The role of stable sward height patches for the productivity, herbage intake and nitrogen cycling of cattle pastures differing in stocking rate

Dissertation

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“The sustainability of grazed systems

is a more fundamental issue than is grazing optimization.”

David D. Briske, 1993

This thesis is dedicated to my family.

Contents

GENERAL INTRODUCTION

Grasslands cover about 40% of the earth's surface (White et al., 2000), one fifth (20.7%) of the total area of the former EU-28 (European Union of 28 Member States in 2015, EUROSTAT, 2020) and nearly 30% of the German agricultural area (Statistisches Bundesamt, 2019). They are a global resource that provides multiple ecosystem services (McGilloway, 2005) and can be highly diverse ecosystems (Rook et al., 2004).

Temperate semi-natural grasslands greatly contribute to the biodiversity of landscapes in Europe (Rook et al., 2004), where wild megaherbivores have maintained grassland vegetation for 1.8 million years (Suttie et al., 2005). They result from low-intensity agricultural usage as pastures or meadows (Isselstein et al., 2005), traditionally fundamental for the feeding and bedding of domesticated animal species (Poschlod, 2017).

European managed grasslands are furthermore recognized for their high productivity and provision of high-quality forage. Also, their potential as a carbon sink is considered large (Pol-van Dasselaar, A. van den et al., 2018). During the last decades, however, the agricultural intensification, including increased fertilization, the conversion of grassland to cropland, as well as the abandonment of marginal grassland sites due to the reduction of livestock numbers (Isselstein et al., 2005) and increased milk yields per cow (Hopkins & Wilkins, 2006), led to a huge loss of biodiversity as well as to related ecological problems (Duru et al., 2015).

Because many ecosystem services, as well as human well-being, depend on biodiversity (Haines-Young & Potschin, 2010), its conservation has gained considerable attention in European research projects and policy during the last years (Duru et al., 2015; Isselstein et al., 2005; Habel et al., 2013; Hopkins & Wilkins, 2006; Marriott et al., 2004; Tscharntke et al., 2005), dealing with trade-offs and synergies between management intensity and ecosystem services also in agricultural systems (Bengtsson et al., 2019; Power, 2010).

There is evidence that a reduced management intensity can improve the relationship between agronomy and ecology in grasslands (Jerrentrup et al., 2020). Low-input semi-natural grasslands are agro-ecosystems targeting both agronomic production and ecological benefits (Isselstein et al., 2005). They are either used as meadows, pastures or grazed meadows (Hejcman et al., 2013), with low-intensity grazing, especially, showing potential to reduce biodiversity losses (Gilhaus et al., 2014) while maintaining adequate agronomic output (Rook & Tallowin, 2003). In particular, this will be true for marginal sites, where the withdrawal of agriculture is ongoing (Rosenthal et al., 2012).

Low-input pastures are characterized by structurally diverse swards developing under sufficiently low stocking rates (Rook et al., 2004). Then, the grazing animals are able to pursue their preference for palatable, high-quality fodder (Dumont, 1997) and therefore they frequently re-visit previously defoliated areas of the pasture, while rejecting others (Cid & Brizuela, 1998; Dumont et al., 2007; Ren et al., 2015). This phenomenon is called patch-grazing, as described by Adler et al. (2001). Patch-grazing, thus, leads to positive feedback between defoliation and forage quality, i.e., the grazing animals create fodder nutrient conditions beneficial to themselves (Gilhaus et al., 2014). In this way, they create and maintain mosaic structures composed of patches differing in sward height (Adler et al., 2001; Cid & Brizuela, 1998; Parsons & Dumont, 2003; Tonn et al., 2019a; Willms et al., 1988).

Due to frequent defoliation, vegetation in short patches is kept in an early phenological stage, providing high-quality forage throughout the season (Gilhaus et al., 2014). Light limitation in short patches is weak, which allows several species to coexist (Strodthoff & Isselstein, 2001) and potentially reach ceiling yield (Lemaire et al., 2000). Because light limitation is strong, vegetation in tall patches is generally dominated by competitive, fast-growing grass species (Olff & Ritchie, 1998). Due to the lack of defoliation, tall patches show comparatively high levels of standing biomass (Correll et al., 2003) and litter (Şahin Demirbağ et al., 2009), with herbage of comparatively low quality (Roguet et al., 1998).

