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A plant trait analysis of responses to grazing in a long-term experiment

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Summary

1. There are few long-term experimental studies of plant community responses to changes in grazing intensity. Here we report species' changes in a mesotrophic grassland after 12 years of a grazing experiment and relate these changes to species' life-history traits.

2. The experiment was set up in 1986 on an extensified species-poor grassland in lowland UK. Treatments comprised sheep grazing vs. no grazing in winter, grazing vs. no grazing in spring, and two grazing intensities in summer, in a $2 \times 2 \times 2$ factorial design with two replicate blocks.

3. Point quadrat surveys in 1998 showed responses to grazing treatments by 17 of the 22 most common species. Species showed different responses, many of which were specific to a grazing season. Community changes were similar under spring and winter grazing, but the heavier summer grazing had different consequences. Species richness was increased by spring grazing, decreased by heavier summer grazing and unaffected by winter grazing.

4. More species responded to treatments in the 1998 survey compared with a survey in 1990. Furthermore, the whole experimental grassland had changed between the surveys, probably as a result of falling soil fertility. The two dominant grasses had declined drastically and most other species had increased in abundance. Five new species were found in 1998.

5. Intensive surveys of dicotyledonous species in 1998 showed five of the 12 most common species had responded to grazing treatments. In most cases dicotyledonous species had increased in abundance under heavier grazing in one or more season, and species richness was increased by spring and winter grazing. Compared with a 1991 survey, the number of species responding to treatments had increased by 1998 and seven new species were found.

6. We tested whether species' responses to grazing were linked to life-history traits according to three hypotheses: that heavier grazing would disadvantage (i) species grazed preferentially, (ii) species less able to colonize gaps or (iii) more competitive species. Mechanisms differed among seasonal treatments. Responses to heavier summer grazing were linked strongly to gap colonization ability. Responses to spring and winter grazing were positively related to grazer selectivity, a surprising result that might be explained if selectivity was positively related to plant regrowth ability.

7. This study shows the need for long-term experimental analyses of community responses to grazing as vegetation responses may develop over a long time. The traits analysis suggests it may be possible to predict changes in species composition under grazing through an understanding of the mechanisms of plant responses. Grassland managers require such information in order to manipulate grazing regimes to achieve, for example, diversification or weed control.

Key-words: diversity, gap colonization, grazer selectivity, long-term study, mesotrophic grassland.

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Introduction

Management of semi-natural communities to manipulate plant species composition requires accurate information on the effects of alternative management practices (Spellerberg, Goldsmith & Morris 1991). In temperate grasslands grazing is the major management activity, for economic or conservation objectives. The effect of grazing regime on animal production in agriculturally improved pastures has been thoroughly researched (Sheath & Clark 1996), but managers of unimproved or extensive grasslands may need information on vegetation responses in order to, for example, enhance biodiversity or control pasture weeds. The consequences of removal of grazers are well documented (Ward & Jennings 1990; Hill, Evans & Bell 1992; Stohlgren, Schell & Vanden Heuvel 1999; Humphrey & Patterson 2000) but much less is known about the ways in which different seasons and intensities of grazing, species, breeds and reproductive status of grazers, stock management procedures, etc., affect plant communities (Bullock & Marriott 2000).

Experiments on vegetation responses to grazing management in temperate grasslands have studied the effects of season of sheep grazing on regenerating chalk grassland (Gibson, Watt & Brown 1987; Gibson & Brown 1992), season of sheep and cattle grazing on mesotrophic meadows (Smith & Rushton 1994; Smith *et al.* 1996, 2000), intensity of cattle or sheep grazing on hill pasture (Grant *et al.* 1996a; Hulme *et al.* 1999) and the species of grazer and intensity of grazing on hill pasture (Grant *et al.* 1996b). Bullock *et al.* (1994a) looked at changes in a mesotrophic species-poor grassland in an experiment that contrasted two sheep grazing intensities in each of three seasons. Four years after imposition of the treatments, Bullock *et al.* (1994a) found that species' responses were complex, although dicotyledonous species (dicots) generally increased under heavier grazing, and there was little evidence for treatment effects through colonization by new species. Watt, Treweek & Woolmer (1996) examined the experiment 3 years later and found the same general effects, although their survey was less intensive and could not detect the more subtle responses found by the earlier study.

This paper reports vegetation changes in the experiment after 12 years, using the intensive methodology of Bullock *et al.* (1994a). The experiments listed above studied effects of different grazing treatments up to a maximum of 8 years. This long-term study is important because responses to management such as grazing may evolve over many years (Hill, Evans & Bell 1992). Population decline of long-lived perennial species in response to unsympathetic management can exhibit a considerable lag (Rose, Clarke & Chapman 1998), and Bullock, Clear Hill & Silvertown (1994b) showed that although grasses can exhibit rapid tiller turnover within years, population changes between years in response to grazing treatment were much slower. Increase of rare or colonizing species under favourable conditions may take a long time because low initial plant numbers can hinder population growth (Stephens & Sutherland 1999). Finally, a depauperate seed bank, as found at their site by Bullock *et al.* (1994a), means that major community changes through colonization by new species could be slow and dependent on seed dispersal from external sources.

Given the paucity of grazing experiments it is important to attempt to generalize from existing studies. Smith & Rushton (1994) related species' responses under grazing treatments to plant life-history strategies as characterized by Grime, Hodgson & Hunt (1988), while other authors have tried to link a wide range of attributes to species' responses to grazing and other factors (Trémont 1994; Lavorel *et al.* 1997; McIntyre *et al.* 1999). To refine such analyses it is useful to frame them in terms of an understanding of how grazers affect plant communities, by processes such as direct damage to plants, changed competitive interactions, gap creation or altered nutrient dynamics (Briske 1996; Augustine & McNaughton 1998; Bullock & Marriott 2000). Here we propose and test three hypotheses of how species' traits affect their responses to grazing treatment.

1. *Selective grazing*. Species that are grazed preferentially will show relative declines under more intense grazing, while less preferred species will increase.

2. *Colonization ability*. Because more intense grazing increases the number of vegetation gaps (Silvertown & Smith 1989), the species increasing under heavier grazing will be those with a greater ability to colonize gaps.

3. *Competitive ability*. Under less intense, or no, grazing the vegetation becomes more rank and competition for light is more severe (Bullock 1996a). Therefore species with a greater ability to compete for light will increase under low grazing pressure.

Methods

SITE DESCRIPTION

The experiment is described in detail by Bullock *et al.* (1994a). It was set up at Little Wittenham Nature Reserve in Oxfordshire, UK (National Gird reference SU568924, latitude 15°37′ N, longitude 1°10′ W), on a mesotrophic grassland upon a calcareous clay loam. The site had a temperate climate with a mean annual rainfall of 620 mm, spread evenly through the year. Temperatures were highest in July (mean maximum 21·6 °C, minimum 11·6 °C) and lowest in January (mean maximum 6 °C, minimum 1 °C). The grassland was species-poor and dominated by fast-growing grasses typical of agriculturally improved sites, such as *Lolium perenne*, *Agrostis stolonifera* and *Poa trivialis* (nomenclature follows Stace 1997). It was classified as transitional between British National Vegetation Classification (NVC; Rodwell 1992) vegetation types MG7 *Lolium perenne* ley and MG6c *Lolium perenne–Cynosurus cristatus* grassland, *Trisetum flavescens* subcommunity. The site had been resown in the 1940s and was intensively managed using sheep grazing and inorganic fertilizers until 1984 when fertilizer applications ceased.

