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Control of *Molinia caerulea* by cutting management on sub-alpine grassland

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ABSTRACT

There has been a considerable expansion of *Molinia caerulea* after the cessation of cutting management of *Nardus stricta* sub-alpine grasslands in the Giant Mts. (Krkonoše/Karkonosze/Riesengebirge, the Czech Republic) in the last 50 years. The aim of this study was to investigate whether the reestablishment of traditional management (one cut per year in late July) could reverse *Molinia* encroachment and help to restore the original *Nardus* grassland.

The cover of *Molinia* significantly decreased from 79% to 7%, the height of the canopy from 45 to 14 cm, biomass production from 313 to 54 g m^{-2} and panicle density from 129 to 18/m^2 after 6 years of cutting management. During the course of the experiment, no seedlings of *Nardus* were recorded in mown plots, although *Nardus* was common in the neighborhood. After *Molinia* retreat bare ground was partly colonized by *Avenella flexuosa* and partly remained free of vegetation. No significant effect of cutting management on species richness per 1 m^2 was recorded. Cutting significantly decreased K availability in the soil, although the amount of K removed was only 8 g/m^2 over 6 years. The N:P, N:K and K:P ratios in the plant biomass were not significantly affected by mowing compared to the unmanaged control, indicating P and K limitation but not N limitation in both treatments.

Reestablishment of traditional management (one cut per year in late July) reversed *Molinia* encroachment but did not increase species richness or restore the original *Nardus* grassland over 6 years.

Introduction

In recent decades, *Molinia* encroachment has been recorded in moorlands, fens, heathlands and in temporary wet low-productive grasslands in many European countries (Aerts, 1989; Berendse et al., 1994; Brys et al., 2005; Critchley et al., 2008; Hájková et al., 2009; Marrs et al., 2004). Under high N deposition, many plant species are limited by phosphorus (P) and cannot increase biomass production if their foliar N:P ratio is higher than 13–16 (Güsewell, 2004; Olde Venterink et al., 2003; Klaudisová et al., 2009). This is not the case for *Molinia* as this grass has a high phosphorus use efficiency (Aerts, 1990) and is able to positively respond to N addition albeit its foliar N:P ratio is higher than 40 (Tomassen et al., 2004). Furthermore, *Molinia* is able to re-translocate 75–85% of N and P from senescent leaves before their abscission and to store them in the root system and basal internodes for use in the following season (Morton, 1977; Thornton and Millard, 1993; van Heerwaarden et al., 2005). This makes *Molinia* a very successful competitor in unmanaged swards with low P and K availability and high N deposition (Havlová, 2006; Lepš, 1999; Taylor et al., 2001).

There have been frequent attempts to control *Molinia* encroachment by various management methods. Todd et al. (1999) concluded that herbicide (glyphosate) treatment is the most effective compared to burning or sheep grazing. Grant et al. (1996) showed that defoliation intensity and frequency were more important for the decline of *Molinia* than the timing of defoliation. Burning followed by herbicide application and consequent intensive sheep grazing (1.5 ewes/ha) reduced the frequency of *Molinia* in a study by Ross et al. (2003). Critchley et al. (2008) recorded a substantial decline in *Molinia* under mixed cattle and sheep grazing, but an increase if sheep were grazing alone. According to Hájková et al. (2009), *Molinia*-invaded fen can be restored by mowing twice a year instead of the annual late mowing that is traditionally used on *Molinia* grasslands in Central Europe. Fire increased sexual reproduction and seedling growth of *Molinia* in a study by Jacquemyn et al. (2005). Mowing of resprouted plants before flowering was recommended to stop the extensive spread of *Molinia* after fire.

In the Giant Mts. (Krkonoše, Karkonosze and Riesengebirge in Czech, Polish and German, respectively), there has been a considerable expansion of *Molinia* since the cessation of mowing of the sub-alpine grasslands in the last 50 years (Hejcman et al., 2006b). In the past, *Molinia* dominated only on the edges of springs and peat

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bogs and on snow beds where snow cover persisted longer than in other areas, supplying the vegetation with additional water during late spring (Bercíková, 1976; Hejcman et al., 2006a). Recently, species-poor stands of *Molinia* have completely replaced grasslands dominated by *Nardus stricta* at many sites, especially in the surroundings of water courses and in other temporarily wet localities. Encroachment started by seedling establishment, followed by a circular enlargement of the *Molinia* patches, leading to total elimination of light-demanding *Nardus* under the closed and tall *Molinia* canopy.

Sub-alpine *Nardus* grasslands (*Nardo strictae-Caricion bigelowii* alliance) are widespread in the Scandinavian Mountains, and the southern limit of their distribution is in Central Europe on the top of the Giant Mts. (Chytrý, 2007). They cover there only several hundred hectares, and therefore they are of high conservation value, and *Molinia* encroachment is incompatible with their conservation.

The aim of this study was to investigate whether the reestablishment of traditional management (one cut per year in late July) could reverse *Molinia* encroachment and help to restore the original *Nardus* grassland.