Thus, in the agroecological-targeted grazing system, short patches constitute the animals' main feeding stations (WallisDeVries et al., 1999), while tall patches are of minor relevance for the agronomic production of the grazing system and may even lower pasture utilization (Chapman et al., 2007). However, tall-grown vegetation stands can represent high carbon mass (Smith et al., 2014) potentially playing a critical role for carbon sequestration in the agroecologically targeted grazing system as their low-degradable biomass has a comparatively long residence time in soil (Rossignol et al., 2011a).

Biomass growth (Parsons et al., 2011) of low-input pastures differs from that of intensively managed grazing systems (Parsons & Chapman, 2000). It is strongly heterogenous as short and tall patches differ not only in the proportion of herbage removed by the grazing animals, but also in their productivity (Cid et al., 2008). Şahin Demirbağ et al. (2009) found short patches to be more productive than tall patches, presumably due to the frequent removal of plant tissue stimulating biomass growth (Ferraro & Oesterheld, 2002; Hilbert et al., 1981). In contrast, net growth rates in tall patches decline during the course of the season and approach zero as they reach peak standing crop (Parsons & Chapman, 2000).

Once the patch pattern is established, the mosaic structure is likely to be temporally and spatially stable over multiple years (Tonn et al., 2019b; Willms et al., 1988). Because the heterogeneous pattern of defoliation (Adler et al., 2001; Dumont et al., 2012) differs from the likewise heterogeneous pattern of excrement placement on pasture (Auerswald et al., 2010), soil nutrients are frequently translocated away from short patches, potentially inducing a lack of soil nutrients in the frequently defoliated patches (Schnyder et al., 2010). Soil nutrient availability is a crucial factor for biomass productivity. In short patches, a lack of soil nutrient availability could counteract the positive effect of frequent defoliation on biomass productivity. Also, interactions of soil nutrient availability and defoliation regime may induce shifts in vegetation composition, replacing productive, grazing tolerant species by unproductive plant species (Rossignol et al., 2011b) pursuing a stress-tolerating strategy (Grime, 2001). Consequently, plant growth for agricultural production may be reduced in long-term low-intensity grazing systems due animal-mediated changes in soil nutrient availability.

However, stocking rate is a major driver of both biomass dynamics and soil nutrient cycling as it determines herbage intake (Dumont et al., 2007; Parsons & Dumont, 2003) and, in this way, strongly influences nutrient pathways (Boddey et al., 2004; Haynes & Williams, 1993; Thomas, 1992). With increased stocking rate and herbage intake, the frequently defoliated area enlarges, while the rarely defoliated area decreases (Tonn et al., 2019b). Also, homogeneity of both sward utilization (Hirata, 2002; Ludvíková et al., 2015) and excrement placement, i.e., soil nutrient return, increase with stocking rate (Haynes & Williams, 1993; Peterson & Gerrish, 1996). Increased stocking therefore leads to an accelerated and more efficient nutrient cycling as the more easily available soil nutrients recycled through dung and urine can be used for regrowth in frequently defoliated short patches. Additionally, a sufficient soil nutrient availability also in short patches might promote grazing-tolerant, productive species with comparatively high nutritive value. Subsequently, this may increase the overall biomass productivity as well as turnover of both above- and below-ground plant biomass on pasture.

Thus, adjusting stocking rate may lead to an optimization of both agronomic output through increased productivity of short patches and ecological goals, as carbon storage through a greater productivity in tall patches increases total carbon flow from the atmosphere to the soil.

So far, research on low-intensity grazing in the context of mitigating ecological problems has been frequently focussed on either the effect of grazing management on biodiversity (Filazzola et al., 2020; Marriott et al., 2004; Rook et al., 2004) or on agronomic aspects of biodiversity-targeted grazing systems (Isselstein et al., 2005). In contrast, grazing effects on both biomass growth for agronomic output and carbon storage of structurally heterogeneous pastures have only rarely been studied.

Therefore, we revisited the cattle grazing experiment initially investigated by Şahin Demirbağ et al. (2009) to study the effects of stocking rate (moderate, lenient, very lenient) on aboveground net primary productivity in patch types (short, medium, tall) after 12 years of low-intensity cattle grazing (Chapter I). To evaluate the agronomic and ecological potential of the grazing systems, we analysed the influence of stocking rate on herbage productivity, herbage intake and herbage utilization (Chapter II). To gain knowledge on animal-mediated dynamics of carbon pools on long-term low-input pastures, we moreover focussed on the influence of stocking rate on the seasonal dynamics of live, dead and belowground biomass as well as the C:N ratio in different sward height patches (Chapter III).