Table 1. The experimental design, of three grazing seasons and two sheep grazing intensities in each season. In winter and spring alternatives were either no grazing (–) or grazing (+) by two sheep per 50 × 50-m paddock. In summer, grazing was to a 3-cm sward height (heavy) or a 9-cm height (light)

	Summer heavy grazing			Summer light grazing	
Treatment	Winter	Spring	Treatment	Winter	Spring
A	–	–	E	–	–
B	–	+	F	–	+
C	+	–	G	+	–
D	+	+	H	+	+

Responses to season and intensity of sheep grazing were investigated in an experiment that contrasted three grazing seasons and within each season two grazing intensities in a 2 × 2 × 2 factorial design (Table 1). Seasons were: winter, 2 November–21 March; spring, 22 March–21 May; and summer, 22 May–1 November. The two intensities in winter and spring comprised no grazing or grazing by two Suffolk × Mule ewes per paddock. All paddocks were grazed in the summer, but two intensities were applied: light, to a sward height of 9 cm, or heavy, to a height of 3 cm. Summer sward heights were achieved and maintained by adjusting stocking rates following weekly or fortnightly height measurements with an 'HFRO sward stick' (Barthram 1986). The eight treatments (Table 1) were applied in a randomized block design with two blocks, in 16 paddocks of 50 × 50 m. The experiment was set up in 1986 and there were no initial differences in species composition between treatments (Treweek, Watt & Hambler 1997).

VEGETATION SURVEYS

A point quadrat survey of the vegetation in each paddock was carried out between 4 and 13 August 1998. This was a repeat, using identical techniques, of the survey between 6 and 10 August 1990 reported by Bullock *et al.* (1994a). For the earlier study we surveyed the experiment in January 1990 in addition to the summer survey, in order to compensate for seasonal variation. However, it was not possible to repeat both surveys, so a summer survey was used to facilitate detection of annual and non-winter green species and make use of the peak in biomass to detect rarer species. Point quadrat frames (Bullock 1996b) were placed at 64 positions at 4-m intervals on an 8 × 8 grid in each paddock. The grid was centred, giving an 11-m buffer within the perimeter of each paddock that allowed avoidance of edge effects. A point quadrat frame comprised a line of 10 pins of 1 mm diameter that were 5 cm apart. Presence/absence of every vascular plant species was recorded for each pin, with presence occurring if the pin was touched by any live part of a plant. The pins were taller than the vegetation maximum height. The total number of pins touched by a species in a paddock (maximum 640) was divided by the sum of the total touches for all species to give a relative frequency measure of abundance for that species. *Poa* species (*P. trivialis* and *P. pratensis*) were combined to avoid errors due to misidentification, as were *Phleum pratense* and *Phleum bertolonii.*

Dicots were rare in the earlier point quadrat survey (Bullock *et al.* 1994a) and were subject to additional surveys to provide better data on abundances. This was done by recording rooted presence/absence of each dicot species in 100 1-m^2 frame quadrats (Bullock 1996b) placed 3 m apart on a 10 × 10 grid in each paddock. This gave a 10-m buffer within the perimeter of a paddock to allow for edge effects. Bullock *et al.* (1994a) recorded dicots at four times of the year, but found no difference in treatment effects among seasons. Therefore, we recorded dicots only once, between 15 and 17 July 1998. This survey was contrasted to the dicot survey carried out in July 1991.

SPECIES' TRAITS

Data were obtained for the 17 most common species in the experiment (those present in at least eight of the 16 paddocks, see the Results) on traits that we considered to be related to grazer selectivity, colonization ability or competitive ability. There were no data available for *Phleum bertolonii*, so *Phleum* spp. were assigned values for *Phleum pratense*. For *Poa* spp. we used means of the trait values for *Poa trivialis* and *Poa pratensis* unless a value was only available for one species, in which case we used that value.

Grazer selectivity was defined as the degree to which grazers remove species biomass in proportions different to the relative abundances of species in the vegetation (Ivins 1952; Leps *et al.* 1995). Selectivity may be affected by a number of traits: (i) 'apparency' to grazers, which may be related to relative height, abundance and leaf size (Black & Kenney 1984; Grant *et al.* 1985); (ii) preference by grazers, which may be related to digestibility and nutritive value (Scehovic 1991), the roughness, silica content or spininess of leaves (Cid *et al.* 1989) or the concentration of secondary metabolites (Augustine & McNaughton 1998); (iii) the ability to resist biomass removal, which may be related to leaf fracture properties (Aranwela, Sanson & Read 1999). It is unclear how these factors interact to affect grazer selectivity (Scehovic 1995; Augustine & McNaughton 1998) so we used only direct measures of selectivity taken in the field. Three measures were used. (i) Davies (1925) measured relative selection among nine of our 17 species in terms of the choice made by sheep among pure plots of the species and the time spent on each plot. Species were given scores relative to 100 for the most selected species. (ii) Diaz & Ford (2000) scored selection among 10 of our species in terms of proportion of plants eaten by rabbits in a series of field experiments where pot-grown plants were planted out at 10 sites. (iii) Finally, Spedding & Diekmahns (1972) made qualitative statements about the greater or lesser degree of grazer selection among species that we converted to a score of less selected (1), selected (2), or more selected (3). Information was given on only 10 of our species, but this was supplemented using Grime, Hodgson & Hunt (1988) who made statements about the preference of grazers for the remaining species.

Colonization ability was defined as the ability of a species to colonize vegetation gaps or other disturbances. Two measures were used. (i) Bullock *et al.* (1995) measured this for all 17 species within the grazing experiment by opening vegetation gaps of 3–9 cm diameter in treatments C, D, G and H (Table 1). The number of ramets or plants of a species in each gap after 50 weeks was divided by the number in the intact vegetation found in a 2-cm wide annulus around the gap at the time of gap creation. This gave an index of gap colonization ability. (ii) A more general measure was obtained using Grime's strategy theory (Grime, Hodgson & Hunt 1988). According to this theory, species have life-history strategies that are combinations of ruderality (R), competitiveness (C) and stress tolerance (S). Each strategy is characterized by a set of ecological, morphological and physiological traits and species with a particular strategy are associated with a particular habitat. More ruderal species are found in disturbed vegetation, where disturbance is the partial or total destruction of plant biomass caused, for example, by grazing. We used ruderality as a measure of the ability to colonize disturbances. The ruderality of a plant as given by Grime, Hodgson & Hunt (1988) was converted to a numerical value, as done by Tofts & Silvertown (2000). Wholly ruderal (R) plants were given a score of 12 and species with intermediate strategies were given an intermediate score as appropriate. Thus, CR plants were given an R-value of 6, CSR plants a value of 4 and C plants a value of 0. Grime, Hodgson & Hunt (1988) assigned two strategies to some species, for example CR and CSR. In such cases we took the mean score of the two strategies, for example CR and CSR gave a mean R-value of 5. Data were available for all 17 species.