Material and methods

Study site

The study site lies above the upper tree line at an altitude of 1370 m a. s. l. in the western part of the Giant Mts. close to the spring of the Elbe River (50°46′12″N, 15°32′12″W). The soil types are podzols, developed on medium grain porphyric granite or granodiorite. The locality lies on a moderate south slope with an inclination of up to 2°. The mean annual temperature is 2 °C and the mean annual precipitation is 1380 mm (Vrbatova Bouda Meteorological Station, period 1960–1990). According to long-term measurements made by Budská et al. (2000), in a neighboring locality, the range of annual wet N deposition was estimated as being 20–40 kg/ha. High year-to-year variability in deposition was caused particularly by the variation in precipitation. According to phytosociological nomenclature (Chytrý, 2007), the vegetation of the experimental grassland was classified as a *Nardo strictae-Caricion bigelowii* alliance. The species present before the start of the experiment were *Molinia caerulea* (cover 79%), *Avenella flexuosa* (26%), *Carex bigelowii* (4%), *Nardus stricta* (2%), *Galium saxatile* (1%) and *Anthoxanthum alpinum* (0.3%). The nomenclature of plant species follows Kubát et al. (2002). The site was used for haymaking and cattle grazing at least from the 17th century until World War II and has been without any agricultural management since 1945 (Lokvenc, 2001).

Experimental design

A randomized complete block experiment with four replicate plots (each 5 m × 5 m) for each treatment was established. To eliminate the edge effect, central 1 m × 1 m plots, using a continuous grid of nine square subplots, were used for data collection. There were two treatments: unmanaged control (control) and cutting management (cut) performed once per year in the last week of July in each year. The cutting height was 2 cm above the soil surface.

Data collection

The percentage cover of all vascular species, the density of *Molinia* panicles and the height of the *Molinia* canopy before cutting were counted or measured separately in all subplots of each 1 m^2 central plot. Species richness (number of species per 1 m^2) was determined by counting all species present in each central 1 m^2 plot. Baseline data were collected in 2002 for each plot before the first experimental manipulation. The height of the *Molinia* canopy was taken as the mean of the highest leaves of ten randomly chosen *Molinia* plants. The biomass samples were collected after vegetation sampling. Samples were oven dried for 48 hours at 85 °C and then weighed. To avoid disturbing the permanent 1 m^2 plots in the control treatment, nearby biomass samples were collected in different places within 5 m × 5 m experimental plots each year. This was done in the close vicinity of the permanent 1 m^2 plots to minimize bias in the data. All data were collected in the last week of July each year.

Soil samples were taken in July 2007. In each plot, four separate samples were taken from 0 to 10 cm depth after removing plant residues, and combined to form one representative sample. The soil samples were air-dried, ground in a mortar, and sieved to 2 mm after removal of living roots. Plant-available Ca, K, Mg and P were extracted by the Mehlich III reagent (Mehlich, 1984) and then determined by ICP-OES. Total N concentration was determined spectrophotometrically after Kjeldahl digestion.

Total N concentration in the plant biomass was determined spectrophotometrically after Kjeldahl digestion, and total Ca and P concentrations were determined spectrophotometrically or by emission flame spectrometry after digestion in sulphuric acid. All chemical analyses were performed in an accredited national laboratory (Ekolab Žamberk).

Data analysis

Treatment effects on all collected data were evaluated by one-way ANOVA or by repeated measures ANOVA using the STATISTICA 7.0 software (StatSoft, Tulsa). Multivariate methods were not used as only four species were analyzed.

Results

Soil chemical properties

In 2007, after 6 years of biomass removal, there was no significant effect of treatment on soil pH, total nitrogen content, plant-available P, Ca or Mg content, but cutting significantly decreased the K content in the soil (Table 1).

Cover data

According to repeated measures ANOVA, there was no significant effect of treatment, year or the treatment × year interaction on species richness. Based on all plots and all years, the mean species

Table 1
Results of one-way ANOVA of soil and biomass chemical properties in 2007. Numbers represent average of four replicates ± standard error of the mean (SE).

Tested variable	ANOVA	Control	Cut
Soil properties (mg kg^{-1})			
pH/H_2O	n.s.	4.07 ± 0.02	4.12 ± 0.03
Nitrogen	n.s.	16570 ± 666	15414 ± 305
Phosphorus	n.s.	52 ± 2	56 ± 6
Potassium	*	756 ± 27	556 ± 60
Calcium	n.s.	591 ± 89	523 ± 20
Magnesium	n.s.	178 ± 12	155 ± 14
Biomass properties (g kg^{-1})			
Nitrogen	n.s.	24 ± 0.4	25 ± 0.8
Phosphorus	n.s.	1.15 ± 0.06	1.05 ± 0.03
Potassium	n.s.	10.0 ± 0.3	9.8 ± 0.3
Calcium	n.s.	1.7 ± 0.1	1.7 ± 0.1
Magnesium	n.s.	1.2 ± 0.1	1.0 ± 0.1
N:P ratio	n.s.	21.3 ± 1.2	23.5 ± 0.8
N:K ratio	n.s.	2.4 ± 0.1	2.6 ± 0.04
K:P ratio	n.s.	8.8 ± 0.5	9.4 ± 0.5

n.s. – not significant, * – significant at α 0.05.

