Ann. Bot. Fennici 39: 159–166 ISSN 0003-3847
Helsinki 24 June 2002

Management of semi-natural grassland vegetation: evaluation of a long-term experiment in southern Sweden

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Received 20 August 2001, accepted 20 December 2001

Wahlman, H. & Milberg, P. 2002: Management of semi-natural grassland vegetation: evaluation of a long-term experiment in southern Sweden. — *Ann. Bot. Fennici* 39: 159–166.

Vascular plants were recorded in a long-term (28-year) experiment on semi-natural grassland vegetation comparing six treatments: continued grazing, mowing every year, mowing every third year, annual spring burning, removal of woody plants, and untreated control. The treatments had created very different vegetation types: the annually mown and grazed plots had the highest species number while the untreated plots had the lowest. The species' ordination scores correlated with Ellenberg indicator values for nutrient status and light: species indicating poor nutrient conditions were mainly in grazed and mown plots, and shade-tolerant species were mainly in untreated and grazed plots. The original aim of this experiment was to evaluate alternative ways of maintaining semi-natural grassland vegetation, but there were no satisfactory long-term alternatives to annual mowing or grazing. An ordination contrasted annual mowing and grazing, ranking species from those associated with mowed plots (e.g. *Leucanthemum vulgare*, *Luzula pilosa*, *Campanula persicifolia*, *Ajuga pyramidalis*) to those associated with grazed plots (e.g. *Ranunculus* spp., *Geum* spp., *Vicia sepium*).

Key words: burning, grassland, grazing, management, mowing, partial RDA, Sweden

Introduction

Semi-natural grasslands in central and northern Europe are very rich in species (e.g. Hæggström 1983, Losvik 1988, Kull & Zobel 1991). However, due to changes in agricultural practices, such grasslands are rapidly diminishing in Scandinavia (Skånes 1990, Bengtsson-Lindsjö *et al*. 1991). Meadows and pastures have been planted with trees, converted to arable land or, if kept open, intensively fertilised, which have decreased their biological diversity and conservation value (Losvik 1988, Glimskär & Svensson 1990, Bengtsson-Lindsjö *et al*. 1991). Since the resources for preservation of semi-natural grasslands and their numerous endangered species (Gärdenfors 2000) are limited, it is important to manage them as efficiently as possible.

In the early 1970s, a group of experiments comparing different management methods of semi-natural grassland vegetation were carried out in southern Sweden (Steen 1976, Fogelfors 1982, Hansson 1991). One of these experiments is still running (2001) but has so far not been subjected to a thorough evaluation of treatment effects. The aim of the present study was to compare the different treatments. We used species characteristics (Ellenberg *N* and *L* values; Ellenberg *et al*. 1992) to evaluate the treatment effects. In addition, we wanted to contrast the treatments of grazing and mowing annually. The most likely conservation management decision will be between these two, but little is known as to what extent and in what way the two treatments differ (Tamm 1956, Hansson & Fogelfors 2000).

Materials and methods

Study area

The study site is a part of a nature reserve situated near Sättra (58°16´N, 14°49´E; 19 ha in size), 55 km WSW of Linköping in the county of Östergötland, in the boreo-nemoral region of southern Sweden. Mean annual precipitation is 550 mm and the mean annual temperature is 6.0 °C (Alexandersson *et al*. 1991). The growing period is 180–190 days (Sjörs 1999). The area has probably been annually mown for many centuries (Hansson 1991). In the 10–15 years before the initiation of the experiment in 1973, the area had been grazed by cattle. The reserve contains a mosaic of species-rich wooded meadows and pastures with scattered stands of *Quercus robur, Betula pendula* and *Corylus avellana*. The soil is a relatively nutrient-poor till.

