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The effect of mowing on a previously abandoned meadow: a ten-year experiment

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Abstract: Meadows in the Bílé Karpaty Mountains, SE Czech Republic, are extremely species-rich, with up to 70 species of vascular plants per m^2. In the past decades regular management ceased in some valuable areas and the meadows were abandoned. As a result, *Molinia arundinacea* became a strong dominant there and species diversity markedly declined. Here we present data based on a ten-year observation of such a grassland where management was resumed to restore the high species diversity. After 10 years regular mowing strongly suppressed the dominant *M. arundinacea* but above-ground biomass have not changed significantly. The leaf area index decreased to one half and the proportion of living plant biomass in the layer below 20 cm increased. The mown plot was colonised by plants from neighbouring meadows. The first colonisers were often myrmecochorous. Later plants with higher light demands arrived. The speed of colonisation was constant during the years. The number of species increased with about a factor 4, both in 0.09 and 2.25 m^2 plots. However, the species richness recorded in the neighbouring meadows has not been reached yet. Assuming a constant increase of species richness, we predict that six more years are needed at a scale of 2.25 m^2 and 23 more years at a scale of 0.09 m^2 to attain the species richness of the neighbouring meadows. If species accumulation declines in the meadows which are already species-rich, as predicted by more realistic non-linear models, the restoration process is supposed to take much longer time.

Keywords: long-term experiment, *Molinia arundinacea*, monitoring, mowing, species-rich grassland

Nomenclature: EHRENDORFER (1973)

Introduction

Grasslands are probably the most species-rich plant communities in temperate Europe. Due to a coincidence of historical (WILMANNS 1997) and environmental (JANSSENS et al. 1998) factors, and appropriate management (DUTOIT & ALARD 1996, OOMES & VAN DER WERF 1996, SCHLAPFER et al. 1998) the grasslands in the southern part of the Bílé Karpaty Mountains, SE Czech Republic, are among the richest in Europe (KLIMEŠ et al. 1999). In

Mountains, SE Czech Republic, are among the richest in Europe (KLIMEŠ et al. 1999). In the Bílé Karpaty Mts. several National Nature Reserves (NNR), up to 700 ha in size, have been designated, where species-rich grasslands with scattered *Quercus* trees form the most widespread vegetation type (KOS & MARŠÁKOVÁ 1997). For example, in NNR Čertoryje, including an area of 694.87 ha, over 450 species of vascular plants have been found. Out of them about 40 species are endangered in the Czech Republic (JONGEPIER & JONGEPIEROVÁ 1990). Most rare plants are grassland species, and are concentrated on south-west-faced slopes where up to 70 species have been found per m^2 and 90 species in plots 4 m^2 in size (KLIMEŠ et al. 1999).

The factors responsible for this high species richness are not completely known. Plant co-existence itself can be explained using the available models (PALMER 1994). However, it is not easy to explain why particularly here the regional species pool (ZOBEL 1997) is so large. On the other hand, the daily practice of experts working in nature conservation shows that several factors may reduce the high species richness considerably within a short time (TLUSTÁK 1972, HILLIER et al. 1990). Particularly any type of fertilisation, mulching, and abandonment have serious negative consequences (WILLEMS et al. 1993, HUBER 1994, WILSON et al. 1995, WILLEMS & VAN NIEUWSTADT 1996). The cessation of regular management deserves special attention because at present it is potentially the most significant risk to species-rich grasslands in many regions of Europe (GIBSON & KIRKPATRICK 1989, RYSER et al. 1995, KOTILUOTO 1998, LINUSSON et al. 1998), including Bílé Karpaty. Mesic unmown meadows in the south of the Bílé Karpaty Mts. are usually dominated by *Molinia arundinacea*, until shrubs colonise the abandoned stands. Consequently, the original species richness declines with about a factor of 10 (JONGEPIEROVÁ et al. 1994) or even more in closed-canopy scrub. After the scrub is removed and regular management of the *Molinia* stands is resumed, the species-rich grassland may partly be restored. However, details about the restoration process are poorly known.

In this paper we focus on restoration of abandoned grasslands, not being mown for decades but not yet overgrown by shrubs. We address the following questions:

1. What is the effect of mowing on the structure of the abandoned grassland dominated by *Molinia arundinacea*?
2. Is grassland restoration a continuous process with a constant speed or does the speed change in time?
3. How much time is needed to restore a previously abandoned meadow after regular mowing is resumed?

The study area

The studied grassland is situated in NNR Čertoryje, the Bílé Karpaty Mts., Czech Republic (48° 54' N, 17° 25' E), at an altitude of 440 m. Mean monthly temperatures were 9.4 °C and the mean annual precipitation was 464.1 mm during the last 10 years (meteorological station at Strážnice, 8 km from the plot). The experimental plots were established in a small grassland area, about 0.1 ha, on a SW-faced slope with an inclination of 5°, surrounded by a wood dominated by *Quercus* spp. trees. Except for two narrow meadow strips, each about 5 m wide, there was no direct connection to the neighbouring meadows, situated about more detailed description of the species composition of the surrounding area is given in JONGEPIEROVÁ et al. (1994) and KLIMEŠ et al. (1995).

