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Effects of restoration with cattle grazing on plant species composition and richness of semi-natural grasslands

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Abstract. Restoration of semi-natural grasslands by cattle grazing is among the most practical options for reversing the decline of northern European floristic diversity, but no studies on this subject are available. In this work the success of restoration of abandoned, privately owned mesic semi-natural grasslands by farmers receiving support from the EU agri-environmental support scheme was studied in southwestern Finland. Three kinds of grasslands were compared: old (continuously cattle grazed), new (cattle grazing restarted 3–8 years ago) and abandoned pastures (grazing terminated >10 years ago). Plant species composition of the three pasture types was floristically different in multivariate analyses (non-metric multidimensional scaling). Total species richness, richness of grassland plants, indicator plants and rare plants were highest in old and lowest in abandoned pastures in all studied spatial scales (0.25–0.8 ha, 1 and 0.01 m^2). The results were congruent with different scales and species list definitions, suggesting that species density scale (1 m^2) can be used as a partial surrogate for large scale species richness. Species richness of new pastures was 20% higher on 0.25–0.8 ha, 40–50% higher on 1 m^2 and 30% higher on the 0.01 m^2 scale compared to abandoned grasslands. Rare species showed insignificant response to resumed grazing. Despite problems in management quality, this study showed promising results of restoration of abandoned grasslands by cattle grazing on private farms. However, populations of several rare grassland plants may not recover with present cattle grazing regimes. Management regulations in the agri-environmental support scheme need to be defined more precisely for successful restoration.

Introduction

Decrease in the amount of semi-natural grasslands and their flora and fauna is among the key problems for European biodiversity (Hillier et al. 1990; Beaufoy et al. 1994; Bignal and McCracken 1996; Pykälä 2000). The need for restoration of grasslands has thus been stressed frequently (Bakker 1989; Bakker and Berendse 1999; European Environment Agency 1999), and restoration of grasslands with grazing and mowing is an important part of nature management policy in many European countries (Mortimer et al. 1998; WallisDeVries et al. 1998).

Studies have shown the constraints of restoration of species-rich grasslands from former arable land and heavily fertilized grasslands (Bakker 1989; Gibson and Brown 1991; Berendse et al. 1992; Mortimer et al. 1998; Poschlod et al. 1998; Bakker and Berendse 1999; Smith et al. 2000). Common and some rare grassland species may disperse to them in a relatively short time, but none of the studies have reported successful restoration of vegetation, i.e. a species composition similar to that of semi-natural species-rich grasslands. One of the main problems is the high nutrient levels in cultivated soils. In particular, high levels of phosphorus are difficult to suppress to the level of semi-natural grasslands (Marss 1993; Janssens et al. 1998).

More successful results can be obtained by restoring abandoned semi-natural grasslands (Bobbink and Willems 1993; Willems and Bik 1998; Barbaro et al. 2001; Mitlacher et al. 2002). In these grasslands, nutrient levels and soil structure may be comparable to continuously managed semi-natural grasslands and many grassland plants occur as remnant populations or in the soil seed bank (Bakker 1989; Bekker et al. 1997). Several plants considered to be extinct from the locality may reappear under appropriate management regimes (Gibson 1986). However, studies on restoration of arable land and heavily fertilized grasslands have been much more common than on restoration of abandoned semi-natural grasslands.

Restoration studies have monitored the changes in vegetation or species richness, but areas under restoration have very seldom been compared to continuously grazed species-rich grasslands, i.e. to the type of vegetation which is the goal of restoration measures (but see Gibson and Brown 1992). Usually restoration studies include only species density scale (0.01–4 m^2). It is commonly assumed that increase in species density indicates increase in species richness on wider spatial scales, although contradictory results have also been reported (Chaneton and Facelli 1991; Olff and Ritchie 1998).

Most European studies on restoration of plant species composition or richness of semi-natural grasslands have focused on wet grasslands and fen-meadows (Bakker 1989; Hald and Vinther 2000; Klötzli and Gootjans 2001), wooded meadows (Austad and Skogen 1990; Austad and Losvik 1998; Kotiluoto 1998; Mitlacher et al. 2002), or seashores (Vestergaard 1985, 1994). The most diverse and species-rich types of grasslands – dry and mesic grasslands – have been the subject of only a few studies (Bobbink and Willems 1993; Willems and Bik 1998; Stampfli and Zeiter 1999; Willems 2001), and in northern Europe only two single site studies are available (Losvik 1992; Huhta et al. 2001).