Treatments

The long-term experiment, initiated in 1973, aimed at evaluating the effects of seven management methods: (i) continued grazing, (ii) mowing once a year, (iii) mowing every third year, (iv) burning once a year, (v) mechanical removal of woody plants, (vi) herbicide treatment of woody plants (not evaluated in the present study), and (vii) untreated control. The grazing treatment involved grazing by cattle, ranging free in a large enclosure (7 ha), from May to October. Grazing patterns varied among years, as did the stocking density. There was one animal per hectare in the late 1980s (Hansson 1991) and in 2000, a density lower than that recommended for this type of grassland (Alexandersson *et al*. 1986). Mowing was done with a scythe and a mower in late July or early August and the hay was removed. The plots mowed every third year were mown during the year of the present study (2000). A bush saw was used to mechanically remove woody plants in early spring, when considered appropriate by the manager (approximately once every 2–3 years). The burning was done before the growth season but after snowmelt (March or April). Burnt plots were also cleared of woody plants if needed. The treatment of the plots with “herbicide treatment of woody plants” changed in 1986, when the use of agrochemicals was abandoned in favour of mechanical removal. Therefore, this treatment was excluded from our study. Further information on the site, experimental design and treatments are given by Steen (1976), Fogelfors (1982) and Hansson (1991).

The treatment plots were 5 m × 20 m and randomly placed within a block design with two replicates. All plots except the grazed ones were within a fenced enclosure. The vegetation in the experiment was superficially documented in 1973 (Steen 1976). In 1980 and 1986, analyses took place using five 1-m^2 samples per treatment plot (Fogelfors 1982, Hansson 1991). A detailed evaluation of the vegetation in the grazed and untreated plots was done in 1991 in conjunction with a soil seed bank study (Milberg 1995). Until the present study, no detailed simultaneous evaluation of all treatments had been conducted.

Sampling

To reduce possible border effects (e.g. due to shading and vegetative spread from neighbouring plots), we ignored a 0.5-m wide verge of each treatment plot. The remaining area, i.e. 19 m × 4 m, was divided into 152 sample plots of 0.5 m × 1 m. Fieldwork was conducted from 20 August to 25 September 2000, i.e. after mowing. Plants were identified to species level wherever possible and presence/absence of a species was recorded for each sample plot. Using presence/absence instead of percentage cover is likely to reduce seasonal differences due to plant phenology as well as observer differences, which we considered important in case of a future follow up. We gave priority to this detailed method for comparing treatments, rather than one that would allow comparison with records made in 1973 or 1980 and 1986. Only some grasses could, with certainty, be identified to species-level (*Avenula pratensis*, *Dactylis glomerata, Deschampsia cespitosa*) while other grass taxa were merged (*Deschampsia flexuosa/ Festuca ovina*) or noted as "other grasses". The last category was not used in the ordination analyses (described below). Nomenclature follows Tutin *et al*. (1964–1980).

Data analysis

ANOVA was used to evaluate differences among treatments regarding the number of species per 0.5 m^2 and the total number of species. Due to the very low number of replications, LSD post hoc tests were conducted if the ANOVA revealed $P < 0.1$.

An initial partial Detrended Correspondence Analysis, treating blocks as covariables, established that gradients were relatively short, and we therefore evaluated the treatment effects with a partial Redundancy Analysis (pRDA; treating blocks as covariables). A separate pRDA was also calculated to evaluate the block effect. The analyses were performed with the CANOCO 4 program (ter Braak & Smilauer 1998) using default options except for square-root transformation of species and 1999 permutation in the Monte-Carlo test (permuting within blocks).

Treatment effects were also evaluated by examining the ordination scores of species and their indicator value according to Ellenberg *et al*. (1992). We used *N* values, indicating preference for nutrient status, and *L* values, indicating preference of light.

A separate pRDA (again with blocks as covariables) was conducted to contrast mowing with grazing, the two most common alternatives in conservation management. Due to the low number of plots involved, no meaningful permutation test could be conducted comparing the treatment plots (it would not be possible to reject an incorrect null hypothesis since too many of the permutations would turn out identical to the observed data). Therefore, since no strict test could be conducted, we used data from each sample plot instead of that from treatment plots.

