Flora 206 (2011) 1020–1029

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.de/flora

Effect of long-term cutting versus abandonment on the vegetation of a mountain hay meadow (Polygono-Trisetion) in Central Europe

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ARTICLE INFO

Article history:
Received 7 January 2011
Accepted 13 May 2011

Keywords:
Grassland management
Functional groups
Plant species composition
Diversity and richness
Jizera Mountains

ABSTRACT

The aim of this study was to identify changes in the plant species richness, diversity and composition of a mountain hay meadow (alliance Polygono bistortae-Trisetion flavescentis) after abandonment in comparison with a control cut once per year. The experiment was carried out from 1999 to 2008 in a mountain hay meadow in the Bukovec nature reserve in the north-eastern part of the Jizera Mountains (Jizerské hory, Góry Izerskie, Isergebirge), Czech Republic.

The number of vascular plants species with cover greater than or equal to 1% remained almost the same throughout the study period; however, the total number of vascular plants was higher in the cut treatment after the first four years of the study. The cover of *Festuca rubra*, *Agrostis capillaris*, *Anthoxanthum odoratum*, *Briza media* and *Trifolium repens* was positively affected by cutting. On the other hand, the cover of *Cirsium heterophyllum*, *Geranium sylvaticum*, *Hypericum maculatum*, *Trisetum flavescens* and *Luzula luzuloides* was higher on the abandoned treatment plots.

The main effect of the abandonment on plant species composition was the shift in cover of the dominant species. Despite ten years of contrasting management, changes in the vegetation were relatively small with no shift to a different plant community. Therefore the cutting regime combined with several years of no management may be a suitable management strategy for the maintenance of Polygono-Trisetion grasslands and will not be detrimental to the preservation of the target vegetation.

Introduction

In agricultural regions throughout Europe considerable changes in the utilization of grassland have occurred within the past 100 years. The decline in grassland diversity over the last few decades is threatening the overall biological diversity and is a major conservation problem. Such decline is due to changes in agricultural management (intensive milk husbandry in cowsheds), as only a small proportion of grasslands are now being used for forage production and large areas of marginal grasslands have been abandoned (Hejcman et al., 2008, 2010a; Isselstein et al., 2005). The situation is the worst in less accessible mountain areas with low productivity, where semi-natural grasslands predominate.

Regular cutting or grazing management is necessary to maintain a desirable grassland community structure and cutting is often preferred in cases where high species richness is a primary concern (Hansson and Fogelfors, 2000). Another possible strategy favouring nature conservation is periodic cutting (syn. intermittent), which may maximize faunal and floristic diversity (Billeter et al., 2003), as many species can finish reproducing in those years in which cutting does not take place. On the other hand, the absence of grassland defoliation frequently leads to a decrease in plant species diversity (Pavlů et al., 2005; Pecháčková and Krahulec, 1995), and the abundance of tall species tends to increase as litter accumulation elevates nutrient availability and hinders seedling recruitment (Hejcman et al., 2009; Huhta et al., 2001; Rosenthal, 2010). The responses of individual plant species to grassland abandonment are not straightforward and vary widely. For example Eler et al. (2005) reported an increase in cover of grasses and a decrease in cover of forbs and legumes after abandonment while other authors recorded completely different results (see Gaisler et al., 2004; Hejcman et al., 2005; Huhta et al., 2001; Pavlů et al., 2006). Such differences may be not only due to environmental conditions and the original species composition but also to the management history (Chýlová and Münzbergová, 2008; Moog et al., 2002; Semelová et al., 2008). However, the majority of studies have confirmed that changes in the structure of vegetation can be fatal when management ceases for long periods because of the disparate behaviour of many taxa upon abandonment.

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doi:10.1016/j.flora.2011.07.008

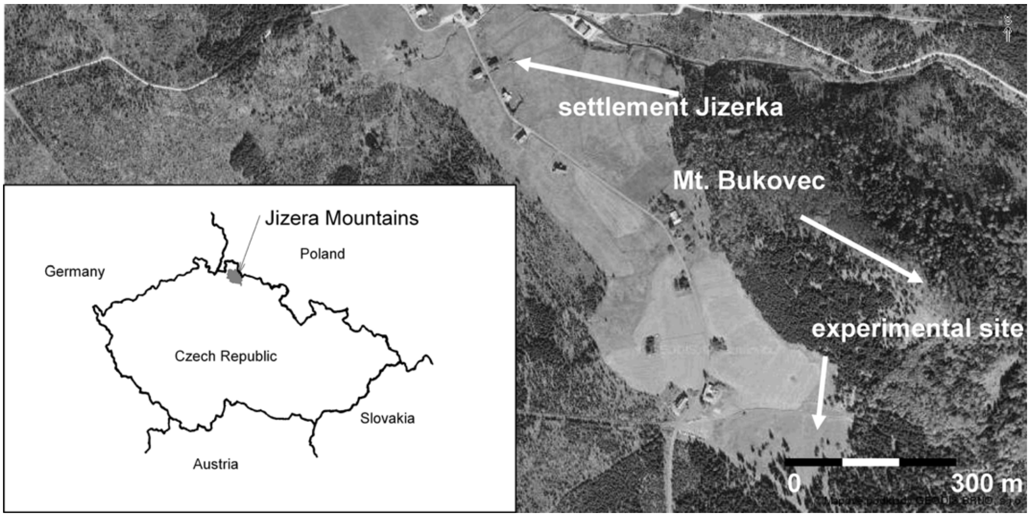

Fig. 1. Location of the Jizera Mountains within the Czech Republic and aerial view (source ©Geodis Brno s.r.o.) of the study area and its surrounding.

Long-term management studies are indispensable because changes in plant species composition after initial management intervention can take many years and periods of early resistance can occur (Bakker et al., 2002; Pavlů et al., 2007). There is a need to determine the underlying factors that control vascular plant species richness and composition in managed grasslands (Klimek et al., 2007).

Mountain hay meadows (alliance Polygono-Trisetion) remain common in the Alps, but in the past, such meadows were also common in the western part of the middle mountains of Central Europe (Chytrý, 2007). However, they are disappearing due to changes in land use involving extensive ploughing and grassland renovation. This occurred rather intensely in the second half of the twentieth century. Nowadays they are threatened by no or inappropriate management and large areas of meadows have been degraded (Chytrý, 2007; Dierschke and Peppler-Lisbach, 2009; Krahulec et al., 1996).

Given the actual low demand for forage from mountain hay meadows and the high cost of management, it is essential to determine how long these grasslands can be left unmanaged without losing their species richness. To address this question, we established a long-term grassland management experiment in the Jizera Mountains on the border between the Czech Republic and Poland.

The following research questions were addressed: (1) How do plant species composition and functional traits change in the ten years after cessation of cutting of mountain hay meadows? (2) How rapidly and when do these changes occur?

