PLANT ANIMAL INTERACTIONS

Ek del-Val · Michael J. Crawley

What limits herb biomass in grasslands: competition or herbivory?

Abstract Competition and herbivory are two of the main forces shaping plant communities. Although several studies have investigated their impact on plant populations separately, few investigations have examined how they might interact. With the purpose of clarifying the combined roles of competition and herbivory on herb biomass in a grassland, we assessed the effects of different herbivores with reduced grass competition. We conducted a field experiment in 2000-2001 in a British acid grassland (Oak Mead), where we experimentally reduced grass biomass and excluded rabbits, insects and molluscs in a factorial design. Removing the grasses from Oak Mead dramatically increased herb biomass and total above-ground biomass. Herbivore exclusions (i.e. rabbits, insects and molluscs) did not affect total above-ground biomass, but they altered relative abundance of several species. Grass removal and rabbit exclusion had positive interactions on biomass of several herb species, and there were some subtle interactions between different herbivore groups: monocots benefitted when both rabbits and molluscs were excluded, and some herb species had greater biomass when insects and rabbits were absent. We then compared the results with a 10-year experiment that manipulated similar variables in neighbouring grassland (Nash's Field). The comparison between Oak Mead and Nash's Field showed that cessation of herbicide application returns the system to its previous state of grass dominance after 3 years. Therefore, even when herbs were more abundant, they could not prevent reinvasion of the grasses once external factors were removed.

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Introduction

The impact of herbivores on plant communities can be seen as the change in the abundance and composition of species. Herbivores can directly modify recruitment of seedlings by altering seed number or species composition in the seed rain and seed bank (Edwards and Crawley 1999a; Hanley et al. 1995). Herbivores can also alter plant population structure depending on the ontogenic stage of the plant and the timing of the attack (Augustine and McNaughton 1998; Coley and Barone 1996; Maschinski and Whitham 1989; Obeso and Grubb 1994). Vertebrate herbivores are particularly influential on plant communities because of the amount they eat (Augustine and McNaughton 1998; Edwards and Crawley 1999b; Edwards et al. 1999; McNaughton 1979, 1983, 1986; Milchunas et al. 1988; Sinclair 1995; Stebbins 1981; Vesk and Westoby 2001), but invertebrates can also have significant effects. In particular, molluscs are known to prefer seedlings rather than mature plants, and they prefer dicots to monocots (Cottam 1986; Dirzo and Harper 1980, 1982; Hanley et al. 1995). Therefore, the selective influence they exert on plant populations is greater than the amount of biomass they consume because they can prevent plants from establishing and becoming adults (Hanley and Fenner 1997; Rodriguez and Brown 1998). Insect herbivores have more subtle effects in grasslands than vertebrates, but they can also affect plant population dynamics as they alter relative competitive abilities (Crawley 1989; Latsch 1997; Trumble et al. 1993; Tscharntke and Greiler 1995), particularly root feeding insects (Brown and Gange 1992).

Many of the deleterious consequences of herbivore attack are related to changes in competitive hierarchies amongst plant species. Competition between plant species is known to be a major force determining composition and relative abundance in nearly every plant community (Goldberg and Novoplansky 1997; Grime 1977, 1979; Smith and Huston 1989; Tilman 1988, 1990, 1994) but field experiments often have failed to find the imprint of competition (Law and Watkinson 1989).

Competition and herbivory interact in dynamic ways to shape plant communities. The effects of herbivory are sometimes magnified by competition (McEvoy et al. 1993; Wardle and Barker 1997) or not affected by it (Reader 1992). Herbivores are known to have a differential impact on plant diversity depending on the nutrient and light availability of the system. Two recent reviews conclude that under high grazing pressure plant species richness decreases in nutrient-poor ecosystems while it increases in nutrient-rich systems (Proulx and Mazumder 1998; Worm et al. 2002).

In most cases, the effects of herbivores on plant species richness is thought to be positive because of the palatability/competitive ability trade-off. Palatable species will reduce diversity when herbivores are absent because they are stronger competitors (Rees et al. 2001). Herbivory can also change the ability of a plant to acquire limiting resources by altering key morphological traits (Louda et al. 1990), or can prevent competitive exclusion in fertilized plots (Gough and Grace 1998). It has been documented that preferential herbivory changes dominance (Cottam 1986), and exclosures from grazers normally lead to shifts in species composition (Bullock et al. 2001; Crawley 1990; Edwards and Crawley 1999a; Hilbert et al. 1981; McNaughton 1979). Other studies have found that a plant's regrowth capacity after herbivore damage is also diminished under competition (Shabel and Peart 1994).

The aim of this study is to clarify the combined roles of competition and herbivory in limiting herb biomass and distribution in a grassland community, and to assess effects of different herbivores with respect to variations in the competitive environment. Herbs are considered all dicot species growing in the grassland. We performed a field experiment with a split-split plot design combining four factors: (1) grass competition, (2) rabbit grazing, (3) mollusc herbivory and (4) insect herbivory.

Our specific questions were: (1) How does the removal of the dominant grasses affect herb biomass and composition in the community? (2) Do these effects on the herb community persist when grasses are allowed to reinvade? (3) How does the removal of grass competitors interact with herbivore effects on herb biomass and composition? (4) How do the effects of vertebrate herbivores (rabbits) interact with the effects of invertebrate herbivores (molluscs and insects) on herb biomass and composition?