Results

Species richness

In total 94 taxa were found in the plots. The ANOVAs revealed larger differences in species number among treatments at the smaller sampling scale (0.5 m^2) than at the larger scale (76 m^2): $F_{(5,5)} = 9.63$, ($P = 0.01329$) and $F_{(5,5)} = 4.15$ ($P = 0.0722$), respectively. The mown and grazed plots had the highest species number while the untreated plot had the lowest (Table 1).

Table 1. Number of species per treatment plot (76 m^2), average number of species per 0.5 m^2 in treatment plots. The paired values represent Block 1/Block 2. The outcome of post hoc comparisons of treatment means (within columns) is indicated by the letters: treatments followed by the same letter are not significantly different (LSD, $P < 0.05$).

Treatment	Spp/76 m^2	Spp/0.5 m^2
Grazing	61/59 a	19.3/14.5 ab
Mowing	53/58 ab	21.0/18.9 a
Mowing 3 y	39/57 ab	11.4/14.7 bc
Burning	40/48 ab	11.3/10.3 cd
Mechanical	44/48 ab	9.0/10.8 cd
Untreated	38/48 b	5.9/8.2 d

Vegetation composition

There were clear and significant differences in species composition among treatments (Table 2). The treatments that deviated most were mowing, grazing and untreated control (longest arrows in Fig. 1 as well as the greatest separation along axis 1). Furthermore, grazing and especially mowing were the treatments with the largest number of species that were indicative (note that only species with long arrows, i.e. a good fit to the treatment matrix, are shown in Fig. 1).

Distribution of species attributes

Ellenberg *N* numbers were highly correlated with axis 1 of the ordination while axis 2 correlated with Ellenberg *L* numbers (Table 3).

Contrasting grazing and mowing

The pRDA ranked species according to their association with either grazing or mowing (Appendix). The species most clearly associated with the mown plots were *Leucanthemum vulgare, Luzula pilosa, Deschampsia flexuosa/Festuca ovina, Plantago lanceolata/media, Carex montana* and *Campanula persicifolia*. At the "grazing end" of the gradient, we found *Ranunculus* spp., *Geum rivale/urbanum, Aegopodium podagraria* and *Vicia sepium.* There were more species clearly associated with mowing than were associated with grazing (17 vs. 7 spp. with a score beyond the mean ± SD), suggesting that mowing would maintain more species than grazing, which in turn would have fewer indicative species.

Table 2. ANOVA of treatment effects according to two pRDAs. *P*-values were established in Monte Carlo permutation tests with 1999 permutations.

Independent variables (*n*)	Covariables	Explained variance (%)	*P*-value
Treatments (6)	Blocks	68.5	0.0025
Blocks (2)	–	8.5	0.4455

Discussion

Treatment effects

The grazing and mowing treatments both had high species richness while it had decreased in the other treatments and particularly in the untreated plots (Table 1). This was expected and conforms to reports from other experiments and observations in grasslands (cf. Bakker 1989, Borgegård & Persson 1990, Huhta 1996, Hansson & Fogelfors 2000 and references therein).

The vegetation in mown plots, and to some extent in the grazed ones, contained many species with low Ellenberg *N* values (Fig. 1 and Table 3). This seems logical since biomass is removed each year from mown plots, thus impoverishing the soil (Sjörs 1954). The amount of removal of mineral nutrients from grazed plots, however, is probably smaller. The high correlation between *N* values and "mowing" (partly "grazing") indicates that, when management is relaxed, soil nutrient status improves, leading to a shift in species composition. Another interpretation is that the distribution of Ellenberg *N* values in the ordination does not reveal an actual change in soil nutrient status, but an indirect shift in dominance due to a change in competition among species. It is important to note that Ellenberg values indicate the "realised niche" and not the "fundamental niche" (Thompson *et al*. 1993, Roy *et al*. 2000).