Methods

The experiment started in June 1989 when two permanent plots were fixed, each 1.5 m × 1.5 m in size. The control (unmown) plot was placed randomly in a fenced area, about 30 m^2 in size. The other plot, mown once a year after the first census in 1989, was randomly placed near the centre of the grassland area, about 8 m from the control plot. The position of the permanent plots was fixed by means of plastic pipes, 1.5 cm in diameter, buried in the soil. During recording, wooden sticks were inserted into the pipes, and on the sticks the corners of a frame were put so that the position of the frame was fixed 2 to 3 centimetres above soil surface. The plot delimited by the frame was divided into 25 subplots, 0.09 m^2 each, by a cord. In these subplots presence of rooted vascular plants was recorded during the second week of June, from 1989 to 1998, usually 1 to 3 weeks before the meadows were cut. Recordings of the individual subplots were made by two to three observers each year, to avoid species omission. The control plot was unmown, except for 1995, when it was mown by mistake, but the hay was left at the plot. Data from the year after were excluded from the regression analyses.

Living above-ground biomass in the mown and unmown stands was estimated using 6 + 6 circular plots, 34 cm in diameter, randomly located nearby the permanent plots. Plants rooting in the circles were cut at the soil surface, separated into layers, each 20 cm thick, and to monocotyledonous (mostly graminoids) and dicotyledonous plants, dried at 90° to constant weight in a drying chamber and weighed. In a single randomly selected sample taken in the mown and control grasslands the leaf area index (LAI) was estimated in the field, using a portable leaf area meter (LI–3000A, LI–COR, inc.).

Meteorological data (mean month temperatures and month sum of precipitation) from the station of Strážnice, 8 km from the plot, were used to assess the effect of the weather on biomass from 1989 to 1998.

Statistical analyses

The effect of mowing was tested by Repeated Measures of ANOVA using the GLM module of SPSS, with treatment (mowing) as between-subject factor and years as within-subject variables ($n = 10$). The year-to-year changes in species composition were evaluated using Detrended Canonical Analysis–DCA (HILL 1979). Species frequency (SF) based on the 25 subplots [%], log transformed before the DCA analysis (log(100*SF+1)), was used as input data. The transformation decreased the impact of plants with higher frequency and increased the effect of rare plants.

Results

In the unmown stand above-ground living biomass did not change from 1989 to 1998 ($y = 10.602 * \text{Year} - 20734$, $r = 0.435$, $P > 0.05$; regression analysis). Similarly, no trend was found for the mown stand ($y = 0.6943 * \text{Year} - 1059.8$, $r = 0.03$; regression analysis).

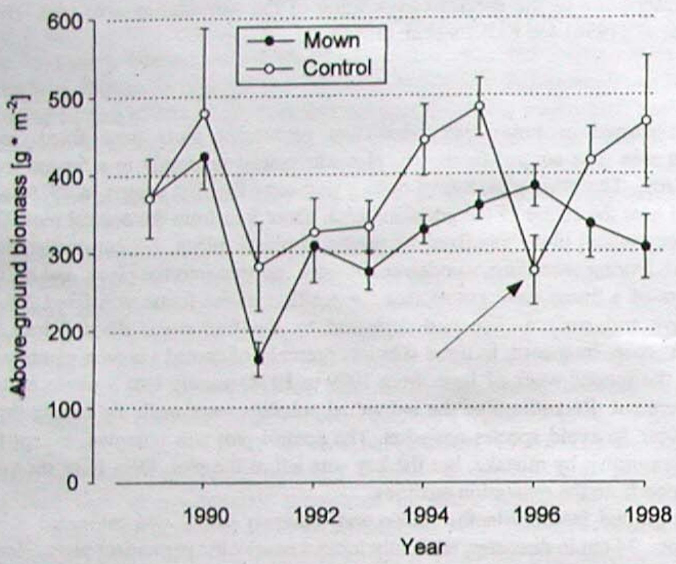

Fig. 1. Above-ground living biomass (mean ± S.E.) of mown and unmown stands from 1989 to 1998. The arrow points to the accidentally mown control plot in 1995.

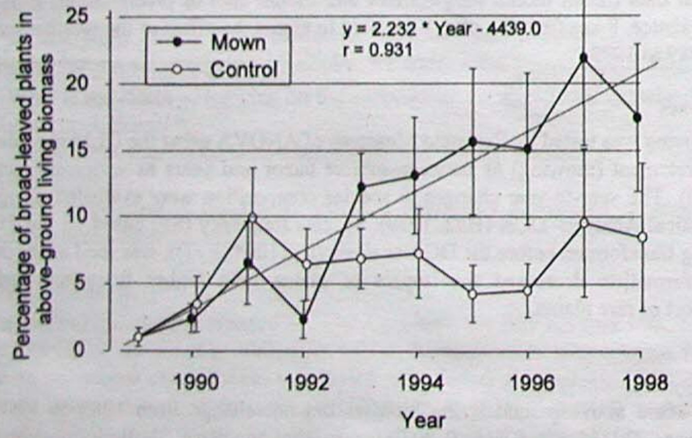

Fig. 2. Percentage of broad-leaved plants (mean ± S.E.) in above-ground living biomass in the mown and unmown stands from 1989 to 1998. The slope of the line fitting the relationship between year and biomass percentage for the unmown stand was not significantly different from zero.

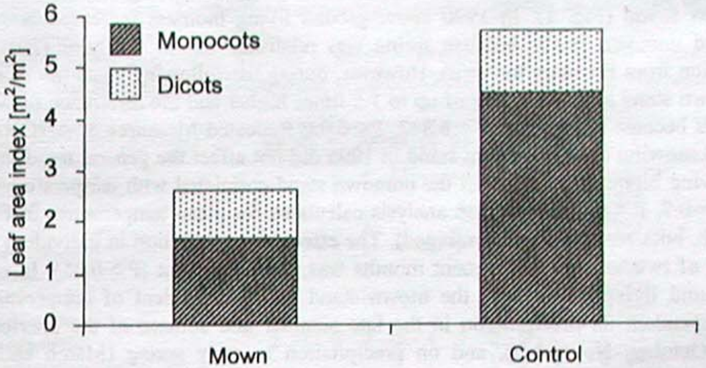

Fig. 3. Representation of mono- and dicotyledonous plants in the leaf area index (LAI) estimated in mown and unmown stands in June 1998.

