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Relationship between soil and biomass chemical properties, herbage yield and sward height in cut and unmanaged mountain hay meadow (Polygono–Trisetion)

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ABSTRACT

Little is known about the effects of either long-term cutting with herbage removal or no management on the nutritional status of *Agrostis capillaris* and *Festuca rubra* meadows. We asked how management affected soil and herbage chemical properties, herbage yield and sward height. The experiment with cutting (C) and unmanaged (U) treatments was undertaken from 1999 to 2009 in the Jizera Mts., Czech Republic. Soil and herbage samples were taken from 2003 to 2009.

Potassium was the only nutrient for which the soil concentration decreased under the C treatment. Soil K concentration was 175 and 210 mg kg^{-1} in the C and U treatments, respectively, in the last year of the experiment. Herbage yield as well as sward height were significantly higher in the unmanaged than in the cutting treatment in all years. Concentrations of P and K in the herbage biomass were lower in the cutting than in the unmanaged treatment, but concentrations of N were lower only in some years. Concentrations of Ca and Mg were not affected by the different treatments. A strong positive relationship between concentration in soil and herbage was recorded only for K.

In contrast to K, ten years of contrasting management was too short a period to affect plant-available (Mehlich III) P, Ca and Mg concentrations, but it was long enough to affect herbage chemical properties and yield.

Introduction

Contrasting grassland management causes changes in plant species composition and species diversity (Bakker et al., 2002; Eler et al., 2005; Gaisler et al., 2004; Hejcman et al., 2010c; Pavlů et al., 2011b; Ryser et al., 1995; Valkó et al., 2012), but may also highly affect nutrient availability. In abandoned grasslands where nutrients are not exported by the harvested herbage, nutrient availability in the soil may increase because of the input of nutrients from atmospheric deposition, mineralization of soil organic matter or by weathering of soil minerals (Köhler et al., 2001). On the other hand, regular cutting with herbage removal can cause depletion of nutrients from the soil (Schnitzler and Muller, 1998). However, only a small percentage of the total nutrient pool is removed by the harvested herbage (Bakker, 1989, and citations therein). Nevertheless, several authors recorded a substantial decrease in the pool of plant-available K in the soil following long-term herbage removal (Alfaro et al., 2004; Hejcman et al., 2010b; Øien and Moen, 2001). In the case of N and P, it is not possible to detect the effect of herbage removal performed over several years by analysis of total N or plant-available P in the soil (Bakker, 1989) and therefore the soil nutrient status may be better indicated by herbage chemical properties rather than by soil analysis (Oomes, 1990).

According to Schaffers (2002), K is the only nutrient which shows a strong relationship between plant-available soil and biomass concentrations. On the other hand, N and P herbage concentrations do not depend predominantly on their availability in the soil but are also affected by other factors such as shading intensity, soil pH and moisture. In addition, N and P concentrations in the plant herbage are also affected by the supply N and P ratio (Hejcman et al., 2010d; Janssens et al., 1998; Koerselman and Meuleman, 1996). Herbage removal does not accelerate depletion of soil P if performed only for a few years, but long-term herbage removal can substantially reduce concentrations of plant-available P in the soil (Perring et al., 2009).

To evaluate how the management regime affects nutrient availability, it is necessary to determine which nutrient limits herbage production because the limiting nutrient is taken up by plants as soon as it becomes available (Köhler et al., 2001). Limitation

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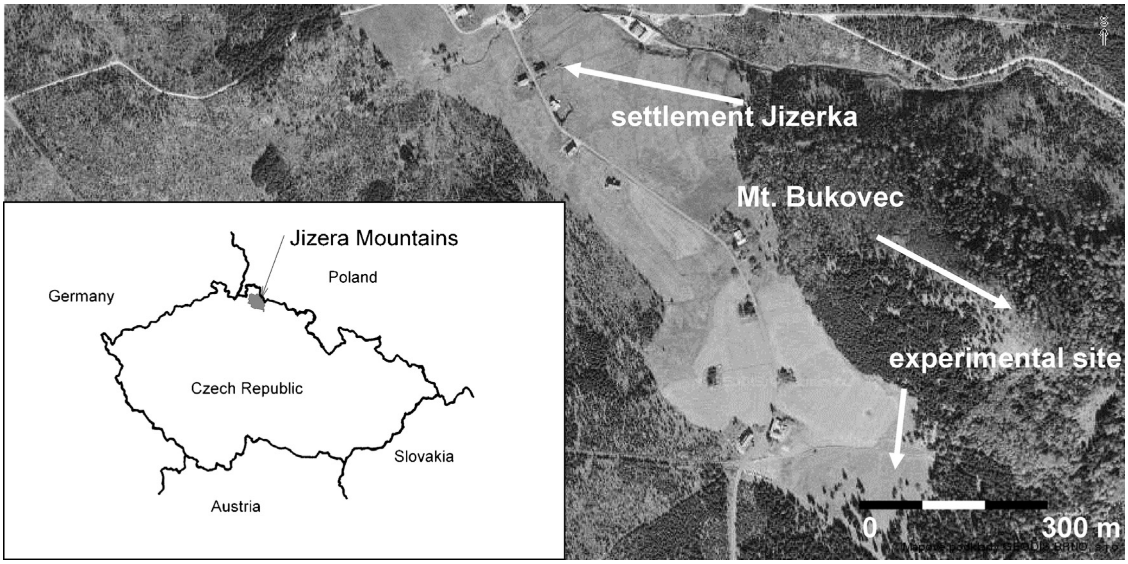

Fig. 1. Location of the Jizera Mountains within the Czech Republic and an aerial view of the study area.

