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An experimental study of the effects of sheep grazing on vegetation change in a species-poor grassland and the role of seedling recruitment into gaps

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Summary

1. An experiment was set up in 1986 on a species-poor grassland in Oxfordshire to determine the effect of sheep grazing management on vegetation change after cessation of fertilizer applications. Three seasons of grazing (winter, spring and summer) were applied, each with two grazing intensities, in a $2 \times 2 \times 2$ factorial design with two blocks in 16 paddocks.

2. Point quadrat surveys in 1990 showed that the grassland vegetation was dominated by perennial grasses and that the frequency distribution of species was highly skewed. Dicotyledonous species ('dicots') were extremely rare, having an overall frequency of only 0.43%.

3. The frequencies of eight of the 10 dominant grasses were significantly affected by grazing intensity although these effects depended on the grazing season, were species-specific and were generally small.

4. Intensive surveys of the dicots in 1990–91 discovered 40 species although most of these were rare. The dicots exhibited stronger and more consistent responses than the grasses, their abundances being significantly increased by increased grazing in one or more grazing periods. Dicot species number was significantly increased by increased grazing intensity in all periods.

5. The potential was studied for seedling establishment in gaps to bring about vegetation change. Regular monitoring of the natural recruitment of seedlings into artificially created gaps was carried out in each paddock. Comparison between the species composition of seedlings emerging in gaps where the soil had been replaced with a sterile loam and that of gaps formed over the original soil showed no evidence of a persistent seed bank and that all seeds were probably derived from recent seed rain.

6. No species novel to the vegetation emerged in the gaps and the species composition of seedlings in the gaps was significantly and positively correlated with that of the vegetation in a majority of the paddocks. However, some species differences in the contribution to the seed rain were noted. In particular, the dicots were over-represented. The number of grass seedlings in the gaps was decreased by increased summer grazing.

7. Therefore, grazing had complex effects on vegetation change. Change is likely to be slow, especially while fertility is high, because of the small responses of the grasses to the grazing treatments and the lack of input of novel species from a seed bank. However, the dicots may continue to increase under increased grazing because of their high seed production and the effects of grazing in increasing gap frequencies.

Key-words: grazing season, regeneration, seed bank, seed rain, species composition.

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Introduction

Two processes are important in determining the species composition of a plant community: the survival and vegetative spread of plants and the establishment of seedlings from the seed bank. The first is very important in most grasslands; grazing encourages the clonal growth of perennial grasses and halts the succession to woodland. However, the intensity of grazing affects the balance between these two processes; as grazing intensity increases, the growth of the dominant grasses is suppressed and gaps are opened in the sward (Watt & Gibson 1988; Silvertown & Smith 1989a). These gaps allow seedlings to establish (Rapp & Rabinowitz 1985; Silvertown & Smith 1988) and, if recruitment occurs from a seed bank with a different composition to that of the vegetation (e.g. Chippindale & Milton 1934), species diversity may be increased. Studies of pastures from which grazers have been excluded have shown that initially the perennial grasses increase, resulting in a rapid decline in species diversity (Rawes 1981; Sykora, van der Kragt & Rademakers 1990; Hill, Evans & Bell 1992). A high intensity of grazing is important in maintaining (Wells 1971) or developing (Gibson, Watt & Brown 1987a; Gibson *et al.* 1987b) the high diversity of chalk grasslands.

The increased application of fertilizers to British grasslands since the 1940s has resulted in dense, productive swards dominated by a few perennial grasses (Fuller 1987). In these grasslands there must be very intensive grazing to suppress grass growth sufficiently to allow 'useless and weedy' species to establish from the seed bank (Jones 1933). To increase the diversity of such improved grasslands cessation of fertilization must be coupled with grazing (Willems 1983; Bakker 1987, 1989). These studies have compared the effects of grazing with no grazing and with other management techniques such as cutting. However, an experiment by Gibson *et al.* (1987a, b) on early succession on land formerly under arable cultivation has shown that both the season and intensity of grazing are likely to affect vegetation change through differential effects on species (see also Bacon 1990). In order to understand the effects of grazing on vegetation change and to direct this change towards conservation objectives, studies must be carried out in which the season and intensity of grazing are both varied experimentally.

We report here on an experiment on a grassland in which three seasons of sheep grazing (winter, spring and summer) were applied, each with two grazing levels, in a randomized block design. This design avoids the error of pseudoreplication, often committed in grazing experiments and other ecological studies (Fowler 1990). The grassland studied was representative of much of British grassland. It had been fertilized since the 1940s and as a result

it was species-poor (Treweek 1990). However, fertilizing had recently ceased, providing an opportunity to study how such a site can be managed to increase species diversity.

The experiment was designed to detect the effects of seasonal grazing treatments, and of interactions between the treatments, on the abundance of all the main plant species in the vegetation. Also studied was the potential for vegetation change mediated by effects of grazing treatment on plant recruitment from seed into gaps. The relative contributions of the seed rain and the seed bank to this recruitment were also determined.

Materials and methods

SITE DESCRIPTION

The grazing experiment was set up at Little Wittenham Nature Reserve in Oxfordshire, England (SU568924) in 1986 (Treweek 1990). The site is situated on the Berkshire Downs and the soil is a calcareous clay loam. Cultivation last occurred in the 1940s and subsequently the site was seeded with an agricultural grass mixture. It was grazed by sheep and received regular applications of fertilizers. When the Northmoor Trust purchased the site in 1984 all application of agrochemicals stopped (Tennyson 1992).

The grazing experiment was designed to determine the effect of the timing and intensity of grazing on vegetation change using recognized grazing seasons and to allow the processes of vegetation change to be determined with statistical rigour. There were three grazing periods in the year: 'winter' (1 November–21 March), 'spring' (21 March–21 May) and 'summer' (21 May–1 November). These grazing periods were chosen because it is reported that grazing in these seasons affects vegetation change differently (Bacon 1990). Within each period there were two levels of grazing. In winter and spring grazing two Suffolk \times Mule ewes per paddock were either present or absent and in summer grazing the sward height was maintained at either 3 cm or 9 cm by weekly measurement followed by adjustment of the stocking rate. The experiment was fully factorial with a $2 \times 2 \times 2$ structure and two randomized blocks assigned over 16 (2×8) paddocks of 50×50 m (Table 1). This design allowed analysis of results by three-way ANOVA of a variable to determine the main effects, i.e. the grazing level in each season, and interaction effects of the grazing levels in the three grazing seasons. This structure was used in the ANOVA analysis of data in this paper. Treweek (1990) found no differences in initial species composition between the grazing treatments.

In 1986 and 1991 the soil chemistry in each paddock was analysed using standard ADAS techniques (ADAS 1986), giving the concentration of mineral

Table 1. Design of the grazing experiment. A minus sign indicates no grazing and a plus sign indicates grazing during the relevant period. All paddocks were grazed in summer to either 3 cm or 9 cm in height

Treatment	Summer 3 cm		Treatment	Summer 9 cm	
	Winter	Spring		Winter	Spring
A	—	—	E	—	—
B	—	+	F	—	+
C	+	—	G	+	—
D	+	+	H	+	+

nutrients in mg per litre of soil from soil cores to a depth of 15 cm. Despite the cessation of fertilization there had been no drop in fertility over this time and concentrations of P (35 mg l^{-1}), K (424 mg l^{-1}) and Mg (113 mg l^{-1}) were all high. ANOVA indicated that the grazing treatments had not affected these levels.

SURVEYS

In conjunction with long-term measurements of sward change (Treweek 1990), the vegetation composition and the seed bank of each paddock were determined several years after setting up the experiment using the techniques described below. In all sampling the 10-m-wide perimeter around each paddock was avoided to reduce edge effects.

Two point-quadrat surveys of the vegetation were carried out over the periods 5–31 January and 6–10 August 1990. Two sample dates were used to compensate for seasonal changes in composition. In each paddock 64 sites 4 m apart on a grid of 8×8 sites were sampled using a point quadrat of 10 pins 5 cm apart. The pins had a diameter of 1 mm. The number of pins touched by any live part of each species was noted on each quadrat; the maximum touches for a species on a quadrat would therefore be 10. The total number of touches by each species in each paddock was used to calculate its fractional abundance in each paddock by dividing the total touches by that species by the total for all species. *Poa annua* (nomenclature follows Clapham, Tutin & Moore 1987), *P. pratensis* and *P. trivialis* were indistinguishable when young and were therefore combined as *Poa* spp.

