Search for optimal mowing regime — slow community change in a restoration trial in northern Finland

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Mowing is frequently used for restoring plant communities in abandoned meadows which were previously managed by cattle grazing and mowing. The aim of this study was to search for the most optimal mowing treatment maximising plant species richness in a dry-mesic meadow in northern Finland. In an earlier restoration attempt at the same study site, traditional mowing in mid to late August was applied for five years (1993–1997). Because this first attempt had negligible effects on plant community structure, a new five-year experiment was conducted (1998–2003) in order to test for the effects of different mowing regimes (early mowing in June, late mowing in August, late mowing + soil disturbance in August, and untreated control plots). In spite of considerable species turnover at the level of individual plots, the treatments had no statistically significant effect on species turnover and species richness per plot. Mowing did not suppress the cover of tall herbs. Late mowing even favoured the early flowering *Geranium sylvaticum*. Restorative mowing is ineffective against tall competitors if the propagule input from the neighbourhood remains high. Early mowing and late mowing + soil disturbance, which most strongly decreased vegetation height, tended to favour competitively inferior small herbs. A reason for a slow response in species richness may lie in seed limitation as only one new species appeared during the study. To enhance species richness, mowing could be combined with propagule addition in cases where the local species pools of meadow species have been exhausted.

Key words: abandonment, disturbance, grassland management, seed limitation, species diversity, species turnover.

Introduction

In the old traditional agriculture, semi-natural meadows formed the basis for animal husbandry. After the hay was collected, in Finland usually in

early August, the cattle were allowed to graze the aftermath (Vainio *et al*. 2001). These management practices created suitable conditions for many plant and animal species (Pykälä 2001). In Finland, the area of semi-natural meadows

reached its peak of 1.6 million ha during the 1880s after which it declined due to the changes in agricultural practices (Soininen 1974). This downgrade of meadows continued insidiously until it was noticed in the 1980s that the area of traditional meadows had drastically declined. In the national inventory of traditional rural biotopes in the early 1990s, only 18 690 ha semi-natural habitats were found. Only 2% of this area was regularly mown and 56% was grazed (Vainio *et al.* 2001), the rest being abandoned. Because of the lack of available grazing cattle, mowing is often the only alternative as a management tool for these areas.

Mowing has been shown to be an effective tool to increase and maintain species richness in dry and mesic semi-natural meadows (Willems 1983, Zobel *et al.* 1996, Fenner & Palmer 1998, Klimeš *et al.* 2000, Wahlman & Milberg 2002). Typically, mowing favours low-growing, rosette forming plant species as well as species with annual or biennial life-history (Ekstam *et al.* 1988). Traditionally-managed unfertilized meadows are characterised by a large number of species which are rather evenly distributed, i.e. usually no single species gains dominance (Persson 1984). In an Estonian wooded meadow, up to 70 vascular plant species may grow in a square metre (Kull & Zobel 1991). A similar diversity has been found in the grasslands of the Carpathian Mountains in the Czech Republic (Klimeš *et al.* 2000). In Finland, 46 vascular plant species per m^2 were found in a hay meadow that was mown and aftermath grazed at least for 50 years (Pykälä 2001).

Mowing time is critical to the development of vegetation (Smith & Jones 1991). If it is carried out too late, tall-growing, tussock-forming and broad-leaved perennial species may gain dominance. Mowing performed too early prevents many meadow species from setting seed and this may lead to their disappearance. On the other hand, early mowing may be used to decrease the dominance of some undesirable species (cf. Bobbink & Willems 1991) because early mowing weakens their ability to store resources below-ground for overwintering (Ekstam *et al.* 1988). Late mowing has been observed to mainly maintain the prevailing vegetation (Huhta *et al.* 2001). Until recently there were rather few stud-

ies comparing the effects of mowing and grazing (e.g. Tamm 1956) but during the last years new results were reported (Hansson & Fogelfors 2000, Wahlman & Milberg 2002, Jantunen 2003). Often both grazing and mowing seem to maintain the most species-rich communities but in some cases mowing is slightly preferable to grazing (Hansson & Fogelfors 2000, Wahlman & Milberg 2002).