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of herbage growth by N, P and K supplies can be estimated from their concentrations in the herbage and also from their N:P, N:K and K:P ratios, but the results of such studies are frequently not straightforward (Güsewell, 2004; Lawniczak et al., 2009; Øien and Moen, 2001; Tessier and Raynal, 2003).The management regime influences not only soil and herbage nutrient properties and plant species composition but also sward height and standing biomass production (Hejcman et al., 2010a; Klimeš and Klimešová, 2002; Köhler et al., 2001; Øien and Moen, 2001; Pavlů et al., 2011a). Lower sward height and standing biomass are influenced by disturbance rather than by stress due to nutrient depletion (Øien and Moen, 2001), and it seems that plant species composition is more influenced by competitive relationships in different light conditions and under different management regimes (Ilmarinen and Mikola, 2009; Köhler et al., 2001).The relationship between plant-available nutrients in the soil and their concentrations in the herbage under different management regimes have been studied, especially in wet meadows (e.g. Güsewell et al., 2003; Olde Venterink et al., 2003; Wassen et al., 1995), but little attention has been paid to mountain meadows (Hejcman et al., 2010a).

In order to study the effects of either cutting or no management, respectively, on plant species composition of species-rich mountain hay meadows (Polygono–Trisetion), we established a long-term experiment in the Bukovec Nature Reserve in the Jizera Mts., at the border of the Czech Republic and Poland in 1999. Over the following ten years, forbs cover substantially increased and grass cover decreased in the unmanaged treatment; the outcome was *vice versa* for the cutting treatment (for details see Pavlů et al., 2011a).

The objective of this paper was to analyze the effects of long-term cutting with herbage removal in comparison with the effects of no management on soil and herbage chemical properties (N, P, K, Ca and Mg), herbage yield and sward height. Within this context, we aimed to answer the following research questions: (i) how are related soil and herbage chemical properties? (ii) how are herbage chemical properties related to herbage yield? (iii) how do different management regimes affect N:P, N:K and P:K ratios in the herbage? (iv) how does nutrient depletion by herbage removal affect nutrient limitation? (v) can be nutrient depletion by herbage removal detectable better according to the soil or the herbage chemical properties?

Material and methods

Study site

The experiment was carried out from 1999 to 2009 in a mountain hay meadow in the Bukovec Nature Reserve in the north-eastern part of the Jizera Mts. (Jizerské hory, Góry Izerskie, Isergebirge in Czech, Polish and German, respectively), 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 soil type is Cambisol. The following soil chemical properties were recorded in the upper 0–10 cm at the beginning of the study (2004): pH/KCl, 4.4; concentration of plant-available P, 15 mg kg^{-1} (very low); plant-available K, 198 mg kg^{-1} (good); and plant-available Mg, 300 mg kg^{-1} (good) – extracted by Mehlich III reagent (Mehlich, 1984). The experimental meadow was cut once per year and herbage had been removed each year since at least 50 years before the start of the experiment.

The experimental grassland was classified as a Polygono bistortae–Trisetion flavescentis (short name Polygono–Trisetion) alliance. The dominant species at the beginning of the experiment were *Festuca rubra*, *Agrostis capillaris*, *Trisetum flavescens*, *Cirsium heterophyllum* and *Geranium sylvaticum*. The mean cover of the main grasses, legumes and forbs in both treatments for the years 2003–2009 is given in Table 1.

Experimental design

The experiment was established in five completely randomized blocks with an individual experimental plot of size 5 m × 5 m. The treatments investigated were: one cut per year with removal of the cut biomass in mid-July (cutting treatment); and unmanaged grassland (unmanaged treatment). Cutting treatment was considered as the control because the grassland was cut before establishment of the experiment.

Soil chemical properties

Soil samples were collected in July in the years 2004–2009. Three soil sub-samples were collected from the upper 10 cm of

Table 1
Cover (in %) of grasses, legumes and forbs and cover of the most abundant species in each functional group. Numbers represent mean values in cutting (C) and unmanaged (U) treatments for the years 2003–2009 (for detail see Pavlů et al., 2011a).

Species	Treatment	
	C	U
Total cover of grasses	**53.2**	**32.7**
Agrostis capillaris	17.4	10.2
Briza media	4.9	1.8
Festuca rubra	19.9	7.1
Luzula luzuloides	4.6	6.8
Trisetum flavescens	6.4	6.8
Total cover of legumes	**13.3**	**3.2**
Trifolium repens	9.3	0.7
Trifolium pratense	2.0	0.1
Vicia cracca	2.0	2.5
Total cover of forbs	**63.9**	**98.5**
Alchemilla sp.	6.8	8.4
Bistorta major	4.4	5.7
Cirsium heterophyllum	17.9	32.6
Crepis mollis	5.3	4.8
Geranium sylvaticum	12.2	18.1
Hypericum maculatum	3.4	18.7
Meum athamanticum	9.5	6.7
Potentilla erecta	4.4	3.5

the soil profile per each 5 × 5 m monitoring plot. The soil samples were air-dried, biomass residues and roots were removed and the sample was then ground in a mortar and sieved to 2 mm. All chemical analyses were performed in an accredited laboratory Ekolab Žamberk (www.ekolab.cz); plant-available P, K, Ca and Mg were extracted by Mehlich III (Mehlich, 1984) reagent (composition: 0.2 M CH_3COOH + 0.25 M NH_4NO_3 + 0.013 M HNO_3 + 0.015 M NH_4F + 0.001 M EDTA, usage: 25 cm^3 reagent per 2.5 cm^3 soil) and then determined by inductively coupled plasma–optical emission spectrometry (ICP–OES). Total N was analyzed by the Kjeldahl method and organic C by means of colorimetry (AOAC, 1984). The mean of three sub-samples per monitoring plot was used for statistical analyses.

