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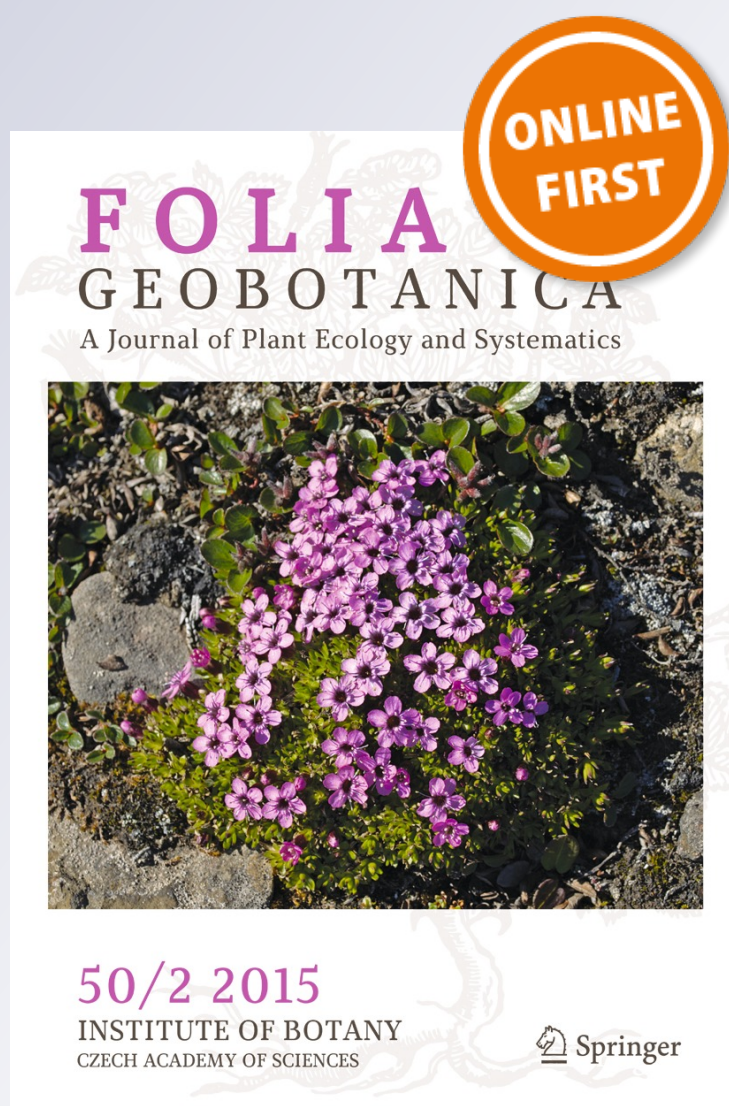
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Sward-height patches under intensive and extensive grazing density in an *Agrostis capillaris* grassland

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Abstract Patchiness is one of the important features of grazed temperate grasslands, but little is known about the structure of sward height patches under different grazing intensities. The present study examined the effect of continuous intensive and extensive stocking of heifers on the proportions of sward-height patch categories (short ≤ 5 cm, moderate 5.5–10 cm, tall ≥ 10.5 cm) and their plant species composition in an *Agrostis capillaris* grassland. A four-year study was performed on an upland grassland maintained under a long-term grazing experiment in the Jizerské hory Mts (Jizera Mountains), Czech Republic. The contrasting stocking densities form the differences in the proportion of sward-patch categories and generated a similar level of patch heterogeneity, which was mainly affected by the proportion of tall- and short-sward patches. The floristic composition of patches within the same sward height category depended upon stocking density. Moderate and tall patches under a given stocking density had similar botanical composition. Vegetation within short patches differed considerably from that of other patches under extensive grazing whereas under intensive grazing the differences between short, moderate

and tall sward-height patches were small. The findings show that grazing intensity is a key driver of the proportion as well as the floristic composition of sward-height patches in grasslands dominated by *A. capillaris*. These findings have implications for nature conservation, as they support the recommendation for extensive management of upland grasslands.

Keywords floristic composition · heifer grazing · pasture · patch category · RDA · vegetation

Introduction

Grazing by large herbivores is the most common use for grasslands worldwide. In contrast to cut grasslands, grazed grasslands are influenced by several factors including trampling, in situ nutrient addition by urine and faeces, seed dispersal, and selective defoliation by animals (Rook et al. 2004). Grazing management therefore usually leads to enhanced structural heterogeneity of the sward canopy, and the specific effects of grazing depend on the type of grazing animal, grazing pressure, and the timing and duration of stocking (Ausden 2007). Because herbivores may graze selectively on certain species and on certain plant parts (Rook and Tallowin 2003), they create a heterogeneous sward structure with a mosaic of different heights (Bakker et al. 1984). Generally, sward height is recognized as an important predictor of plant responses to defoliation intensity (e.g. Diaz et al. 2001; Pavlů et al. 2003; Pykälä 2004; Naujeck et al. 2005).