Because of their rarity, dicotyledonous species ('dicots') were poorly represented in the point quadrat surveys (see below) and therefore a different technique was used to sample them more fully. Presence or absence of rooted plants of each dicot species in 1-m^2 quadrats was noted at 100 sites 3 m apart on a grid of 10×10 sites in each paddock, giving a maximum score of 100 per paddock for a species. Eight surveys were carried out, in the middle of February, April, July and November, from February 1990 until November 1991 inclusive.

Vegetative plants of *Ranunculus bulbosus* and *R. repens* were indistinguishable and were therefore combined as *Ranunculus* spp.

EXPERIMENTAL GAPS

The natural recruitment of seedlings into artificially created gaps was also studied. On 26 September 1990 two transects were laid out in each paddock parallel to the North–South fences. Starting 10 m along a transect, 10 sampling sites 3 m apart were marked. At each site all above-ground vegetation (including buried shoot bases) within a 10-cm diameter circle was removed with as little soil disturbance or removal as possible. Two 'seed source' treatments were applied. Half of the 20 gaps created in each paddock were assigned at random to a 'rain' treatment for which all the soil within the gap was removed to a depth of 15 cm and replaced with sterile loam (John Innes Seed Compost). The remaining gaps were left intact and were assigned to a 'bank + rain' treatment. This technique allowed separation of the two sources of the seedlings emerging into the gaps: the immediate seed rain as measured in the 'rain' treatment and the more persistent seed bank, buried in the soil and determined by comparing the numbers of seedlings from both sources, measured in the 'bank + rain' treatment, with the seed rain.

Two weeks later all seedlings in each gap were identified and removed. The gaps were monitored and any clonal ingrowth was removed every few weeks, depending on the rate of seedling emergence, until a final census on 10 January 1992. The census dates were collated into five approximately equal periods: 1 October 1990–1 January 1991, 2 January 1991–1 April 1991, 2 April 1991–1 July 1991, 2 July 1991–1 October 1991 and 2 October 1991–10 January 1992. For each species the sum of seedlings over the 10 gaps of each 'seed source' treatment was calculated for each paddock.

Results

POINT QUADRAT SURVEYS

Twenty-five species were detected over the whole experiment in the point quadrat surveys (Fig. 1a), 18 of which were grasses. The frequency distribution of species was extremely skewed with four species accounting for over 80% of touches. Dicot species were extremely rare in all the paddocks, having a combined frequency of 0.43% (the mean value per paddock).

Split-plot ANOVA of the arcsine transformed frequency data was used to determine the effects of the grazing treatments (upper stratum) and survey period (lower stratum) on the frequencies of species. Because the factor time involved repeated sampling of the paddocks, conservative degrees of freedom

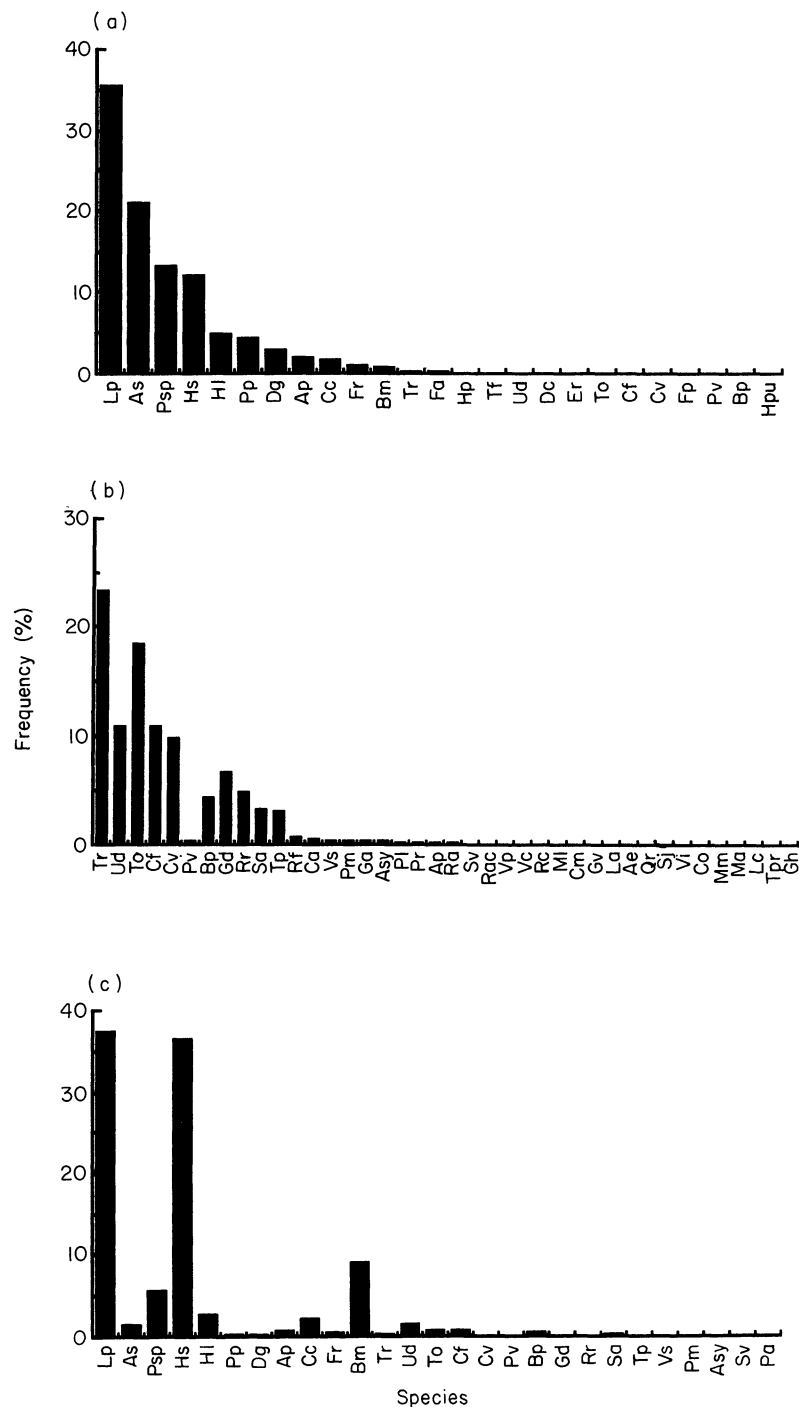


Fig. 1. Frequency distributions of species in each of the three surveys: (a) point quadrat surveys; (b) dicot surveys; (c) survey of the seedling emergence in gaps. The first six species from the origin in (b) were found in the point quadrat survey and are ranked according to their ranks in the point quadrat survey. Similarly, the species in the gap survey are ranked according to their ranks in the two vegetation surveys, except *Polygonum aviculare* which was unique to the gaps. All values are non-zero but those below 0.1% do not show on the figures. Species key: Ae, *Agrimonia eupatoria*; Ap, *Alopecurus pratensis*; Aps, *Acer pseudoplatanus*; As, *Agrostis stolonifera*; Asy, *Anthriscus sylvestris*; Bm, *Bromus mollis*; Bp, *Bellis perennis*; Ca, *Cirsium arvense*; Cc, *Cynosurus cristatus*; Cf, *Cerastium fontanum*; Cm, *Crataegus monogyna*; Co, *Convolvulus arvensis*; Cv, *Cirsium vulgare*; Dc, *Deschampsia cespitosa*; Dg, *Dactylis glomerata*; Er, *Elymus repens*; Fa, *Festuca arundinacea*; Fp, *Festuca pratensis*; Fr, *Festuca rubra*; Ga, *Galium aparine*; Gd, *Geranium dissectum*; Gh, *Glechoma hederacea*; Gv, *Galium verum*; Hl, *Holcus lanatus*; Hp, *Avenula pratensis*; Hpu, *Avenula pubescens*; Hs, *Hordeum secalinum*; La, *Leontodon autumnalis*; Lc, *Lotus corniculatus*; Lp, *Lolium perenne*; Ma, *Malus* spp.; Ml, *Medicago lupulina*; Mm, *Matricaria matricarioides*; Pa, *Polygonum aviculare*; Pl, *Plantago lanceolata*; Pm, *Plantago media*; Pp, *Phleum pratense*; Pr, *Potentilla reptans*; Psp, *Poa* spp.; Pv, *Prunella vulgaris*; Qr, *Quercus* spp.; Ra, *Rumex acetosa*; Rac, *Ranunculus acris*; Rc, *Rumex crispus*; Rf, *Ranunculus ficaria*; Rr, *Ranunculus repens* & *bulbosus*; Sa, *Sonchus asper*; Sj, *Senecio jacobaea*; Sv, *Senecio vulgaris*; Tf, *Trisetum flavescens*; To, *Taraxacum officinale*; Tp, *Trifolium pratense*; Tpr, *Tragopogon pratense*; Tr, *Trifolium repens*; Ud, *Urtica dioica*; Vc, *Veronica chamaedrys*; Vi, *Vicia* spp.; Vp, *Veronica persica*; Vs, *Veronica serpyllifolia*.

