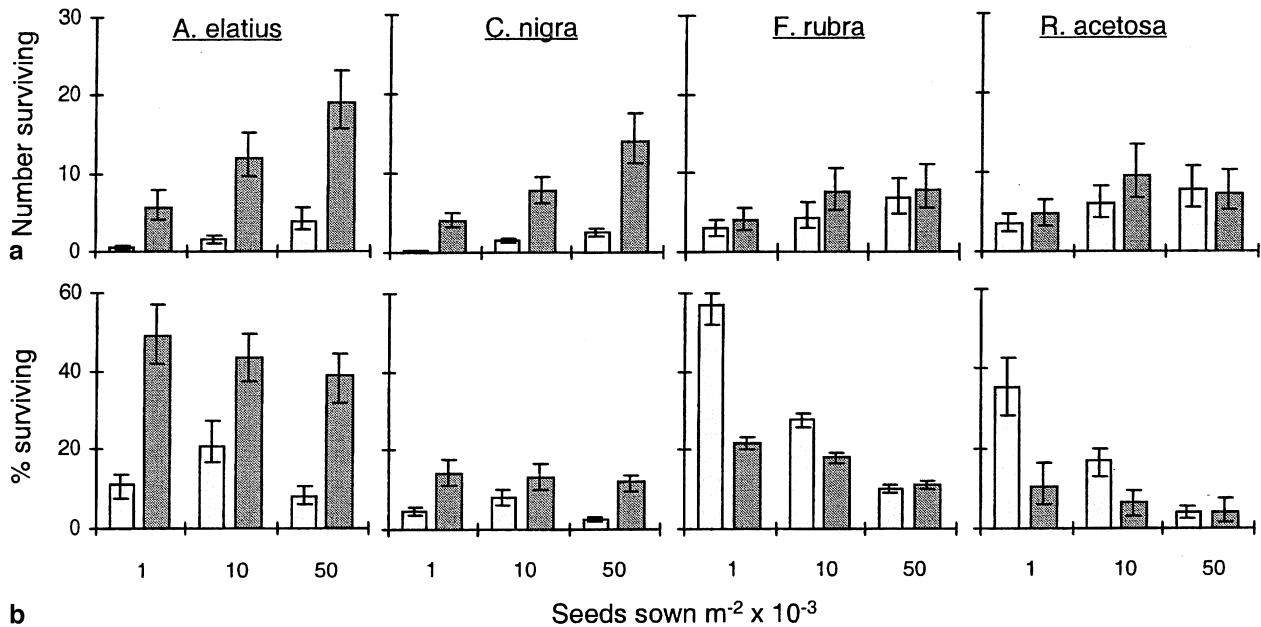


Fig. 4 Seedling survival for seeds sown in autumn. The effect of rodent enclosure cages and the density of sown seeds on the mean number of seedlings (per 0.25×0.25 m, \pm SE, $n = 4$, back-transformed from logs) that were present in winter (December) 1996 (**a**) and the mean percentage (\pm SE, $n = 4$, back-transformed from logits) of sown seedlings that emerged in spring 1995 that survived until winter 1996 (**b**) (open bars rodent exposed, closed bars rodent protected)

R. acetosa and *F. rubra*, there were no significant effects of seed density or rodent exclusion on seedling density in December 1996 (Fig. 4a). However, there was a significant effect of the seed density \times rodent exclusion interaction on the proportion of seedlings that survived ($F_{2,18}$: *F. rubra* = 4.0, *R. acetosa* = 4.3, $P < 0.05$; Fig. 4b). The proportion surviving decreased with increasing seed density, and was increased by rodents at 1000 and 10,000 seeds m^{-2} but not at 50,000 seeds m^{-2} .

There were no significant effects of rodent exclusion or seed density on the number of flowering stems of *F. rubra* or *R. acetosa* in June 1996 (mean flowering stems per 25×25 cm; *F. rubra*: exposed = 26.4, protected = 28.9; *R. acetosa*: exposed = 0.4, protected = 0.5, $P > 0.1$, GLIM with Poisson errors). A total of 14 *C. nigra* capitula were counted on three plants and these were all in plots from which rodents had been excluded. A total of 18 *A. elatius* flowering stems were counted on six plants, 14 of which were found where rodents had been excluded. There were too few flowering stems of *C. nigra* and *A. elatius* to analyse statistically.

Seedling emergence and survival of species not sown

Plots sown in spring

There was little emergence in spring 1995 of species that were not sown. We found only four seedlings of

P. lanceolata, three of *Agrostis capillaris*, three of *Leontodon autumnalis* L. and four of *Taraxacum officinale* (Weber), and none of these seedlings survived past the end of summer 1995. In autumn 1995, a total of 135 seedlings emerged, consisting mainly of *P. lanceolata*, *H. lanatus* L. and *G. saxatile*. Analysis of the total number of seedlings that emerged in autumn 1995 showed that there were fewer seedlings in the plots to which rodents had access (Table 2; $\chi^2 = 10.1$, $df = 1$, $P < 0.01$, analysis based on all 128 quadrats; 64 rodent access plus 64 rodent exclusion). As with the sown species, we recorded little emergence in the plots in spring 1996 (total seedlings emerged = 8). There were fewer marked seedlings surviving in June 1996 where rodents had access ($\chi^2 = 4.8$, $df = 1$, $P < 0.05$; Table 2), but rodents had no effect on the proportion of seedlings that survived from autumn 1995 to summer 1996 ($\chi^2 = 0.5$, $df = 1$, $P > 0.1$; Table 2).

