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RESEARCH ARTICLE

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Effect of 15-year sward management on vertical distribution of plant functional groups in a semi-natural perennial grassland of central Europe

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Abstract

Aims: The nutrient concentration in herbage and biomass productivity analyses are dependent on the vertical distribution of different sward layers where the sampling is done. Notably, a majority of studies indicate clipping biomass to the ground level without any consideration of the vertical distribution. This study examined the effect of cutting and grazing intensities on the vertical distribution of plant functional groups.

Location: Oldřichov Grazing Experiment, northern Czechia.

Methods: During a 15-year experiment: (a) intensive and (b) extensive grazing without cutting; (c) cutting in June followed by intensive and (d) extensive grazing; and (e) undefoliated treatment were applied throughout the vegetation season. Biomass data were collected at two layers in the sward (below and above 3 cm) and separated into five functional groups. Biomass data were analysed to examine the succession and effects of treatments on vertical distribution of functional groups.

Results: Treatment effects were differentiated after 2–3 years from the introduction of management, but the composition of functional groups fluctuated over time. Treatments significantly affected total biomass of all functional groups and the vertical distribution within swards of most groups. Particularly intensive grazing significantly decreased the total biomass of graminoids, forbs, and dead biomass in favour of legumes (which increased). This led to a shift in the relative biomass distribution from the upper sward layer to the lower layer for most functional groups except for legumes and mosses.

Conclusion: The high proportion of dead biomass in the lower sward layer suggests the need for a methodological approach that considers clipping of biomass only above 3 cm when sampling for productivity and forage quality analysis. This approach would avoid including biomass from below 3 cm or the lower layer, which would be ungrazed by cattle. Many previous studies may have reported a distorted or inflated value in herbage productivity or forage quality results.

KEYWORDS

Central Europe, cutting, functional groups, grassland management, grazing intensity, heifers, sward structure

1 | INTRODUCTION

Although the relationship between biodiversity and grassland productivity remains a passionately contested topic (Adler et al., 2011; Grace et al., 2012), it is still assumed that in agricultural settings higher plant diversity has lower economical value for farmers as it is often associated with lower forage quality and biomass yield (Bruinenberg et al., 2002; Isselstein et al., 2005). Therefore, several studies have been conducted focusing on grassland productivity and forage quality. However, accurate measurement with a clear methodology is critical when it comes to productivity and forage quality assessments. Unfortunately, which layer to incorporate during sampling and analysis of data from grazing or cutting experiment remains vague or largely unanswered.

Grazing management is a highly complex process that affects the grazers as well as the sward structure. Vegetation structure (where height of the sward is the main criterion determining structure) is one of the main factors that affects the quantity as well as the quality of available forage resources for grazing animals. Therefore, the performance of the grazers is directly affected by their nutrient intake from the vegetation structures (Fleurance et al., 2016). In mixed-species swards, the vertical structure also affects grazing intake as well as influencing inter-species competition for light (Schulte & Lantinga, 2002). For instance, in temperate grasslands the biomass intake by cattle is significantly influenced by sward structure through several factors of grazing behaviour including bite mass (Casey et al., 2004), intake rate (Barrett et al., 2003) and amount of energy utilized during grazing (Illius et al., 1995). Intake and grazing behaviour are also influenced by morphological changes in sward structure, which was observed as having a direct relationship between grazing activity and sward structure of lucerne (*Medicago sativa*) and cocksfoot (*Dactylis glomerata*) in a New Zealand silvopastural site (Peri et al., 2001). Hence, greater emphasis on the management of sward structure has increasing relevance in the context of grassland utilization, as the direct influence of sward structure on herbage intake ultimately affects animal production (Gordon & Benvenutti, 2006).

The promotion of certain managements such as grazing or long-term exclusion of grazing could lead to a change in dominance of above-ground biomass (different plant functional groups) ultimately affecting the proportion of palatable grasses and unpalatable forbs in temperate ecosystems (Zhao et al., 2019). However, plant competition (del-Val & Crawley, 2005), and grazing behaviour of the animals also influence the composition and perenniality of plant communities (Matches, 1992), the functional groups and the spatial heterogeneity of vegetation (Adler et al., 2001; Bullock et al., 2001; Díaz et al., 2007; Fernández-Lugo et al., 2013) as well as soil physical and chemical properties (Augustine and Frank, 2001; Steffens et al., 2008).

Grassland managers often consider grazing to be one of the most important management tools for manipulating the vegetation, yet the respective management decisions should always be based on a clear set of criteria that includes sward structure. According to Hodgson and Maxwell (1981), sward measurements such as height and growth stage are important for managing grazing systems, and can greatly improve grassland productivity and utilization as well as improving the sward structure (Milchunas & Lauenroth, 1993), by matching sward condition and herbage availability to the requirements of animals. For instance, the relative proportion of flowers, stems and dead material in the different horizons (vertical structure) is one of the main components of structural variation that is open to manipulation (Tallowin et al., 2005). However, sward structure could be very different depending on the types of plant species present. For example, Hodgson (1985), described the vertical structure for a legume (white clover, *Trifolium repens*) and grass (perennial ryegrass, *Lolium perenne*), and observed that the upper horizons of the sward canopy are made up primarily of living leaves, whereas leaf sheaths, stems and dead biomass are concentrated in the lower horizons. In a sub-humid grassland type in Argentina, Sala et al. (1986) investigated the effect of grazing management on plant community structure in seven sward layers and found that in grazed grassland most of the plant material was concentrated in the bottom layer, whereas in undefoliated plots the largest proportion of the leaf area was in the upper layer.

Previous studies and documentation of the vertical structure of swards in temperate areas have mainly considered homogeneous swards of legumes and grasses, such as perennial ryegrass and white clover. The structure of these swards has been shown to consist typically of leaves in the upper layer, while the lower layer mostly comprises stems and dead biomass (Hodgson, 1985). However, grasslands of central Europe, which often have a high species diversity, have been very little studied, and particularly long-term data of mixed-species swards composed of graminoids, forbs, mosses and legumes are lacking. In this paper, we present the results of a long-term study that started in 1998 in the Jizera Mountains (Czech Republic) with the main objective of investigating the effects of different levels of grazing intensity on different functional groups of grassland species at two vertical sward layers. Against this background, and using long-term data, we seek to answer the following questions:

1. What is the successional development of functional groups in different layers of the sward under contrasting grazing intensity and cutting management?
2. What is the effect of treatments on the vertical distribution of functional groups? Is grazing intensity or cutting management the key driver?

2 | METHODS

2.1 | Study site

The study was conducted at the site of the "Oldřichov Grazing Experiment" in the Jizera Mountains, northern Czech Republic

(50°50.34′ N, 15°05.36′ E; elevation 420 m a.s.l.). The site has an average annual precipitation of 803 mm, and a mean annual temperature of 7.2°C (Liberec Meteorological Station). For monthly rainfall and mean monthly temperatures, see Appendix S1.

The geological substratum is granite underlying a low, deep, brown soil (cambisol). The content of plant-available P, K, and Mg at the start of the experiment analysed according to the Mehlich III method (Mehlich, 1984) was 64, 95 and 92 mg/kg respectively (Pavlů et al., 2006a). For plant-available P, K, Mg, Ca and pH/$CaCl_2$ under each treatment for the year 2016 see Appendix S2. In the early 1980s, the area was drained, ploughed and reseeded with productive grasses, namely *Dactylis glomerata*, *Festuca pratensis*, *Lolium perenne*, and *Phleum pratense*. Between 1987 and 1992, rotational grazing was introduced, and fertilizer was applied over the entire experimental site as follows: N (40–140 kg/ha as NH_4NO_3), P (40 kg/ha as $Ca(H_2PO_4)_2$), and K (120 kg/ha as KCl). No fertilizers have been applied since 1992 (Pavlů et al., 2003), and the site remained abandoned until 1998.