Herbage chemical properties, yield and sward height

Herbage samples were taken in the years 2003–2009. Dry matter herbage yield in both the cutting and unmanaged treatment was measured in three sub-plots each of 50 cm × 25 cm within each 5 m × 5 m experimental plot at a stubble height of 3 cm. The sampling site in the unmanaged treatment was a 1-m wide unmanaged strip in the 5 m × 5 m experimental plots. Herbage was collected from different sub-plots in each year in order to avoid any residual effect of herbage collection from the previous year. The harvested herbage was dried until totally desiccated at 85 °C and dry matter yield was then determined. The mean of three sub-samples per experimental plot was used for statistical analyses.

Compressed sward height was measured using a rising plate meter (Castle, 1976). We performed ten measurements per each experimental plot before vegetation sampling in each vegetation season.

N, P, K, Ca and Mg concentrations were determined from the herbage samples collected for analysis of dry matter herbage yield after digestion in *aqua regia* by ICP–OES in the accredited laboratory, Ekolab Žamberk. The amount of N, P, K, Ca and Mg in the herbage was determined by multiplying the herbage dry matter yield by the concentrations of N, P, K, Ca and Mg in the herbage.

Data analysis

A repeated-measures ANOVA was used to evaluate the effect of year, treatment and the year*treatment interaction on soil and biomass chemical properties, herbage yield, sward height and on the amount of nutrients in the herbage. To identify significant differences between treatments in individual years, a one-way ANOVA was used. We used ANOVA as all the required assumptions were met.

The relationships between herbage yield, sward height, soil and biomass chemical properties were analyzed by linear regression analysis. All analyses were performed in Statistica 9.0 program (www.statsoft.cz).

Results

Soil chemical properties

Calculated by repeated-measures ANOVA, a significant effect of year on total N content, plant-available concentrations of Ca and Mg and on pH/KCl was recorded (Table 2). There was no significant effect of treatment or the year*treatment interaction on any of the measured soil chemical properties. The highest total nitrogen content of 9000 mg kg^{-1} was recorded in 2008; this value was very different from the mean value of 7300 mg kg^{-1} recorded in all

Table 2
Results of repeated measures ANOVA (year, treatment, year × treatment) of soil and herbage chemical properties.

		Year		Treatment		Year × Treatment	
		F-ratio	*P*-value	*F*-ratio	*P*-value	*F*-ratio	*P*-value
Soil	pH/KCl	16.46	<0.001	0.04	0.842	0.30	0.909
	C_{org}	2.09	0.083	0.13	0.724	0.20	0.962
	N_{tot}	5.08	0.001	0.28	0.602	0.18	0.970
	P	2.40	0.066	0.01	0.935	0.55	0.703
	K	1.04	0.398	2.65	0.112	0.82	0.523
	Ca	2.96	0.031	0.93	0.342	0.67	0.615
	Mg	8.35	<0.001	2.39	0.130	0.63	0.642
Herbage	Yield	67.94	<0.001	124.39	<0.001	1.87	0.101
	Sward height	5.08	<0.001	331.33	<0.001	1.84	0.107
	N	31.97	<0.001	3.85	0.056	4.59	0.002
	P	2.78	0.028	5.63	0.022	0.64	0.672
	K	3.39	0.011	87.31	<0.001	0.49	0.784
	Ca	2.25	0.065	0.39	0.536	1.63	0.171
	Mg	1.73	0.147	0.54	0.467	0.74	0.595
	N:P	1.30	0.281	2.83	0.099	0.40	0.085
	N:K	3.02	0.019	55.56	<0.001	1.34	0.264
	K:P	1.37	0.253	19.62	<0.001	0.65	0.666

F represents the value derived from *F* statistics in repeated measurements ANOVA and *P* represents the related probability value.