Plots sown in autumn

In autumn 1995, a total of 124 seedlings emerged of species that were not sown, and as with the plots established in spring, these were mainly *P. lanceolata*, *H. lanatus* and *G. saxatile*. Fewer seedlings emerged on plots to which rodents had access ($\chi^2 = 11.5$, $df = 1$, $P < 0.01$; Table 2). There was little emergence in spring 1996 (only 10 seedlings) and compared to autumn 1995, emergence in autumn 1996 was low (21 seedlings, of which 18 died before the following winter). There were fewer marked seedlings surviving in December 1996 where rodents had access ($\chi^2 = 5.5$, $df = 1$, $P < 0.05$; Table 2), but there was no effect of rodent exclusion on the proportion of seedlings that emerged in autumn 1995 which survived until December 1996 ($\chi^2 = 1.1$, $df = 1$, $P > 0.1$; Table 2).

Table 2 The effect of rodent seed predation on the mean number of seedlings that emerged in autumn 1996, the mean number of seedlings surviving and the mean percentage of seedlings surviving of species that occurred only in the natural seed rain. Numbers surviving are for June 1996 for the spring-sowing experiment and December 1996 for the autumn-sowing experiment. Percentage

Experiment	Rodent exclusion	Seedling emergence – autumn 1996 (number per 0.25 × 0.25 m)	Seedlings surviving (number per 0.25 × 0.25 m)	Percentage seedlings surviving from autumn 1995
Spring-sowing experiment	Access	0.54	0.15	31.2
	Excluded	1.66	0.56	34.9
Autumn-sowing experiment	Access	0.43	0.21	35.9
	Excluded	1.51	0.73	41.6

survival is from autumn 1995 to June 1996 for the spring sowing and from autumn 1995 to December 1996 for the autumn sowing. Data for all species have been pooled. Values have been back-transformed from logs for seedling numbers and logits for the percentage surviving

Discussion

Impact of seed loss on emergence

Several field studies have found that rodents are responsible for substantial post-dispersal seed loss in grasslands (Mittlebach and Gross 1984; Reader and Beisner 1991; Hulme 1994a), but it is not always clear whether this seed loss leads to a reduction in seedling emergence (Crawley 1992). Our study showed that rodents reduced emergence of all four species that were sown in autumn 1995, as well as those species that occurred only in the natural seed rain. It is important to note, however, that the reduced emergence we detected might not only reflect the removal of seeds but also seedling herbivory (Hulme 1994b). Seedlings may have emerged and been killed by rodents between census dates, so remaining undetected, and leading to the effects of seed loss being confused with those of seedling herbivory (see Kerley et al. 1997). However, we did find in plots where rodents were excluded in autumn 1995 that the number of seedlings that emerged decreased with decreasing density of sown seeds. Thus, it seems likely that seed loss to rodents did play a role, although the relative importance of this compared to seedling herbivory is difficult to disentangle.

Difference in response to rodents in spring and autumn

The difference in the effect of rodents in autumn, where they reduced emergence of sown and unsown species, and spring, where they had no impact, was striking. There are three possible explanations for this. First, seed predation rates may have been greater in autumn than spring (see Hulme 1994a), so having a greater impact on seedling emergence in autumn. However, we did not detect any difference in seed removal between seasons (Fig. 1), suggesting that seasonal differences in predation rates may not have been the principal cause of the observed pattern. Of course, we do not know how closely our technique of estimating seed predation (e.g.

removal of seed placed in Petri dishes) matches seed predation of seeds from the ground surface hidden amongst the vegetation, or whether the technique is a good measure of rodent abundance. Indeed, at two sites in Silwood Park grasslands, Hulme (1994a) found no relationship between seed predation rates and overall rodent abundance. Second, seasonal variation in some other seedling mortality factor may have masked the effect of rodents on emergence. For instance, seedling herbivores such as molluscs and arthropods, both of which vary seasonally (Hulme 1994a), had access to sites protected from and exposed to rodents. Third, microsite availability and intensity of competition from existing vegetation may have varied between spring and autumn. While we did not measure microsite availability directly in this experiment, we observed that the vegetation in spring 1995 appeared continuous, with few obvious gaps, and that many of the seeds that were sown were trapped by a dense layer of vegetation away from the soil surface (often within the bryophyte layer; see also van Tooren 1988). Thus, emergence in spring was probably limited by the number of microsites, and rodents may have been removing seeds that would otherwise not have contributed to the population (see Crawley 1992). In contrast, we observed that the vegetation in autumn was open, with numerous bare patches of ground, and that most of the seeds that were sown reached the soil surface. The increased microsite availability probably reflected the intensity of the drought in summer 1995 which resulted in the death of perennial ramets, and low plant biomass at the end of the summer (G.R. Edwards, unpublished data). Thus, in autumn where total seedling emergence was seed limited, consumption of seeds by rodents exerted a strong influence.

