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RESEARCH ARTICLE

Soil organic carbon stocks and belowground biomass in patches in heterogeneous grassland

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Abstract

Background: Selective grazing creates stable patches of contrasting sward height, thereby providing different growth conditions for the grass sward above and below ground and potentially affecting soil organic carbon (SOC) stocks. We hypothesized that the presence of patches leads to greater spatial variability in belowground biomass (BGB) and SOC stocks than occurs between pastures managed under different stocking intensities.

Methods: A long-term grazing experiment consisting of three stocking intensities was used for this study. We studied BGB, SOC, and soil total nitrogen (N_{tot}) stocks in the 0–15 cm soil depth. Shannon diversity of plant species, soil bulk density, soil phosphorus, potassium, and magnesium contents were considered.

Results: There were no significant effects of patch or stocking intensity on BGB, SOC, and N_{tot} stocks. Short patches had a greater Shannon diversity than tall patches ($p < 0.05$) and plant-available nutrients in soil correlated positively with sward height ($p < 0.05$).

Conclusions: We conclude from the current results and previous studies that higher plant species diversity with lower soil nutrient contents in short-patch areas and higher nutrient contents together with light competition in tall-patch areas might balance each other out with respect to BGB and SOC stocks.

KEYWORDS
grazing land, roots, seminatural grassland, soil organic matter, stocking rate

INTRODUCTION

Comparisons between grasslands grazed at varied intensities are inconclusive in terms of effects of grazing intensity and soil organic carbon (SOC) management (Reinhart et al., 2021). For instance, Wang et al. (2021) and McSherry and Ritchie (2013) found larger SOC contents in less intensively grazed grassland than intensive grassland. Other studies showed the opposite (Abdalla et al., 2018; Bork et al., 2020; Conant et al., 2017) or found no effects of grazing intensity (Herfurth et al., 2016; Nüsse et al., 2017) on SOC. In replicated and designed field experiments on effects of stocking intensity (in terms of animal units ha^{-1}) under continental-temperate climate, stocking intensity had mostly no significant influence on SOC (see Table S1 for an overview). The influence of grazing intensity depends on pedoclimatic conditions (Piñeiro et al., 2010), nutrient inputs (Fornara & Higgins, 2022; Poeplau et al., 2018), the vegetation (Abdalla et al., 2018), or interactions with local management (Soussana et al., 2004). In some cases, the experimental design was insufficient (Reinhart et al., 2021) or there were unknown reasons (Bai & Cotrufo, 2022). Also, SOC is, in general, a function of the grassland sward age (Johnston et al., 2009). In some studies, the grazing management was tested (e.g., rotational vs. continuous grazing) at the same stocking intensity (Conant et al., 2003) or, often, the reference was grassland in grazing exclusion zones (Phukubye et al., 2022), challenging inference on the effect of stocking intensity on SOC. In grassland, a substantial proportion of the total net primary productivity is allocated below ground, serving as the primary carbon input to SOC from carbon flows related to root turnover or rhizodeposition (Gao et al., 2008; Kuzyakov & Domanski, 2000; Poyda et al., 2020). In low-input grazing systems, patch grazing leads to heterogeneous grass swards (Adler et al., 2001) because cattle prefer short patches (<10.5 cm height) for grazing (Dumont et al., 2007, 2012) and avoid tall grass patches (≥10.5 cm height), and these patches remain very stable over many years (Tonn et al., 2018). Patches represent a heterogeneous vegetation composition resembling a pattern of different sward height classes of tall and mature and shorter mainly vegetative areas (Ludvíková et al., 2015). Short patches can be expected to have fewer resources available to invest in belowground biomass (BGB) production than tall patches as the constant defoliation requires continuous regrowth aboveground (Ebeling et al., 2020; Ganjegunte et al., 2005; Rogers et al., 2005). Regular regrowth after defoliation, on the other hand, requires a versatile root system to enable sufficient uptake of nutrients (Whitehead, 2000), particularly those that are immobile. Tonn et al. (2019) provide evidence for 50% greater soil potassium and 35% greater phosphorus contents under tall patches compared to short ones. This is because there is within-pasture nutrient transfer through the herbivore from herbage ingested explicitly in short patches and excreted at random in short and tall patches. Therefore, in short patches, a trade-off can be identified between aboveground biomass and BGB allocation. Since the plant species in tall patches no longer need to invest resources into the formation of new aboveground biomass, at least from the time of peak crop (Bircham & Hodgson, 1983), investing in belowground organs seems to be an appropriate strategy, particularly when soil nutrient contents are sufficient for growth. However, despite greater nutrient availability in soil under tall patches (Tonn et al., 2019; Wrage et al., 2012), survival under competition for light may pose an equally important environmental force for aboveground investment in tall patches as in short patches. Studies comparing grazed grassland with ungrazed exclusion zones are inconclusive in terms of effects on BGB (López-Mársico et al., 2015; Picon-Cochard et al., 2021). So far, there is no information on whether short and tall patch areas within a pasture differ in BGB and SOC stocks. Within-pasture variation by patch specificity may therefore be a hitherto disregarded source of variation and may be a reason for the apparent contradiction on the effects of grazing intensity management on SOC stocks detected in earlier studies. Comparing exclusion zones against grazed grassland may not be the right approach to answer the question of differences between patches because they disregard potential defoliation in tall patches, effects of trampling on soil bulk density (Hiltbrunner et al., 2012), and within-pasture nutrient transfer. Such an investigation requires long-term stable grazing conditions under varied controlled stocking intensity (Reinhart et al., 2021) with stable patchiness. Hence, one of the few long-term cattle grazing experiments in Europe (Isselstein et al., 2007) with replicated stocking intensities was used as a platform for experimentation to study SOC stocks and BGB. In a study on the same experiment, Grinnell et al. (2023) found that livestock performance was greater with more intensive stocking compared to less intensive grazing (stocking rates of 1.1 vs. 0.6 livestock units ha^{-1}; livestock units, LU). Thus, trade-offs between SOC storage and agronomic performance in relation to stocking intensity can be identified. The present study hypothesizes that BGB and the SOC stocks in extensively grazed grassland have a larger variability due to patches within pastures than between pastures managed under different stocking intensities. The objective was to evaluate whether patch-specific variation in SOC stocks affects pasture-scale carbon inventories.

