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Summary

1 Hay meadows in western Ireland were traditionally mown once a year in late summer with aftermath grazing. To assess how changes in mowing regime affect the plant species composition, productivity and vegetation structure, a long-term mowing experiment was carried out in an *Arrhenatheretum* meadow on a clayey limestone soil in County Galway, Ireland. From 1986 until 1997, a grassland was fenced to exclude grazing, and plots of 12 m^2 were mown every year either in May or in August or at both dates or left unmown ($n = 4$).

2 Vegetation relevés carried out in 1986, 1989, 1991 and 1997 revealed an overall successional trend (e.g. the decrease of some typical pasture species) as well as time-dependent treatments effects: mown and unmown plots diverged initially, with a temporary increase of legumes in mown plots, but differences in species composition largely disappeared until 1997.

3 The effects of mowing on plant species richness (s) were also time-dependent. Until 1991, s increased in mown plots (from a mean of 17.1 species m^{-2} in 1986 to 22.1 in 1991) whereas it decreased in unmown plots (15.5 in 1991). From 1991 to 1997, s strongly decreased in plots mown either in May or in August (12.3 m^{-2}); only plots mown in May and August remained more species-rich (17.5 m^{-2}) than unmown plots (14.5 m^{-2}). The general decrease in species richness might be related to the exclusion of grazing.

4 In July 1997, plots mown in August had a lower biomass, lower graminoid to forb ratio, lower canopy height and a greater proportion of biomass close to soil surface (0–10 cm) than plots mown in May or unmown. The availability of N in soil was 2–3 times higher in unmown than in mown plots, whereas the availability of P was generally high and hardly differed among treatments.

5 We conclude that the maintenance of mowing (possibly associated with grazing) is important for the conservation of species-rich grasslands in Ireland; none of the three mowing regimes appeared clearly preferable, partly because treatments effects were time-dependent.

Keywords: calcareous grassland, canopy structure, diversity, mowing experiment, redundancy analysis, vegetation dynamics

Introduction

The intensification of agriculture, mainly supported by EC policy (Hickie *et al.* 1999), has caused changes in the mowing regime of grasslands in western Ireland. Traditionally, grasslands were cut for hay making once a year, whereas nowadays grass is used for silage, and meadows are often mown twice a year and fertilised. Even in meadows mown only once a year, the time of mowing has often shifted from the traditional dates (late July or August), to earlier dates (mainly May). The effects of fertilizer use on the vegetation of grasslands have been widely investigated, showing that a decrease in species diversity often results from fertilisation (Bobbink 1991; Willems *et al.* 1993; Gough *et al.* 2000). However, changes in mowing regime alone, even without any fertilisation, may also influence the species composition, biomass production and vegetation structure of grasslands (Oomes & Mooi 1981; Bakker 1989; Buttler 1992; Willems *et al.* 1993; Ryser *et al.* 1995) as well as the performance and life history of individual species (Oostermeijer *et al.* 1994; Bühler & Schmid 2001; Kleijn & Steinger 2002). For nature conservation it is important to know which mowing regime is most suitable to preserve the typical species composition and the species richness of the traditional grassland communities.

The effects of management on the vegetation depend on site factors such as soil type, nutrient availability and climate (Georgiadis *et al.* 1989; Huhta 1996; Proulx & Mazumder 1998). At highly productive sites, plant growth rapidly becomes light-limited. As a result, biomass production and species richness are generally enhanced by more frequent mowing or by grazing because the removal of above-ground biomass improves light conditions (de Mazancourt *et al.* 1998; Smith *et al.* 2000). At low-productive (dry or nutrient-poor) sites, plant growth is limited by soil resources, and more frequent mowing tends to reduce the biomass production; species richness may be unaffected or reduced (Bakker *et al.* 2002). Climate determines the length of the growing season and thus, the period during which plants can effectively grow between two cuts of a grassland. In the peroceanic climate of western Ireland, with little or no winter frost, the vegetation grows throughout the year and therefore regenerates rapidly after mowing regardless of the time of management. This contrasts with more continental climates, where summer drought and then low winter temperatures allow little re-growth when grasslands are mown in late summer. It may therefore be expected that the effects of mowing regimes on the limestone grasslands of western Ireland differ from those shown in other parts of Europe, e.g. the southern parts of the Netherlands (Willems 1985; Bobbink *et al.* 1987; Bobbink & Willems 1988) or Switzerland (Ryser *et al.* 1995; Köhler 2001).

