Ann. Bot. Fennici 46: 397–408 ISSN 0003-3847 (print) ISSN 1797-2442 (online)
Helsinki 30 October 2009

Restoration management of a floodplain meadow and its cost-effectiveness — the results of a 6-year experiment

Jaan Liira*, Marge Issak, Ülle Jõgar, Majalis Mändoja & Martin Zobel

*Institute of Ecology and Earth Sciences, University of Tartu. 40 Lai St., Tartu 51005, Estonia (*corresponding author's e-mail: jaan.liira@ut.ee)*

Received 21 Jan. 2008, revised version received 11 Aug. 2008, accepted 28 Aug. 2008

Liira, J., Issak, M., Jõgar, Ü., Mändoja, M. & Zobel, M. 2009: Restoration management of a floodplain meadow and its cost-effectiveness — the results of a 6-year experiment. — *Ann. Bot. Fennici* 46: 397–408.

A key challenge of conservation management in seminatural grasslands is to find ecologically cost-effective management regimes which will maintain the ecological functionality and biodiversity of a community. We studied changes in the plant functional trait composition and diversity of the flooded meadow in the 6-year field experiment in Soomaa National Park, Estonia. Five management regimes were introduced: traditional (cutting with a scythe and hay removal), mowing (machine cutting and hay removal), mulching (machine cutting without hay removal), spring burning and unmanaged control. Unmanaged and burned plots differed from cut plots due to their higher percentage of grasses and sedges, and of C-strategists, and by lower percentage of trampling- and grazing-tolerant species, erosulate species, and vegetatively mobile guerrilla species. Removal of litter enhanced rosette species and winter-green species. Traditional management increased the compositional variability among plots. Species richness remained almost constant in burned plots, and fluctuated in unmanaged plots, while in all cut plots there was a significant increase in species richness. Within cutting treatments, richness increased relatively more in the plots that were cut by a machine. Results from the 6-year field experiment suggest that mulching is the most cost-effective management regime in floodplain meadows, but only in combination with mowing (cutting with removal of the hay crop) every second or third year, providing the best management practice in the long run.

Key words: conservation management, cost-effectiveness, plant diversity, flooded meadow, plant functional type, seminatural grassland

Introduction

The development and persistence of semi-natural grasslands in temperate Europe is associated with a long history of traditional management — the grazing of domestic animals and haymaking over hundreds and even thousands of years (Kull & Zobel 1991, Austerheim *et al.* 1999, Eriksson *et al.* 2002). Due to the abandonment of traditional small-scale farming during the last century, the number, size and species diversity of semi-natural grasslands have dramatically declined in Europe (Willems 2001, van Dijk 1991, WallisDeVries *et al.* 2002, Poschlod *et al.* 2005). Due to their species rich flora and fauna and their cultural value as part of traditional landscapes, semi-natural grasslands have been recognized as important targets in conservation of biodiversity. The importance of floodplain meadows has been emphasised in particular (Leibak & Lutsar 1996, Truus & Tõnisson 1998, Grootjans *et al.* 2002). Relatively large proportion of flooded meadows escaped agricultural conversion as compared with other meadow types in Europe (Wagner *et al.* 2003), thus optimal management of flooded meadows is of primary interest of nature conservation.

Semi-natural grasslands are usually not feasible for modern agricultural use for various reasons, such as low productivity, small size and difficult access with machinery (Poschlod & WallisDevries 2002, Strijker 2005). If management is not applied, an overgrowing succession will start, resulting in the decrease of species diversity and finally the development of secondary woodland (Zobel *et al.* 1996, Austrheim *et al.* 1999, Truus & Tõnisson 1998, Dupre & Diekmann 2001, Pykälä *et al.* 2005). In order to keep semi-natural grasslands open and ecologically highly functional, nature conservation frequently faces the question of how to maintain optimal community structure and maximize biodiversity with minimal cost. Though the continuation of traditional management (e.g. cutting with a scythe or mixed management with cattle herding) may give the best results from the point of view of conservation (Rosen 1982, Kull & Zobel 1991, Mykelstad & Saetersdal 2003, Pykälä 2004), it is usually unrealistic to apply it on a larger scale, due to its high cost and lack of skilled people. Thus, one must seek optimal management solutions that would preserve the typical structure, function and species composition of semi-natural grassland vegetation, but would be realistic to conduct from the practical point of view. There are alternative management regimes which maintain a low vegetation canopy and an open sward, but they might result in quite a different community composition (Poschlod *et al.* 2005). Also, since the effect of management regimes depends on particular edaphic conditions, management experiments have to be conducted in different types of grasslands, including flooded meadows.

In contemporary Europe, the low input agricultural systems are usually maintained by special support schemes to farmers, or by special management efforts in protected areas (Ostermann 1998, Muller 2002, Strijker 2005). Due to the interest of farmers, who use floodplain meadows for haymaking in national parks or under agri-environmental schemes, conservation managers are faced with the question: what is the least resource consuming but still efficient management regime to conserve floodplain plant communities.

In Estonia, the area of flooded meadows in the 1930s was estimated to be 83 000 ha (Laasimer 1965). Later on, a large proportion of semi-natural grassland was converted either into intensive grassland, forested or simply abandoned from 1950 onwards. The area of flooded meadows was 24 587 ha in 1981 (Aug & Kokk 1983). Leibak and Lutsar (1996) estimated that at the beginning of the 1990s, floodplain meadows still covered an area of 12 500 ha in Estonia. Large areas of floodplain meadows are situated in Soomaa National Park (Leibak & Lutsar 1996).

Traditionally, most meadows in the area were used for haymaking in the summer, but since the surrounding wet plains were sparsely populated, and villages with animal herds were located tens of kilometres apart, grazing after haymaking was not a common practice. Hay was stored in barns that were located in floodplain meadows, and carried away in winter, when the frozen land was more accessible.