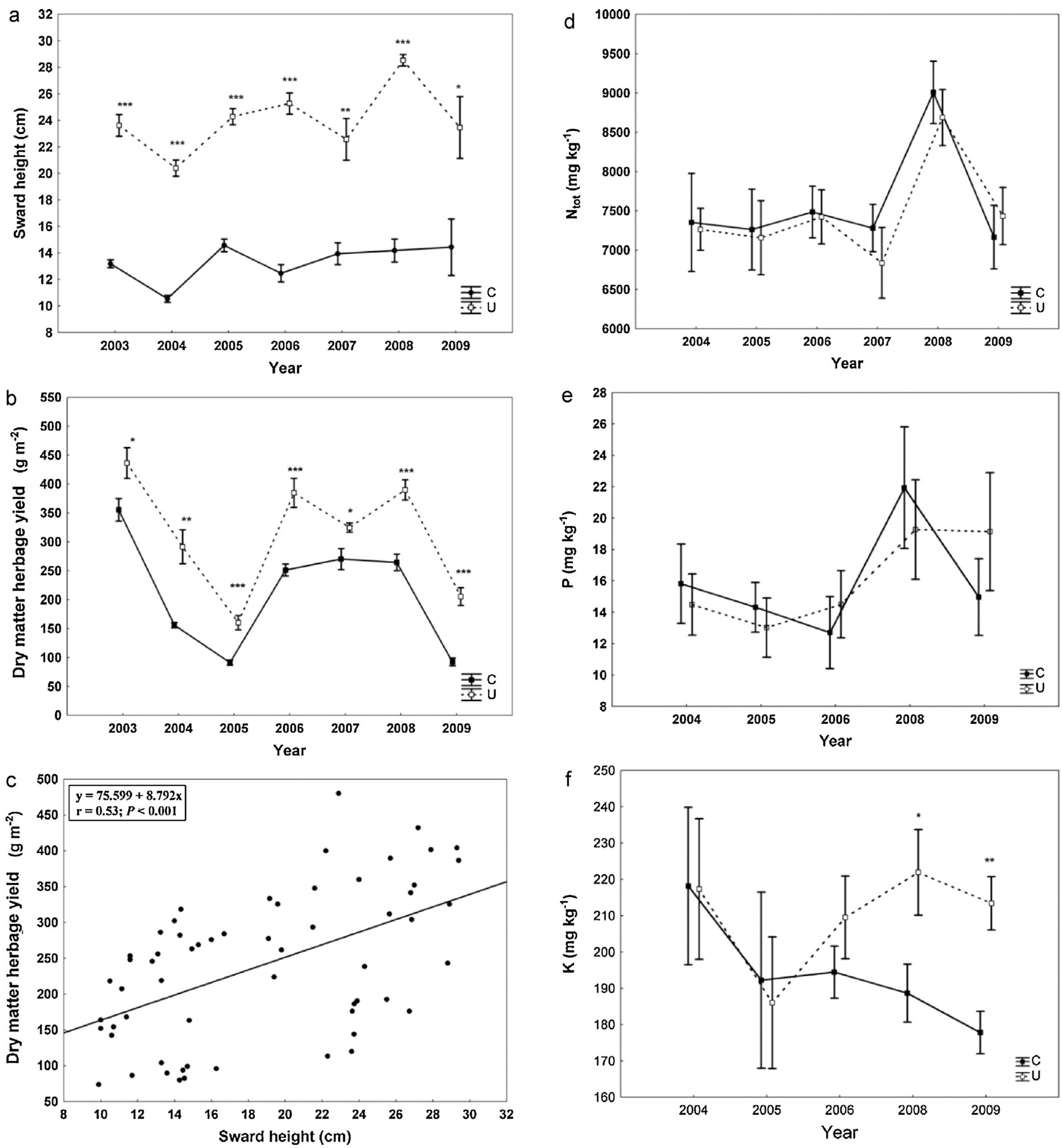

Fig. 2. (a) Sward height, (b) dry matter herbage yield, (c) relationship between sward height and dry matter herbage yield, (d) concentration of total nitrogen in the soil, (e) concentration of Mehlich III phosphorus and (f) potassium in the soil. C – cutting treatment, U – unmanaged treatment. Significant differences between treatments within each year calculated by a one-way ANOVA are indicated by asterisks (* – significant at α 0.05, ** – significant at α 0.01, *** – significant at α 0.001). Error bars represent standard error of the mean (SE).

other years (Fig. 2d) The concentration of plant-available P ranged from 12 to 22 mg kg^{-1}, with the highest values recorded in 2008 (Fig. 2e). The concentration of plant-available K clearly decreased in the cutting treatment, from 220 mg kg^{-1} in 2004 to 175 mg kg^{-1} in 2009 (Fig. 2f). No decrease was recorded in the unmanaged treatment and differences between treatments were significant in 2008 and 2009. Mean values of pH/KCl, organic C, C:N ratio, total N content and plant-available concentrations of P, K, Ca and Mg in both treatments for all years are given in Table 3.

Herbage yield and sward height

Calculated by repeated-measures ANOVA, a significant effect of year and treatment on herbage yield and sward height was recorded. A significant effect of the year*treatment interaction was recorded only in the case of herbage yield (Table 2). Herbage yield and sward height were significantly higher in the unmanaged than in the cutting treatment in all years (Fig. 2a and b). For the years 2003–2008, the mean herbage yield was 231 and

Table 3
Soil and herbage chemical properties.

		Treatment	
		C	U
Soil	pH/KCl	4.4	4.4
	C_{org} mg kg^{-1}	102758	100959
	N_{tot} mg kg^{-1}	7602	7467
	P mg kg^{-1}	15.8	16.1
	K mg kg^{-1}	196	210
	Ca mg kg^{-1}	1177	1242
	Mg mg kg^{-1}	348	378
	C:N	13.6	13.6
Herbage	N g kg^{-1}	16.0	16.5
	P g kg^{-1}	1.7	1.8
	K g kg^{-1}	11.1	14.6
	Ca g kg^{-1}	10.1	10.3
	Mg g kg^{-1}	4.2	4.1
	N:P	9.7	9.2
	N:K	1.5	1.1
	K:P	6.8	8.2

Numbers represent mean values in cutting (C) and unmanaged (U) treatments for the years 2003–2009.

331 g m^{-2} and mean sward height was 13 and 24 cm in the cutting and unmanaged treatments, respectively. Herbage yield was significantly positively correlated with sward height regardless of treatment (Fig. 2c).