Competitive ability was measured using four traits. (i) A score of competitiveness (C) was derived from the score for the competitor strategy of Grime, Hodgson & Hunt (1988) using the same protocol as for the R-value. Plant height or size has been shown to be a good predictor of competitive ability when competition is primarily for light (Keddy 1989; Gaudet & Keddy 1995), so we obtained two measures of plant size. (ii) The maximum foliage height recorded by Grime, Hodgson & Hunt (1988) was available for 16 species. (iii) Tiller weight of 12 grasses was measured by collecting vegetative material from the experiment which was then grown in 4–6 replicate pots in a glasshouse. After 10 weeks tiller weights had stabilized and five tillers were taken from each pot, oven-dried and weighed. (iv) Plant growth rate may indicate a plant's ability to usurp resources and thus its competitive ability (Bullock 1996a). The best available measure of this was that of the seedling relative growth rate (RGR) made by Grime, Hodgson & Hunt (1988) for 13 of our species.

SOIL ANALYSES

Soil was collected from each paddock in August 1998 by removing 38-mm diameter, 75-mm deep cores from 25 points 5 m apart on a 5 × 5 grid. The 25 samples from each paddock were bulked and soil chemistry was analysed using standard ADAS techniques (ADAS 1986). This analysis was repeated in 1986 and 1990 (Bullock *et al.* 1994a).

Results

POINT QUADRAT SURVEY

Sixteen grass species (for simplicity combined *Poa* spp. and combined *Phleum* spp. will each be called single species) and 22 dicot species (*Ranunculus repens* and *Ranunculus bulbosus* were combined as *Ranunculus* spp.) were detected in the point quadrat survey. This compared with 18 grasses and seven dicots in the August 1990 point quadrat data (Fig. 1). In fact three grasses species were detected only in the 1990 survey, although one, *Deschampsia cespitosa*, was represented only by a single tussock in one paddock and was present, although missed by the survey, in 1998. Although *Helictotrichon pratense* and *Helictotrichon pubescens* appeared to have been lost, we now suspect they were misidentified *Festuca pratensis*. *Arrhenatherum elatius* was a new species in 1998. Fifteen extra dicot species were found in 1998, although because 10 of these had been detected in the dicot surveys in 1990 (Bullock *et al.* 1994a) only *Crepis capillaris*, *Achillea millefolium*, *Leontodon hispidus*, *Plantago major* and *Hypochoeris radicata* were truly new. *Leontodon hispidus* (along with *Trifolium dubium* and *Cirsium eriophorum*) was sown into the experiment by Tofts (1998), but the other new species must have colonized from nearby populations.

Differences between the two surveys were analysed by repeated-measures ANOVA, using PROC GLM in SAS (1990). Univariate and multivariate repeated-measures analyses (Maxwell & Delaney 1990) were carried out and gave identical results. The ANOVA had survey year (the repeat factor), block and treatment as factors, but only overall survey year differences are considered here. The experimental paddocks were more diverse in 1998 (Fig. 1 and Table 2), having more species (mean species

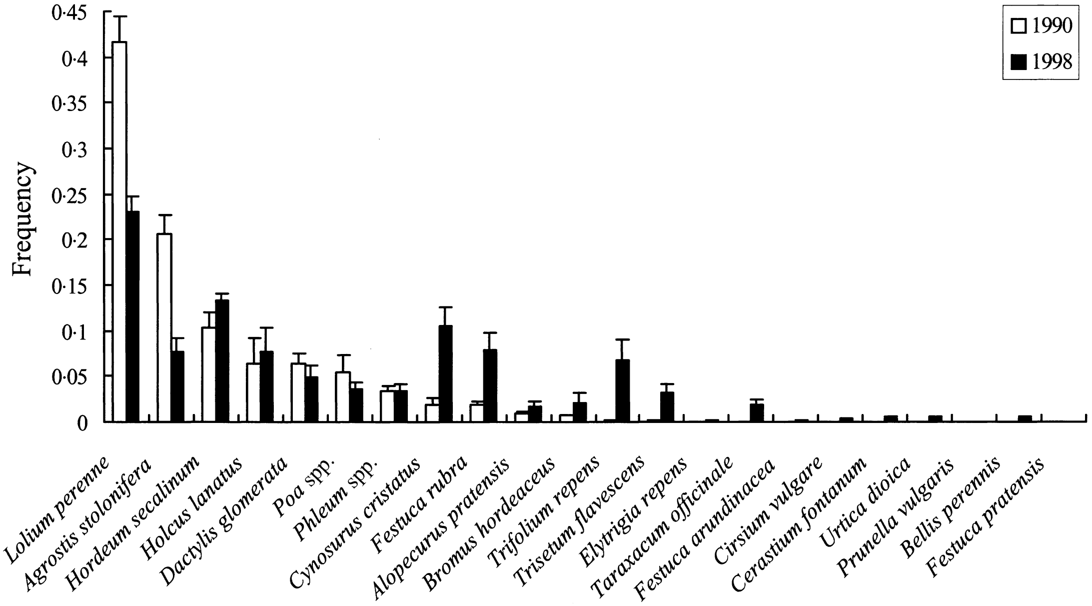

Fig. 1. Mean relative frequencies with one standard error of species in the point quadrat surveys of 1990 and 1998, ranked according to frequencies in 1990. All species shown were present in both surveys. Other species present only in the 1998 survey were (in order of abundance) *Trifolium pratense*, *Arrhenatherum elatius*, *Geranium dissectum*, *Crepis capillaris*, *Ranunculus* spp., *Cirsium arvense*, *Achillea millefolium*, *Galium verum*, *Leontodon hispidus*, *Plantago lanceolata*, *Medicago lupulina*, *Convolvulus arvensis*, *Senecio jacobaea*, *Plantago major*, *Sonchus asper* and *Hypochoeris radicata*.

number per paddock in 1990 = 12; in 1998 = 20·1), an effect that remained after any species added by Tofts (1998) was subtracted from the 1998 total (new mean = 19·9), and having a higher log normal diversity index (Magurran 1988), also calculated without Tofts' species (mean index per paddock in 1990 = 1·77; in 1998 = 3·20). Changes in individual species' frequencies between surveys were analysed using arcsine-transformed frequencies. Only the 22 species that were represented in at least four paddocks in one survey were analysed. Twelve species showed increases in 1998, some of which were substantial, for example for *Cynosurus cristatus*, *Festuca rubra* and *Trifolium repens* (Fig. 1 and Table 2). The only species that had declined by 1998 were *Lolium perenne* and *Agrostis stolonifera*, the dominant species in 1990.