We address changes in plant communities under different management regimes. Instead of species composition, we focus on functional traits, which are recommended as a more general approach (Liira *et al.* 2002, 2008, Diaz *et al.* 2004, Pykälä 2004). The response of plant species to changes of management conditions in grasslands has shown to depend on species dispersal ability, but also on other ecological and functional traits (van der Valk 1981, Eriksson & Jakobsson 1998, Hodgson & Grime 1990, Liira & Zobel 2000, Lindborg & Eriksson 2004, Dzwonko & Loster 2007). There is yet no data about the changes in functional trait composition of flooded meadow plant communities in relation to management.

This paper aims to evaluate the impact of five different management regimes: (1) traditional (cutting with a scythe and hay removal), (2) mowing (machine cutting and hay removal), (3) mulching (machine cutting without hay removal), (4) spring burning, and (5) unmanaged control, on trait composition and species richness of the vegetation in a long-term field experiment. We will consider resulting ecological effects together with relative cost of managements, in order to find the most cost-efficient management regime.

Material and methods

Study site

The study was carried out on the Kuusekäära floodplain meadow on the west side of the Raudna River near the centre of Soomaa National Park (58°26´28´´N, 25°5´50´´E), in southwestern Estonia. Mean annual precipitation in the region is 600–650 mm, the mean annual air temperature is 4.5–5.0 °C, ranging between –6.5 °C in January and 17 °C in July (Aunap 2004). The area is characterised by regular early spring flooding and occasional autumn flooding, which continuation is usually more than one-two weeks.

The Kuusekäära flooded meadow is a about 96 ha, of which 47% is still open sward (M. Suurkask pers. comm.). The meadow was annually mown and hay removed until the late 1980s. Management of the meadow was irregular between 1985 and 2000; on average, it was mown once in three years. The vegetation represents a transition between *Festuco rubrae–Deschampsietum* and *Carici caespitosae–Deschiampsietum* communities of wet floodplain grassland site type (Paal 1997) with predominating *Filipendula ulmaria*, *Festuca rubra* and *Deschampsia caespitosa*. The overgrowing part of the meadow is dominated by willow scrubs e.g. *Salix cinerea*, *S. pentandra* and *S. triandra*. The soil is gleysol with a humus layer of 14–18 cm. Most grassland species in the meadow have a short-term persistent or transient seed bank (Wagner *et al*. 2003).

The data on management cost was provided by Soomaa National Park. In 2005, hay was cut in 289 ha of flooded meadows and 244 ha meadows of which the hay crop was removed. At the same time, the total area of flooded meadows in the Park is 2300 ha, and the ideal target of the maximum managed area is 1800 ha, since the rest of the meadows are either inaccessible or too overgrown.

Experimental design and sampling

In 2000, a management experiment was established. The experiment had a rather complex spatially hierarchical design. First, three similar and homogeneous sampling areas of 20 × 50 m were selected at Kuusekäära flooded meadow. Within each sampling area, five 10 × 20 m experimental plots were randomly assigned one of the five experimental treatments (*see* also fig. 1 in Jõgar & Moora 2008): (1) mulching (machine cutting at a height of approximately 15 cm without hay removal); (2) mowing — machine cutting with hay removal; (3) traditional management (cutting hay with a scythe at a height of approximately 5 cm and removal of the hay); (4) unmanaged; and (5) burning in April. The cutting of hay took place in early August. The burning of treatment (4) was skipped in 2003 and 2005, because of the unusually drawn-out spring floods from March until mid-May.

In each experimental plot, four study plots of 2 × 2 m were established. Study plots were split into sixteen 0.5 × 0.5 m subplots, and the occurrence of vascular plant species in each subplot was recorded at the end of June and the beginning of July. The first recording was made before experimental treatments were applied. In total, 960 subplots were surveyed from 2000 to 2005. The plant species nomenclature follows Krall *et al*. (1999).

To consider the local hydrological and soil conditions variation within the Kuusekäära meadow due to the variation of microtopography, we measured the relative altitude of the study plots.

Data treatment

Since the natural small-scale variation of vegetation was remarkably high due to local tussocks and depressions between them, as well as due to natural variation of soil surface microtopography, we choose to analyze the changes in functional composition and species richness of vegetation at experimental plot scale (10 × 20 m), as optimal scale for robust and easily interpretable results.

Different species traits and functional groups were used to analyse functional change of vegetation in response to various management types. In order to characterise changes in functional structure of vegetation, we analysed traits and functional types (Appendix 1) pointed out by previous studies. We aimed to cover 15 traits formerly addressed by studies of grassland vegetation (Boutin & Keddy 1993, Liira & Zobel 2000, Keddy 2002, Song & Dong 2002, Hellström *et al*. 2003, Nygaard & Ejrnaes 2004, Adriaens *et al*. 2006). Data on plant traits were obtained from various databases: BIOLFLOR (Klotz *et al*. 2002), CLO-PLA (Clonal Plants Database, Klimeš & Klimešova 1999), Ellenberg's data base (Ellenberg *et al*. 1991) and Estonian flora (Krall *et al*. 1999) (list of traits in the Appendix 1).

We intended to analyse a wide range of the functional traits of species as a trait complex. In the analyses we used weighted average values of continuous traits and weighted proportions of selected levels of nominal traits, e.g. growth forms and functional traits (for methodology *see* Liira *et al*. 2008). Species frequency in subplots of a study plots within an experimental plot was used as weighting variable. We had to skip several commonly used traits (lifespan e.g. annual/perennial, Raunkiaer life-form, species region of origin), which had hardly any variability in particular grassland, e.g. 97% of species were perennials.

An indirect gradient analysis was performed for the detection of trait compositional changes in plots 10 × 20 m. As preliminary analyses showed that the main differences in vegetation composition were observed between study areas (20 × 50 m), we removed the main effect of the study area and the ordination analysis was applied on the residual values of traits weighted data. For the selection of the optimal method for ordination, various methods (PCA, DCA and NMS) were applied in PC-Ord ver. 5.10 (McCune & Grace 2002). As the gradient lengths were very short (1.036, 0.688 and 0.466 units for three axes) and all ordination techniques provided nearly identical results, the simplest method — partial PCA (pPCA; ter Braak & Šmilauer 2002) — was chosen. MRPP (Multi-Response Permutation Procedures) based on Sørensen distance measure (McCune & Grace 2002) was applied to determine the differences in the trait composition among the different managements or years.