To investigate how mowing at different dates affects the species composition and species richness of the vegetation, late Dr. Tony Whilde set up a mowing experiment in 1986 in a traditionally managed limestone grassland at Ardnasillagh-Oughterard, western Ireland. The experiment was maintained and monitored over a period of twelve years. In this paper, we assess the long-term effects of four

mowing regimes on plant species composition, species richness, biomass and vegetation structure. We expected that plant species composition and species richness would progressively diverge among the four treatments, with little change under late-summer mowing (the traditional management) and shifts in species composition under the three other treatments. Specifically, we expected mowing in May to reduce plant species richness by promoting grasses with rapid regeneration (Ryser et al. 1995) as well as late-flowering species able to set seeds after the mowing (van Tooren et al. 1987; Bobbink & Willems 1991). Mowing both in early and in late summer was expected to reduce the biomass production of the vegetation by exporting more nutrients with the hay, with or without effect on plant species richness (Bakker et al. 2002; Güsewell 2003a,b). Complete abandonment was expected to cause a greater nutrient availability in soil (Köhler et al. 2001), and thus an increased biomass production, taller canopy, the exclusion of smaller plant species and a reduced species richness (Buttler 1992; Huhta 1996; Prach 1996; Diemer et al. 2001; Bakker et al. 2002).

Methods

EXPERIMENTAL DESIGN

The experiment took place in a traditional species-rich limestone grassland on clay soil situated in Oughterard co. Galway Ireland (53°25'N 09°16'W; Irish grid M166418; Fig. 1). The area has a peroceanic climate with an annual precipitation of 1150–1500 mm, a mean annual temperature of 10.1 °C, and monthly mean temperatures ranging from 5.4 (January or February) to 15.1 (July; Rohan 1986). The geological underground is limestone, over which a fine clay soil with a depth between 20 and 50 cm has developed; the soil pH (H_2O) ranges from 5.5–6 at soil surface to

approximately 8 at 15 cm depth. The vegetation is a moderately productive mesic *Arrhenatheretum* (Ellenberg 1996). Before the start of the experiment, the grassland was mown once per year in late July or early August and subsequently grazed by free-ranging cattle. When the experiment was set up, the grassland was fenced to prevent further grazing.

Sixteen experimental plots (3 m x 4 m) were laid out within the grassland in four rows of four plots separated by paths of 1 m. Four management types were randomly attributed to the plots in a 4 x 4 Latin square design: mown in May-June (M), mown in August (A), mown at both dates (MA) and unmown (U). Mowing was done manually, and the hay was removed immediately. The experiment started in 1986, and the same management schedule was applied every year for a total of eleven years, i.e. until 1996; the final assessment of management effects took place in early July 1997.

DATA COLLECTION

The species composition of the vegetation was surveyed four times during the experi-

Fig. 1. Location of the experimental site in western Ireland. The inset indicates which part of Ireland is represented by the map.

ment: at the start (1986), after three years (1989), after five years (1991) and at the end (1997) in one permanent quadrat of 1m x 1m per experimental plot. Species cover was assessed for all vascular plants on the Braun-Blanquet scale either in June or in August, depending on the time of mowing (cf. Appendix 1). Vegetation relevés were also used to determine the species richness per 1 m^2 as well as the number of forb and of graminoid species.

The above-ground biomass of the vegetation was sampled on 3–4 July 1997 by clipping a 20 cm x 20 cm quadrat just above soil surface. To describe the vegetation structure, the samples were subdivided into layers of 10 cm; the material from each layer was further sorted into forbs and graminoids. All subsamples were dried for 48 h at 70 °C to obtain dry biomass.

To assess nutrient availability, one soil core (6 cm diameter, 5 cm length) was taken in each experimental plot on 3–4 July 1997. The air-dried soil was extracted with 0.2 M KCl for available nitrogen, and with an ammonium lactate-acetic acid solution for plant-available phosphorus (Houba *et al.* 1995; van Oorschot *et al.* 1995). The concentrations of nitrate, ammonium and phosphate in the extracts were measured colorimetrically on an autoanalyzer (Skalar, Breda, The Netherlands).