Materials and methods

The experiment was carried out from 1999 to 2008 in a mountain hay meadow in the Bukovec nature reserve in the north-eastern part of the Jizera Mts. (Jizerské hory, Góry Izerskie, Isergebirge), Czech Republic (50°48′42″N, 15°21′21″E; Fig. 1). The altitude of the study site is 910 m a.s.l., the average annual precipitation is 1500 mm and the mean annual temperature is 4.5 °C. The bedrock of the Jizera Mts. is mainly granite, but patches of basalt occur at the study site. The following soil chemical properties were recorded in the upper 0–10 cm at the beginning of the experiment: pH/KCl 4.4, plant available P content 5 mg kg^{-1} (very low), plant available K content 198 mg kg^{-1} (good) and plant available Mg content 300 mg kg^{-1} (good) – extracted by Mehlich III reagent (Mehlich, 1984). Prior to the start of the experiment the study site was generally cut once per year and biomass was removed (relatively regular management, at least from 1945). According to the phytosociological nomenclature (Chytrý, 2007), the vegetation of the experimental sites belonged to the alliance Polygono bistortae-Trisetion flavescentis. The dominant species at the beginning of the experiment were *Festuca rubra*, *Agrostis capillaris*, *Trisetum flavescens*, *Cirsium heterophyllum* and *Geranium sylvaticum*. The nomenclature of the plant species follows Kubát et al. (2002).

The experimental treatments were one cut per year with the removal of cut biomass in mid-July (control) and no cutting (unmanaged grassland). Vegetation monitoring was carried out annually in five permanent completely randomised blocks with an individual plot size of 5 m × 5 m before being cut in mid-July. The cover of all vascular plant species was recorded using the percentage scale. Based on the mean height of vascular plants in the regional flora (Kubát et al., 2002), all plant species within the study area were *a priori* categorized according to their main traits: short graminoids, tall graminoids, short forbs and tall forbs. The species with a mean height ≥0.5 m were considered tall and those below this threshold were considered to be short (Appendix B). The plant species diversity was assessed by plant species richness, Simpson's (D) species diversity index and Simpson's (E) species evenness index (Begon et al., 2005).

One-way ANOVA was performed to identify significant differences between treatments within each year for the most abundant plant species, main plant traits, species richness, and D and E indices. Repeated-measures ANOVA was used to evaluate plant species richness, cover of individual species, and cover of main plant traits for the whole study period. Redundancy analysis (RDA, Lepš and Šmilauer, 2003) in the Canoco package (ter Braak and Šmilauer, 2002) followed by a Monte Carlo permutation test was used to evaluate trends in plant species composition (Table 1). A split plot design was used in the permutation to cope with repeated measures. We used 999 permutations in all analyses. Our data form repeated observations along with the baseline data (measurements performed before the introduction of treatments), and thus the interactions between treatments and year were the most important variables. A standard biplot ordination diagram as well as the principal response curves (PRC) constructed by the CanoDraw program (ter Braak and Šmilauer, 2002) were used to visualise the results of the analyses. The resulting PRC showed the extent and directions of development of grassland vegetation under experimental treatment compared with the control treatment (Lepš and Šmilauer, 2003). The vertical scores of the PRC curves were based on the scores of environmental variables from RDA; the sampling time

Table 1
Results of the RDA of cover estimates. U (unmanaged), C (cutting) = treatments; plot ID = plot identifier; % explained variability = species variability explained by the 1st (all) ordination axes (which measure the explanatory power of the explanatory variables); *F*-ratio = *F* statistics for each particular analysis; *P*-value = corresponding probability value obtained by the Monte Carlo permutation test. Tested null hypotheses: A1 – the temporal trend in the species composition is independent of the treatment and A2 – there are no directional changes in time in the species composition that are common to both treatments.

Tested hypotheses	Explanatory variables	Covariables	% explained variability 1st (all) axes	*F*-ratio 1st (all) axes	*P*-value 1st (all) axes
A1	Year*U, Year*C	Year, Plot ID, Block	15.5	16.1	0.001
A2	Year, Year*U, Year*C	Plot ID, Block	16.1 (27.3)	16.9 (16.5)	0.001 (0.001)

indicators were used as covariables and the interaction between the treatment levels and sampling times were used as environmental variables.

Results

Species richness

At the beginning of the experiment a total of 59 vascular plant species (18 graminoids and 41 forbs) were recorded across the study site. The mean cover of all recorded species is given in Appendix A. During the ten years of the study 79 vascular plant species were recorded (22 graminoids, 55 forbs and the seedlings of two woody species). In 1999 the mean number of vascular plants with cover ≥1% ± SE (standard error) was 16.8 ± 0.7 and 17.6 ± 0.7 in the unmanaged and cut treatments, respectively. The number of plants in this category was similar in both treatments throughout the study period (Table 2 and Fig. 2). At the beginning of the experiment in 1999 the mean number and ±SE of all species per plot was 34.0 ± 0.9 and 34.0 ± 0.5 in the unmanaged and cut treatments, respectively. The number of all vascular plants, without reference to cover, increased significantly during the study in the cut treatment (Table 2 and Fig. 2).

However, the occurrence of some of the newly recorded species was frequently random and only temporary (*Hieracium pilosella*, *Filipendula ulmaria*, *Veronica officinalis*, *Carex pallescens*, *Nardus stricta*). The cover of the species *Trifolium spadiceum* and *Hieracium aurantiacum* exceeded 1% for only a short time and subsequently decreased below 1%. *Botrychium lunaria* occurred sporadically in some study plots, whereas *Arnica montana* and *Gymnadenia conopsea* occurred only once in the cut plots.

The D species diversity index and E species evenness index were similar at the beginning of the experiment, whereas the D species diversity index was significantly lower in unmanaged treatment plots after seven years compared to the control ($P < 0.05$, one way ANOVA) and the E species evenness index was significantly lower after eight years ($P < 0.05$, one way ANOVA).

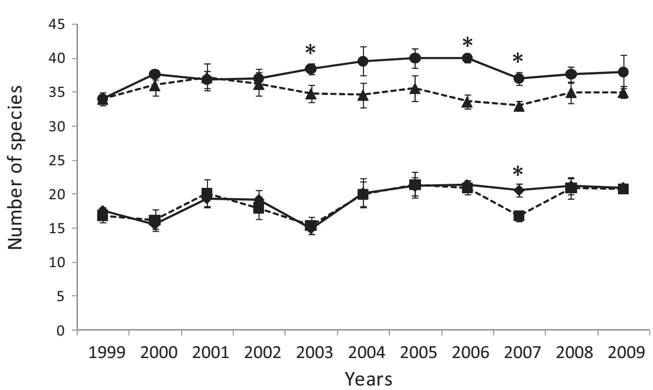

Fig. 2. Number of vascular plant species in treatment plots (per 25 m^2): total species regardless of cover for cutting (●) and unmanaged (▲) treatments, species with cover ≥1% for cutting (♦) and unmanaged (■) treatments for years 1999–2008. Standard errors are indicated by vertical lines. Significant differences between treatments within each year ($P < 0.05$, ANOVA) are indicated by an asterisk.