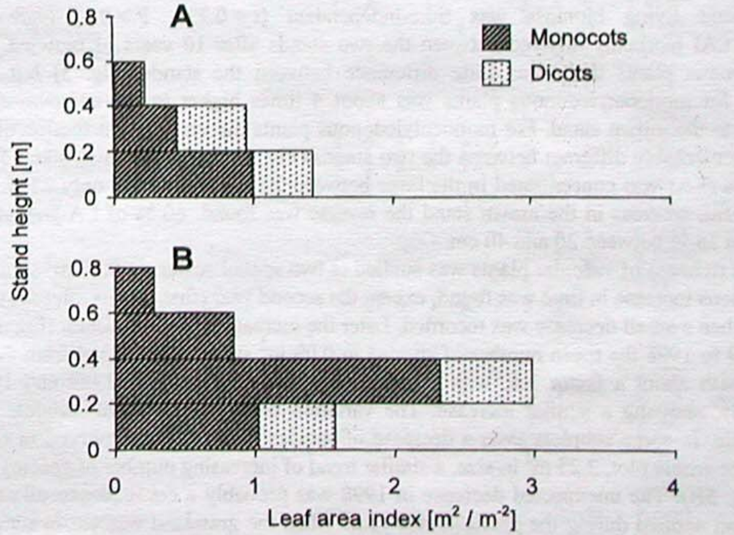

Fig. 4. Vertical distribution of leaf area index (LAI) in the mown (A) and unmown (B) stands in June 1998.

1995 and then declined. However, from 1989 to 1998 no species declined significantly (Table 1). In the control plot one species increased its frequency significantly from 1989 to 1998 (*Carex montana*) and four species declined (*Inula salicina*, *Lathyrus latifolius*, *Potentilla alba* and *Primula veris*).

Before the first mowing no difference between above-ground living biomass of the two stands was found (Fig. 1). In 1990 above-ground living biomass increased both in the mown and unmown stands because spring was relatively wet in that year (105 mm of precipitation from February to April). However, during the following years the biomass of the unmown stand attained values of up to 1.5 times higher and the difference between the two stands became significant ($F = 6.842$, $P < 0.03$; Repeated Measures of ANOVA). The accidental mowing of the unmown stand in 1995 did not affect the general trend in above-ground living biomass. Biomass in the unmown stand correlated with temperatures in late winter ($r \approx 0.7$, $P < 0.05$; regression analysis calculated for mean temperatures in February and March, both separated and combined). The effect of precipitation in individual months and sums of two to three subsequent months was non-significant ($P > 0.05$). In contrast, above-ground living biomass of the mown stand was independent of temperatures but weakly dependent on precipitation in the late summer and autumn of the previous year (August, October, November), and on precipitation in early spring (March and April) ($r \approx 0.7$, $P < 0.05$; regression analysis).

The proportion of dicotyledonous plants in living above-ground biomass of the mown stand increased with time from 1.5 % in 1989 to about 20 % in 1997 (Fig. 2). This increase was strongly significant ($P < 0.0001$), whereas in the unmown stand the course of the above-ground living biomass was time-independent ($r = 0.231$, $P > 0.1$; regression analysis). LAI markedly differed between the two stands after 10 years of mowing. For dicotyledonous plants there was little difference between the stands (Fig. 3) but LAI estimated for monocotyledonous plants was about 4 times higher in the unmown stand compared to the mown stand. For monocotyledonous plants the vertical distribution of the LAI was remarkably different between the two stands (Fig. 4). In the unmown stand 52 % of leaf area (LA) was concentrated in the layer between 20 and 40 cm and only 23 % was below 20 cm, whereas in the mown stand the reverse was found: 60 % of LA was at the ground and 28 % between 20 and 40 cm.

Species richness of vascular plants was studied at two spatial scales. In 0.09 m^2 subplots a monotonous increase in time was found, except the second year (first census after mowing started), when a small decrease was recorded. Later the increase became constant (Fig. 5A). From 1989 to 1998 the mean number of species in 0.09 m^2 subplots increased from 2.2 to 8.0, i. e. with about a factor 3.6, with maxima of 4 and 15 species in 1989 and 1998, respectively, showing a similar increase. The variation between individual subplots was considerable. In some subplots even a decrease of species richness was observed in some years. In the whole plot, 2.25 m^2 in size, a similar trend of increasing number of species was found (Fig. 5B). The unexpected decrease in 1998 was probably a consequence of wrong management applied during the previous two years when the grassland was cut in summer and the hay was left on the plots for several months before it was removed.

The total number of species recorded from 1989 to 1998 in the mown plot was 64 (Table 1) whereas in the control plot 33 species were found (Table 2). In the mown plot the frequency of two out of 23 species significantly increased during the studied period. In 10 species the increase was monotonous. For example, *Agropyron intermedium* was not recorded in 1989 and 1990, but in 1998 it occupied 92 % of the subplots already. An interesting behaviour was observed in *Viola hirta* which reached its maximum frequency in

Table 1: Number of subplots ($n = 25$) occupied from 1989 (89) to 1998 (98) by individual plant species in the mown plot. Tendency of increasing/decreasing number of occupied subplots was tested using linear regression.
r – correlation coefficient. * – P< 0.05, ** – P< 0.01, *** – P< 0.001; non-significant results are not labelled. Dots denote species not recorded in particular years (in calculations replaced by "0").

