Effects of disturbance and rabbit grazing on seedling recruitment of six mesic grassland species

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Abstract

Seeds of two grass (*Arrhenatherum elatius* and *Festuca rubra*), two herb (*Plantago lanceolata* and *Rumex acetosa*) and two legume (*Lotus corniculatus* and *Trifolium repens*) species were sown in summer 1995 at four densities (no seed, 1000, 10 000 and 50 000 seeds m^{-2}) into an established rabbit-grazed grassland given factorial combinations of rabbit fencing (with and without fences) and soil disturbance (with and without cultivation). On plots where no seeds were sown, only the species with persistent seed banks (*P. lanceolata, L. corniculatus* and *T. repens*) showed enhanced seedling emergence in response to disturbance. In disturbed soil, seedling densities of all species increased with increasing density of sown seeds, the effects of which were still evident for plant cover 2 years after seed sowing. In undisturbed vegetation, *A. elatius*, *F. rubra, P. lanceolata* and *R. acetosa* showed increased seedling densities following seed sowing; but in each case, there was an upper asymptote to seedling recruitment, presumably due to microsite limitation. Rabbit grazing reduced seedling densities, with this reduction being more pronounced with disturbance than without. However, the effect of rabbit grazing did not persist for some species; seedling mortality of *R. acetosa*, *P. lanceolata, L. corniculatus* and *T. repens* was higher on plots without rabbit grazing, so that plant densities of these species in summer 1996 and plant cover in summer 1997 were greater on grazed plots. The results indicate interactions between soil disturbance, propagule availability and herbivory, rather than disturbance alone, will play an important role in controlling seedling recruitment and species habitat distributions in grasslands.

Keywords: disturbance, mesic grassland, rabbit grazing, seedling recruitment

Introduction

There is considerable evidence that seedling recruitment in grasslands is strongly dependent on areas of disturbance (Fenner, 1985), with few documented cases of successful seedling recruitment within dense, undisturbed vegetation (Thompson and Baster, 1992). Numerous studies have reported that seedling recruitment of many grassland species is restricted to patches of bare ground created by the death of perennial ramets or the activities of burrowing animals (e.g. Gross and Werner, 1982; Crawley and Nachapong, 1985; Rapp and Rabinowitz, 1985; Bullock *et al*., 1995; Milton *et al*., 1997). Since soil disturbance is the key factor required for seedling recruitment for so many grassland species, it is intuitive that interactions with other factors affecting recruitment (e.g. nutrients, herbivory, shade) will determine which species successfully recruit on to a disturbed site (Silvertown and Tremlett 1989). There have been few studies, however, that have investigated the interaction between disturbance and other factors affecting recruitment (see Collins, 1987; Silvertown and Tremlett, 1989; Carson and Pickett, 1990; Burke and Grime, 1996).

This paper investigates the effect of the interaction between soil disturbance and rabbit grazing on seedling recruitment of two grass (*Arrhenatherum elatius* L. and *Festuca rubra* L.), two herb (*Plantago lanceolata* L. and *Rumex acetosa* L.) and two legume (*Lotus corniculatus* L. and *Trifolium repens* L.) species in a mesic grassland. These six species occur in mesic grasslands subject to different levels of disturbance (Grime *et al*., 1988), and numerous studies have shown that rabbit grazing can influence their abundance and distribution (e.g. Gillham, 1955; Watt, 1981; Crawley, 1990a). Thus, there is reason to believe that the way seedling recruitment responds to the interaction between rabbit grazing and disturbance will be important in determining the abundance and distribution of these species.

One way rabbits might influence seedling recruitment is by grazing flower stems or flowers (Crawley 1990a), thus altering the number and species

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composition of seeds available at the time when the disturbance occurs (Gross, 1980; Hobbs and Mooney, 1985; Kotanen, 1996). Alternatively, rabbit grazing might affect seedling recruitment by impacting on seedling emergence and survival, the effects of which are likely to be complex (see Crawley, 1990a; Silvertown *et al*., 1992). For example, by defoliation of grazing-sensitive seedlings, rabbits might reduce seedling survival (Fenner, 1985). On the other hand, defoliation of neighbouring vegetation might enhance germination (e.g. altered light regimes; Deregibus *et al*., 1994) and increase seedling survival (e.g. reduced competition; Crawley, 1990a; Hanley *et al*., 1995). The effects of rabbit grazing on disturbed sites might be very different to those on undisturbed grassland sites, where fewer seedlings emerge and there is more intense competition from the established, intact vegetation (Crawley and Pacala, 1991).

A factorial experiment (with and without rabbit fencing, with and without soil cultivation, and with and without seed sowing at different seed densities) was carried out in a species-poor acid grassland with a long history of rabbit grazing. The aim was to investigate how rabbit grazing affected seedling emergence and survival under different levels of soil disturbance. For each of the six species studied we asked: What set of conditions of soil disturbance, rabbit grazing and seed availability were necessary and sufficient for recruitment from seed to occur?

Methods

Study area

The study was conducted in Nash's Field, Silwood Park, Berkshire, UK (National Grid reference 41/944691), a species-poor grassland on acid, sandy soil. Visual inspection of the grassland before the experiment began showed the dominant grass species were *Agrostis capillaris* L. and *F. rubra* and the dominant herb species were *Galium saxatile* L. and *R. acetosella* L. (National Vegetation Classification: MG6, Rodwell,1992). The experimental site had a long history of rabbit (*Oryctolagus cuniculus* L.) grazing which kept standing biomass low for most of the year (< 150 g DM m^{-2}) and precluded many plant species from flowering (see Crawley, 1990a). The grassland was occasionally grazed by larger vertebrates, such as muntjac (*Minitacus reeveesi* Oligby.) and roe deer *(Capreolus capreolus* L.). The vegetation cover was continuous, except for small soil disturbances arising from digging by rabbits and European moles (*Talpa europaea* L.); < 2% of ground area was disturbed each year (G.R. Edwards, M.J Crawley and M.S. Heard, unpublished observations). Silwood Park experiences an average annual rainfall of 653 mm with little seasonal pattern. Rainfall in the spring–summer period of 1995 was substantially below the long-term average (Edwards and Crawley, 1999). Nomenclature follows Stace (1997).