Materials and methods

Oak Mead: experimental design

A 2-year field experiment was carried out in Oak Mead, Silwood Park, Berkshire, UK (National Grid reference 41/944691), a species poor grassland on acid, sandy soil. We established the experiment in January 2000 as a split-split plot design. Grass-specific herbicide, insecticide and molluscicide treatments were randomly nested within rabbit exclusion plots (details below). The experiment consisted of four replicates with four nested plot sizes: replicates (large blocks: 50×30 m^2), rabbit exclusion blocks (25×30 m^2), plots for competition-free treatment (plots: 12.5×30 m^2), within which smaller insecticide and molluscicide split-plots were assigned at random (split-plots: 7.5×12.5 m^2; Fig. 1).

Rabbit exclusions were built by fencing four blocks of grassland. The mesh fence was bent outward to prevent rabbit tunnels (see Crawley 1990, for details). In the grass competition-free plots, a grass-specific herbicide (Checkmate from Hortichem: 193 g/l sethoxydim, 100 ml/l water) was sprayed. Smaller plots were treated with insecticide and molluscicide.

For insect exclusion, we used a combination of two insecticides: one systemic, Danadim 40 from Cheminova (400 g/l dimethoate), and one broad-spectrum systemic and contact, Dursban from DowElanco (480 g/l chlorpyrifos). Twenty-five milliltres of each chemical were diluted in 10 l water and then sprayed on the experimental plants. For mollusc exclusion, Mifaslug from Farmers Crop Chemicals (6% metaldehyde) was used at 500 mg molluscicide per 45 m^2 as suggested by the
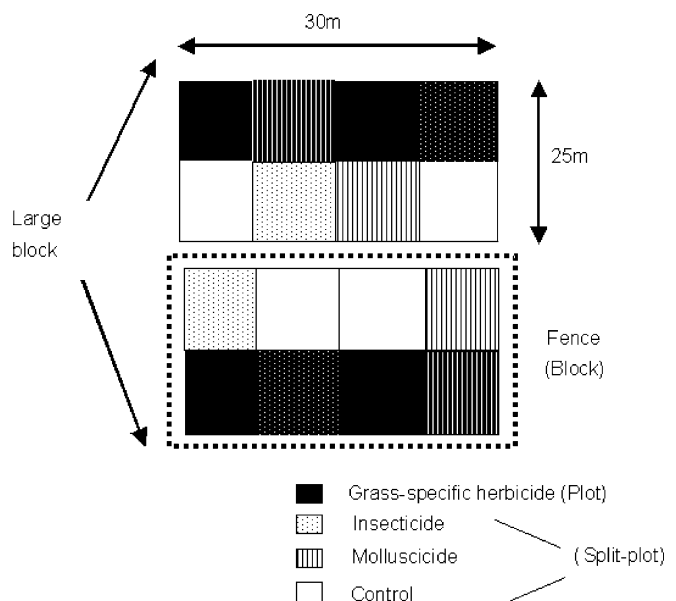

Fig. 1 Experimental design showing replicates (large blocks), rabbit exclusion (blocks), grass-specific herbicide treatment (plots) and molluscicide and insecticide treatments (split-plots)

provider. Herbicide was first applied in March 2000 and it was re-applied several times during the experiment to maximise the reduction in grass cover. Insecticide and molluscicide were applied in April 2000 and re-applied three times during each growing season.

Vegetation sampling was done using a randomly placed metal quadrat of 0.25×0.50 m^2 at the end of the growing season (last week of August) for each split-split plot. All the above-ground biomass contained in the quadrat was cut down and then dried in an oven (80°C) for 48 h. In 2000 only total above-ground biomass per sample was measured. Additionally, in 2001 above-ground biomass was sorted per species and then dried and weighed.

The data were analysed using a split-split plot model in S-PLUS 2000 (MathSoft). We first used total biomass as response variable, and then we analysed biomass per species for those that were present in more than ten plots. In order to analyse biomass results per plant type, we added up biomass of all dicot species to get "herb biomass" and we also added up biomass of grasses, sedges and rushes to get "monocot biomass". Monocot, herb and bryophyte biomass, dead organic matter, total number of species present, number of herb species present and number of monocot species present were also analysed as response variables. The statistical models were built as a split-split plot design including different plot sizes in different error terms. The explanatory variables used were ± rabbits, ± herbicide, ± insects, ± molluscs and the interactions between them. Natural-log and squared-root transformations of the response variables were carried out in different cases in order to find the best model for each analysis. The best model was chosen by model-check plots.

Long term effects: comparison with Nash's Field

In order to understand better the long-term effects of competitor release in grasslands, we compared the results obtained in Oak Mead with another neighbouring grassland, Nash's Field, where similar experiments have been running for 10 years. In 1991 a field experiment was set up to investigate long-term effects of rabbit herbivory and grass competitor release. Rabbit exclusions were built (eight replicates) and grass-free plots were nested inside (see Edwards and Crawley 1999a, for experimental set-up). The experiment is being monitored yearly during the summer and mowed inside the rabbit exclusions every spring.

We used the data from 1992, 1997 and 2000 from Nash's Field and the data from 2000 and 2001 from Oak Mead. It is important to note that herbicide application in Nash's Field stopped in 1994, therefore data from 1997 and 2000 relates to 3 and 6 years after cessation of grass removal, respectively. Effects of herbicide application and rabbit exclusion were assessed in terms of total above-ground biomass, herb biomass and monocot biomass (in total and species by species) and the number of species present.