MATERIALS AND METHODS

Grazing experiment and climatic conditions

The "FORBIOBEN" grazing experiment is located in Central Germany at the experimental farm of the University of Göttingen, in Relliehausen (51°46′56.3″ N, 9°42′11.6″ E), 265–340 m above sea level, and it was conducted between 2018 and 2020 after 16–18 years of experimentation. The experimental site was established in 2002 (Isselstein et al., 2007) and has been maintained in its current form since 2005 without interruption, consequently serving as a platform to study the effects accumulating from long-term grazing management under continuous stocking. The experimental area has been extensively managed over at least 30 years as a permanent pasture grazed by suckler cows without any sward renovation or resowing. There were no applications of fertilizers or pesticides, or any mechanical sward maintenance for at least 10 years before the field experiment was established in 2002. No fertilizer or lime was added to the experimental area, although growth of emerging shrubs was controlled mechanically. The area has an agroclimate on the boundary between humid and continental temperate. The long-term (1991–2020) growing season (April–October) precipitation sum was 427 ± 36 mm, with a long-term average growing-season mean temperature of 13.3 ± 0.7°C (mean ± SD) (German Weather Service Station Moringen-Lutterbeck, 18 km distant). The weather conditions during the growing season in 2018 and 2019 were drier (216 and 350 mm, respectively) and hotter (17.0 ± 4.6°C and 15.2 ± 5.2°C, respectively), whereas in 2020, values were closer to the long-term average (422 mm and 14.9 ± 3.7°C). The year 2018 was extremely dry. The grassland is of moderate species richness, with a mean of 11.2 ± 4.1 vascular plant species per 0.25 m^2, a total of >70 vascular plant species (Perotti et al., 2018), and it is representative of the species association known as *Cynosurion cristati* (Runge, 1973). The most dominant grass, dicotyledonous herbs, and legume were, respectively, *Festuca rubra*, *Urtica dioica* and *Taraxacum officinale*, and *Trifolium pratense*. The soil type is a Vertic Cambisol. In the topsoil layer to 15 cm, contents of clay, silt, and sand of 12.0% ± 8.3%, 76.7% ± 9.9%, and 11.3% ± 4.4% (mean ± SD), respectively, were determined in November 2018. The mean ± SD contents of plant-available nutrients in the oven-dry soil were 94 ± 57 mg P kg^{-1}, 278 ± 179 mg K kg^{-1} (calcium-acetate-lactate [CAL] method), and 376 ± 140 mg Mg kg^{-1} ($CaCl_2$) at a pH of 6.1 ± 0.7 ($CaCl_2$)

(Schüller, 1969). The soil contained no free carbonate as determined by the HCl method (Ad-hoc-AG Boden, 2007).