Plant / Year	89	90	91	92	93	94	95	96	97	98	r
Agropyron intermedium	.	.	5	7	10	12	16	19	20	23	0.994***
Ajuga reptans	.	.	.	.	.	.	.	.	.	1	0.522
Allium scorodoprasum	.	.	.	2	.	.	.	.	1	.	0.027
Anthericum ramosum	.	.	2	2	4	4	3	5	8	6	0.922***
Arabis hirsuta	.	.	.	.	.	.	1	.	.	.	0.174
Asperula cynanchica	.	.	.	1	1	.	.	.	.	.	-0.174
Asperula tinctoria	.	.	.	.	.	.	.	.	.	1	0.522
Betonica officinalis	2	1	2	2	2	4	2	2	2	2	0.224
Brachypodium pinnatum	.	.	.	.	.	.	.	1	3	3	0.777**
Calamagrostis arundinacea	.	.	.	.	.	.	.	.	.	3	0.522
Campanula glomerata	.	.	.	.	1	1	1	1	1	1	0.853**
Carex caryophyllea	.	.	.	.	.	.	.	.	1	1	0.696*
Carex flacca	.	.	.	.	.	.	.	.	1	.	0.406
Carex montana	.	1	2	.	1	.	.	3	3	4	0.658*
Carex tomentosa	.	.	.	.	.	1	3	3	4	14	0.759*
Cerastium holosteoides	.	.	1	.	.	.	.	.	1	.	0.087
Cerastium sp.	.	.	.	.	.	.	.	.	1	.	0.406
Cirsium pannonicum	.	.	.	.	.	1	1	.	.	2	0.577
Cirsium vulgare	.	.	1	.	.	.	.	.	.	.	-0.290
Clematis recta	6	2	8	9	8	9	9	9	7	7	0.423
Colchicum autumnale	1	5	2	2	3	3	4	4	4	5	0.617
Coronilla varia	.	.	.	.	2	3	3	3	3	.	0.561
Crataegus sp.	.	.	.	.	.	.	.	.	2	1	0.625
Cruciata glabra	.	.	.	.	.	1	1	3	2	1	0.746*
Dactylis glomerata	.	.	.	.	.	.	.	1	2	2	0.799**
Erysimum odoratum	.	.	.	.	.	.	5	5	.	.	0.348
Euphorbia cyparissias	.	.	.	1	1	3	3	3	1	.	0.418
Euphorbia virgata	.	.	.	.	.	.	.	.	1	1	0.696*
Festuca rubra	.	.	.	4	2	1	6	.	.	.	0.043
Festuca rupicola	.	.	.	.	.	3	1	1	1	1	0.522
Filipendula vulgaris	1	1	2	2	3	2	2	1	1	1	-0.157
Galium sp.	.	.	.	.	.	.	.	.	1	.	0.406
Galium verum	6	7	10	13	9	12	13	13	14	16	0.901***
Genista tinctoria	.	.	4	4	6	6	3	1	1	2	0.057
Geranium sanguineum	1	.	1	.	.	.	.	.	.	.	-0.609
Gymnadenia conopsea	.	.	.	.	.	.	.	.	7	10	0.698*
Helianthemum ovatum	.	.	.	.	.	.	.	1	.	.	0.290
Inula hirta	.	.	.	.	.	.	.	2	1	2	0.756*
Inula salicina	.	.	1	.	.	.	.	.	.	.	-0.290
Iris graminea	.	.	.	.	.	.	1	1	1	1	0.853**
Knautia kitaibelii	.	.	.	.	.	.	1	1	1	.	0.570
Laserpitium latifolium	2	2	3	4	5	5	4	5	5	6	0.897***
Lathyrus latifolius	4	1	3	5	6	4	6	4	3	4	0.246
Lathyrus niger	.	.	.	.	1	5	2	5	5	1	0.649*
Linum catharticum	.	.	.	.	.	.	1	1	.	.	0.348

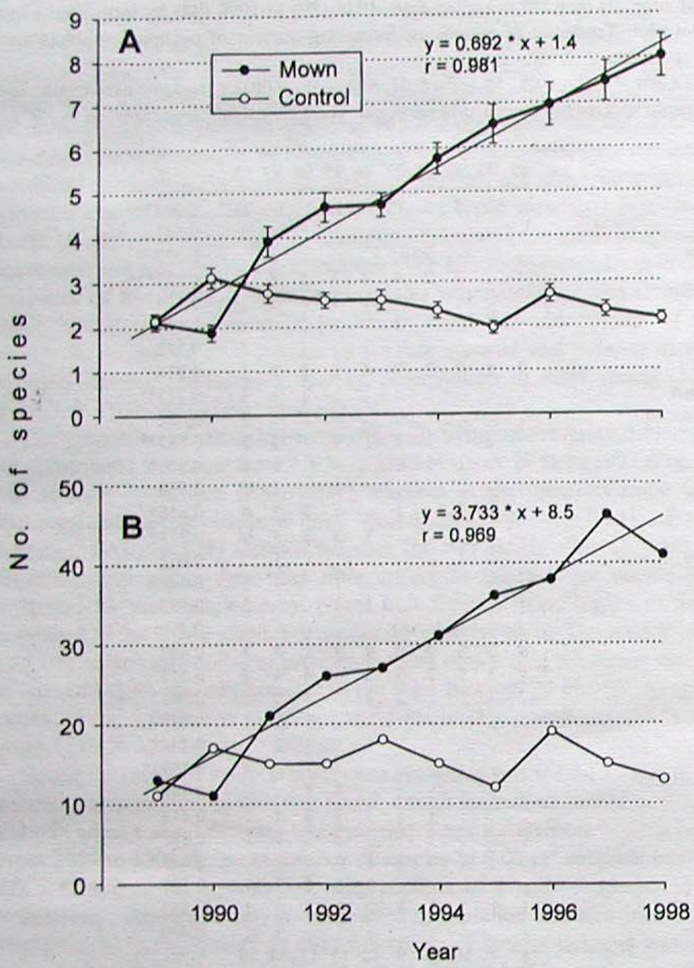

Fig. 5. Number of species (mean ± S.E.) recorded at two scales (A – 0.09 m^2, B – 2.25 m^2) of mown and control plots from 1989 to 1998.