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CHAPTER I: PRIMARY PRODUCTIVITY IN PATCHES OF HETEROGENEOUS SWARDS AFTER 12 YEARS OF LOW-INTENSITY CATTLE GRAZING

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Abstract

In low-intensity grazing systems, patch grazing leads to a mosaic structure of short (frequently defoliated) and tall (rarely defoliated) patches, with the stocking rate determining the proportion of these patch types on the pasture. Little is known about the long-term effects of patch grazing on the productivity of contrasting sward height patches developed under varying stocking rates. On a 12-year low-intensity cattle pasture we investigated aboveground net primary productivity (ANPP) and its seasonal variation in different patch types (‘short’, ‘medium’ and ‘tall’) under three stocking rates (‘moderate’, ‘lenient’ and ‘very lenient’) over two years. Additionally, we determined stocks of soil phosphorus, potassium and magnesium as well as soil pH.

ANPP was affected by an interaction of patch type and stocking rate and ranged from less than 300 g m^{-2} in short patches under very lenient stocking to more than 1000 g m^{-2} in medium patches under moderate stocking. In contrast to observations at the start of the experiment, ANPP in short patches was similar to or less than that in medium and tall patches. As topsoil phosphorus and potassium stocks were lowest in short patches, this indicates a long-term redistribution of nutrients by grazing animals, which limits short-patch productivity. Productivity of medium patches increased with stocking rate, and soil potassium concentration showed a similar trend, pointing towards enhanced nutrient cycling under more intensive stocking. We conclude that nutrient redistribution may lead to increasing trade-offs between ecological and agronomic aims in long-term low-intensity grazing systems.

Keywords: ANPP, continuous stocking, nutrient transport, patch grazing, spatial heterogeneity, herbage growth rates

Introduction

On extensive pastures, spatial heterogeneity in forage intake affects sward structure (Dumont et al., 2012), productivity (Tallowin et al., 2005) and vegetation composition (Gillet et al., 2010; Wrage et al., 2012; Tonn et al. 2019) and is known to promote biodiversity outcomes (Metera et al., 2010; Rook et al., 2004; Wrage et al., 2011). Spatial heterogeneity in forage intake is a consequence of selective grazing (Pauler et al., 2020) with the aim to maximize daily nutrient intake (Fryxell, 1991). Grazers prefer high-quality plant biomass (Hopkins, 2000) and trade off bite mass against digestibility of the plant material (Searle et al., 2005). This can lead to a positive feedback cycle that promotes the continued use of previously grazed parts of the pasture, with frequently grazed short patches providing young and high-quality plant material throughout the grazing season (WallisDeVries et al., 1999). In contrast, lack of defoliation in rejected patches leads to tall vegetation and larger proportions of matured and dead plant material (Dumont et al., 2012; WallisDeVries et al., 1999).

Through this within-paddock variation in grazing intensity, known as 'patch grazing' (Adler et al., 2001), herbivores generate a mosaic of patches differing in sward height (Bakker et al., 1984; Cid & Brizuela, 1998; Şahin Demirbağ et al., 2009; Tonn et al., 2019).

Especially on fertile sites (Dumont et al., 2012), such mosaics can be temporally and spatially stable both over short periods of two successive years (Cid & Brizuela, 1998; Dumont et al., 2012) and over longer periods of four (Willms et al., 1988) or even more than ten years (Tonn et al., 2019).

Patch grazing can be expected to affect biomass productivity. During the first years of a newly established cattle grazing experiment, Şahin Demirbağ et al. (2009) found short patches to be more productive than tall ones, presumably owed to compensatory re-growth after defoliation (Ferraro & Oesterheld, 2002; Hilbert et al., 1981). Continuous, whole-season biomass growth in short patches allows their permanent use for feeding , whereas net growth rates in tall patches will approach zero as they reach peak standing crop (Parsons & Chapman, 2000). On the other hand, Rossignol et al. (2011) found lightly grazed tall patches to be less productive than short patches in several long-term horse- and cattle-grazed grasslands.