Experimental design

The experimental setup represents a one-factor randomized block design with three replicates comparing three stocking intensity treatments, that is, moderate, lenient, and very lenient stocking, on nine 1-ha paddocks, which are similar to typical sizes of managed grassland paddocks in Germany (LFL, 2015). The grazing management was based on continuous stocking. The treatment-specific stocking intensity was defined as that which maintained a target, compressed sward height, which was 6 cm for moderate, 12 cm for lenient, and 18 cm for very lenient stocking on average per year, measured bi-weekly at 50 random points using a rising plate meter (Castle, 1976, 200 g plate weight, 30 cm diameter). Data of the sward height measurements were used for display of the temporal trend of sward height in terms of arithmetic means ± SD (Figure 2). These sward height measurements were coupled with regular calibration cuts, taken near the soil surface, to determine standing herbage on offer (Correll et al., 2003), of which three, five, and six were taken during 2018, 2019, and 2020, respectively. Eight calibration measurements were usually performed per paddock and date. From 2005 until 2020, treatments were grazed at an intensity corresponding to 413 ± 112, 238 ± 70, and 164 ± 48 LU grazing days ha^{-1} $year^{-1}$ (with 1 LU = 500 kg live weight) in moderate (M), lenient (L), and very lenient stocking (VL), respectively. The average stocking rates corresponded to 1.1 ± 0.3, 0.7 ± 0.2, and 0.5 ± 0.1 LU ha^{-1} $year^{-1}$. In a previous study (Ebeling et al., 2015), the herbage utilization efficiency of the standing herbage on offer was 64%, 38%, and 27.5% under moderate, lenient, and very lenient stocking, respectively. In this respect, herbage utilization efficiency refers to the quotient between annual herbage intake and annual herbage accumulation. The paddocks were grazed by pregnant, nonlactating Fleckvieh beef cows (average live weight of 681 kg) during the grazing season from April to October. A put-and-take approach was applied to manage the stocking of the experimental paddocks to maintain the defined treatment-specific target compressed sward heights. Cows grazed on a compensation area surrounding the experimental plots after they were removed from the experimental paddocks during times when the sward heights were too short for grazing. Throughout the grazing season, cows had ad libitum access to water and salt lick. In all three stocking treatments, there were stable mosaic patterns of tightly defoliated short patches and rejected tall patches and these patches were found to be stable over more than 10 years (Tonn et al., 2018). Area proportions of short and tall patches were determined in a study during 2019 and 2020 using rising plate meters at 14 day intervals (Obermeyer et al., 2022). In that study, the authors found that proportions of short patches per 1 ha paddock increase with stocking intensity representing on average 82.2%, 34.8%, and 24.7% of the paddock areas in moderate, lenient, and very lenient stocking, respectively. For the purpose of the present study, tall patches were classified in close similarity to Ludvíková et al. (2015) as areas within pastures of ≥10.5 cm compressed sward height. All areas with a compressed sward height of <10.5 cm were treated as short patches.

Data collection

In November 2018 (end of the growing season), visibly distinct randomly chosen patches, two short and two tall, were sampled per paddock. In 2019, samples were taken monthly from June to August, with one randomly chosen visibly defined tall patch and one short patch per paddock. In late spring, end of June, and in the autumn of 2020 (beginning and end of October), four randomly chosen sampling locations were selected per paddock representing the range of visible patches (from very tall to very short sward height) (Figure 1). An allocation of each sampling point according to tall and short patches was made ex post. At the beginning of October 2020, an additional factor for stratification was included to control for any potential influence of the vegetation composition; thus, there were eight sampling locations per paddock at this occasion. For this, areas dominated by either dicotyledonous (forb-dominated) plant species or grasses (grass-dominated) were sampled. Sampling on each occasion was restricted to areas that had not been sampled previously.

At each sampling location, the compressed sward height was recorded using a rising plate meter (Castle, 1976). Subsequently, the standing aboveground herbage biomass (AGB) within a steel frame placed right beneath the rising plate meter was manually cut close to ground level using electric hand shears (Gardena®). A sample of BGB was taken from the center of the cut area to 15 cm soil depth using the auger method (Böhm, 1979). The auger diameter for sampling was 8 cm, although in November 2018, two BGB samples were obtained per location. In 2018 and 2020, soil sampling was carried out to a depth of 15 cm using a spade as the sampling tool, with three to five soil samples taken from around each sampling area. These were pooled for analysis (Figure 1). The soil sampling did not take place on every occasion (Figure 1) and, in total, 288 BGB samples and 144 soil samples were collected throughout this study. All samples were frozen (−18°C) until further processing. All BGB samples were washed free from soil contaminants in an automatic elutriation system over a 1 mm mesh size and the total amount of standing BGB (live and dead roots) was determined manually in floatation using hand tweezers. All samples of BGB and AGB were then dried (60°C, 48 h) and converted into equivalent dry matter per square meter of soil surface (g DM m^{-2}) to 15 cm soil depth (McNally et al., 2015). All soil samples were homogenized to 0.2 mm particle size and analyzed for contents of total C (=SOC) and total N (N_{tot}) using elemental analysis (Vario el Cube, Elementar Analysensysteme GmbH). The contents of plant-available P and K in the soil were determined using the CAL method in continuous flow analysis coupled to a flame photometer (K) or ultraviolet/visible spectrophotometer (P) (San System). The soil Mg content was determined with the $CaCl_2$ method using atomic absorption spectrometry (AAnalyst 400; PerkinElmer Inc.).