Table 2
Results of repeated measures ANOVA of cover and biomass production of individual species, total biomass production, density of *Molinia* inflorescences, nutrient accumulation in the standing biomass and sward height.

Tested variable	Treatment	Year	Treatment × year
Species richness	n.s.	n.s.	n.s.
Cover of *Molinia*	**	**	**
Cover of *Avenella*	n.s.	**	n.s.
Cover of *Nardus*	**	n.s.	n.s.
Cover of *Anthoxanthum*	**	**	n.s.
Height of canopy	**	**	**
Biomass production	**	**	**
Panicle density	**	**	**
N in biomass	**	**	**
P in biomass	**	**	**
K in biomass	**	**	**
Ca in biomass	**	**	**
Mg in biomass	**	**	**

n.s. – not significant, * – significant at α 0.05, ** – significant at α 0.001.

richness per 1 m^2 was 4. Six vascular plant species were recorded within the experimental area, but only four species were frequent enough to be statistically analyzed.

According to repeated measures ANOVA, the cover of *Molinia* was significantly affected by treatment, year and by the treatment × year interaction (Table 2). The cover of *Molinia* significantly decreased from 79% in both treatments in 2002 to 44% and 7% in the control and cut treatments respectively in 2008. According to one-way ANOVA, the effect of treatment on *Molinia* cover was already significant in 2003 one year after the first experimental manipulation (Fig. 1a).

The cover of *Avenella* ranged from 5% to 27% in all investigated years. It was significantly affected by year (Table 2) and a decrease was recorded in both treatments. From 2004, the cover of *Avenella* was lower in the control compared to the cut treatment. Differences between treatments were significant in only three (2004, 2005 and 2007) of the seven investigated years (Fig. 1b).

The cover of *Nardus* was significantly affected by treatment only (Table 2), but analyses of data from each individual year revealed no significant effect of treatment (Fig. 1c). In 2002, it was 2–3% in both treatments. It was relatively stable in the control, but slightly increased in the cut treatment from 3% to 7% in 2002 and 2008 respectively. No *Nardus* seedlings were recorded in the cut treatment during the 6 years of the study. The cover of *Anthoxanthum* ranged from 0.1% to 2% in all investigated seasons. It was significantly affected by year and treatment as well (Table 2). There was high inter-annual variability within the data – very low cover in both treatments in 2003 and on the other hand high cover in the control that was significantly different from the cut treatment in 2008 (Fig. 1d).

Height of canopy

The height of the *Molinia* canopy was significantly affected by year, treatment and by the treatment × year interaction (Table 2, Fig. 2a). During the course of the experiment, the height of the canopy decreased substantially from 45 to 15 cm in the cut treatment. Differences between treatments were not significant in the baseline data in 2002, but were significant in all other years.

Biomass production

According to repeated measures ANOVA, aboveground biomass production was significantly affected by year, treatment and by the treatment × year interaction (Table 2). Biomass production was approximately 300 g/m^2 in both treatments in 2002 before the