"Grazing" and "untreated control" both pointed upwards along the second axis (Fig. 1), an axis that correlated with Ellenberg *L* values (Table 3). The ground vegetation in the untreated plots was in the deep shade from a tree canopy, so we would expect mainly shade-tolerant species there. It is possible, however, that the grazed plots also contributed to the correlation between *L* number and species ordination scores. The

Table 3. Spearman rank correlation coefficients for two ordination axes and Ellenberg *N* and *L* values. *P*-values within parentheses.

Covariables	*N* (*n* = 60)	*L* (*n* = 65)
Axis 1	–0.465 (< 0.0005)	0.148 (> 0.2)
Axis 2	0.085 (> 0.5)	–0.259 (< 0.05)

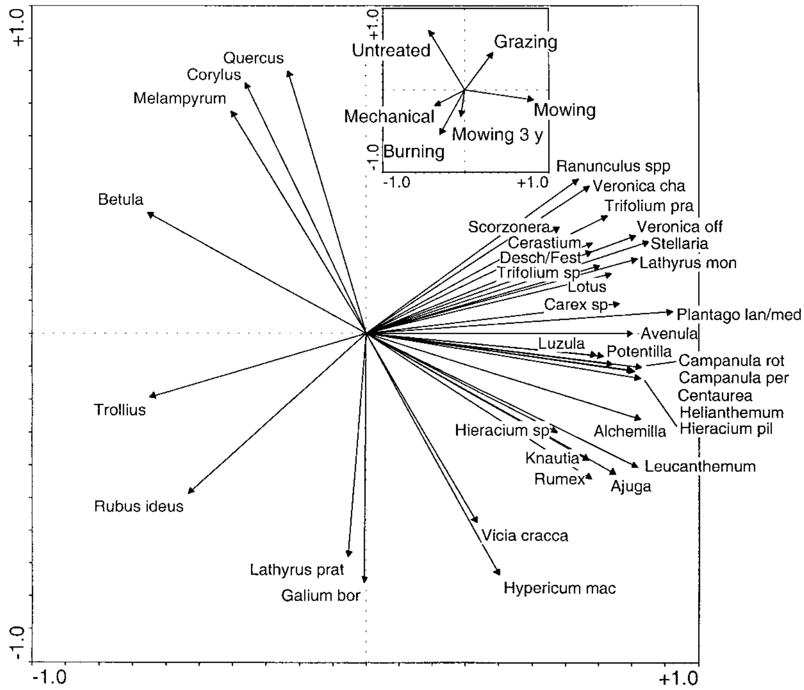

Fig. 1. pRDA of vegetation data from an experiment with six treatments after 28 years. Eigenvalues of axis 1 and 2 were 0.342 and 0.143, respectively. Only the 38 species that best "explained" the treatments are indicated (they have a cumulative fit > 0.40). Full species names are given in Appendix.

reason could be that a few trees and shrubs had been allowed to grow to a large size in one of the grazed plots, thereby out-shading light-demanding species (cf. Einarsson & Milberg 1999). Although cattle to some extent suppress phanerophytes (Hæggström 1990), once shrubs and trees grow to a certain size, grazing no longer controls them. Under traditional management, such individuals would have been removed (Borgegård & Persson 1990, Glimskär & Svensson 1990, Linusson *et al.* 1998).

Mowing every third year created an intermediate community composition (short arrow located near zero on axis 1 in Fig. 1) and intermediate species richness (Table 1). Of the three less-intensive treatments compared, this one had retained most species including 11 considered to indicate traditional management (Naturvårdsverket 1987; there were 17 such species recorded in the experiment). In fact, two of them were quite abundant (*Campanula rotundifolia*, *Lathyrus montanus*). Still, due to the many species losses we do not consider mowing every third year as a long-term management alternative to preserve a flora with conservation value. However, since the loss of species and change in vegetation composition was relatively slow, it is preferred to no management at all. Hence, it might be used to overcome shorter periods of relaxed management (cf. Hansson 1991, Hansson & Fogelfors 2000), e.g. if grazing is difficult to arrange.