Plant species composition

Significant differences between the study treatments and remarkable changes over time independent of treatment were detected by redundancy analysis (Table 1). The species that thrived best under the cut treatment were *Festuca rubra*, *Briza media*, *Trifolium repens* and *Ranunculus acris*. The species associated with the unmanaged treatment were *Alopecurus pratensis*, *Lathyrus pratensis*, *Hypericum maculatum* and *Cardaminopsis halleri*. Those species that were not strongly affected by the treatments were *Potentilla erecta*, *Silene dioica*, *Crepis mollis* subsp. *hieracioides* and *Bistorta major* (Fig. 3).

PRC showed that the diversification in plant species composition created by the different treatments had already begun by the second year of the study (Fig. 4). Species with negative PRC scores had a higher abundance in the cut treatment whereas species with positive PRC scores had a higher abundance in the unmanaged treatment.

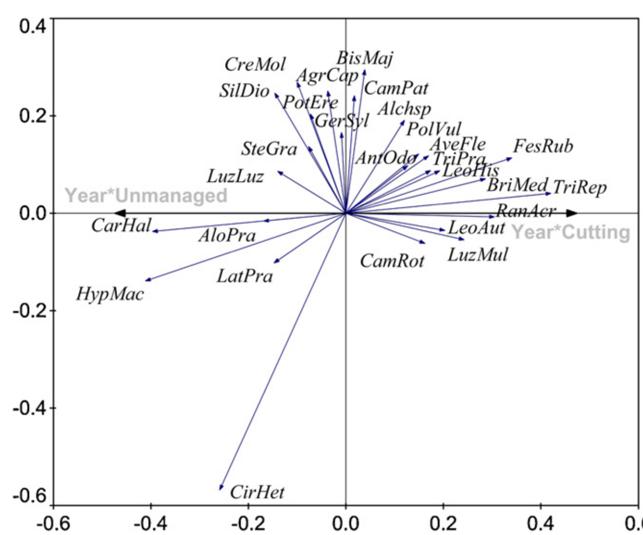

Fig. 3. Ordination diagram showing the results of the RDA. * indicates interaction of environmental variables; species abbreviations: AgrCap – *Agrostis capillaris*, Alchsp – *Alchemilla* sp., AloPra – *Alopecurus pratensis*, AntOdo – *Anthoxanthum odoratum*, AveFle – *Avenella flexuosa*, BisMaj – *Bistorta major*, BriMed – *Briza media*, CamPat – *Campanula patula*, CamRot – *Campanula rotundifolia*, CarHal – *Cardaminopsis halleri*, CirHet – *Cirsium heterophyllum*, CreMol – *Crepis mollis* subsp. *hieracioides*, FesRub – *Festuca rubra*, GerSyl – *Geranium sylvaticum*, HypMac – *Hypericum maculatum*, LatPra – *Lathyrus pratensis*, LeoAut – *Leontodon autumnalis*, LeoHis – *Leontodon hispidus*, LuzLuz – *Luzula luzuloides*, LuzMul – *Luzula multiflora*, PolVul – *Polygala vulgaris*, PotEre – *Potentilla erecta*, RanAcr – *Ranunculus acris*, RumAce – *Rumex acetosa*, SilDio – *Silene dioica*, SteGra – *Stellaria graminea*, TriFla – *Trisetum flavescens*, TriPra – *Trifolium pratense*, and TriRep – *Trifolium repens*.

Table 2
Results of repeated measurements ANOVA (time, treatment, time × treatment) of dominant plant species, functional groups and number of plant species. *F* represents value derived from *F* statistics in repeated measurements ANOVA and *P* represents related probability value.

	Effects					
	Time		Treatment		Time × treatment	
	F-ratio	*P*-value	*F*-ratio	*P*-value	*F*-ratio	*P*-value
Agrostis capillaris	2.62	0.010	50.63	<0.001	3.52	0.001
Alopecurus pratensis	3.37	0.002	4.74	0.032	1.35	0.220
Anthoxantum odoratum	3.80	<0.001	10.40	0.002	0.93	0.500
Bistorta major	1.75	0.091	2.67	0.106	0.45	0.903
Briza media	4.29	<0.001	46.40	<0.001	1.87	0.070
Cardaminopsis halleri	6.88	<0.001	25.96	<0.001	4.58	<0.001
Cirsium heterophyllum	0.43	0.91	38.71	<0.001	1.38	0.210
Festuca rubra	5.33	<0.001	222.23	<0.001	10.23	<0.001
Geranium sylvaticum	1.57	0.14	30.56	<0.001	0.82	0.600
Hypericum maculatum	10.18	<0.001	175.93	<0.001	10.18	<0.001
Luzula luzuloides	1.18	0.316	5.03	0.028	1.04	0.417
Meum athamanticum	2.54	0.01	9.53	0.003	0.40	0.931
Ranunculus acris	3.61	<0.001	5.74	0.019	4.83	<0.001
Rhinanthus minor	5.21	<0.001	40.78	<0.001	4.80	<0.001
Rumex acetosa	3.59	0.001	6.96	0.010	1.54	0.149
Trifolium repens	8.99	<0.001	77.56	<0.001	6.74	<0.001
Trisetum flavescens	12.00	<0.001	7.34	0.008	1.40	0.200
Total graminoids	1.87	0.069	81.41	<0.001	2.64	0.010
Tall graminoids	3.41	0.001	21.96	<0.001	1.34	0.231
Short graminoids	3.60	<0.001	75.54	<0.001	4.13	<0.001
Total forbs	8.40	<0.001	83.87	<0.001	4.81	<0.001
Tall forbs	3.14	0.003	2003.18	<0.001	6.74	<0.001
Short forbs	5.23	<0.001	31.33	<0.001	2.52	0.013
Number of all plant species	2.06	0.043	16.08	<0.001	1.92	0.06
Number of plant species ≥1%	9.00	<0.001	0.16	0.687	1.36	0.22

Graminoids

The cover of graminoids (both tall and short) was significantly higher in the cut than in the unmanaged treatment during the experiment (Fig. 5a and b). Short graminoids responded significantly to the cut treatment after two years whereas tall graminoids responded significantly after nine years. *Festuca rubra*, *Agrostis capillaris*, *Briza media* and *Anthoxanthum odoratum* in particular showed a significant increase in cover in the cut treatment (Fig. 6). On the other hand the cover of *Luzula luzuloides* and *Alopecurus pratensis* in the cut treatment significantly decreased throughout the study, with an initially rapid decrease after which it was maintained at a lower level over the course of the experiment. The cover of *T. flavescens* decreased in both the cut and unmanaged treatment but the cover in the latter remained significantly higher.