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The floristic composition and heterogeneity of vegetation in temperate grasslands are usually related to grazing intensity together with animals' preferences (Pettit et al. 1995; Sasaki et al. 2005) and result in a patchy structure of swards. Shorter patches are preferentially grazed by cattle due to their higher quality of biomass in comparison with patches of taller herbage that are either ungrazed or rarely grazed, and the selection for short patches increases over the course of the grazing season (Dumont et al. 1995; Correll et al. 2003; Dumont et al. 2007; Rossignol et al. 2011). The patchy structure thereby becomes reinforced (Pavlů et al. 2006c) and can remain stable for months (Cid and Brizuela 1998; Rossignol et al. 2011). Under extensive grazing management, patches neglected by herbivores predominate, as the available forage supply is higher than the herbivores' demand (Dumont et al. 1995; Pavlů et al. 2006a). These non-grazed patches can increase total species diversity while at the same time providing niches for generative reproduction of species less tolerant to grazing (Correll et al. 2003).

The immediate effect of grazing on the heterogeneity of vegetation depends on the interaction between the pre-existing spatial pattern of vegetation and the spatial pattern of grazing, not only at the paddock scale (Adler et al. 2001), but also at the landscape scale (Kohler et al. 2006a). If the spatial heterogeneity of grazing is stronger than the spatial heterogeneity of vegetation, then the spatial heterogeneity of vegetation will increase after grazing, and stable patches will thus be formed (Adler et al. 2001). Thus, variations in grazing intensity within a paddock may be greater than that among paddocks (Wallis De Vries et al. 1998). However, there are few references regarding the structure of patchiness, even though it is one of the most important indicators of pasture conditions (Bakker et al. 1984) and one which distinguishes pastures from meadows. Detailed vegetation studies focusing directly on sward-height patches are not common (see Willms et al. 1988; van den Bos and Bakker 1990; Sasaki et al. 2005; Dumont et al. 2007; Marion et al. 2010), and studies from temperate species-rich grasslands in Central Europe are even rarer (Sahin Demirbag et al. 2009). To date, there have been only a few studies examining the relationship between stocking intensity and the height structure of sward patches in detail (Wrage et al. 2012; Dumont et al. 2012; Tonn et al. 2013).

If grazing is spatially heterogeneous (patch grazing *sensu* Adler et al., 2001), which involves repeated

grazing of short patches due to increasing forage quality of such patches, then the relative cover of short patches will increase at the expense of moderately grazed patches during the vegetation season, but the relative cover of tall ungrazed patches will remain the same. The total spatial heterogeneity will thus increase. Stocking density is thus expected to affect mainly the relative cover of different classes of sward-height patches without changing the overall characteristics of the patches. We suppose that if a given sward-height patch category is grazed at the same intensity regardless of stocking density, it will therefore display the same floristic composition between stocking density treatments.

Given the importance of the structure of patchiness as outlined above, we focus in our paper on two basic questions: (1) What is the effect of two contrasting grazing densities on the structure of different sward-height patch categories?; (2) How do the two contrasting grazing densities affect the plant species composition of particular sward-height patch categories?

Material and methods

Study site

The study site was situated in an experimental grassland on an exposed north-westerly slope in the Jizerské hory Mts (Jizera Mountains), 10 km north of the city of Liberec in the northern part of the Czech Republic (50°50.34' N, 15°05.36' E, 420 m a.s.l.) at the village of Oldřichov v Hájích. The bedrock is formed of locally widespread biotic granite and overlain by a typical brown shallow soil (cambisol) with a pH (KCl) of 5.45 and an organic C content of 4.53 %. As analysed according to the Mehlich III method (Mehlich 1984), the contents of plant available P, K, Ca and Mg per 1 kg of soil were 28 mg, 67 mg, 1,728 mg and 58 mg, respectively. Average total annual precipitation is 803 mm, and the mean annual temperature is 7.2°C (data from the meteorological station in Liberec). The grassland was classified as a mesophile upland hay meadow (alliance *Arrhenatherion*; Chytrý 2007). There were about 24 vascular plant species per m² with the following dominant species: *Agrostis capillaris*, *Festuca rubra* agg., *Trifolium repens* and *Taraxacum* spp. The total number of vascular plant species recorded during the field sampling was about 60.