Repeating Bullock *et al.* (1994a), we analysed grazing treatment effects on arcsine-transformed species' frequencies by three-way ANOVA. This contrasted the three main effects, i.e. winter grazing vs. no grazing, spring grazing vs. no grazing and summer heavy vs. light grazing, and interactions between seasonal grazing treatments. In 1998, of the 14 grasses and eight dicots analysed, 11 grasses and six dicots showed main treatment effects (Table 2). Responses to grazing treatments were varied. Of 28 main treatment effects, there were three negative and five positive responses to winter grazing, four negative and four positive responses to spring grazing, and eight negative and four positive responses to heavier summer grazing. Furthermore, while some species showed similar responses to heavier grazing in different seasons (for example *Agrostis stolonifera*, *Alopecurus pratensis* and *Cirsium vulgare*), most responded differently in different seasons, either showing different responses to grazing intensity (for example *Bellis perennis*) or showing no response at all in one season (for example *Trisetum flavescens*). Species number was decreased by heavier summer grazing and increased by spring grazing, and this effect remained after the species sown by Tofts (1998) were subtracted from the total.

The same analysis of the 1990 data revealed many fewer treatment effects, among only eight species. There were two negative and three positive responses to winter grazing, one negative and two positive responses to spring grazing and one case each of positive and negative responses to heavier summer grazing (Table 2). Six of these responses remained in 1998, but four were lost (i.e. no significant response in 1998) and one was reversed. Bullock *et al.* (1994a) analysed combined summer and winter survey data for 1990 and there were some differences between that analysis and this one using only the summer data. Seven responses were the same in both analyses, three were new to this analysis and one was unique to the previous analysis.

In both analyses, there were few significant effects of interactions among seasonal grazing treatments on species' frequencies. In 1990 none of 72, and in 1998 four of 84 comparisons were significant.

DICOT SURVEY

This survey detected 34 dicot species, compared with 21 in July 1991 (Fig. 2). Three species found in 1991 were lost by 1998, but 16 species were new in 1998 (Fig. 2). However, if all eight surveys reported by Bullock *et al.* (1994a) were considered only *Trifolium dubium*, *Cirsium eriophorum*, *Hypochoeris radicata*, *Achillea millefolium*,

Table 2. Point quadrat survey. Differences between grazing treatments and survey years in species' percentage frequency and species diversity. Mean values for the main grazing treatment contrasts are shown for each survey year, with the significance of the treatment effect (ANOVA, $^{***}P < 0{\cdot}001$, $^{**}P < 0{\cdot}01$, $^{*}P < 0{\cdot}05$; no superscript, no significant difference) with the second of the pair of means. Species not recorded in 1990 are represented by –. Survey year effects, where significant in repeated-measures ANOVA, are indicated by the year with the higher value. No year effect is shown by –. Species marked † were used in the traits analysis (see text)

	1990						1998						
	Winter		Spring		Summer		Winter		Spring		Summer		
Species	+	–	+	–	3 cm	9 cm	+	–	+	–	3 cm	9 cm	Survey year
†*Agrostis stolonifera*	19·2	22·1	25·4	15·9*	17·5	23·9	3·9	11·3***	5·8	9·5*	4·3	11·0***	90***
†*Alopecurus pratensis*	1·3	0·55	0·59	1·2*	0·77	1·1	0·65	2·6**	0·66	2·6*	0·65	2·6**	–
Arrhenatherum elatius	–	–	–	–	–	–	0·24	0·15	0·09	0·30	0·02	0·38*	98**
†*Bromus hordeaceus*	0·57	0·86	0·69	0·75	0·71	0·73	1·4	2·9	0·65	3·6	3·0	1·3	–
†*Cynosurus cristatus*	1·8	2·2	2·1	1·9	1·7	2·2	11·3	9·5	11·5	9·4	16·5	4·4***	98***
†*Dactylis glomerata*	8·8	3·9*	5·8	7·0	5·0	7·7	7·1	2·9*	5·5	4·5	1·8	8·1**	–
Elytrigia repens	0·06	0·05	0·07	0·04	0·03	0·08	0·07	0·12	0·01	0·18	0·04	0·15	–
†*Festuca rubra*	2·3	1·2*	2·4	1·2	1·1	2·5	7·7	8·1	9·7	6·2	3·8	12·1*	98***
†*Holcus lanatus*	2·12	10·6*	4·7	8·1	3·7	9·1	1·2	14·2**	6·2	9·2	7·4	8·0	–
†*Hordeum secalinum*	15·0	5·6**	10·8	9·8	12·6	8·0	14·2	12·4	13·1	13·5	13·3	13·2	98*
†*Lolium perenne*	36·0	47·2*	39·2	44·0	48·0	35·2*	24·1	22·0	23·3	22·8	28·6	17·4***	90***
†*Phleum* spp.	4·0	2·7	4·9	1·8**	2·5	4·1*	3·3	3·5	4·6	2·3*	1·78	5·1***	–
†*Poa* spp.	8·4	2·6	2·9	8·0	6·1	4·8	2·8	4·2	2·1	5·0*	3·1	5·0	–
†*Trisetum flavescens*	0·09	0·07	0·08	0·08	0·04	0·12	4·9	1·6*	2·0	4·5	3·4	3·1	98***
Bellis perennis	0	0·02	0	0·02	0	0·02	0·69	0·02*	0·12	0·58	0·69	0·01*	98*
†*Cerastium fontanum*	0·04	0·03	0·07	0	0·07	0	0·41	0·50	0·39	0·53	0·78	0·13*	98*
†*Cirsium vulgare*	0·03	0·06	0·03	0·06	0·06	0·03	0·57	0·13*	0·55	0·15*	0·45	0·25	98**
Ranunculus spp.	–	–	–	–	–	–	0·03	0·04	0·05	0·02	0·03	0·03	–
†*Taraxacum officinale*	0·04	0·07	0·03	0·08	0·04	0·07	2·3	1·3	0·5	3·1**	2·7	0·89*	98***
Trifolium pratense	–	–	–	–	–	–	0·34	0·18	0·49	0·03***	0·02	0·50***	98***
†*Trifolium repens*	0·19	0	0·16	0·03	0·03	0·16	11·7	1·7***	11·8	1·5***	7·1	6·3	98***
†*Urtica dioica*	0	0·05	0·03	0·02	0·05	0	0·53	0·42	0·40	0·56	0·54	0·42	98***
Species number	11·9	12·1	12	12	11·8	12·3	21·1	19·1	21·5	18·8*	18·8	21·5*	98***
Species number minus sown species	11·9	12·1	12	12	11·8	12·3	21	18·9	21·1	18·8*	18·6	21·3*	98***
Log normal diversity	1·74	1·80	1·79	1·75	1·70	1·85	3·36	3·03	3·43	2·96	3·00	3·39	98***