The botanical diversity at the experimental site can be considered as high with up to 24 vascular plant species per m^2. The dominant species are *Agrostis capillaris*, *Festuca rubra* aggr., *Trifolium repens* and *Taraxacum* spp. (Ludvíková et al., 2015).

2.2 | Experimental layout and grazing trial

The experiment was established in two adjacent completely randomized blocks in 1998 (Pavlů et al., 2007). Each block consisted of five treatment paddocks, each of 0.35 ha, except the undefoliated plot, which was 0.12 ha. Different management regimes were applied in each paddock. The treatments were (Table 1): (a) extensive grazing (EG), where the stocking rate (SR) was adjusted to achieve a mean target sward surface height >10 cm; (b) intensive grazing (IG), in which SR was adjusted to achieve a mean target sward surface height <5 cm; (c) cutting in June followed by extensive grazing (ECG) for the rest of the growing season; (d) cutting in June followed by intensive grazing for the rest of the growing season (ICG); and (e) the undefoliated control (U). The percentage cover (%) of the graminoids, forbs and legumes under different treatments for the years 2001–2012 are shown in Appendix S3.

In order to adjust the stocking density for IG and EG treatments, while also keeping the stock numbers constant, the size of grazed areas was adjusted by moving the fences continuously throughout the grazing season. Since its establishment, the design of the experiment, its layout and SR remained unchanged. All paddocks of treatments (a) and (b) were continuously stocked with young heifers with initial live weights of about 200 kg from early May until late October, and from mid-June to late October in the case of treatments (c) and (d).

2.3 | Measurements and sward structure

In early May (before cutting or the start of grazing) from 1998 to 2012 (15 years), six samples were collected from a 50 cm × 25 cm steel frame randomly placed within each treatment plot (paddock). In each, the biomass from two vertical sward layers was collected using electric clippers within the area of the steel frame: (a) lower 0–3 cm (stable non-grazed layer) and (b) upper >3 cm (grazed layer). Experimental evidence (Laca et al., 1994; Ungar, 1998) indicated that animals favourably graze the highest or upper part of the sward. For instance, in our experimental site under IG treatment, the average sward during the grazing season is typically between 3 cm and 4 cm, which was identified from weekly measurements of compressed sward heights across the experiment's plots (100 measurements per plot). Hence, the lowest layer, which is left ungrazed in our experiment, is considered under 3 cm in all plots.

Accordingly, the plant material that were collected from the two layers was then sorted into different functional groups: living biomass, separated into forbs (without legumes), graminoids, legumes and mosses, and undifferentiated dead material. Total living biomass of vascular plants was calculated as the sum of graminoids, forbs and legumes (hereafter referred to as living biomass). Finally, the samples were oven-dried for 48 hr at 70°C and weighed. In total, 1,800 samples (120 samples per year) were analysed over the 15-year experimental period. The experimental site can be classified as a low-productive site with herbage biomass production in the years 1998 to 2001 ranging from 3.33 t/ha to 3.90 t/ha under IG and 2.20 t/ha to 3.35 t/ha under EG (Pavlů et al., 2006a).

TABLE 1 Description of treatments at the study site

				One-way design	Two-way design	
Treatment description	**Sward height**	**Start of cutting**	**Start of grazing**	**Treatment**	**Intensity**	**Management**
Extensive grazing	>10 cm	No cut	Mid-May	EG	E	N
First cut followed by extensive grazing	>10 cm	Early June	Late June	ECG	E	C
Intensive grazing	<5 cm	No cut	Early May	IG	I	N
First cut followed by intensive grazing	<5 cm	Early June	Mid-June	ICG	I	C
Undefoliated	Uncontrolled	No cut	No grazing	U	–	–

Abbreviations: C, Cut; E, Extensive; G, grazing; I, Intensive; N, No cut; U, Undefoliated.

2.4 | Data analysis

The succession in the composition of functional groups in the two vertical layers was analysed using a partial principal components analysis (pPCA) with blocks as covariate and excluding the variable living biomass, as it is the sum of other variables. pPCA was performed using Canoco 5 (ter Braak & Šmilauer, 2012).

To investigate the effects of the treatments on differences between the vertical sward layers, the ratio of the biomass in the upper layer to the sum of the biomass in both layers was calculated for each functional group. The effects of the treatments on total biomass and on the upper biomass of each functional group, and their ratios were analysed using two sets of general linear models (GLMs). The first set of models included all five treatments (including undefoliated — U) in one factor, and the Tukey honestly significant difference test was applied to identify the differences between them. The second set excluded treatment U, thereby enabling us to test for the effect of grazing and cutting separately, including their interaction. In addition, "year" and all its interactions were included as random factor in both sets of models to account for the large between-year fluctuations. The first three years of data were excluded from this analysis due to the substantial change in vegetation that followed the introduction of management at the site. Block was excluded from the models, as it had no significant effect. The total biomass was log-transformed [$X^{/} = \log_{10}(X + 1)$] and the proportion of the upper layer was arcsin-transformed {$X^{/} = \mathrm{asin}\,[\mathrm{sqrt}\,(X)]/\mathrm{asin}\,(1)$} to improve normality of the data. We applied Benjamini–Hochberg's procedure to control for false discovery rate (FDR; Verhoeven et al., 2005). Additional GLMs were used to evaluate the effect of treatments on the ratio of living to dead biomass for the two sward layers separately. The ratio was log-transformed [$X^{/} = \log_{10}(X)$] and "infinity" ratios in samples with zero dead biomass were replaced by the maximum value of each respective treatment. The same model setting was applied as in the GLMs with all treatments described above (year as random factor, Tukey post-hoc test). GLMs were conducted using Statistica 13.1 (Dell Inc., 2016).

3 | RESULTS

3.1 | The successional development

The pPCA shows the overall differentiation in vegetation composition through the course of the experiment (main pattern in Figure 1, detailed successional trajectories in Appendix S4). The first axis (explaining 36% of variation) differentiated the intensive grazing (IG, ICG) from extensive grazing or no management (EG, ECG, U) with additional slight differences within the latter group. The start of all successional trajectories is close to the undefoliated control, and rapid changes in vegetation were observed for the two-year period following the establishment of management, especially in the intensively grazed plots. The vegetation of the undefoliated or extensively grazed treatments is largely characterized by large amounts of dead biomass in both layers, and graminoids and forbs dominate in the upper layer, while legumes were mostly absent. Intensive grazing treatments are characterized by lower amounts of dead biomass in both layers, while legumes were largely present in both layers. The second axis (explaining 19% of the variation) represents mostly random between-year fluctuations, which were generally consistent in all treatments. Most of this variation is attributed to mosses and forbs in the lower layer, and these are generally more abundant in ECG.