Burnt plots were poor in species (Table 1) and were dominated by a few species: *Trifolium medium*, *Hypericum maculatum*, *Dactylis glomerata*, *Aegopodium podagraria* and *Galium boreale* (only the latter species was indicative of this treatment; Fig. 1). What direct effects could be expected from an early spring fire? Individuals of species that support aboveground foliage all-year-round or woody structures would be killed, but the mortality levels of other species would probably be small at this time of the year. Another direct effect is that removal of litter through burning will affect light and temperature conditions near the soil surface, possibly affecting the growth conditions in the early spring. An indirect effect of burning is on soil nutrient status, especially a depletion of N (Blair *et al.* 1998). The Ellenberg N values of the five dominants listed above varied between 2 and 8, suggesting no clear trend in this attribute of vegetation composition. The community structure created by burning, with a few dominating species, is very unlike that under traditional management. Burning is, therefore, not an alternative to grazing or mowing.

The treatment plots with mechanical removal of woody plants had lower species richness (Table 1), and a drastically different species composition (Fig. 1), with many nutrient-demanding species (Table 3). Mechanical removal of woody plants is a much-needed complement to the grazing and mowing of traditional management (Einarsson & Milberg 1999). It is, however, not a viable management option by itself.

The untreated plots were very different from the other plots (Fig. 1), having a closed canopy of trees (20 m tall), and being the least species-rich treatment (Table 1). The transition from species-rich semi-natural grassland to trivial deciduous forest vegetation has occurred in less than 30 years. The transition was discernible already in 1986 (Hansson 1991) and apparent in 1991 (Milberg 1995). Hence, untreated grasslands will quickly lose populations of traditional semi-natural grassland species (Persson 1984, Huhta 1996, Huhta & Rautio 1998, Hansson & Fogelfors 2000). How fast an untreated area is taken over by phanerophytes, however, is largely dependent on the starting composition of species and land history (Glimskär & Svensson 1990).

Comparing mowing and grazing

Despite being the two main management options for semi-natural grasslands in northern Europe, few field studies have been conducted comparing annual mowing and grazing. Theory would predict grazing to be more selective than mowing: mowing cuts all plants at a specific height above ground while animals can be selective in avoiding species if, for example, they are prickly or unpalatable (Leps *et al*. 1995). In the present data set, there were few species of the type that one should expect to be rejected or non-preferred by animals. Still, there was a clear separation between the mowed and grazed treatment plots, mowed plots having e.g. *Leucanthemum vulgare, Luzula pilosa, Plantago lanceolata/media, Carex montana, Campanula persicifolia, Ajuga pyramidalis, Lathyrus montanus, Avenula pratensis, Rumex acetosa, Campanula rotundifolia* and *Primula veris*. In contrast, at the other end (in Appendix) were some species associated with grazed plots, e.g. *Deschampsia cespitosa, Trifolium medium, Fragaria vesca, Ranunculus* spp., *Geum* spp. and *Vicia sepium*. *Ranuculus* is a genus avoided by grazers because of its bad taste, while *Deschampsia cespitosa* is not preferred because of its high silica content (Grime *et al*. 1988), and both have previously been recorded as typical for grazed areas (Tamm 1956).

Another difference between mowing and grazing treatments is that animals create dung/urine patches as well as small areas with bare ground by trampling, facilitating regeneration from seeds (Coffin & Lauenroth 1988, Detling 1998). One would expect short-lived, nitrophilous species to be the ones benefiting from this small-scale spatial variation created by large animals. In the present data, however, there were no ephemeral annuals, although several species are present in low abundance in the seed bank in the area (Milberg 1995). Finally, when comparing grazing and mowing, we should keep in mind that in traditional management, grazing often commenced after mowing, but that this was not the case in the present experiment. Hence, in an area under traditional management (i.e. mowing followed by grazing), the differences compared with pure grazing should be less pronounced.