Experimental design

The experimental site was located on the site of the long-term Oldřichov Grazing Experiment, established on a formerly abandoned grassland with an initially homogeneous plant species composition across the entire experimental site in 1998 (Pavlů et al. 2007). Since 1998, the experimental pasture had been continuously stocked with young heifers each year from May to October. Two contrasting stocking densities were applied: (1) extensive grazing (EG), where the stocking rate was adjusted to achieve a mean target sward surface height of greater than 10 cm; and (2) intensive grazing (IG), in which the stocking rate was adjusted to achieve a mean target sward surface height of less than 5 cm. The mean stocking rates were approximately 500 kg live weight (two heifers) per 1 ha and 1,000 kg live weight (four heifers) per 1 ha for the EG and IG treatments, respectively. Compressed sward height was measured weekly across each experimental plot (100 measurements) using a rising plate meter (Correll et al. 2003), and stocking density was adjusted accordingly by increasing or decreasing the area available for grazing by moving fences with a set number of stock per plot (Pavlů et al. 2007). The experiment was arranged in two completely randomized blocks of experimental plots. Each experimental plot (core area) was approximately 0.35 ha. To study sward-height patches, two permanent transects lines of 42 m per plot were established in 2003 in areas that were available for grazing throughout the grazing season.

Measurements

Measurements were performed at 40 fixed sampling points at 1 m intervals along linear transects. The percentage cover of all vascular species, bare ground and faeces was estimated up to 100 % within circles 30 cm in diameter. Plant species nomenclature follows Kubát et al. (2002). Because of identification problems related to grazing, *Poa pratensis*, *P. annua* and *P. trivialis* were pooled together under *Poa* spp. Compressed sward height was measured in the same circles in which the cover was recorded. According to sward height, we arbitrarily assigned patch height categories. The following patch categories were identified: (a) short patches, height from 0 to 5 cm; (b) moderate patches, height from 5.5 to 10 cm; and (c) tall patches, height ≥ 10.5 cm. This arbitrary approach is based on experience with sward

response to grazing and is commonly used in temperate grasslands (Bakker et al. 1984; Scimone et al. 2007; Sahin Demirbag et al. 2009). The data from the transects were collected in 2003, 2004, 2006 and 2007 two times in each year during both the summer (S) and autumn (A) grazing seasons. There were 2,560 botanical records in total ($2 \text{ stocking densities} \times 2 \text{ blocks} \times 2 \text{ transects} \times 40 \text{ points per transect} \times 2 \text{ times per year} \times 4 \text{ years}$).

Data analysis

The relative proportions of specific sward-height patch categories between the treatments were evaluated by repeated measures ANOVA. The following effects were tested: year, season, stocking density, and the interaction of stocking density with year and season. The relative proportions data were arcsine-transformed to meet the assumptions of ANOVA. Repeated measures ANOVA was used to evaluate dominant species. The following effects were tested: stocking density, season, patch category, the interaction between patch category and year, and the interaction between stocking density and season. Three multivariate analyses were carried out (A1, A2, A3) to detect the key driver for plant species composition of grazed swards. Patches with different sward-height formed as a results of the primary manipulated factor (stocking density), but the effect of stocking density differed depending on the sward-height patch. The effects of stocking density and sward-height patches were therefore tested separately, and to distinguish these effects, their interaction was tested, too. Redundancy analysis (RDA) as implemented in CANOCO 5 (ter Braak and Šmilauer 2012) was used and followed by a Monte Carlo permutation test. These tests were carried out for the whole experimental period. The permutation scheme was adjusted to the repeated measures design. The individual points along the transects are split plots, and the whole-plot factors examined are: (1) stocking density in analysis A1 and (2) one transect in one study year in analyses A2 and A3. The following permutations were performed (1) no permutations within whole-plots and freely exchangeable permutations within split plots in analysis A1; (2) linear transect permutations within whole plots and freely exchangeable permutations within split plots in analysis A2; and (3) no permutations within whole plots and linear transect permutations within split plots in analysis A3. Each analysis was performed with 999 permutations. The species data were log-transformed $y' = \log_{10}(y + 1)$. The blocks

and years were treated as covariates. Biplot ordination diagrams in CANOCO 5 (ter Braak and Šmilauer 2012) were used to visualize the results of the analyses. Only the species with the highest fit are shown in the ordination diagram.