As a second step in analyses, a General Linear Mixed Model analysis was applied for the estimation of the treatment dependent differences in successional changes in species richness and trait composition in 2 × 2 m plots during 6 years. Only linear trend of change in traits was tested since a relatively short experimental period cannot accurately estimate non-linearity (variable year was in model as a continuous fixed factor). The relative altitude of the vegetation plot was used as a covariate and 20 × 50 m study areas as fixed factor. Repeated model design with an unstructured covariance matrix was used to correct for hierarchical design in the experiment. In the model of species richness, year was treated as a fixed categorical factor, as non-linear changes could be expected. The analysis was performed in the procedure MIXED in SAS (SAS Institute Inc. 1989).

The cost-effectiveness analysis was performed by comparing the four management treatments and the unmanaged control, using similarity estimates of pair wise comparisons in MRPP at the end of the experiment (2005) (McCune & Grace 2002). In comparisons we used trait residual composition data partitioned by the main effect of the study area (pPCA; ter Braak & Šmilauer 2002). MRPP statistic was chosen for comparisons, as it takes the variation among plots within a management type into account. The management costs in Soomaa National Park were treated in relative units, based on the costs in 2005 and taking a unit of cost to be equal to the cost of cutting hay with a tractor without hay removal (mulching), as most available management type.

Results

Trait composition

The first three axes of the pPCA describe 62.5%

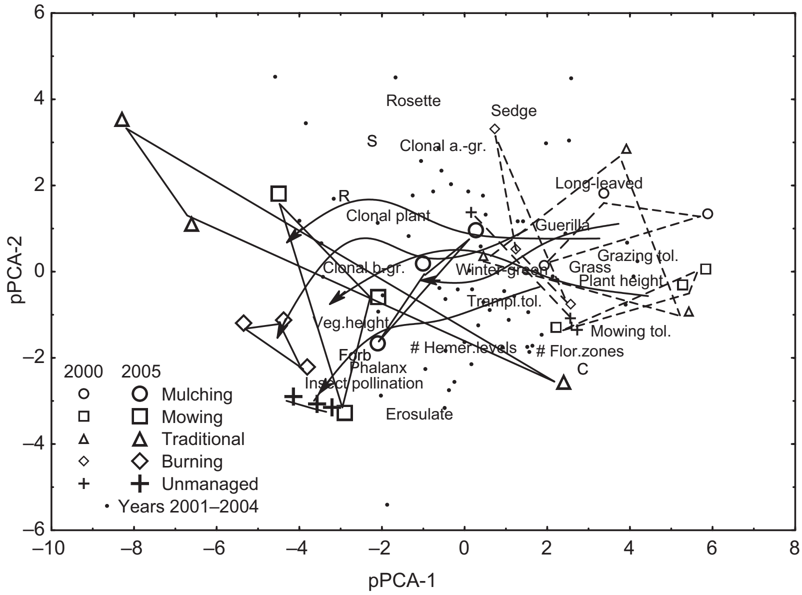

Fig. 1. pPCA ordination of the five experimental treatments in the experimental plots (10 × 20 m) in Kuusekäära flooded meadow, Soomaa National Park. Trend vectors illustrate the average change over three plots of each management type from the year 2000 to 2005. The first pPCA axis describes 32.9% of total variation, and the second pPCA axis combines 16.8%.

(32.9%, 16.8% and 12.8%) of the total variability in functional trait composition (Fig. 1). Experimental plot position along the first pPCA axis could be explained by changes in functional trait composition under management treatments. According to the results of the MRPP test, the functional trait composition between the initial vegetation (2000) and last two years of experiment (2004 and 2005) are significantly different (multiple comparison $P < 0.0034$ with Bonferroni correction).

The trait composition of plant communities in all management regimes resulted in similar successional changes, which is reflected by parallel trajectories on the ordination diagram (Fig. 1). One has to note that in the last year of experiment, a clustering of plots within unmanaged control and burned treatment, as well as high variability in traditional scythe-managed plots, became evident.

The mixed model analysis showed that the proportion of grasses and sedges decreased and the proportion of forbs and insect pollinated plants increased during six years (Table 1). Meadow management, except burning, resulted in significantly lower sward height as compared with unmanaged control. Models revealed also significant treatment-specific changes in trait proportions. In machine-mowed plots, grasses lost their abundance the least and in the traditionally managed plot the most. The average trampling tolerance changed as well, while the most evident increase of the proportion of trampling-tolerant species was in plots mowed with machine, and the smallest in burned plots. Mowing tolerance of vegetation decreased only in unmanaged and burned plots, while increases in traditionally managed plots. We also observed a linear shift from C-strategist to S-strategists in traditionally managed plots, while the opposite was observed in burned and control plots (Table 1).

In the early stages of the experiment, there was higher abundance of phalanx (turf or tussock plants) species, while in the late stages of the experiment, the proportion of guerrilla (vegetatively mobile) species increased.

Long-leaf species loose in their abundance against simple-leaved plants. Erosulate species exhibited uniform positive change in all plots. Rosette species gained mostly in plots with litter removal (mowed and traditionally managed plots) and increased only slightly in plots where litter was not removed (mulched and burned plots) and did not show any change in unmanaged control plots. The effect of litter was similar in the case of winter-green plants, which lost their proportion compared to only-summer-green plants in mulching and control plots, where litter accumulated over years.

Ecological plasticity did not seem to play a

Table 1. GLM test results about responses of plant traits on plot-ID, elevation, treatment and yearly changes (left-hand-side half of the table). In case of significant interaction term Year × Treatment or Year, the slope estimates for significant successional effects are provided (right-hand-side half of the table). Detailed information about slopes by treatment is provided only in the case of significant interaction term Year × Treatment in the model. Parameter significance labels: ns = non-significant, *P < 0.05, **P < 0.01, ***P < 0.001.