The data were also analysed using S-PLUS 2000 (MathSoft). The statistical models were built up as a split-split plot design including different sites, years and plot sizes in the error terms. The response variables were natural-log (biomass) and number of species per plot; the explanatory variables used were site, year, ± herbicide, ± rabbits and the interactions between them. High order non-significant interactions were removed from the model and only the simplified models are reported here.

Results

Oak Mead

Thirty-two plant species were recorded in the study area, 9 monocots and 23 dicots (Table 1). Analysis of individual species was performed only when the species was present in more than ten plots. Thus only seven monocot and eight dicot species were analysed separately.

Grass-specific herbicide

In summer 2000, herbicide treatment did not show any significant effect on plant biomass (Table 2, Fig. 2). Nonetheless in summer 2001 (after two consecutive years of treatment), herbicide was the treatment that caused the greatest effect, suggesting that competitor release had a big impact on the community. We found that where grasses were removed total biomass and herb biomass were greater (Table 2). In terms of individual species, four out of eight herb species increased significantly in biomass on herbicide plots (*Cerastium fontanum*, *Senecio jacobaea*, *Stellaria graminea*, and *Veronica serpyllifolia*; Table 3). Bryophyte biomass and dead organic matter were not affected. Even though the herbicide was effective against most of the grasses, three species of monocots (out of seven) were not reduced by the herbicide: *Poa pratensis*, *Luzula campestris* and *Festuca rubra* subsp. *rubra*.

Total number of species per 0.50×0.25-m^2 quadrat was not affected by herbicide (Table 2), but nevertheless the average number of herb species was greater where grasses were killed (6.04 ± 0.25 species/plot and 4.46 ± 0.27 species/plot, respectively).

Rabbit exclusion

Rabbit exclusion had a positive effect on plant biomass in summer 2000 (Table 2, Fig. 3). Total biomass on fenced plots was 57.1 ± 2.29 g (456.8 g/m^2) and unfenced 44.3 ± 2.24 g (354.4 g/m^2). Nevertheless, in 2001, the effect of rabbit exclusion on above-ground biomass was no longer significant but the tendency was in the same direction. Neither herb biomass nor monocot biomass were significantly affected by rabbit exclusion, nor were dead organic matter or bryophytes. Neither total number of species present nor the number of herb species

Table 1 List of species found in Oak Mead, Silwood Park during summer 2001 (total number of plots = 60; information from Peat and Fitter 2002)

Species	Family	Type	Life form	No. of plots present in
Senecio jacobaea	Asteraceae	Dicot	Biennial	53[a]
Stellaria graminea	Caryophyllaceae	Dicot	Perennial	48[a]
Festuca rubra subsp. *rubra*	Poaceae	Monocot	Perennial	47[a]
Trifolium repens	Fabaceae	Dicot	Perennial	37[a]
Veronica chamaedrys	Scrophulariaceae	Dicot	Perennial	37[a]
Luzula campestris	Jucaceae	Monocot	Perennial	32[a]
Agrostis capillaris	Poaceae	Monocot	Perennial	30[a]
Ranunculus repens	Ranunculaceae	Dicot	Perennial	26[a]
Holcus lanatus	Poaceae	Monocot	Perennial	25[a]
Cerastium fontanum	Caryophyllaceae	Dicot	Perennial	22[a]
Rumex acetosella	Polygonaceae	Dicot	Perennial	20[a]
Poa pratensis	Poaceae	Monocot	Perennial	16[a]
Anthoxanthum odoratum	Poaceae	Dicot	Perennial	12[a]
Veronica serpyllifolia	Scrophulariaceae	Monocot	Perennial	11[a]
Holcus mollis	Poaceae	Monocot	Perennial	10[a]
Lotus corniculatus	Fabaceae	Dicot	Perennial	7
Cirsium arvense	Asteraceae	Dicot	Perennial	5
Prunella vulgaris	Lamiaceae	Dicot	Perennial	5
Taraxacum officinale	Asteraceae	Dicot	Perennial	5
Urtica dioica	Urticaceae	Dicot	Perennial	4
Achillea millefolium	Asteraceae	Dicot	Perennial	3
Vulpia bromoides	Poaceae	Monocot	Perennial	3
Crepis capillaris	Asteraceae	Dicot	Perennial	3
Myosotis discolor	Boraginaceae	Dicot	Perennial	3
Vicia sativa subsp. *nigra*	Fabaceae	Dicot	Annual	3
Ornithopus perpusillus	Fabaceae	Dicot	Perennial	2
Carex muricata subsp. *lamprocarpa*	Cyperaceae	Monocot	Perennial	1
Hypochaeris radicata	Asteraceae	Dicot	Perennial	1
Lathyrus pratensis	Fabaceae	Dicot	Perennial	1
Aphanes australis	Rosaceae	Dicot	Perennial	1
Quercus robur	Fagaceae	Dicot	Perennial	1
Rubus fruticosus	Rosaceae	Dicot	Perennial	1

[a] Species analysed separately

were affected by rabbit exclusion, but number of monocot species increased when rabbits were present (fenced 2.79 ± 0.41 monocot species/plot and unfenced 3.75 ± 0.33 monocot species/plot). Rabbit exclusion led to increased biomass of *Holcus mollis*, *Stellaria graminea* and *Festuca rubra* subsp. *rubra* whereas *Luzula campestris* had greater biomass in unfenced plots (Table 3).