The aim of this study was to find out how different mowing treatments affect species diversity in a hay meadow. In a previous restoration attempt in the same study site, traditional mowing in mid to late August was applied for five years between 1993 and 1997 (Huhta *et al.* 2001). Mowing reduced litter accumulation, but caused negligible changes within the plant community. Furthermore, late mowing was unable to control early-flowering tall herbs, such as *Geranium sylvaticum*, which are competitively superior to small herbs. Because the first attempt had only minor effects on plant community structure and diversity, new treatments were introduced (1998–2003) in part of the experimental plots, whereas the previous treatments continued in the remaining plots. We used four treatments and hypothesised that: (1) in unmown control plots the species richness would decrease slowly due to accumulating litter layer that prevents the growth and germination of many small growing meadow species (Huhta *et al.* 2001), (2) in early mown plots (late June) the species richness would increase as this treatment allows smaller meadow species to gain space and germinate, (3) in late mown plots the prevailing situation would remain but this treatment was not expected to prevent the invasion of some tall competitive species (Huhta *et al.* 2001), and (4) in heavily disturbed plots, breaking the soil surface (combined with late mowing) simulates the mechanical disturbance effect of grazing animals' hoofs on the soil surface and would thus provide new germination niches for seeds.

Further, we chose three model species to represent plant groups that are expected to have different responses to mowing. The criterion was that the species has to be abundant enough in order to reliably evaluate its response to treatments. *Geranium sylvaticum* was chosen as a model species of tall herbs (C-strategists, *sensu*

Grime 1977) that were expected to be disfavoured by early mowing (e.g. Huhta *et al.* 2001), while *Campanula rotundifolia*, a small-growing meadow herb, was used as an example of stress tolerators or S-strategists *sensu* Grime *et al.* (1988) which can be expected to be favoured by mowing due to reduced above-ground competition as well as drier growth conditions at mown plots (*see* Huhta *et al.* 2001). Third model species, *Agrostis capillaris*, a common grass of hay meadows, has been shown to be favoured by grazing (Hellström *et al.* 2003) but not by mowing (Bakker *et al.* 1983).

Material and methods

Study site and experimental design

The study site, Kiiminki Haaraoja meadow (65°10´N, 25°50´E) lies in the middle boreal vegetation zone, ca. 20 km from the Gulf of Bothnia in northern Finland. Small dry meadow patches on small hillocks around abandoned fields were grazed by cattle until 1985. The meadow was evaluated as a provincially valuable semi-natural grassland in the national inventory of rural biotopes in the early 1990s, and its restoration was started by annual mowing in 1993. Mowing was performed annually in August using scythes in 1993–1997, and the present management practices (*see* below) were applied in 1998–2003. The former control plots of the first experiment (Huhta *et al.* 2001) were left untreated during the present experiment too, i.e. these plots had been without mowing for 18 years by the end of this study (2003). The experimental plots, which were previously mown in August, were randomly allocated among three treatments as described below. It should thus be noted that, although we here report only the results obtained from 1998 onwards, our experimental plots have actually been subjected to mowing treatments since 1993, i.e. for 10 years.
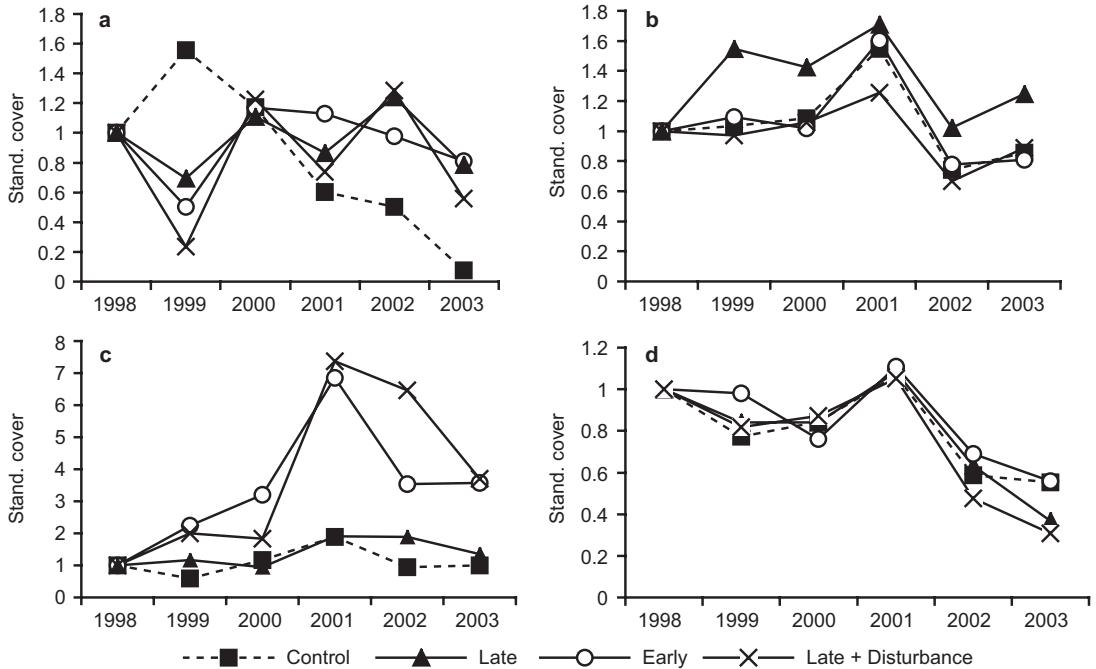
The experimental design consisted of four treatments that were applied into 40 permanent plots (10 plots of size 0.25 m² per treatment): (1) early mowing (in late June), (2) late mowing (in August), (3) late mowing and disturbance (soil surface broken by spade, ca. 25% bare soil of the