The general trend in species composition is reflected by the DCA scatter plot (Fig. 6). Year-to-year changes of co-ordinates of the mown plot were chaotic and relatively small. In contrast, the distance between positions of the mown plot in subsequent years was approximately the same in the ordination diagram, and the distance to the first census increased until 1998. This indicates a divergence in species composition of the two plots.

Molinia arundinacea	25	25	25	25	25	25	25	25	25	25	–
Myosotis arvensis	.	.	.	1	1	1	.	.	.	.	-0.114
Peucedanum cervaria	1	.	1	2	1	2	2	2	2	2	0.753*
Potentilla alba	2	1	3	6	5	5	5	6	5	4	0.631
Primula veris	.	.	.	1	1	1	5	5	4	10	0.870**
Pulmonaria mollis	.	.	.	.	.	.	.	.	2	1	0.625
Pulmonaria obscura	.	.	.	1	.	.	.	.	.	.	-0.174
Ranunculus polyanthemos	.	.	.	.	.	.	1	2	3	2	0.840**
Salvia pratensis	.	.	.	1	.	.	.	.	.	.	-0.174
Sanguisorba officinalis	1	1	1	1	1	2	2	2	2	2	0.870**
Silene nutans	.	.	.	.	.	.	.	.	1	.	0.406
Symphytum tuberosum	.	.	8	5	2	5	5	8	9	12	0.808**
Tanacetum corymbosum	.	.	.	.	.	3	2	1	1	1	0.533
Taraxacum sect. *Ruderalia*	.	.	.	.	1	3	1	2	1	3	0.751*
Traunsteinera globosa	.	.	.	.	.	.	.	.	.	1	0.522
Trifolium campestre	.	.	.	.	.	2	.	.	.	.	0.058
Trisetum flavescens	.	.	.	.	.	1	1	3	2	.	0.572
Vincetoxicum hirundinaria	1	.	.	1	1	1	1	1	1	1	0.522
Viola hirta	.	.	13	14	15	14	21	19	20	15	0.803**
Number of species in 25 subplots	13	11	21	25	27	32	36	38	46	41	

The order in which species successively colonised the mown plot showed an interesting pattern. The species occurring in the stand at the beginning of the experiment (in 1989) were either large-sized, capable to grow through the closed canopy of *Molinia arundinacea* (e.g., *Clematis recta, Laserpitium latifolium, Lathyrus latifolius, Peucedanum cervaria, Vincetoxicum hirundinaria*) or were shade tolerant (*Betonica officinalis, Colchicum autumnale, Potentilla alba, Sanguisorba officinalis*). The first colonisers, recorded in 1990 and 1991, were represented by species abundant in the neighbourhood of the mown plot, such as *Carex montana* and *Viola hirta.* Shade-tolerant plants with frequent generative reproduction and abundant seedlings were represented by *Symphytum tuberosum*. Three out of the six species which colonised the plot in 1991 and persisted until 1998 were myrmecochorous (*Carex montana, Symphytum tuberosum, Viola hirta*). During recent years many plants of open-canopy stands, which are infrequent in the neighbouring meadows, but may spread efficiently, colonised the mown plot (*Arabis hirsuta, Carex flacca, Erysimum odoratum, Euphorbia virgata, Helianthemum ovatum, Iris graminea, Knautia kitaibelii, Linum catharticum, Pulmonaria mollis, Ranunculus polyanthemos*).

Discussion

In abandoned grasslands nutrients are not removed by mowing. Therefore, plants are better supplied with nutrients, especially potassium, nitrogen and phosphorus (Schaffers et al. 1998), and their above-ground biomass increases. A dense canopy is formed, shading the ground, and excluding light-demanding plants (Bakker et al. 1980, Mitchley & Willems 1995, Kotanen 1997). The effect of litter accumulation is usually even more pronounced. In the *Molinia* stands between 40 to 80 % of above-ground biomass is composed of litter

Table 2: Number of subplots (n = 25) occupied from 1989 (89) to 1998 (98) by individual plant species in the control plot. Tendency of increasing/decreasing number of occupied subplots was tested using linear regression.
r – correlation coefficient. * – P< 0.05, ** – P< 0.01, *** – P< 0.001; non-significant results are not labelled. Dots denote species not recorded in particular years (in calculations replaced by "0").