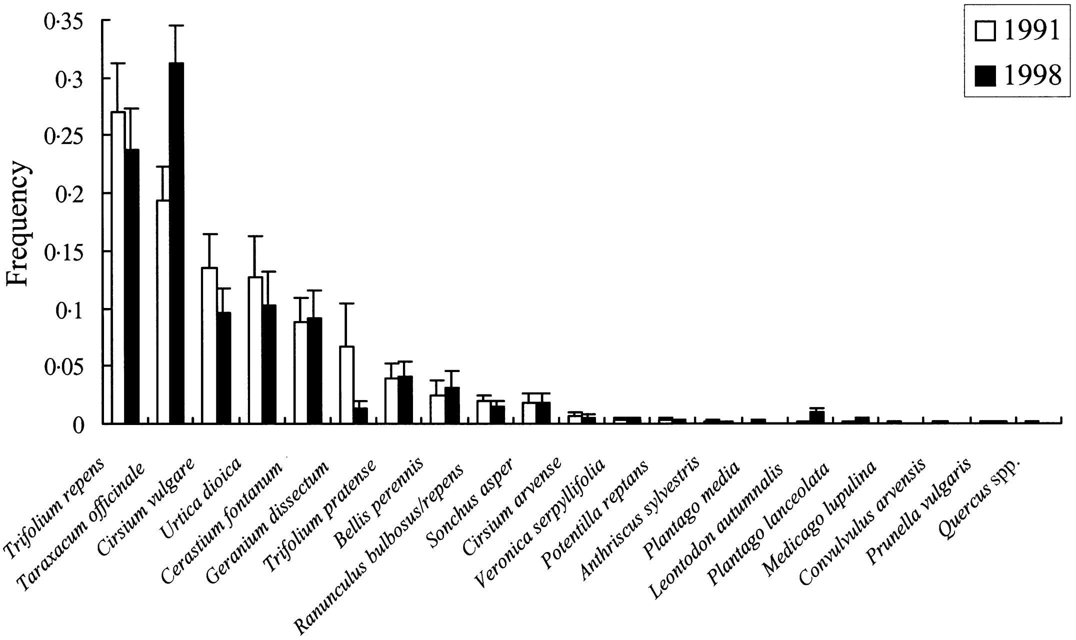

Fig. 2. Mean relative frequencies with one standard error of species in the dicot surveys of 1991 and 1998, calculated from the total number of occupied quadrats in a paddock divided by the sum of this total across all species. All species shown were present in both surveys, except for *Convolvulus arvensis*, *Quercus* spp. and *Plantago media*, which were present only in 1991. Other species present only in the 1998 survey were (in order of abundance) *Trifolium dubium*, *Rumex crispus*, *Cirsium eriophorum*, *Hypochoeris radicata*, *Senecio jacobaea*, *Achillea millefolium*, *Ranunculus acris*, *Leontodon hispidus*, *Tragopogon pratense*, *Rosa* sp., *Veronica chamaedrys*, *Vicia* sp., *Galium verum*, *Prunus spinosa*, *Veronica persica* and *Agrimonia eupatoria.*

Ranunculus acris, *Rosa* spp. and *Prunus spinosa* were truly new, and two of these (*Trifolium dubium* and *Cirsium eriophorum*) were sown by Tofts (1998). Mean species number per paddock was higher in 1998 than in July 1991 (after subtracting Tofts' species: 1991 = 9·94; 1998 = 11·75; Table 3). Repeated-measures ANOVA on species' frequencies (number of occupied quadrats) was carried out on species that were present in at least four paddocks in 1 year. Of the 12 suitable species nine had increased by 1998 (Table 3).

Three-way ANOVA of frequencies in 1998 of the 12 most common species resulted in 10 main treatment effects, distributed among five species (Table 3). All but two effects were positive responses to grazing or increased grazing intensity. Three species, *Cirsium vulgare*, *Trifolium pratense* and *Trifolium repens*, showed positive responses to both winter and spring grazing. Both spring and winter grazing increased dicot species number. Eight species provided sufficient data in both point quadrat and dicot surveys for comparison of ANOVA results. Nine treatment effects were common to both surveys, two were unique to the point quadrat survey and one was unique to the dicot survey.

There were nine main treatment effects in the 1991 survey, and eight of these were positive responses to grazing or increased grazing intensity. Five responses were repeated in the 1998 survey, but four were lost (Table 3). As in the point quadrat surveys, there were few significant effects of interactions among seasonal grazing treatments on species' frequencies (in 1991 three of 40, and in 1998 two of 48, comparisons were significant).

CORRELATION OF SPECIES' RESPONSES WITH TRAITS

Measures of species' responses to winter grazing intensity were derived from the 1998 point quadrat data as follows:

$$\text{winter grazing response ratio (species } i) = WF_{Gi}/WF_{Ui} \qquad \text{eqn 1}$$

where WF_{Gi} is the mean proportionate frequency of species i in winter grazed paddocks and WF_{Ui} is the corresponding mean for non-winter grazed paddocks. A spring grazing response ratio and a summer grazing response ratio (henceforth spring ratio and summer ratio) were calculated for each species in the same way. These ratios indicated the extent to which grazing (winter or spring) or heavier grazing (summer) in each season caused increases (ratio > 1) or decreases (ratio < 1) in the frequency of a species. To ensure accurate estimates of responses to treatment, ratios were calculated only for the 17 species that were present in at least half the paddocks. These were also the most common species in 1998, and are marked in Table 2. The ratios were log-transformed to achieve normality and homogeneity of variances, but the means presented below were back-transformed.

The winter and spring ratios of species were positively correlated (Pearson correlation $r = 0{\cdot}53$, d.f. = 15, $P < 0{\cdot}05$), indicating species' responses to spring and winter grazing were similar. However, both spring and winter ratios were unrelated to the summer ratios (winter

Table 3. Dicot survey. Differences between grazing treatments and survey years in the percentage frequency of the more common species and species number. The layout is as for Table 2

	1991						1998						
	Winter		Spring		Summer		Winter		Spring		Summer		
Species	+	–	+	–	3 cm	9 cm	+	–	+	–	3 cm	9 cm	Survey year
Bellis perennis	4·6	1·5	2·6	3·5	2·6	1·5	13·1	14*	5·8	8·8	11·0	3·5	98**
Cerastium fontanum	16·3	5·3*	10·8	10·8	13·9	7·6	23·9	16·9	16·1	24·5	30·0	10·6*	98*
Cirsium vulgare	25·8	17·4*	23·1	10·0	25·3	7·9	41·5	8·4**	35·3	14·6*	30·6	19·3	98*
Geranium dissectum	14·4	1·9*	11·9	4·4	6·1	10·1	6·6	0·50	6·8	0·38	0·88	6·3	98*
Leontodon autumnalis	–	–	–	–	–	–	2·4	2·1	4·1	0·4	1·3	3·3	98*
Ranunculus spp.	2·5	2·1	2·3	2·4	3·0	1·6	3·1	2·3	2·0	3·4	2·9	2·5	–
Sonchus asper	1	3·5	3·6	0·88	2·4	2·1	1·0	6·0	5·8	1·3	4·3	2·8	–
Taraxacum officinale	38·8	8·8**	15·4	32·1*	35·1	12·4*	57·3	52·0	37·6	71·6*	57·0	52·3	98**
Trifolium dubium	–	–	–	–	–	–	1·9	0·25	2·0	0·13	1·1	1·0	–
Trifolium pratense	5·9	3·6	8·0	1·5	1·5	8·0	16·1	4·4*	18·9	1·6**	4·0	16·5*	98*
Trifolium repens	44·9	21·8**	45·1	21·5**	37·8	28·9	78·5	26·0***	73·6	30·9***	46·5	58·0	98**
Urtica dioica	14·6	16·6	11·4	19·9	12·0	19·3	19·3	19·6	16·1	22·8	15·1	23·8	98**
Species number	12·0	7·9*	11·3	8·6	11·1	8·8	14·8	10·1**	14·4	10·5*	11·8	13·1	98*
Species number minus sown species	12·0	7·9*	11·3	8·6	11·1	8·8	13·9	9·6**	13·3	10·3*	11·6	11·9	98*

vs. summer $r = 0·19$, $P > 0·05$; spring vs. summer $r = 0·12$, $P > 0·05$), meaning species showed different responses to grazing in summer than they did to spring or winter grazing. The same ratios were calculated for the 1990 data to investigate whether responses in 1998 were correlated with those in 1990. Correlations, with d.f. = 15, were high and positive, but were not significant at the 5% level (winter $r = 0·40$, spring $r = 0·37$, summer $r = 0·46$), indicating species' responses to grazing after 12 years were different (1998) to the responses after 4 years (1990).