Experimental design, treatments and study species

The design of the experiment was $2 \times 2 \times 4$ factorial with two levels of rabbit grazing, two levels of soil cultivation and four levels of seed density. The experiment was laid out in a split plot design and was replicated in four blocks. The same experiment was carried out for six species: *A. elatius*, *F. rubra*, *L. corniculatus*, *P. lanceolata*, *R. acetosa* and *T. repens*. These species were chosen because they represent a range of life histories and have contrasting patterns of abundance in rabbit-grazed and rabbit-fenced plots in Nash's Field (Table 1).

Four blocks, each measuring 8 m × 8 m, were laid out at random within Nash's Field, and one half (4 m × 8 m) of each block was randomly allocated to be fenced to exclude rabbits and larger vertebrates in mid June 1995. The rabbit fences were 1 m high and were constructed of 3-cm square wire mesh, supported by wooden posts every 4 m. The bottom 15 cm of wire was turned outwards towards the rabbits so that they encountered the wire as soon as they started digging. The fences were highly effective at excluding rabbits but larger vertebrates, for example roe and muntjac deer, occasionally jumped over them. Furthermore, the fences did not exclude moles, which tunnelled underneath, or rodents, which entered through the wire mesh (Hulme, 1994).

One half (4 m × 4 m) of each fenced and grazed plot was randomly allocated to be cultivated to a depth of 15 cm in late June 1995, giving four fencing–cultivation treatment combinations (fenced–cultivated, fenced–grassland, grazed–cultivated, grazed–grassland). Two passes were made over the vegetation with a rotavator, one to break down the perennial vegetation and one to cultivate deeper into the soil profile. This treatment effectively destroyed the above-ground vegetation but fragments of perennial plants like *F. rubra*, *Holcus mollis* L. and *R. acetosella* remained. The aim was for shoots regenerating from these fragments, along with seedlings arising from the seed bank, to provide competition for seedlings arising from sown seeds, thus simulating natural soil disturbances (e.g. molehills), where recently dispersed seeds compete with vegetation regenerating from fragments and the soil seed bank. Following cultivation and the erection of the fences in late June, no further treatments were imposed on the plots until late September 1995 when seeds were sown. At the time of sowing, there were marked differences in the amount of bare ground and sward height due to the fencing and cultivation treatments. The percentage of

Table 1. Comparative life histories of the six species studied. All are perennial and polycarpic. The final two columns of the table show the biomass of the six species in rabbit-grazed and rabbit-fenced plots in Nash's Field before the experiment began in summer 1995

Species	Family	Seed bank[1]	Seed weight[2] (mg)	Emergence time[3]	Biomass in Nash's Field[4] (g DM m^{-2}) Grazed	Biomass in Nash's Field[4] (g DM m^{-2}) Fenced
Arrhenatherum elatius	Gramineae	Transient	2.28	Summer/autumn	0.0	1.1
Festuca rubra	Gramineae	Transient	0.83	Autumn	14.6	70.5
Plantago lanceolata	Plantaginaceae	Persistent	1.81	Autumn/spring	2.4	1.3
Rumex acetosa	Polygonaceae	Transient	0.71	Autumn	4.5	3.8
Lotus corniculatus	Leguminosae	Persistent	1.61	Autumn/spring	0.6	0.2
Trifolium repens	Leguminosae	Persistent	0.59	Autumn/ spring	0.1	0.0

[1] Data taken from Thompson and Grime (1979), Grime *et al.* (1988) and G.R. Edwards and M.J. Crawley (unpublished results). Classification of seed banks: transient = present during the summer; persistent = present throughout the year with some seeds older than 1 year.

[2] Mean weight calculated by weighing a sample of 1000 seeds.

[3] Taken from Grime *et al.*, 1988.

[4] Means calculated from six replicate 0.25 m × 0.5 m quadrats taken at random from within each of six 10 m × 10 m blocks that had been fenced against rabbits since 1986 or grazed by rabbits during the same period. Each quadrat was cut to ground level with scissors, sorted to species, oven dried and weighed (see Crawley, 1990a for further details).

bare ground, as determined by the number of first touches on soil from 200 point quadrats taken at random in each of the 16 plots, was greater on cultivated than grassland plots ($F_{1,6} = 285.3$, $P < 0.01$) and on rabbit-grazed than rabbit-fenced plots ($F_{1,3} = 51.6$, $P < 0.01$; mean % bare ground: fenced–cultivated = 30.1, fenced–grassland = 3.0, grazed–cultivated = 52.5, grazed–grassland = 7.4). The height of the vegetation, as determined by measuring the height of the tallest leaf (non-extended) above the soil surface at 200 random locations in each of the 16 plots, was greater on grassland than cultivated plots ($F_{1,6} = 30.2$, $P < 0.01$) and on rabbit-fenced than rabbit-grazed plots, although this effect was only significant at the 10% level ($F_{1,3} = 7.1$, $P = 0.07$; mean height (cm): fenced–cultivated = 7.3, fenced–grassland = 12.6, grazed–cultivated = 4.5, grazed–grassland = 9.8).