Among North European nature conservation managers, cattle grazing is considered more suitable for plant diversity than sheep or horse grazing (e.g. Johansson and Hedin 1991). This is mainly due to the fact that cattle grazes less selectively than sheep and horses (Pykälä 2000). In European grassland restoration studies the grazing animal has mainly been sheep, or areas have been mowed. Surprisingly, no European study has focused on restoration of dry or mesic grasslands using cattle. Restoration and management of privately owned grasslands is a key issue for maintaining biodiversity, as it is not feasible to maintain biodiversity of agricultural areas with state-owned nature conservation areas only. Management of semi-natural grasslands and other areas formed by traditional animal husbandry is one measure in the agri-environmental programme of Finland as well as in several other European countries (e.g. Ovenden et al. 1998). In Finland the agri-environmental programme is the main means to accomplish management of grassland types of the EU Habitats

Directive included in the Natura 2000 network (Salminen and Kekäläinen 2000). Studies on the success of restoration of grasslands with the help of agri-environmental subsidies are urgently needed. Monitoring results of vegetation change due to the restarted grazing will be available only after several years. This difficult time-delay in obtaining results can only be circumvented by studying areas where grazing has started earlier, if available.

In the present study the vegetation of areas with resumed grazing was compared with that of old pastures and overgrowing, abandoned grasslands. The possible differences in restoration success on different spatial scales were studied by comparing plant composition and species richness on three spatial scales. Furthermore, occurrences of indicator and rare species were used as a surrogate for the success of restoration on the landscape scale.

On the basis of the studies cited above the following hypotheses were formulated. First, species richness is highest in old pastures on all scales used in the study. Second, if restoration of abandoned grasslands with cattle grazing proceeds well, positive results (change in vegetation towards old pastures and increase in species richness) can be seen already a few years after resumed grazing. Thirdly, species richness patterns and recovery of species richness will be manifested differently on different spatial scales. Finally, different species groups show different levels of recovery.

Material and methods

Sites

Mesic semi-natural grasslands in which grazing by cattle had been restarted ≥ 3 years ago after more than 10 years of abandonment were intensively searched in southern Finland from the biogeographical provinces Regio aboënsis, Nylandia and Tavastia australis during 1999–2000 (for Finnish biogeographical provinces, see Hämet-Ahti et al. 1998). Grasslands found in the national inventory of semi-natural grasslands and those for which subsidies have been granted for management were checked in the field. Ten suitable areas with similar ecological conditions were found. Thereafter old and abandoned pastures similar to these were located close to new pastures.

The study sites were situated on the border of the hemiboreal and southern boreal vegetation zones in inland southwestern Finland, 20–50 km from the coast. Three kinds of mesic semi-natural grasslands were studied: (1) continuously seasonally cattle grazed ($n = 10$), (2) seasonal cattle grazing restarted 3–8 years (mean: 5 years) ago after >10 years of abandonment ($n = 10$), and (3) overgrowing, >10 years ago abandoned ($n = 11$). In 1999 in the river Rekijoki valley (the largest area of mesic grasslands in Finland; Kontula et al. 2000), 18 sites (six triplets of all the three types of study areas) were studied. In 2000, 13 additional sites (four old, four new and five abandoned pastures) were studied.

In 1999 the area of the studied grassland sites varied from 0.25 to 0.8 ha (mean:

0.4 ha in each of the three groups; $n = 6 \times 3 = 18$). In 2000 a uniformly sized area (0.25 ha) was studied from each site ($n = 13$).

Differences in abiotic conditions between the sites were minimized. All study sites were situated by rivers and brooks with the same soil type (clay soil) and on rather steep slopes with high incident radiation (facing S, W, or E, mainly SW or SE). The maximum distance between the sites was ca. 100 km. The flora in the river valleys of inland southwestern Finland is rather homogenous, with only minor differences between species pools.

Most sites were grazed by dairy heifers (mainly Ayshire). Four new pastures were grazed by beef cattle (heifers or cows and calves). In all farms semi-natural grasslands were used as additional pastures complementing cultivated pastures. Therefore grazing pressure in the grasslands was not constant between different years, although according to the farmers, grazing management was in most areas rather similar between different years. During the study year grazing was started in most old pastures (70%) in late spring or early summer. In three sites grazing started in July and in one in August. In four new pastures grazing was started in late spring or early summer, in two in July, in two in August and two were not grazed at all during 2000. Animals were usually moved to other pastures when food in the semi-natural grasslands was becoming depleted.

All but two study sites were privately owned. None were protected for nature conservation, but 2/3 of them were included in the Natura 2000 network. The grasslands were mainly Fennoscandian lowland species-rich dry to mesic grasslands as defined in the EU Habitats Directive. All of the resumed pastures as well as most old pastures were included in the EU agri-environmental support scheme of management of traditional rural biotopes.