Insect exclusion

Insect exclusion did not affect total above-ground biomass in summer 2000 and in summer 2001 was only important for some species, but not in the general trends (total above-ground biomass, herb and monocot biomass, nor dead organic matter or

Table 2 Analysis of variance of the experimental treatments and interactions on total biomass (2000 and 2001), monocot biomass, herb biomass, bryophyte biomass, dead organic matter, total number of species present, number of herb species present and number of monocot species in Oak Mead. Values shown are F statistics with degrees of freedom. Statistical analyses were performed with natural log-transformed data

	Total biomass		Monocot biomass 2001	Herb biomass 2001	Bryophytes 2001	Dead organic matter 2001	Total no. of spp. 2001	No. herb spp. 2001	No. monocot spp. 2001
	2000	2001							
Rabbits ($F_{1,3}$)	11.19**	0.08	1.77	0.13	0.44	3.34	1.05	0.27	17.45**
Herbicide ($F_{1,6}$)	3.32	13.05**	66.8****	169.14****	3.48	1.46	0.12	14.28****	9.52**
Insects ($F_{1,24}$)	0.007	0.74	0.32	1.24	0.11	0.67	0.36	0.07	> 0.0001
Molluscs ($F_{1,24}$)	1.45	0.38	0.6	0.02	0.04	1.72	0.11	1.57	> 0.0001
Rabbits × herbicide ($F_{1,6}$)	0.007	2.95	4.6*	1.17	0.16	0.76	0.28	0.71	0.76
Rabbits × insects ($F_{1,24}$)	1.49	1.05	0.13	0.59	0.24	0.23	0.05	0.51	0.35
Rabbits × molluscs ($F_{1,24}$)	0.09	0.1	6.75**	0.12	0.02	0.001	1.42	0.94	0.58
Herbicide × insects ($F_{1,24}$)	0.003	1.22	0.11	1.81	0.0002	1.41	0.24	0.55	0.99
Herbicide × molluscs ($F_{1,24}$)	0.75	0.11	0.41	0.002	0.1	4.73**	5.4**	0.37	1.53
Rabbits × herbicide × insects ($F_{1,24}$)	1.06	0.001	4.2*	0.16	0.04	0.75	0.19	0.75	1.12

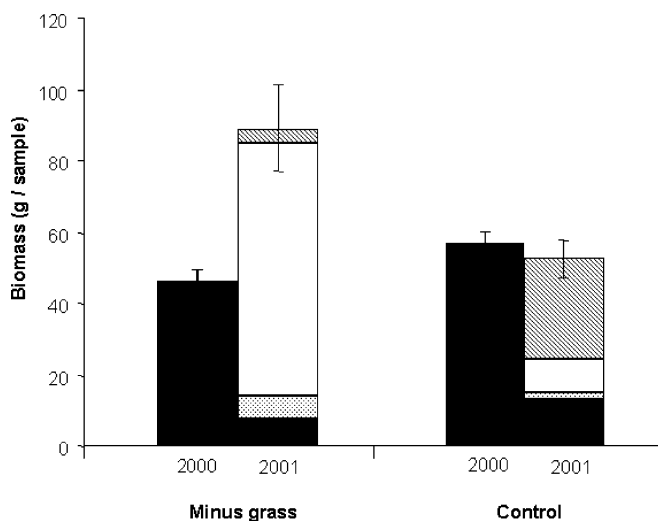* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$; **** $P < 0.001$

Fig. 2 Effects of grass-specific herbicide on two consecutive years, showing Mean ± 1SE of total biomass per plot (g). For summer 2001, biomass is divided into vegetation components: *diagonal shading* monocot, *unshaded* herbs, *stippling* bryophytes, *black* dead organic matter. Monocot and herb biomass are significantly different between treatments ($P < 0.05$), whereas dead organic matter and bryophytes are not

bryophytes). *Holcus mollis* increased when insects were excluded (Table 3).

In other cases there was an interaction between insect exclusion and herbicide application: *Ranunculus repens* biomass was greater when herbicide and insecticide were applied together (10.45 ± 5.68 g/plot) compared with only herbicide (3.93 ± 2.9 g/plot). There was also a significant interaction between insecticide and fencing treatments: *R. repens* biomass was greater on fenced insecticide plots (10.75 ± 5.62 g/plot) compared with only fenced (3.58 ± 2.9 g/plot). *Veronica chamaedrys* also increased when insecticide and herbicide were applied together (5.1 ± 2.3 g/plot) compared with only herbicide (2.6 ± 2.3 g/plot). Insect exclusion also interacted with rabbit exclusion for *Stellaria graminea*, with greater biomass in plots where both insects and rabbits were excluded (4.66 ± 1.14 g/plot) in comparison with only insect exclusion (0.41 ± 0.21 g/plot) or rabbit exclusion (0.41 ± 0.2 g/plot). *Rumex acetosella* was negatively affected by insecticide application.

Mollusc exclusion

Molluscicide did not affect total above-ground biomass in either year (Table 2). Monocot biomass was not affected by mollusc exclusion, but there was an interaction between rabbit exclusion and mollusc exclusion. There was greater monocot biomass when both were in place: molluscicide + fencing > fencing only. Bryophytes benefited by the same interaction.

Molluscicide application showed impact on various species: *Rumex acetosella* grew better when molluscs were excluded and benefited even more when molluscicide was applied in addition to herbicide or to rabbit fencing

(Table 3). *Anthoxanthum odoratum* had greater biomass on plots where molluscs were present. *Ranunculus repens* and *R. acetosella* also benefited from simultaneous herbicide and molluscicide application. *Holcus lanatus* increased when molluscicide, fencing and herbicide were applied. *Stellaria graminea* had greater biomass when applying molluscicide + herbicide + rabbit exclusion and also with a combination of fencing and molluscicide.