plot area), and (4) untreated control (abandonment). Mown plant material was carefully raked away from the plots. The plots were placed 5 m from each other in 2–3 lines (2 m space between the lines) in two hillocks. The treatments were randomly allotted to plots. The percentage cover (scale: 0.25%, 0.5%, 1%, 2%, 3%, 5%, 7%, 10%, 15%, 20%, 25%, 30%, 40%, …, 100%) of all vascular plant species and ground layer species (mosses and lichens) were estimated annually. The inventory was done every year in late June before carrying out the early mowing. The nomenclature of taxa follows the Finnish Field Flora (Hämet-Ahti *et al.* 1998). In late June 2003, the average vegetation height was estimated in each plot with a "meadow ruler" (*see* Ekstam & Forshed 1996), and also the maximum height of each plant species in every plot was measured at the same time. We also studied the effects of different mowing treatments on the abundance and maximum height of the three model species (*Geranium sylvaticum*, *Campanula rotundifolia* and *Agrostis capillaris*) that differ in their expected responses to mowing.

Statistical analysis

Because the data of 1998 did not yet include the new treatment effects, we took the values of 1998 as a base line for the variables presented in Figs. 1a and 2. The values obtained for 1999–2003 were divided by those of 1998, and hence in Figs. 1a and 2, deviations from the value of 1 indicate an increasing (> 1) or a decreasing (< 1) trend with time. Temporal trends in species richness and abundances of species and species groups were analysed by using repeated measures analysis of variance (ANOVA) with plots (40) as subjects, time (years 1999–2003) and time × treatment interaction as within-subject factors, and treatment (four levels) as a between-subject factor. If the assumption of circularity of the variance-covariance matrix was not met, significance levels were confirmed by using the multivariate approach (MANOVA) that is known to be robust for the above assumption (Norušis 1993, Tabachnick & Fidell 1996). As the multivariate tests did not change interpretation of the results as compared with univariate repeated

measures ANOVA, only the latter are reported (Tabachnick & Fidell 1996). Because there were no significant treatment effects (neither significant year × treatment interaction) no *post hoc* comparisons were performed.

Species turnover index (T) was calculated to study the amount of change in species composition in different treatments during this 5-yr study. This index was calculated as $T = (A + D)/n$, where A is the number of arrived new species in a plot during the study, D is the number of disappeared species in the plot and n is the total number of species at the beginning of the study period (Berlin *et al.* 2000). Temporal changes in the abundance of the model species were studied by computing Spearman's rank correlation (r_s) between its abundance in a particular year and time in years (1–6) since the beginning of the study. This was performed separately for different treatments. Significant positive correlation tells that the abundance of the species has increased, and significant negative correlation that it has declined during the study period (*see* also Hellström *et al.* 2003). The effects of the treatments on plant height of the three model species in the end of the experiment (2003) were tested with one-way ANOVA, and *post hoc* tests (control *vs.* treatments) were carried out with the LSD procedure (Saville 1990). If the homogeneity of variances was not met the data were transformed with natural logarithm. In case ln-transformation did not improve variance homogeneity the data were rank transformed. The average vegetation height (measured in 2003) within the plots was tested with the same procedure.