There were more species occurring preferentially in mown plots than in grazed ones, suggesting that mowing would preserve more species, confirming a similar notion by Tamm (1956). In both that and the present study, the swards had been mown for centuries while grazing throughout the season was a new phenomenon. This could possibly be reflected in the larger number of species with “mowing preference”.

Acknowledgements

We thank the foresighted Eliel Steen for establishing this long-term experiment and Håkan Fogelfors and Margareta Hansson (SLU) for securing its continued survival. We also acknowledge the manual labour of numerous people over the years conducting the treatments. Dan Nilsson at the County Administration Board gave us permission to work at Sättra. We thank Karl-Olof Bergman, Ylva Langemar and a referee for comments on the manuscript and Joakim Lydig, Jenny Eriksson, Ludwig Odbrant and Cecilia Berg for logistic support.

References

Alexandersson, H., Ekstam, U. & Forshed, N. 1986: *Stränder vid fågelsjöar. Om fuktängar, mader och vassar i odlingslandskapet.* — LTs Förslag, Stockholm. 112 pp.

Alexandersson, H., Karlström, C. & Larsson-McLann, S. 1991: *Temperaturen och nederbörden i Sverige 1961-1990. Referensnormaler.* — Sveriges Meteorologiska och Hydrologiska Institut, SMHI Meterologi No. 81. 87 pp.

Bakker, J. P. 1989: *Nature management by grazing and cutting. On the ecological significance of grazing and cutting regimes applied to restore former species-rich grassland communities in the Netherlands.* — Kluwer Acad. Publ., Dordrecht. 400 pp.

Bengtsson-Lindsjö, S., Ihse, M. & Olsson, E. G. A. 1991: Landscape patterns and grassland species diversity in the 20th century. — *Ecol. Bull.* 41: 388–396.

Blair, J. M., Seastedt, T. R., Rice, C. W. & Ramundo, R. A. 1998: Terrestrial nutrient cycling in tallgrass prairie. — In: Knapp, A. K., Briggs, J. M., Hartnett, D. C. & Collins, S. L. (eds.), *Grassland dynamics. Long-term ecological research in tallgrass prairie*: 222–243. Oxford Univ. Press, New York.

Borgegård, S.-O. & Persson, S. 1990: Vegetational gradients and the effects of management in the wooded meadow of Allekvia, Gotland, Sweden. — *Svensk Bot. Tidskr.* 84: 87–103. [In Swedish with English summary].

Coffin, D. P. & Lauenroth, W. K. 1988: The effects of disturbance size and frequency on a shortgrass plant community. — *Ecology* 69: 1609–1617.

Detling, J. K. 1998: Mammalian herbivores: ecosystem-level effects in two grassland national parks. — *Wildlife Soc. Bull.* 26: 438–448.

Einarsson, A. & Milberg, P. 1999: Species richness and distribution in relation to light in wooded meadows and pastures in southern Sweden. — *Ann. Bot. Fennici* 36: 99–107.

Ellenberg, H., Weber, H. E., Dull, R., Volkmar, W., Werner, W. & Paulißen, D. 1992: Zeigewerte von Pflanzen in Mitteleuropa. — *Scripta Geobot.* 18: 1–258.

Fogelfors, H. 1982: *Det marginella odlingslandskapets öppethållande. Del II. Resultat och utvärdering av långvariga försök med olika skötselmetoder.* — Swedish Univ. Agric. Sci., Dept. Ecol. & Env. Res., Report 11. 83 pp.

Glimskär, A. & Svensson, R. 1990: *Vegetation changes following fertilization and changed management. Thirty-five-year-old field-experiments in natural pasture.* — Swedish Univ. Agric. Sci., Dept. Ecol. & Env. Res., Report 38. 71 pp. [In Swedish with English summary].

Grime, J. P., Hodgson, J. G. & Hunt, R. 1988: *Comparative plant ecology: a functional approach to common British species.* — Unwin Hyman Ltd., London. 739 pp.