In the centre of each cultivated and grassland area, one plot measuring 3 m × 2 m was laid out and was divided into six contiguous strips, each measuring 0.5 m × 2 m. The area around the outside of each 3 m × 2 m plot acted as a guard strip. Each strip was randomly allocated to one of the six species to be sown (Table 1). The strips were further divided into four quadrats, each measuring 0.5 m × 0.5 m, and these were randomly allocated to four seed sowing densities: 0 (non-sown control), 1000, 10 000, 50 000 seeds m^{-2}. These seed densities encompass the normal range of localized seed densities for the species in Nash's Field (M.S. Heard, unpublished observations). Seeds were sown by hand on to the soil surface in late September 1995, and no attempt was made to cover seeds with soil or vegetation. Seeds were provided by John Chambers' Wild Flower Seeds, Kettering, UK. Germination percentages of seed samples in glasshouse tests, as determined by 100 seeds placed on compost, were greater than 85% for all species.

From the time fences were erected in June 1995 until seed sowing, flowering stems and flowers of the six study species were removed from the experimental plots prior to seed dispersal; this allowed us to control seed density by seed sowing. The date of seed sowing in late September was later than the six species normally disperse seeds in Nash's Field (M.S. Heard, unpublished observations). We sowed seeds at this time to minimize rodent seed predation (Hulme, 1994) by reducing the time between sowing and germination.

Measurements

Seedling recruitment was measured in a 0.25 m × 0.25 m quadrat that was permanently marked out in the centre of each 0.5 m × 0.5 m seed sowing plot; the outer area was considered to be a buffer zone between plots. Originally our aim was to tag and follow the fate of all seedlings that emerged. However, the considerable space and replication in the experiment, and the large number of seedlings that emerged soon after sowing (up to 400 seedlings per 0.25 m × 0.25 m quadrat), made it logistically impossible for this to be carried out at the first census in late October 1995 (see Fenner (1987) for a summary of difficulties encountered in seedling monitoring experiments). As a compromise, all seedlings were counted at the first census. During autumn 1995, there was considerable seedling mortality, so by the time of the second census in late December (winter) 1995, it was possible to tag all seedlings. This was carried out by recording the location of the seedling on a map of the quadrat using a 5 × 5 grid of 5 cm square cells as a guide. Further seedling surveys were made in April (spring) and July (summer) 1996. At each survey, any new seedlings were tagged, and any existing seedlings were recorded as present or absent. It was not possible to assign a cause of death to seedlings, as seedlings were either very desiccated or missing completely. In July 1997, the percentage cover of all species in each quadrat was scored by visual assessment.

Statistical analysis

All statistical analyses was carried out in GLIM 3.77 (NAG, 1985). Seedling densities in October (autumn) 1995 and July (summer) 1996 were analysed using Poisson errors with a log link. These analyses were based on seedling counts totalled at each plot size of the split plot design. The seedling density value analysed in July 1996 was the number of seedlings that emerged in autumn 1995 and spring 1996 that survived until July 1996. The proportion of seedlings that survived from December (winter) 1995 to July 1996 was analysed using log-linear models with binomial errors. As in the analysis of seedling counts, survival analysis was based on seedling counts totalled at each level of the split plot design. Where models were over-dispersed (residual deviance greater than residual degrees of freedom), an empirical scale parameter was estimated, and F tests rather than χ^2 tests were carried out (Crawley, 1993). The percentage cover of each species at the end of the experiment in July 1997 was analysed as a split-plot analysis of variance (ANOVA) following an arcsine transformation of the percentage.

Results

The density of seedlings of each species, at four survey dates during the experiment, in factorial combinations of rabbit fencing and soil cultivation, are shown in Figure 1. The percentage cover of each species at the end of the experiment in July 1997 is also given. Almost all seedlings emerged in autumn 1995 soon after seed sowing. Only *T. repens* and *L. corniculatus* (56 and 76 seedlings in total over the four replicates, respectively) showed any emergence in spring 1995. Few seedlings emerged from seeds arising from the seed bank or the natural seed rain on the non-sown plots of *F. rubra* (two seedlings), *A. elatius* (one seedling) and *R. acetosa* (one seedling) (Table 2). In contrast, there was considerable emergence on the non-sown plots of *P. lanceolata* (21 seedlings), *L. corniculatus* (57 seedlings) and *T. repens* (41 seedlings) (Table 2). Seedling mortality occurred predominantly during the rapid growth phase of the existing vegetation in the spring and early summer months (January–July) of 1996 (Fig. 1). The dominant existing vegetation that grew during this time was *Anthoxanthum odoratum* L. on cultivated plots and *F. rubra* on grassland plots. The two grasses (*A. elatius* and *F. rubra*) showed similar patterns with respect to the rabbit grazing, cultivation and seed sowing treatments, as did the two herbs (*P. lanceolata* and *R. acetosa*) and the two legumes (*L. corniculatus* and *T. repens*). Therefore, results for each pair of species are described together. Results of statistical tests are given in Table 3.

A. elatius *and* F. rubra

For these two species, cultivation had a strong positive effect on the density of seedlings in autumn (October) 1995 (Table 3). Cultivation interacted with rabbit grazing, which had a larger negative effect on the abundance of seedlings with disturbance than without (Fig. 1). There was also a significant interaction between the effects of cultivation and seed density (Table 3). On cultivated plots, the abundance of seedlings increased with increasing seed density (Table 2). On grassland plots, sowing seeds also enhanced seedling densities, but seedling densities did not differ between plots sown at different seed densities (Table 2).

Seedling survival from winter (December) 1995 to summer (July) 1996 was greater on fenced plots (*A. elatius*: grazed = 62.1%, fenced = 71.3%; *F. rubra*: grazed = 23%, fenced = 39%; Table 3, Fig. 1). The interaction between the effects of rabbit grazing and cultivation evident for seedling densities in autumn 1995 was still significant for seedling densities in summer 1996 (Table 2). Seedling survival reduced with increasing seed density for *F. rubra* (66, 42 and 26% for 1000, 10 000 and 50 000 seeds m^{-2}, respectively) but was unaffected by seed density for *A. elatius* (66.6, 74.3 and 65.0% for 1000, 10 000 and 50 000 seeds m^{-2}, respectively). The interaction between the effects of cultivation and seed density evident for seedling densities in autumn 1995 was still significant for seedling densities in summer 1996 (Table 2).