Plant / Year	89	90	91	92	93	94	95	96	97	98	r
Anthericum ramosum	.	.	.	.	.	.	.	2	2	.	0.522
Arabis hirsuta	.	.	.	.	.	.	.	5	.	.	0.290
Betonica officinalis	3	1	1	1	1	1	1	1	1	1	-0.522
Brachypodium pinnatum	.	3	2	.	.	.	.	.	.	.	-0.527
Carex montana	.	.	.	.	1	2	1	1	1	1	0.680*
Cirsium pannonicum	.	.	.	.	.	.	.	1	1	.	0.522
Cirsium vulgare	.	.	.	1	.	.	.	.	.	.	-0.174
Clematis recta	.	8	8	7	4	5	3	3	4	4	-0.205
Colchicum autumnale	1	3	1	2	2	1	2	2	2	3	0.373
Crataegus sp.	.	2	2	1	1	1	1	1	1	1	-0.097
Euphorbia virgata	.	.	.	.	.	.	.	1	.	.	0.290
Filipendula vulgaris	3	5	2	3	3	3	3	2	3	2	-0.482
Geranium sanguineum	1	.	.	.	.	.	.	.	.	.	-0.522
Gymnadenia conopsea	.	.	.	.	.	.	.	.	.	1	0.522
Inula salicina	1	1	.	.	.	.	.	.	.	.	-0.696*
Knautia kitaibelii	.	.	.	.	.	.	.	.	.	1	0.522
Laserpitium latifolium	.	.	.	.	.	.	1	.	.	.	0.174
Lathyrus latifolius	1	1	.	.	.	.	.	.	.	.	-0.696*
Lathyrus niger	.	1	1	1	1	1	.	1	1	.	-0.114
Molinia arundinacea	25	25	25	25	25	25	25	25	25	25	–
Myosotis arvensis	.	.	.	1	.	.	.	.	.	.	-0.174
Peucedanum cervaria	6	6	4	6	7	5	5	6	6	5	-0.087
Potentilla alba	5	5	5	5	6	5	1	2	1	1	-0.817**
Primula veris	2	5	5	4	1	1	1	.	.	.	-0.788**
Pulmonaria mollis	.	1	1	1	1	.	.	.	.	.	-0.569
Rosa gallica	.	.	.	.	1	.	.	.	.	.	-0.058
Salvia pratensis	.	1	1	1	1	1	.	.	.	.	-0.522
Sanguisorba officinalis	6	7	8	6	6	6	5	7	6	6	-0.334
Symphytum tuberosum	.	3	3	.	1	.	.	3	3	3	0.317
Taraxacum sect. *Ruderalia*	.	.	.	.	.	1	.	1	.	.	0.261
Trifolium or *Medicago* (jv.)	.	.	.	.	.	.	.	1	.	.	0.290
Vicia tetrasperma	.	.	.	.	1	.	.	.	.	.	-0.058
Viola hirta	.	.	.	.	2	1	.	3	2	.	0.453
Number of species in 25 subplots	11	17	15	15	18	15	12	19	15	13	

whereas in regularly mown meadows it is 30–40 % only (KLIMEŠ, unpubl. data). Litter accumulation significantly reduces species richness (MILTON et al. 1997, FOSTER & GROSS 1998, but see HUHTA & RAUTIO 1998), especially at smaller scales (KLIMEŠ, unpubl. data).

The increase of above-ground living biomass in the control plot was small and non-significant. However, it would be stronger if the plot had not accidentally been mown in

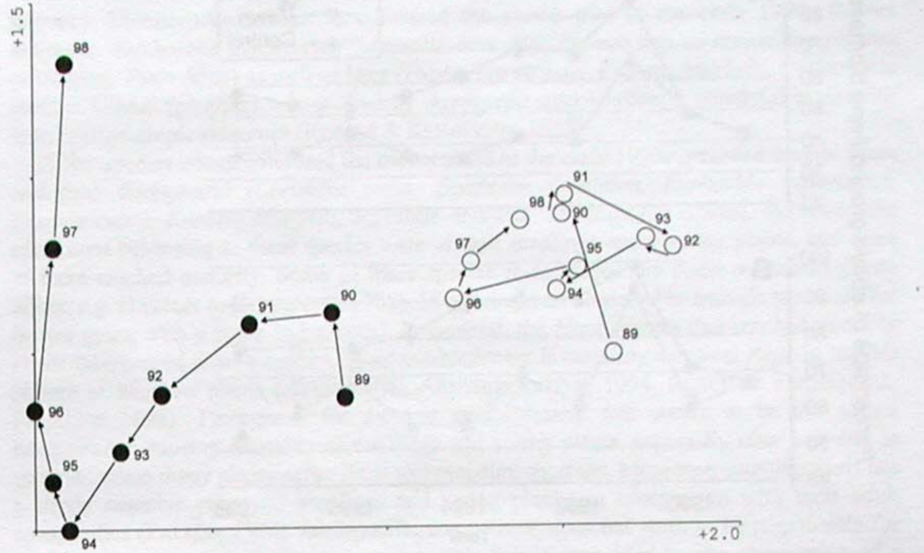

Fig. 6. DCA ordination of mown (full circles) and control (open circles) plots. Input values were species frequencies calculated from 25 subplots, and log transformed before the analysis. The first two axes were used in the scatter diagram.

1995 and the spring in 1991 had not been so dry. Grassland deterioration due to increasing biomass of a dominant plant is known from other types of grasslands (BOBBINK & WILLEMS 1987, DE KROON & BOBBINK 1997). In contrast, the considerable changes in species composition of the mown plot were not accompanied by any change of above-ground living biomass. Our analysis suggests that low early spring temperatures may reduce above-ground biomass in the unmown stand and drought periods may reduce above-ground biomass in the mown stand. Similar effects have been reported by STAMPFLI (1995) from grasslands dominated by *Bromus erectus*. In more open grasslands even stronger effects of drought have been reported by VAN DER MAAREL & SYKES (1997).