Results

Proportion of patches

The relative proportion of all sward-height patch categories differed between IG and EG stocking density (Table 1). Time effects (season and year) tested by repeated measures ANOVAs were significant only for short and tall sward-height patches, but non-significant for moderate sward-height patches. The relative proportion of short sward-height patches was increased whereas the relative proportion of tall sward-height patches was decreased under both stocking densities during all

Table 1 Results of repeated measures ANOVAs for the relative proportion of sward-height patch categories. *D.f.* = degrees of freedom, residual (denominator) *f*degrees of freedom for individual tests, *F*-ratio = *F*-statistics for the test of a particular analysis, *P*-value = corresponding probability value. * indicates interaction of environmental variables. Abbreviations: StockDen = stocking density; SH = short, MO = moderate, TA = tall sward-height patch categories.

Tested variable	Effect	<i>D.f.</i>	<i>F</i> -ratio	<i>P</i> -value
SH	Year	3	7.16	0.002
	Season	1	21.01	< 0.001
	StockDen	1	378.36	< 0.001
	Year*StockDen	3	7.81	< 0.001
	Season*StockDen	1	2.09	0.163
	Residuals	22		
MO	Year	3	1.52	0.236
	Season	1	0.19	0.666
	StockDen	1	27.34	< 0.001
	Year*StockDen	3	6.64	0.002
	Season*StockDen	1	6.08	0.022
	Residuals	22		
TA	Year	3	3.91	0.022
	Season	1	16.97	< 0.001
	StockDen	1	74.47	< 0.001
	Year*StockDen	3	0.26	0.855
	Season*StockDen	1	0.25	0.622
	Residuals	22		

seasons, except the year 2004 under EG (Table 2). By contrast, the tested interactions (between stocking density and year and between stocking density and season) were significant for the moderate sward-height patch category and were not significant for the tall sward-height patch category (Table 1). The relative proportion of moderate sward-height patches decreased during all seasons under IG and remained almost unchanged under EG. The interaction between stocking density and season was also non-significant for the short sward-height patch category, but the interaction between stocking density and year was significant.

Plant species composition

Based on RDA analyses, the interaction between stocking density and the patch category explained the largest proportion of vegetation data in comparison with solely the patch category or stocking density (Table 3). On average, stocking density had a larger effect on plant species composition (Table 3, analysis A1) than the patch categories (Table 3, analysis A2); however, in both cases the explanatory power was relatively small. A similar plant species composition was found between the taller patch categories (moderate and tall) under IG as well as between the same patch categories under EG (Fig. 1). Under EG, but not under IG, the short patch category substantially differed in botanical composition from the moderate and tall categories. The botanical composition of moderate and tall patch categories differed considerably between the two stocking densities (Table 3, analysis A3). Bryophytes frequently occurred in short patch categories under EG. Tall forbs (e.g. *Aegopodium podagraria*, *Cirsium palustre*, *Galium album*, *Hypericum maculatum*, *Lathyrus pratensis*, *Rumex acetosa*, *Ranunculus acris*, *Veronica chamaedrys* and *Vicia cracca*) as well as tall graminoids (e.g. *Alopecurus pratensis*, *Festuca rubra*, *Holcus lanatus* and *Holcus mollis*) occurred in taller swards, and thus had higher abundance in moderate and tall patch categories under EG (Fig. 1). The highest cover of bare ground was present in the tall patch category, especially in EG plots, as indicated in Fig. 1. The largest amounts of heifer faeces were recorded in the moderate and tall patch categories in IG plots.

The results of repeated measures ANOVAs (Table 4) show that the abundance of *F. rubra* differed between the stocking densities and that it changed over the years and seasons. However, the interaction between patch

Sward-height patches under intensive and extensive grazing

Table 2 Mean sward height (cm) in summer (S) and autumn (A), standard error of the mean (*SE*), and number of observations (*n*) for short (SH), moderate (MO), or tall (TA) sward patches under intensive (IG) and extensive (EG) stocking density in each study year.

Year/ Season	Stocking density	Patch category	Mean	<i>SE</i>	<i>n</i>
2003 S	IG	SH	3.63	0.085	116
		MO	7.08	0.212	36
		TA	13	0.567	8
	EG	SH	4.33	0.667	3
		MO	8.67	0.154	64
		TA	14.74	0.368	93
	IG	SH	2.91	0.088	144
		MO	6.63	0.202	16
		TA	–	–	0
2003 A	EG	SH	3.96	0.195	24
		MO	7.77	0.111	128
		TA	12.75	0.526	8
	IG	SH	4.11	0.096	72
		MO	7.59	0.164	59
		TA	13.34	0.382	29
	EG	SH	4.4	0.169	20
		MO	8.11	0.151	80
		TA	14.6	0.478	60
2004 A	IG	SH	3.69	0.093	102
		MO	7.685	0.167	54
		TA	11.75	0.479	4
	EG	SH	4.16	0.206	19
		MO	8.31	0.147	80
		TA	13.05	0.324	61
2006 S	IG	SH	3.68	0.123	72
		MO	7.85	0.144	74
		TA	12.21	0.405	14
	EG	SH	3.85	0.308	10
		MO	8.69	0.142	81
		TA	13.56	0.509	69
2006 A	IG	SH	3.51	0.109	91
		MO	7.26	0.172	63
		TA	11.5	0.516	6
	EG	SH	4.23	0.253	15
		MO	8.42	0.141	85
		TA	13.7	0.559	60
2007 S	IG	SH	3.91	0.106	66
		MO	7.88	0.184	60
		TA	13.53	0.398	34
	EG	SH	4	0.366	6
		MO	8.21	0.168	68
		TA	15.59	0.550	86