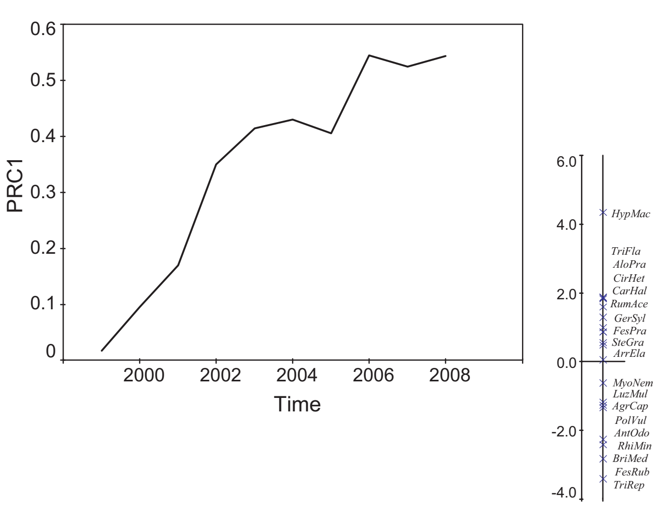

Fig. 4. Principal response curves for the unmanaged treatment (—) during the experiment. The *x*-axis corresponds to time, and the *y*-axis is the first principal component, showing the main differentiation of the plant communities. The cutting treatment was taken as a reference – zero line (thus the score for parameters in the cutting treatment is 0 in all times, and consequently, is represented with a line identical to the *x*-axis). The one-dimensional diagram on the right shows the species scores on the RDA axis. The species showing the best fit to the model are plotted as crosses on the line to the right of the graph. For species abbreviations see Fig. 3.

The proportions of the majority of graminoids differed significantly over the years, with the exception of *Luzula luzuloides* (Table 2).

There was a significant effect of the time and treatment interaction on the proportions of total and short graminoids, but not in the case of tall graminoids (Table 2). Only two graminoids, *Festuca rubra* and *Agrostis capillaris*, were significantly influenced by the interaction between time and treatment.

Forbs

The absence of management significantly increased the cover of tall forbs over the course of the experiment, but the cover of short forbs was significantly higher in the cut treatment. The proportion of tall forbs started to increase significantly in the unmanaged treatment after one year without management. However, the response of short forbs was not as straightforward, as their cover in the cut treatment increased significantly after seven years (Fig. 5c and d).

The cover of *Cirsium heterophyllum*, *Geranium sylvaticum*, *Hypericum maculatum* and *Rumex acetosa* (tall forbs) was significantly higher in the unmanaged treatment (Table 2 and Fig. 7). On the contrary the cover of *Meum athamanticum*, *Trifolium repens* and *Rhinanthus minor* (short forbs) significantly increased in the cut treatment over the course of the experiment. The proportions of other less abundant forb species, such as *Bistorta major*, *Veronica*

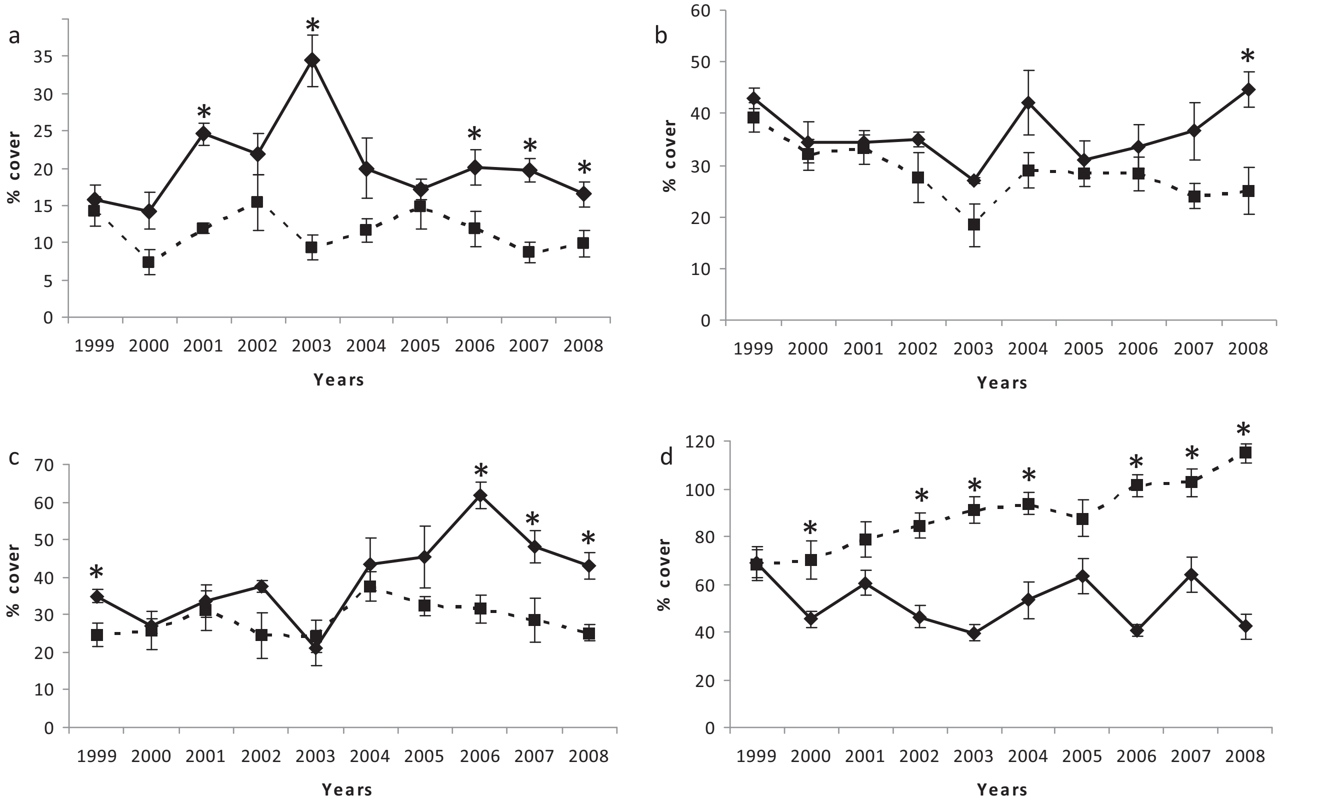

Fig. 5. Changes in cover (%) of functional groups: (a) short graminoids, (b) tall graminoids, (c) short forbs, and (d) tall forbs for cut (♦) and unmanaged (■) treatments for years 1999–2008. Standard errors are indicated by vertical lines. Significant differences between treatments within each year ($P < 0.05$, ANOVA) are indicated by an asterisk.