Herbage chemical properties

Calculated by repeated-measures ANOVA, a significant effect of year on concentrations of N, P and K was recorded. A significant effect of treatment on the concentrations of P and K was recorded; a significant effect of the year*treatment interaction was recorded only for N concentrations (Table 2). The concentrations of N ranged from 13 to 19 g kg^{-1} and were significantly higher in the unmanaged treatment only in 2003 and 2007 (Fig. 3a) The concentration of P ranged from 1.5 to 2.0 g kg^{-1} and was generally slightly higher in the unmanaged treatment, but differences between treatments were not significant in individual years (Fig. 3b). The concentration of K was significantly higher in the unmanaged than in the cutting treatment in all years (Fig. 3c). The mean K concentration over all years was 11 and 15 g kg^{-1} in the cutting and unmanaged treatments, respectively. The mean concentrations of Ca and Mg over all years are given in Table 3.

The mean N:P ratio for all years was 9.7 and 9.2 in the cutting and unmanaged treatments, respectively, and differences between treatments were not significant in individual years (Fig. 3d). The mean N:K ratio for all years was 1.5 and 1.1 in the cutting and unmanaged treatments, respectively, and differences between treatments were significant in all years (Fig. 3e). The mean K:P ratio for all years was 6.8 and 8.2 in the cutting and unmanaged treatments, respectively, and differences between treatments were significant only in 2007 and 2008 (Fig. 3f).

In both treatments, the concentration of N in the herbage decreased with increasing herbage yield (Fig. 4a) Concentrations of P and K decreased with increasing herbage yield only in the cutting treatment (Fig. 4b and c). In both treatments, a negative relationship between total soil N content and concentration of N in the biomass was recorded (Fig. 4d). The concentration of P in the herbage was positively related to the concentration of plant-available P in the soil only in the cutting treatment (Fig. 4e). Concentrations of K in the herbage were positively related to the concentration of plant-available K in the soil in both treatments (Fig. 4f).

Amount of nutrients in the herbage

Calculated by repeated-measures ANOVA, a significant effect of year and treatment on the amount of N, P, K, Ca and Mg in the harvestable herbage was recorded. The interaction of year*treatment was significant only in the case of K (Table 4). With the exception of Ca and Mg in 2003, the quantity of nutrients in the herbage was significantly higher in the unmanaged than the cutting treatment.

Discussion

Soil chemical properties

Ten years of observing different management regimes was too short a period to affect significantly total N content and plant-available concentrations of P, Ca and Mg in the soil. The result of there being almost no effect over the ten years of the cutting regime on plant-available concentrations of P, Ca and Mg is in agreement with other grassland management studies (Hansson and Fogelfors, 2000; Hejcman et al., 2010a; Ilmarinen and Mikola, 2009; Köhler et al., 2001; Øien and Moen, 2001; Perring et al., 2009; Schaffers et al., 1998). A decrease in plant-available concentrations of P, Ca and Mg by cutting and herbage removal management is a long-term process, as the amount of annually removed P, Ca and Mg is relatively low (Pavlů et al., 2011b). It seems that it was the type of management regime rather than nutrient depletion that could have been the key factor for vegetation changes in the mountain hay meadow, at least in the initial period after the contrast management regimes were introduced.

Furthermore, the soils under the cutting management regime, where plant-available P concentrations in the soil were reduced by biomass removal, are more exposed to freezing and thawing. These soils therefore freeze earlier in the autumn and frost penetrates deeper than it does under unmanaged grassland, so the availability of P in these soils can be increased (Øien and Moen, 2001); this results in there being a similar amount of plant-available P in the soil under the cutting and as well as under the unmanaged treatments. As recorded in this study and also by other authors (Novák et al., 2013; Pavlů et al., 2012), a high cover of the short grass *A. capillaris* is a very good indicator of low P availability in the grassland soil.Ten years of cutting and herbage removal management was sufficient significantly to decrease plant-available concentrations of K in the soil. The decrease in K availability under the regime of regular cutting and biomass removal is in accordance with results obtained from several other grassland studies (Alfaro et al., 2003, 2004; Koerselman et al., 1990; Schaffers et al., 1998). A possible explanation for this is that soil with high organic matter and low clay content was not able to release enough K by weathering of clay minerals in order to compensate for the K removed by the harvested herbage (Kayser and Isselstein, 2005). A substantial decrease in plant-available concentrations of K in our experiment was recorded despite the K concentration being evaluated as "good" for productive grasslands (Budňáková et al., 2004). The same result of a substantial decrease in the concentration of K under the cutting management regime, despite "very high" K concentrations in the soil, was recorded by Hejcman et al. (2010a) after six years of cutting and herbage removal management in mountain grassland of low productivity on organic soil. It seems that the Mehlich III extraction procedure does not correctly predict the amount of plant-available K in soils with high organic matter content.

Herbage yield and sward height

The studied grassland was classified as being of low productivity, as the mean dry matter herbage yield in both treatments over