DATA ANALYSIS

Changes in plant species composition between 1986 and 1997 and their dependence on management were analysed with Redundancy Analysis, a constrained ordination method (ter Braak 1994). Because the relevés had been carried out either in June or in August, the analysis was mainly based on the presence or absence of species, which would change less in the course of the season than

species cover. Thus, all Braun-Blanquet codes greater than 1 were transformed into 1, the code + into 0.5, and the code r into 0.2, and species absence into 0. Thirteen plant species that occurred in less than five relevés were excluded from the analysis to reduce noise. Explanatory variables were management (df = 3), years (nominal, df = 3) and their interaction (df = 9). The percentage of variation explained by each of them was quantified through a series of partial RDA's (Økland & Eilertsen 1994), and their relationship with plant species composition was represented in an ordination biplot. These analyses were done with the software package CANOCO (ter Braak 1987–1992).

The effect of management on vascular plant species richness (total, forbs, graminoids) was analysed with univariate repeated-measures Anova (between-subject factor management, within-subject factors year and management x year); no adjustment of residual df was required (Mauchly criterion, $P > 0.10$). Management effects on above-ground biomass, the ratio of graminoid to forb biomass, as well as N and P contents of the soil in 1997 (all log-transformed) were analysed with one-way Anova. If the Anova was significant, treatment means were compared pairwise with Tukey-Kramer tests, separately for each year in the case of species richness. The statistical package JMP version 3.2.2. was used for all univariate tests (SAS Institute, Cary, NC, USA). Vegetation structure was compared qualitatively among treatments by drawing structure diagrams based on the biomass data.

Results

The species composition of the vegetation changed considerably between 1986 and 1997. There was an overall successional trend

characterised by the decrease or total disappearance of several grass and forb species (*Festuca rubra, Agrostis tenuis, Holcus lanatus, Stellaria graminea*) and by the increase of a few forb species such as *Conopodium majus, Linum catharticum, Leontodon autumnalis* (cf. Appendix 1). In the ordination biplot (Fig. 2), this trend was apparent as a general shift of plots from negative to positive values along the x axis (first RDA axis).