On both grassland and cultivated plots, there was a strong negative effect of grazing on the percentage cover of both species in summer (July) 1997 (Table 3, Fig. 1). There was also a significant interaction between the effects of rabbit grazing, seed density and cultivation (Table 3). The percentage cover of both species was reduced by cultivation on non-sown grazed and fenced plots, and also on sown, grazed plots for *F. rubra* (Fig. 2). In contrast, cultivation increased the percentage cover on fenced, sown plots for *F. rubra*, and on both grazed and fenced sown plots for *A. elatius* (Fig. 2).

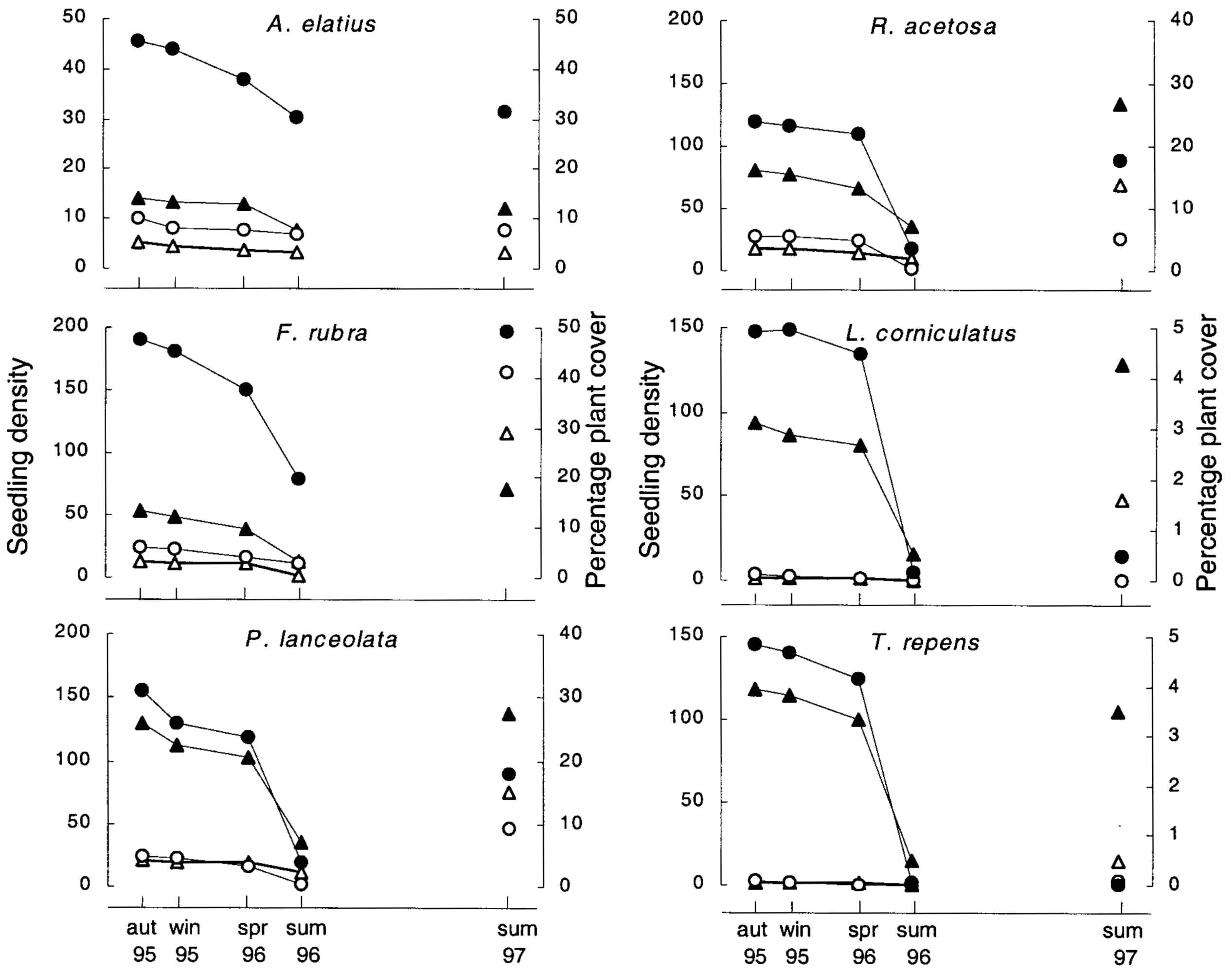

Figure 1. The effect of rabbit fencing and cultivation on seedling densities (mean per 0.25 × 0.25 m back-transformed from logs) of the six species studied from autumn (September) 1995 to summer (July) 1996. Seedling densities are the number of seedlings present at each census and so represent the net of seedling emergence and seedling mortality. The mean plant cover (% ground area back-transformed from arcsine percentages) of each species at the end of the experiment in summer (July) 1997 is also shown in the final column of data. Cover and seedling density values are averaged across the four levels of seed density. △ grazed–grassland, ○ fenced–grassland, ▲ grazed–cultivated, ● fenced–cultivated. Note the different scales for seedling densities and plant cover for the different species. Rabbit fences were erected and cultivation was carried out in June 1995. Seeds were sown in late September 1995.

Like seedling densities, the percentage cover of both species increased with seed density on cultivated plots, but was an asymptotic function of seed density on grassland plots (Table 2).

P. lanceolata *and* R. acetosa

For these two species, cultivation had a strong positive effect on the density of seedlings in autumn 1995 (Table 3). There was also a significant interaction between the effects of cultivation and rabbit grazing on the density of seedlings (Table 3). For *P. lanceolata*, rabbit grazing reduced the number of seedlings on cultivated plots but not on grassland plots (Fig. 1). For *R. acetosa*, the negative effect of rabbit grazing on the abundance of seedlings was greater with cultivation than without (Fig. 1). The interaction between the effects of cultivation and seed density was also significant (Table 3). On cultivated plots, the abundance of seedlings increased with increasing seed density (Table 2). On grassland plots, sowing seeds also enhanced seedling densities, but seedling densities did not differ between plots sown at different seed densities (Table 2).