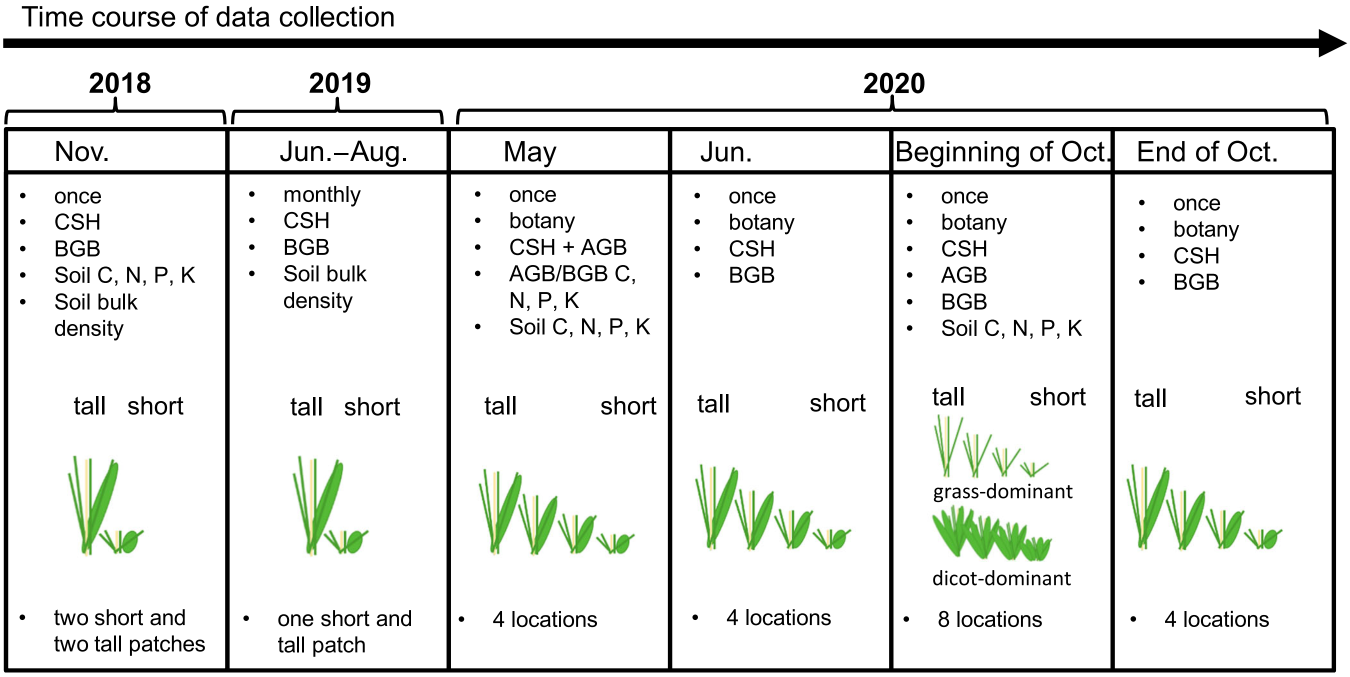

FIGURE 1 Time course and occasions of data collection with locations, referring to the number of samples obtained per paddock. AGB, aboveground herbage biomass; BGB, belowground biomass; C, soil organic carbon; N, total soil nitrogen; P, soil phosphorus; K, soil potassium; CSH, compressed sward height (cm); C, total carbon; N, total nitrogen; P, phosphorus; K, potassium, in live AGB and in BGB (see Table S4 for details); live AGB = live green herbage biomass (>90% green).

Soil bulk density

A first bulk density determination was performed during February 2014, where one tall and one short patch sample in each paddock were sampled from a duplicate sampling in 5–15 cm with 100 cm^{-3} standard steel cylinders and subsequent drying to a constant weight at 105°C (Hartge & Horn, 2009). The same procedure was followed in 2018. However, two pairs of each tall and short patches were sampled per paddock in 2018 (Figure 1). Thus, there were 18 soil bulk density samples in 2014 and 36 in 2018. Details are presented in the supplement (Tables S2 and S3). The SOC and N_{tot} stocks (kg m^{-2}) to 15 cm soil depth were calculated according to Dlamini et al. (2016) using the measured soil bulk densities of 1.41 g cm^{-3} for short patches and 1.40 g cm^{-3} for tall patches (Tables S2, S3, and below).

Botanical composition

To estimate the botanical composition, the three dominant vascular plant species were determined using the dry-weight-rank method ('t Mannetje, 2000) at exactly each sampling point of sward height recording in 2020. The three highest-yielding plant species based on their dry matter content were estimated for this and assigned to ranks 1–3. If there were only two plant species in a location, only two ranks were filled. For each species, the number of ranks 1, 2, and 3 were multiplied by 8.04, 2.41, and 1, respectively ('t Mannetje, 2000) and accumulated to obtain the totally weighted sum per species, patch, and paddock across sampling occasions. The multipliers underlying the calculation of yield proportions of any species determined within the dry-weight ranking are derived from long-term experimental evidence by 't Mannetje and Haydock (1963) from studies of the relationship between actual and ranked dry-weight composition. Their use has been thoroughly validated on a large number of grasslands with different botanical compositions ('t Mannetje, 2000). The weighted rows for all species were accumulated. The value recorded for each species was then divided by the total of the weighted column to obtain the yield proportion for each species and paddock. These data were used to calculate the Shannon diversity (H') according to Equation (1) and Shannon evenness according to Equation (2) following Magurran (2004) using the following formulas:

$$H' = -\sum\left[\left(\frac{n}{N}\right)\ln\left(\frac{n}{N}\right)\right], \quad (1)$$

$$Evenness = \frac{H'}{\ln(N)}, \quad (2)$$

where n represents the percentage cover per species and N is the total percentage plant cover. For this, each sampling location was assigned to a patch (short and tall) and analyzed across dates.