were used to determine the significance of its effects (Hand & Taylor 1987; pp 56–57). According to this method the degrees of freedom were changed to 1, $a-1$, where a is the number of subjects (in this case, 8 grazing treatment combinations). Only 10 species were common enough for analysis, namely *Alopecurus pratensis*, *Agrostis stolonifera*, *Cynosurus cristatus*, *Dactylis glomerata*, *Festuca rubra*, *Holcus lanatus*, *Hordeum secalinum*, *Lolium perenne*, *Phleum pratense* and *Poa* spp. Five of the species were significantly affected by the survey period although this rarely changed the effects of the grazing treatments qualitatively (only five of 70 survey period \times grazing treatment interactions were significant; results are not shown). There were several significant main effects of the grazing treatments on the species (Fig. 2), more than expected by chance (eight of 30 comparisons). There was great variation among the species in the effect of grazing period and the direction of the response to grazing. However, there were very few significant interaction effects of the grazing treatments (one of 40 comparisons; results are not shown). The grazing treatments did not affect grass species number.

DICOT SURVEYS

Forty species of dicot were found in the surveys (Fig. 1b) and again these had a highly skewed frequency distribution with six species accounting for over 80% of scores. The data for the 2 years were separated and split-plot ANOVA used to determine the effects of the grazing treatments (upper stratum) and survey date ('time'; lower stratum) on the abundance of each species in each year. Only eight species were common enough for this analysis, namely *Bellis perennis*, *Cerastium fontanum*, *Cirsium vulgare*, *Geranium dissectum*, *Ranunculus* spp., *Taraxacum officinale*, *Trifolium repens* and *Urtica dioica*. Because the factor time involved repeated sampling of the paddocks, conservative degrees of freedom were again used to determine the significance of time effects (see above).

Although there were significant time effects on the abundances of most species the patterns of these effects were not consistent between the 2 years (Fig. 3). The species generally increased in abundance in the summer months during 1991 but decreased in the summer of 1990, probably because there was a severe drought in the summer of 1990 (rainfall May–September 1990 was 45% of the 1951–91 average, whereas the same measure for 1991 was 117%). There were many significant main grazing treatment effects (21 of 48 comparisons) which were similar in both years (Fig. 4). Only *Ranunculus* spp. and *Urtica dioica* were unaffected by grazing. In all cases, except spring grazing on *Taraxacum officinale*, abundances were increased by an increased grazing intensity. Some grazing treat-

ment interactions were significant (12 of 64 comparisons) and these reflected the synergistic nature of the grazing treatment effects. There were no more significant time \times grazing treatment interactions than expected by chance (5 of 112 comparisons).

The dicot species number was significantly increased by winter grazing in 1990 and by increased grazing in all treatments in 1991 (Fig. 5).

SEEDLING RECRUITMENT INTO GAPS

14720 seedlings of 27 species were found in the gaps over the whole experiment during the 15 months (summed over the two 'seed source' treatments). The frequency distribution of species was highly skewed; more than 70% of the seedlings were of two species only (Fig. 1c). Although there were 16 dicot species their seedlings were few in number, making up only 4.2% of all seedlings. The 11 grass species found in the gaps were the dominant species in the point quadrat surveys. All the dicot species on the gaps were also found in the dicot surveys except the single seedling of *Polygonum aviculare*. Thus, 25 dicot species present in the vegetation were not detected in the gaps. The dicot species found in the gaps were generally those most common in the dicot surveys (Fig. 1b, c).

Therefore, the species composition of seedlings emerging in the gaps seems to have been similar to that of the vegetation. This similarity was tested by determining the Spearman rank correlation in each paddock of the abundances in the point quadrat surveys (averaged over the two surveys) with the abundances in the gaps (using only the 'bank + rain' treatment and summed over the year covering the last four censuses) of the 11 commonest grasses and the sum of all the dicots. Because of the rarity of the dicot species, to provide data for each paddock the total numbers of all dicot species were summed for each paddock. The correlation was positive and significant in 11 of the 16 paddocks and when abundances were summed across the paddocks (Table 2). The relationship between the vegetation and gap seedling compositions was investigated further by calculating the ratios of abundances in the point quadrat survey to those in the gaps for the 12 species (calling dicots a species) in each paddock. By using the 16 paddocks as replicates it was seen that different species had consistently different ratios (Kruskal Wallis test, $H = 125.8$, $P < 0.001$). *Agrostis stolonifera*, *Phleum pratense* and *Dactylis glomerata* all had consistently high ratios, i.e. they were under-represented in the gaps. *Bromus mollis*, *Cynosurus cristatus* and the dicots all had consistently low ratios, indicating that they were over-represented in the gaps (Table 3).

The correspondence between the species compositions in the dicot surveys and the dicots in the gaps was also investigated by Spearman rank