Seedling survival of both species from winter 1995 to summer 1996 was greater on grazed plots

Table 2. The effect of soil cultivation and seed sowing density (per m^2) on the mean density of seedlings (per 0.25 × 0.25 m, back-transformed from logs) in autumn (October) 1995 and summer (July) 1996, and the mean percentage cover (back-transformed from arcsine percentages) in summer (July) 1997 of the six species studied. Seedling densities are the number of seedlings present at each census and so represent the net of seedling emergence and seedling mortality. Cover and seedling density values are averaged across the rabbit grazing and rabbit fencing treatments

	Grassland				Cultivated			
Species	0	1000	10 000	50 000	0	1000	10 000	50 000
A. elatius								
Seedlings: autumn 1995	0.1	7.6	10.6	11.9	0.0	20.6	37.9	60.8
Seedlings: summer 1996	0.0	4.9	7.4	7.6	0.0	12.5	25.9	38.1
Cover: summer 1997	2.5	5.7	6.9	6.7	0.1	10.7	35.1	54.8
F. rubra								
Seedlings: autumn 1995	0.1	20.0	22.5	26.9	0.1	35.0	141.3	310.4
Seedlings: summer 1996	0.0	8.9	9.0	10.3	0.0	25.3	74.5	84.0
Cover: summer 1997	25.3	36.6	37.9	38.3	7.0	31.6	40.3	57.9
P. lanceolata								
Seedlings: autumn 1995	1.1	21.8	26.5	28.8	2.6	42.9	128.5	397.0
Seedlings: summer 1996	0.6	4.6	5.4	4.3	1.6	8.0	27.8	57.7
Cover: summer 1997	6.7	17.6	16.9	19.1	11.0	23.3	33.0	49.3
R. acetosa								
Seedlings: autumn 1995	0.0	26.4	36.8	34.6	0.1	39.8	104.9	254.6
Seedlings: summer 1996	0.0	4.8	5.8	6.9	0.1	13.8	29.8	55.9
Cover: summer 1997	3.1	10.5	12.0	12.9	1.3	18.4	33.7	44.7
L. corniculatus								
Seedlings: autumn 1995	2.3	2.8	2.5	2.4	4.9	30.6	172.5	279.3
Seedlings: summer 1996	0.4	0.5	0.4	0.6	0.8	2.0	5.4	9.5
Cover: summer 1997	0.4	0.9	0.9	1.1	1.0	1.6	2.4	4.0
T. repens								
Seedlings: autumn 1995	1.1	0.9	1.9	2.0	4.0	35.5	183.0	348.3
Seedlings: summer 1996	0.0	0.1	0.0	0.1	0.9	2.1	8.9	15.0
Cover: summer 1997	0.1	0.1	0.3	0.3	0.8	0.9	1.4	2.2

(*P. lanceolata*: grazed = 25.0%, fenced = 14.1%; *R. acetosa*: grazed = 41%, fenced = 12.0%; Table 3, Fig. 1). By summer 1996, the significant interaction between the effects of cultivation and rabbit grazing had disappeared, leaving significant main effects of rabbit grazing and cultivation for seedling numbers in summer 1996 (Table 2). In contrast with autumn 1995, seedlings were now more abundant on grazed plots (Fig. 1). This effect of rabbit grazing was still significant for plant cover in summer 1997 (Fig. 1). Seedling survival was lower on sown than non-sown plots for *P. lanceolata* but did not differ between plots sown at different seed densities (74, 20, 22 and 17%, for 0, 1000, 10 000 and 50 000 seeds m^{-2}, respectively; Table 3). There was no significant effect of seed density on seedling survival of *R. acetosa* (29, 24 and 22%, for 1000, 10 000 and 50 000 seeds m^{-2}, respectively; Table 3). The interaction between cultivation and seed density evident in autumn 1995 was still significant for seedling densities in summer 1996 and for plant cover in summer 1997 (Table 2).

L. corniculatus *and* T. repens

For these two species, cultivation had a strong positive effect on the density of seedlings in autumn 1995 (Table 3). Cultivation interacted with rabbit grazing, which reduced the density of seedlings on cultivated plots but had no significant effect on grassland plots (Fig. 1). The interaction between the effects of cultivation and seed density was also significant (Table 3). The abundance of seedlings increased with increasing seed density on cultivated plots but was unaffected by seed sowing on grassland plots (Table 2).

Seedling survival from winter 1995 to spring 1996 was greater on grazed plots (*L. corniculatus*: grazed = 7.1%, fenced = 1.9%; *T. repens*: grazed = 5.0%, fenced = 1.1%, Table 3). By summer 1996, the significant interaction between the effects of cultivation and rabbit grazing had disappeared, leaving only significant main effects of rabbit grazing and cultivation (Table 3). In contrast with autumn 1995,

Table 3. Results of statistical analysis for the effects of rabbit grazing (G), soil cultivation (C) and the density of sown seeds (S) on the number of seedlings in autumn (October) 1995 and summer (July) 1996, the proportion of seedlings surviving from winter (December) 1995 to summer 1996 and plant cover in summer 1997. Seedling data were analysed in GLIM using Poisson errors for seedling densities and binomial errors for seedling survival. Plant cover values were analysed by split-plot ANOVA following an arcsine transformation of the percentage. NS = not significant, *$P < 0.05$, **$P < 0.01$