Measurements

Presence–absence data of vascular plants were collected from each of the study areas during July and August. A total of 15 sample plots of 1 m^2 were randomly selected within each study site, and cover percentages of vascular plants were visually estimated. Total cover of field and ground layers, litter and the proportion of vegetation grazed <10 cm high were estimated and the mean height of vegetation was measured. In some study areas patches of moist grassland vegetation (0–15% of the study area) occurred. The proportion of moist grassland was estimated visually. Presence–absence of plants of sample plots of 0.01 m^2 inside 1 m^2 sample plots (one in each) was noted. At the end of September, data on grazing intensity were collected from 15 randomly selected sample plots per 0.25 ha: mean height of vegetation, proportion of vegetation grazed <10 cm high, cover of field layer and cover of ground layer.

Land use history and the present land use (e.g. grazing regime, number of years grazed during the last 50 years, fertilization, use of supplementary forages) were recorded by interviewing landowners. The time of starting of grazing during the study year was classified: 5 = before 15.6, 4 = 15.6–30.6, 3 = 1.7–14.7, 2 = 15–31.7, 1 = after 31.7 or not grazed.

The community species pools of species of dry and mesic grasslands of southern Finland (in the study sites $n = 105$) and indicator species ($n = 37$) of biologically valuable grasslands were delimited as in Pykälä (2001). Indicator species are grassland plants which occur infrequently in habitats other than semi-natural grasslands. This list was compiled from Nordic botanical literature and from the results of a national inventory of semi-natural grasslands. These species benefit from grazing and/or mowing.

Rare species ($n = 17$) designations and taxonomic nomenclature followed the Field Flora of Finland (Hämet-Ahti et al. 1998). Rare natives and archaeophytes in either of the biogeographical provinces Ab and Ta were included. All of them prefer grasslands in southwestern Finland. Archaeophytes were included because the origin of most of them is obscure, in other words they may also be natives (Pykälä 1998). Moreover, many of them are considered as good indicators of grasslands with conservation value.

Because of identification problems *Alchemilla* and *Galeopsis* species (in the study sites *G. bifida* and *G. speciosa*) were pooled, but in the field the easily recognizable *A. glaucescens* and *A. samuelssonii* were kept separated. *Poa pratensis* coll. includes *P. angustifolia*, *P. pratensis*, *P. alpigena* and *P. subcaerulea* (the last two are rare in the study area).

Data analysis

Species compositions (mean cover of each species) of the three types of study areas were compared using global non-metric multidimensional scaling (NMDS) with the program PC-ORD version 4 (McCune and Mefford 1999). The distance measure used was the Bray–Curtis index, the number of runs with real data 100, maximum number of iterations 500 and number of randomized runs 100. NMDS runs were repeated 50 times with random starting configurations in one to four dimensions, and the solution with the lowest amount of stress was chosen. In all ordinations the first two dimensions provided the best solution.

Species richness and density, vegetation height and cover of litter and ground-layer of old, new and abandoned pastures were compared using Kruskall–Wallis one-way ANOVA and its *a posteriori* test between pairs using the program Statistix 7. Furthermore, the six most abundant species in abandoned pastures and differences in their cover between the three pasture types were compared.

Results

Species composition

In the NMDS ordination the three groups were separated (Figure 1). The r^2 values for axes 1 and 2 were 0.57 and 0.26, respectively. NMDS revealed a clear grazing–abandonment gradient parallel to the first ordination axis. Measures of grazing pressure (height of vegetation, cover of litter and ground layer, number of years grazed, time of starting of grazing) had a strong correlation with the first axis, but all variables were only weakly related to the second axis (Table 1). Species of abandoned grasslands (e.g. *Aegopodium podagraria*, *Calamagrostis epigejos*, *Cirsium arvense*, *Urtica dioica*) showed the highest and small plants such as *Potentilla crantzii*, *Plantago major* and *Prunella vulgaris* the lowest first axis scores (Figure 2).

Environmental variables and land use

The mean cover of litter, cover of bryophyte-dominated ground layer and vegetation height differed between the three pasture types (Table 2). The amount of litter was very variable between different pastures, mainly because of differences in grazing pressure during the previous year.