Long term effects: comparison with Nash's Field

Biomass was greater in rabbit exclusion plots at both Oak Mead and Nash's Field (Table 4, Fig. 4). Because results from Nash's Field encompass data from years with and without herbicide application, herbicide treatment was not significant as a main effect but there was a significant herbicide × year interaction ($P < <0.001$). In the second year of herbicide application (i.e., 1992 for NF and 2001 for OM), we observed opposite trends, greater biomass in control plots for Nash's Field and greater biomass in minus-grass plots in Oak Mead (Fig. 5). Average number of species present increase somewhat in the control plots in both sites ($P = 0.08$).

Rabbit exclusion did not affect herb biomass but grass-specific herbicide effect had a large impact on herbs ($P = 0.002$) and there was a significant interaction between herbicide and site ($P << 0.001$) and herbicide and year ($P = 0.006$). The increase in herb biomass after removing the grasses was particularly evident in 2001 Oak Mead and 1992 Nash's Field. In contrast, number of herb species per plot was not affected by herbicide as a main effect but there was a significant interaction between herbicide application and site: in Oak Mead herbicide plots had 6.0 ± 0.2 herb species/plot and control plots only 4.4 ± 0.3 herb species/plot ($P << 0.001$). For the number of herb species there was also an interaction between herbicide and rabbit exclusion: fencing the plot and applying herbicide increased the number of herb species (4.6 ± 0.4 herb species/plot) compared with only fencing (3.4 ± 0.4 herb species/plot; $P << 0.001$).

Rabbit exclusion also had no effect on monocot biomass ($P > 0.05$) while herbicide reduced grass biomass as expected ($P << 0.001$). There was also a significant interaction between herbicide and rabbit exclusion: monocot biomass was greater in plots with rabbit fencing and no herbicide ($P = 0.04$). Because Oak Mead showed a greater response after removing grasses than Nash's Field we also find two significant interactions for monocot biomass: herbicide and site ($P << 0.001$) and herbicide and year ($P = 0.02$). Average number of monocot species present per sample was also significantly lower in plots with herbicide ($P << 0.001$) and the interaction between herbicide and year was also significant ($P = 0.004$).

Analysing the two sites together several herb species were favoured when grasses were excluded: *Ranunculus repens* ($F_{1,119} = 4.24$, $P = 0.04$), *Senecio jacobaea* ($F_{1,119} = 29.34$, $P << 0.001$), *Stellaria graminea* ($F_{1,117} = 8.18$,

Table 3 Analysis of variance for individual species biomass under experimental treatments and interactions in Oak Mead, 2001. Values shown are F statistics with degrees of freedom. Statistical analyses were performed with natural log-transformed data

Species	Rabbits $(F_{1,3})$	Herbicide $(F_{1,6})$	Insects $(F_{1,24})$	Molluscs $(F_{1,24})$	Rabbits × herbicide $(F_{1,6})$	Rabbits × insects $(F_{1,24})$	Rabbits × molluscs $(F_{1,24})$	Herbicide × insects $(F_{1,24})$	Herbicide × molluscs $(F_{1,24})$	Rabbits × herbicide × insects $(F_{1,24})$	Rabbits × herbicide × molluscs $(F_{1,24})$
Monocots											
Agrostis capillaris	1.97	22.09****	1.83	0.09	0.41	0.06	0.37	0.05	2.14	0.17	0.17
Anthoxanthum odoratum	0.46	11.98**	0.08	25.68****	0.74	1.8	0.07	0.08	25.69****	1.79	0.04
Festuca rubra subsp. rubra	10.02**	2.36	0.17	>0.001	0.63	0.57	0.01	0.15	0.03	0.002	2.87
Holcus lanatus	0.003	94.58****	2.7	1.01	>0.001	3.73*	5.94**	0.12	1.23	2.66	5.46**
Holcus mollis	21.95**	8.57**	9.08***	0.46	5.64*	3.5*	0.46	3.23*	0.46	0.43	0.46
Luzula campestris	22.54***	0.13	0.25	0.35	0.24	0.47	0.14	0.02	1.24	0.53	0.58
Poa pratensis	0.34	0.84	0.3	0.22	1.58	1.34	0.02	0.01	>0.001	0.07	2.95*
Herbs											
Cerastium fontanum	1.51	8.66**	1.13	0.94	0.001	2.12	0.16	0.02	0.85	0.62	0.01
Rumex acetosella	8.27*	2.46	7.03**	6.6**	0.7	10.76****	2.45	3.87*	8.73****	0.34	1.57
Ranunculus repens	8.87*	0.27	2.67	0.65	0.36	11.69****	1.59	7.2**	6.12**	0.73	0.18
Stellaria graminea	64.98****	14.14***	>0.001	1.65	5.62*	6.16**	3.41*	4.38**	1.11	5.06**	5.98**
Senecio jacobaea	5.11	123.73****	0.93	0.002	3.02	0.28	0.05	0.64	0.002	>0.001	0.96
Trifolium repens	4.2	1.84	0.06	0.009	1.84	0.08	0.74	2.87	0.86	0.18	1.61
Veronica chamaedrys	5.87*	1.76	0.26	0.2	0.22	1.24	0.01	7.68**	0.02	0.1	0.03
Veronica serpyllifolia	2.82	7.36**	0.36	0.32	3.09	1.2	0.28	0.2	0.1	0.64	0.29