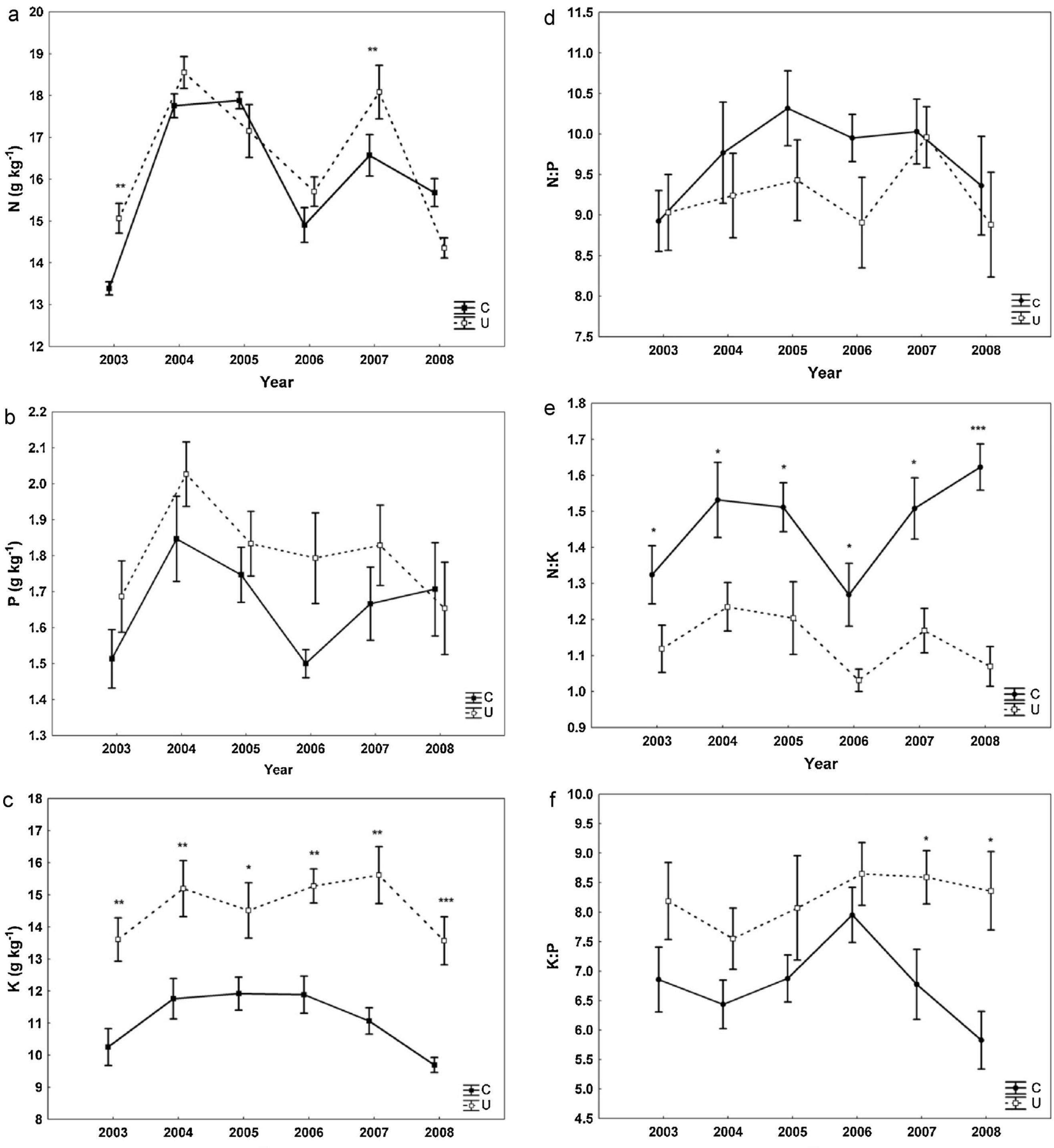

Fig. 3. Concentration of (a) N, (b) P, (c) K in the herbage and (d) N:P, (e) N:K and (f) K:P rations in the herbage. C – cutting treatment, U – unmanaged treatment. Significant differences between treatments within each year calculated by a one-way ANOVA are indicated by asterisks (* – significant at α 0.05, ** – significant at α 0.01, *** – significant at α 0.001). Error bars represent standard error of the mean (SE).

all years was below 300 g m^{-2}, the limit for low productive grasslands in Central Europe (Hejcman et al., 2010d). The low production potential of the grassland was also in accordance with the C:N ratio in the soil, which was 13.6, and this is in accordance with the conclusions of Hejcman et al. (2010b), that is, that a C:N ratio below 10 is characteristic for highly productive and above 10 for less productive grasslands. Low biomass production was also indicated by the dominance of low productive *A. capillaris* in the sward because of the generally low nutrient availability. Another typical feature of this mountain grassland was the very high year-to-year variability in herbage production, similar to other mountain grasslands in the borderland between the Czech Republic and Poland (Hejcman et al., 2009, 2010a).

The positive correlation between the compressed sward height and herbage yield (r = 0.53) was lower than the correlation recorded in monoculture stands of *Medicago sativa* (r = 0.85; Hakl et al., 2012). This relatively weak correlation can be explained by the heterogeneous vegetation structure that occurred due to the presence of