Fig. 1. — **a**: The effects of different mowing treatments (Control = unmown, Early = mown in June, Late = mown in August, and Late + Disturbance = mown and soil surface broken in August) on the number of vascular plant species per plot in Kiiminki Haaraoja meadow in 1998–2003. The species numbers in 1999–2003 have been standardized in relation to the value of 1998 that was set as one. — **b**: Average species turnover index in different treatments between 1998 and 2003 (mean ± SE).

Results

Species richness and turnover

The number of vascular plant species per plot remained practically unchanged during the study (year × treatment interaction, $P = 0.504$, Table 1).

Table 1. Results of repeated measures ANOVA where the effects of the treatments on different community parameters and species groups were studied in 1999–2003. Proportional values were used, i.e. the values in 1999–2003 were divided by that of year 1998.

	df	Species no.		Ground layer		Tall herbs		Small herbs		Grasses	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Within-subjects effects											
Year	4	10.86	< 0.001	1.54	0.194	18.34	< 0.001	4.61	0.002	19.61	< 0.001
Year × Treatment	12	0.95	0.504	1.03	0.429	0.49	0.917	1.05	0.406	0.51	0.903
Error	132										
Between-subjects effects											
Treatment	3	1.25	0.306	0.09	0.963	1.89	0.150	1.13	0.351	0.18	0.911
Error	33										

Fig. 2. The standardized cover of (**a**) ground layer vegetation, (**b**) tall herbs, (**c**) small herbs, and (**d**) grasses in the study plots in 1998–2003. The values in 1999–2003 have been standardized as in Fig. 1a (value 1 indicating the level in 1998). For statistics *see* Table 1.

However, there was a slight (but not significant) decrease in late mowing and abandonment (control) treatments (Fig. 1a). The average number of species per 0.25 m² plot (*n* = 40) was 13.8 ± 0.8 (mean ± SE) in 1998 and 12.2 ± 0.6 in 2003. The total number of vascular plant species in all plots together (area of 10 m²) was 55 in 2003.

Only one new species appeared during the study of five years. *Mentha arvensis* was not observed in the meadow before it invaded one plot in 2001. Some species, e.g. *Arabis glabra* and *Geum rivale*, were present elsewhere in the community and spread occasionally into the study plots. Even though the turnover of species at community level (i.e all the 40 plots together) was rather small, 0.14, it was higher at the level of individual plots, on an average 0.58. The turnover index between the years 1998 and 2003 was rather similar between the treatments (ANOVA: $F_{3,36}$ = 1.158, *P* = 0.339). It was lowest in unmown plots and highest in early mown plots (Fig. 1b). When studying the turnover rate between 1993 and 2003 the rate remained rather constant as compared with that

in the present five-year study; it was 0.18 in all plots together and on average 0.75 at individual plots. The most interesting species invading the plots during that time period was the annual hemiparasite *Rhinanthus minor*.