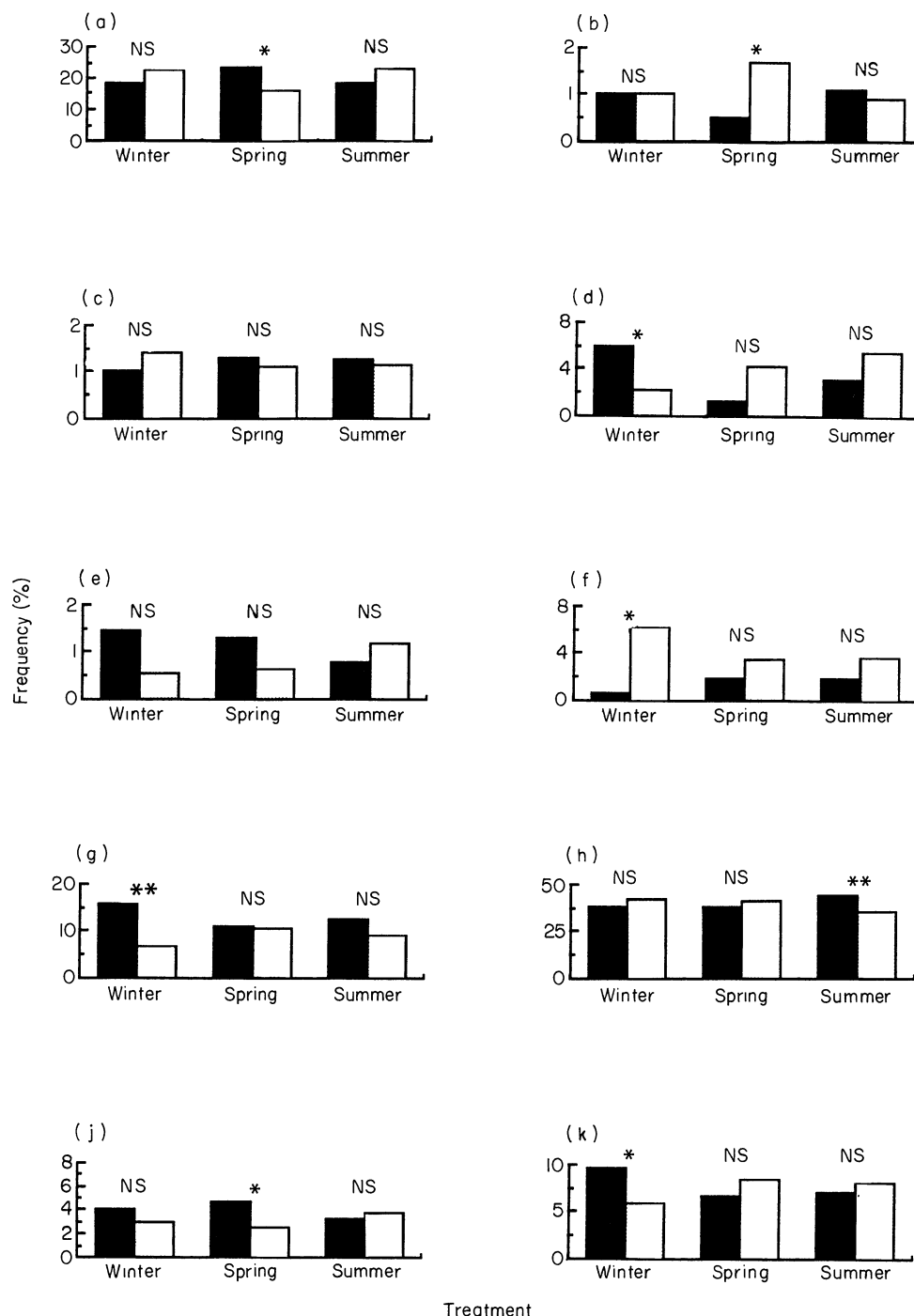


Fig. 2. Means corresponding to the main effects of the three seasonal grazing treatments on the relative frequencies of the 10 dominant grass species as measured in the point quadrat surveys. ■, Grazed in spring (paddocks B, D, F & H), grazed in winter (paddocks C, D, G & H) or grazed to 3 cm in summer (paddocks A, B, C & D), □ Ungrazed in spring (paddocks A, C, E & G), ungrazed in winter (paddocks A, B, E & F) or grazed to 9 cm in summer (paddocks E, F, G & H). (a) *Agrostis stolonifera*. (b) *Alopecurus pratensis*. (c) *Cynosurus cristatus*. (d) *Dactylis glomerata*. (e) *Festuca rubra*. (f) *Holcus lanatus*. (g) *Hordeum secalinum*. (h) *Lolium perenne*. (j) *Phleum pratense*. (k) *Poa* spp. Degrees of freedom are all 1,7. NS, not significant; * $P < 0.05$; ** $P < 0.01$.

correlation. Because few dicots emerged in the gaps only one analysis was carried out using the sum of abundances over all 16 paddocks. The species below rank 22 (Fig. 1b, c) in the dicot survey were not found in the gaps and were therefore excluded from the analysis. The correlation was positive and significant ($R_s = 0.774$, $P < 0.001$).

ANOVA was used to determine the effects on the grazing and 'seed source' on the number of seedlings of each species summed over all censuses. A split-plot model was used with grazing treatments on the upper stratum and 'seed source' treatments on the lower stratum. The species common enough for analysis were *Alopecurus pratensis*, *Agrostis*

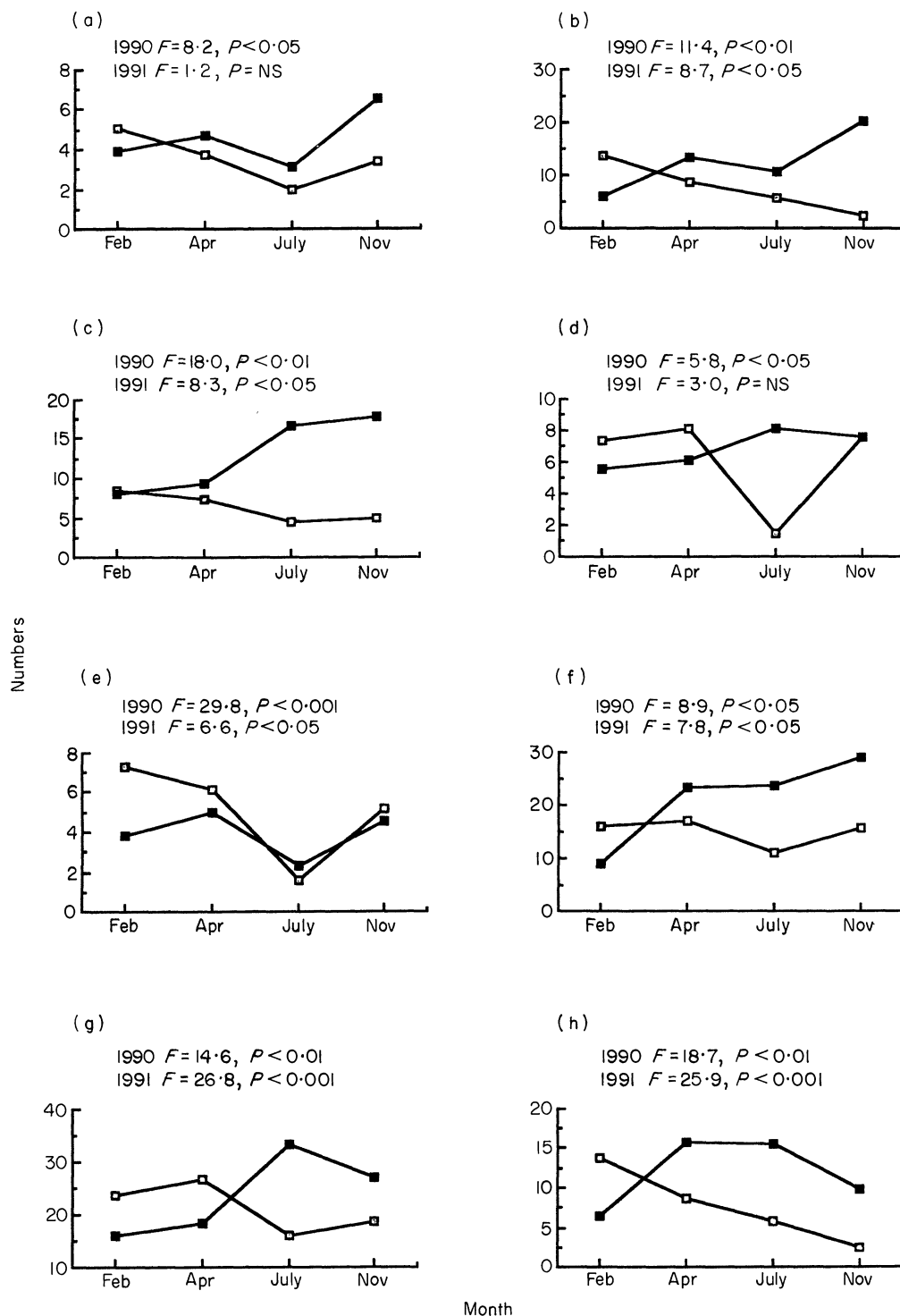


Fig. 3. Seasonal changes in the numbers of the eight dominant dicot species measured in the dicot surveys in 2 years. The number is the per paddock mean number of quadrats in which the species was found. 100 quadrats were sampled in each paddock. □, 1990. ■, 1991. The F-values and significances of the seasonal effects in each year are shown. Conservative degrees of freedom are all 1,7. (a) *Bellis perennis*. (b) *Cerastium fontanum*. (c) *Cirsium vulgare*. (d) *Geranium dissectum*. (e) *Ranunculus* spp. (f) *Taraxacum officinale*. (g) *Trifolium repens*. (h) *Urtica dioica*.

stolonifera, *Cynosurus cristatus*, *Holcus lanatus*, *Hordeum secalinum*, *Lolium perenne*, *Poa* spp., *Cerastium fontanum*, *Taraxacum officinale* and *Urtica dioica*. Other variables analysed were the total number of seedlings of all species, the total

number of grass seedlings, the total number of dicot seedlings, the number of grass species and the number of dicot species. There were few significant grazing-treatment effects on these 15 variables (Table 4). Five variables were decreased by increased