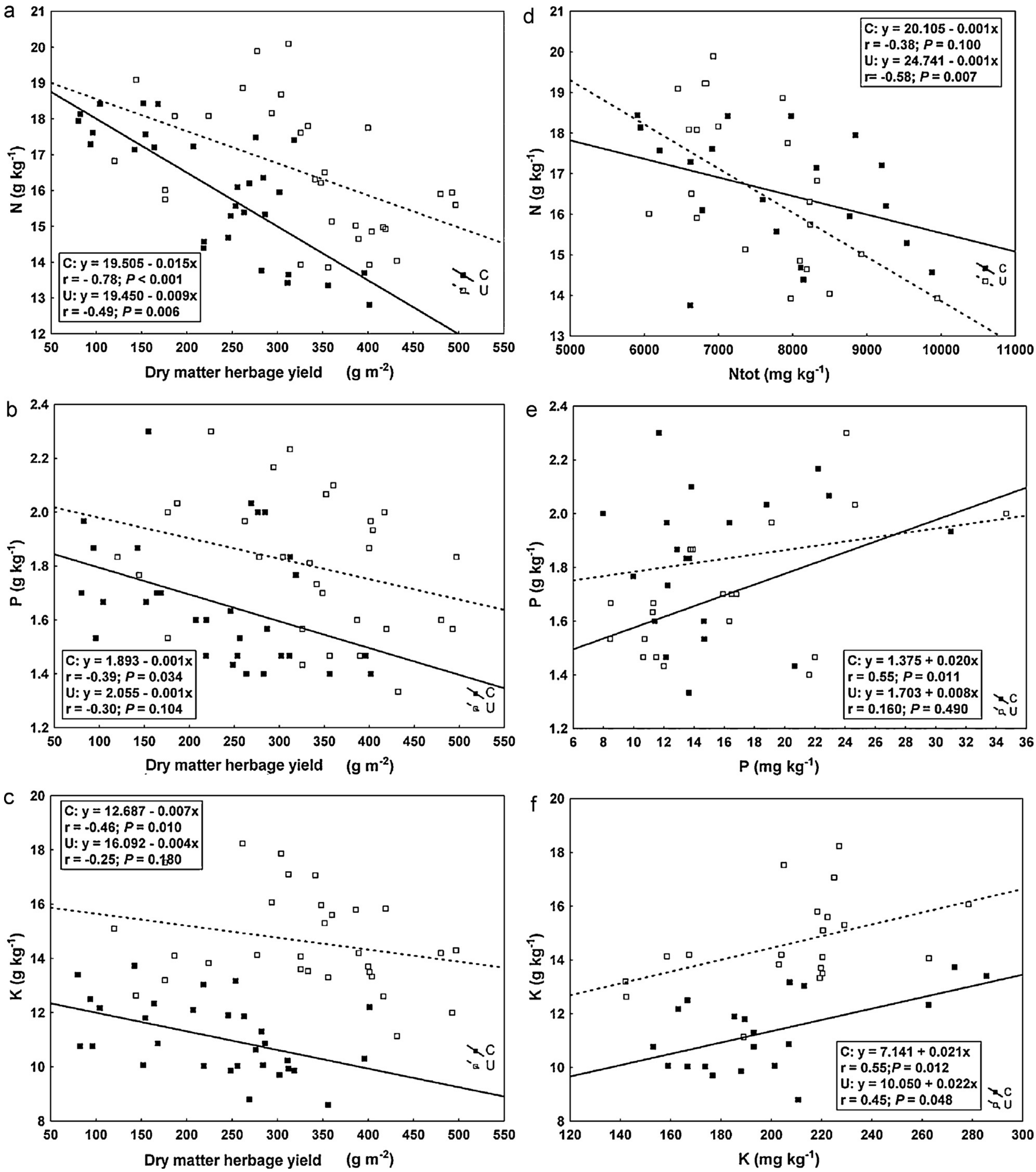

Fig. 4. Relationships between (a) nitrogen, (b) phosphorus and (c) potassium concentration in the herbage and herbage yield and relationships between (a) nitrogen, (b) phosphorus and (c) potassium concentrations in the soil and in the herbage. C – cutting treatment, U – unmanaged treatment. Significant differences between treatments within each year calculated by a one-way ANOVA are indicated by asterisks (* – significant at α 0.05, ** – significant at α 0.01, *** – significant at α 0.001). Error bars represent standard error of the mean (SE).

species with different heights (Pavlů et al., 2011a). Therefore, the use of the compressed sward height in the precise prediction of herbage yield could be problematic in semi-natural species rich grasslands.

Herbage chemical properties

The forage quality of the herbage was generally low, and the herbage from this low productivity grassland was not suitable for feeding high yielding milk cows. This is because the recorded concentrations of N (16 to 16.5 g N kg^{-1}) and P (1.7 to 1.8 g P kg^{-1}) were far below the optimal N and P concentrations for dairy cow nutrition, which range from 19 to 25.8 g N kg^{-1} and from 2.3 to 3.7 g P kg^{-1} (Whitehead, 2000). In addition, the low forage quality of the herbage was also indicated by the above-optimum K, Ca and Mg concentrations. The concentration of K ranged from 11 to 14 g K kg^{-1} compared to the optimum 3 to 8 g K kg^{-1}, the concentration of Ca ranged from 10.1 to 10.3 g Ca kg^{-1} with an optimum of

Table 4
Nutrient content in the above-ground herbage per m^2, results of one-way ANOVA for each year from 2003 to 2008, and ANOVA repeated measures.

Year	Treatment	Nutrient				
		K g m^{-2}	Ca g m^{-2}	Mg g m^{-2}	P g m^{-2}	N g m^{-2}
2003	C	3.66	3.34	1.45	0.53	4.75
	U	5.93	4.70	1.73	0.74	6.61
		**	n.s.	n.s.	*	*
2004	C	1.83	1.72	0.68	0.29	2.77
	U	4.40	3.09	1.25	0.58	5.39
		***	*	**	***	***
2005	C	1.09	0.99	0.40	0.16	1.63
	U	2.33	1.46	0.61	0.30	2.75
		**	**	**	**	**
2006	C	2.97	2.34	1.02	0.38	3.74
	U	5.84	3.61	1.48	0.68	6.03
		***	*	*	***	***
2007	C	2.96	2.43	1.02	0.45	4.48
	U	5.05	3.34	1.36	0.59	5.85
		***	*	*	*	**
2008	C	2.56	2.82	1.23	0.45	4.16
	U	5.26	4.58	1.74	0.65	5.60
		***	**	**	*	**
Effect of ANOVA repeated measures	T	***	***	***	***	***
	Y	***	***	***	***	***
	T × Y	*	n.s.	n.s.	n.s.	n.s.