Data analysis

Data analysis was performed in R studio (version 4.1.2) (R Core Team, 2021). We used the sward height as a covariate representative of patch in the data analysis.

This analysis allowed us to test the hypothesis of within-pasture variation without risk of unbalanced data among patches and years. For this, analyses of covariance in a repeated-measures design were implemented using linear mixed-effects models in the package "nlme" (Pinheiro et al., 2022). The sward height was treated as a continuous additive covariate in the models and the fixed effects and the interaction of stocking intensity and year were included. The sampling pair nested in paddock nested in block was used as a random effect to account for repeated measures over time on the same paddock. A sampling pair represented the smallest observational unit, namely, the sampling locations within a paddock, patch, and occasion. A separate variance was allowed for each year in the model of BGB and soil N_{tot} stocks and for each year and stocking intensity in the model of SOC stocks to meet the distributional requirements of variance homogeneity and to account for variation in the amount of data points per year. All variables were log-transformed before analysis. A separate analysis of the data from October 2020, where grass- and forb-dominated areas were distinguished (Figure 1), showed no significant effect of the vegetation and is therefore not shown. Soil bulk density data of the Years 2014 and 2018 were modeled on the fixed and interaction effects of stocking intensity, patch, and year. The random effect constituted the sampling pair, nested in paddock, and nested in block. Separate variances were allowed for each patch, stocking intensity, and year in that model. To be able to assess the distribution of sward height among stocking intensities, the sward height measurements at each calibration cutting during 2019 and 2020 were analyzed in a model with stocking intensity and year as fixed and interaction effects. The paddock nested in block was used as a random effect. Corresponding arithmetic mean values ± SD for the year 2018, which were not included in the statistical analysis of sward height, were retrieved for reasons of comparison. In addition, AGB of the calibration cutting during 2018 until 2020 were square-root transformed and analyzed using a linear mixed effects model with the main and interaction effects of stocking intensity and year. The paddock nested in block served as random effect. Shannon diversity H' and Shannon evenness were analyzed in linear mixed-effects models with patch and stocking intensity as additive fixed effects, while paddock nested in block was modeled as a random effect. For this analysis, patch was assigned a categorical factor according to the sward height measurements into two levels (short and tall; see above) rather than assuming a linear increase of Shannon diversity H' with sward height (Wrage et al., 2012) and performing analysis of covariance. The models were then analyzed in Type III sum of squares analysis of variances because of unbalanced data points among patches. Residuals of each model were inspected for homoscedasticity and normality by inspection of model residuals in QQ plots in the package "rstatix" (Kassambara, 2021). Comparison of means for significant influencing variables was performed using least-squared means in the "predictmeans" package (Luo et al., 2021). The least significant difference was used to separate significant means from each other at an α-level of <0.05 using Tukey's adjustment for pairwise comparisons. Robust winsorized correlations were calculated in the "WRS2" package (Mair et al., 2022) to test for correlations of soil nutrient contents (P, K, Mg contents) with (i) stocking intensity, (ii) compressed sward height, (iii) SOC stocks, and (iv) BGB.

RESULTS

Soil bulk density

There were no significant effects of year or stocking intensity, but there was a marginally significant effect of patch for soil bulk density (Tables S2 and S3, $p = 0.0942$). Thus, the soil bulk density remained stable over years and for different stocking intensities, without interaction between treatments. According to the comparison of means, the soil bulk density under short patches was $1.41 \pm 0.03\ g\,cm^{-3}$ and that for tall patches was $1.4 \pm 0.03\ g\,cm^{-3}$ ($p = 0.518$).

BGB, SOC, and N_{tot} stocks

The analysis of covariance indicated no significant effect of sward height for BGB, SOC, and soil N_{tot} stocks (Table 1). There was a significant main effect of year for BGB and a marginal significant effect on SOC

TABLE 1 Output of analyses of variance of BGB, SOC stocks, and N_{tot} stocks in the 0–15 cm soil layer on the patch scale as affected by the main effects of sward height, stocking intensity, year, and the interaction of year × stocking intensity, and of AGB as affected by stocking intensity, year and the interaction of both.