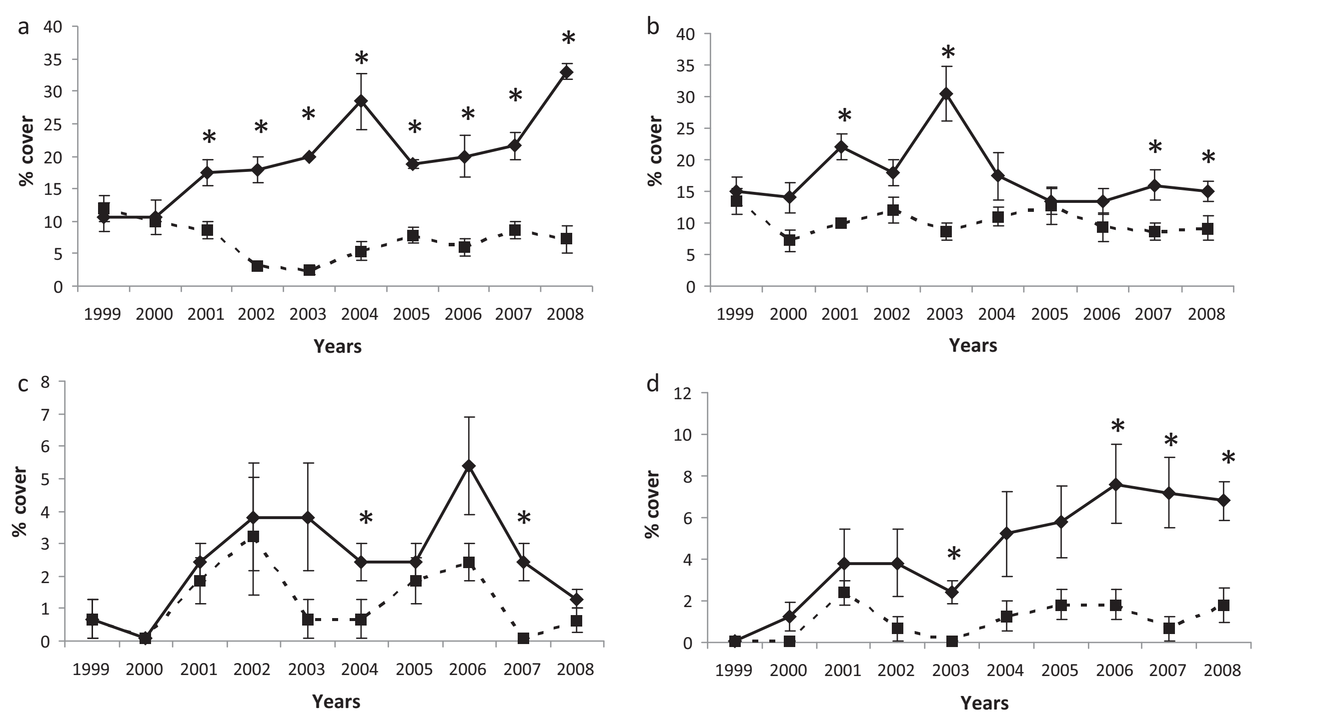

Fig. 6. Changes in cover (%) of (a) *Festuca rubra* agg., (b) *Agrostis capillaris*, (c) *Anthoxanthum odoratum*, and (d) *Briza media* for cut (♦) and unmanaged (■) treatments for years 1999–2008. Standard errors are indicated by vertical lines. Significant differences between treatments within each year ($P < 0.05$, ANOVA) are indicated by an asterisk.

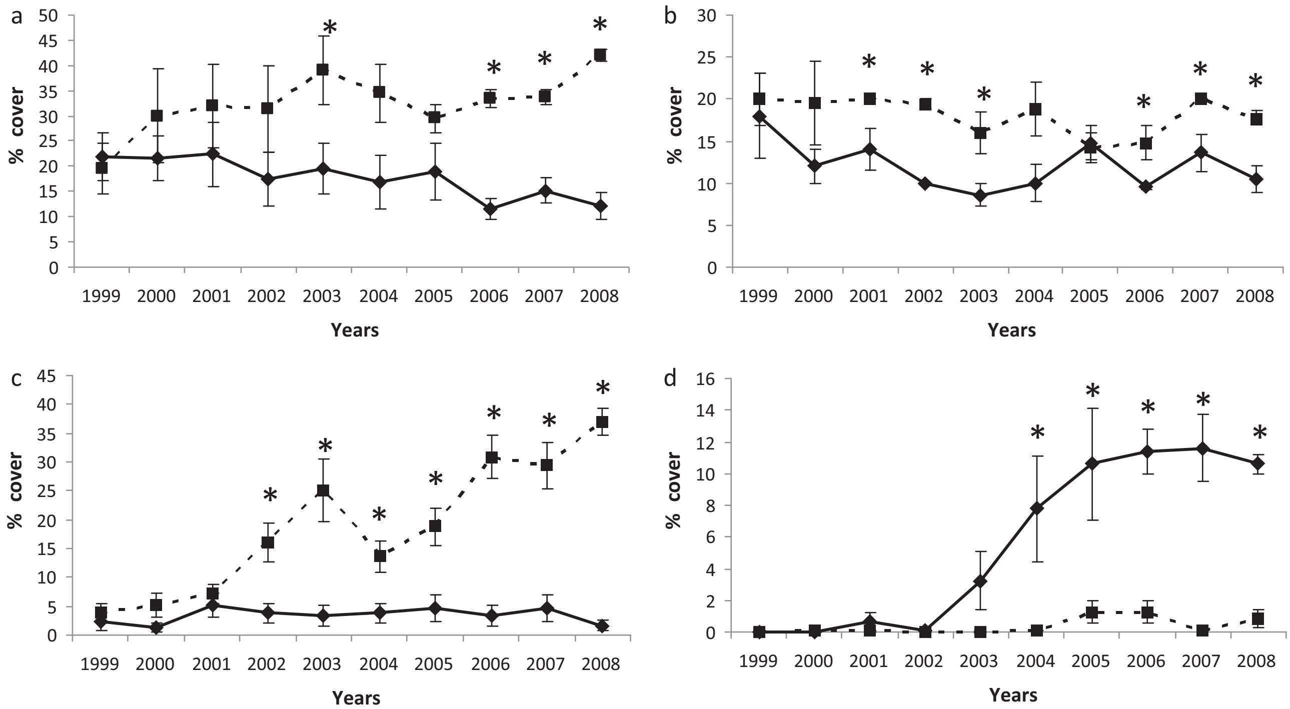

Fig. 7. Changes in cover (%) of (a) *Cirsium heterophyllum*, (b) *Geranium sylvaticum*, (c) *Hypericum maculatum*, and (d) *Trifolium repens* for cut (♦) and unmanaged (■) treatments for years 1999–2008. Standard errors are indicated by vertical lines. Significant differences between treatments within each year ($P < 0.05$, ANOVA) are indicated by an asterisk.

chamaedrys, *Vicia cracca*, *Potentila erecta*, *Crepis mollis* subsp. *hieracioides* and *Achillea millefolium*, did not change significantly under either treatment during the experiment.