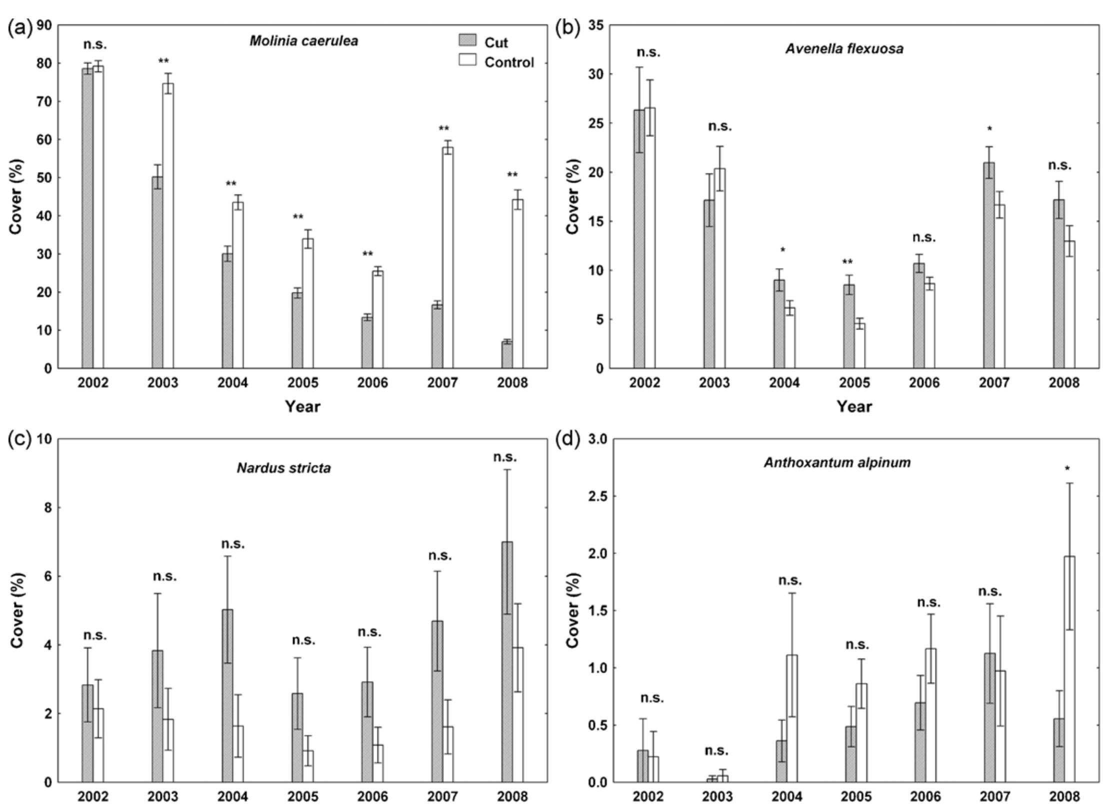

Fig. 1. Effect of cut and control treatments on cover of *Molinia caerulea* (a), *Avenella flexuosa* (b), *Nardus stricta* (c) and *Anthoxanthum alpinum* (d). Error bars represent SE. n.s. – result of one-way ANOVA was not significant, * – result significant at α 0.05 and ** – result significant at α 0.001.

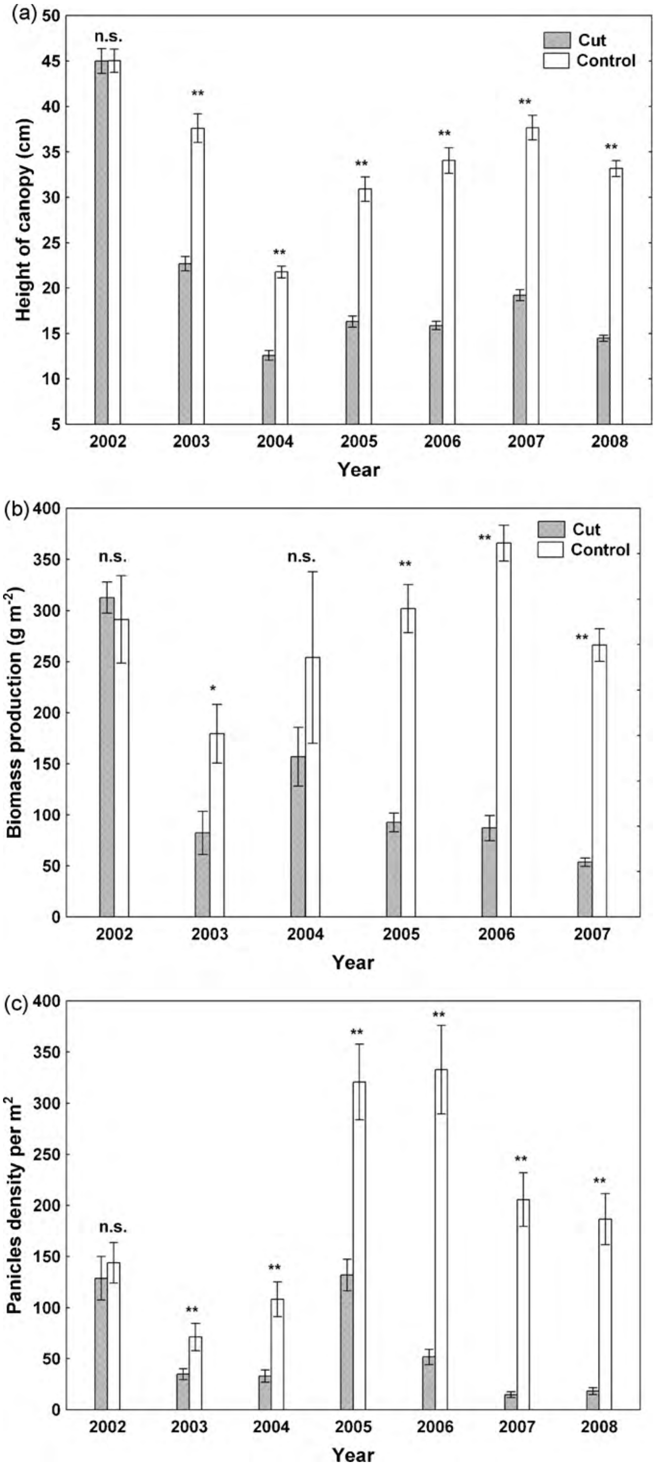

Fig. 2. Effect of cut and control treatments on height of *Molinia* canopy (a), aboveground biomass production (b) and density of *Molinia* panicles (c). Error bars represent SE. n.s. – result of one-way ANOVA was not significant, * – result significant at α 0.05 and ** – result significant at α 0.001.