We did not repeat the seed-sowing experiment in autumn 1996, so we can only speculate as to whether rodents would have had the same impact on the sown species each autumn. However, it is noteworthy that emergence of the species that were *not* sown was increased by rodent exclusion in autumn 1995 (Table 2) but not in autumn 1996 following a slightly wetter summer when total biomass was higher. Furthermore, we have found in other seed-sowing studies in Nash's

Field that seedling emergence was much higher in autumn 1995 than in autumn 1996 (G.R. Edwards, unpublished data). Therefore, while the drought in summer 1995 may have caused considerable mortality among mature plants and seedlings (100% mortality of seedlings emerging in spring 1995 in this experiment), it may have had an important positive impact on plant recruitment by causing increased microsite availability and higher subsequent rates of seedling recruitment.

Impact of seed density

At low seed densities (1000 and 10,000 seeds m^{-2}), a negative effect of rodents on seedling emergence was apparent. In contrast, at the highest seed density (50,000 seeds m^{-2}), no effect of rodents was apparent in the field, despite the finding from our seed removal study (i.e. Petri dishes) that the highest proportion of seeds was removed at the highest seed density (i.e. positive density-dependent seed predation). The failure to detect any effect of rodents on seedling emergence at the seed density of 50,000 seeds m^{-2} probably points to other constraints acting on seedling emergence at high seed density (e.g. microsite availability; Crawley 1992), as indicated by the decrease in the proportion of sown seeds that emerged as seed density increased (Fig. 3). Although rodents may have removed more seeds at the high seed density, they are likely to have been seeds that would have died in any case for other reasons (Crawley 1992).

Seedling survival

Whether seed predators ultimately affect plant populations depends on the extent to which there is compensatory density-dependent seedling survival. For *F. rubra* and *R. acetosa*, the proportion of seedlings surviving from emergence in spring 1995 to 15 months of age declined with increasing seed density, and was lower in sites where rodents were excluded. Thus, no differences in seedling density remained, confirming the predictions of Harper (1977) and Crawley (1992), that density-dependent seedling survival at subsequent stages can compensate for early seed losses.

In contrast, for *A. elatius* and *C. nigra*, there was no effect of seed density on seedling survival, and seedling survival was greater where rodents were excluded. This accentuated the effect of rodent exclusion on seedling emergence at 1000 and 10,000 seeds m^{-2} and created a new effect of rodent exclusion at 50,000 seeds m^{-2} (where initial seedling densities were not different). The reduced seedling survival in sites exposed to rodents confirms previous studies that rodents are not only important as seed predators but also as seedling predators in grasslands (Pyke 1987; Hulme 1994a,b). It is noteworthy that evidence of seedling predation was only found for the two species with the largest seedlings

(*C. nigra* and *A. elatius*). This supports the broad relationship that rodent seedling predation is more pronounced in species with large seedlings (Hulme 1994b).

Conclusion

To answer the question, whether or not seed predators are important to plant community structure requires long-term seed predator exclusion studies where the fates of seedlings are followed to assess whether differences in seedling densities persist to become differences in mature plant densities. Our study showed that seedling emergence of four perennial grassland species could be increased by rodent exclusion, but that these differences in seedling densities only persisted to maturity for two of the species, *A. elatius* and *C. nigra*. We consider that the *A. elatius* and *C. nigra* seedling data, combined with the tentative indication of increased flowering for both species in sites protected from rodents, constitutes reasonable evidence that rodents can limit plant recruitment of these species, and may play an important role in maintaining these two species at the very low densities observed within Nash's Field (*C. nigra* < 1 plant per 1000 m^2 , *A. elatius* < 1 plant per 100 m^2). It turns out that both of the rare species tested here show reduced recruitment under rodent herbivory. This is not to be taken as arguing that all of the rare species in Nash's Field are rare because of rodent seed and seedling predation. Other factors (e.g. rabbit grazing, invertebrate herbivory) may be important for other species and these are currently being investigated. The failure of the statistically significant differences in seedling densities to persist for *F. rubra* and *R. acetosa* stresses the need for caution when interpreting the effect of seed predators on plant dynamics based on seedling emergence data alone. Our study further showed that seed predators only affected plant recruitment for seeds sown in autumn, where a summer drought had increased microsite availability, and not for seeds sown in spring, where microsite availability was low. This finding highlights that in future studies we must not only address the question of whether or not seed predators reduce plant recruitment but under what conditions they might be expected to do so.

Acknowledgements The research is supported by a research grant from the Natural Environmental Research Council. We would like to thank Matt Heard, Mike Hay, Joanna Dixon, Philip Hulme and two anonymous referees for their helpful comments on the manuscript.

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