	Treatment effects						
Response variable	G	C	S	G × C	G × S	C × S	C × G × S
A. elatius							
Seedlings: autumn 95	**	**	**	**	NS	**	NS
Seedlings: summer 96	**	**	**	**	NS	**	NS
Seedling survival[1]	**	NS	**	NS	NS	NS	NS
Cover: summer 97	**	*	**	**	**	**	**
F. rubra							
Seedlings: autumn 95	**	*	**	**	NS	**	NS
Seedlings: summer 96	**	**	**	**	NS	**	NS
Seedling survival[1]	**	NS	**	NS	NS	NS	NS
Cover: summer 97	**	*	**	**	**	**	**
P. lanceolata							
Seedlings: autumn 95	**	*	**	*	NS	**	NS
Seedlings: summer 96	**	*	**	NS	NS	**	NS
Seedling survival	*	NS	*	NS	NS	NS	NS
Cover: summer 97	**	**	**	NS	NS	**	NS
R. acetosa							
Seedlings: autumn 95	**	*	**	*	NS	**	NS
Seedlings: summer 96	**	*	**	NS	NS	**	NS
Seedling survival[1]	*	NS	NS	NS	NS	NS	NS
Cover: summer 97	**	**	**	NS	NS	**	NS
L. corniculatus							
Seedlings: autumn 95	**	**	**	**	NS	**	NS
Seedlings: summer 96	**	**	**	NS	NS	NS	NS
Seedling survival	**	NS	*	NS	NS	NS	NS
Cover: summer 97	NA	NA	NA	NA	NA	NA	NA
T. repens							
Seedlings: autumn 95	**	**	**	**	NS	**	NS
Seedlings: summer 96	**	**	**	NS	NS	NS	NS
Seedling survival	**	NS	*	NS	NS	NS	NS
Cover: summer 97	NA	NA	NA	NA	NA	NA	NA

NA = not assessed as species present on too few plots.

[1] analysis based only on those plots where seeds were sown.

seedlings were now more abundant on grazed plots (Fig. 1). Seedling survival from winter 1995 to summer 1996 decreased with increasing seed density for both species (*L. corniculatus*: 21.1, 8.2, 5.1 and 3.2%; *T. repens*: 26, 6, 4 and 3%, for 0, 1000, 10 000 and 50 000 seeds m^{-2}, respectively; Table 3). However, the abundance of seedlings on cultivated plots in summer 1996 still increased with increasing seed density (Table 2). Almost all of the plants had died by the end of the experiment; *L. corniculatus* was found in seven quadrats and *T. repens* in eight quadrats, all on grazed plots. These species were present on too few plots at the end of the experiment to allow statistical analysis.

Discussion

The question of whether on not plant recruitment is seed-limited is a crucial issue in plant population dynamics (see Crawley, 1990b), and in many cases we do not know whether an increase in seed production would lead to an increase in the number of seedlings, let alone an increase in the number of adult plants. Recruitment might not be seed-limited because there is too little disturbance (microsite-limited), too much competition from adult or seedling plants of the same or different species (competition-limited) or too much seed and seedling predation (herbivore-limited). For

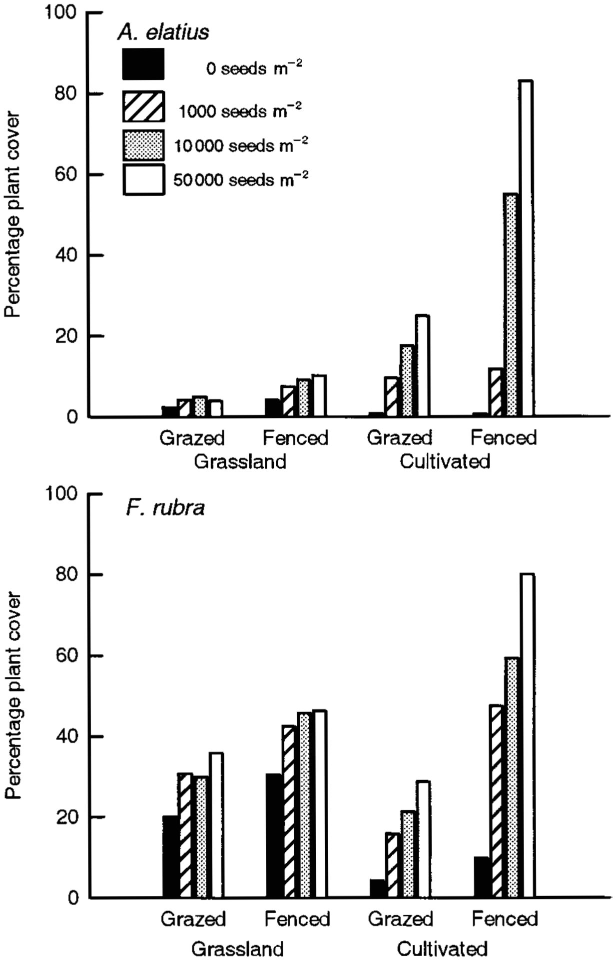

Figure 2. The effect of rabbit grazing, cultivation and seed sowing density (per m^2) on the mean percentage cover (back-transformed from arcsine percentages) in summer (July) 1997 of *A. elatius* and *F. rubra*. There was a significant rabbit grazing × soil cultivation × seed density interaction for both species.

the six species sown in a mesic grassland in this study, we observed a wide variety of responses. Seed density, soil disturbance and rabbit grazing all affected recruitment, but to differing degrees and in differing ways for different species.