From some areas rather detailed information on previous land use was available, whereas from others this data was scarce. However, previous land use appears to have been similar between the three pasture types. According to the landowners ca. 1/3 of the study areas had earlier (before 1950 or between 1950 and 1991) been fertilized. Fertilization had been occasional, and accurate data on fertilization levels was not available. According to the interviews as well as on the basis of present vegetation in these sites, the fertilization levels had been low to moderate. Four areas had been partly used as cultivated fields before 1960. Commonly some

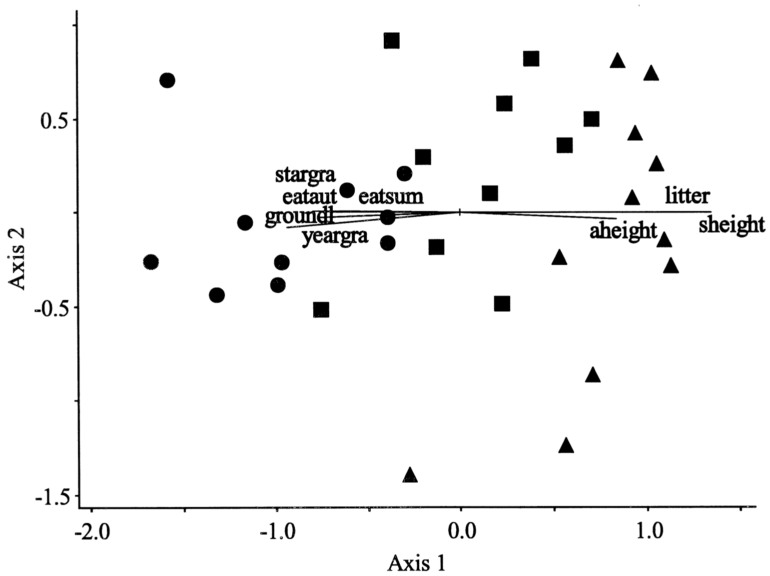

Figure 1. NMDS ordination of the 31 study areas. (●) Old pastures, (■) new pastures, (▲) abandoned pastures. Correlations between axis scores and environmental variables with r^2 values >0.20 are shown. For abbreviations of the environmental variables see Table 1.

Table 1. Kendall correlations with NMDS ordination axes (abbreviations for the variables included in Figure 1 are in parentheses).

	Axis 1	Axis 2
Height of vegetation, summer (sheight)	0.751	0.105
Cover of litter (litter)	0.620	0.112
Cover of groundlayer (groundl)	−0.596	−0.061
Number of years grazed (yeargra)	−0.565	−0.190
Time of starting of grazing started during summer (stargra)	−0.552	−0.017
Proportion of vegetation <10 cm, autumn (eataut)	−0.549	0.021
Proportion of vegetation <10 cm, summer (eatsum)	−0.529	0.008
Height of vegetation, autumn (aheight)	0.527	0.002
Cover of bare soil	−0.427	0.014
Cover of vascular plants	0.233	0.168
Former use as arable land	−0.107	0.045
Proportion of moist grassland	0.042	−0.066
Study year	−0.006	−0.346
Fertilization	0.000	−0.128

supplementary forages were now or earlier given to animals. Sometimes semi-natural grasslands had been fenced with cultivated pastures.

Species richness and density

The total number of observed plant species in all the study sites was 252 (old pastures 209, new pastures 173, abandoned areas 156). A total of 50 species were exclusive to old, 13 to new and 19 to abandoned pastures. Most of these exclusive species were found only in one or two sites.

Mean number of species, grassland species, indicator species and rare species were all highest in old and lowest in abandoned pastures on all studied spatial scales (Table 2). Mean numbers of species in the study areas were 80.2 in 2000 and 68.7 in 1999, although the area studied was larger in 1999 (mean: 0.4 versus 0.25 ha). No statistical differences occurred in species richness and density between years. The highest density in all sample plots was 44 species per m^2 for old, 31 species per m^2 for new and 26 species per m^2 for abandoned pastures.

The three groups differed significantly in richness of all species, species of dry and mesic grasslands and indicator species. All these differences were significant both on the scale of the whole study site and on the scale of the 1 m^2 study plot (Table 2). Total species richness and richness of species of dry and mesic grasslands were also significantly different among the three types of study areas on the scale of 0.01 m^2. The number of rare species differed only on the scale of 1 m^2. *A posteriori* comparison between the groups revealed that statistical differences occurred mainly between old and abandoned pastures (Table 2). Old and new pastures differed in the total species richness and richness of grassland plants per m^2 and in the richness of grassland plants per 0.01 m^2. Species richness of new pastures was 20% higher on 0.25–0.8 ha, 40–50% higher on 1 m^2 and 30% higher on the 0.01 m^2 scale compared to abandoned grasslands.