Only four of the forbs (*Cirsium heterophyllum*, *Geranium sylvaticum*, *Bistorta major* and *Potentila erecta*) remained relatively stable with no significant changes over the course of the study.

There was a significant effect of the time and treatment interaction on the total cover of forbs (both tall and short) (Table 2). Species that were affected by this interaction were *Hypericum maculatum*, *Ranunculus acris*, *Trifolium repens* and *Rhinanthus minor*.

Discussion

Species richness

The 79 plant species recorded during the ten years of this experiment comprised 75.5% of the total species richness of the surrounding grasslands detected by Pavlů and Burda (1999). The floristic composition was affected by the local micro-relief, which allows small-scale floristic differentiation, reflecting spatially variable moisture conditions (Nardion < Trisetion) and the presence of basalt in the dominant granite bedrock. Therefore, although the study area belongs to the alliance Polygono-Trisetion some species from the alliance Nardion (e.g. *Botrychium lunaria*, *Arnica montana*, *Nardus stricta*) also occurred, as they are present in the vicinity of the experimental area.

Despite abandonment, none of the species with a cover ≥1% disappeared from the study plots during the experiment, although their proportions changed considerably. This shows the high plasticity of the existing species to a change in management. Our study revealed that the number of vascular plants with a cover ≥1% was not affected by the different treatments whereas the total number of vascular plants, regardless of cover, was higher in the cut treatment after the first four years of the study. It should be noted that three new species that appeared during the study with a low frequency of occurrence (*Botrychium lunaria*, *Gymnadenia conopsea* and *Arnica montana*) are considered threatened in the Czech Republic (Holub and Procházka, 2000). *Botrychium lunaria* and *Arnica montana* predominantly occur in the alliance Nardion. *Botrychium lunaria* is a rhizome-geophyte and may develop from belowground organs; therefore it can remain invisible for several years. Nevertheless, the presence of sparse species was subject to variation. Therefore interpretation of results based on species with low cover should be carried out with care because of the potential to confuse the conclusions. Moreover it seems that a ten-year study period is too short to reveal substantial changes. However, the higher total species richness in the cut than in the unmanaged treatment recorded in our study is consistent with the results of other authors (Hansson and Fogelfors, 2000; Pavlů et al., 2005; Ryser et al., 1995; Smith and Rushton, 1994; Wahlman and Milberg, 2002).

In contrast to our results, Hellström et al. (2006), Bakker et al. (2002) and Hejcman et al. (2010b) found no effect of abandonment on the number of vascular plant species and Huhta and Rautio (1998) even reported higher species diversity in unmanaged meadows. A possible explanation for their results could be that their cutting regime eliminated tall growing species, which did not happen in our experiment. Therefore a temporary increase in species richness due to management cessation in some short-term studies may create the illusion that abandonment is more desirable from the nature conservancy point of view (Bakker et al., 2002).

Plant traits and plant species composition

Only tall forbs increased their cover due to abandonment because, as strong competitors, they do not tolerate disturbance.

However, short graminoids and short forbs preferred managed grassland due to the better light conditions with more opportunity to colonise the open space. It seems that this mechanism is the key factor for promoting plant coexistence, as reported by Klimeš and Klimešová (2002). However, different species responses and functional traits were observed by other authors (e.g. Eler et al., 2005; Hellström et al., 2006; Huhta et al., 2001). These different responses may be due not only to site-specific situations and different time of cutting, but also to the oceanity-continentality gradient and as well as the South-North gradient covered by the different investigated sites. It should also be noted that the effect of past land use may be even more important than the effect of some abiotic conditions (Chýlová and Münzbergová, 2008).

The positive effect of cutting on the cover of *Festuca rubra* and *Agrostis capillaris* is well documented by other studies of temperate grasslands in mountain areas [e.g. Pecháčková and Krahulec, 1995 (Nardo-Agrostion); Krahulec et al., 2001 (Nardion and Polygono-Trisetion); Huhta and Rautio, 1998; Hellström et al., 2006]. On the other hand, Mašková et al. (2009) observed a positive effect of abandonment on the proportion of *Agrostis capillaris* in an acidophilous meadow (Polygono-Trisetion) in the Šumava Mts, and Stampfli (1992) on poor soil in Switzerland (Mesobromion/Trisetion). This was probably due to the timing of cutting, as *Agrostis capillaris* is a late-growing species that is favoured by late cutting. Moreover it seems that the cover of *Agrostis capillaris* depends not only on management, but also on the nutrient status of the soil, as mentioned by Olde Venterink and Güsewell (2010). And finally, it should be noted that although *Agrostis capillaris* was more abundant on managed plots in the study by Huhta and Rautio (1998), it also occurred frequently on all of their experimental grasslands. This is consistent with our experiment in which *Agrostis capillaris* was also remarkably abundant in all unmanaged plots, where its cover remained relatively constant during the experiment.

The positive effect of cutting on *Anthoxanthum odoratum* is consistent with the results of Hansson and Fogelfors (2000), who reported an increase in *Anthoxanthum. odoratum* in cut meadows in southern Sweden on soils with a medium nutrient status and pH of 5.5. However it contradicts the results of Huhta and Rautio (1998) and Stampfli (1992). These differences could be due to the different types of plant community according to local nutrient and moisture conditions. The high sensitivity of *Anthoxanthum odoratum* to shading in tall grassland might explain the positive effect of cutting on its abundance. On the other hand abandonment may create better conditions for *Anthoxanthum odoratum* on dry and nutrient poor soils.

Broad-leaved forbs usually suppress other plants in abandoned meadows that lack expansive tall grasses (Huhta et al., 2001). In our experiment the diagnostic species of the Polygono-Trisetion alliance (Chytrý, 2007), *Cirsium heterophyllum*, was the dominant tall forb, and thus suppressed other plants.

The rapid increase in the proportion of *Hypericum maculatum* in the unmanaged treatment is consistent with the results of other authors from investigations in mountain hay meadows in Central Europe (Hejcman et al., 2005; Krahulec et al., 2001; Pavlů et al., 2007). However Mašková et al. (2009) found no significant difference in the cover of *Hypericum maculatum* between cut and abandoned mountain grasslands (Polygono-Trisetion) in the Šumava Mts after ten years. The higher altitude (1150 m a.s.l.), a very nutrient-poor acid soil, and the dominance of *Deschampsia cespitosa* in the Šumava stand are probably responsible for these differences.