3.2 | Effect of all treatments on the biomass and its vertical distribution

The five treatments had significant effects on total biomass of all functional groups and on the vertical distribution of most groups except legumes and mosses (Table 2). Except for mosses, treatment also had a significant effect on the upper layer of all functional groups. Compared to the managed treatments (explored in more detail in the next section), the undefoliated treatment in the total showed the lowest biomass of graminoids (shared with intensive grazing) and legumes, but the highest amount of dead biomass. The sum of living biomass was only marginally different and the undefoliated treatment had intermediate values. Regarding the vertical

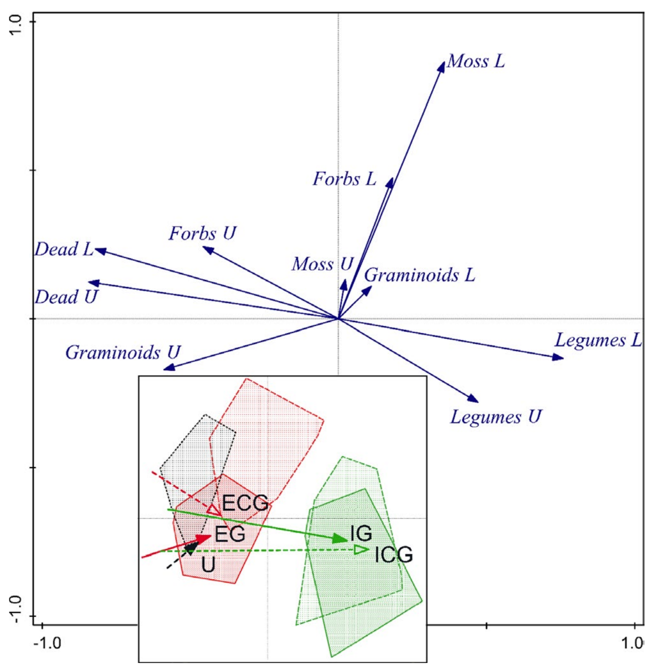

FIGURE 1 Partial principal components analysis (pPCA) of the plant functional groups for the upper (>3 cm) and lower (<3 cm) sward layers. Arrows indicate the main successional direction of treatments (from 1998 to 2012); envelopes encompass the region where the treatments were fluctuating after their initial divergence (from 2001 to 2012, i.e. excluding the first three years consistently with our general linear models). For detailed plot, see Appendix S4. Group labels include group name and layer abbreviation: L – lower, U – upper. For treatment abbreviations, see Table 1

distribution, in the undefoliated treatment the living biomass was present in the upper layer more than in the case of managed treatments. This holds for both the graminoid and forb components (legumes were almost absent in U, preventing reliable evaluation of their vertical distribution). Dead biomass was low in the U treatment, in contrast to extensive grazing.

Furthermore, our results showed an overall higher proportion of living biomass in the upper layer than in the lower layer. The IG and ICG treatments provided a significantly higher proportion of living biomass relative to EG, ECG and U treatments (Figure 2). In terms of dry standing matter, graminoids provided the highest amount among all functional groups throughout the entire experimental period (Appendix S5).

3.3 | Effect of grazing intensity and cutting management on the biomass and its vertical distribution

Grazing intensity significantly affected the upper layer biomass (>3 cm) of all functional groups except for mosses (Table 3). Extensive grazing increased biomass in graminoids, forbs, sum of living biomass (mostly composed of graminoids and forbs) and dead matter, while legumes decreased (Figure 3a). Apart from forbs, management and its interaction with grazing intensity had no effect on the functional groups of the upper layer. A higher ratio of biomass in the upper layer to total biomass was also observed under extensive treatment for graminoids, forbs, living and dead (Figure 3c), which in combination with higher total biomass in extensive treatment in these groups (Figure 3b) results in a more pronounced pattern in the upper layer alone (Figure 3a) compared to the pattern observed with total biomass. Overall, very little dead biomass was present in the upper layer while mosses were effectively absent from the upper layer (Figure 3a).

Grazing and cutting treatments significantly affected the total biomass of most functional groups (some of the main effects were only marginally significant; grazing intensity was not significant for mosses due to the contrasting effect of interaction; Table 3; Figure 3b). Intensive grazing suppressed both living and dead biomass, specifically through its effect in decreasing graminoids and forbs, while there was higher moss biomass in the cut plots. In contrast, intensive grazing resulted in a marked increase in legumes, and it also led to an increased occurrence of moss in the uncut plots. Cutting supported forbs (largely), legumes (slightly, and only when combined with intensive grazing), and mosses (largely, only when combined with extensive grazing), and suppressed graminoids and resulted in less dead biomass (only in extensive grazing).

TABLE 2 Result of general linear model for the effect of all treatments on the total biomass, on the upper layer biomass (>3 cm) and on the ratio of biomass in the upper layer (>3 cm) to total biomass for all functional groups

	df	*F*	*p*	IG	ICG	EG	ECG	U
Functional group total biomass								
Graminoid	44	6.51	**<0.001**	bc	bc	a	b	c
Forb	44	10.69	**<0.001**	d	c	c	a	bc
Legume	44	63.74	**<0.001**	a	a	c	b	d
Living	44	3.6	0.012	c	bc	ab	a	bc
Dead	44	113.96	**<0.001**	d	d	b	c	a
Moss	44	7.2	**<0.001**	b	b	c	a	bc
Ratio: >3 cm/total biomass								
Graminoid	44	9.82	**<0.001**	c	c	b	b	a
Forb	44	19.41	**<0.001**	c	c	ab	b	a
Legume	46.1	1.15	0.344	-	-	-	-	-
Living	44	15.95	**<0.001**	c	c	b	b	a
Dead	44	6.97	**<0.001**	b	b	a	a	b
Moss	44.9	0.94	0.448	-	-	-	-	-
> 3 cm biomass								
Graminoid	44	6.5929	**<0.001**	b	b	a	a	a
Forb	44	19.0508	**<0.001**	d	c	b	ab	a
Legume	44	27.80724	**<0.001**	a	a	b	b	c
Living	44	10.6314	**<0.001**	b	b	a	a	a
Dead	44	40.608	**<0.001**	c	c	a	b	a
Moss	44	1.276594	0.293	-	-	-	-	-

Results are summarized by denominator degrees of freedom *df* (numerator *df* was 4 in all tests), *F* ratio and *p*-value. Significant results (after table-wise Benjamini–Hochberg false discovery rate correction) are highlighted in bold. Significant differences between treatments (for abbreviations, see Table 1) in a Tukey test are indicated by different lowercase letters (alphabetic order represents decreasing values of means, i.e. a represents the largest mean).

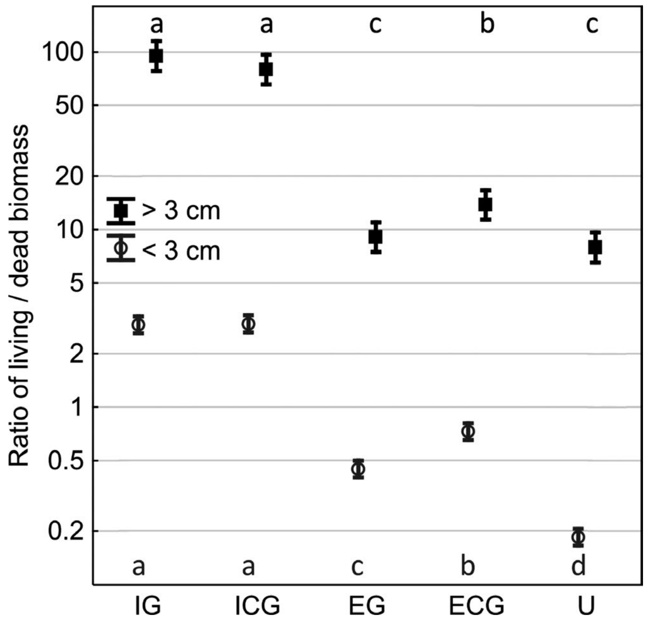

FIGURE 2 The effect of treatments on the herbage ratio of living biomass and dead biomass in two different sward layers (<3 and >3 cm). Error bars indicate model-based 95% confidence intervals. Different lowercase letters indicate significant differences between treatments in a Tukey test. For treatment abbreviations, see Table 1

Similar to the upper-layer biomass, cutting and its interaction with grazing intensity had no effect on the vertical biomass distribution for any of the functional groups (Table 3). In contrast, intensive grazing significantly suppressed the proportion of biomass in the upper layer in the functional groups of graminoids, forbs, living and dead biomass (Figure 3c). Neither grazing intensity nor cutting management had any significant effect on the vertical distribution of legumes or of mosses.