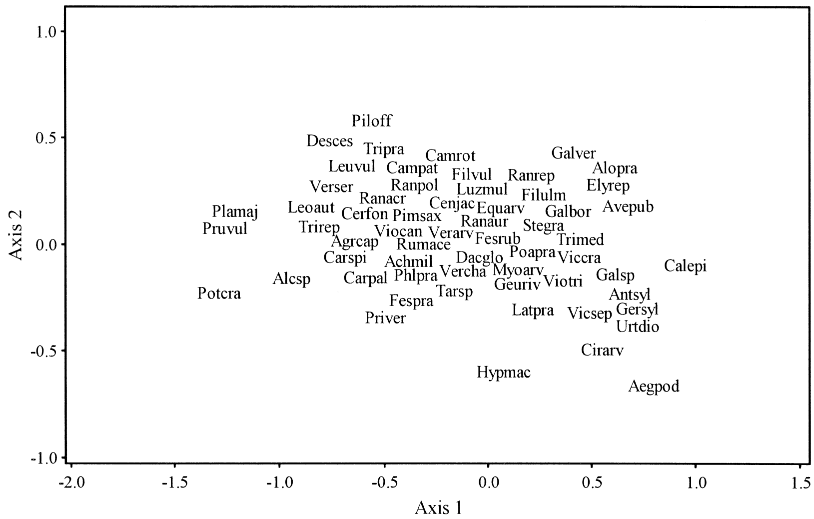

Figure 2. NMDS ordination of the species. Species with >10% frequency per m^2 in one of the three groups are included. Abbreviations for the species: Achmil – *Achillea millefolium*, Aegpod – *Aegopodium podagraria*, Agrcap – *Agrostis capillaris*, Alcsp – *Alchemilla* spp., Antsyl – *Anthriscus sylvestris*, Avepub – *Avenula pubescens*, Calepi – *Calamagrostis epigejos*, Campat – *Campanula patula*, Camrot – *Campanula rotundifolia*, Carpal – *Carex pallescens*, Carspi – *C. spicata*, Carcar – *Carum carvi*, Cenjac – *Centaurea jacea*, Cerfon – *Cerastium fontanum*, Cirarv – *Cirsium arvense*, Dacglo – *Dactylis glomerata*, Desces – *Deschampsia cespitosa*, Elyrep – *Elymus repens*, Equarv – *Equisetum arvense*, Fespra – *Festuca pratensis*, Fesrub – *F. rubra*, Filvul – *Filipendula vulgaris*, Filulm – *F. ulmaria*, Galsp – *Galeopsis* spp., Galbor – *Galium boreale*, Galver – *G. verum*, Gersyl – *Geranium sylvaticum*, Geuriv – *Geum rivale*, Hypmac – *Hypericum maculatum*, Latpra – *Lathyrus pratensis*, Leoaut – *Leontodon autumnalis*, Leuvul – *Leucanthemum vulgare*, Myoarv – *Myosotis arvensis*, Phlpra – *Phleum pratense*, Piloff – *Pilosella officinarum*, Pimsax – *Pimpinella saxifraga*, Plamaj – *Plantago major*, Poapra – *Poa pratensis* coll., Potcra – *Potentilla crantzii*, Priver – *Primula veris*, Prunvul – *Prunella vulgaris*, Ranacr – *Ranunculus acris*, Ranaur – *R. auricomus*, Ranpol – *R. polyanthemos*, Ranrep – *R. repens*, Rumace – *Rumex acetosa*, Stegram – *Stellaria graminea*, Tarsp – *Taraxacum* spp., Trimed – *Trifolium medium*, Tripra – *T. pratense*, Trirep – *T. repens*, Urtdio – *Urtica dioica*, Verarv – *Veronica arvensis*, Vercha – *V. chamaedrys*, Verser – *V. serpyllifolia*, Viccra – *Vicia cracca*, Vicsep – *V. sepium*, Viocan – *Viola canina*, Viotri – *V. tricolor*.

Species richness per study site and per m^2 showed a clear positive correlation in old (r_s = 0.681, P = 0.03) and new (r_s = 0.866, P = 0.001) pastures, but not in abandoned pastures (r_s = 0.178, P = 0.6). In new pastures the number of indicator (r_s = 0.843, P = 0.002) and rare (r_s = 0.775, P = 0.008) species per study site and per m^2 were also significantly correlated.

Division of rare species into tall (>50 cm high) and low species (<50 cm high) revealed that rare species with low stature benefitted from grazing, whereas the frequency of species with high stature was similar among all three groups (Table 3).

Cover of the six most abundant species in abandoned grasslands was 54.5% (Table 4), which was 75% of all plant cover in abandoned grasslands. Total cover

Table 2. Kruskall–Wallis one-way ANOVA comparisons for the species numbers and densities and vegetation height (mean and std) among the three types of study areas.