The species used for the traits analysis comprised 12 grasses and five dicots (Table 2). One-way ANOVAS showed that dicots had higher winter ratios (dicot mean = 2·21, grass mean = 0·73, $F_{1,15} = 4·6$, $P < 0·05$) and summer ratios (dicot mean = 2·17, grass mean = 0·74, $F_{1,15} = 5·5$, $P < 0·05$) than grasses, but the spring ratios were not significantly different (dicot mean = 1·17, grass mean = 0·71, $F_{1,15} = 0·9$, $P > 0·05$). The ancient evolutionary divergence of grasses (monocots) and eudicots (Bremer *et al.* 1998) means that there are many trait differences between the two groups and there is the risk of spurious correlation of phylogenetically correlated traits with response to grazing (Silvertown, Franco & Harper 1997). To correct for this we carried out ANOVA on each of the logged grazing ratios with taxonomic group (dicot or grass) as the treatment. The residual ratio values for each species from the ANOVAS were used as measures of the response to grazing after the effect of taxonomic group on grazing response had been removed.

Differences in residual ratios between the three Spedding selectivity levels (Spedding & Diekmahns 1972) were analysed by ANOVA. Otherwise, regression was used to test for relationships between the residual ratios and each of the plant traits. The trait values were log-transformed.

Of the three traits indicating grazing selectivity, the only significant relationships were of Davies' selectivity (Davies 1925), with the winter and spring ratio residuals (Table 4). These relationships were positive, contrary to the hypothesized negative effect of selectivity on response to grazing. The Davies and Diaz (Diaz & Ford 2000) selectivity values were not correlated (Pearson correlation $r = 0·05$, d.f. = 7, $P > 0·05$), but while the Diaz selectivity values did not differ significantly among the three levels of Spedding selectivity (ANOVA $F_{2,7} = 1·11$, $P > 0·05$), the Davies and Spedding values were positively related (ANOVA $F_{2,6} = 6·23$, $P < 0·05$).

Gap colonization ability and ruderality, traits indicating colonization ability, both had positive relationships with the summer ratio residual, and the former had a particularly high r^2. However, neither of these traits explained a significant amount of variance in either the winter or spring residuals. The two traits were significantly correlated (Pearson correlation $r = 0·67$, d.f. = 15, $P < 0·01$).

Finally, the only significant regression for the traits related to competitive ability was a negative effect of competitiveness on the summer ratio residual. The competitiveness trait was not correlated with any of the other three traits related to competitive ability (tiller weight $r = 0·22$, d.f. = 10, $P > 0·05$; RGR $r = 0·18$, d.f. = 11, $P > 0·05$; height $r = 0·31$, d.f. = 14, $P > 0·05$).

SOIL ANALYSES

The 1998 soil samples were analysed for pH and phosphate (P), potassium (K), magnesium (Mg) and nitrogen (N) (both ammonium–nitrogen and nitrate–nitrogen) concentrations. The first four properties were also analysed in 1986 and repeated-measures ANOVA showed that pH and K had remained unchanged by 1998 but P had increased and Mg had decreased (Table 5). However, these changes, while significant, were very small and probably had little biological importance. These soil properties were unaffected by grazing treatment in 1986 or 1998 (Table 5). NH_4-N was in relatively low concentrations in 1998, and was unaffected by treatment. However, NO_3-N was at higher concentrations (mean NO_3-N : NH_4-N ratio = 5·3) and was increased by winter grazing and heavier summer grazing (Table 5).

Table 4. Results of regressions of the plant traits on the residual ratios for winter, spring and summer grazing treatments (both ratios and trait values were logged). $^{***}P < 0·001$, $^{**}P < 0·01$, $^{*}P < 0·05$; no superscript, no significant difference. Where the relationship was significant, the value of the regression slope is given. †The Spedding selectivity data were analysed using ANOVA (see text), so the statistic given is the *F*-value

			Winter ratio		Spring ratio		Summer ratio	
Hypothesis	Trait	*n*	r^2	Slope	r^2	Slope	r^2	Slope
Selective grazing	a) Davies	9	48·9*	+3·3	51·1*	+ 2·7	5·5	
	b) Diaz	10	0·1		8·0		0·9	
	c) *Spedding*†	*17*	*1·32*		*0·06*		*1·52*	
Colonization ability	a) Gap colonization ability	17	4·5		9·9		51·9***	+0·90
	b) Ruderality	17	0·1		1·7		26·9*	+0·74
Competitive ability	a) Competitiveness	17	2·3		16·8		43·7**	–0·95
	b) Height	16	0·2		0·4		10·3	
	c) Tiller weight	12	5·0		2·3		19·4	
	d) RGR	13	14·4		5·7		3·2	

Table 5. Differences between survey years and grazing treatments (main effects) in soil chemistry. The means for each treatment or year are given and the significance of the difference (***$P < 0·001$, **$P < 0·01$, *$P < 0·05$; no superscript, no significant difference) is given with the second of the pair of means

			Soil chemistry pH	P (mg l^{-1})	K (mg l^{-1})	Mg (mg l^{-1})	NH_4-N (mg kg^{-1})	NO_3-N (mg kg^{-1})
	Survey year	1986	7·48	29·50	426·8	116·6	–	–
		1998	7·43	31·56*	407·4	109·1**	3·41	13·81
1986	Winter grazing	+	7·56	30·13	459·6	116·3	–	–
		–	7·39	28·88	393·9	117·0	–	–
	Spring grazing	+	7·55	25·50	405·5	112·5	–	–
		–	7·40	33·50	448·0	120·8	–	–
	Summer grazing	3 cm	7·49	26·88	395·8	113·6	–	–
		9 cm	7·46	32·13	457·8	119·6	–	–
1998	Winter grazing	+	7·70	28·00	416·9	101·3	2·28	18·85
		–	7·15	35·13	397·9	116·9	4·55	8·78*
	Spring grazing	+	7·66	26·75	369·4	104·0	3·13	16·94
		–	7·19	36·38	445·4	114·1	3·70	10·69
	Summer grazing	3 cm	7·34	32·50	405·5	108·1	3·83	17·33
		9 cm	7·51	30·63	409·3	110·0	3·00	10·30*

Discussion

VEGETATION CHANGES OVER TIME

Complicating any vegetation responses to grazing treatment were the large changes in diversity over the whole grassland between 1990–91 and 1998: a 67% increase in species number per paddock and an 80% increase in the log normal diversity in the point quadrat survey. Such increases might be expected in extensified grasslands, where species number can increase rapidly after cessation of fertilizer inputs (Olff & Bakker 1991; Mountford, Lakhani & Holland 1996) as a result of declines in soil fertility and therefore productivity (Olff, Berendse & de Visser 1994). We found no declines over 12 years in the few nutrients measured, although the change in nitrogen, probably the limiting nutrient in such grasslands (Olff, Berendse & de Visser 1994), was not measured.