Target variable	Factors	numDF	denDF	*F*	*p*
BGB	Sward height	1	161	0.5	0.469
	Stocking	2	4	2.6	0.190
	Year	2	93	15.1	<0.001
	Stocking × year	4	93	1.0	0.423
SOC stocks	Sward height	1	107	0.1	0.772
	Stocking	2	4	0.1	0.916
	Year	1	24	3.9	0.061
	Stocking × year	2	24	0.2	0.832
N_{tot} stocks	Sward height	1	107	0.7	0.402
	Stocking	2	4	0.4	0.694
	Year	1	24	2.3	0.142
	Stocking × year	2	24	0.2	0.823
AGB	Stocking	2	4	25.3	0.005
	Year	1	562	7.1	<0.001
	Stocking × year	4	562	1.6	0.173

Note: Degrees of freedom, *F*, and *p* of the ANOVA output are shown.

Abbreviations: AGB: aboveground biomass; BGB, belowground biomass; denDF, degrees of freedom in the denominator; N_{tot}, soil total nitrogen; numDF, degrees of freedom in the numerator; SOC, soil organic carbon.

stocks (Table 1), but not for soil N_{tot} stocks. However, comparison of means revealed significantly greater soil SOC and N_{tot} stocks in 2018 compared to 2020 (Table 2). The BGB was significantly lower in 2019 compared to the other years (Table 2). The AGB was significantly affected by the year (Table 1) with significantly lower AGB in 2020 compared to 2018 and 2019 (Table 2). The AGB was also significantly affected by the stocking intensity (Table 1) because of lower values under moderate stocking intensity compared to the other treatments. The AGB declined in the following order M < L and VL (126 ± 11.2 < 210 ± 14.5 and 236 ± 15.4 g DM m^{-2}) (not shown).

Grass sward height

The sward heights increased from 2019 to 2020 and decreased with stocking intensity (Figure 2). Analysis of variance showed that there was a significant year × stocking intensity interaction ($F(2, 421) = 3.6$, $p = 0.0292$). The interaction was characterized by a smaller difference between patch types in the M stocking intensity treatment. Estimated means ± SEs during 2019 and 2020 were 7.4 ± 0.5 and 9.0 ± 0.6 cm for M, 9.4 ± 0.5 and 13.0 ± 0.6 cm for L, and 10.0 ± 0.5 and 14.0 ± 0.6 cm for VL, respectively. Corresponding arithmetic mean values ± SD for the year 2018 were 6.1 ± 1.2, 8.9 ± 1.2, and 10.3 ± 1.8 cm in M, L, and VL, respectively (Figure 2).

TABLE 2 Estimated means ± standard errors of means for each year of AGB, BGB, SOC stocks, and N_{tot} stocks in the 0–15 cm soil layer on the patch scale.

Target variable	2018	2019	2020
AGB (g DM m^{-2})	210 ± 13.1b	195 ± 13.5b	160 ± 11.5a
BGB (g DM m^{-2})	428 ± 55a	189 ± 25b	359 ± 41a
SOC stocks (kg m^{-2})	9.2 ± 1.0a	-	7.4 ± 0.8b
N_{tot} stocks (kg m^{-2})	0.9 ± 0.08a	-	0.8 ± 0.06b

Note: Different lowercase letters indicate significantly different means among years ($p < 0.05$).

Abbreviations: AGB, aboveground biomass; BGB, belowground biomass; N_{tot}, soil total nitrogen; SOC, soil organic carbon.

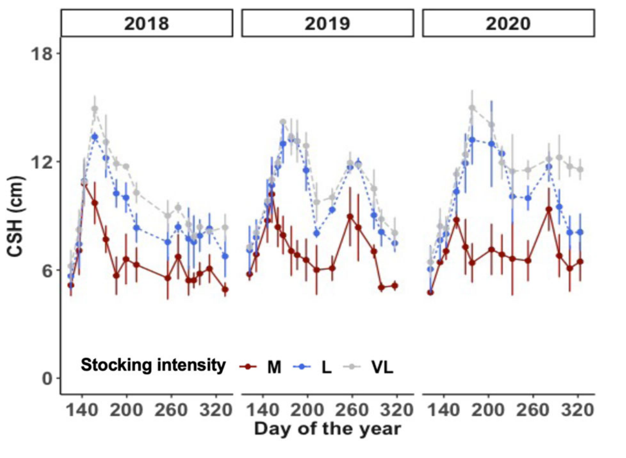

FIGURE 2 Arithmetic means ± SD of compressed sward heights (CSH, cm) measured approximately every 14 days on 50 locations per paddock over the Years 2018 till 2020. L, lenient; M, moderate; VL, very lenient stocking.

Botanical composition

In total, 25 genera of vascular plant species were found across samplings in 2020, and among these, 31 plant species were identified. A significant patch effect was found for the H' ($F(1, 26) = 13.1$, $p = 0.0013$), and comparison of means revealed a greater H' in short patches than in tall patches (0.72 ± 0.03 vs. 0.63 ± 0.03, estimated means ± SE). The Shannon evenness was not affected by patch type or stocking intensity (not shown). Besides phytodiversity, the dominant plant species differed considerably between patches. In tall patches, among the dominant species, *F. rubra* accounted for 36%, *Dactylis glomerata* for 23%, and *U. dioica* for 9% of the recording points (not shown). In short patches, *F. rubra* reached 27%, followed by *T. pratense* with 22% and *Cynosurus cristatus* with 9%.