Experimental treatments brought about considerable differences in species composition between mown and unmown plots during the first five years of the experiment, as seen by the shifts of plots along the y axis (second RDA axis) in Fig. 2. The unmown plots changed little between 1986 and 1991, except for the temporary appearance of *Dactylis glomerata*. In the mown plots, there was a temporary increase of legumes (*Trifo-*
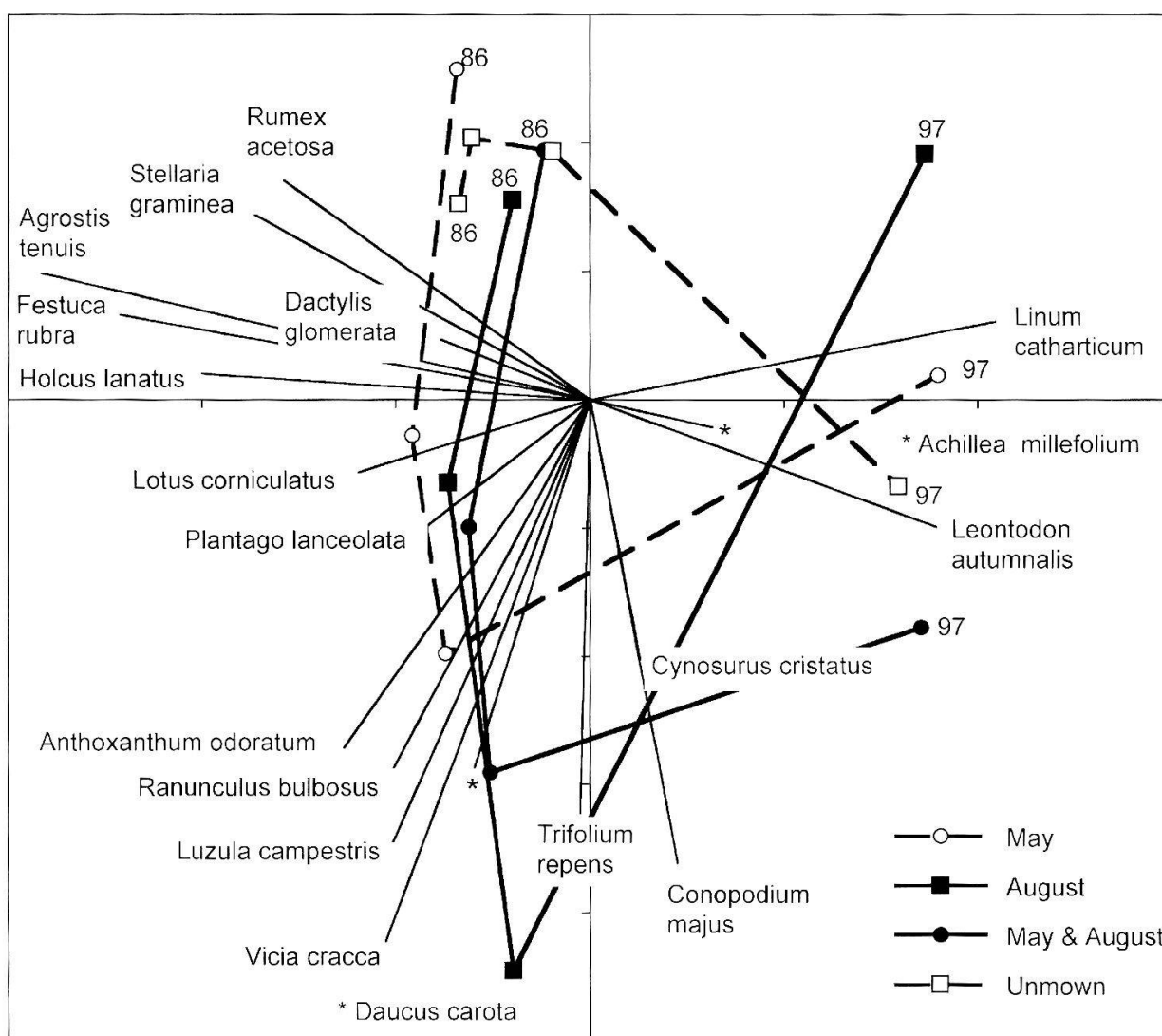
Fig. 2. Ordination biplot resulting from Redundancy Analysis of species data with management and years as explanatory variables. The first two ordination axes are shown, representing 19.6% and 9.8% of total variation in species data, respectively. Shifts in plant species composition between 1986 and 1997 under the four management regimes are visualised by shifts of the mean scores of the four relevés per management and year; symbols for 1986 and 1997 are labelled as '86' and '97'; those for 1989 and 1991 are intermediate. Species scores are shown by lines if at least 50% of a species' variance is explained by the ordination.

Table 1. Repeated measures Anova for the effects of management and years on species richness in 1-m^2 plots (all vascular plant species, forbs and graminoids). Data are F-ratios and significance levels (***, P $<$ 0.001; **, P $<$ 0.01; *, P $<$ 0.05;°, P $<$ 0.1; no symbol, P $>$ 0.10).

Effect	df	All	Forbs	Graminoids
Between subjects				
Management	3	3.1 °	2.3	1.3
Plot [Management][1]	12	2.8 **	3.9 ***	1.0
Within subjects				
Year	3	37.0 ***	22.8***	20.4***
Management x Year	9	7.2 ***	5.6***	2.4*
Residual	36			

[1] Between-subject residual

lium repens, Lotus corniculatus, Vicia cracca) and of *Anthoxanthum odoratum*. These species decreased between 1991 and 1997, causing mown and unmown plots to become similar again. Differences in species composition between the three mowing regimes were minor at all times (Fig. 2).

Of the total variance in species data, 55% were explained by the effects of years, management and their interaction. Differences among years accounted for the largest part of

the explained variance (28.5%). The temporary appearance of differences between mown and unmown plots was reflected in a weak overall management effect (8.6% of variance) and a stronger management x year interaction (17.9% of variance).