Despite these changes in species number per paddock, we found only 10 new species in the grassland since the 1990–91 surveys, including three sown by Tofts (1998). Furthermore, these new species were rare, having a total frequency of 0·3% in the point quadrat survey. Bullock *et al.* (1994a) suggested that colonization of the grassland at this site by new species would be slow because the seed bank and seed rain contained no species not already found in the vegetation. Therefore, while high soil fertility may be an important inhibitor of grassland diversification (Marrs 1993), dispersal limitation may also play a major role. The fact that three (*Leontodon hispidus*, *Trifolium dubium*, *Cirsium eriophorum*) of four (the fourth was *Rumex obtusifolius*) species artificially introduced by Tofts (1998) have established in the grassland supports this conclusion.

Community change was manifest mostly as increases or decreases in the abundance of the dominant species. *Lolium perenne* was still dominant, but nearly halved in abundance. It, and the second dominant *Agrostis stolonifera*, were generally replaced by other grasses. The greatest increases were by *Cynosurus cristatus*, *Festuca rubra* and *Trisetum flavescens*, finer grasses that, along with the increase in dicots, indicate change towards a plant community typical of slightly less fertile conditions (NVC MG6c *Lolium perenne–Cynosurus cristatus* grassland, *Trisetum flavescens* subcommunity; Rodwell 1992) and away from the community dominated by vigorous, agriculturally desirable, grasses that was present at the start of the experiment (NVC MG7 *Lolium perenne* ley). However, the grassland is still a long way short of dicot-rich diverse grassland (NVC MG5 *Cynosurus cristatus–Centaurea nigra* grassland or MG6 *Lolium perenne–Cynosurus cristatus* grassland) that may have been typical on these circum-neutral soils before the advent of intensive farming practises.

GRAZING TREATMENT EFFECTS OVER TIME

Comparison of the 1990–91 surveys with those in 1998 suggests that, to understand fully vegetation responses to grazing, it is important to continue experiments over a long period. Treatment effects in the point quadrat survey nearly tripled between 1990 and 1998 and had increased in significance; for example, nine were significant at $P < 0·001$ in 1998 compared with none in 1990. Furthermore, more species were affected by treatments in 1998, 17 compared with eight in 1990. The changes between the two surveys were caused mostly by strengthening of effects found in 1990 and emergence of new effects in 1998. However, five of 11 effects found in the 1990 point quadrat survey and four of nine in the 1991 dicot survey were lost in 1998. These discontinuities and the large number of new responses meant that vegetation responses in 1990 were poor predictors of responses in 1998, as shown by the poor correlations between the 1990 and 1998 grazing ratios.

We cannot predict when vegetation in the different paddocks will cease exhibiting new treatment effects over time, i.e. when treatment effects will stabilize. Hill, Evans & Bell (1992) reported on exclosure experiments in Welsh hill pastures that had lasted up to 33 years and found that, although most major changes occurred in the first 7 years, the vegetation continued changing throughout the recording period. However, ungrazed grassland undergoes succession to shrub-dominated vegetation, whereby there is a large change in species composition. Changes in response to different grazing intensities will be less profound and may therefore stabilize more rapidly.

The data presented are not a long time series, but from two points in time. It may be dangerous to assume that treatment responses in 1998 represent a gradual evolution since 1990–91. There is evidence that year-to-year fluctuations in plant communities can be large (Ward & Jennings 1990; Dodd *et al.* 1995), so an extreme scenario may be that differences between 1998 and 1990–91 represent variation around a mean that has stayed constant over the years. However, the great change over the whole grassland (see above) and the large increase in treatment effects suggest we are seeing a true time trend, although some individual species' responses may be transitory. This conclusion is supported by the fact that surveys of frequencies in two 1-m^2 quadrats per paddock showed increases in the number of treatment effects over time between 1986, 1987, 1989 and 1993 (Watt, Treweek & Woolmer 1996; Treweek, Watt & Hambler 1997). Furthermore, as found in the Park Grass experiment (Tilman *et al.* 1994), although there may be temporal variation in species' abundances, responses of species to experimental treatments can be relatively consistent between years.

GRAZING TREATMENT EFFECTS ON DIVERSITY AND INDIVIDUAL SPECIES

Where studies have compared grazed and ungrazed treatments it is usual to find that grazing increases plant species diversity (Hill, Evans & Bell 1992; Bullock & Pakeman 1997; Humphrey & Patterson 2000), and Olff & Ritchie (1998) have suggested this is a general effect of large grazers in temperate fertile systems. In our experiment, where all paddocks were grazed, but at different seasons and intensities, effects on diversity were not so straightforward. While winter and spring grazing increased dicot species number, the point quadrat survey showed no effect of winter grazing, a positive effect of spring grazing and a negative effect of heavier summer grazing on species number of all vascular plants. Most other studies have found no effect of grazing season or intensity on species richness: Smith & Rushton (1994) comparing autumn grazed only, spring grazed only and autumn and spring grazed treatments in a mesotrophic meadow; Smith *et al.* (1996) comparing autumn grazing vs. autumn and spring grazing treatments in another mesotrophic meadow; Gibson & Brown (1991) comparing autumn vs. spring grazing and long vs. short grazing periods on a chalk grassland. However, Smith *et al.* (2000) found that a combination of spring and autumn grazing increased species number in a mesotrophic meadow. We also found the log normal diversity index was unaffected by treatment. These complexities of diversity responses result from the variety of individual species' responses to grazing treatments in different seasons. Thus, responses that might lead to higher species diversity under heavier grazing, such as increase of the uncommon *Trisetum flavescens* under winter grazing or the decline of the dominant *Agrostis stolonifera* under heavier grazing in any season, were counteracted by effects such as the increase of the dominant *Lolium perenne* under heavier summer grazing. The rare species showed a similar variety of responses: the coarse grass *Elytrigia repens* was nearly 20 times more abundant in non-spring grazed paddocks, but the low-growing dicot *Medicago lupulina* was found only in spring grazed paddocks.

Aside from community-level responses, the treatment effects on particular species may be important in terms of management requirements. While the general increase in dicot species number and abundance of individual dicots under heavier grazing pressure (see also Bullock, Clear Hill & Silvertown 1994c) might be seen as desirable for biodiversity, the enormous increase in *Cirsium vulgare* under heavier grazing in any season is undesirable in terms of stock management and animal production (Hartley 1983). In one particular paddock that was grazed in winter and spring and heavy grazed in the summer, *Cirsium vulgare* was found in 82 of the 100 dicot survey quadrats. This level of infestation reflects the emerging weed problems in heavily grazed pastures that have been extensified as a result of the UK government's Environmentally Sensitive Areas scheme (Pywell *et al.* 1998).