	Factor's test P value						The estimated slope of regression					
Trait	Plot	Year × Plot	Elevation (log)	Treatment	Year	Year × Treatment	Pooled trend	Mulching	Mowing	Trad. man.	Burned	Unman. control
Veg. Height												
Vegetation height (log)	0.002	0.002	0.005	0.004	0.009	0.004		–0.010*	–0.010*	–0.010*	–0.010*	–0.010*
Pot. height of plants	0.092	0.098	0.923	0.003	0.009	0.003		–0.183*	–0.298**	–0.483***	–0.050ns	0.065ns
Growth form												
Grass%	0.097	0.100	0.872	0.040	< 0.001	0.040		–1.017***	–0.959***	–1.455***	–1.135***	–1.239***
Sedge%	0.082	0.082	0.489	0.706	< 0.001	0.701	1.486***					
Forb & Legume%	0.019	0.019	0.220	0.078	< 0.001	0.077	–0.689***					
Leaf types												
Long-leaved%	0.002	0.002	0.001	0.658	< 0.001	0.655	–2.201***					
Winter-green%	0.334	0.340	0.036	0.011	0.001	0.011		–1.376***	–0.212ns	0.809ns	–0.521ns	–1.457**
Rosette%	0.315	0.331	< 0.001	0.022	< 0.001	0.023		0.221*	0.412**	0.525***	0.239*	0.067ns
Erosulate%	0.162	0.156	0.043	0.067	< 0.001	0.066	0.756***					
Vegetative spread												
Clonal plant%	< 0.001	< 0.001	0.003	0.024	< 0.001	0.024		–0.048ns	0.133ns	0.676**	0.019ns	0.343*
Phalanx%	0.843	0.839	0.434	0.851	< 0.001	0.858	–1.032***					
Guerilla%	0.031	0.031	0.661	0.970	< 0.001	0.970	0.375***					
Vegetative spread — Above	0.455	0.449	0.606	0.022	0.396	0.022		0.044ns	0.098ns	0.280ns	–1.158**	–1.069*
Vegetative spread — Below	< 0.001	< 0.001	0.003	< 0.001	< 0.001	< 0.001		1.737***	1.670***	1.861***	3.381***	1.615***
Strategies												
Mowing tolerance	0.001	0.001	0.749	0.003	0.057	0.003		0.004ns	0.000ns	0.006*	–0.007*	–0.013**
Grazing tolerance	0.029	0.028	0.028	0.079	< 0.001	0.077	–0.026***					
Trampling tolerance	0.001	0.001	0.035	0.014	< 0.001	0.014		–0.045***	–0.054***	–0.053***	-0.040***	–0.048***
C-stategy	< 0.001	< 0.001	0.108	< 0.001	< 0.001	< 0.001		0.001ns	–0.001ns	–0.005***	0.003***	0.003***
R-stategy	< 0.001	< 0.001	0.000	0.041	< 0.001	0.041		–0.002ns	–0.001ns	< 0.001ns	–0.004**	< 0.001ns
S-stategy	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001		–0.001*	< –0.001ns	0.003***	–0.003***	–0.003***
Pollination type												
Insect pollinated%	0.066	0.067	< 0.001	0.401	< 0.001	0.398	1.887***					
Ecological plasticity												
# floristic zones	0.325	0.321	0.956	0.410	0.001	0.408	–0.004***					
# hemeroby levels	0.196	0.193	0.065	0.084	0.217	0.084						

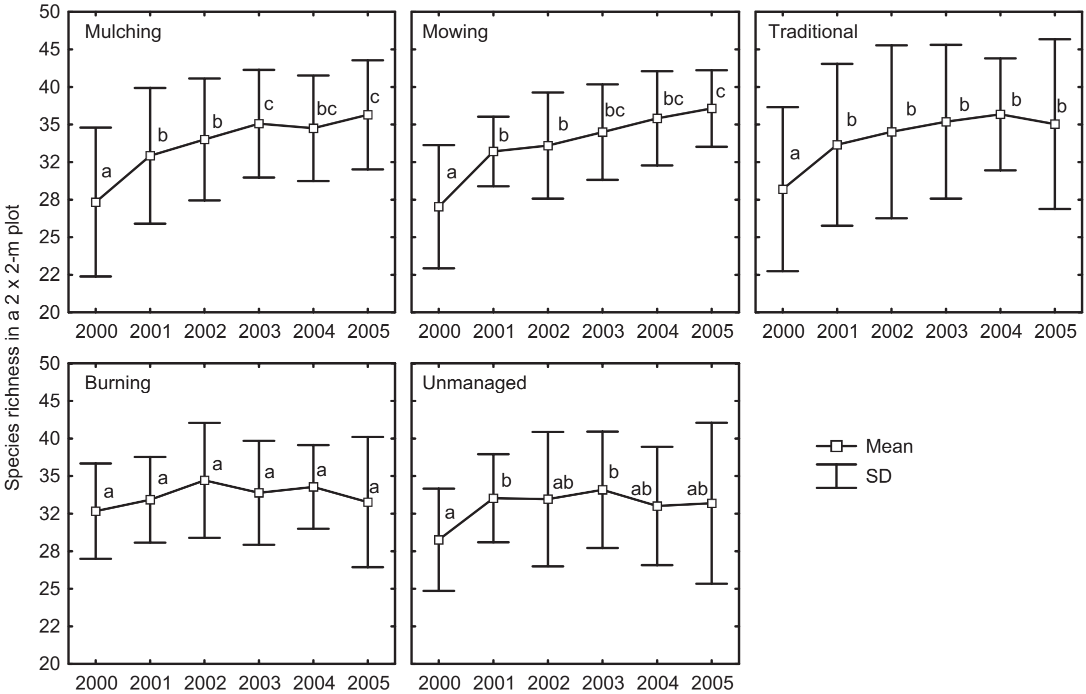

Fig. 2. Average species richness in 12 study plots (2 × 2 m) of the five different management treatments in Kuusekäära flooded meadow. Letters denote homogeneity classes within treatment according to the result of the Tukey multiple comparison test. The vertical axis is log-scaled.

major role in plant response, as weighted number of hemeroby levels did not change during experiment. Local specific species gained in all treatments, as average weighted number of vegetation zones where the species occurs tended to decrease in time.