A total of 46 plant species were recorded in the experimental plots, of which 11 were grass species (Appendix 1). The species number differed significantly among years, and the effects of management regimes upon it also dif-
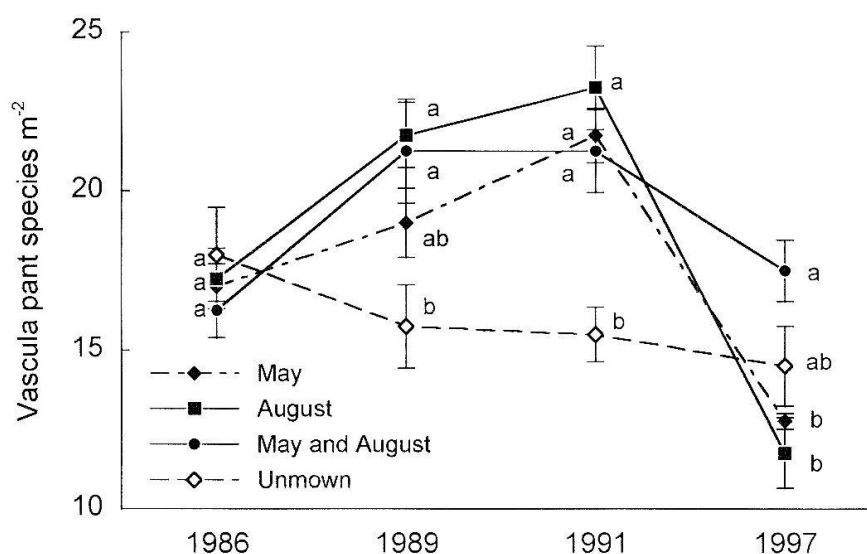

Fig. 3. Changes in plant species richness in relation to management regime (number of vascular plant species m^{-2}, means ± SE, n = 4). Within each year, pairwise differences between treatments were evaluated with the Tukey HSD test; treatments which do not share a common letter differ significantly (P $<$ 0.05).

Table 2. Above-ground biomass of the vegetation for each management in July 1997 as well as ratio of graminoid to forb biomass and the available N and P contents in the top 5 cm of soil (means ± SE, n = 4). For biomass, means that do not share the same letter differ significantly (Tukey-Kramer test, P < 0.05); the other variables did not differ significantly among management types.

Management	Biomass g m^{-2}	Gramin:Forb	N (mg m^{-2})	P (mg m^{-2})
May	506.0 ±122.5[b]	2.0 ±1.9	35.8 ±13.3	66.0 ±19.7
August	235.9 ± 36.2[a]	1.1 ±0.6	31.0 ±12.1	52.7 ±10.6
May & August	367.4 ± 78.5[ab]	0.8 ±0.1	36.8 ±10.6	64.8 ±26.4
Unmown	609.8 ± 52.0[b]	3.1 ±1.1	77.0 ±25.5	91.3 ±19.6

fered among years, as shown by significant management x year interactions (Table 1). In contrast, overall management effects were only marginally or not significant. Patterns were essentially the same for all species together or for graminoids and forbs separately. In 1986, plots all had a similar number of species (Fig. 3). Between 1986 and 1991, the species number increased in the mown plots but not in the unmown ones, so that species richness differed significantly between mown and unmown plots in 1989 and 1991 (Fig. 3). Between 1991 and 1997, however, the species number decreased again, especially in the treatments M and A. In 1997, the plots mown twice a year (MA) were more species-rich than those mown once a year (M or A), and control plots were intermediate. The overall

mean of the 16 plots initially increased from 17.1 species m^{-2} in 1986 to 20.4 species m^{-2} in 1991, and decreased thereafter to 14.1 species m^{-2} in 1997. Likewise, the total number of species found in the 16 plots (i.e. 16 m^2) in a particular year first increased from 32 to 37 and then decreased to 31 species.