Six species disappeared from the 40 plots during the study (treatment in parentheses: E = early mowing, L = late mowing, D = late mowing + disturbance and C = unmown control plot): *Angelica sylvestris* (E), *Betula pubescens* (D, C), *Carex nigra* (C), *Deschampsia cespitosa* (E, L), *Ranunculus repens* (L) and *Rubus idaeus* (E, C). However, the disappeared species were not very abundant at the start (cover ≤ 3%) and none of them disappeared from the community. Late mowing and abandonment were unfavourable for some small rosette-forming herb species. For instance, *Pilosella officinarum* disappeared from four late mown and three unmown plots during the study. In early mown plots, it disappeared from one and invaded one plot. Early mowing tended to favour low-growing *Fragaria vesca* as it invaded three new plots. *Vicia cracca* seemed to be sensitive to heavy disturbance
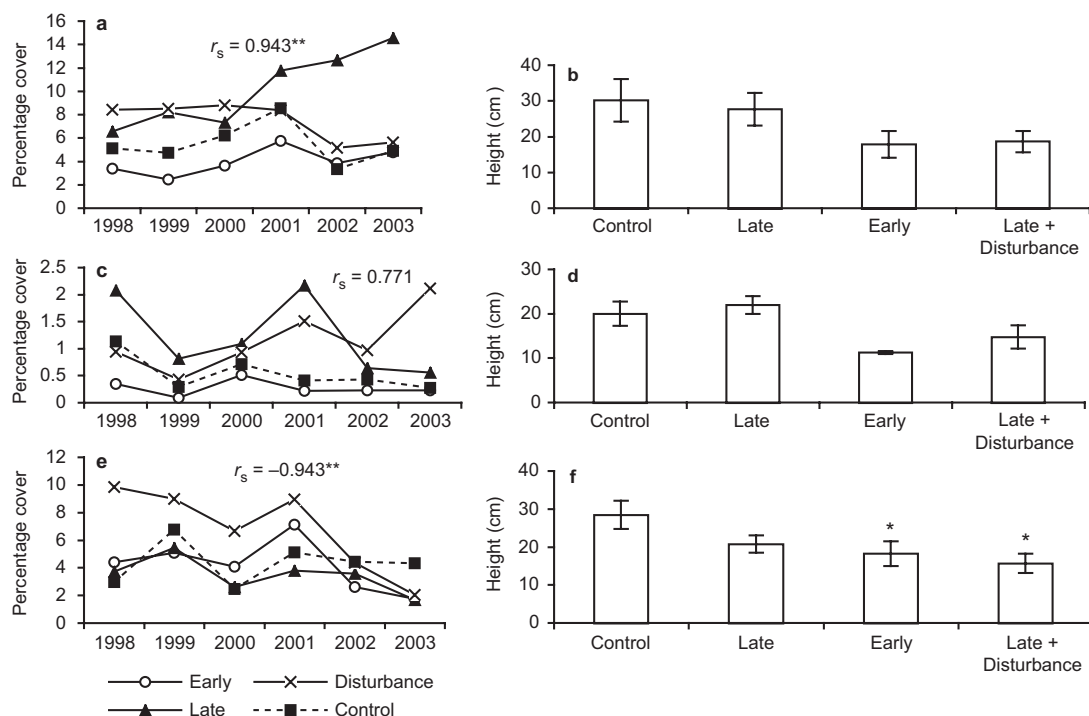
Fig. 3. The effects of different mowing regimes on the performance of the three model species in 1998–2003. *Geranium sylvaticum*: (**a**) average percentage cover and (**b**) mean height (± SE); *Campanula rotundifolia*: (**c**) average percentage cover and (**d**) mean height (± SE); *Agrostis capillaris*: (**e**) average percentage cover and (**f**) mean height (± SE). Temporal trends with time in a specific treatment are indicated by Spearman's correlation coefficient (r_s). Significant correlations are indicated with asterisks. Differences in plant height between different treatments in 2003 were tested with LSD procedure (asterisk indicates treatments significantly different from the control ($P < 0.05$).

because it disappeared from four late mown + disturbed plots. The two most abundant species, *Geranium sylvaticum* and *Achillea millefolium* did not show any drastic changes in their occurrences: *Achillea* persisted in all the plots while *Geranium* disappeared from one and invaded two plots.

Community structure and species responses

Ground layer species cover fluctuated greatly in unmown plots (Fig. 2a). Abandonment seemed to be especially harmful for ground layer species. In abandoned plots their cover decreased to a very low level by the end of the study (Fig. 2a). Repeated measures ANOVA, however, did not yield any statistically significant temporal trends between the treatments (Table 1). Although the cover of tall herbs tended to be above their initial

cover in late mown plots (Fig. 2b) and the cover of small herbs tended to increase, especially in 2001–2003, in response to early mowing and to late mowing combined with disturbance (Fig. 2c), year × treatment interactions were not statistically significant in either case (Table 1). In grasses, the treatments did not cause any major differences (Table 1), but there was a remarkable decrease (ca. 58 %) in their cover during the last two study years 2002–2003 irrespective of the treatments (significant time effect, Table 1; Fig. 2d).