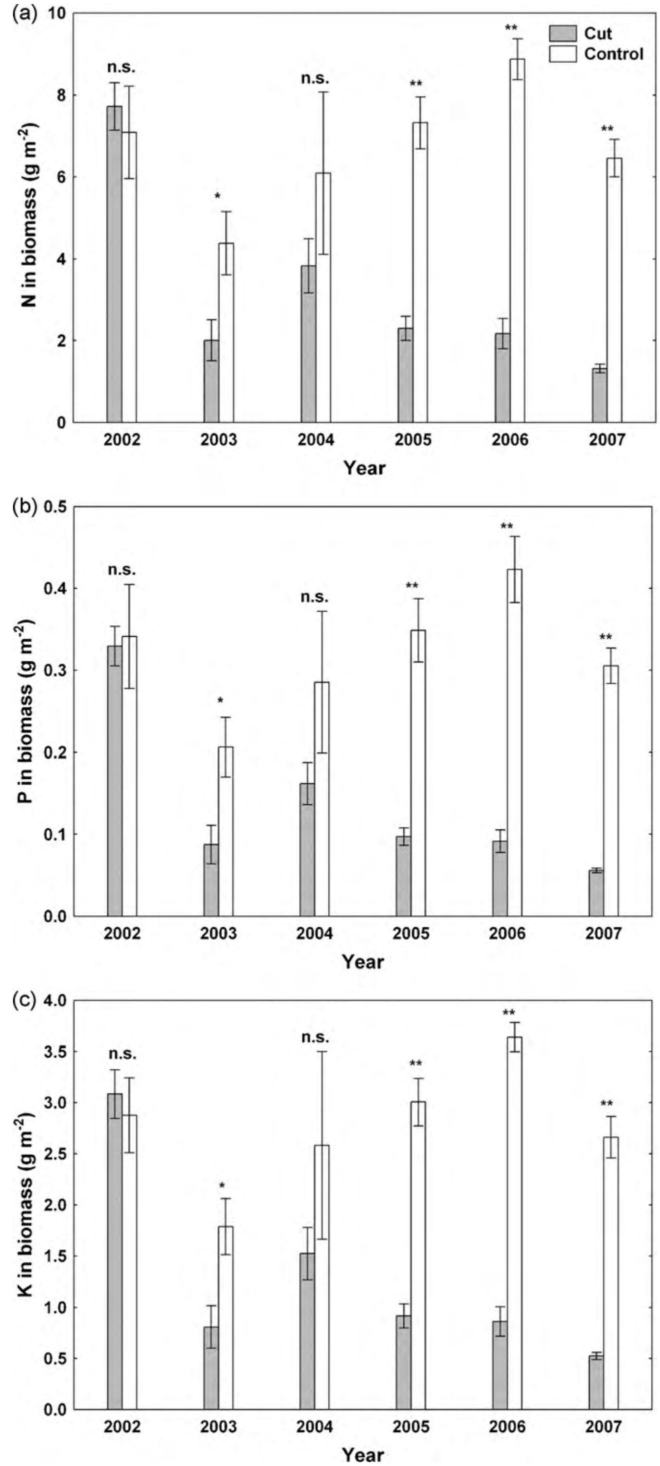

Fig. 3. Effect of cut and control treatments on amount of nitrogen (a), phosphorus (b) and potassium (c) accumulated in aboveground biomass. Error bars represent SE. n.s. – result of one-way ANOVA was not significant, * – result significant at α 0.05 and ** – result significant at α 0.001.

first experimental manipulation. In the following years, biomass production substantially decreased in the cut treatment, but was relatively stable in the control (Fig. 2b). According to one-way ANOVA, the effect of treatment on biomass production was not significant in 2002 or 2004.

Panicle density

There was high inter-annual variability in the density of *Molinia* panicles. Panicle densities were significantly affected by year, treatment and by the treatment × year interaction (Table 2). The highest densities of approximately 320–330 panicles/m^2 were recorded in the control in 2005 and 2006. However, 2002, 2003 and 2004 were less favorable for flowering. Differences between treatments were

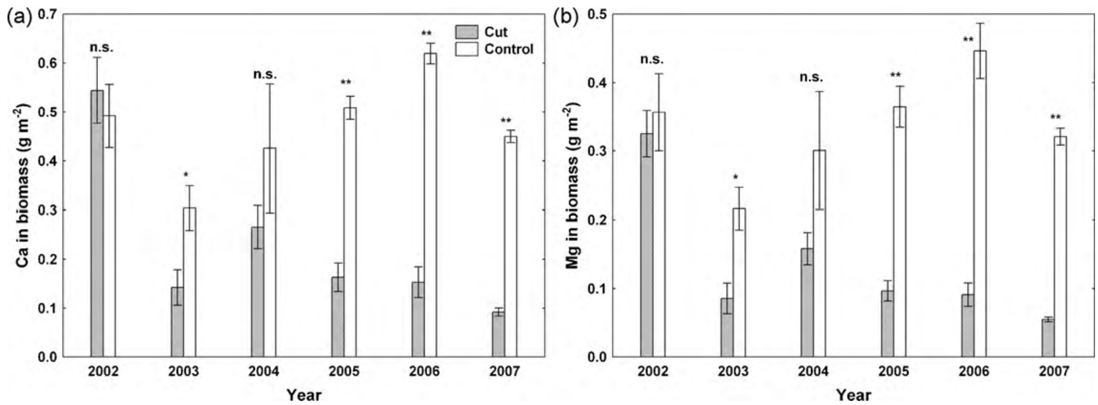

Fig. 4. Effect of cut and control treatments on amount of calcium (a) and magnesium (b) accumulated in aboveground biomass. Error bars represent SE. n.s. – result of one-way ANOVA was not significant, * – result significant at α 0.05 and ** – result significant at α 0.001.

significant from 2003 onwards (Fig. 2c). Panicle density decreased from approximately 130 to 18/m^2 after 6 years of cutting management.