Above-ground biomass in July 1997 was significantly greater in the unmown plots (U) or those mown only in May (M) than in plots mown in August (A). Plots mown in May and August (MA) had an intermediate biomass (Table 2). The biomass of graminoids was on average 2–3 times greater than that of forbs in the treatments M and U whereas the two groups had a similar biomass in the treatments A and MA; however, the graminoid:forb ratio did not differ significantly
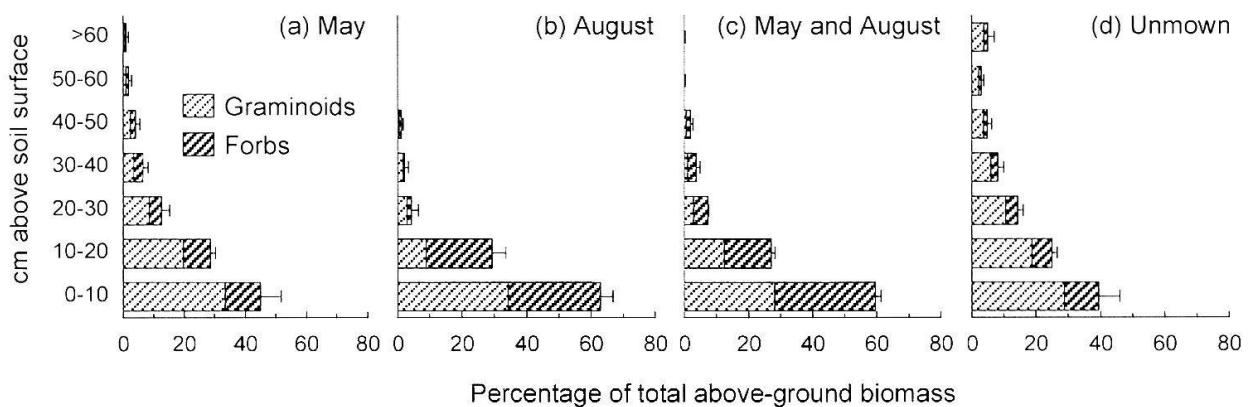

Fig. 4. Vertical distribution of plant biomass in July 1997, with the biomass of graminoids and forbs in each canopy layer expressed as percentage of total above-ground biomass (means, n = 4). Error bars represent SE for the percentage of biomass (both graminoids and forbs) in each layer.

among treatments. There was no correlation between biomass and species richness in 1997 across the 16 plots ($r = 0.17$, $P = 0.53$), nor between the graminoid:forb ratio and species richness ($r = -0.19$, $P = 0.48$).

Soil analyses showed that 2–3 times more N was available in the soil of unmown plots than in mown ones, yet the difference failed to be significant due to large variation among the unmown plots (Table 2). The three mowing regimes did not differ from each other. The available P content was high in all plots and did not differ among treatments (Table 2). Nutrient contents are given per soil area in Table 2; based on soil mass, available N content ranged from 7 to 17 mg kg^{-1} dry soil, and available P content from 12 to 20 mg kg^{-1}.

The canopy structure in July 1997 differed clearly among treatments (Fig. 4). Plots mown in August (treatments A or MA) had more than 60% of their biomass close to the soil surface (0–10 cm), and canopy height was generally less than 50 cm (Fig. 4b,c). In contrast, plots not mown in August (treatments M or U) only had 40–50% of their biomass close to the soil surface, and canopy height often exceeded 60 cm (Fig. 4a,d).

Discussion

VEGETATION DYNAMICS ONLY PARTLY EXPLAINED BY MOWING REGIME

The vegetation of the investigated grassland was dynamic, with pronounced changes in plant species composition during the twelve-year experiment. At the last survey in 1997, new species still appeared which had not been observed until 1991. Because species composition was surveyed only at four times during the experiment, the observed changes must be interpreted with some caution as they may partly represent fluctuations. A year-to-year replacement of 20–30% of the species is commonly observed in 1-m^2 plots within semi-natural vegetation (van der Maarel & Sykes 1993; Pärtel & Zobel 1995; Ryser et al. 1995; Güsewell et al. 1998).

Even if some of the observed changes in plant species composition may represent intrinsic fluctuations, the vegetation dynamics probably included successional trends caused by the experimental management. The grassland was grazed before the experiment, whereas cattle were excluded after 1986. This could have caused the replacement of typical grazing-tolerant species by more competitive species (Smith & Rushton 1994; Jutila 1999). However, the trends observed in our experiment contrasted with the differences between grazed and ungrazed plots found elsewhere. For example, in our experiment Festuca rubra decreased and Leontodon autumnalis increased after the cessation of grazing, whereas in a British grassland with similar species composition, F. rubra was more abundant in ungrazed and L. autumnalis in grazed plots (Smith & Rushton 1994); both F. rubra and L. autumnalis were most abundant in grazed plots in Finnish shoreline meadows (Jutila 1999). The effects of grazer exclusion obviously depend on the context of the site, e.g. climatic factors, seed sources, nutrient availability (Smith & Rushton 1994; Ritchie & Tilman 1995; Proulx & Mazumder 1998; Jutila 1999), and even 'meaningful' associations between plant traits and responses to grazing may be a coincidence (Smith & Rushton 1994). Successional trends after grazer exclusion are therefore difficult to explain end even more difficult to predict.