Table 2 (continued)

Year/ Season	Stocking density	Patch category	Mean	<i>SE</i>	<i>n</i>
2007 A	IG	SH	3.48	0.105	101
		MO	7.47	0.172	54
		TA	11.6	0.400	5
	EG	SH	4.32	0.205	11
		MO	8.54	0.153	67
		TA	14.62	0.352	82

category and season was insignificant. *Festuca rubra* had a higher cover in moderate and tall patch categories under EG (Fig. 2a). Dominant species *Taraxacum* spp. (Fig. 2b) and *Trifolium repens* (Fig. 2c) together with other short forbs (*Plantago lanceolata*, *Veronica serpyllifolia* and *Cerastium holosteoides*) and short grasses (such as *A. capillaris*; Fig. 2d) were present in all patch categories under IG. All effects on the abundance of *A. capillaris* tested by repeated measures ANOVAs were significant except for season and the interaction between patch category and season (Table 3).

Trifolium repens had a high cover also in the short patch category under EG and IG stocking density. The RDA analysis revealed that other short forbs (*Cerastium holosteoides*, *Hypochaeris radicata*, *Leontodon autumnalis* and *Ranunculus repens*) had higher abundance under IG than under EG and they occurred especially in the short category. Although nearly all the study factors had a significant effect on the cover of *T. repens*, the cover of another short forb, *Taraxacum* spp., had a tendency to be more stable throughout the season and more independent of patch category (see Table 3). The most common grass species of the sward, *A. capillaris*, dominated in all patch categories under IG (Fig. 2d).

Discussion

Proportions of patches

Intensive stocking density indeed resulted in a higher proportion of short-sward patches, but spatial heterogeneity did not differ with increasing grazing intensity from spatially heterogeneous grazing so typical for extensive stocking densities. This means that the differences in the proportions of sward-patch categories were affected by the

Table 3 Results of redundancy analyses for three different H_0 analyses (A1, A2, A3), A1 – Stocking density has no effect on plant species composition; A2 – Patch categories have no effect on plant species composition; A3: The interaction of stocking density and patch categories has no effect on plant species composition;

Analysis	Explanatory variable	Covariables	% expl.	F-ratio	P-value
A1	stocking density	Block Year	9.90	281.0	0.001
A2	patch categories	Block Year	7.34 (7.40)	202.0 (102.0)	0.001 (0.001)
A3	patch categories * stocking density	Block Year	11.60 (12.50)	333.0 (73.9)	0.001 (0.001)

% expl. – variation explained by axis 1 (adjusted explained variation by all ordination axes), a measure of the explanatory power of the explanatory variables; F-ratio – F-statistics for the test of a particular analysis; P-value – corresponding probability value obtained by the Monte Carlo permutation test.

contrasting stocking densities, and both treatments generated a similar level of heterogeneity in sward