Seedling densities

All six of the species studied showed significantly enhanced seedling densities when soil disturbance and seeds were experimentally provided, and this had significant effects upon the final abundance of all species 2 years later. This result supports the findings of a large number of studies (Elton, 1958; Crawley 1986; Drake *et al*., 1989; Burke and Grime, 1996; Kotanen, 1997) that have related disturbance events to invasion in plant communities. Seedling emergence was not, however, restricted entirely to disturbed plots; *A. elatius*, *F. rubra*, *P. lanceolata* and *R. acetosa* all showed significantly enhanced seedling densities when extra seeds were sown into undisturbed grassland. However, in each case there were fewer seedlings than on disturbed plots, and unlike disturbed plots, where seedling densities increased with increasing seed density, seedling densities were an asymptotic function of seed density (Table 2). The most obvious explanation for the higher seedling densities on disturbed plots is that the destruction of the perennial cover, mainly *F. rubra* and *A. capillaris*, increased the availability of establishment microsites and reduced the intensity of competition from the perennial vegetation (Crawley, 1990a). However, we cannot rule out the possibility that the difference between disturbed and grassland plots was due to an indirect effect of the removal of vegetation (rather than a direct one). For example, the abundance of seed and seedling predators, such as molluscs and small mammals, has been shown to be positively correlated with the degree of vegetation cover (Montgomery, 1980; Godan, 1983), leading to the expectation that they might have a greater impact on grassland plots. Separation of these direct and indirect effects would require factorial experiments involving soil disturbance (with and without) and predator exclusion (with and without seed and seedling predators) (e.g. Bonser and Reader, 1998).

There were marked differences between species in their response to disturbance on plots where no extra seeds were sown. *P. lanceolata*, *L. corniculatus* and *T. repens* all showed enhanced seedling densities, whereas *A. elatius*, *F. rubra* and *R. acetosa* did not show any significant emergence. The differences in emergence between species probably reflects the capacity of the three species that did emerge to form persistent seed banks (Table 1), and so have viable seeds present in the soil at the time when the disturbance occurred. These differences had important implications for the final abundance of these species; although there was some regeneration of *A. elatius*, *F. rubra* and *R. acetosa* from vegetative fragments after cultivation (G.R. Edwards, unpublished observations), all three species had a lower final abundance on non-sown plots that were disturbed than non-sown plots in intact grassland. This result, in conjunction with the finding that all species were enhanced by disturbance where seeds were sown, confirms previous results, that revegetation following disturbance will be constrained by the abundance and type of propagules available at the disturbed site (Gross, 1980; Hobbs and Mooney, 1985; Kotanen, 1996).

The difference in the impact of rabbit grazing on seedling densities between disturbed and grassland plots was striking. On disturbed plots there was a marked negative effect of grazing (Fig. 1). In contrast, on grassland plots there was no effect or a very small negative effect (Fig. 1). This difference could be due simply to higher seedling densities; because more seedlings emerged on disturbed plots, there was a greater chance of detecting an impact of rabbit grazing (Crawley and Pacala, 1991). Alternatively, the degree of exposure of seedlings to rabbits might be important. Seedlings emerging on the bare soil of cultivated plots would be particularly prone to grazing, whereas those emerging in grassland would be protected from grazing by the associated vegetation.

The result that rabbit grazing reduced or had no impact on seedling emergence bears comparison with the seedling emergence studies of Bakker and de Vries (1992), conducted in a salt marsh, and Watt and Gibson (1988), conducted in a chalk grassland. These studies recorded more emergence on plots grazed by sheep and cattle than mown or non-grazed plots. This was attributed to the grazed plots having more bare ground and a shorter, less competitive canopy. The difference between these studies and ours might reflect the short period of time (3 months) that fences were erected before seed sowing; there was little growth during this period due to the summer drought, and only small differences existed in plant cover and vegetation height at the time of seed sowing. Alternatively, differences in the capacity of the animals to graze selectively might be important. Because rabbits have small mouth parts, they might be able to graze seedlings that are too small for sheep and cattle to eat.

Seedling survival

In this study, seedling mortality occurred predominantly in the spring and early summer months of 1996 (Fig. 1), a time that was associated with the vigorous growth of *A. odoratum* and *R. acetosella* on disturbed plots and *F. rubra* on grassland plots. This result supports previous studies which have shown that mortality of both seedlings and mature plants of grassland species is greater when swards are growing most actively (Saruhkan and Harper, 1973; Hawthorn and Cavers, 1976; Howe and Snaydon, 1986; Silvertown *et al*., 1992), and therefore at a time when there is the most intense competition for limiting resources.

Previous studies have suggested that seedling survival may be related to seed size, with large-seeded species having an advantage over small-seed species as they have more food for the seedlings (Thompson, 1984; Gross and Werner, 1982; Goldberg and Werner, 1983). However, in this study there was no simple relationship between seed size and seedling survival. Although *A. elatius*, which has the largest seed size, had the greatest seedling survival (Fig. 1), *L. corniculatus* had the poorest seedling survival, despite having a seed size similar to that of *P. lanceolata* and larger than that of *T. repens*.

Feeding trials have shown that rabbits prefer grass species to dicotyledon species, with *F. rubra* being highly preferred (Williams *et al*., 1974; Bhadresa, 1977). Our seedling survival data are consistent with these results, and also with the hypothesis that palatability and competitive ability are positively correlated (Crawley, 1990a; Pacala and Crawley, 1992). Seedling survival of the most palatable species, the grasses, was higher on plots protected from grazing. In contrast, survival of the less palatable species, the herbs and legumes, was greater on plots exposed to grazing; by summer 1996, seedlings of *P. lanceolata* and *R. acetosa* were more numerous on grazed plots. Moreover, high density seedling populations of *T. repens* and *L. corniculatus* on fenced, cultivated plots went extinct within 2 years of emergence. Apparently, the herb and legume species benefited from competitive release as a result of preferential grazing of associated species; on fenced plots, survival was probably lower due to greater competition for light, moisture or nutrients arising from the accumulation of non-grazed biomass of the established vegetation (Cook, 1985; Rabinowitz and Rapp, 1985; Howe and Snaydon, 1986; Aguilera and Lauernroth, 1993; Potvin, 1993). However, the response of seedling survival to fencing for the herb and legume species could also be due to indirect effects of fencing on other seedling mortality factors. More litter, for instance, which can reduce seedling survivorship (e.g. Gross and Werner, 1982; Bergelson, 1990), was observed on fenced plots at the end of the experiment. Furthermore, Rice (1987) has elegantly demonstrated that rodent abundance may be higher within fenced exclosures, and that their grazing effects may be confused with those of plant–plant interactions.