	Pasture type			K–W *P*
	Old (1) ($n = 10$)	New (2) ($n = 10$)	Abandoned (3) ($n = 11$)	
Spatial scale and the measure of species richness				
0.25–0.8 ha				
All species	87.1 ± 18.9[a]	74.0 ± 12.1[ab]	60.6 ± 11.9[b]	0.002
Grassland species	55.9 ± 7.7[a]	44.1 ± 6.8[ab]	37.5 ± 7.2[b]	<0.001
Indicator species	9.1 ± 4.0[a]	6.2 ± 2.4[ab]	4.7 ± 2.6[b]	0.016
Rare species	3.8 ± 1.8[a]	3.1 ± 1.9[a]	2.6 ± 1.5[a]	0.280
1 m^2				
All species	24.7 ± 3.2[a]	16.4 ± 3.7[b]	11.2 ± 2.2[b]	<0.001
Grassland species	22.6 ± 3.7[a]	14.0 ± 3.2[b]	9.0 ± 2.4[b]	<0.001
Indicator species	2.3 ± 1.5[a]	1.3 ± 0.8[ab]	0.5 ± 0.4[b]	0.001
Rare species	0.9 ± 0.7[a]	0.3 ± 0.3[ab]	0.2 ± 0.3[b]	0.014
0.01 m^2				
All species	6.5 ± 1.8[a]	4.2 ± 1.6[ab]	3.2 ± 1.5[b]	0.001
Grassland species	6.1 ± 1.5[a]	3.7 ± 1.6[b]	2.6 ± 1.3[b]	0.001
Indicator species	0.31 ± 0.29[a]	0.19 ± 0.17[a]	0.09 ± 0.08[a]	0.098
Rare species	0.08 ± 0.17[a]	0.04 ± 0.08[a]	0.04 ± 0.10[a]	0.676
Vegetation height				
Mean height (cm)[1]	13.7 ± 7.9[a]	29.5 ± 12.0[a]	49.1 ± 6.5[b]	<0.001
Proportion <10 cm height (%)[1]	38.7 ± 22.9[a]	16.0 ± 27.3[ab]	0[b]	<0.001
Mean height (cm)[2]	10.3 ± 7.5[a]	19.3 ± 15.6[a]	44.5 ± 8.1[b]	<0.001
Proportion <10 cm height (%)[2]	65.8 ± 29.1[a]	43.0 ± 33.9[ab]	0[b]	<0.001
Cover of litter (%)[1]	27.2 ± 19.2[a]	40.4 ± 23.2[a]	89.6 ± 6.4[b]	<0.001
Cover of groundlayer (%)[1]	31.0 ± 18.5[a]	5.5 ± 4.7[b]	1.1 ± 1.9[b]	<0.001

The letter code indicates the location of significant differences among the classes according to *a posteriori* tests. Only classes not sharing a letter differed from each other. [1]Summer; [2]autumn.

Table 3. Kruskall–Wallis one-way ANOVA comparison for the number of rare plant species per m^2 among the three types of study areas.

Plant height	Pasture type			*P*-value
	Old (1)	New (2)	Abandoned (3)	
<50 cm	0.71[a]	0.14[b]	0.04[b]	0.002
>50 cm	0.18[a]	0.14[a]	0.15[a]	0.600
Total	0.89[a]	0.27[ab]	0.19[b]	0.013

For the letter code, see Table 2. Plant height according to Hämet-Ahti et al. (1998). Height <50 cm: *Ajuga pyramidalis*, *Alchemilla samuelssonii*, *Carex caryophyllea*, *C. spicata*, *Filipendula vulgaris*, *Luzula campestris*, *Poa compressa*, *Primula veris*, *Trifolium aureum*, *Vicia tetrasperma*. Height >50 cm: *Agrimonia eupatoria*, *Allium oleraceum*, *Avenula pubescens*, *Carex atherodes*, *C. disticha*, *Centaurea phrygia*, *Veronica longifolia*.

of these species was lower in new pastures (cover 32.2%) and even lower in old pastures (14.0%). Two of these species (*Anthriscus sylvestris* and *Cirsium arvense*) showed significant decline in cover in new pastures (Table 4).

Table 4. The six most abundant species in abandoned pastures and differences of their cover (%) (mean + std) between the three pasture types (Kruskall–Wallis one-way ANOVA; for the letter code, see Table 2).