The different management regimes created differences in biomass, vegetation structure and phenology. Contrary to expectation, we found no relationship between the flowering time of individual species and their responses to mowing (data not shown). Probably in-situ

seedling recruitment was low in many species regardless of the treatments. Species that established from outside would depend more on conditions for germination (e.g. presence of gaps or open soil at the right time) than on conditions for seed set (Smith & Rushton 1994). And species with successful seed production could certainly disperse among plots with different management given the small plot size (cf. Güsewell *et al.* 1998).

Data from 1997 suggest that differences in the availability of N developed between mown and unmown plots. In the unmown plots, the absence of N exports would cause N availability to increase due to the mineralisation of N from the litter (Köhler *et al.* 2001). This may have promoted the nutrient-demanding, fast-growing grass *Dactylis glomerata*. In contrast, the continued removal of biomass from the mown plots maintained a low N availability, which was perhaps even strengthened by the exclusion of cattle. Cessation of grazing together with low N and high P availability may have favoured some legumes, which became more abundant in the mown plots between 1986 and 1991 (Ritchie & Tilman 1995). Why these species declined again between 1991 and 1997 is not clear here. Strong fluctuations in legume abundance were also reported by Ritchie & Tilman (1995), who explained them with climatic factors.

SPECIES RICHNESS IN RELATION TO BIOMASS AND SEED AVAILABILITY

Overall, the studied grassland showed a relatively high level of diversity, especially in 1991, with up to 29 species per m^2. Both the moderate (N-limited) biomass production and the base-rich soil certainly contributed to the species richness (Olde Venterink *et al.* 2001). Many studies found species richness in grasslands to be maximal at an intermediate biomass of 450–600 g m^{-2} (e.g. Grime 1979;

Vermeer & Berendse 1983; Oomes 1992; Smith & Rushton 1994; Zobel & Liira 1997). According to Willems & van Nieuwstadt (1996) the optimum might be lower in limestone grasslands: they found maximal species richness at 330 g m^{-2}. This suggests that in the unmown plots of our site, the rather high biomass (mean of 600 g m^{-2}) contributed to the decrease in species richness observed between 1986 and 1997. An additional factor was certainly the accumulation of litter. While virtually no litter was present in the mown plots, a dense litter layer of up to 118 g m^{-2} covered the unmown plots in July 1997. This would inhibit seed germination and seedling establishment, e.g. through shading and reduced temperature fluctuations (Foster & Gross 1997; Foster & Gross 1998; Spacková *et al.* 1998).

Species richness first increased and then decreased again in the mown plots, although vegetation biomass was low in 1997. This suggests that seed availability was too low to maintain the diversity. Mowing mainly enhances the species diversity by improving the conditions for new species to establish from seeds (Foster 2001). This requires that viable seeds are either present in the soil or able to immigrate (Hald & Vinther 2000; Smith *et al.* 2000). The movement of machines or animals between meadows can be an important source of seeds (Stender *et al.* 1997; Strykstra *et al.* 1997; Bakker *et al.* 2002). Before 1986, our experimental plots certainly received a regular seed input from the cattle which moved across the area. This seed input stopped when the plots were fenced in 1986. The decrease in species richness after 1991 may be at least partly due to the depletion of the initial seed bank combined with the lack of seed dispersal. Alternatively, conditions for seed germination may not have been improved sufficiently by manual mowing be-

cause the latter did not create patches of bare soil, unlike trampling by cattle (Spacková et al. 1998).