Correlation of soil nutrient with stocking intensity, sward height, SOC stocks, and BGB

Stocking rate was positively correlated with soil P and K contents and negatively correlated with soil Mg content (Table 3a). The correlation of soil K content with sward height was significantly positive, whereas soil Mg correlated negatively with sward height (Table 3b). All soil nutrients correlated significantly positive with SOC stocks (Table 3c). The BGB correlated positively with soil P and K contents (Table 3).

TABLE 3 Correlation analysis between (a) stocking rate (LU ha^{-1} $year^{-1}$), (b) sward height (cm), (c) SOC stocks (kg m^{-2}), and (d) BGB (g DM m^{-2}) with soil phosphorus, potassium, and magnesium contents (P, K, Mg, mg kg^{-1} soil).

Variables	Item	Soil P	Soil K	Soil Mg
(a) Stocking rate	*r*	0.34	0.20	−0.52
	p	<0.001	=0.019	<0.001
	CI	[0.19, 0.49]	[0.03, 0.36]	[−0.63, −0.41]
(b) Sward height	*r*	0.11	0.34	−0.22
	p	<0.186	<0.001	=0.009
	CI	[−0.07, 0.30]	[0.16, 0.48]	[−0.36, −0.04]
(c) SOC stocks	*r*	0.46	0.28	0.56
	p	<0.001	=0.0009	<0.001
	CI	[0.31, 0.59]	[0.15, 0.43]	[0.44, 0.67]
(d) BGB	*r*	0.30	0.18	−0.07
	p	=0.0002	=0.035	=0.43
	CI	[0.14, 0.45]	[0.02, 0.33]	[−0.22, 0.10]

Note: The correlation coefficients *r*, *p*, and CIs are shown.

Abbreviations: BGB, belowground biomass; CI, confidence interval; LU, livestock unit; SOC, soil organic carbon.

DISCUSSION

More spatial variation of SOC stocks within pastures than among pastures of different grazing intensity?

We hypothesized that the SOC stocks under heterogeneous low-input grasslands have a greater variability due to the presence of patches of different sward height within pastures than between pastures managed under different stocking intensities. However, based on the results from this continuous grazing experiment, managed for nearly two decades, this hypothesis was not confirmed (Table 1). The present study goes beyond the scope of an earlier study of continuously grazed pastures (Nüsse et al., 2017) because variation caused by patch grazing was not considered before. According to Obermeyer et al. (2022), in a study during 2019 and 2020 of the same experiment, short patches accounted for 82%, 35%, and 25% of the paddocks per ha under moderate, lenient, and very lenient stocking, respectively. If SOC stocks are determined and recorded, and stratified according to patches as was done in the present study, then the weighting of SOC stocks according to patch types can be scaled to the paddock level of, for example, 1 ha size. On the other hand, SOC stocks determined at the paddock scale can be obtained from average values taken across paddocks (Nüsse et al., 2017) irrespective of patch types. The resulting paddock-scale SOC stocks from patch-wise weighing or random averaging differ by 1.9 t SOC ha^{-1}. Differences in topsoil SOC stocks among stocking intensities in previous studies range from up to 2 to <0.5 t ha^{-1} (Bork et al., 2020; Conant et al., 2017; Herfurth et al., 2016; Nüsse et al., 2017; Pringle et al., 2014; Silveira et al., 2013). To extrapolate to a paddock level, it is, according to our data from measurements at patch level under the given conditions, therefore recommended that the proportions of patches should be taken into account if possible.

No effects of grazing intensity on SOC stocks

The absence of any effect of stocking intensity on SOC stocks is in accordance with previous studies (Herfurth et al., 2016; Picon-Cochard et al., 2021; Wright et al., 2004). For instance, Herfurth et al. (2016) found no differences after 7 years of varied grazing intensity on SOC stocks. Bork et al. (2020), on the contrary, found a positive relationship between stocking rate and SOC storage in Canadian grasslands, which they attributed to overcompensation of net primary production through defoliation (Hempson et al., 2015). Our long-term study with 16–18 years of varied stocking intensity shows that over a longer time interval, the stocking intensity has no effect on SOC stocks. Over the years, the moderate stocking intensity was significantly more productive than the other stocking intensities, as was determined in a study on livestock performance (Grinnell et al., 2023). The higher productivity under moderate grazing compared to more lenient grazing was consequently clearly without any adverse effect on topsoil carbon storage. Consequently, we found no trade-off between agronomic performance and SOC storage. Overall, the grazing intensity is extensive, with herbage utilization efficiencies of only 64% in the moderate stocking intensity to as low as 27.5% in the very lenient stocking intensity (Ebeling et al., 2015). Under the given low-input extensive grazing management, a more output-oriented but still extensive farming can obviously promote income without compromising climate protection goals through carbon storage. The moderate stocking intensity treatment was managed under a long-term stocking rate of 1.1 LU ha^{-1} at approximately 6 cm sward height, which can be used as an orientation for management.