4 | DISCUSSION

4.1 | Successional development

The pPCA demonstrated large temporal fluctuations of functional group composition. It is interesting that these fluctuations were similar in all treatments, suggesting that they were not just random. A possible explanation could be changes and fluctuations in the environment (Lepš et al., 2018), such as weather conditions within seasons or climatic differences between years, which may benefit or suppress individual functional groups regardless of the treatment. Similarly, a study by Fischer et al. (2020) reported year-to-year changes in species composition due to seasonal fluctuations in temperature and precipitation, confirming weather is a dominant driver of local vegetation dynamics. For instance, *Festuca rubra* (one of the dominant grass species in our experimental site), which has many ecotypes (Grime et al., 1988) in comparison with other common grass species, is well adapted to various abiotic conditions including drought. Its variability in time can be explained by compensatory dynamic (Lepš et al., 2018) in which cover of species like *Festuca rubra* can increase even under dry conditions (Titěra et al., 2020) while compensating for the possible decline in cover of other species like *Poa trivialis*, which is less tolerant to drought (Peeters et al., 2004). Gaisler et al. (2018) also reported similar results from a long-term experiment (13 years) in which different functional groups such as tall graminoids and tall forbs fluctuated without any clear stable trend for any particular treatment. Despite the large variability in the present study, the main patterns found by pPCA largely overlap with GLM results, and in just 2–3 years after the introduction of management the succession was close to that of the final composition.

4.2 | Composition of total biomass

Several studies have reported on the impacts of grazing on plant communities, especially in terms of the role of long-term grazing in eliminating those species that are less resistant to the effects of grazing (Dorrough et al., 2004). Therefore, the ability of plant communities to respond to changes in the environment is heavily affected by the grazing history, including changes to grazing intensity (Mack & Thompson, 1982). After 15 years of different treatments of grazing and cutting management at our experimental site, a clear pattern was seen: both the IG and ICG treatments had a positive effect on total biomass of legumes, whereas forbs and graminoids, and also dead biomass, were present in greater amounts and were apparently supported by the management of the ECG and EG treatments.

Graminoids showed a remarkable dominance in terms of dry-matter standing biomass throughout the 15-year experimental period. This outcome can be explained by two effects: (a) the ability of graminoids to suppress other functional groups like forbs, because of their superior competitive ability (del-Val & Crawley, 2005); and (b) the dominance of *Agrostis capillaris*, which is largely promoted by grazing especially in grasslands of low productivity (Louault et al., 2005). Hence, it outcompetes species that are less tolerant of frequent defoliation (Gaisler et al., 2013). Grazing is generally expected to increase the dominance or abundance of graminoids (Puchetaet al., 1992). Frequent removal of the biomass of graminoids, as occurs under grazing, stimulates sward regrowth by increasing the amount of available light reaching the base of the sward (Deregibus et al., 1985).

The highest amount of total dead plant biomass was found in the undefoliated treatment. In the treatments with grazing, the frequent cutting leads to regrowth and reduces the opportunity for senescence of plant tissue. This outcome is not only unique to temperate grasslands. Altesor et al. (2005) for grasslands of Uruguay and Sala et al. (1986) for the Argentine Pampa also reported similar findings, where grazed and ungrazed treatments were compared. In addition, intensive grazing was able to reduce the standing dead biomass in both layers and shift its allocation to the lower layer, which ultimately helped to increase the living biomass proportion by promoting overall growth (Balph & Malechek, 1985).

TABLE 3 Result of general linear model for the effect of grazing intensity and cutting management in factorial design on the total biomass, on the upper layer biomass (>3 cm) and the ratio of biomass in the upper layer (>3 cm) to total biomass for all functional groups

	Functional group total biomass			Ratio: >3 cm/total biomass			>3 cm biomass		
Effect	***df***	***F***	***p***	***df***	***F***	***p***	***df***	***F***	***p***
Graminoid									
Intensity	11	9.11	**0.01**	11	14.99	**0.003**	11	15.22	**0.002**
Management	11	7.05	0.02	11	0.44	0.522	11	4.19	0.065
Intensity × management	11	0.37	0.55	11	0.39	0.544	11	0.002	0.960
Forb									
Intensity	11	19.15	**<0.001**	11	20.78	**<0.001**	11	41.57	**<0.001**
Management	11	184.6	**<0.001**	11	4.68	0.053	11	52.64	**<0.001**
Intensity × management	11	0.21	0.65	11	2.54	0.139	11	1.92	0.192
Legume									
Intensity	11	61.26	**<0.001**	14.1	3.2	0.095	11	38.46	**<0.001**
Management	11	8.24	**0.015**	14.7	0.43	0.52	11	1.49	0.246
Intensity × management	11	3.04	0.108	14	0.00	1.000	11	2.89	0.117
Living									
Intensity	11	7.52	0.02	11	18.83	**<0.001**	11	17.60	**<0.001**
Management	11	4.09	0.07	11	0.57	0.466	11	0.18	0.681
Intensity × management	11	0.38	0.55	11	0.02	0.896	11	0.23	0.641
Dead									
Intensity	11	98.95	**<0.001**	11	18.4	**<0.001**	11	75.61	**<0.001**
Management	11	6.51	0.03	11	0.2	0.663	11	4.30	0.062
Intensity × management	11	8.68	**0.01**	11	0.1	0.76	11	2.25	0.161
Moss									
Intensity	11	0.01	0.9	11	2.04	0.18	11	1.66	0.224
Management	11	20.68	**<0.001**	11	1.37	0.266	11	1.85	0.200
Intensity × management	11	36.81	**<0.001**	11	0.00	0.954	11	0.48	0.501

Results are summarized by denominator degrees of freedom *df* (numerator *df* was 1 in all tests), *F* ratio and *p* value. Significant results (after table-wise Benjamini–Hochberg false discovery rate correction) are highlighted in bold. See Figure 3 for effect directions.

The total amount of legumes (mainly *Trifolium repens*) found in the undefoliated plots was very low. This may be attributed, at least in part, to their low ability to compete for light unless their leaves can reach the upper canopy of the sward. Thus, in the present study, white clover occurred predominantly in the IG and ICG treatments (Appendix S3). The explanation for its very low presence in undefoliated plots may, however, be highly complex as several factors, including winter survival as well as competition for light and nutrients, are known to affect clover growth, flowering and survival (Parsons and Chapman, 2000). Furthermore, when legumes are present in swards under intensive management, some may be annual species (such as *Trifolium dubium* in our experiment) that have the advantage of continuing to survive by producing new seedlings after established plants die or are removed by grazing livestock. The strategy of annuals provides a survival advantage relative to perennial plants that are grazed during their longer life cycle (Díaz et al., 2007). This is, however, in contradiction with other studies such as Matches (1992), who found that legume content was lower under increased grazing intensity, whereas light grazing favoured legumes rather than forbs or grasses (Qu et al., 2016). These disparities between different studies may be explained by differences in experimental sites' environments such as nutrient supply, water or light/shade conditions (Milchunas & Lauenroth, 1993; Borer et al., 2014). Especially leguminous species are generally known for their positive response to P and K and negative response to the high inputs of N, NP or NPK (e.g., Čop & Eler, 2019; Titěra et al., 2020).