Seed limitation in undisturbed grassland

A surprising feature of our results was that four of the six species were seed-limited in intact, undisturbed grassland. This result contrasts with the general view that seedlings rarely, if ever, establish in closed turf (for a review see Wells *et al*., 1989). The difference between our study and others is difficult to explain. One possibility is that our results reflect the effect of the severe drought in summer 1995, which resulted in the death of perennial ramets and low plant biomass (G.R. Edwards, unpublished observations) at the time of sowing. Thus, as microsite availability was high, and competition from existing vegetation low, seedling recruitment might have been more pronounced than in other moister years. In support of this argument, we found that out of 60 herb species sown at a rate of 1000 extra seeds m^{-2} into undisturbed mesic grassland at Silwood Park in the following slightly wetter year (1996), only three were seed-limited (M.J. Crawley, G.R. Edwards and L. Turnbull, unpublished results). Thus, while the drought in summer 1995 caused considerable mortality amongst mature plants, it may have had an important positive impact on plant recruitment by causing increased microsite availability and higher subsequent rates of seedling recruitment.

Implications of results

The effects of rabbit grazing and soil disturbance on seedling recruitment that we observed are consistent with the patterns of abundance of the six species in Nash's Field. The finding that *T. repens* and *L. corniculatus* were found almost exclusively on grazed, disturbed sites is in keeping with the observation from Nash's Field that these two species occur predominantly on grazed areas around the edge of disturbances (e.g. molehills) and that they only persist for short periods of time (G.R. Edwards, unpublished results). The other four species studied are more widely distributed in Nash's Field, as would be predicted by their capacity to establish in intact vegetation. The reduced survival of *R. acetosa* and *P. lanceolata* on fenced plots is consistent with the observation that these species are increasers under rabbit grazing (Crawley, 1990a), and with the finding that removal of grasses with herbicide allows competitor release of these species (M.J. Crawley, unpublished observations). In the case of *F. rubra* and *A. elatius*, reduced seedling recruitment on grazed plots may be an important factor preventing these species from dominating these plots.

The conditions of seed density, disturbance and herbivory under which plant populations are seed-limited has implications for predicting what impact seed loss due to herbivores (e.g. seed and flower feeders) has on plant recruitment (Anderson, 1989; Crawley, 1992). Seed loss in all six species would be expected to have a marked effect on the number of plants that recruit to the juvenile population in grasslands subject to heavy disturbance (e.g. heavy mole infestation). However, this prediction would depend on the level of grazing; as an example, at our study site *P. lanceolata* and *R. acetosa* would be more sensitive to seed predation on sites exposed to rabbits. The same level of seed loss would be expected to have much less of an impact in intact grassland. For the four species with an upper asymptote to seedling recruitment, seed loss is likely to have little impact until seed density is reduced to some (unknown) threshold below 1000 seeds m^{-2} where seed density limits recruitment. Moreover, as *L. corniculatus* and *T. repens* were not seed-limited in intact grassland, heavy seed losses may have little measurable impact on population size for these species, unless it interfered with the establishment of a seed bank capable of exploiting future disturbances (Anderson, 1989). Clearly, the important question is not so much whether or not these herbivores will affect recruitment, but under what circumstances of disturbance and subsequent levels of herbivory they will affect recruitment (see Maron and Simms, 1997; Rees and Paynter, 1997).

Our results also have practical implications for attempts to diversify species-poor grasslands by introducing seed, particularly of dicot species (Wells *et al*., 1981; Wells, *et al*., 1989). In agreement with previous recommendations (Wells *et al*., 1989), our experiments demonstrate that the most successful way of establishing dicot species is to sow seeds where the existing vegetation has been disturbed (e.g. by partial or complete rotavation or by harrowing, see Pywell *et al*., 1997), and to use grazing or cutting to control the competing vegetation, particularly that of perennial grasses (Jones and Hayes, 1997). We do not agree entirely, however, with the general view that soil disturbance is always needed for establishment of sown seeds (Wells *et al*., 1989); both *P. lanceolata* and *R. acetosa* established from seed in intact grassland in our study (see also Thompson and Baster, 1992). Moreover, for these two species, seedling recruitment was an asymptotic function of seed density, and populations of around 50 plants m^{-2} were established with seed densities as low as 1000 seeds m^{-2}. This highlights the potential for using low seed rates combined with minimal soil disturbance to establish populations when the availability of suitable seed is limited and no soil disturbance is desired (see discussion in Stevenson *et al*., 1995).

Conclusion

This study supports the general conclusion of a substantial body of field work that seedling recruitment in grasslands is enhanced by soil disturbance (Burke and Grime, 1996; Silvertown and Tremlett, 1989). Although in contrast to many studies, seedlings of some species did occur in closed vegetation (see also Thompson and Baster, 1992). Our study highlights that species abundance and distribution patterns will not only reflect the history of disturbance but also the interaction between disturbance and other factors, here rabbit grazing and propagule supply. Our study shows that rabbit grazing could affect seedling recruitment on disturbances by altering the number and species composition of seeds dispersed to disturbances, as well as through direct (e.g. seedling herbivory) and indirect effects (e.g. defoliation of competitors) on seedling survival. As Silvertown and Tremlett (1989) note, it is likely that seedling recruitment in many grassland species will depend on the interaction between soil disturbance and another factor, be it herbivory, shade (Silvertown and Tremlett, 1989) or nutrient availability (Carson and Pickett, 1990; Burke and Grime, 1996). We must explore these interactions in greater detail if we are to make advancements in understanding what determines the distribution and abundance of species in grasslands.

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