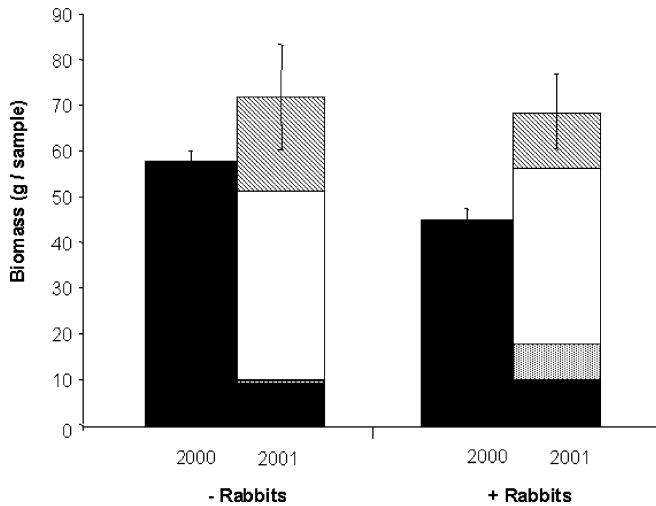* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$; **** $P < 0.001$

Fig. 3 Effects of rabbit exclusion on two consecutive years, showing Mean ± 1 SE of total biomass per plot (g). For summer 2001, biomass is divided into vegetation components: *diagonal shading* monocot, *unshaded* herbs, *stippling* bryophytes and *black* dead organic matter. There were no significant differences between any of the biomass components for rabbit exclusion ($P > 0.05$)

$P = 0.005$), *Trifolium repens* ($F_{1,118} = 5.54$, $P = 0.02$), *Cerastium fontanum* ($F_{1,119} = 7.86$, $P = 0.006$) and *Veronica serpyllifolia* ($F_{1,119} = 6.31$, $P = 0.01$). Interestingly *Rumex acetosella* showed opposite reactions when grazed than when ungrazed. Grazed plant biomass was greater on the non-herbicide plots whereas plants in ungrazed plots had greater biomass on the herbicide plots (fence × herbicide: $F_{1,118} = 5.6$, $P = 0.02$). *Plantago lanceolata* benefited from competitor release only in 1992 (year × herbicide: $F_{3,117} = 4.13$, $P = 0.008$). No effect for rabbit exclusion was found in terms of number of herb species present in a plot.

Discussion

Oak Mead

After two consecutive years of herbicide application we saw a clear signature of competitor release in the grassland: herb biomass increased 7.8-fold and total above-ground biomass increased 1.7-fold when grasses were experimentally reduced. This supports the idea that grasses in general are superior competitors in this system and that they are suppressing herb biomass. Several studies in grassland communities have found that more diverse plots were more productive (reviewed by Rees et al. 2001). However, in our case, biomass production increased but average number of species per plot did not change under manipulation as found in a greenhouse experiment by Wardle and Barker (1997). Relative species biomass changed radically and this was sufficient to increase total above-ground biomass (i.e., the identity of the most abundant species changed under herbicide treatment).

Herb species are able to coexist in a grassland even under intense competition, but they benefit when grasses are killed and increase in biomass, either by recruitment from seed or by vegetative growth. We demonstrated that for several herb species (i.e., *Cerastium fontanum*, *Stellaria graminea*, *Senecio jacobaea*, *Veronica chamaedrys* and *V. serpyllifolia*) competition is the main mechanism restricting its biomass; when removing the grasses they increased substantially in biomass. The inhibiting factors when major competitors are present could be several. Our results suggest that competition for light could be an important factor in the system because besides the decrease in monocot biomass, we found a tendency towards less dead organic matter in grass-specific-herbicide plots that could be shading plants (a result also found by Suding and Goldberg 2001). In addition Van der Wal et al. (2000) also found that competition for light was more important than grazing for *Triglochin maritima*. Another possible explanation could be that grasses may be superior competitors for nutrients (Tilman 1982). Several studies have demonstrated that established plants inhibited germination and reduced the probability of herb recruitment (Fenner 1978; Rees and Brown 1991). An increase in available germination sites could also explain the rapid increase in herb biomass in our experiment. An additional component that could have influenced the increase in herb biomass is the extra nutrient input

Table 4 Analysis of variance for total biomass, herb and monocot biomass, total number of species, and number of herb and monocot species, including data from Oak Mead and Nash's Field. Values shown are F statistics. Biomass analyses were performed with natural log-transformed data. For herb biomass, monocot biomass and number of species only the year 2001 from Oak Mead was used. Values of *df* are given in *parentheses*. The effects of site, year and year × site were not evaluated because of lack of replication