Biomass chemical properties

In 2007 there was no significant effect of treatment on concentrations of N, P, K, Ca or Mg or on the N:P, N:K or P:K ratio in the aboveground biomass (Table 1). The amount of macro-nutrients (N, P, K, Ca and Mg) accumulated in the aboveground biomass was significantly affected by year, treatment and the year × treatment interaction (Table 2, Figs. 3 and 4). For all analyzed nutrients, there were no differences in the amount of nutrients accumulated in the aboveground biomass before the first experimental manipulation in 2002, but substantial differences showed up in subsequent years. Differences between treatments increased with the duration of the experiment as the biomass production in the cut treatment decreased substantially. In the cut treatment, the mean amount of N, P, K, Ca and Mg removed over 6 years was 19.3, 0.82, 7.7, 1.4 and 0.81 g/m^2, respectively.

Discussion

Chemical properties of soil and biomass

Although cutting management was performed for 6 years before soil sample collection, there was no effect of treatment on P, Ca or Mg availability in the upper soil layer. The availability of the above-mentioned nutrients was therefore probably still high enough to support the growth of *Molinia* in the cut treatment after 6 years. Decreasing the plant-available concentrations of the above-mentioned elements by cutting management is evidently a long-term process even on low-productive mountain podzol soils. Furthermore, the insignificant decrease in P, Ca and Mg availability was probably connected with the low biomass production and therefore the low annual removal of nutrients compared to productive grasslands.

Six years of cutting management was sufficient to significantly decrease K availability, although the amount of K removed was only 7.7 g/m^2 over the 6 years. This greatly contrasts with grasslands on clay soils where the annual removal of K in harvested biomass can be much higher than in this study and the effect on K concentration in the soil is minimal or non-existent (see Hrevušová et al., 2009). The low ability of the podzol soil to supply the vegetation with high amounts of K was probably connected with the accumulation of organic matter in the upper soil layer as K limitation frequently occurs on organic and mineral poor sandy soils (Kayser and Isselstein, 2005; Madaras and Lipavský, 2009; Olde Venterink et al., 2009). K limitation was also indicated by high biomass N:K ratios, which were higher than 2.1 – a threshold value for harmonic nutrition (Olde Venterink et al., 2003). Furthermore, high N:P ratios above 14.5 and K:P ratios above 3.4 indicated P limitation and the adaptation of *Molinia* to conditions with low P availability.

There was no effect of cutting management on total N content in the soil, although 19.3 g/m^2 of N were removed by cutting management over the 6 years of the study. In the studied soil, the total N pool was too high to be affected by N removal and in addition N was supplied not only from the soil, but also from aerial dry and wet deposition. N deposition can thus compensate for removal of N in harvested biomass and cutting can further stimulate the rate of N mineralization as demonstrated for sub-alpine grasslands by Robson et al. (2007). Our results are consistent with the conclusions of Olde Venterink et al. (2002) that haymaking prevents N enrichment, but does not decrease the soil N pool in low-productive ecosystems due to N compensation by aerial deposition.

Plant species composition

During the experiment, the decrease in cover of *Molinia* and year-to-year fluctuations in control were probably caused by the different habitus of the plants in each year due to weather conditions. In the control, the decrease in cover was only partly reflected by a decrease in the height of the canopy, but was not reflected by a decrease in biomass production of *Molinia*. Furthermore, in the control, the lowest cover of *Molinia* was associated with exceptionally high panicle density in 2005 and 2006. In the control, the estimate of cover thus probably reflected the different proportions of leaves, stems and panicles in each year relatively well. The reintroduction of traditional cutting management quickly reduced the cover, biomass and flowering of *Molinia*, but after 6 years, cutting management did not increase species richness or restore the original *Nardus* dominated sub-alpine grassland. This result is consistent with several other studies demonstrating that the restoration of target grassland communities by cutting is a long-term process (Galvánek and Lepš, 2008; Ilmarinen et al., 2009; Mašková et al., 2009; Stampfli and Zeiter, 1999). After the retreat of *Molinia*, empty gaps were only partly colonized by *Avenella* or remained free of vegetation. No seedlings of *Nardus* were recorded, although *Nardus* was common in the neighborhood. This indicates the low ability of *Nardus* to colonize bare ground and probably the low seed production of *Nardus* under harsh climatic conditions. According to Málková and Matějka (2004), the production of germinable seeds of *Nardus* is low in sub-alpine grasslands in the Giant Mts. and restricted to favorable years. The decrease in vitality of *Molinia* after 6 years of cutting indicates its high sensitivity to defoliation under the harsh climatic conditions of the study site.