The higher cover of *Trifolium repens* in the cut treatment probably reflected its intolerance of shade (Grime et al., 1988). The positive effect of defoliation management on the cover of *T. repens* is consistent with other studies from various grasslands throughout Europe (Belsky, 1992; Correll et al., 2003; Hejcman et al., 2010b). However, Stampfli (1992) included *T. repens* as one of the species that increased their cover on abandoned plots because of their ability to use the improved nutrient and water resources. This difference in the behaviour of *T. repens* may be due to differences in the ecological conditions of the study stands. Moreover, Stampfli (1992) studied the grasslands for only four years and thus it is not known whether this result can be extrapolated into later years. In our experiment, *Trifolium repens* started to increase progressively in the cut treatment after only five years.

Our results confirmed that *Geranium sylvaticum* is a characteristic species of abandoned meadows, as reported for meadows in the middle boreal zone (Huhta and Rautio, 1998), the Central European mountains (Krahulec et al., 2001) and the European Alps (Spiegelberger et al., 2006). It is generally regarded as a problematic species in recently abandoned meadows because it often spreads at the expense of uncommon or rare plant species characteristic of traditionally managed meadows. However, it is notable that, in England, *Geranium sylvaticum* is a rare species and is accepted as an indicator of good ecological conditions in British hay meadows (Pacha and Petit, 2008).

Conclusions

Our ten-year study assessed the impact of the cessation of cutting on the plant species diversity and the composition of vegetation in a species-rich mountain hay meadow (Polygono-Trisetion). The total number of plant species regardless of cover was higher in the cut treatment after the first four years of the study. However the number of species with a cover $\geq$1% was the same in both treatments throughout the experiment. The main effect of the abandonment on plant species composition in our experiment was the change in abundance of some of the dominant species (e.g. *Festuca rubra*, *Cirsium heterophylum*, *Geranium sylvaticum*, *Hypericum maculatum*), but there was no change in the overall plant community. Ten years of contrasting management resulted in relatively small changes in plant species composition, but these rather slow changes are still in progress and therefore monitoring of grassland management requires really long-term studies. The main practical message of the study is that some types of mountain grasslands can be left unmanaged for several years without substantial changes in plant species composition and, that such lack of management is not detrimental to the preservation of the target vegetation. Given the contemporary low demand for forage from Polygono-Trisetion grasslands and the high price of grassland management, cutting management combined with several years of no management may be a suitable strategy for the maintenance of Polygono-Trisetion grasslands.

Acknowledgements

The study was supported by the projects VaV ME SP/203/179/07 and MA 0002700604. We gratefully acknowledge Karel Prach and the anonymous reviewers for their useful comments. We are grateful to Antonín Urban, František Paška, Oliver Correll and Renata Hujerová for their help with the fieldwork.

Appendix A. Average percentage cover of species for cutting (C) and unmanaged (U) treatments (five replicates each) for years 1999–2008. "+" indicates cover less than 1%.

	1999		2000		2001		2002		2003		2004		2005		2006		2007		2008	
	C	U	C	U	C	U	C	U	C	U	C	U	C	U	C	U	C	U	C	U
Agrostis capillaris	15	13	14	7	22	10	18	12	31	9	17	11	13	13	13	9	16	9	15	9
Achillea millefolium	5	5	+	2	+	+	+	+	+	+	2	1	2	2	2	+	4	2	2	+
Alchemilla sp.	7	7	7	9	7	9	4	7	4	9	7	11	8	11	7	7	8	9	9	5
Alopecurus pratensis	8	4	4	3	+	2	+	4	+	3	0	+	+	2	+	2	+	2	0	2
Anemone nemorosa	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthoxanthum odoratum	+	+	+	+	2	2	4	3	4	+	2	+	2	2	5	2	2	+	1	+
Arnica montana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	0
Arrhenatherum elatius	+	+	+	+	+	+	+	+	+	+	+	+	+	1	+	+	+	1	0	1
Avenella flexuosa	+	+	+	+	+	+	+	+	+	0	+	+	+	+	1	+	2	+	1	0
Bistorta major	5	6	3	4	6	8	3	7	2	4	7	8	7	5	4	4	5	7	2	4
Botrychium lunaria	0	0	0	0	+	+	0	0	+	0	+	+	+	+	+	0	0	0	0	0
Briza media	+	+	1	+	4	2	4	+	2	+	5	1	6	2	8	2	7	+	7	2
Campanula patula	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Campanula rhomboidalis	0	+	+	+	+	+	+	+	+	+	0	+	+	0	+	+	+	+	0	0
Campanula rotundifolia	+	+	+	+	+	+	+	+	+	+	+	+	2	1	3	+	1	+	+	+
Cardaminopsis halleri	+	+	+	+	2	1	3	3	+	1	2	2	+	2	+	2	+	3	+	3
Carex ovalis	+	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex pallescens	0	0	+	+	+	0	0	0	+	0	+	0	+	+	+	0	0	0	+	0
Carex pilulifera	+	0	+	0	0	0	0	0	0	0	+	0	+	+	+	0	0	0	+	0
Carlina acaulis	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cerastium holosteoides	+	+	0	0	0	0	+	0	0	0	0	+	+	0	0	0	0	0	0	0
Cirsium heterophyllum	22	20	22	30	22	32	18	31	20	39	17	35	19	30	12	33	15	34	12	42
Crepis mollis subsp. *hieracioides*	6	4	3	2	6	3	4	2	2	2	6	9	7	7	4	6	8	6	7	7
Deschampsia cespitosa	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Elytrigia repens	+	0	0	+	0	0	0	+	0	+	0	+	0	+	+	+	0	+	0	+
Epilobium montanum	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0	+	0	0
Euphrasia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	0
Festuca pratensis	+	+	+	+	+	+	+	+	+	+	0	1	0	1	0	1	+	+	+	+
Festuca rubra	11	12	11	10	17	9	18	3	20	2	28	5	19	8	20	6	22	9	33	7
Filipendula ulmaria	0	0	0	+	+	+	0	+	+	+	0	+	0	+	0	+	0	+	0	+
Galeopsis sp.	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium mollugo agg.	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0
Galium saxatile	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Geranium sylvaticum	18	20	12	20	14	20	10	19	9	16	10	19	15	14	10	15	14	20	10	18
Gymnadenia conopsea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	0	0	0
Hieracium aurantiacum	0	0	0	0	+	+	+	0	+	+	+	0	+	+	+	0	+	0	+	+
Hieracium laevigatum	+	+	0	+	+	+	0	+	0	+	+	+	+	0	+	0	+	+	+	+
Hieracium pilosella	0	0	0	0	+	0	+	0	0	0	+	0	+	0	+	0	+	0	+	0
Holcus mollis	+	+	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Hypericum maculatum	2	4	1	5	5	7	4	16	3	25	4	14	5	19	3	31	5	29	2	37
Juncus filiformis	0	0	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Lathyrus pratensis	0	0	0	+	0	+	0	+	0	+	0	+	0	+	0	+	+	+	0	+
Leontodon autumnalis	0	+	0	+	0	+	0	0	0	+	0	0	0	0	0	+	+	0	0	0
Leontodon hispidus	1	+	+	3	+	1	+	+	+	1	+	1	2	+	3	+	1	+	2	1
Leucanthemum ircutianum	+	+	+	+	+	+	+	+	+	+	+	0	+	+	+	+	+	0	+	+
Luzula luzuloides	12	7	4	3	4	10	4	7	3	7	4	8	4	6	4	9	4	6	3	5
Luzula multiflora	+	+	+	+	+	+	+	+	+	+	+	+	1	+	1	+	1	+	+	+
Lychnis flos-cuculi	+	0	0	+	+	+	+	+	+	0	+	0	+	+	+	0	+	0	+	+
Meum athamanticum	11	7	10	5	6	6	10	6	6	5	10	7	7	6	15	11	10	7	10	7
Myosotis nemorosa	+	+	+	+	+	2	+	+	+	+	+	2	+	+	0	+	0	+	0	+
Nardus stricta	0	0	0	0	+	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0
Phyteuma spicatum	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Plantago lanceolata	0	+	+	+	+	+	0	0	+	0	+	0	+	0	+	0	+	0	+	+
Poa chaixii	0	3	0	2	0	4	0	3	0	2	0	2	0	2	+	2	+	2	0	4
Poa pratensis	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Poa trivialis	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygala vulgaris	+	+	+	+	1	+	1	0	+	+	1	0	3	+	4	0	+	+	1	0
Potentilla erecta	5	2	4	2	4	4	4	4	1	2	6	5	4	3	7	3	4	7	5	3
Ranunculus acris	2	4	2	3	4	4	4	2	2	1	4	3	3	3	2	3	10	2	5	4
Ranunculus repens	+	+	+	0	0	0	0	+	0	+	0	0	+	0	0	0	0	0	0	+
Rhinanthus minor	+	+	1	+	4	+	11	+	1	+	3	+	2	+	3	+	4	+	1	+
Rumex acetosa	4	3	+	+	+	+	+	3	+	1	1	4	2	2	+	3	+	1	+	+
Senecio nemorensis agg.	0	+	0	+	0	+	0	+	0	+	0	+	0	+	0	+	0	+	0	+
Silene dioica	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Stellaria graminea	+	+	0	0	0	0	+	+	+	+	+	5	+	+	0	0	0	+	+	+
Taraxacum sect. *Ruderalia*	+	0	+	+	+	+	+	+	+	+	+	0	0	0	0	0	+	0	+	0
Trifolium pratense	+	+	+	+	+	+	+	+	+	+	+	+	1	+	3	+	+	+	+	+
Trifolium repens	+	0	+	+	+	+	+	+	3	+	8	+	11	1	11	1	12	+	11	+
Trifolium spadiceum	0	0	0	0	+	0	0	0	+	0	+	0	2	0	+	0	+	+	0	0
Trisetum flavescens	11	13	14	13	7	4	7	9	+	4	3	10	1	6	+	5	2	2	+	2
Trollius altissimus	+	+	+	+	+	1	+	+	+	1	+	+	+	+	+	+	+	+	0	+
Vaccinium myrtillus	+	0	0	0	0	0	0	0	0	0	+	0	0	0	+	0	0	0	0	0
Veratrum album subsp. *lobelianum*	0	+	0	+	0	+	0	+	0	+	0	+	0	+	0	+	0	0	0	+