Numbers represent average of five replicates; n.s. – result of ANOVA was not significant, * – result significant at α 0.05 and ** – result significant at α 0.01,*** – result significant at α 0.001; C – cutting and U – unmanaged treatments; Y – year, T – treatment.

2.9 to 5.8 g Ca kg^{-1} and, finally, the concentration of Mg ranged from 4.2 to 4.1 g kg^{-1} with an optimum of 1.6 to 2 g Mg kg^{-1} (Whitehead, 2000). Herbage from this *A. capillaris* and *F. rubra* dominated grassland can rather be used for feeding beef cattle or sheep, which have lower forage quality requirements than have a high milk yielding dairy cattle.

Concentrations of N and P in the herbage were comparable with values recorded in *F. rubra*-dominated grasslands by Pavlů et al. (2012) or with those for low productivity wetlands (Wassen et al., 1995). According to Wassen et al. (1995), concentrations of N in wetlands of below 14 g kg^{-1} and concentrations of P below 0.7 g kg^{-1} at the peak of growing season are indicators of N and P limitation. The importance of N, P co-limitation for the existence of low productive grasslands was demonstrated also in grassland landscape studies by Klaus et al. (2011, 2013) or by a long-term fertilizer experiment by Oelmann et al. (2009). Regional differences preclude generalization, but the regional replication is of major importance for studies seeking general insights into productivity-diversity relationships (Klaus et al., 2013).

The similar concentrations of N found in the herbage in both treatments were probably a result of the N removed in the harvested herbage being compensated by N_2 fixation, as the cover of N_2 fixing legumes (*Trifolium repens* and *T. pratense*) was substantially higher in the cutting than in the unmanaged treatment. For example, the apparent transfer of N from legumes to grasses can exceed 100 kg N ha^{-1} per year (Elgersma and Hassink, 1997). In addition, a higher proportion of N-rich legumes, together with a lower proportion of N-poor stems in the cutting compared to the unmanaged treatment is another possible explanation for there being similar concentrations of N in the herbage from both treatments.

High year-to-year fluctuations in N concentrations can be explained by the different herbage production in particular years and also by year-to-year differences in plant species composition. Generally, in years with a high herbage production, lower concentrations of N in the herbage were recorded. This negative relationship between herbage yield and herbage N concentration is called the dilution effect; it indicates that the N concentration in the herbage must be evaluated with respect to the herbage yield, which is in turn directly related to the phenological stage of the individual species (Duru and Ducrocq, 1997; Hejcman et al., 2010d).

The existence of a negative relationship between total soil N content and the concentration of N in the herbage, means that the total content of N is a negative indicator of N availability in the soil in our experiment. High total N content in the soil is connected with poor soil quality, resulting in an accumulation of soil organic matter and its slow mineralization.

The slightly higher concentration of P in the herbage from the unmanaged compared to the cutting treatment could be explained by the continuous removal of P from the grassland in latter treatment. This removal was not reflected in the concentration of plant-available P in the soil extracted by a relatively strong Mehlich III solution. Ten years under different management was not a sufficiently long period of time to detect these small changes in the soil P status; this observation is in accordance with several other long-term studies using CAL extraction (Hejcman et al., 2010c; Pavlů et al., 2011b). Moreover, small differences in plant-available concentrations of P in the soil extracted by Mehlich III solution can result in very high differences in herbage P concentrations, as was also recorded in mountain grasslands by Hejcman et al. (2007) and Semelová et al. (2008). Higher P concentrations in the herbage from the unmanaged treatment can at least partly be explained by the higher forb cover there (Pavlů et al., 2011a), with forbs generally being more P-rich than are grasses (Pirhofer-Walzl et al., 2011). The negative relationship between herbage yield and P concentration was explained by the dilution effect described for P by Duru and Ducrocq (1997).

The significantly higher concentration of K found in the herbage from the unmanaged compared to the cutting treatment is consistent with a gradual decrease in the concentration of plant-available K in the soil. The decrease in herbage K concentrations was recorded substantially earlier than the decrease in plant-available K concentrations in the soil. It seems that soil analyses of plant-available K are not as sensitive as analyses of herbage K concentrations, and soil K status can be better predicted by the herbage K analysis: this was also noted by Oomes (1990). This result is consistent with the conclusion of Schaffers (2002), who found K to be the nutrient with the strongest relationship between the soil and herbage concentration.

In addition to the low N concentration in the herbage, a relatively low availability of N in the studied grassland was also indicated by the N:P ratio in the herbage, which was below 11 in both treatments over all years, indicating that the herbage production was N-limited. According to the experience of Koerselman and Meuleman (1996), Olde Venterink et al. (2003) and Güsewell (2004), N-limitation of herbage production is to be expected if the N:P ratio is below 14 in wet grasslands. Klaus et al. (2011) confirmed validity of this threshold also for mesic managed grasslands Nitrogen limitation of herbage production was also indicated by the biomass N:K ratios, which were lower than 2.1, a threshold value for harmonic nutrition in wet grasslands (Olde Venterink et al., 2003).

Conclusion

Despite ten years of nutrient depletion by herbage removal, K was the only nutrient of which the plant-available concentration significantly decreased. Likewise, K was the only nutrient with strong relationship between the soil and herbage concentration. Long-term cutting management can induce N, P and K limitation in herbage production, which can be better analyzed using biomass rather than soil chemical properties.

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