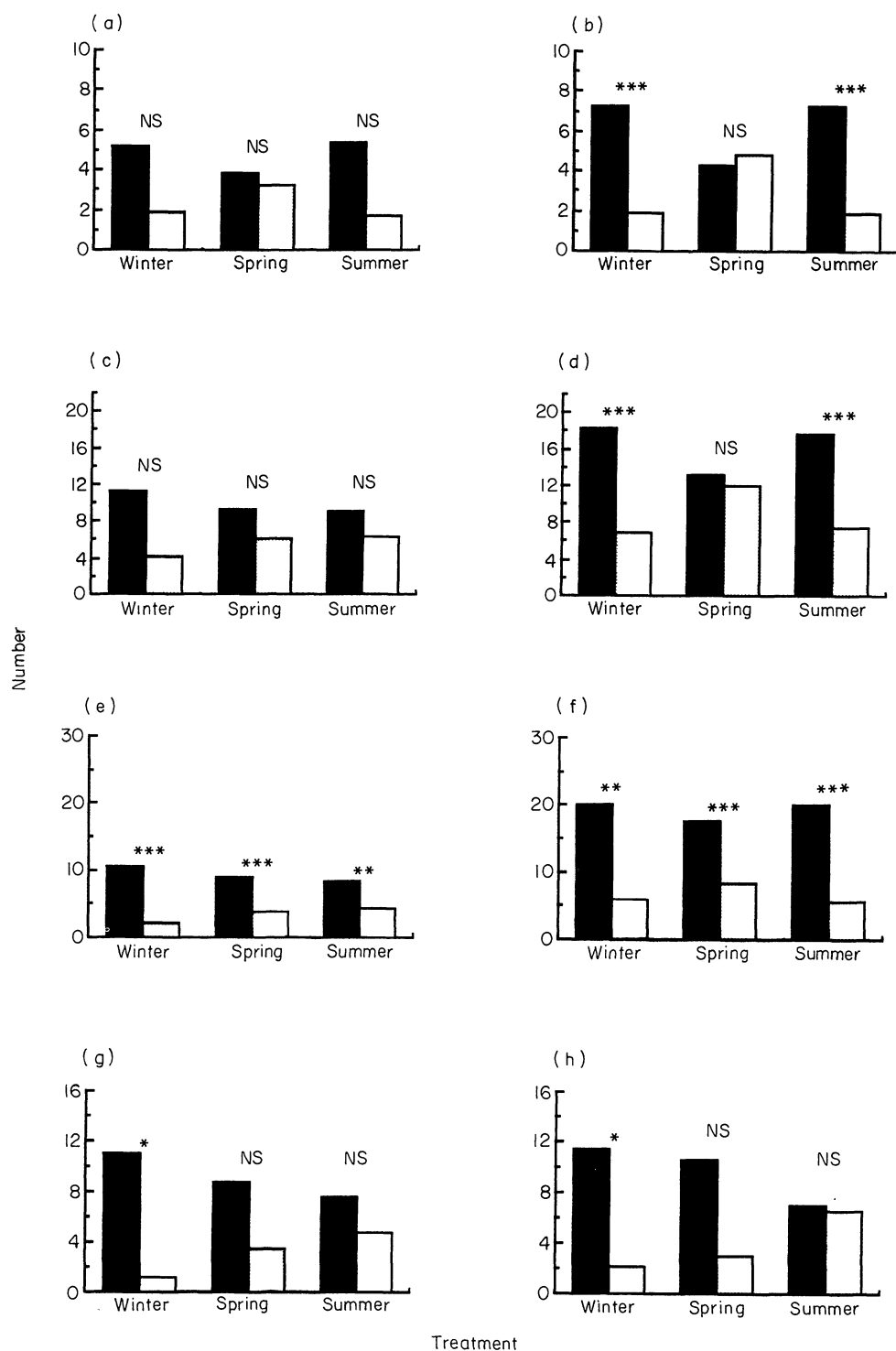


Fig. 4. Means corresponding to the main effects of the three seasonal grazing treatments on the relative frequencies of the eight dominant dicot species as measured in the dicot surveys in 1990 and 1991. ■, Grazed in spring or winter or grazed to 3 cm in summer. □, Ungrazed in spring or winter or grazed to 9 cm in summer. (a) *Bellis perennis* in 1990. (b) *Bellis perennis* in 1991. (c) *Cerastium fontanum* in 1990. (d) *Cerastium fontanum* in 1991. (e) *Cirsium vulgare* in 1990. (f) *Cirsium vulgare* in 1991. (g) *Geranium dissectum* in 1990. (h) *Geranium dissectum* in 1991. (i) *Ranunculus* spp in 1990. (j) *Ranunculus* spp in 1991. (l) *Taraxacum officinale* in 1990. (m) *Taraxacum officinale* in 1991. (n) *Trifolium repens* in 1990. (o) *Trifolium repens* in 1991. (p) *Urtica dioica* in 1990. (q) *Urtica dioica* in 1991. Degrees of freedom are all 1,7. NS, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

summer grazing; winter grazing increased numbers in five variables; and spring grazing decreased two variables. The 'bank + rain' treatment significantly increased seedling numbers in nine variables

(Table 4). There were no more significant grazing-treatment interactions (three of 68 comparisons) or grazing treatment \times 'seed source'-treatment interactions (four of 119) than expected by chance.

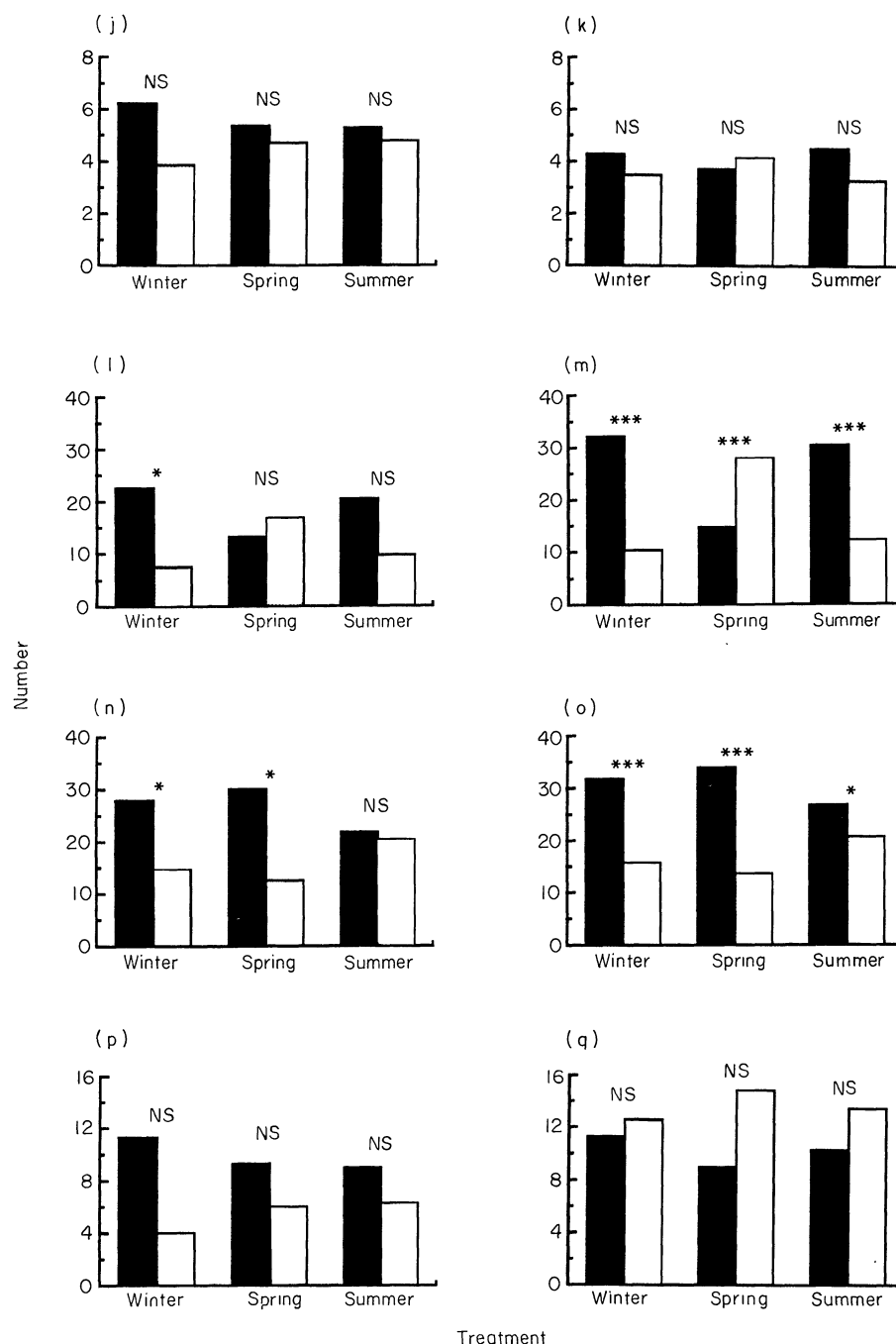


Fig. 4. (cont'd)