Treatments had some clear effects on the abundance of the three model species. *Geranium sylvaticum* was favoured by late mowing (Fig. 3a, significant correlation), and plants in late mown plots were as tall as in unmown plots (Fig. 3b). Late mowing combined with disturbance treatment tended to increase the abundance of the small herb *Campanula rotundifolia* (Fig. 3c, $r_s = 0.771$, $P = 0.07$), while treatments had no effect on plant height (Fig. 3d). Late mowing
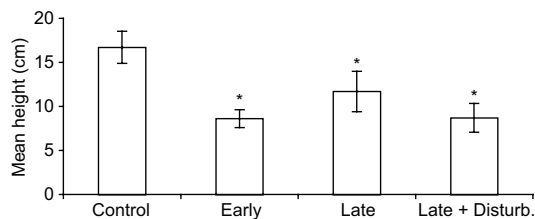
Fig. 4. Mean vegetation height (± SE) (cm) in June 2003 after different mowing treatments conducted in 1998–2002. Asterisk indicates treatments significantly (*P* < 0.05) different from the control (according to the LSD procedure).

combined with disturbance reduced the cover of *Agrostis capillaris* (Fig. 3e). In unmown plots its cover remained rather constant. Early mowing as well as late mowing + disturbance decreased its height significantly (Fig. 3f). All mowing treatments (1998–2002) decreased the height of the vegetation measured in June 2003 (ANOVA: $F_{3,36}$ = 4.73, *P* = 0.007). The vegetation height in early mown and late mown + disturbed plots was only about half of the height in control plots (Fig. 4). In late mown plots, the vegetation was somewhat taller compared to other mowing treatments but it was still lower than in control plots.

Discussion

Slow changes in the meadow plant community

Changes in species composition during this (1998–2003) and a previous study (1993–1997, Huhta *et al.* 2001) remained very small, despite altogether 18 years of abandonment (control plots) and ten years of mowing (managed plots). This is surprising because abandonment usually leads to a decrease in species number as tall species outcompete smaller species (Grime 1977, Olff & Ritchie 1998). In addition to overgrowing, litter accumulation is also a common feature of abandoned meadows (Bakker 1998). This is harmful for many short-lived meadow species as it chemically prevents the growth of seedlings (Facelli & Facelli 1993) and generates a mechanical barrier for many small-growing species (Hutchings & Booth 1996). Species diversity is often highest shortly after abandon-

ment because the true meadow species are still abundant while some indicators of abandonment are starting to gain space. When the succession proceeds, the litter layer gets thicker and a few tall herb and grass species gain dominance thus shading out smaller species. This leads to lower species richness under mesotrophic and eutrophic soil conditions (Bakker 1998). Species number in a meadow abandoned for 20–30 years has been shown to drop to one third as compared with that in continuously managed sites (Losvik 1999, Wahlman & Milberg 2002). Sometimes the decrease may be more gentle, for instance 15% during 15 years (Hansson & Fogelfors 2000).

It is often difficult to predict the development of a plant community after abandonment. An abandoned meadow may stay in a rather unchanged state for decades (Persson 1984), or it may be overgrown by a deciduous forest within 20 years (Wahlman & Milberg 2002). The rate of succession in an abandoned meadow depends e.g. on the species composition of the meadow before abandonment, nutrient content of the soil and management history (cf. Persson 1984). For instance, meadows with a long management history can sometimes be more resistant to species invasions (Bakker 1998), and succession following abandonment is often slower in nutrient poor and dry sites (Milberg & Hansson 1993, Huhta 2001). According to the long-term simulation results by Huhta *et al.* (2001), the succession dynamics of our abandoned plots from 1993 onwards for the next 30 years were expected to be characterized by (i) a transient phase with rather rapid changes for the first five to ten years and (ii) a more stationary phase with very slow changes in the cover of small herbs, tall herbs and grasses. First, small herbs were expected to decline from 1993 to 1998 in abandoned plots and to remain more or less unchanged there after (1998–2003). Second, tall herbs were expected to increase in cover first rapidly (1993–1998) and then more slowly (1998–2003). Third, grasses were expected to decline in cover from 1993 to 2003. Indeed, the cover of small as well as tall herbs remained more or less unchanged in abandoned plots during the present study. The decline of grasses that had begun already during 1993–1998 continued in 1998–2003, especially steeply during the last two study years. However,

there may well be some climatic factors (e.g. dry summers 2002 and 2003) behind this decline, because the cover of tall herbs also decreased during the last two study years.