The total biomass of mosses under the ECG treatment was relatively high compared to that in the other managed treatments, and this is attributed mainly to the inability of mosses to tolerate the effects of trampling by grazing heifers (Ludvíková et al., 2014), especially for *Rhytidiadelphus squarrosus*, which is the dominant species at the experimental site. Our result also showed treatment had no effect on the upper layer (>3 cm) for mosses, which could imply they are not really present in the upper layer neither in the managed nor in the undefoliated plots (Table 2; Figure 3). Similarly, total forbs and total graminoids were also more abundant, and total living biomass

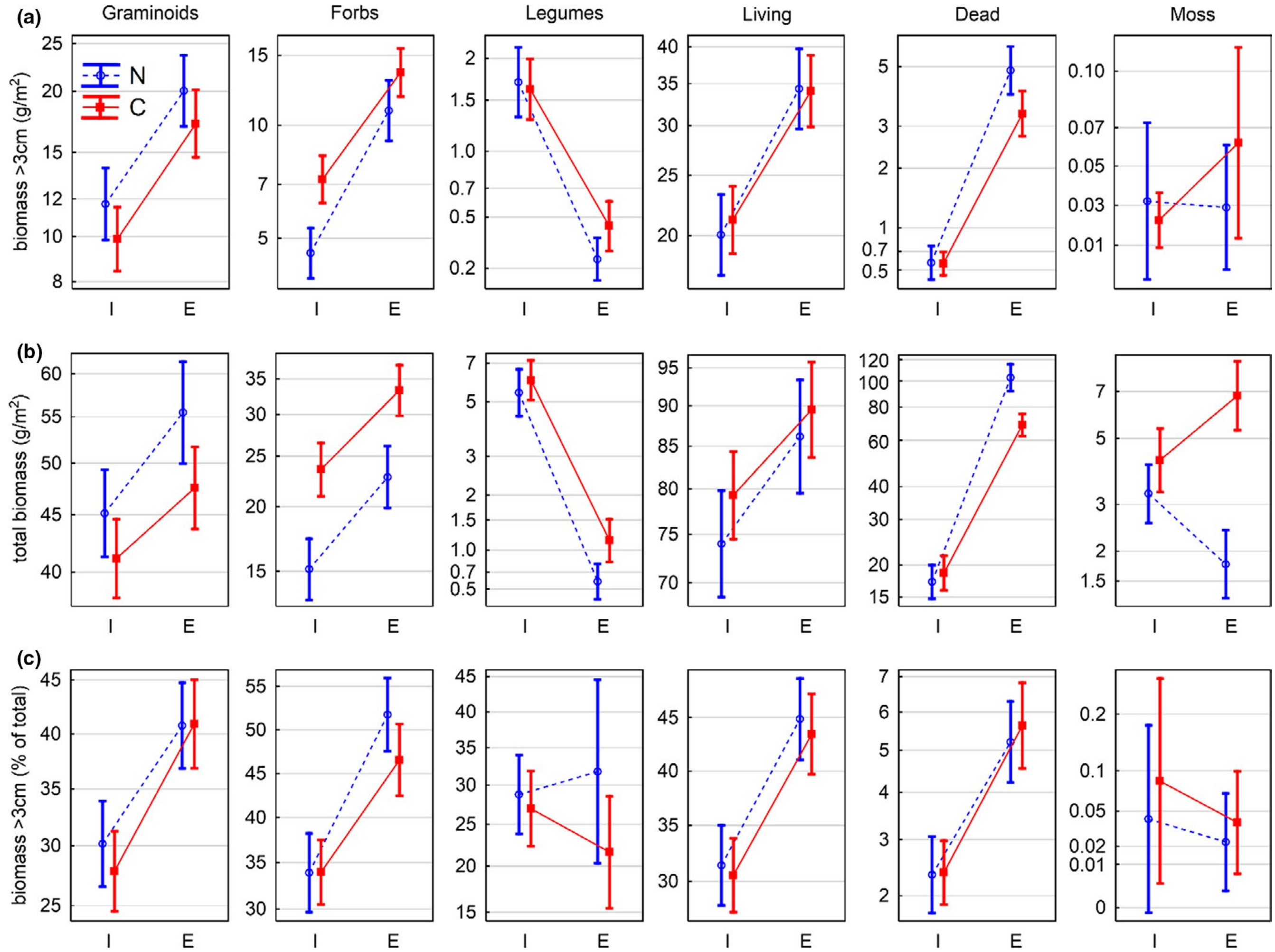

FIGURE 3 The effect of grazing intensity and cutting management on (a) upper layer biomass (>3 cm), (b) total biomass and (c) ratio of biomass in upper layer (>3 cm) to total biomass of each functional group. Abbreviations on the *x*-axis and in legend: N = No Cutting, C = Cutting, I = Intensive, E = Extensive. Error bars indicate model-based 95% confidence intervals. See GLM results in Table 3

was greater, in the extensive treatment. These findings are consistent with results of Correll et al. (2003), who also found a higher proportion of forbs under extensive grazing. It is well understood that many forb species typically benefit from reduced grazing intensity (Wahren et al., 1994). In our experiment, the most dominant forb species are *Taraxacum* spp., which are generally shade-intolerant species (Grime et al.,1988). In tall-growing swards, as represented by the undefoliated plots in this study, the growth of forbs like *Taraxacum* spp. is adversely affected by reduced light at lower sward depths. However, many forbs are able to develop well under management with frequent defoliation (Louault et al., 2005; Pavlů et al., 2007), and can adapt quickly to the changing trophic regime of soil under extensive management.

4.3 | Vertical distribution of sward

Grazing intensity had strong and significant effects on the vertical distribution of several functional groups. A high proportion of living biomass in the upper layer was revealed by the analysis (Figure 2) and this is a common phenomenon. As growing herbage gradually reaches maturity, a greater proportion of green matter will be found in the upper layer and dead biomass accumulates at the bottom layer. The higher proportion of living biomass in the upper layer, compared to the lower layer, raises another crucial issue in relation to experimental procedures and field assessments. Several reported studies have followed procedures of cutting or hand plucking close to the ground level, or clipping biomass at the soil surface, as the basis for determining herbage biomass per unit area (e.g., Grant et al., 1996; Fleurance et al., 2016) or when sampling for forage quality (e.g., White et al., 2014). Procedures that include herbage samples from the bottom layer that would normally be left ungrazed (<3 cm) could potentially result in disputable conclusions being drawn with regard to overestimation of the available biomass or the accuracy of forage quality.

The higher allocation of dead material to the upper sward layer under extensive grazing, with the resulting taller sward, was consistent with Wright and Whyte (1989), who also found a higher proportion of dead material with increasing sward height, and also with Bircham and Hodgson (1983), who identified higher rates of senescence in tall swards, typical for extensive grazing management and for ungrazed plots. In contrast to the high proportion of total biomass of forbs under extensification, more forbs were allocated to the upper layer in undefoliated plots and there was lower forb biomass under both the intensively grazed treatments (ICG > IG). This can be attributed to more grazing-tolerant species occurring within the forbs group and appearing frequently in the grazed areas (Bermejo et al., 2012). This different response by forbs as a functional group may possibly be explained by the heterogeneous features and wide range of morphological traits of the group, thereby enabling species within the group to respond to the various disturbances or conditions (Bermejo et al., 2012).