The 'seed source' treatment effects were investigated further by examining changes in the numbers of seedlings emerging in the gaps over the five time periods using a three level split-plot ANOVA with time on the third stratum. Because the factor time involved repeated sampling of the gaps, conservative degrees of freedom were used to determine the significance of its effects (see above). Only *Agrostis stolonifera*, *Hordeum secalinum*, *Lolium perenne*, *Poa* spp., total dicot seedlings and total seedlings provided enough data for this analysis. The data for the rarer species, *Alopecurus pratensis*, *Bromus*

mollis, *Cynosurus cristatus*, *Holcus lanatus*, *Cerastium fontanum* and *Urtica dioica*, were summed across the paddocks and analysed for 'seed source' and time effects using conservative split-plot ANOVA. Although there were significant 'seed source' treatment effects such that more seedlings were found in the 'bank + rain' treatment for *Agrostis stolonifera*, *Alopecurus pratensis*, *Cynosurus cristatus*, *Poa* spp., *Urtica dioica*, total dicots seedlings and total seedlings (Table 4), all these (except *Alopecurus pratensis*) showed significant 'seed source' treatment \times time interactions (Fig. 6). There were significantly

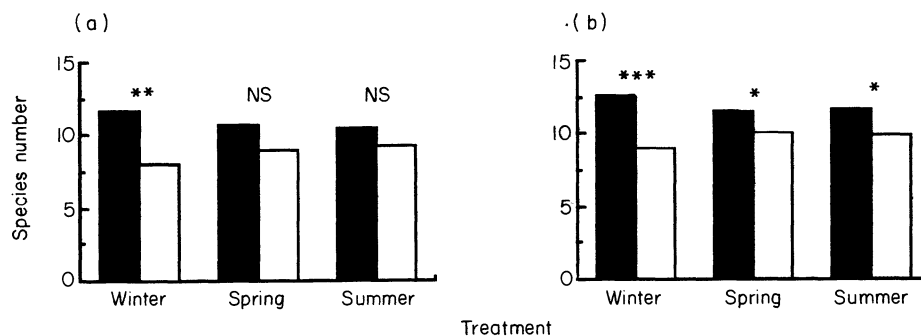


Fig. 5. Means corresponding to the main effects of the three seasonal grazing treatments on the number of dicot species per paddock as measured in the dicot surveys in (a) 1990 and (b) 1991. ■, Grazed in spring or winter or grazed to 3 cm in summer. □, Ungrazed in spring or winter or grazed to 9 cm in summer. Degrees of freedom are all 1,7. NS, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2. Spearman rank correlation coefficients between the abundances of the species listed in Table 3 in the point quadrat survey and in the gaps. For each paddock and for the abundances summed across the paddocks. Significance levels: * $P < 0.05$. $n = 12$

Paddock	R_s	
	Block 1	Block 2
A	0.198	0.626*
B	0.642*	0.626*
C	0.360	0.617*
D	0.625*	0.324
E	0.629*	0.585*
F	0.587*	0.686*
G	0.625*	0.287
H	0.323	0.585*

Table 3. Ranks of the ratio of abundance of a species in the point quadrat survey to its abundance in the gaps for each of 12 species averaged over the 16 paddocks. High ranks indicate over-representation in gaps

Species	Mean rank
<i>Agrostis stolonifera</i>	1.9
<i>Phleum pratense</i>	2.5
<i>Dactylis glomerata</i>	2.9
<i>Poa</i> spp.	5.5
<i>Festuca rubra</i>	6.3
<i>Holcus lanatus</i>	6.4
<i>Alopecurus pratensis</i>	6.8
<i>Lolium perenne</i>	6.9
<i>Hordeum secalinum</i>	8.4
<i>Cynosurus cristatus</i>	9.3
<i>Bromus mollis</i>	9.9
Dicot species	11.2

Table 4. Main effects of the grazing treatments and the 'seed source' treatment on the abundance of each species and other variables in the gaps. The paddocks (Table 1) corresponding to each treatment are shown. Interaction effects are not shown (see text). The mean for each treatment is shown and the significance of the difference between the means calculated by ANOVA is shown in the right hand column of each comparison. Degrees of freedom are 1, 7 for grazing effects and 1, 8 for 'seed source' effects

Variable	Winter grazing		Spring grazing		Summer grazing		Seed source effect	
	+	–	+	–	3 cm	9 cm	bank +	rain
	CDGH	ABEF	BDFH	ACEG	ABCD	EFGH	rain	rain
<i>Agrostis stolonifera</i>	5.8	6.9 ^{NS}	6.2	6.6 ^{NS}	5.0	7.8 ^{NS}	8.1	4.7**
<i>Alopecurus pratensis</i>	3.8	1.8*	1.3	4.4**	1.9	3.8 ^{NS}	4.8	0.9**
<i>Bromus mollis</i>	65.9	17.6 ^{NS}	29.3	54.2 ^{NS}	39.1	44.4 ^{NS}	41.6	41.9 ^{NS}
<i>Cynosurus cristatus</i>	10.6	8.9 ^{NS}	9.1	10.4 ^{NS}	5.6	13.9 ^{NS}	15.1	4.4*
<i>Holcus lanatus</i>	0.6	23.1 ^{NS}	4.6	19.1 ^{NS}	0.8	22.9 ^{NS}	19.7	3.9 ^{NS}
<i>Hordeum secalinum</i>	267	70.6**	209	128 ^{NS}	92.6	245*	176	161 ^{NS}
<i>Lolium perenne</i>	227	119**	192	154 ^{NS}	136	211*	166	181 ^{NS}
<i>Poa</i> spp.	20.6	30.1 ^{NS}	16.2	34.5 ^{NS}	20.7	30.0 ^{NS}	35.7	15.0**
<i>Cerastium fontanum</i>	3.3	2.9 ^{NS}	3.9	2.3 ^{NS}	3.7	2.4 ^{NS}	2.6	3.5 ^{NS}
<i>Taraxacum officinale</i>	2.9	3.0 ^{NS}	0.5	5.4**	3.3	2.6 ^{NS}	3.4	2.9 ^{NS}
<i>Urtica dioica</i>	7.0	6.5 ^{NS}	5.4	8.1 ^{NS}	5.5	8.0 ^{NS}	10.8	2.7**
Total seedlings	623	297**	487	433 ^{NS}	319	601**	504	416*
Total grass seedlings	606	281**	473	414 ^{NS}	303	584**	482	404 ^{NS}
Total dicot seedlings	17.1	15.9 ^{NS}	13.7	19.3 ^{NS}	16.1	16.9 ^{NS}	21.5	11.5*
Grass species	8.4	8.0 ^{NS}	8.4	8.1 ^{NS}	7.5	8.9*	8.9	7.6**
Dicot species	4.1	3.9 ^{NS}	3.8	4.3 ^{NS}	4.0	4.0 ^{NS}	4.4	3.6*

NS = non significant; * $P < 0.05$; ** $P < 0.01$.