Gärdenfors, U. (ed.) 2000: *The 2000 redlist of Swedish species.* — Artdatabanken, Uppsala. 397 pp. [In Swedish with English summary].

Hæggström, C.-A. 1983: Vegetation and soil of the wooded meadows in Nåtö, Åland. — *Acta Bot. Fennica* 120: 1–66.

Hæggström, C.-A. 1990: The influence of sheep and cattle grazing on wooded meadows in Åland, SW Finland. — *Acta Bot. Fennica* 141: 1–28.

Hansson, M. 1991: *Management of seminatural grassland. Results of fifteen-year-old field-experiments in south and central Sweden.* — Swedish Univ. Agric. Sci., Dept. Ecol. & Env. Res., Report 45. 124 pp. [In Swedish with English summary].

Hansson, M. & Fogelfors, H. 2000: Management of seminatural grassland; results from a 15-year-old experiment in southern Sweden. — *J. Veg. Sci.* 11: 31–38.

Huhta, A.-P. 1996: Vegetation changes in semi-natural meadows after abandonment in coastal northern Finland. — *Nordic J. Bot.* 16: 457–472.

Huhta, A.-P. & Rautio, P. 1998: Evaluating the impacts of mowing: a case study comparing managed and abandoned meadow patches. — *Ann. Bot. Fennici* 35: 85–99.

Kull, K. & Zobel, M. 1991: High species richness in an Estonian wooded meadow. — *J. Veg. Sci.* 2: 711–714.

Leps, J., Michalek, J., Kulisek, P. & Uhlik, P. 1995: Use of paired plots and multivariate analysis for the determination of goat grazing preference. — *J. Veg. Sci.* 6: 37–42.

Linusson, A.-C., Berlin, G. A. I. & Olsson, E. G. A. 1998: Reduced community diversity in semi-natural meadows in southern Sweden, 1965–1990. — *Pl. Ecol.* 136: 77–94.

Losvik, M. H. 1988: Phytosociology and ecology of old hay meadows in Hordaland, western Norway in relation to management. — *Vegetatio* 78: 157–187.

Milberg, P. 1995: Soil seed bank after 18 years of succession from grassland to forest. — *Oikos* 72: 3–13.

Naturvårdsverket 1987: *Inventering av Ängs- och Hagmarker.* — Swedish Env. Prot. Agency, Stockholm. 225 pp.

Persson, S. 1984: Vegetation development after exclusion of grazing cattle in a meadow area in the south of Sweden. — *Vegetatio* 55: 65–92.

Roy, D. B., Hill, M. O., Rothery, P. & Bunce, R. G. H. 2000: Ecological indicator values of British species: an application of Gaussian logistic regression. — *Ann. Bot. Fennici* 37: 219–226.

Sjörs, H. 1954: Meadows in Grangärde Finnmark, SW Dalarna, Sweden. — *Acta Phytogeogr. Suecica* 34: 1–135. [In Swedish with English summary].

Sjörs, H. 1999: The background: geology, climate and zonation. — *Acta Phytogeogr. Suecica* 84: 5–14.

Skånes, H. 1990: Changes in the rural landscape and the impact on flora: A retrospective case study using aerial photographs. — *Geogr. Ann.* 72: 129–134.

Steen, E. 1976: *Det marginella odlingslandskapets öppethållande. Dokumentation i långvariga försök med olika skötselmetoder.* — Lantbrukshögskolan, Avdelningen för ekologisk miljövård, Uppsala. 105 pp.

Tamm, C. O. 1956: Composition of vegetation in grazed and mown sections of a former hay-meadow. — *Oikos* 7: 144–157.

ter Braak, C. J. F. & Smilauer, P. 1998: *CANOCO reference manual and user's guide to CANOCO for Windows: Software for Canonical Community Ordination (Version 4).* — Microcomputer Power, Ithaca. 352 pp.

Thompson, K., Hodgson, J. G., Grime, J. P., Rorison, I. H., Band, S. R. & Spencer, R. E. 1993: Ellenberg numbers revisited. — *Phytocoenologia* 23: 277–289.