	Pasture type			*P*-value
	Old (1)	New (2)	Abandoned (3)	
Alopecurus pratensis	7.06 ± 7.49^{a}	19.26 ± 11.34^{ab}	22.58 ± 15.53^{b}	0.020
Anthriscus sylvestris	0.21 ± 0.29^{a}	1.07 ± 0.98^{a}	4.26 ± 2.66^{b}	<0.001
Calamagrostis epigejos	0.09 ± 0.15^{a}	2.08 ± 5.26^{a}	6.41 ± 9.06^{a}	0.370
Cirsium arvense	0.24 ± 0.42^{a}	0.73 ± 0.80^{a}	6.68 ± 6.55^{b}	<0.001
Elymus repens	0.79 ± 1.88^{a}	3.61 ± 5.25^{a}	4.08 ± 5.85^{a}	0.063
Trifolium medium	5.59 ± 4.35^{a}	5.43 ± 5.09^{a}	10.06 ± 12.03^{a}	0.682
Total	54.07^{a}	32.18^{ab}	13.98^{b}	<0.001

Discussion

Most studies on restoration of grasslands are from nature conservation areas or from research farms. There is a lack of studies on privately owned non-protected areas in which grasslands are agriculturally exploited. This is a major drawback, because the future of biodiversity in European agricultural landscapes relies much on how biodiversity can be maintained in farming practices (Krebs et al. 1999; Sutherland 2002). It is crucial to study the effects of restoration in areas managed by private farmers (Dolek and Geyer 2002). Disfavour of privately owned areas is probably largely caused by the lack of possibility to standardize grazing pressure and other land use variables, and to obtain exact information of previous land use. This has the result that not all of the underlying factors behind the vegetation change can be effectively extracted.

In the present study, considerable effort was made to find areas in which environmental conditions and previous land use were as similar as possible. Thus, differences in plant species composition between the three groups of pastures were most probably caused by differences in grazing management.

All the results showed clear differences between new, old and abandoned pastures, although the differences may have been slightly obscured by differences in weather conditions between the years 1999 and 2000. The summer of 1999 was dry, whereas that of 2000 was rainy. This probably explains the slightly higher mean species richness and density in 2000.

Species composition

Multivariate analyses (NMDS) revealed a strong grazing–abandonment gradient along the first ordination axis. The lack of nutrient-enrichment gradient may be due to the fact that data on land use history were insufficient from several areas.

Multivariate analysis illustrated that the species compositions of the three groups were distinctly different. In the ordination plot, species composition of new pastures was between that of old and abandoned pastures (Figure 1). In the ordination plot, some new pastures were situated close to old pastures, suggesting that restoration had succeeded well, but some new pastures were close to abandoned grasslands. Three abandoned grasslands were located separately from the others in the lower right corner of the ordination. The probable reason for this was the low abundance of *Alopecurus pratensis* in these sites.

The comparison between old and abandoned pastures revealed that only very few new species invaded abandoned grasslands. Only *Epilobium angustifolium* tended to be confined to abandoned areas. The cover and frequency of a few tall species, already frequently present in old pastures, heavily increased after abandonment (e.g. *Alopecurus pratensis*, *Anthriscus sylvestris*, *Calamagrostis epigejos*, *Cirsium arvense*, and *Elymus repens*). The critical role of a few competitive species in causing the decline of other species as well as in retarding the success of restoration has often been emphasized (e.g. Bobbink and Willems 1987, 1993).

Cover of *Anthriscus sylvestris* and *Cirsium arvense* declined considerably after resumed grazing. The sensitivity of *Anthriscus* to grazing is well known (e.g. Grime et al. 1988). *Cirsium arvense* has often been reported as resistant to or even benefitting from grazing (e.g. Grime et al. 1988; Schalitz et al. 1995; Scholz 1995), but in this study it was among the species most sensitive to grazing. A potential explanation for these differences is that *C. arvense* may be more resistant to grazing in nutrient-enriched habitats, or may be avoided by cattle in sites where grazing is started late in the growing season.

The most abundant species in abandoned areas, *Alopecurus pratensis* (ca. 32% of all vascular plant cover), showed no response to restoration. The abundance of this species may effectively retard the progress of restoration. *Alopecurus pratensis* seems thus to be a negative key species in abandoned mesic grasslands, due to its ability to suppress species richness.

Species richness and density

Numerous studies have demonstrated the positive effects of grazing on plant species richness on a small scale (generally ≤ 10 m^2) (see e.g. Bakker 1989, 1998), but the effects on larger scales have rarely been studied. In this study the total species richness as well as the richness of grassland, indicator and rare plants were higher in grazed than in abandoned areas on all the studied spatial scales. Thus cattle grazing appears to be beneficial to plant species richness independently of the study scale. The difference was more pronounced on small scales (species density scale), consistently with other studies of mesic and moist grasslands (Persson 1984; Bakker 1998). Grazing increases the equitability of species, causing a fine-grained mixture of evenly distributed species in grasslands (Bakker 1998).

Species richness is sensitive to environmental heterogeneity. Because of this, species density per m^2 may be more suitable for evaluating grassland quality for nature conservation than species richness. Species richness may recover more easily than species density, as can be seen from the results of Austrheim and Olsson (1999). However, in new pastures the number of species in the study areas and the number of species per m^2 showed a strong correlation. This supports the assumption that species density per m^2 can be a useful surrogate for larger scale species richness when the progress of grassland restoration is evaluated.