Such contrasting observations might be caused by animal-mediated shifts in soil nutrient availability within each patch type. Preferred grazing of short compared to tall patches means that the nutrient removal is larger in short than in tall patches. Nutrient return through urine and dung, on the other hand, occurs not only when animals are grazing but also during other behaviour (Auerswald et al., 2010) for which they show no patch-specific preferences but rather are influenced by other drivers, such as topography or watering places (Hirata et al., 1987; Schnyder et al., 2010; Yoshitake et al., 2014). This may lead to soil nutrient redistribution from short to tall patches, decreasing the potential for compensatory regrowth of short patches in the long term. Reduced biomass productivity due to low soil nutrient availability would occur especially in summer months when soil nitrogen stocks fed from over-winter litter decomposition have already been taken up. As short patches constitute the main forage resource, their productivity throughout the season is of particular relevance for both agricultural production and patch stability over the long term. Nevertheless, patch-dependent biomass productivity of such multi-annual systems has been reported only scarcely, especially for temperate pastures in Europe.

The effect of patch grazing on pasture productivity is further influenced by stocking rate, both at the paddock and at the patch scale. At the paddock scale, it determines the proportion (Cid et al., 2008; Dumont et al., 2007; Jerrentrup et al., 2014; Ludvíková et al., 2015; Tonn et al., 2019) and the size (Tonn et al., 2019) of different patch types on the pasture area. Generally, the proportion (Dumont et al., 2007) and the size (Tonn et al., 2019) of frequently defoliated short patches increase with increased stocking rate, while those of rarely defoliated tall patches decrease. The stability of the patch pattern responds to stocking rate and seems to depend on individual patch sizes as well (Tonn et al., 2019). At the patch scale, the local grazing intensity within patch types may differ as stocking rate affects the herbivore’s foraging behaviour (Dumont et al., 2007). For example, short patches grazed under higher stocking rates may be defoliated less frequently or less severely than short patches grazed under lower stocking rates, because selection for short patches decreases (Dumont et al., 2007).

Further, the speed of nutrient cycling generally increases with the stocking rate (Boddey et al., 2004). Nutrients become available faster after ingestion and excretion by animals than through litter decomposition (Haynes & Williams, 1993; Thomas, 1992), and the amount of nutrients cycled through the herbivore pathway increases with stocking rate. At the same time, excrements are distributed more homogeneously over the pasture area under higher stocking rates (Peterson & Gerrish, 1996). They may therefore be beneficial for sward productivity of low-input pastures.

We revisited the cattle grazing experiment initially investigated by Şahin Demirbağ et al. (2009) to study the aboveground net primary productivity of different patch types after 12 years of cattle grazing at three different stocking rates. We hypothesised that –in contrast to the results of from the beginning of this 12-year grazing experiment (Şahin Demirbağ et al., 2009)– frequently defoliated short patches would have a lower aboveground net primary productivity (ANPP) than infrequently defoliated tall patches (hypothesis I). Nevertheless, we expected ANPP to be distributed more evenly over the grazing season in short patches than in tall patches (hypothesis II), because accumulating herbage would reduce ANPP of tall patches later in the season, while short patches show frequent regrowth following defoliation events. Moreover, we hypothesized ANPP to increase with increasing stocking rate, irrespective of patch type (hypothesis III), based on an enhanced nutrient cycling and a better soil nutrient availability under higher stocking rates (Haynes & Williams, 1993).

Material and methods

Experimental site and design

We conducted this experiment on a permanent low-intensity cattle pasture with a continuous stocking system, located in Relliehausen (51°46′N, 9°42′E, 250 m a.s.l.), Lower Saxony, Germany. The long-term (2002-2014) mean annual temperature is 8.8 °C (meteorological station: Moringen-Lutterbeck, Deutscher Wetterdienst, DWD) and the annually accumulated precipitation is 816 mm (meteorological stations: Moringen-Lutterbeck, 2002-2010, Dassel, 2011-2014, DWD). Precipitation and temperature in 2013 and 2014 are summarized in Table 1. The soil type is a Vertic Cambisol (IUSS Working Group WRB, 2006). Soil texture ranges between a silt loam and a clay soil (Nüsse et al., 2017). The vegetation type of the mesotrophic hill grassland is a Lolio-Cynosuretum. Main species are Lolium perenne, Trifolium repens, Taraxacum sect. Ruderale, Dactylis glomerata, Ranunculus repens and Agrostis stolonifera (Wrage et al., 2012). For at least 10 years prior to the setup of the experiment in 2002, there had not been any fertilizer or herbicide application and the sward had been treated uniformly with rotational grazing and cutting, inhibiting the formation of a sward mosaic driven by patchy grazing (Cid & Brizuela, 1998; Tonn et al., 2019). Scrubs have been removed mechanically when necessary.