Similarly, more graminoids were found in the bottom layer of almost all treatments except the undefoliated plot. This could be explained by the effects of long-term grazing on the study site, as grazing results in the removal of leaf material from the upper layers of the sward, thereby reducing the canopy height, and in the long term it affects the competitive balance within the community so that shorter-growing species replace taller species (Fahnestock & Detling, 2000). Thus, the sward composition evolves with selection for species that are well suited to survive or are adapted to intensive grazing.

In contrast, management (cutting or non-cutting) had no discernible effect on the vertical distribution or on the upper-layer biomass (except for forbs) of any of the functional groups, although it had significant effects on the total harvested biomass. This is mainly because the increased frequency of defoliation rather than the type of defoliation (such as cutting in spring) influences total biomass more, increasing the densities of all sward components like grass tillers (Pavlů et al., 2006b).

A limitation to the study is the choice of a broad functional group approach for the samples collected in the two layers. Although all species within a functional group will not behave the same, it was not possible to collect the data at the species level. This is mainly because identifying species in the lower layer is nearly impossible after the top layer is already cut or sampled. Due to this, it was not possible to evaluate the species richness and detailed botanical composition in relation to the vertical distribution. However, a study by Pavlů et al. (2007) and Pavlů et al. (2016) conducted at the same experimental site concluded that grazing and cutting management has changed the plant species composition, leading to an increased proportion of short grasses and prostate forbs. Specifically, tall forbs (such as *Aegopodium podagraria*, *Galium album*, *Senecio* aggr.) and tall grass (such as *Alopecurus pratensis*, *Elytrigia repens)* were more abundant under U treatment. *Dactylis glomerata*, *Festuca rubra* aggr. and *Phleum pratense* were largely supported by both grazing treatments (IG and EG), while *Agrostis capillaris*, *Taraxacum* spp., *Trifolium repens*, *Ranunculus acris* and *Cirsium vulgare* were supported by both cut treatments (ICG and ECG). Overall, this study benefits from the long-term experimental data. Due to the multifunctionality of grasslands, environmental and biodiversity outputs require long-term studies, since processes in soil, vegetation and microorganisms are long-term in relation to any change in management (Lemaire, 2007).

Regarding the applicability of our results to other grazing animals in different grassland types, more research may be necessary due to differences in site conditions such as climate, plant composition, biomass productivity and anatomy of the grazing animal. For instance, cattle and sheep have different requirements for forage quality and selectivity which can be influenced by vegetation composition and diversity (Wrage et al., 2011). Furthermore, characteristic anatomical differences such as in the mouth and tongue allow sheep to graze close to the ground on top of their considerable selectivity for high-quality plants (Rook et al., 2004). Hence, these grazing differences between different grazers may have different effects on the vertical distribution and require further investigation.

5 | CONCLUSION

The final composition of functional groups 15 years after the introduction of management at the experimental site was similar to that reached in the first three years, although large temporal fluctuations were still observed subsequently. Long-term studies are therefore needed to evaluate changes in community structure. Treatments significantly affected total biomass and upper-layer biomass of all functional groups and the vertical distributions within swards of most groups. In addition, large proportions of biomass from all functional groups (except mosses and legumes) were allocated to the upper layer in undefoliated swards and swards under extensive management. Intensity of management was found to be the key driver affecting the vertical distribution of the groups, whereas type of defoliation (grazing or cutting) had little effect. Although similar patterns were observed between upper biomass, total and the ratios, the trends are much more pronounced in the upper layer when the bottom layer biomass was excluded from the analysis. Given the high proportion of live biomass in the upper layer and the high proportion of dead biomass in the lower layer, we suggest that careful biomass sampling procedures are needed to take account of differences in the different layers of a sward, and thereby ensure accurate results are provided to support appropriate management strategies for both agricultural utilization and other objectives such as nature conservation.

AUTHOR CONTRIBUTIONS

VP and LP conceived the study; PB, VP and TK designed the methodology; VP and LP collected the data; TK and PB analysed and interpreted the data; TK, VP, KP, and PB wrote and edited the manuscript. All authors contributed critically to the manuscript and gave approval for publication.

DATA AVAILABILITY STATEMENT

Data necessary to reproduce all results and figures are available in Appendix S6.

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REFERENCES

Adler, P.B., Raff, D.A. & Lauenroth, W.K. (2001) The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia*, 128, 465–479. https://doi.org/10.1007/s004420100737

Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hectos, A. et al. (2011) Productivity is a poor predictor of plant species richness. *Science*, 333, 1750–1752. https://doi.org/10.1126/science.1204498

Altesor, A., Oesterheld, M., Leoni, E., Lezama, F. & Rodriguez, C. (2005) Effect of grazing on community structure and productivity of a Uruguayan grassland. *Plant Ecology*, 179, 83–91. https://doi.org/10.1007/s11258-004-5800-5

Augustine, D.J. & Frank, D.A. (2001) Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. *Ecology*, 82, 3149–3162. https://doi.org/10.2307/2679841

Balph, D.F. & Malechek, J.C. (1985) Cattle trampling of crested wheatgrass under short duration grazing. *Journal of Range Management*, 38(3), 226–227. https://doi.org/10.2307/3898971

Barret, P.D., Mcgilloway, D.A., Laidlaw, A.S. & Mayne, C.S. (2003) The effect of sward structure as influenced by ryegrass genotype on bite dimensions and short-term intake rate by dairy cows. *Grass and Forage Science*, 58, 2–11. https://doi.org/10.1046/j.1365-2494.2003.00345.x

Bermejo, L.A., de Nascimento, L., Mata, J., Fernández-Lugo, S., Camacho, A. & Arévalo, J.R. (2012) Responses of plant functional groups in grazed and abandoned areas of a Natural Protected Area. *Basic and Applied Ecology*, 13(4), 312–318. https://doi.org/10.1016/j.baae.2012.05.004

Bircham, J.S. & Hodgson, J. (1983) The influence of sward conditions on rates of herbage growth and senescence in mixed swards under continuous grazing management. *Grass and Forage Science*, 38, 323–331. https://doi.org/10.1111/j.1365-2494.1983.tb01656.x

Borer, E.T., Seabloom, E.W., Gruner, D.S., Harpole, W.S., Hillebrand, H., Lind, E.M. et al. (2014) Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, 508, 517–520. https://doi.org/10.1038/nature13144

ter Braak, C.J.F. & Šmilauer, P. (2012) *Canoco 5, Windows release (5.00). [Software for canonical community ordination]*. Ithaca, NY: Microcomputer Power.