Species richness

An average species richness of plants in the study plots varied between 28 and 36 species. There was no significant main effects of the management treatment ($F_{4,7}$ = 0.26, P = 0.896) and of the relative altitude of the study plot ($F_{1,7}$ = 0.01, P = 0.946) on species richness in the study plots (2 × 2 m). However, we observed a significant overall change in richness over the years ($F_{5,7}$ = 7.77, P = 0.009), and a significant interaction between the year and the treatment ($F_{20,7}$ = 12.32, P = 0.0012). Species richness remained almost constant in burned plots, and fluctuated in unmanaged plots, while in all cut plots there was a significant increase in species richness (Fig. 2). Within the three hay cutting treatments, richness increased relatively more in the machine-cut plots than in traditionally managed. In both machine treatments, whether the hay crop was removed or not, species richness increased from 28 species to 37 species. In traditionally managed plots, the increase in richness was not as evident. However, the great variability among study sites obscured significant differences between treatments in the last years of the experiment.

Management costs and managed areas in Soomaa National Park

The management costs in Soomaa National Park were treated in relative units, based on the costs in 2005. Management costs were transformed into relative units, taking a unit to be equal to the cost of cutting hay on one hectare with a machine (mulching), as the most common man-

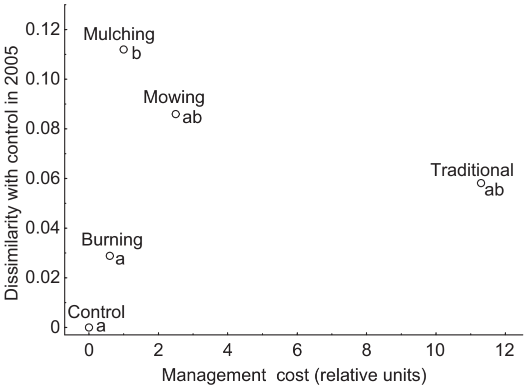

Fig. 3. Dissimilarity of managed plots from unmanaged controls plotted versus relative cost of management. Labels denote significant differences among treatments according to MRPP test with the Bonferroni correction ($P < 0.0125$).

agement practice in recent years. According to this, the cost of control management was 0 units, mulching 1 unit, cutting with a scythe 11.3 units, mowing with removal of hay 2.5 units and controlled burning approximately 0.6 units per ha.

The cost of management *versus* dissimilarity among control and managed plots in 2005 (Fig. 3) one can see that mulching is the most cost-effective in terms of changing the trait composition of grassland.

Discussion

Experimental management in a previously irregularly managed flooded meadow resulted in various changes of community composition. Similarly to Eek and Zobel (1997), and Hellström *et al.* (2006), we realised that changes in plant communities after re-start of the management were slow. Although certain changes in species composition were observed in all plots, the impact of experimental treatments was, however, slightly obscured by the high local environmental variability of the meadow community. At the same time, changes in trait composition were more evident.

Although the connection between trait composition of the vegetation and management is widely accepted (Diaz *et al.* 2004, Liira *et al.* 2008), studies of the response of species with specific traits in temperate or boreal grasslands is rather scarce and comes from grazed grasslands. For instance, Dupre and Diekmann (2001), Hellström *et al.* (2003) and Pykälä (2004) reported several differences in the representation of functional types between abandoned and grazed grasslands — grazing favours therophytes and species regenerating from the seed bank, while abandonment enhances geophytes and vegetatively regenerating plants. We observed a uniform increase of the abundance of guerrilla type species in all plots through time, but we could not detect management dependent response of vegetative regeneration as has been pointed out by Prach and Pyšek (1994) and Köhler (2001).

Our results show that management by hay cutting resulted in lowered canopy height, but revealed also differences in functional trait structure in differently managed grasslands in more detail. Our results suport those of Liira and Zobel (2000), Huhta *et al.* (2001) or Hellström *et al.* (2003) that species with low canopy height — in our case rosette species — are vulnerable to accumulation of the litter on the ground. Cutting with a machine resulted in a higher proportion of grasses, while traditional management favoured more forbs. These differences might be explained by the different cutting heights: on average 15 cm with a tractor and 5 cm with a scythe. The first does not lead to the removal of taller herb species from the community, but mostly suppression of their growth, leaving lower leaves untouched, because non-stratified structure of grassland's herb layer (Liira *et al.* 2002). Generally, management increased the proportion of mowing-tolerant species, but machine-management specifically increased trampling-tolerant species. There was a shift from C-strategist to S-strategist, notably in traditionally managed stands.

Species richness in 2×2 m study plots was significantly influenced by management treatments. In unmanaged and burned plots, richness did not change directionally, while in cut plots, an increase in richness was observed. The most evident increase in species richness was recorded in plots cut by machine, both when the hay crop was removed or not. Traditional management did not result in as steep an increase in richness. The lower cut frees the seedlings from light competition, but evidently results in higher evaporation, which may lead to increased water stress of seedlings (Eckstein 2005). Hölzel and Otte (2004) showed that majority of floodplain meadow resident species need simultaneously light and high moisture for germination and establishment. That hypothesis is supported by the experimental sowing of rare plant *Gladiolus imbricatus* in the same experiment which showed that seedling establishment was enhanced by cutting treatments but it was most successful in the mulching treatment (Jõgar & Moora 2008).