Marrs (1993) suggested grazing might be used to decrease soil nutrients in extensified pastures and other fertile systems to allow development of more desirable plant community types, but the lack of grazing responses by most soil nutrients in this study indicates this is not a useful method. In fact nitrogen was higher under heavier grazing. This is commonly found and is probably the result of excretal return increasing available nitrogen (Dormaar & Willms 1998).

SPECIES' TRAITS AND RESPONSES TO GRAZING

Wishing to describe vegetation responses to grazing in terms of functional groups, Lavorel *et al.* (1997) suggested that responses to grazing can be correlated to life history (grazing increases short-lived species), morphology (grazing increases short and rosette species) and regeneration type. This implies responses to grazing are controlled mostly by: (i) grazer selectivity, in that shorter plants avoid biomass removal by large grazers; and (ii) disturbance, in that short-lived plants or good dispersers can colonize disturbances caused by grazers, while longer-lived plants are damaged by grazing and cannot exploit openings. This classification has been supported by studies comparing grazed vs. ungrazed or light vs. heavy grazed temperate (Trémont 1994; McIntyre, Lavorel & Trémont 1995; Lavorel, McIntyre & Grigulis 1999), mediterranean (Noy Meir, Gutman & Kaplan 1989; Sternberg *et al.* 2000) and arid (Landsberg *et al.* 1999) grasslands, which have shown that grazing encourages species that are short-lived, have a flat-rosette growth form and/or have seeds that disperse well (for example are small or have pappi). Correlating grazing response with coarse classes of growth form and life history may be useful where extremes of grazed vs. ungrazed or very heavily vs. lightly grazed are compared. However, this may be irrelevant within the usual range of grazing regimes imposed by agricultural or conservation managers on temperate pastures. In our grassland, which is typical of temperate improved pasture, there were few species and few functional groups; almost all species were polycarpic perennial hemicryptophytes (perennial buds in the soil surface), with a few short-lived species and some chamaephytes (perennial buds just above the soil surface). This suggests grazing *per se* has already restricted the range of life forms in the pasture (see also Tofts & Silvertown 2000). The less extreme variations in grazing intensity of our study produce more subtle correlations. The use of functional groups is useful where there is a diversity of groups (for example Sternberg *et al.* 2000 had 10 functional groups and 166 species) and poor quantitative information on species' traits. However, functional groups are distinguished using an array of traits and so it is difficult to determine exactly which traits are determining the response to grazing. The use of quantitative traits is more informative and rigorous than the use of functional groups.

Briske (1996) and Augustine & McNaughton (1998) considered traits rather than functional groups and suggested there are two conflicting mechanisms causing community change under grazing compared with no grazing. (i) Avoidance, whereby species less preferred by grazers increase under grazing. Selection is controlled by biochemical deterrents (for example secondary chemicals) and/or morphology (for example growth form). (ii) Tolerance, whereby species more able to regrow, and regrow more rapidly, after grazing are able to dominate. One factor controlling the balance between these two mechanisms is the possibility that fast regrowers may gain an advantage under the greater nitrogen availability under heavier grazing.

This dichotomy may be too simplistic. Our study suggests the mechanism of response can vary, even within the same grassland, depending on the type of grazing contrast considered. The lack of a correlation of the summer ratios with those for winter or spring grazing suggests the mechanism controlling community responses to summer grazing treatment was different to that controlling responses to winter or spring grazing. However, the latter two responses were correlated, suggesting a common mechanism.

The summer grazing mechanism was clearly through the opening of vegetation gaps, and superior gap colonizers showed a more positive response to heavier grazing. Our direct measure of gap colonization ability was the best predictor of summer grazing response. However, the fact that Grime's ruderality score (Grime, Hodgson & Hunt 1988) was also significant and was correlated with our gap colonization ability measure means that there is a generally available measure that might be used to predict response to grazing. The negative effect of competitive ability, as measured by Grime's C-value, on summer grazing response probably does not indicate a second mechanism. This is because the other measures of competitive ability were not correlated with response to grazing and the C-value and R-value were negatively correlated (Pearson $r = -0{\cdot}84$, d.f. = 15, $P < 0{\cdot}001$). The latter finding is a general problem caused by the constrained geometry of Grime's triangular model (Loehle 1988), which reduces its usefulness for a study such as ours.

The importance of colonization ability supports our previous statements about the major role of gap dynamics in herbaceous communities (Silvertown & Smith 1988; Bullock *et al.* 1994a, 1995). Smith & Rushton (1994) and Smith *et al.* (1996) also found that grazing responses were linked to gap colonization, with heavier grazing favouring more ruderal species (i.e. competitor ruderals and stress-tolerant ruderals). It is interesting that the avoidance/tolerance theory put forward by Briske (1996) and Augustine & McNaughton (1998) ignores gap creation.

The surprising positive correlations of spring and winter grazing ratios with grazing selectivity may be spurious. Accurate measures of selection are extremely hard to make, and grazer choice can vary depending on a wide range of factors, including animal condition, previous grazing environment, season, and species, breed and gender of grazer (Illius & Gordon 1993). However, the correlation of the Davies (Davies 1925) and Spedding (Spedding & Diekmahns 1972) selectivity values indicates they have some generality for large grazers (the Diaz & Ford 2000 data suggest rabbits use different criteria). Another explanation for the positive correlation is that selectivity score may be a surrogate for another process that controlled response to grazing. In a review of studies of a wide range of habitats, Augustine & McNaughton (1998) found some cases of increases in biochemically unpalatable species under grazing, but other cases of no change, or even an increase in more palatable species. They explained the latter case by suggesting there is a trade-off between biochemical palatability and regrowth ability, which means that avoidance and tolerance may be alternative strategies. There is ample evidence of a negative relationship between a plant's growth rate and its ability to defend itself chemically (Hartley & Jones 1997). In our system, where grazing is intense during winter and spring grazing, and we have observed sheep eating even well-defended species such as *Urtica dioica* and *Cirsium vulgare*, tolerance may be a more successful strategy than avoidance.

Over and above these correlations of particular traits with performance under grazing was the difference between dicots and grasses, with the former generally increasing, and the latter generally decreasing, under winter grazing or heavy summer grazing. This seemed to be a general difference between the taxa because the sum of the frequencies of the rarer 17 dicots (i.e. those not included in the trait analysis) was increased by grazing in any season (mean ratio = 2·93) whereas the sum of the frequencies of the rarer four grasses was decreased by grazing (mean ratio = 0·81; paired *t*-test on ratios for each main grazing treatment, $t = 4{\cdot}1$, d.f. = 2, $P < 0{\cdot}05$). The positive effect of grazing on dicots was noted in the previous surveys (Bullock *et al.* 1994a) but, given the wide range of life histories exhibited by the dicot species, it is unclear why this should be such a general effect. It does mean, however, that heavier grazing in any season will move the grassland towards the more dicot-rich community desired by conservationists.

This study has shown that vegetation changes due to grazing will differ depending on the exact grazing regime, season and intensity being important. These differences are due to changes in the mechanism of response to grazing. An ability to adjust the grazing regime in order to direct vegetation change towards particular targets, such as increasing dicot diversity or weed control, will require greater understanding of the mechanisms by which plants are responding to grazing.

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