Bruinenberg, M.H., Valk, H., Korevaar, H. & Struik, P.C. (2002) Factors affecting digestibility of temperate forages from semi natural grasslands: a review. *Grass and Forage Science*, 57, 292–330. https://doi.org/10.1046/j.1365-2494.2002.00327.x

Bullock, M.J., Franklin, J., Stevenson, J.M., Silvertown, J., Coulson, J.S., Gregory, J.S. et al. (2001) A plant trait analysis of responses to grazing in a long-term experiment. *Journal of Applied Ecology*, 38, 253–267. https://doi.org/10.1046/j.1365-2664.2001.00599.x

Casey, I.A., Laidlaw, A.S., Brereton, A.J., McGilloway, D.A. & Watson, S. (2004) The effect of bulk density on bite dimensions of cattle grazing micro swards in the field. *Journal of Agricultural Science*, 142, 109–121. https://doi.org/10.1017/s0021859604003910

Čop, J. & Eler, K. (2019) Effect of fertiliser application and cutting regime on temporal differentiation of mesic semi-natural grassland vegetation. *Italian Journal of Agronomy*, 14, 153–161. https://doi.org/10.4081/ija.2019.1405

Correll, O., Isselstein, J. & Pavlů, V. (2003) Studying spatial and temporal dynamics of sward structure at low stocking densities: the use of an extended rising-plate-meter method. *Grass and Forage Science*, 58, 450–454. https://doi.org/10.1111/j.1365-2494.2003.00387.x

Dell Inc. (2016) *Dell Statistica (Data Analysis Software System), Version 13.1 Software*. dell.com. Tulsa, OK: Dell Inc.

del-Val, E. & Crawley, M.J. (2005) What limits herb biomass in grasslands: competition or herbivory? *Oecologia*, 142, 202–211. https://doi.org/10.1007/s00442-004-1719-8

Deregibus, V.A., Sanchez, R.A., Casal, J.J. & Trlica, M.J. (1985) Tillering responses to enrichment of red light beneath the canopy in a humid natural grassland. *Journal of Applied Ecology*, 22, 199–206. https://doi.org/10.2307/2403337

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G. et al. (2007) Plant traits responses to grazing: a global synthesis. *Global Chang Biology*, 13, 313–341. https://doi.org/10.1111/j.1365-2486.2006.01288.x

Dorrough, J., Ash, J. & McIntyre, S. (2004) Plant responses to livestock grazing frequency in an Australian temperate grassland. *Ecography*, 27, 798–810. https://doi.org/10.1111/j.0906-7590.2004.04004.x

Fahnestock, J.T. & Detling, J.K. (2000) Morphological and physiological responses of perennial grasses to long-term grazing in the Pryor Mountains, Montana. *American Midland Naturalist*, 143(2), 312–320.

Fernández-Lugo, S., Bermejo, L.A., de Nascimento, L., Méndez, J., Naranjo-Cigala, A. & Arévalo, J.R. (2013) Productivity: key factor affecting grazing exclusion effects on vegetation and soil. *Plant Ecology*, 214(4), 641–656. https://doi.org/10.1007/s11258-013-0196-8

Fischer, F.M., Chytrý, K., Těšitel, J., Danihelka, J. & Chytrý, M. (2020) Weather fluctuations drive short-term dynamics and long-term stability in plant communities: A 25-year study in a Central European dry grassland. *Journal of Vegetation Science*, 31, 711–721. https://doi.org/10.1111/jvs.12895

Fleurance, G., Farruggia, A., Lanore, L. & Dumont, B. (2016) How does stocking rate influence horse behaviour, performances and pasture biodiversity in mesophile grasslands? *Agriculture, Ecosystem & Environment*, 231, 255–263. https://doi.org/10.1016/j.agee.2016.06.044

Gaisler, J., Pavlů, V., Pavlů, L. & Hejcman, M. (2013) Long-term effects of different mulching and cutting regimes on plant species composition of Festuca rubra grassland. *Agriculture Ecosystems & Environment*, 178, 10–17. https://doi.org/10.1016/j.agee.2013.06.010

Gaisler, J., Pavlů, L., Nwaogu, C., Pavlů, K., Hejcman, M. & Pavlů, V. (2018) Long-term effects of mulching, traditional cutting and no management on plant species composition of improved upland grassland in the Czech Republic. *Grass and Forage Science*, 74, 463–475. https://doi.org/10.1111/gfs.12408

Gordon, I.J. & Benvenutti, M. (2006) Food in 3D: how ruminant livestock interact with sown sward architecture at bite scale. In: Bels, V. (Ed.) *Feeding in domestic vertebrates: from structure to behaviour*. Wallingford, UK: CAB International, pp. 263–277.

Grace, J.B., Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y. et al. (2012) Response to comments on "Productivity is a poor predictor of plant species richness". *Science*, 335, 1441. https://doi.org/10.1126/science.1214939

Grant, S.A., Torvell, L., Common, T.G., Sim, E.S. & Small, J.L. (1996) Controlled grazing studies on Molinia grasslands: effects of different seasonal patterns and levels of defoliation on Molinia growth and responses of swards to controlled grazing by cattle. *Journal of Applied Ecology*, 33(6), 1267–1280. https://doi.org/10.2307/2404769

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative plant ecology: a functional approach to common British species*. London: Unwin Hyman.

Hodgson, J. (1985) The control of herbage intake in the grazing ruminant. *Proceedings of the Nutrition Society*, 44(2), 339–346. https://doi.org/10.1079/PNS19850054

Hodgson, J. & Maxwell, T.J. (1981) *Grazing research and grazing management*. *Biennial Report*. Midlothian, VA: Hill Farming Research Organisation. pp. 169–187.

Illius, A.W., Gordon, I.J., Milne, J.D. & Wright, W. (1995) Costs and benefits of foraging on grasses varying in canopy structure and resistance to defoliation. *Functional Ecology*, 9, 894–903. https://doi.org/10.2307/2389988

Isselstein, J., Jeangros, B. & Pavlů, V. (2005) Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe—a review. *Agronomy Research*, 3, 139–151.

Laca, E.A., Ungar, E.D. & Demment, M.W. (1994) Mechanisms of handling time and intake rate of a large mammalian grazer. *Applied Animal Behavioral Science*, 39, 3–19. https://doi.org/10.1016/0168-1591(94)90011-6

Lemaire, G. (2007) Research priorities for grassland science: the need of long term integrated experiments networks. *Revista Brasileira de Zootecnia*, 36(suppl), 93–100. https://doi.org/10.1590/S1516-35982007001000012

Lepš, J., Májeková, M., Vítová, A., Doležal, J. & de Bello, F. (2018) Stabilizing effects in temporal fluctuations: management, traits, and species richness in high-diversity communities. *Ecology*, 99(2), 360–371. https://doi.org/10.1002/ecy.2065

Louault, F., Pillar, V.D., Aufrere, J., Garnier, E. & Soussana, J.F. (2005) Plant traits and functional types in response to reduced disturbances in a semi-natural grasslands. *Journal of Vegetation Science*, 16(2), 151–160. https://doi.org/10.1111/j.1654-1103.2005.tb02350.x

Ludvíková, V., Pavlů, V., Gaisler, J., Hejcman, M. & Pavlů, L. (2014) Long-term defoliation by cattle grazing with and without trampling differently affects soil penetration resistance and plant species composition in *Agrostis capillaris* grassland. *Agriculture, Ecosystems & Environment*, 197, 204–211. https://doi.org/10.1016/j.agee.2014.07.017

Ludvíková, V., Pavlů, V., Pavlů, L., Gaisler, J. & Hejcman, M. (2015) Sward-height patches under intensive and extensive grazing density in an *Agrostis capillaris* grassland. *Folia Geobotanica*, 50, 219–228. https://doi.org/10.1007/s12224-015-9215-y

Mack, R.N. & Thompson, J.N. (1982) Evolution in steppe with few large, hooved mammals. *The American Naturalist*, 119(6), 757–773. https://doi.org/10.1086/283953

Matches, A.G. (1992) Plant response to grazing: a review. *Journal of Production Agriculture*, 5, 1–7. https://doi.org/10.2134/jpa1992.0001

Mehlich, A. (1984) Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant. *Communication in Soil Science and Plant Analysis*, 15, 1409–1416. https://doi.org/10.1080/00103628409367568

Milchunas, D.G., Lauenroth, W.K. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, 63(4), 327–366. https://doi.org/10.2307/2937150

Parsons, A.J. & Chapman, D.F. (2000) The principles of pasture growth and utilisation. In: Hopkins, A. (Ed.) *Grass: Its Production and Utilisation*. *British Grassland Society*. Oxford: Blackwell Scientific Publications, pp. 31–89.