Our results show that regular management will result in increased species richness and changes in trait composition of plant communities. Traditional management — cutting with a scythe and removing of the hay crop — did not give better results from the conservation point of view within the investigated time-scale. The use of a machine for cutting was justified for its cost-effectiveness. Removal of the hay crop had no significant impact on species richness, although different response of growth forms (e.g. smaller abundance of rosette species in mulched plots) may lead to more evident differences in community composition in the future. It has been suggested that the search for optimal restoration methodology should be based on long-term experiments (Hellström *et al*. 2006, Aavik *et al*. 2008). Mulching has been recommended as a feasible management regime also by Kahmen *et al*. (2002), who generalized the results of the 25-year experiment. On the other hand, mulching may nevertheless cause changes in the composition of the flooded meadow plant community via suppression of the emergence of new seedlings, especially those that germinate in autumn (Kupferschmid *et al*. 2000, Poschlod *et al*. 2005) but, the relationship between germination success and litter presence or absence in a wet meadow has proven to be species specific (Kotorova & Lepš 1999, Eckstein & Donath 2005). For example, species with large seeds tend to react more positively to litter presence than species with small seeds (Donath *et al*. 2006). Thus, a longer observation period is needed to study the impact of mulching.

We may conclude, as did Hansson and Fogelvors (2000) and Kahmen *et al*. (2002) in the case of mesophyte grasslands, that burning is not an effective means of management in flooded meadows. It may eliminate the accumulation of litter and invading wooded plants from the meadow, but burning had no positive effect on species richness.

A key challenge of conservation management in seminatural grasslands is to find ecologically reasonable management regimes that require a low financial input (WallisDeVries *et al*. 1998, Hodgson *et al*. 2005, Köhler *et al*. 2005, Poschlod *et al*. 2005). The experimental results indicate that all types of green biomass cutting (independent of the removal of hay crop) caused positive changes in species richness and functional trait composition of the vegetation. At the same time, the cost of mowing exceeds more than twice the cost of mulching, and the cost of traditional management was even higher. In combining the effect of management on vegetation composition and the cost of management, one may argue that mulching may be recommended as an effective means of flooded meadow management. Accumulating hay may result in long-term changes in community composition. But given a relatively high cost of hay removal, 2.5 times the costs of mulching, we recommend that the hay is removed irregularly, e.g. every second year. This should reduce litter-accumulation in the long run and may be used to enlarge the area of managed flooded meadows in the national park.

Acknowledgements

This project was supported by Tartu University (SF0180098s08) and the Estonian Science Foundation (ETF5809, ETF7366). We would like to thank the administration of Soomaa National Park, Jaan Palisaar, Meelis Suurkask, Jaana Vaino and Kai Rünk for their help in establishing the management experiment and gathering field data. Mari Moora, Alexander Harding and two anonymous referees kindly commented the first draft of the manuscript.

References

Aavik, T., Jõgar, Ü., Liira, J., Tulva, I. & Zobel, M. 2008: Plant diversity in a calcareous wooded meadow — management continuity and colonization debt. — *Journal of Vegetation Science* 19: 475–484.

Adriaens, D., Honnay, O. & Hermy, M. 2006: No evidence of a plant extinction debt in highly fragmented calcareous grasslands in Belgium. — *Biological Conservation* 133: 212–224.

Aug, H. & Kokk, R. 1983: *Eesti NSV looduslike rohumaade levik ja saagikus*. — ENSV ATK Informatsiooni ja Juurutamise Valitsus, Tallinn.

Aunap, R. 2004: *Eesti atlas*. — Avita, Tallinn.

Austrheim, G., Olsson, G. A. & Grontvedt, E. 1999: Land-use impact on plant communities in semi-natural sub-alpine grasslands of Budalen, central Norway. — *Biological Conservation* 87: 369–379.

Boutin, C. & Keddy, P. A. 1993: A functional classification of wetland plants. — *Journal of Vegetation Science* 4: 591–600.

Diaz, S., Hodgson, J., Thompson, K., Cabido, M., Cornelissen, J., Jalili, A., Montserrat-Marti, G., Grime, J., Zarrinkamar, F., Asri, Y., Band, S., Basconcelo, S., Castro-Diez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Perez-Harguindeguy, N., Perez-Rontome, M., Shirvany, F., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martinez, M., Romo-Diez, A., Shaw, S., Siavash, B., Villar-Salvador, P. & Zak, M. 2004: The plant traits that drive ecosystems: evidence from three continents. — *Journal of Vegetation Science* 15: 295–304.

Donath, T. W., Hölzel, N. & Otte, A. 2006: Influence of competition by sown grass, disturbance and litter on recruitment of rare flood-meadow species. — *Biological Conservation* 130: 315–323.

Dupre, C. & Diekmann, M. 2001: Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. — *Ecography* 24: 275–286.

Dzwonko, Z. & Loster, S. 2007: A functional analysis of vegetation dynamics in abandoned and restored limestone grasslands. — *Journal of Vegetation Science* 18: 203–212.

Eckstein, R. L. 2005: Differential effects of interspecific interactions and water availability on survival, growth and fecundity of three congeneric grassland herbs. — *New Phytologist* 166: 525–535.

Eckstein, R. L. & Donath, T. W. 2005: Interactions between litter and water availability affect seedling emergence in four familial pairs of floodplain species. — *Journal of Ecology* 93: 807–816.

Eek, L. & Zobel, K. 1997: Effects of additional illumination and fertilization on seasonal changes in fine-scale grassland community structure. — *Journal of Vegetation Science* 8: 225–234.

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W. & Paulissen, D. 1991: Ziegerwerte von Pflanzen in Mitteleuropa. — *Scripta Geobotanica* 18: 1–248.

Eriksson, O., Cousins, S. A. O. & Bruun, H. H. 2002: Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. — *Journal of Vegetation Science* 13: 743–748.

Eriksson, O. & Jakobsson, A. 1998: Abundance, distribution and life histories of grassland plants: a comparative study of 81 species. — *Journal of Ecology* 86: 922–933.

Grootjans, A. P., Bakker, J. P., Jansen, A. J. M. & Kemmers, R. H. 2002: Restoration of brook valley meadows in the Netherlands. — *Hydrobiologia* 478: 149–170.

Hansson, M. & Fogelvors, H. 2000: Management of a semi-natural grassland: results from a 15-year-old experiment in southern Sweden. — *Journal of Vegetation Science* 11: 31–38.