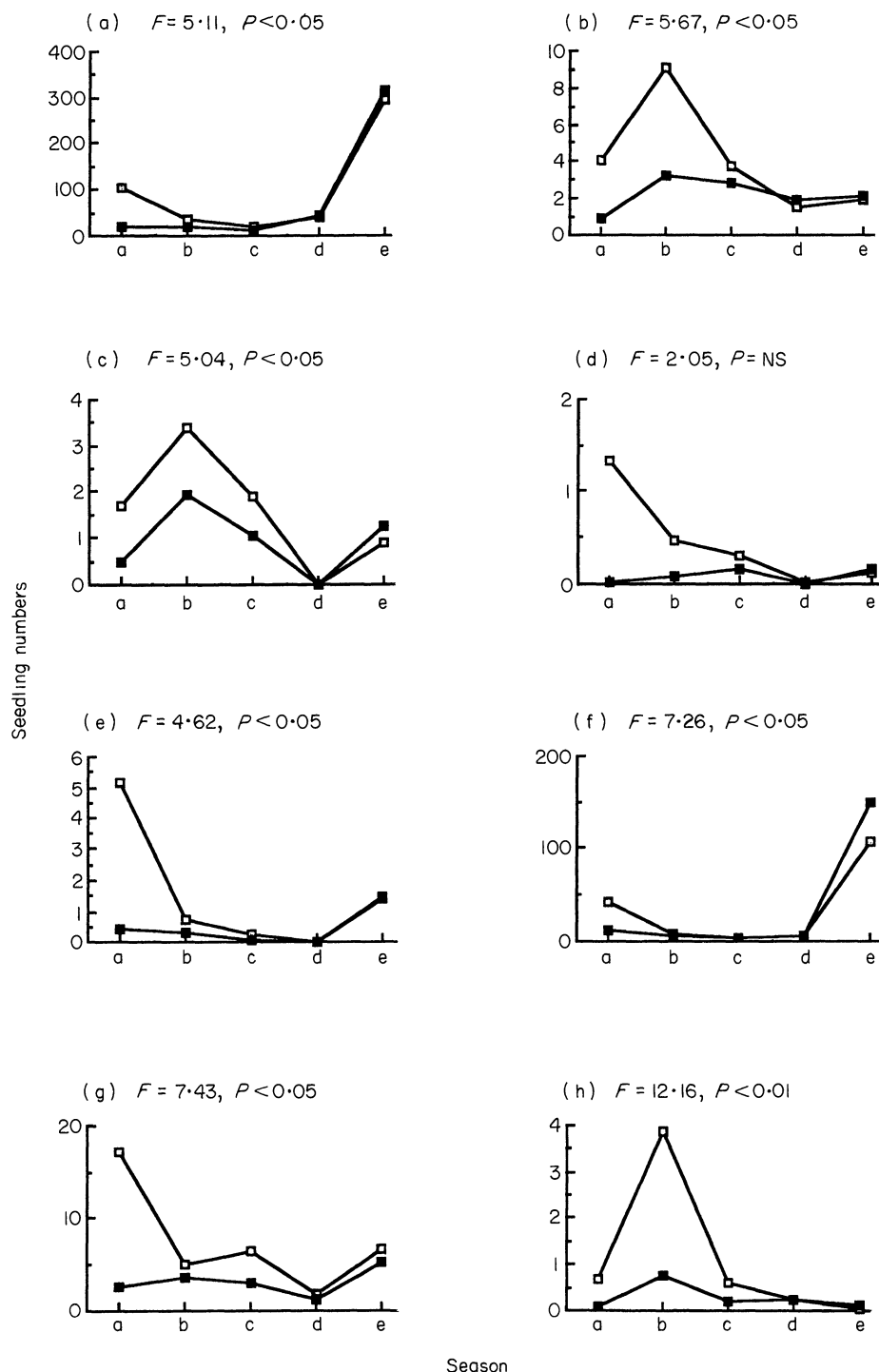


Fig. 6. Changes in the 'seed source' treatment effects over the five seasons on the number of seedlings found in the gaps expressed as the mean per paddock over each season: a = October 1990–January 1991; b = January 1991–April 1991; c = April 1991–July 1991; d = July 1991–October 1991, and e = October 1991–January 1992. ■, 'rain' treatment. □, 'bank + rain' treatment. The F -values and significances of the 'seed source' treatment \times season interaction are shown. Conservative degrees of freedom are all 1,15. (a) Total seedlings. (b) Total dicot seedlings. (c) *Agrostis stolonifera*. (d) *Alopecurus pratensis*. (e) *Cynosurus cristatus*. (f) *Lolium perenne*. (g) *Poa* spp. (h) *Urtica dioica*.

more seedlings in the 'bank + rain' treatment only in the first, and sometimes the second, time period. In subsequent periods there were similar seedling numbers in both 'seed source' treatments.

Of the 27 species found in the gaps three were unique to the 'bank + rain' treatment: *Geranium*

dissectum (3 seedlings), *Polygonum aviculare* (1 seedling) and *Trifolium repens* (26 seedlings). Two species were unique to the 'rain' treatment: *Ranunculus* spp. (1 seedling) and *Anthriscus sylvestris* (1 seedling). This pattern may therefore be due to sampling error resulting from low numbers rather

than to a genuine difference between the two 'seed source' treatments. The numbers of *Trifolium repens* found might seem to counter this conclusion; but 22 of these seedlings were found in one gap, indicating that the discrepancy was due to spatial heterogeneity of seed density.

Discussion

GRAZING EFFECTS ON THE VEGETATION

The study showed that the season and intensity of grazing had significant effects on species composition. The dicot species numbers and the abundances of individual dicot species were generally increased by an increased grazing intensity in all seasons (Figs 4 & 5), although the season during which grazing was effective depended on the species. However, although eight of the 10 grass species analysed responded to grazing, these responses were generally small and differed strongly between species (Fig. 2). Increased grazing intensity did not decrease any of the dominant grasses and grass species numbers were unaffected by grazing. Therefore, the less common grasses and the dicots were extremely rare in all treatments. This might be expected because the experiment had been running for only 5 years and the soil was still very fertile. Grazing is unlikely to affect fertility rapidly (Bakker 1989) and it may be many years before fertility will fall to a level at which grazing can diminish the dominant grasses.

These differences in the response to the grazing treatments between the two species groups, grasses and dicots, may be related to differences in their life histories. Grazing brings about species change through direct effects on growth, indirect effects via competitive interactions, and effects of gap creation on seedling establishment and plant growth. The simple responses of the eight commonest dicot species to grazing occurred because disturbance was probably the overwhelmingly important factor affecting their numbers, through its effects on seedling establishment and/or clonal spread. This is surprising because these species represent a variety of life history types, comprising five clonal perennials (*Bellis perennis*, *Cerastium fontanum*, *Ranunculus* spp., *Trifolium repens* and *Urtica dioica*), two short-lived perennials (*Cirsium vulgare* and *Taraxacum officinale*) and one annual (*Geranium dissectum*). One might expect that the clonal perennials would show more complex responses to grazing, noting also that *Ranunculus* spp. and *Urtica dioica* showed no responses. However, studies at Little Wittenham on *Cerastium fontanum* (Clear Hill, unpublished data), *Cirsium vulgare* (Silvertown & Smith 1989b; Bullock, Clear Hill & Silvertown 1994), and *Geranium dissectum* (Silvertown *et al.* 1992) have shown

that in these species population sizes are controlled by gap-dependent seedling emergence and establishment. The clonal growth of other species may also respond positively to disturbance (e.g. *Trifolium repens*; Solangaraachi & Harper 1987; Sackville Hamilton & Harper 1989). The species differences in seasonal grazing effects may be explained by life-cycle differences. *Geranium dissectum* germinates in spring and therefore responds to gaps created by grazing in the previous winter (Fig. 4g, h), whereas *Cerastium fontanum* germinates in winter and spring and therefore responds to summer and winter grazing (Fig. 4c, d). *Trifolium repens* (Fig. 4n, o) responds to gaps by clonal growth all year round (Sackville Hamilton & Harper 1989). Modelling showed that the population size of *Cirsium vulgare* might respond exponentially to increases in the disturbance rate (Silvertown & Smith 1989b); such an effect may explain the relatively large responses to the grazing treatments by the dicot species in comparison to the grasses.