	Total biomass (g)	Total number of species	Monocot biomass (g)	Number of monocot species	Herb biomass (g)	Number of herb species
Rabbits	24.4** (1,3)	0.66 (1,1)	10.2 (1,1)	1.44 (1,1)	3.1 (1,1)	0.29 (1,1)
Herbicide	0.04 (1,158)	3.15* (1,114)	53.62**** (1,114)	23.69**** (1,114)	9.69*** (1,114)	2.47 (1,114)
Site × herbicide	5.19** (1,158)	0.41 (1,114)	55.2**** (1,114)	8.6*** (1,114)	26.37**** (1,114)	12.03**** (1,114)
Year × herbicide	8.8**** (3,158)	0.35 (2,114)	3.97** (2,114)	2.6* (2,114)	5.39*** (2,114)	3.47** (2,114)
Site × rabbits	0.23 (1,158)	0.005 (1,1)	14.7 (1,1)	0.88 (1,1)	0.17 (1,1)	0.61 (1,1)
Rabbits × herbicide	1.3 (1,158)	3.45* (1,114)	4.3** (1,114)	0.26 (1,114)	12.9 (1,114)	10.06*** (1,114)
Site × rabbits × herbicide	1.1 (1,158)	0.25 (1,114)	3.1* (1,114)	0.19 (1,114)	2.44 (1,114)	1.24 (1,114)
Year × rabbits × herbicide	1.81 (2,158)	0.38 (1,114)	0.02 (1,114)	1.1 (1,114)	0.29 (1,114)	>0.0001 (1,114)

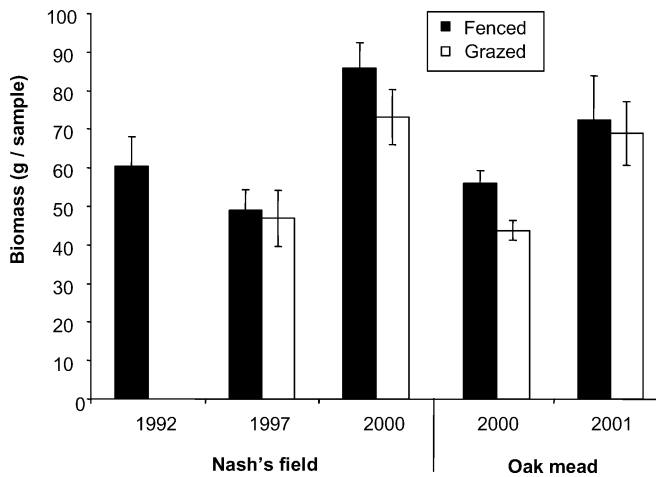* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$; **** $P < 0.001$

Fig. 4 Rabbit exclusion effect on biomass with data from Oak Mead and Nash's Field. Showing Mean ±1 SE of total biomass per plot (g). In Nash's Field 1992, only biomass in fenced plots was assessed
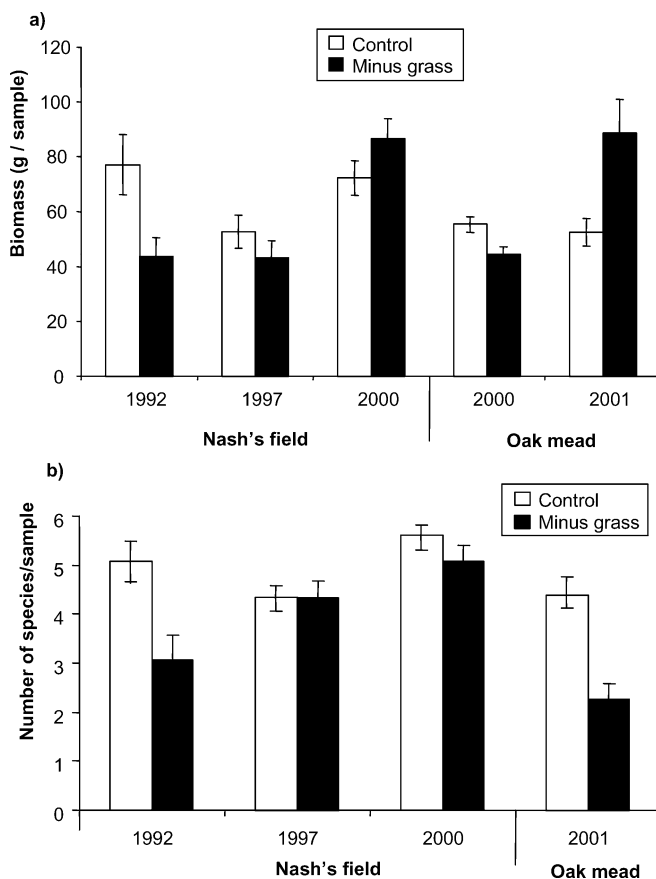

Fig. 5 Herbicide effect in different years in Oak Mead and Nash's Field. **a** Mean ±1 SE of total biomass (g) per sample (0.25×0.50 m²) in control and minus-grass plots; **b** Mean ±1 SE number of species per sample (0.25×0.50 m²) in control and minus-grass plots

through the dead tillers from grasses. Several studies have found that dead organic material produced by plants (i.e. in these case grass residues) enhance nitrogen

mineralization in the soil (van der Krift and Berendse 2002; Wedin and Tilman 1990). All of the above factors may have played some role. *Festuca rubra* subsp. *rubra* was resistant to herbicide application. Therefore this grass species also benefited from competitor release in the "minus grass" treatment. The effects of competitor release on herbs would likely have been even greater if *Festuca* had been killed.

Changes in species richness due to mammal grazing have been found in several studies (Bullock et al. 2001; Latsch 1997; Rambo and Faeth 1999; Schuman et al. 1999), and some authors have proposed that herbivores can increase plant diversity because of the palatability/competitive ability trade-off (Pacala and Crawley 1992; Rees et al. 2001). However, the direction of herbivore impact on plant richness depends on the nutrient availability of the system (Proulx and Mazumder 1998; Worm et al. 2002). In this particular study, we did not find any change in species richness. There were some changes in species relative biomass but the average species number between grazed and ungrazed areas remained the same.