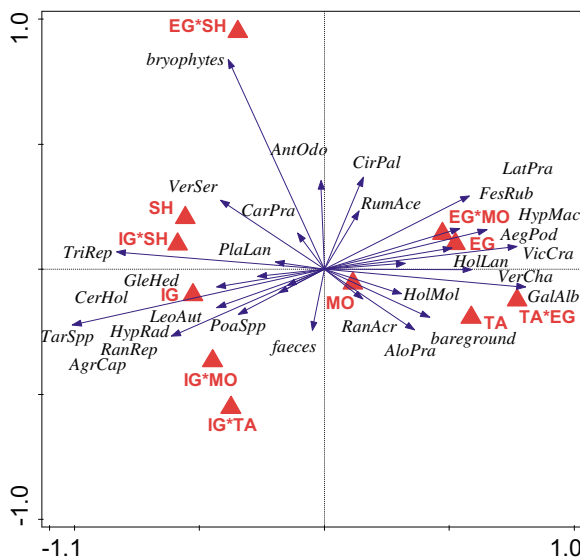


Fig. 1 Ordination diagrams showing the results of redundancy analysis of plant species composition data. Arrows represent species data; * indicate interactions of environmental variables. Abbreviations: EG = extensive grazing; IG = intensive grazing; SH = short, MO = moderate, TA = tall sward-height patch categories; AegPod = *Aegopodium podagraria*; AgrCap = *Agrostis capillaris*; AloPra = *Alopecurus pratensis*; AntOdo = *Anthoxanthum odoratum*; CarPra = *Cardamine pratensis*; CerHol = *Cerastium holosteoides*; CirPal = *Cirsium palustre*; FesRub = *Festuca rubra*; GalAlb = *Galium album*; GleHed = *Glechoma hederacea*; HolLan = *Holcus lanatus*; HolMol = *Holcus mollis*; HypMac = *Hypericum maculatum*; HypRad = *Hypochaeris radicata*; LatPra = *Lathyrus pratensis*; LeoAut = *Leontodon autumnalis*; PlaLan = *Plantago lanceolata*; PoaSpp = *Poa* spp.; RanAcr = *Ranunculus acris*; RanRep = *Ranunculus repens*; RumAce = *Rumex acetosa*; TarSpp = *Taraxacum* spp.; TriRep = *Trifolium repens*; VerCha = *Veronica chamaedrys*; VerSer = *Veronica serpyllifolia*; VicCra = *Vicia cracca*.

structure because it was generated by similar proportions of contrasting sward height classes. On the other hand, Berg et al. (1997) reported contrasting sward micro-patterns occur especially on extensively grazed pastures with high sward-height variability. This variability in extensively grazed pastures was also noted in previous studies based on the Oldřichov Grazing Experiment (e.g. Correll et al. 2003; Pavlu et al. 2006c, 2009) and was also observed in Argentinian pastures (Cid and Brizuela 1998; Cid et al. 2008). This micro-pattern indicates variability in plant species. However, as demonstrated by our study, a certain degree of variability among different sward-height patches also exists on intensively grazed pastures, although it is initially not as obvious as on extensively grazed ones. Confirming our first conceptual hypothesis, short patches dominated under IG across all study seasons; tall patches were represented only sporadically under this treatment, the reverse being observed under EG. Similar results were observed in the study of Tonn et al. (2013). This showed that in the case of continuous intensive grazing the availability of forage did not significantly exceed demand; cattle grazed less selectively, and therefore the percentage of short patches increased. Under high grazing pressure from intensive stocking, when animals repeatedly overgraze short vegetation, the grazing of tall patches is restricted by the presence or absence of faeces or thistles (Cid and Brizuela 1998; Rossignol et al. 2011). The proportion of moderate patches was relatively stable under particular stocking densities and was not significantly affected by the season and year. This shows that patch heterogeneity under specific stocking densities is mainly affected by the proportion of tall and short patches.

In autumn 2003 the swards were shorter than in the autumns of the other years. The absence of tall patches under IG and their reduction to only 5 % under EG in

Table 4 Results of repeated measures ANOVAs for the percentage cover of four dominant species. *D.f.* – degrees of freedom, residual (denominator) degrees of freedom for individual tests, *F*-ratio – *F*-statistics for the test of a particular analysis, *P*-value – corresponding probability value. * indicate interactions of environmental variables. Abbreviations: StockDen – stocking density, PatchCat – patch category.

Tested variable	Effect	<i>D.f.</i>	<i>F</i> -ratio	<i>P</i> -value
<i>Festuca rubra</i>	Year	3	141.02	< 0.001
	StockDen	1	348.52	< 0.001
	Season	1	40.33	< 0.001
	PatchCat	2	15.39	< 0.001
	PatchCat*Year	6	14.50	< 0.001
	PatchCat*StockDen	2	3.41	0.033
	PatchCat*Season	2	0.65	0.520
	Residuals	2,853		
<i>Taraxacum</i> spp.	Year	3	5.25	< 0.001
	StockDen	1	519.80	< 0.001
	Season	1	0.01	0.933
	PatchCat	2	2.88	0.056
	PatchCat*Year	6	3.74	< 0.001
	PatchCat*StockDen	2	36.57	< 0.001
	PatchCat*Season	2	0.32	0.727
	Residuals	2,853		
<i>Trifolium repens</i>	Year	3	49.93	< 0.001
	StockDen	1	304.02	< 0.001
	Season	1	62.78	< 0.001
	PatchCat	2	26.44	< 0.001
	PatchCat*Year	6	8.60	< 0.001
	PatchCat*StockDen	2	24.92	< 0.001
	PatchCat*Season	2	3.29	0.038
	Residuals	2,853		
<i>Agrostis capillaris</i>	Year	3	27.83	< 0.001
	StockDen	1	471.81	< 0.001
	Season	1	0.46	0.496
	PatchCat	2	8.25	< 0.001
	PatchCat*Year	6	8.11	< 0.001
	PatchCat*StockDen	2	2.11	0.122
	PatchCat*Season	2	0.62	0.539
	Residuals	2,853		

autumn 2003 can be explained by insufficient precipitation in August 2003, during which rainfall was only 14.5 mm, compared with the 30-year average of 88 mm (Liberec meteorological station). This extraordinary drought reduced the usual aboveground sward biomass growth and standing biomass substantially.