The number of species recorded in the mown grassland was relatively high, if compared with data from other regions and countries (GRIME et al. 1988). After ten years the number of species increased with about a factor of 4, reaching 45 species in 1997. This corresponds to about 30 species in an area of 1 m^2 (based on a species-area relationship, calculated for combined subplots: number of species = 43.66 * area $[m^2]^{0.295}$ – 13.880, R^2 = 0.995, DF = 9). Species richness in grasslands of temperate Europe is often comparable or even lower. For example, HOBOHM & HARDTLE (1997) give a mean of 10 species per m^2 in plant communities of Germany. Therefore, the restoration seems to be quite successful. However, in comparison with the number of species found in the neighbouring meadows, where between 60 and 70 species per m^2 have been recorded, the results are rather poor. If the linear trend in species accumulation is retained until the final number of species is reached,

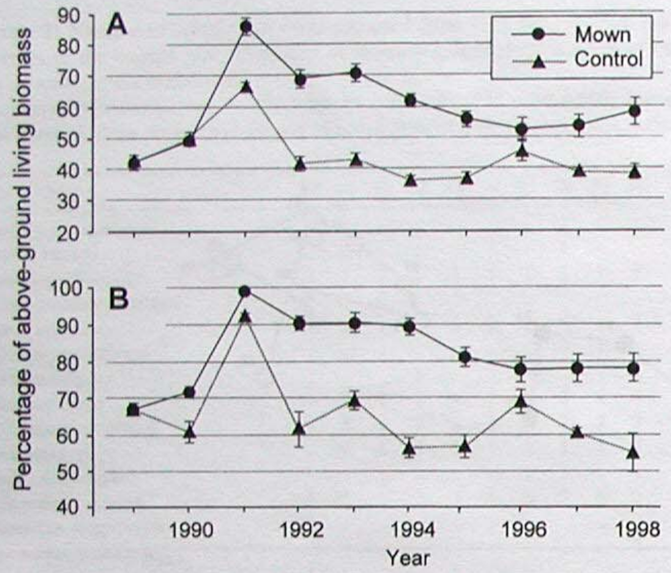

Fig. 7. Percentage of above-ground living biomass (mean ± S.E.) concentrated in the layer 0–20 cm (A) and between 20–40 cm (B) in the mown and unmown stands from 1989 to 1998. In A 100 % corresponds to the total living above-ground biomass, in B to that above 20 cm.

the restoration takes another six years in the 2.25 m^2 plot and 23 years at the scale of 0.09 m^2. Unfortunately, this prediction is not very realistic. It is very likely that sooner or later the accumulation process will slow down, because all easily dispersing plants and plants occurring in the close surroundings will already be present in the restored plot, and a stronger competition in the stand, nearly species-saturated, may also be expected. Therefore, the speed of species accumulation will slow down in future. As a result, the restoration process will be longer than predicted by the previous model, possibly up to several times. Other authors also estimated that the expected species richness in meadows will be restored in 50 years or more (ZOBEL et al. 1996, KINDSCHER & TIESZEN 1998).

The mechanisms of restoration processes are complex and probably change with time. At the beginning seed banks play an important role (MILBERG & HANSON 1993, WILLEMS & BIK 1998, DAVIES & WAITE 1998), together with efficient diaspore dispersal by ants (POSCHLOD et al. 1998) and short-distance spreading in clonal growth (HENSEN 1997). However, the seed bank in species-rich meadows includes only a small proportion of species present in the vegetation (BEKKER et al. 1997, DAVIES & WAITE 1998, KALAMEES & ZOBEL 1998). An analysis of germinating seeds in the soil of the studied grassland at the beginning of the experiment showed that several plants which appeared in the mown plot early after the first mowing, have a large seed bank which was an important source for the establishing populations (e. g., of *Cerastium holosteoides, Campanula glomerata, Carex tomentosa, Festuca rupicola, Primula veris, Ranunculus polyanthemos, Symphytum tuberosum, Tanacetum corymbosum, Taraxacum* sect. *Ruderalia, Viola hirta* – Klimeš,

unpubl.). Myrmecochorous plants colonised the mown plot in the early 1990s (*Carex montana, Euphorbia cyparissias, Myosotis arvensis, Pulmonaria obscura, Symphytum tuberosum, Viola hirta*) as well as later (*Euphorbia virgata, Knautia kitaibelii, Pulmonaria mollis*). Clonal spreading was utilised by *Agropyron intermedium*, a perennial grass with long hypogeotropic rhizomes (KLIMEŠ & KLIMEŠOVÁ 1998).

A few species which colonised the mown stand in the early 1990s persisted several years and then disappeared (*Coronilla varia, Erysimum odoratum, Euphorbia cyparissias, Festuca rubra, Knautia kitaibelii, Myosotis arvensis, Trisetum flavescens*). However, the specimens belonging to these species were always seedlings and younger plants, and none of them reached maturity. Some of these species re-colonised the stand repeatedly (mass effect; e.g. HATTON & CARPENTER 1986). 18 species were recorded in a single year only (or in two years, with a break in between). In contrast, the plant species that reached maturity never disappeared from a subplot. Plant establishment is certainly a critical stage in the life history of meadow plants (RYSER 1990, ARNTHÓRSDÓTTIR 1994, RUSCH & FERNÁNDEZ-PALACIOS 1995). The reason for the low establishment rate seems to be the severe environment, causing mortality of seedlings and young plants, especially after mowing in summer, when many plants suffer from soil moisture shortage. Moreover, mowing itself has a strong negative effect on seedlings and young plants, in comparison with their adult conspecifics (PALMER 1994). Interspecific competition does not seem to be responsible for the high extinction rate in the mown plot. This fact is supported by the observation of a successful establishment of several synanthropic plants in autumn 1994 in plots with a much higher species richness (KLIMEŠ, unpubl.), indicating that niche limitation is hardly a serious problem in the studied plant community (KLIMEŠ et al. 1995). The speed of a restoration process can be increased if seeds from neighbouring meadows are collected and sown in the restored plot (CULLEN et al. 1998). We did not apply this procedure because firstly, natural restoration promoted by the appropriate management is less costly and therefore more attractive for utilisation in other areas, and secondly, we expected the large species pool in the surroundings of the experimental plots to speed up the colonisation process.