The high defoliation sensitivity of *Molinia* is in accordance with other studies demonstrating the negative effect of cutting or intensive grazing on *Molinia* performance in various plant communities (Grant et al., 1996; Jacquemyn et al., 2005; Critchley et al., 2008). The highly negative effects of single cut management at least partly conflict with the recommendation by Hájková et al. (2009) that cutting twice a year is better for quick reduction of *Molinia* instead of the late annual cutting that was traditionally carried out in *Molinia* meadows in the Czech Republic. It must be noted that this recommendation does not apply to *Molinia* stands under sub-alpine conditions as the vegetation season is too short and *Molinia* regrowth after the first cut is limited by low temperatures.

In the cut treatment, the decrease in *Molinia* cover, height and biomass production significantly supported the growth of short *Avenella* in several years. This is consistent with the conclusion reached by Klimeš and Klimešová (2002) that cutting is highly selective as it removes a higher proportion of the aboveground biomass of tall than short species. Tall *Molinia* evidently suffers from regular cutting management similarly to *Calamagrostis villosa*, another tall grass that is common under sub-alpine conditions in the region (Hejcman et al., 2009). According to Hájková et al. (2009), carbohydrate depletion seems to play a more important role than nutrient export in the suppression of *Molinia* in mown plots. This probably explains why such a big retreat of *Molinia* was recorded after 6 years of mowing although the amount of nutrients removed was relatively low.

Conclusion

Reestablishment of traditional management (one cut per year in late July) reversed *Molinia* encroachment, but over 6 years did not increase species richness or restore the original *Nardus* grassland.

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References

Aerts, R., 1989. Aboveground biomass and nutrient dynamics of *Calluna vulgaris* and *Molinia caerulea* in a dry heathland. Oikos 56, 31–38.

Aerts, R., 1990. Nutrient use efficiency in evergreen and deciduous species from heathlands. Oecologia 84, 391–397.

Berciková, M., 1976. Rostlinná společenstva s účastí Molinia coerulea v alpínském stupni Krkonoš [Plant communities with *Molinia caerulea* in alpine zone of the Giant Mts.]. Opera Corcon. 13, 95–129.

Berendse, F., Schmitz, M., de Visser, W., 1994. Experimental manipulation of succession in heathland ecosystems. Oecologia 100, 38–44.

Brys, R., Jacquemyn, H.R., de Blust, G., 2005. Fire increases aboveground biomass, seed production and recruitment success of *Molinia caerulea* in dry heathland. Acta Oecol. 28, 299–305.

Budská, E., Franče, P., Světlík, I., 2000. Monitoring of atmospheric deposition in the area of the Krkonoše Mountains. Opera Corcon. 37, 47–54.

Chytrý, M., 2007. Vegetation of the Czech Republic 1. Grassland and Heathland Vegetation. Academia, Prague.

Critchley, C.N.R., Adamson, H.F., McLean, B.M.L., Davies, O.D., 2008. Vegetation dynamics and livestock performance in system-scale studies of sheep and cattle grazing on degraded upland wet heath. Agric. Ecosyst. Environ. 128, 59–67.

Galvánek, D., Lepš, J., 2008. Changes in richness pattern in mountain grasslands: abandonment versus restoration. Biodiv. Conserv. 17, 3241–3253.

Grant, S.A., Torvell, L., Common, T.G., Sim, E.M., Small, J.L., 1996. Controlled grazing studies on *Molinia* grassland: effects of different seasonal patterns and levels of defoliation on *Molinia* growth and responses of swards to controlled grazing by cattle. J. Appl. Ecol. 33, 1267–1280.

Güsewell, S., 2004. N:P ratios in terrestrial plants: variation and functional significance. New Phytol. 164, 243–266.

Hájková, P., Hájek, M., Kintrová, K., 2009. How can we effectively restore species richness and natural composition of a *Molinia*-invaded fen? J. Appl. Ecol. 46, 417–425.

Havlová, M., 2006. Syntaxonomical revision of the *Molinion* meadows in the Czech Republic. Preslia 78, 87–101.

Hejcman, M., Dvořák, I., Kociánová, M., Pavlů, V., Nežerková, P., Vítek, O., Rauch, O., Jeník, J., 2006a. Snow depth and vegetation pattern in a late-melting snow-bed analyzed by GPS and GIS in the Giant Mountains, Czech Republic. Arct. Antarct. Alp. Res. 38, 90–98.

Hejcman, M., Pavlů, V., Hejcmanová, P., Gaisler, J., Hakl, J., Rauch, O., 2006b. Farmer decision making and its effect on subalpine grassland succession in the Giant Mts., Czech Republic. Acta Soc. Bot. Pol. 75, 165–174.

Hejcman, M., Klaudisová, M., Hejcmanová, P., Pavlů, V., Jones, M., 2009. Expansion of *Calamagrostis villosa* in sub-alpine *Nardus stricta* grassland: Cessation of cutting management or high nitrogen deposition? Agric. Ecosyst. Environ. 129, 91–96.

Hrevušová, Z., Hejcman, M., Pavlů, V., Hakl, J., Klaudisová, M., Mrkvička, J., 2009. Long-term dynamics of biomass production, soil chemical properties and plant species composition of alluvial grassland after the cessation of fertilizer application in the Czech Republic. Agric. Ecosyst. Environ. 130, 123–130.