Over the course of the vegetation season, the proportion of short patches usually increased under both stocking densities through to the end of the grazing season, which is similar to the findings of Dumont et al. (2007). It is known from previous studies (Ring et al. 1985; Gibb and Ridout 1988) that at the end of the vegetation season cattle still continue to feed on previously grazed areas, as occurred under both of our stocking densities. This supports the creation and maintenance of a mosaic sward structure (Adler et al. 2001; Rossignol et al. 2011).

According to our sward height measurements, heifers under the EG treatment repeatedly grazed short patches in particular, which corroborates the findings of Cid and Brizuela (1998). In our experiment carried out as part of the Oldřichov Grazing Experiment, the maximum proportion of such patches under EG was only 15 % in paddocks, demonstrating greater forage availability. Repeated grazing of the same patches is not only driven by the mechanical and momentary necessity to graze high-quality sward that short patches provide, as mentioned above, but it could also be conditioned by the spatial memory of cattle (Bailey et al. 1989; Laca 1998). Cattle can, to a certain degree, remember the location of preferred patches but the limits of their spatial memory are still not known (Dumont 1997).

Plant species composition

In accordance with previous studies, the short grass *A. capillaris* was promoted by grazing in low-productivity grasslands (e.g. Hellström et al. 2003; Louault et al. 2005; Pavlů et al. 2006b, 2007). Especially under the IG treatment, it became the dominant sward species of short and moderate patches, as occurred in our study conducted as part of the Oldřichov Grazing Experiment. Jewell et al. (2005) also found that *A. capillaris* occurred mostly in intensively and heavily grazed plots. Grime et al. (1988), however, characterized *A. capillaris* as a common species in permanent pastures, and especially in mountain grasslands. It is regarded as a patch-forming species. Several prostrate or short species (*Taraxacum* spp., *T. repens*, *H. radicata*, *Glechoma hederacea*, *V. serpyllifolia* and *R. repens*) were represented especially in short patches subjected to both stocking densities, where the availability of light is an important factor determining the presence of these species (ter Heerdt et al. 1991). Such species are intolerant to shading