Hellström, K., Huhta, A. P., Rautio, P., Tuomi, J., Oksanen, J. & Laine, K. 2003: Use of sheep grazing in the restoration of semi-natural meadows in northern Finland. — *Applied Vegetation Science* 6: 45–52.

Hellström, K., Huhta, A.-P., Rautio, P. & Tuomi, J. 2006: Search for optimal mowing regime — slow community change in a restoration trial in northern Finland. — *Annales Botanici Fennici* 43: 338–348.

Hodgson, J. G. & Grime, J. P. 1990: The role of dispersal mechanisms, regenerative strategies and seed banks in the vegetation dynamics of the British landscape. — In: Bunce, R. G. H. & Howard, D. C. (eds.), *Species dispersal in agricultural habitats*: 65–81. Belhaven Press, London.

Hodgson, J. G., Montserrat-Marti, G., Tallowin, J., Thompson, K., Diaz, S., Cabido, M., Grime, J. P., Wilson, P. J., Band, S. R. & Bogard, A. 2005: How much will it cost to save grassland diversity? — *Biological Conservation* 122: 263–273.

Hölzel, N. & Otte, A. 2004: Ecological significance of seed germination characteristics in flood-meadow species. — *Flora* 199: 24.

Huhta, A.-P., Rautio, P., Tuomi, J. & Laine, K. 2001: Restorative mowing on an abandoned semi-natural meadow: short-term and predicted long-term effects. — *Journal of Vegetation Science* 12: 677–686.

Jõgar, Ü. & Moora, M. 2008: Re-introduction of a rare plant (*Gladiolus imbricatus*) population to a river floodplain — how important is meadow management? — *Restoration Ecology* 16: 382–385.

Kahmen, S., Poschlod, P. & Schreiber, K. F. 2002: Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. — *Biological Conservation* 104: 319–328.

Keddy, P. 2002: Relative competitive performance of 63 species of terrestrial herbaceous plants. — *Journal of Vegetation Science* 13: 5–16.

Klimeš, L. & Klimešova, J. 1999: CLO-PLA2 — a database of clonal plants in central Europe. — *Plant Ecology* 141: 9–19.

Klotz, S., Kühn, I. & Durka, W. 2002: *BIOLFLOR — Eine Datenbank mit biologish-ökologischen Merkmalen zur Flora von Deutschland*. — Bundesamt für Naturschutz, Bonn.

Kotorova, I. & Lepš, J. 1999: Comparative ecology of seedling recruitment in an oligotrophic wet meadow. — *Journal of Vegetation Science* 10: 175–186.

Krall, H., Kukk, T., Kull, T., Kuusk, V., Leht, M., Oja, T., Reier, Ü., Sepp, S., Zingel, H. & Tuulik, T. 1999: *Eesti taimede välimääraja*. — EPMÜ ZBI, Eesti Loodusfoto, Tartu.

Kull, K. & Zobel, M. 1991: High species richness in an Estonian wooded meadow. — *Journal of Vegetation Science* 2: 711–714.

Kupferschmid, A. D., Stampfli, A. & Newbery, D. M. 2000: Dispersal and microsite limitation in an abandoned calcareous grassland of the southern Prealps. — *Folia Geobotanica* 35: 125–141.

Köhler, B. 2001: *Mechanisms and extent of vegetation changes in differently managed limestone grasslands*. — Ph.D. thesis, ETH Zürich.

Köhler, B., Gigon, A., Edwards, P. J., Krusi, B., Langenauer, R., Lüscher, A. & Ryser, P. 2005: Changes in the species composition and conservation value of limestone grasslands in northern Switzerland after 22 years of contrasting managements. — *Perspectives in Plant Ecology, Evolution and Systematics* 7: 51–67.

Laasimer, L. 1965: *Eesti NSV taimkate*. — Valgus, Tallinn.

Leibak, E. & Lutsar, L. 1996: *Eesti ranna- ja luhaniidud*. — Kirjameeste Kirjastus, Tallinn.

Liira, J., Schmidt, T., Aavik, T., Arens, P., Augenstein, I., Bailey, D., Billeter, R., Bukacek, R., Burel, F., De Blust, G., De Cock, R., Dirksen, J., Edwards, P. J., Hamersky, R., Herzog, F., Klotz, S., Kühn, I., Le Coeur, D., Miklova, P., Roubalova, M., Schweiger, O., Smulders, M. J. M., van Wingerden, W. K. R. E., Bugter, R. & Zobel, M. 2008: Plant functional group composition and large-scale species richness in the agricultural landscapes of Europe. — *Journal of Vegetation Science* 19: 3–14.

Liira, J. & Zobel, K. 2000: Vertical structure of a species-rich grassland canopy, treated with additional illumination, fertilization and mowing. — *Plant Ecology* 146: 183–193.

Liira, J., Zobel, K., Mägi, R. & Molenberghs, G. 2002: Vertical structure of herbaceous canopies: the importance of plant growth-form and species-specific traits. — *Plant Ecology* 163: 123–134.

Lindborg, R. & Eriksson, O. 2004: Effects of restoration on plant species richness and composition in scandinavian semi-natural grasslands. — *Restoration Ecology* 12: 318–326.

McCune, B., Grace, J. B. & Urban, D. L. 2002: *Analysis of ecological communities*. — MjM Software Design, Gleneden Beach, OR.

Muller, S. 2002: Appropriate agricultural management practices required to ensure conservation and biodiversity of environmentally sensitive grassland sites designated under Natura 2000. — *Agriculture, Ecosystems and Environment* 89: 261–266.

Mykelstad, A. & Saetersdal, M. 2003: Effects of reforestation and intensified land use on vascular plant species richness in traditionally managed hay meadows. — *Annales Botanici Fennici* 40: 423–441.

Nygaard, B. & Ejrnaes, R. 2004: A new approach to functional interpretation of vegetation data. — *Journal of Vegetation Science* 15: 49–56.

Ostermann, O. P. 1998: The need for management of nature conservation sites designated under Natura 2000. — *Journal of Applied Ecology* 35: 968–973.