Possibly, more drastic changes in abandoned plots would need invasion of woody plants. Meadow communities are often resistant to the invasion of woody plants because tree seedlings have difficulties in finding regeneration patches within the dense grass sward (Persson 1984). This may be the reason for the small changes we observed in the abandoned plots. Zobel *et al.* (1996) made an important distinction between coarse-scale and fine-scale interactions between plants which are spatially separated (e.g. trees *vs.* herbaceous plants) or not (e.g. among herbaceous plants of roughly similar height). When the spatial structure of the community changes, coarse-scale interactions may lead to drastic changes in species composition. For instance, the invasion of woody plants changes light conditions in a way that favours shade-tolerant species. This species-pool is often less species-rich than that of light-demanding true meadow species. According to Zobel *et al.* (1996), coarse-scale interactions determine the direction of rapid changes during the first stages of community succession. On the other hand, as in our case, changes may remain very slow as long as fine-scale interactions among herbaceous plants dominate in the community.

Species responses to management

Different mowing regimes had some distinct effects on vegetation but not as pronounced as we expected. Late mowing favoured tall herbs, especially *Geranium sylvaticum*. At the time of late mowing *G. sylvaticum* had already set seed and probably started to translocate resources into the below-ground parts. It benefitted from the removal of litter when mown material was raked after mowing. In unmown plots a thick litter layer probably suppressed its growth. Instead, early mowing and also late mowing combined with mechanical disturbance of the soil seemed to keep its abundance in control. *G. sylvaticum* is a forest species but it seems to benefit from the opening of the tree cover (Hansson & Fogelfors 2000). It also benefitted from the restoration of

wooded meadows (including clearing, mowing and aftermath grazing) in SW Finland (Kotiluoto 1998). Wahlman and Milberg (2002) found that *G. sylvaticum* is more closely associated with grazing than mowing. Late season grazing is also ineffective in controlling its abundance (Hellström *et al.* 2003). Usually tall herbs decline when management is restarted because as strong competitors (C-strategy *sensu* Grime 1977) they do not tolerate disturbance. Our results deviate from these expectations because *G. sylvaticum* is able to set seed in late mown plots and/or late mown plots receive continuous seed input from the surroundings. Moreover, perennial tall herbs may survive vegetatively in mown plots for years in spite of cutting of their flowering shoots.

We expected that early mowing and late mowing combined to disturbance would favour small growing herbs but only a slight trend to this direction was observed. *Campanula rotundifolia* that was used as a model species of small herbs benefitted from late mowing combined with the disturbance treatment. Mowing has been found to favour this species in other studies as well (Huhta & Rautio 1998, Kahmen *et al.* 2002, Wahlman & Milberg 2002). Mowing has also been shown to promote the growth of rosette-forming herbs (Tamm 1956, Wahlman & Milberg 2002, Jantunen 2003), as they have most of their biomass close to the ground and mowing removes a smaller proportion of their above-ground biomass than in species with leafy stem. Our results support this view as *Pilosella officinarum* disappeared from many unmown and late mown plots but persisted in early mown plots. Long-continued mowing also favours smaller species growing on nutrient poor soil as nutrients are removed from the community via the cut hay (cf. Wahlman & Milberg 2002). Species indicating nutrient poor soil in our study include e.g. *Antennaria dioica*, *Anthoxanthum odoratum*, *Campanula rotundifolia*, *Pilosella officinarum* and *Nardus stricta* that persisted or even gained space in mown plots.

Constraints on successful meadow restoration

Because the present management treatments had favourable effects on the habitat of small herbs
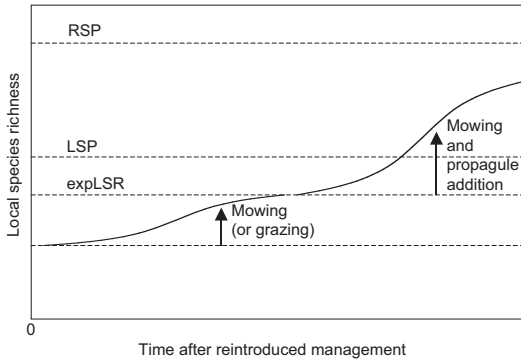
Fig. 5. Hypothetical effect of mowing (or grazing) on the local species richness of semi-natural meadows. Time after reintroduced management is on the *x*-axis. Local species richness is influenced by the local species pool (LSP) and the regional species pool (RSP). By mowing (or grazing), the local species richness (LSR) could be increased to an expected level (expLSR). Addition from the regional species pool is needed to further increase diversity in the presence of mowing above LSP. For simplicity, it is assumed that LSP and RSP remain constant over time.