Plant establishment in the mown plot was promoted by a remarkable decline of LAI which decreased to 50 % (Fig. 3). The vertical distribution of the LAI was appropriate for young and small plants in the mown plot because most leaves were situated close to the ground so that plants could relatively easily reach the canopy whereas in the control stand the high concentration of leaves between 20 and 40 cm was very unfavourable for smaller and young plants. The vertical distribution of LAI corresponded to the vertical distribution of biomass. About 40 % of above-ground living biomass was concentrated in the layers between 0 and 20 cm, and between 20 and 40 cm at the beginning of the experiment (Fig. 7). The exceptionally dry spring in 1991 reduced plant biomass to about 60 % in the unmown and 40 % in mown stand (Fig. 1). Accordingly, nearly 90 % of above-ground biomass became accumulated in the layer between 0 and 20 cm in the mown stand whereas in the unmown stand it was less than 70 % (Fig. 7A). In 1992 this accumulation returned to the initial 40 % in the unmown stand whereas in the mown stand it decreased very slowly until 1997 and finally, in 1998, it was higher by nearly 20 % than in the unmown stand. Therefore, in the mown stand the ground was not shaded by a dense canopy, and the establishment of new colonisers was easier. Percentage of above-ground biomass in the layer between 0 and 20 cm continuously declined in the mown stand, indicating that the conditions for seedling establishment became worse. This trend was even more pronounced if expressed as the ratio between the biomass in the 20–40 cm layer and the total biomass above 20 cm (Fig. 7B). The remarkable peak observed in 1991 possibly determined the development of the stand during the following 7 years. It seems that without this sharp biomass decrease the canopy would not have been opened so much and the restoration process would have been much slower. The effect of an exceptional season on long-term vegetation development can be expected but has been rarely documented in literature (but see SCHMIDT 1994, VAN DER MAAREL & SYKES 1997).

The experimental plots were situated in a grassland which is more or less surrounded by a woodland. Therefore, plant colonisation from neighbouring meadows was relatively difficult, if compared with grasslands attached to regularly managed areas. Accordingly, in comparison with those cases the restoration process was relatively slow (JONGEPIEROVÁ, unpubl. results). Thus, our results should not be directly transferred to different situations (cf. MULLER et al. 1998). On the other hand, the exceptionally large species pool enhanced colonisation rates. We believe that the restoration process depends very much on local conditions, such as the period of time without management, position and width of barriers limiting diaspore dispersal, density of animal agents dispersing diaspores, soil conditions, etc. To build up a comprehensive model including these factors much more information based on field experiments is needed.

Conclusions

1. The effect of mowing on a meadow abandoned for a long time was remarkable, no matter whether expressed in terms of above-ground biomass, leaf area or species richness.

2. Species richness increased linearly during the first 10 years after regular management was resumed. However, it is predicted that the speed of species accumulation will decrease in future so that it will take several decades, at least, until the stand is completely restored, especially if species richness at small scales is considered.

3. Exceptional events, such as spring drought, which reduce the production of dominant grasses, may speed up the effect of resumed management. It is suggested that they may affect the restoration process over many subsequent years.

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Vliv obnovení pravidelného kosení na louky v Bílých Karpatech

Pravidelné kosení je ve střední Evropě nutnou podmínkou pro existenci luk. Po přerušení pravidelného obhospodařování většinou rychle převládnou vzrůstem vysoké a mohutné druhy a dojde k drastické redukci druhové pestrosti. Proces obnovy louky, která nebyla po řadu let kosena, sice závisí na typu lučního porostu, ale je v každém případě mnohem pomalejší.

Obnova louky kosením byla sledována na jihozápadním svahu v Bílých Karpatech, kde by se v případě pravidelného kosení a při vyloučení hnojení vyskytovaly druhově velmi bohaté louky. Pokus prokázal, že převládající bezkolenec (*Molinia arundinacea*) je sice možno pravidelným kosením potlačit, ale přesto zůstává i po jedné dekádě výraznou dominantou. Počet druhů v průběhu pokusu rostl lineárně, takže je naděje, že při zachování současného typu obhospodařování i v dalších letech bude počet druhů na sledované ploše přibývat. Nicméně, k žádoucímu stavu, tj. k obnově druhové pestrosti srovnatelné s typickými bělokarpatskými loukami, nedojde dříve než za čtvrt století, pravděpodobně mnohem později. Proces obnovy je pravděpodobně možno urychlit, např. doséváním druhů, které se pomalu šíří, vhodným načasováním seče (v letech s teplým létem později) nebo kosením 2× ročně v prvních letech po obnovení kosení. Tím dojde k urychlení první fáze obnovy. Ta však probíhá v každém případě nejrychleji. V důsledku toho se celková doba obnovy zkrátí jen málo.

Obnova mezofilních luk je velmi populární a často úspěšná v mnoha koutech Evropy. Naše výsledky však ukazují, že původně druhově velmi bohaté louky, nyní nekosené a porostlé bezkolencem, obnovit pomocí pravidelného kosení vzhledem k obvyklému trvání projektů prakticky nelze. Z tohoto důvodu nemá udržování pravidelného kosení z hlediska ochrany přírody žádnou alternativu.

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