Paal, J. 1997: *Eesti taimkatte kasvukohatüüpide klassifikatsioon*. — Keskkonnaministeeriumi Info- ja Tehnokeskus, Tallinn.

Poschlod, P., Bakker, J. P. & Kahmen, S. 2005: Changing land use and its impact on biodiversity. — *Basic and Applied Ecology* 6: 93–98.

Poschlod, P. & WallisDeVries, M. F. 2002: The historical and socioeconomic perspective of calcareous grasslands: lessons from the distant and recent past. — *Biological Conservation* 104: 361–376.

Prach, K. & Pyšek, P. 1994: Clonal plants — what is their role in succession? — *Folia Geobotanica et Phytotaxonomica* 29: 307–320.

Pykälä, J. 2004: Cattle grazing increases plant species richness of most species trait groups in mesic semi-natural grasslands. — *Plant Ecology* 175: 217–226.

Pykälä, J., Luoto, M., Heikkinen, R. K. & Kontula, T. 2005: Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. — *Basic and Applied Ecology* 6: 25–33.

Rosen, E. 1982: Vegetation development and sheep grazing in limestone grasslands of south Öland, Sweden. — *Acta Phytogeographica Suecica* 72: 1–108.

SAS Institute Inc. 1989: *SAS/STAT® User's guide, version 6*. — SAS Institute Inc., Cary, NC.

Song, M. & Dong, M. 2002: Clonal plants and plant species diversity in wetland ecosystems in China. — *Journal of Vegetation Science* 13: 237–244.

Strijker, D. 2005: Marginal lands in Europe — causes of decline. — *Basic and Applied Ecology* 6: 99–106.

ter Braak, C. J. F. & Šmilauer, P. 2002: *CANOCO reference manual and CanoDraw for Windows user's guide: Software for Canonical Community Ordination (version 4.5)*. — Microcomuter Power, Ithaca.

Truus, L. & Tõnisson, A. 1998: The ecology of floodplain grasslands in Estonia. — In: Joyce, C. B. & Wade, P. M. (eds.), *European wet grasslands: biodiversity, management and restoration*: 49–60. J. Wiley & Sons, New York.

van der Valk, A. G. 1981: Succession in wetlands: a Gleasonian approach. — *Ecology* 62: 688–696.

van Dijk, G. 1991: The status of semi-natural grasslands in Europe. — In: Goriup, P. D. (eds.), *The conservation of lowland dry grassland birds in Europe*: 15–36. JNCC Publ., Newbury.

Wagner, M., Poschlod, P. & Setchfield, R. P. 2003: Soil seed bank in managed and abandoned semi-natural meadows in Soomaa National Park, Estonia. — *Annales Botanici Fennici* 40: 87–100.

WallisDeVries, M. F., Bakker, J. P. & van Wieren, S. E. 1998: *Grazing and conservation management*. — Kluwer Academic Press, Dordrecht.

WallisDeVries, M. F., Poschlod, P. & Willems, J. H. 2002: Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. — *Biological Conservation* 104: 265–273.

Willems, J. H. 2001: Problems, approaches and results in restoration of Dutch calcareous grassland during the last 30 years. — *Restoration Ecology* 9: 147–154.

Zobel, M., Suurkask, M., Rosen, E. & Pärtel, M. 1996: The dynamics of species richness in an experimentally restored calcareous grassland. — *Journal of Vegetation Science* 7: 203–210.

Appendix 1. List of traits with reference on data sources, where the data about species was obtained.

Trait	Comment	Data source
Veg. height		
Vegetation height	Upper limit of vegetation in a study plot	Estimated in field
Pot. height of plants	Weighted average of plant species	Krall *et al*. 1999
Growth form	Grass, sedge, legumes and other forbs, pteridophyte, tree and shrub	Krall *et al*. 1999, BIOLFLOR (Klotz *et al*. 2002)
Leaf types		
Leaf shape	Long-leaved (grass-like, long), simple-leaved (simple, lobate) or pinnate-leaved	BIOLFLOR (Klotz *et al*. 2002)
Leaf persistence over seasons	Winter-green vs leaves only during spring, summer or autumn	Ellenberg *et al*. 1991
Leaf location	Rosette (leaved at shoot base), erosulate (leaves on upright stem) or hemirosette (rosette with leaved stem)	BIOLFLOR (Klotz *et al*. 2002)
Vegetative spread		
Propagation type	Dominant propagation type of plant: clonal, sexual or both. In analyses we use the weighted proportion of ability for clonal propagation	BIOLFLOR (Klotz *et al*. 2002), CLO-PLA (Klimeš & Klimešova 1999)
Clonal growth type	Phalanx, guerilla, both, none	BIOLFLOR (Klotz *et al*. 2002), CLO-PLA (Klimeš & Klimešova 1999)
Vegetative spread		
Above	Clonal growth organs are above-, below-ground or both	BIOLFLOR (Klotz *et al*. 2002), CLO-PLA (Klimeš & Klimešova 1999)
Plant strategies		
Mowing tolerance	Weighted average of plan species tolerance to mowing (1 = low; 5 = high)	BIOLFLOR (Klotz *et al*. 2002)
Grazing tolerance	Weighted average of plan species tolerance to grazing (1 = low; 5 = high)	BIOLFLOR (Klotz *et al*. 2002)
Trampling tolerance	Weighted average of plan species tolerance to trampling (1 = low; 5 = high)	BIOLFLOR (Klotz *et al*. 2002)
CSR-strategies	C, S and R weight variables (value 0 … 1), summing up to 1	BIOLFLOR (Klotz *et al*. 2002)
Pollination type		
Insect pollinated%	Abundance weighted proportion of insect pollinated plant species *vs.* wind and self pollinated plants	BIOLFLOR (Klotz *et al*. 2002)
Ecological plasticity		
No. floristic zones	Weighted average number of floristic zones, where plant species is present	BIOLFLOR (Klotz *et al*. 2002)
No. hemeroby levels	Weighted average number of hemeroby levels (measure of departure from naturalness) listed in BIOLFLOR data base for plant species	BIOLFLOR (Klotz *et al*. 2002)