(reduced vegetation height, removal of litter, breaking the soil surface), it is likely that the reason of slow responses in the cover of small herbs lies somewhere else than the conditions required for successful establishment of seedlings and survival and reproduction of adult plants (*see* also Stampfli & Zeiter 1999). First, the five-year time period may have been too short for the spread of these species and changes in vegetation may occur slowly in northern areas as the growing season ($> +5\,°C$) in the study region is at maximum 150 days per year (cf. Zobel *et al.* 1997). On the other hand, part of the plots had been mown and raked already for 10 years by the end of this study. That time period seems long enough if changes are going to occur (cf. Huhta *et al.* 2001, Hellström *et al.* 2003). Second, the abandoned study plots were rather small to show successional dynamics, for instance, to provide suitable growing conditions for woody plants. Even if the plots had a 50-cm buffer zone, edge effect is large in such 50×50 cm plots. For instance, light and moisture conditions can be very different in those plots than in a larger area. Third, changes did occur at the level of individual plots as the turnover index within individual plots was fairly high, on average 0.58.

Mowing enhances turnover as it incurs a disturbance in vegetation removing some plants but simultaneously providing space for new individuals. Because many meadow species are rather short-lived they can disappear from one place and emerge in another micro-site. This pattern is known as the carousel model (van der Maarel & Sykes 1993) that may explain the rather high turnover rate in many meadow communities. To compare, in the restoration of an overgrown meadow, Jantunen (2003) found a high turnover index (1.09) during a 6-yr mowing period; while in a 25-yr study, Berlin *et al.* (2000) reported an average turnover index of 0.56 measured in 25-m^2 squares. Milberg and Hansson (1993) reported 0.46–0.63 turnover rates in limestone grassland where 1 m^2 sized grazed and abandoned plots had similar turnover rates.

Consequently, in spite of habitat changes and species turnover at the plot level, the species composition at community level remained rather constant during our five-year study. Hardly any new species invaded the site. Breaking soil surface could be expected to provide germination sites for seeds but no such effect was observed here. Obviously, the appearance of new species either as a consequence of germination from seed bank or long distance spread occurs very infrequently. In such situations, all mowing regimes may remain ineffective in increasing species richness in a meadow where community changes are limited by propagule availability. However, from the three mowing regimes used, early mowing seems to be the most optimal restoration tool in meadows where tall herbs have gained dominance. We suggest that mowing (or grazing) can increase the local species richness (LSR) to a level determined by local species pool (expected LSR in Fig. 5). The meadow we studied had probably reached this state. To further increase species richness, propagule addition from the regional species pool (RSP) is needed in the presence of management (Fig. 5). The local species richness cannot reach, under mowing, the level determined by the local species pool, and when propagules are added, species richness will not reach the regional species pool because certain environmental and biotic filters sort part of the species out from the community (Zobel 1997). This kind of seed limita-

tion may well be common in Finland because of the small amount of managed meadows and long distances between them. In our study site, for instance, no other managed meadows are left in its vicinity. In a larger regional scale, there is, however, potential for new species to spread there as only 18% of the species of the total regional pool (i.e. 55 out of ca. 300 species) of inland meadows on mineral soil in this province were recorded in our study plots (data from Huhta & Rautio 2005).

Very little is known about the original species richness of meadows in northern Finland. We also do not know the species composition of this site in 1985 when management ceased. In southern Finland 30–40 vascular plant species may grow in a square metre in a herb-rich mesic meadow used for decades (Vainio *et al.* 2001) but in northern Finland the meadows are probably inherently less species-rich due to poorer growing conditions and more acidic soil. We recommend that the possibility of seed limitation will be rigorously tested in restoring species richness of meadow plant communities in Finland when mowing and grazing appear to be ineffective in restoring the original species richness and community structure.

Acknowledgements

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