Pavlů, V., Hejcman, M., Pavlů, L. & Gaisler, J. (2003) Effect of rotational and continuous grazing on vegetation of an upland grassland in the Jizerské hory Mts, Czech Republic. *Folia Geobotanica*, 38, 21–34. https://doi.org/10.1007/bf02803125

Pavlů, V., Hejcman, M., Pavlů, L., Gaisler, J. & Nezerkova, P. (2006a) Effect of continuous grazing on forage quality, quantity and animal performance. *Agriculture Ecosystems and Environment*, 113, 349–355. https://doi.org/10.1111/j.1365-2494.2006.00506.x

Pavlů, V., Hejcman, M., Pavlů, L., Gaisler, J., Hejcmanova-Nezerkova, P. & Meneses, L. (2006b) Change in plant densities in a mesic species-rich grassland after imposing different grazing management treatments. *Grass and Forage Science*, 16(1), 42–51. https://doi.org/10.1111/j.1365-2494.2006.00506.x

Pavlů, V., Hejcman, M., Pavlů, L. & Gaisler, J. (2007) Restoration of grazing management and its effect on vegetation in an upland grassland. *Applied Vegetation Science*, 10(3), 375–382. https://doi.org/10.1111/j.1654-109x.2007.tb00436.x

Pavlů, V., Pavlů, L., Gaisler, J., Supek, S., Hujerova, R., Hejcman, M. et al. (2016) Effect of long-term intensive and extensive grazing on plant species composition. *Grassland Science in Europe*, 21, 563–566.

Peeters, A., Vanbellinghen, C. & Frame, J. (2004) *Wild and Sown Grasses. Profiles of a Temperate Species Selection: Ecology, Biodiversity and Use*. Rome: Food and Agriculture Organization of the United Nations and Blackwell Publ.

Peri, P.L., Varella, A.C., Lucas, R.J. & Moot, D.J. (2001) Cocksfoot and Lucerne productivity in *Pinus radiata* silvopastoral system: a grazed comparison. *Proceedings of the New Zealand Grassland Association*, 63, 139–147.

Pucheta, E., Diaz, S. & Cabido, M. (1992) The effect of grazing on the structure of a high plateau grassland in central Argentina. *Coenoses*, 7, 145–152.

Qu, T., Du, W., Yuan, X., Yang, Z., Liu, D., Wang, D. et al. (2016) Impacts of grazing intensity and plant community composition on soil bacterial community diversity in a steppe grassland. *PLoS One*, 11(7), e0159680. https://doi.org/10.1371/journal.pone.0159680

Rook, A., Dumont, B., Isselstein, J., Osoro, K., Wallis DeVries, M., Parente, G. et al. (2004) Matching type of livestock to desired biodiversity outcomes in pastures: a review. *Biological Conservation*, 119, 137–150. https://doi.org/10.1016/j.biocon.2003.11.010

Sala, O.E., Oesterheld, M., León, R.J.C. & Soriano, A. (1986) Grazing effects upon plant community structure in subhumid grasslands of Argentina. *Vegetatio*, 67, 27–32. https://doi.org/10.1007/BF00040315

Schulte, R.P.O. & Lantinga, E. (2002) Mechanistic simulation of the vertical structure of mixed swards. *Ecological Modeling*, 149(3), 229–246. https://doi.org/10.1016/s0304-3800(01)00438-0

Steffens, M., Kölbl, A., Totsche, K.U. & Kögel-Knabner, I. (2008) Grazing effects on soil chemical and physical properties in a semiarid steppe of Inner Mongolia (P.R. China). *Geoderma*, 143, 63–72. https://doi.org/10.1016/j.geoderma.2007.09.004

Tallowin, J.R.B., Rook, A.J. & Rutter, S.M. (2005) Impact of grazing management on biodiversity of grasslands. *Animal Science Journal*, 81(2), 193–198. https://doi.org/10.1079/asc50780193

Titěra, J., Pavlů, V.V., Pavlů, L., Hejcman, M., Gaisler, J. & Schellberg, J. (2020) Response of grassland vegetation composition to different fertilizer treatments recorded over ten years following 64 years of fertilizer applications in the Rengen Grassland Experiment. *Applied Vegetation Science*, 23, 417–427. https://doi.org/10.1111/avsc.12499

Ungar, E.D. (1998) Changes in bite area and bite depth during patch depletion by cattle. In: Gibb, M.J. (Ed.) *European Intake Workshop on Techniques for Investigating Intake and Ingestive Behaviour by Farm Animals*. North Wyke: IGER, pp. 81–82.

Verhoeven, K.J., Simonsen, K.L. & McIntyre, L.M. (2005) Implementing false discovery rate control: increasing your power. *Oikos*, 108, 643–647. https://doi.org/10.1111/j.0030-1299.2005.13727.x

Wahren, C.H., Papst, W.A. & Williams, R.J. (1994) Long-term vegetation change in relation to cattle grazing in subalpine grassland and heathland on the Bogong High Plains: an analysis of vegetation records from 1945 to 1994. *Australian Journal of Botany*, 42(6), 607–639. https://doi.org/10.1071/BT9940607

White, S.R., Cahill, J.F. Jr & Bork, E.W. (2014) Implications of precipitation, warming, and clipping for grazing resources in Canadian Prairies. *Agronomy Journal*, 106, 33–42. https://doi.org/10.2134/agronj2013.0085

Wrage, N., Strodthoff, J., Cuchillo, H.M., Isselstein, J. & Kayser, M. (2011) Phytodiversity of temperate permanent grasslands: ecosystem services for agriculture and livestock management for diversity conservation. *Biodiversity Conservation*, 20, 3317–3339. https://doi.org/10.1007/s10531-011-0145-6

Wright, I.A. & Whyte, I. (1989) Effect of sward surface height on the performance of continuously stocked spring-calving beef cows and their calves. *Grass and Forage Science*, 44, 259–266. https://doi.org/10.1111/j.1365-2494.1989.tb02163.x

Zhao, L.-P., Wang, D., Liang, F.-H., Liu, Y. & Wu, G.-L. (2019) Grazing exclusion promotes grasses functional group dominance via increasing of bud banks in steppe community. *Journal of Environment Management*, 251, 109589. https://doi.org/10.1016/j.jenvman.2019.109589

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. (a) Monthly precipitation and (b) mean monthly temperature recorded at the study site

Appendix S2. Plant-available pH/$CaCl_2$, P, K, Ca, Mg under each treatment for the year 2016

Appendix S3. Mean botanical composition (%) of the most abundant graminoids, legumes and forbs for the years 2001–2012

Appendix S4. Partial principal components analysis (pPCA) of the plant functional groups for the upper (>3 cm) and lower (<3 cm) sward layers, from 1998 to 2012

Appendix S5. The effect of treatments on dry matter standing biomass for the different functional groups showing changes over the period 1998 to 2012

Appendix S6. Primary data to reproduce all results and figures

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