Our study was preceded by a continental-wide drought period (the Year 2018) (Buras et al., 2019) with 49% less precipitation than the long-term average, which may explain the large BGB allocation in that year (Table 2) (Poorter & Nagel, 2000). In the post drought year of 2019, the BGB was 51% smaller than in 2018 (Table 2), and this likely reflects relocation towards aboveground production (Figure 2). With the return in 2020 of climatic conditions comparable to long-term values, the BGB increased by 43% from 2019 until 2020, which reflects the more favorable growing conditions (+21% more precipitation during 2020 compared to 2019), enabling resources for BGB production.

Sources of variation of SOC stocks and BGB within pastures

López-Mársico et al. (2015) found increased BGB in grazed sites compared to ungrazed exclusion zones, while Picon-Cochard et al. (2021) found no differences but a large interannual variation of roots. Tall patches are basically comparable to grazing exclusions. Exclusion zones, however, are not subject to potential defoliation in tall patches, effects of trampling on soil bulk density (Hiltbrunner et al., 2012), and within-pasture nutrient transfer. Greater nutrient availability in tall patches (Table 3) and lower Shannon diversity are in accordance with previous studies (Perotti et al., 2018; Tonn et al., 2019; Wrage et al., 2012). The content of mobile potassium and the relatively immobile phosphorus are both reduced in short patches compared to tall patches (Table 3; Tonn et al., 2019). For plant survival in short patch areas, investment in a versatile root system that can capture nutrients (P and K; Table 3) is consequently relatively more important than in tall patches. Compared to natural grassland and heathlands, contents of on average 94 mg P kg^{-1} and 278 mg K kg^{-1} soil as in the present study are still comparably large (Riesch et al., 2018) and they indicate that both nutrients are available in sufficient quantity for plant growth (Agricultural Chamber, 2018; Wiesler, 2018). Analyses of a subset of live AGB point to nutrient supply in growing herbage tissue (Table S4). There, the N:P ratios of below 0.8 (Hejcman et al., 2012) and N:K ratios of below 2.1 (Olde Velterink et al., 2003) indicate N limitation of the present grassland (Table S4). These ratios are at the lower end of ranges reported in other studies (Hrevušová et al., 2014; Pavlů et al., 2019). Our data (Table S4) consequently show that plant growth is generally N limited. Investment in BGB for nitrate uptake is consequently important irrespective of patches and this may also affect deeper soil layers. Grazing can trigger belowground C-exudation (Reeder et al., 2004), thereby activating microbial communities in the rhizosphere that may immobilize available N. The increased C:N ratio of AGB and BGB in short patches compared to tall patches (Table S4) suggests that plants in short patches were more limited with respect to N uptake than plants in tall patches.

The frequent defoliation of short patch areas has changed the botanical composition compared to tall patch areas and increased the Shannon diversity compared to tall patches, which is in accordance with other studies (Schuman et al., 1999). There is a positive relationship between species richness and SOC storage (Bai & Cotrufo, 2022; Yang et al., 2019), so that the soil under short patches is potentially able to store more SOC than soil under tall patches. Differences in plant species identities among patches affect BGB, biological N fixation, litter input (De Deyn et al., 2011; Reeder & Schuman, 2002), and SOC stocks. In addition, plants require sufficient light to grow. In the absence of defoliation, less light may reach lower sward strata. Consequently, a few very fast-growing species dominate over short-stature species. For instance, Eskelinen et al. (2022) used artificial light sources in lower sward strata of grassland and found that competition for light is a major driver of species selection in grassland in the absence of defoliation. Consequently, tall-patch C input and associated C flows may be indifferent to short patches because there is a strong aboveground competition for light (Cleland et al., 2019), an aspect that also requires further investigation that also considers deeper soil layers (Cougnon et al., 2017; Rauber et al., 2021).

CONCLUSIONS

As one of the few replicated long-term grazing experiments in Europe, this study shows that under long-term continuous grazing under low-input management without fertilizer input or sward maintenance, under temperate climate conditions, maintaining a sward height of 6 cm has no adverse effect on SOC stocks compared to more extensive grazing with 12–18 cm sward heights. Future studies are needed to determine whether higher plant species diversity combined with lower soil nutrient contents in short patch areas, against larger soil nutrient contents in combination with light competition in tall patch areas, are able to balance each other out with respect to variation in BGB and SOC stocks among patches.

AUTHOR CONTRIBUTIONS

Martin Komainda: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; supervision; visualization; writing—original draft; writing—review and editing. **Eliana Mohn**: Investigation. **Klára Kajzrová**: Investigation; writing—review and editing. **Kilian Obermeyer**: Investigation; writing—review and editing. **Jan Titěra**: Investigation; writing—review and editing. **Vilém Pavlů**: Funding acquisition; writing—review and editing. **Johannes Isselstein**: Conceptualization; funding acquisition; investigation; methodology; resources; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All research data of the current study are accessible from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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