Treweek (1990) carried out less intensive but more frequent surveys of the grazing experiment in March, June and September 1986 and 1987 and in September 1989 in two 1-m² permanent quadrats placed in each paddock. Dicot species were too rare to be detected in these samples but her surveys did show grazing treatment effects on some grass species. However, these effects varied through time: *Agrostis stolonifera* was decreased by spring grazing in June 1987; *Dactylis glomerata* was increased by spring grazing in June 1987 and by winter grazing in September 1990. There were interaction effects of grazing treatments on *Bromus mollis* and *Poa* spp. in September 1987 and on *Cynosurus cristatus* and *Hordeum secalinum* in September 1989. The other species recorded, *Lolium perenne*, *Festuca rubra* and *Phleum pratense*, showed no responses to the treatments. The differences between our surveys and Treweek's may be caused partly by differences in sampling procedures; but the inconsistencies within Treweek's study and the small effects of the treatments on the grass species in our study indicate that the changes in the grass species under the grazing treatments have been temporally extremely variable. All the grasses except *Bromus mollis* and *Poa annua* are perennials and it is likely that the most important grazing effect is on competitive interactions, resulting in complex and slow-acting effects on species abundances. Our studies of the two dominant grasses, *Agrostis stolonifera* and *Lolium perenne*, have shown that the effects of the grazing treatments on their tiller dynamics are also temporally variable (Bullock, Clear Hill & Silvertown, unpublished).

The results presented here show some agreement with those of Gibson *et al.* (1987a, b) who studied grazing effects on grassland succession from formerly ploughed land on a skeletal soil. Annual and short-

lived perennial dicots and annual grasses were increased by spring and/or autumn grazing but perennial grasses and dicots showed various responses. Bakker (1989) investigated the effects of continuous sheep grazing versus no grazing over 10 years in a grassland dominated by a few perennial grass species and on which fertilizer application had stopped. His results were generally similar to those of this study in that dicots and species diversity were generally increased by grazing and the grasses showed a variety of responses. A comparison of the responses of individual species between our study and Bakker's shows that some species were similarly affected by grazing in both studies (*Bellis perennis*, *Cirsium vulgare*, *Holcus lanatus*, *Poa trivialis* and *Trifolium repens*) but others were affected differently (*Cerastium fontanum*, *Cynosurus cristatus*, *Lolium perenne*, *Phleum pratense*, *Ranunculus repens* and *Taraxacum officinale*). These results and the temporal inconsistency of grazing effects on species at Little Wittenham conflict with the attempt to correlate species responses to grazing with their CSR life history strategies by Buttenschön & Buttenschön (1982), who concluded that 'competitor' species responded negatively and 'ruderal' species positively to increased grazing. Although the responses to grazing of short-lived species are predictable because of their need for gaps, the responses of species with more complex life cycles will depend on the exact grazing treatment, the community structure and the environmental conditions.

POTENTIAL FOR VEGETATION CHANGE BY SEEDLING RECRUITMENT INTO GAPS

A seedling that establishes in a gap may derive from the recent seed rain or from the buried seed bank, and the 'bank + rain' and 'rain' treatments were designed to differentiate the two processes. However, there was no obvious difference in species composition between the two treatments; the only difference was in the seedling number of some

species and this was only in the first and sometimes the second census period (Fig. 6). These differences were not large compared with the overall number of seedlings found, which suggests that they were due to the accumulation of the recent seed rain which was removed in the 'rain' treatment and that there was no persistent seed bank.

Even if there were no persistent seed bank, the seed rain could influence vegetation change by introducing novel or rare species from outside the community or through species-related differences in seed production which change the relative frequency of species in the seed rain as compared to the vegetation. There is no evidence for the introduction of novel species in the rain during the time of this survey (*Polygonum aviculare*, although found in the seed rain but not in the dicot survey, was seen as adult plants in the paddocks). However, such an event would be uncommon and some of the rare species found growing in the paddocks may have been colonizing in this way. *Sonchus asper* may be a case in point. While most dicots were fairly stable in numbers over the 2 years of the surveys the numbers of this annual increased from no plants in the first survey to 80, spread over 12 paddocks, in the final survey (Fig. 7). This may indicate that an influx of wind-borne seeds from external sources allowed rapid population build up.

There have been many surveys of the seed bank in a variety of grasslands which have shown a poor correspondence between the composition of seed bank and vegetation (Chippindale & Milton 1934; Champness & Morris 1948; Major & Pyott 1966; Thompson & Grime 1979; Schenkeveld & Verkaar 1984; Williams 1984; Bakker 1989). However, these studies must be extended if one is to determine how seedling recruitment into gaps created by grazing or other factors may influence vegetation change. For such influence to occur, seeds in the seed bank must not merely be present in the soil but must be able to germinate and establish as plants. Our study has shown that the input of seedlings from the seed

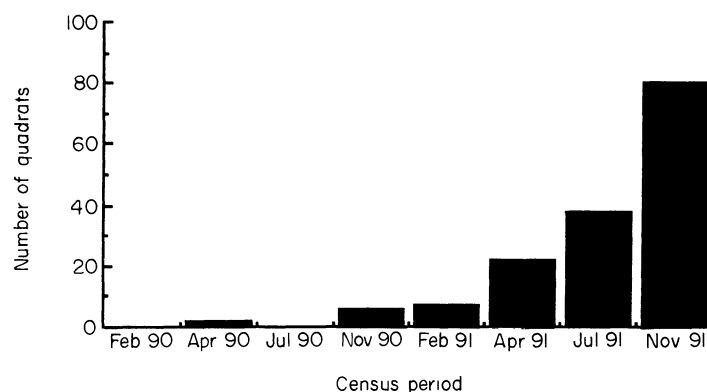


Fig. 7. Change in the number of quadrats containing *Sonchus asper* in the dicot surveys over time, totalled over all 16 paddocks.

bank was so rare as to be undetectable, despite the fact that nearly 15 000 seedlings were monitored. Recruitment was entirely attributable to the seed rain which, as Rabinowitz (1981) has shown in a quite different grassland, had the same species composition as the vegetation. The seed bank was unimportant, either because it was unusually depauperate compared with other grasslands of similar age and history (e.g. Chippindale & Milton 1934; Champness & Morris 1948), or because movement of seed to the soil surface was extremely rare.

Nevertheless, this study did show differences between the abundances of some species in the vegetation and their seedlings in the gaps (the seed rain). Some species were over-represented in the gaps (*Bromus mollis*, *Cynosurus cristatus* and the dicot species) and some were under-represented (*Agrostis stolonifera*, *Dactylis glomerata* and *Phleum pratense*). These differences were probably due to life-history differences; annuals and short-lived perennials (*Bromus mollis* and some of the dicots) probably produce large amounts of seed whereas stoloniferous grasses (*Agrostis stolonifera* and *Phleum pratense*) may produce few seeds. Studies of seed bank composition have found annuals better represented than perennials (Major & Pyott 1966) and dicots better represented than grasses (Chippindale & Milton 1934; Champness & Morris 1948).

The effects of grazing treatments on the species composition of seedlings in the gaps rarely corresponded with their effects on the same species in the vegetation (Figs 2 & 4; Table 4). This is probably because grazing effects on the grass species were slight. However, because of the consistent effects of grazing on all dicots, one might have expected there to be more dicot seeds in the more intensively grazed paddocks. That this is not the case may be due to the rarity of dicots in the vegetation. The grazing effects occurred mainly by affecting seed production, since summer grazing and occasionally also spring grazing decreased abundances of many species in the seed rain. This was probably caused by removal of flowers and flower stalks by sheep, as also found by O'Connor & Pickett (1992) and Williams (1984). By affecting only some species these grazing effects on seed production may be an added mechanism by which grazing can effect vegetation change. It is particularly interesting that, by decreasing the seed numbers of the dominant grasses, harder summer grazing increased the fraction of dicot seeds ($F = 6.97$, $P < 0.05$) in the total seed count.

CONCLUSIONS

The regeneration of species-rich grasslands is a slow process on fertile sites (Bakker 1989). At Little Wittenham the different grazing seasons and grazing intensities brought about only small divergences

among the paddocks in the frequencies of the dominant species, although increased grazing generally increased the dicots. The experiment must be long-term in order to determine how these changes will develop, whether the dicots will continue to increase under grazing, whether the dominant grasses will eventually decrease and how falling fertility will affect these processes. Changes beyond these, and the development of a species-rich grassland, are hampered by the domination of the same grasses in the seed rain as in the vegetation and by the lack of recruitment of novel species from a seed bank. Such a problem may be addressed by the sowing of alien seed to increase diversity (Wells 1983). However, the differences among the species in their input to the seed rain may also bring about vegetation change.

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