Implications for management

Despite suboptimal management quality in most new pastures, the results of this study are promising for restoration of grasslands with cattle grazing. During ca. 5 years, the species composition clearly altered in the desired direction. Positive changes in species richness were more prominent than in other Nordic studies of mesic grasslands (Huhta et al. 2001) or mesic wooded meadows (Austad and Losvik 1998; Kotiluoto 1998), or in studies on restoration of agriculturally improved grasslands in the temperate region (Bakker 1989; Smith et al. 2000).

However, the vegetation of new pastures was more similar to abandoned than to old pastures, and most target species (rare and indicator species) showed no or only slight recovery. It is known that restoration of semi-natural grasslands will take a long time (Gibson and Brown 1992; Zobel et al. 1996; but see Willems and Bik 1998). The results obtained in only 5 years must be treated as preliminary. A much longer time period is needed for the evaluation of the long-term effectiveness of restoration.

The history of land use is very important in evaluating the suitability of areas for restoration (Bakker and Berendse 1999). Here, the aim was to choose areas representing non-fertilized semi-natural grasslands, but this was not fully successful. Interviews with landowners revealed that in most areas low to moderate levels of nutrient enrichment had occurred in the past.

Nutrient enrichment has long-term effects on species richness in grasslands (Willems and van Nieuwstadt 1996). It may retard the progress of restoration in new pastures as well as suppress species richness in old pastures. Three sites partly cultivated prior to 1960 still showed the lowest species densities per m^2 among abandoned and old pastures. The low species density (18.7 species per m^2) in one studied old pasture was probably caused by the use of supplementary forages. Nutrient enrichment may decrease the differences between the three treatments by suppressing the species richness and density of managed areas, but on the other hand it may speed up overgrowth after abandonment.

Several studies have reported more prominent recovery of common than rare species in grassland restoration (e.g. Bakker 1989; Kotiluoto 1998). Several reasons can be proposed for insignificant recovery of rare species in this study: (1) rarity in the data set. Mean numbers of rare species were slightly higher in new than in abandoned pastures: 3.1 versus 2.6 on the study site scale and 0.3 versus 0.2 in the m^2 study plots (the latter a 42% higher value). This tendency was caused by the increase of small rare plants in new pastures. Small rare plants are dependent on management, but tall plants appear tolerant to overgrowth if the grasslands remain open. (2) Previous nutrient enrichment may retard the recovery of rare species, because the soil nutrient levels may be too high for them. (3) Relatively low grazing pressure in several new pastures may also cause lack of recovery of small-sized rare species. (4) It is also possible that their recovery has a time delay, and that better results will be obtained after e.g. 10 years of management. (5) Some of the rare species have already disappeared from all abandoned areas (e.g. *Luzula campestris*), and their dispersal back is probably slow if they do not occur in the soil seed bank, or are not able to reappear from it.

Most grassland plants do not have a long-persistent seed bank (Bakker et al. 1996; Bakker and Berendse 1999). Although seeds of most of the rare species in the study sites may persist for long periods in the soil (e.g. *Ajuga pyramidalis*, *Alchemilla samuelssonii*, *Carex* sp., *Luzula campestris*, *Potentilla crantzii*, *Trifolium aureum*, *Vicia tetrasperma*), the resumption of grazing appears not to have been effective for promoting their germination and re-establishment.

The quality of management of areas under the agri-environmental scheme in Finland has been shown to be commonly inappropriate for biodiversity (Salminen and Kekäläinen 2000). This is mainly due to the lack of clear management instructions to landowners. In this study, management quality showed considerable variability between areas. In some areas grazing intensity was very low, and in some areas supplementary forages had been given to animals, causing nutrient enrichment. Even if the quality of management is only moderate for nature conservation, plant species richness appears to increase after resumed cattle grazing. However, present management practices may be inappropriate for the recovery of uncommon and rare species. For these, management regimes need to be defined more precisely (e.g. grazing pressure, timing of grazing, no nutrient enrichment allowed). To decrease soil nutrient levels, mowing may be needed in some areas.

Grassland areas included in the Natura 2000 network in Finland are mainly intended to be managed with the EU agri-environmental support scheme (Salminen and Kekäläinen 2000). This study showed that efficient restoration of Natura 2000 areas with the agri-environmental scheme is possible, but that the quality of management needs to be improved in order to successfully manage grassland types of the EU Habitats Directive. Further development of regulations as well as studies on the effects of different management regimes are needed for successful restoration of abandoned species-rich grasslands.

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