Tutin, T. G., Heywood, V. H., Burges, N. A., Valentine, D. H., Walters, S. M. & Webb, D. A. (eds) 1964–1980: *Flora Europaea, Volumes 1–5.* — Cambridge Univ. Press, London.

Appendix. Species ordination scores in a pRDA contrasting annually mown and grazed plots (treating blocks as covariables). Species are ranked from those occurring predominantly in mowed plots (–) to those occurring in grazed plots (+). There were 152 observation plots in each of two replicates per treatment.

	pRDA score	Freq. (%)
Leucanthemum vulgare	–0.776	44
Luzula pilosa	–0.706	54
Deschampsia flexuosa/ Festuca ovina	–0.682	62
Plantago lanceolata/media	–0.565	62
Carex montana	–0.445	54
Campanula persicifolia	–0.430	73
Ajuga pyramidalis	–0.419	20
Lathyrus montanus	–0.416	71
Hieracium sp.	–0.408	22
Avenula pratensis	–0.373	54
Rumex acetosa	–0.331	74
Campanula rotundifolia	–0.331	23
Primula veris	–0.302	12
Anthriscus sylvestris	–0.279	13
Knautia arvensis	–0.277	31
Alchemilla spp.	–0.274	70
Vicia cracca	–0.249	28
Hieracium pilosella	–0.227	6.1
Achillea millefolium	–0.193	38
Potentilla erecta	–0.189	56
Helianthemum nummularium	–0.164	2.6
Hypericum maculatum	–0.087	59
Carex sp.	–0.083	7.1
Galium album	–0.081	0.7
Centaurea jacea	–0.070	0.5
Geranium robertianum	–0.070	0.5
Pimpinella saxifraga	–0.070	0.5
Vaccinium vitis-idaea	–0.070	0.5
Galium boreale	–0.068	37.2
Glechoma hederacea	–0.062	1.8
Veronica officinalis	–0.060	18
Dactylis glomerata	–0.051	63
Scorzonera humilis	–0.048	64
Salix sp.	–0.041	0.2
Sorbus aucuparia	–0.041	0.2
Leontodon hispidus	–0.018	0.8
Cerastium fontanum	–0.012	7.9
Hypochoeris maculata	0.000	1.0
Rubus saxatilis	0.013	7.2
Lotus corniculatus	0.015	1.5
Juniperus communis	0.041	0.2
Maianthemum bifolium	0.041	0.2
Rosa canina	0.041	0.3
Viola canina/riviniana	0.050	44
Trifolium sp.	0.056	9.5
Melampyrum pratense/ sylvaticum	0.057	0.3
Populus tremula	0.058	4.1
Platanthera sp.	0.062	1.8
Stellaria sp.	0.066	27
Plantago major	0.070	0.5
Succisa pratensis	0.070	0.5
Cirsium sp.	0.081	0.7
Galium verum	0.081	0.7
Quercus robur	0.089	6.1
Prunella vulgaris	0.104	1.6
Carex pallescens	0.104	3.1
Pyrola rotundifolia	0.112	3.8
Ranunculus repens	0.129	1.6
Veronica chamaedrys	0.142	92
Lathyrus pratensis	0.148	17
Hepatica nobilis	0.159	2.5
Trollius europaeus	0.159	2.5
Filipendula ulmaria	0.192	5.3
Taraxacum officinale	0.196	29
Geranium lucidum	0.207	4.1
Carex flacca	0.221	5.2
Trifolium pratense	0.227	16
Trifolium repens	0.232	5.1
Deschampsia cespitosa	0.243	20
Trifolium medium	0.283	50
Corylus avellana	0.304	9.0
Fragaria vesca	0.305	13
Geranium sylvaticum	0.345	63
Ranunculus acris/auricomus/ polyanthemos	0.368	51
Geum rivale/urbanum	0.479	20
Aegopodium podagraria	0.604	54
Vicia sepium	0.638	39