Ilmarinen, K., Mikola, J., Nissinen, K., Vestberg, M., 2009. Role of soil organisms in the maintenance of species-rich seminatural grasslands through mowing. Restor. Ecol. 17, 78–88.

Jacquemyn, H., Brys, R., Neubert, M.G., 2005. Fire increases invasive spread of *Molinia caerulea* mainly through changes in demographic parameters. Ecol. Appl. 15, 2097–2108.

Kayser, M., Isselstein, J., 2005. Potassium cycling and losses in grassland systems: a review. Grass Forage Sci. 60, 213–224.

Klaudisová, M., Hejcman, M., Pavlů, V., 2009. Long-term residual effect of short-term fertilizer application on Ca, N and P concentrations in grasses *Nardus stricta* L. and *Avenella flexuosa* L. Nutr. Cycl. Agroecoesyst. 85, 187–193.

Klimeš, L., Klimešová, J., 2002. The effects of mowing and fertilisation on carbohydrate reserves and regrowth of grasses: do they promote plant coexistence in species-rich meadows? Evol. Ecol. 15, 363–382.

Kubát, K., Hrouda, L., Chrtek, J., Kaplan, Z., Kirschner, J., Štěpánek, J., 2002. Klíč ke květeně České republiky [Identification key to the flora of the Czech Republic]. Academia, Prague.

Lepš, J., 1999. Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow. J. Veg. Sci. 10, 219–230.

Lokvenc, T., 2001. Budní hospodářství Labské louky [Mountain farming on Labská Meadow]. Z. Českého Ráje a Podkrkonoší 14, 69–90.

Madaras, M., Lipavský, J., 2009. Interannual dynamics of available potassium. in a long-term fertilization experiment. Plant Soil Environ. 55, 334–343.

Málková, J., Matějka, K., 2004. Selected grass dominant germination in the Giant Mountains. Opera Corcon. 41, 250–255.

Marrs, R.H., Phillips, J.D.P., Todd, P.A., Le Duc, M.G., 2004. Control of *Molinia caerulea* on upland moors. J. Appl. Ecol. 41, 398–411.

Mašková, Z., Doležal, J., Květ, J., Zemek, F., 2009. Long-term functioning of a species-rich mountain meadow under different management regimes. Agric. Ecosyst. Environ. 132, 192–202.

Mehlich, A., 1984. Mehlich No. 3 soil test extractant: a modification of Mehlich No. 2. Commun. Soil Sci. Plant Anal. 15, 1409–1416.

Morton, A.J., 1977. Mineral nutrient pathways in a *Molinietum* in autumn and winter. J. Ecol. 65, 993–999.

Olde Venterink, H., Pieterse, N.M., Belgers, J.D.M., Wassen, M.J., De Ruiter, P.C., 2002. N, P, and K budgets along nutrient availability and productivity gradients in wetlands. Ecol. Appl. 12, 1010–1026.

Olde Venterink, H., Wassen, M.J., Verkroost, A.W.M., De Ruiter, P.C., 2003. Species richness-productivity patterns differ between N-,P- and K-limited wetlands. Ecology 84, 2191–2199.

Olde Venterink, H., Kardel, I., Kotowski, W., Peeters, W., Wassen, M.J., 2009. Long-term effects of drainage and hay-removal on nutrient dynamics and limitation in the Biebrza mires, Poland. Biogeochemistry 93, 235–252.

Robson, T.M., Lavorel, S., Clement, J., Le Roux, X., 2007. Neglect of mowing and manuring leads to slower nitrogen cycling in subalpine grasslands. Soil Biol. Biochem. 39, 930–941.

Ross, S., Adamson, H., Moon, A., 2003. Evaluating management techniques for controlling *Molinia caerulea* and enhancing *Calluna vulgaris* on upland wet heathland in northern England, UK. Agric. Ecosyst. Environ. 97, 39–49.

Stampfli, A., Zeiter, M., 1999. Plant species decline due to abandonment of meadows cannot easily be reversed by mowing. J. Veg. Sci. 10, 151–164.

Taylor, K., Rowland, A.P., Jones, H.E., 2001. *Molinia caerulea* (L.) Moench. J. Ecol. 89, 126–144.

Thornton, B., Millard, P., 1993. The effects of nitrogen supply and defoliation on the seasonal internal cycling of nitrogen in *Molinia caerulea*. J. Exp. Bot. 44, 531–536.

Todd, P.A., Phillips, J.D.P., Putwain, P.D., Marrs, R.H., 1999. Control of *Molinia caerulea* on moorland. Grass Forage Sci. 55, 181–191.

Tomassen, H.B.M., Smolders, A.J.P., Limpens, J., Lamers, L.P.M., Roelofs, J.G.M., 2004. Expansion of invasive species on ombrotrophic bogs: desiccation or high N deposition? J. Appl. Ecol. 41, 139–150.

van Heerwaarden, L.M., Toet, S., van Logtestijn, R.S.P., Aerts, R., 2005. Internal nitrogen dynamics in the graminoid *Molinia caerulea* under higher N supply and elevated CO_2 concentrations. Plant Soil 277, 255–264.