Herbivory, rather than competition, seems to be the main mechanism regulating the biomass for only a few species in this system, similar to what other authors have shown in different systems (Olofsson 2001, 2002; Reader 1992). *Holcus mollis* grew better when insects were excluded. This species is known to have a specialist aphid (*Holcaphis holci*) that considerably reduces its growth under natural conditions (M.J. Crawley, unpublished data). *Rumex acetosella* and *Anthoxanthum odoratum* had greater biomass when molluscs were excluded.

One species increased in biomass under rabbit grazing: *Luzula campestris*. Various factors may explain these findings, but a plausible explanation for the increase of this species is rabbit avoidance; *L. campestris* has long hairs on the leaves that can function as a physical defence (Clapham et al. 1962).

Interestingly, competitor release effects were magnified by herbivore exclusion for some species as found for *Salicornia europaea* (Ellison 1987) and some herb species in British grasslands (Crawley 1990). *Ranunculus repens* and *Veronica chamaedrys* increased only if monocots were killed and insects were excluded; they increased 400-fold and 4-fold, respectively, when competitors were removed and insects were excluded. *Rumex acetosella*, *Ranunculus repens* and *Anthoxanthum odoratum* also had greater biomass when competitors were killed and molluscs excluded.

The interaction between vertebrate and invertebrate herbivores was not pronounced. Monocot biomass was greater when both molluscs and rabbits were excluded. We found some interesting interactive effects of herbivore exclusions: *Stellaria graminea*, *Rumex acetosella* and *Ranunculus repens* were disproportionately favoured when both rabbits and insects were excluded and *Rumex acetosella* was also favoured when protected from rabbits and molluscs. Therefore, individual species biomass can be substantially modified by the combined grazing

of different kinds of herbivores that would not be predictable from the response to exclusion of one herbivore alone, as has been shown for other systems (Palmisiano and Fox 1997).

These results could misleadingly suggest that in absence of herbivores, monocots will still be the dominants of this system. However, we know from previous experiments that after a few years of herbivore-free environment, tree seedlings start to establish and outcompete grassland species (M.J. Crawley, unpublished data). Rabbit grazing prevents woodland succession but insects and molluscs do not appear to prevent recruitment of woody plants. Because grasslands in this latitude are not climatically driven but maintained by external factors (i.e., vertebrate herbivores or agricultural practices), we could expect a community shift towards a forest (Milchunas et al. 1988).

Comparison with Nash's Field

Long-term data from Nash's Field offer an important perspective of interpreting short term results from Oak Mead. Both studies showed that grasses are superior competitors. Even though the herbicide effects disappeared in Nash's Field after 3 years (when herbicide application stopped), the same effects were observed in the first year of herbicide application in both sites: herb species significantly increased in biomass when grasses were killed (Fig. 6). Apparently, however, Nash's Field quickly returned to the normal grassland stage following the cessation of herbicide application. Thus, even though herbs benefited greatly from removal of grasses and increased overall grassland biomass in the short term, they do not have the ability to dominate the grassland system in the long term. Grasses rapidly reinvaded once herbicide treatment was stopped.

This study provides strong support for the importance of competitive hierarchies in grasslands; monocot species are stronger competitors than herbs, hence when removing grasses, herb species increase in biomass. The effects of competitor release were strong and conspicuous, contrary to some earlier reviews which suggested that evidence of interspecific competition was hard to obtain in field situations (Law and Watkinson 1989). Likewise, although effects of competitor release were large, they were clearly transient (we were able to witness the rapid return to a typical grassland once the experimental manipulation was relaxed).

This study also presents evidence for a better understanding of the relative magnitude of competition and herbivory in this grassland. With the level of rabbit herbivory that these grasslands experience, interspecific plant competition is the primary factor determining community structure. Notwithstanding that insects and molluscs had smaller effects than rabbits as previously known, their effects were substantial enough to alter the biomass of several individual species particularly when competition is diminished, so their effects should be considered in any study examining changes in biomass and distribution of grassland species.

Fig. 6 Herbicide effect in different years in Oak Mead and Nash's Field. Mean monocot biomass and mean herb biomass for control and minus-grass plots in g per sample (0.25×0.50 m²)

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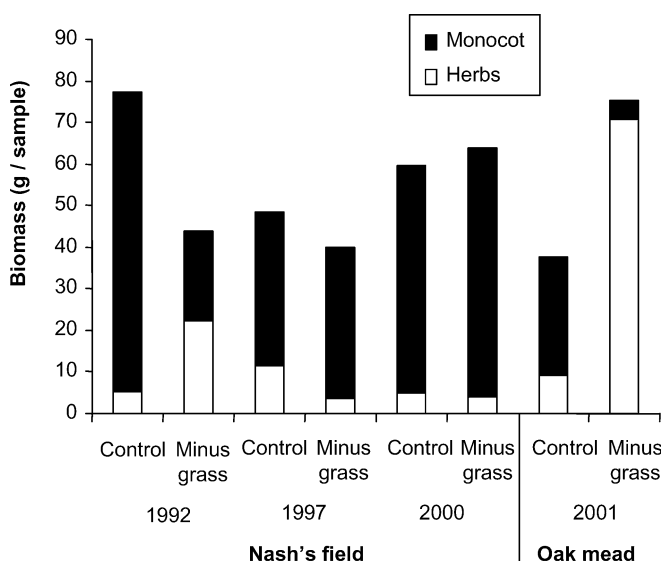
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