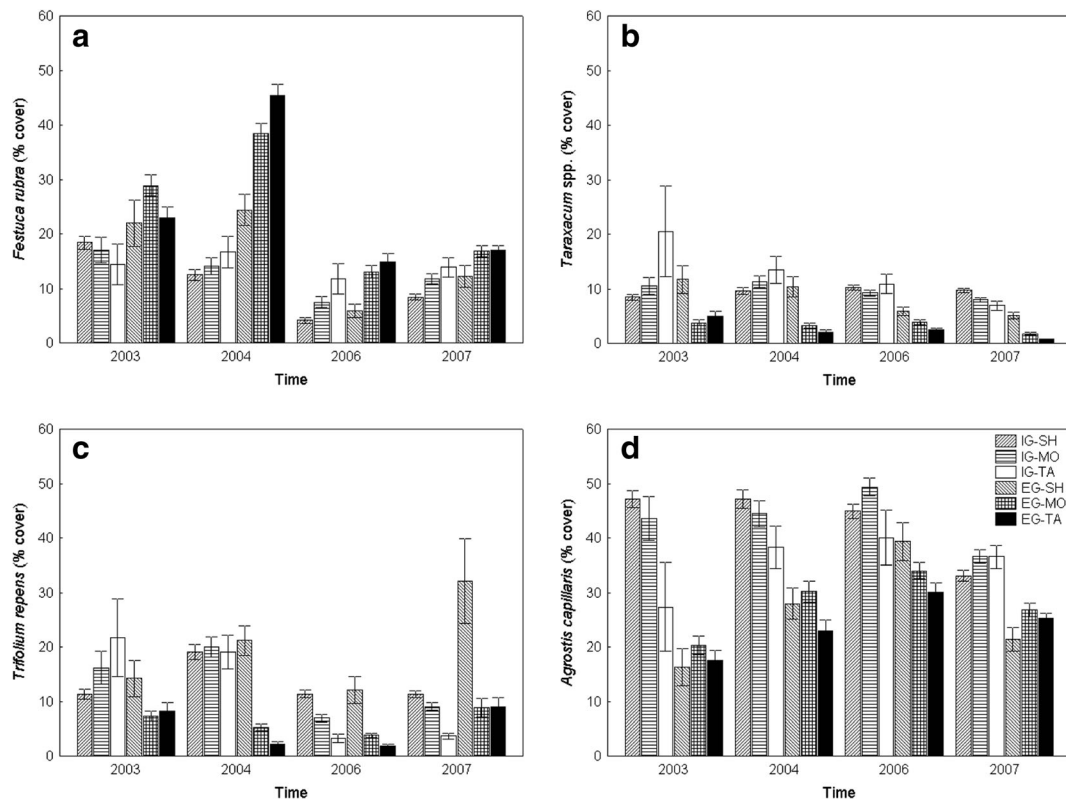


Fig. 2 Changes in coverage (%) of dominant tall graminoid *Festuca rubra* (a), short forbs *Taraxacum* spp. (b), *Trifolium repens* (c), and short graminoid *Agrostis capillaris* (d) under

different treatments from 2003 to 2007. Standard errors are indicated by vertical lines. For abbreviations, see Fig. 1.

and would be outcompeted by taller species. On the other hand, they are very resistant to intensive grazing and trampling (Grime et al. 1988). Therefore, prostrate species such as *Taraxacum* spp., *T. repens* or *V. serpyllifolia* are very promptly able to colonize non-shaded areas (Pavlů et al. 2003; Hejčman et al. 2005) or newly created gaps (Kohler et al. 2006b) with short sward height. Selective grazing of prostrate forbs (*Taraxacum* spp. and *T. repens*) can explain the stability of patches over the course of the grazing season, especially in lightly grazed grasslands (Rossignol et al. 2011). Nevertheless, these species could also dominate in tall patches under IG. This was because a majority of this patch category under the IG treatment was formerly short vegetation littered with faeces and was consequently refused by animals (personal observation). The floristic composition in moderate and tall patch categories under the IG treatment was very similar, and the abundance of species present in such patches changed during the season. This is probably affected

by micro-successions caused by small-scale dung pats, where plant communities react rapidly to changes in nutrient availability at the seasonal scale (Cid and Brizuela 1998; Gillet et al. 2010). By contrast, most tall patches under EG were usually made up of non-grazed vegetation because the amount of forage on offer exceeded the demand of the grazing animals. Tall forbs and tall graminoids, such as *Aegopodium podagraria*, *G. album*, *H. maculatum*, *A. pratensis* and *Holcus mollis*, were associated with tall and moderate patches under the EG treatment, where grazing is light or null (Correll et al. 2003; Pavlů et al. 2007). Such patches are characterized by species with a strong ability to compete for light. Forage offered by tall patches is usually poor in quality, yet it is a highly available resource from which in periods of food scarcity (e.g. summer droughts and late autumn) animals can benefit by exploiting reproductive swards to satisfy part of their forage requirements (Dumont et al. 1995). Sometimes, taller or rarely grazed patches do not

consist of a single species, but have nearly the same plant species as do short or heavily grazed patches (Bakker et al. 1984), as also occurred in our experiment under IG. They differ, however, in the relative cover of tall and short species with different resistance to grazing. This contradicts recent studies (Wrage et al. 2012; Tonn et al. 2013) conducted on a *Lolium-Cynosuretum* grassland. They concluded that differences between patch types were larger than those within the same patch type between different grazing intensities. The type of vegetation can probably affect the composition and structure of patches considerably even under similar grazing density.

Conclusion

In this study, two contrasting stocking densities caused differences in the proportion of patches with different sward height and generated a similar level of patch heterogeneity, which was mainly affected by the proportion of tall and short patches. The floristic composition of patches belonging to the same sward height category was strongly dependent on stocking density. Moderate and tall sward-height patches under particular stocking densities were similar in botanical composition. It therefore seems that moderate sward-height patches resulted from partly grazed tall ones. The floristic composition of short-sward patches differed considerably from other patches under extensive grazing. Under intensive grazing, however, the differences among short-, moderate- and tall-sward patches were small. The absence of large differences in floristic composition among sward height patches under intensive grazing may suggest that this stocking density promotes botanical homogeneity despite heterogeneity in sward height structure. Grazing intensity is a key driver of both the proportion and the floristic composition of sward-height patches in grasslands dominated by *A. capillaris*. These findings have implications for nature conservation, as they support the recommendation for extensive management of species-rich grasslands.

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