Veronica chamaedrys	9	6	3	4	6	4	3	2	2	3	3	2	3	3	4	3	4	1	2	3
Veronica officinalis	0	0	0	0	0	+	0	0	0	0	+	0	0	0	0	0	0	0	+	0
Vicia cracca	3	3	2	3	2	1	1	2	+	+	2	1	2	3	2	5	2	+	+	2
Viola tricolor	0	0	0	0	0	0	+	0	0	0	0	+	+	0	+	0	0	0	0	0
Seedlings																				
Acer pseudoplatanus	0	0	0	0	0	0	0	0	0	0	+	+	0	0	0	0	0	0	+	+
Picea abies	0	0	0	0	0	0	0	+	0	+	0	+	0	+	0	0	0	0	0	+

Appendix B. Functional groups of the study sward.

Tall graminoids	Short graminoids	Tall forbs	Short forbs
Alopecurus pratensis	*Agrostis capillaris*	*Achillea millefolium*	*Alchemilla* sp.
Arrhenatherum elatius	*Anthoxanthum odoratum*	*Bistorta major*	*Anemone nemorosa*
Avenella flexuosa	*Briza media*	*Cirsium heterophyllum*	*Arnica montana*
Deschampsia cespitosa	*Carex ovalis*	*Crepis mollis* subsp. *hieracioides*	*Campanula patula*
Elytrigia repens	*Carex pallescens*	*Epilobium montanum*	*Campanula rhomboidalis*
Festuca pratensis	*Carex pilulifera*	*Filipendula ulmaria*	*Campanula rotundifolia*
Festuca rubra	*Juncus filiformis*	*Galium mollugo* agg.	*Cardaminopsis halleri*
Holcus mollis	*Luzula multiflora*	*Geranium sylvaticum*	*Carlina acaulis*
Luzula luzuloides	*Nardus stricta*	*Gymnadenia conopsea*	*Cerastium holosteoides*
Poa chaixii		*Hiearacium laevigatum*	*Euphrasia* sp.
Poa pratensis		*Hypericum maculatum*	*Galeopsis* sp.
Poa trivialis		*Lathyrus pratensis*	*Galium saxatile*
Trisetum flavescens		*Leucanthemum ircutianum*	*Hieracium aurantiacum*
		Phyteuma spicatum	*Hieracium pilosella*
		Ranunculus acris	*Leontodon autumnalis*
		Rumex acetosa	*Leontodon hispidus*
		Senecio nemorensis agg.	*Lychnis flos-cuculi*
		Trollius altissimus	*Meum athamanticum*
		Vicia cracca	*Myosotis nemorosa*
		Veratrum album subsp. *lobelianum*	*Plantago lanceolata*
			Polygala vulgaris
			Potentilla erecta
			Ranunculus repens
			Rhinanthus minor
			Silene dioica
			Stellaria graminea
			Taraxacum sect. *Ruderalia*
			Trifolium pratense
			Trifolium repens
			Trifolium spadiceum
			Vaccinium myrtillus
			Veronica chamaedrys
			Veronica officinalis
			Viola tricolor

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