The vegetation structure can also influence species richness. For limestone grasslands in the Netherlands, Willems & van Nieuwstadt (1996) proposed that species richness is negatively related to the graminoid:forb ratio. Similarly, in a Swiss limestone grassland, mowing in autumn reduced the graminoid:forb ratio and increased the species richness compared to mowing in early summer (Ryser et al. 1995). The same was not found in our study, where the plots mown in August had a low biomass, canopy height and graminoid:forb ratio but still the lowest species richness of all treatments in 1997. This is another indication that in the mown plots, species richness was limited by seed availability or by the lack of bare soil rather than by competition (Smith et al. 2000; Zobel et al. 2000).

PRODUCTIVITY, NUTRIENT AVAILABILITY AND BIOMASS PRODUCTION

The differences in above-ground biomass and canopy height found among treatments in July 1997 did not indicate a clear effect of mowing on biomass production. In particular, the non-significant difference between the biomass and N availability of plots mown in August and of those mown in May and August shows that nutrient exports with hay had little impact upon the productivity of the vegetation (as in Bakker et al. 2002) – otherwise biomass should have been greater in the plots mown only in August (Güsewell 2003a). The lack of effect is not surprising as nutrient exports with mowing are generally small relative to nutrient capitals in clayey soils (Marrs 1993). The greater biomass in unmown plots than in mown ones might reflect a greater availability of nitrogen in soils of unmown plots (cf. Table 2), but it could also simply reflect the accumulation of biomass over more than one year in the absence of mowing. Repeated harvests would have been needed to confirm either possibility.

Compared to N availability, which seemed to be higher in unmown plots, P differed even less between mown and unmown plots, probably due to the very high P content of the clay soil. In a neighbouring grassland with similar substrate and management, high availability of P and K relative to N was shown by mean nutrient concentrations in plant biomass: 7.9 mg g^{-1} N, 1.5 mg g^{-1} P, and 12.5 mg g^{-1} K ($n =$ 7 species; B. Beltman, unpublished data). The corresponding N:P ratio (5.3) and N:K ratio (0.6) indicate clearly that biomass production was limited only by N (Koerselman & Meuleman 1996; Pegtel et al. 1996). This contrasts with limestone grasslands in the Netherlands and in Switzerland, where the supply of P is generally limiting or co-limiting (Bobbink 1991; Willems et al. 1993; Köhler et al. 2001). The high K concentrations in plant biomass correspond to the absence of K limitation found in the Swiss and Dutch grasslands (Bobbink 1991; Köhler et al. 2001). The combination of high P and K availability with a relatively high species richness in these Irish hayfields shows that species-rich grasslands are not restricted to sites with low P availability (less than 5 mg P kg^{-1}), as proposed by Janssens et al. (1998).

CONCLUSIONS FOR CONSERVATION MANAGEMENT

Considerable differences in species composition and species richness developed between mown and unmown plots from 1986 to 1991, suggesting that mowing (regardless of the time) was essential for the conservation of species-rich grassland vegetation. In 1997, however, differences among treatments were

much smaller, and only mowing twice per year had a positive effect on species richness. These contrasting results are difficult to interpret from a conservational point of view; they stress the importance of long-term studies with regular surveys to assess the effects of management on the vegetation (Bakker et al. 1996, 2002).

Biomass production and nitrogen availability in soil appeared enhanced in unmown plots compared to the mown ones, suggesting that in the long term, complete abandonment would lead to a loss of species by increasing the productivity of the vegetation. The final plant species composition differed only little among the mowing regimes, and species richness decreased in all treatments. We have tentatively explained this result by a poor seedling recruitment, possibly as a consequence of grazer exclusion, suggesting that the maintenance of some grazing in addition to mowing might be important for the conservation of species-rich grasslands in Ireland.

Acknowledgements

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Electronic Appendix

Appendix 1. Vegetation relevés carried out at the start of the experiment (1986), after three and five years of treatments (1989, 1991), and at the end of the experiment (1997). As the date of survey varied, it is given as 'year–month'. For each treatment and date, species cover in the four replicate plots is indicated by four Braun-Blanquet codes (5 = 76–100% cover, 4 = 51–75%, 3 = 26–50%, 2 = 6–25%, 1 = 1–5%, + = less than 1%, r = single individuals, . = absent). Species are ordered according to their dynamics during the experiment (cf. Fig. 2).

The Appendix can be downloaded as PDF file at
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