Since 2005, the experimental area has been stocked with dry Simmental cows. Three stocking rates have been applied to maintain different mean target sward heights at the paddock level: moderate stocking (MS), lenient stocking (LS) and very lenient stocking (VLS), with 6, 12 and 18 cm compressed sward height (CSH, Castle, 1976, Correll et al., 2003). During 2013 and 2014, target sward heights resulted in average stocking rates of 607 (MS), 342 (LS) and 221 (VLS) kg live weight ha^{-1} a^{-1}.

Target sward heights have been maintained by adjusting livestock numbers after measuring mean paddock sward heights in a two-week interval. Each time, we took fifty CSH measurements per paddock with a rising-plate meter (Correll et al., 2003). If mean paddock sward heights differed from the paddocks' target sward heights, we put cattle on or took them off the pasture area in response (put-and-take system).

The experiment was arranged in a randomized block design with three replications, comprising nine paddocks with a size of 1 ha each in total.

Table 1. Duration of growth periods in 2013 and 2014, mean daily precipitation (mm), mean daily temperature (°C) during growth periods and sward height class thresholds (cm compressed sward height) at the beginning of each growth period.

Year	GP	Start	End	P	T	Sward height class threshold	
						Short-medium	Medium-tall
2013*	1	20-Apr	16-May	1.4	11.4	5.0	7.0
	2	17-May	11-Jun	4.7	11.7	8.0	14.0
	3	12-Jun	9-Jul	1.6	16.6	6.0	16.5
	4	10-Jul	21-Aug	1.1	18.5	6.0	12.0
	5	22-Aug	1-Oct	1.5	13.8	5.0	12.0
	6	2-Oct	30-Oct	2.4	10.5	5.0	11.0
2014†	1	1-Apr	13-May	2.2	10.3	5.5	9.5
	2	14-May	13-Jun	3.5	14.9	14.5	20.0
	3	14-Jun	11-Jul	3.4	15.0	9.0	13.0
	4	12-Jul	21-Aug	3.3	17.8	8.0	15.0
	5	22-Aug	23-Sep	2.9	14.5	8.0	14.0
	6	24-Sep	14-Oct	2.1	12.8	6.8	12.0
	7	15-Oct	3-Nov	2.6	10.7	6.0	9.0

Note Abbreviations: GP Growth period, P Precipitation, T Temperature *Mean daily precipitation (2.1, 1.9, 1.0 mm) and temperature (-0.2, -0.8, -1.1 °C) in Jan, Feb, Mar †Mean daily precipitation (2.4, 1.5, 0.8 mm) and temperature (1.6, 4.0, 6.4) in Jan, Feb, Mar

From 2002 to 2005, the experiment had been run with slightly different stocking rates and cattle breeds: One lenient stocking (LS) variant grazed by growing German Angus, a second LS variant grazed by growing Simmental steers and one moderate stocking (MS) variant grazed by growing Simmental steers (Isselstein et al., 2007). Today's very lenient stocking (VLS) variant was established out of the LS variant grazed by growing German Angus in 2005. More information about the study site is published in Isselstein et al. (2007).

An overview of stocking rates in earlier years of this 12-year experiment is given in Jerrentrup et al. (2014).

In addition to adjusting livestock numbers, we used the fortnightly CSH measurements to define three different patch types: 'short', 'medium' and 'tall'. To this end, we calculated the 0.33 quantile and the 0.67 quantile out of the 450 CSH measurements taken at each date across the nine paddocks and defined them as sward height class thresholds (short to medium and medium to tall). Averaged over 2013 and 2014, we classified 60, 31 and 17% of the paddock area as short and 15, 36 and 59% of the paddock area as tall under moderate, lenient and very lenient stocking, respectively. Sward height class thresholds during the experiments are shown in Table 1. Proportions of patch types over the long term are given in Tonn et al. (2019).

Field sampling

Aboveground biomass

The method for the determination of ANPP and its seasonal distribution followed that of Şahin Demirbağ et al. (2009), combining an exclosure method with sward height measurements and converting the increase in height to an increase in herbage mass as follows:

We placed one exclusion cage (2 m × 1 m) per patch type and paddock (Figure S.2), comprising 27 exclusion cages in total, in a random manner and left the cages standing for a duration (growth period) which length was predetermined and adapted to the seasonal biomass productivity (Table 1). We chose short growth periods during spring, when high growth rates can occur, to ensure that sward structure within cages did not diverge too much from the surrounding patch type. Later in the year, we extended the growth periods to permit the accumulation of measurable biomass increments. We placed the cages at different locations repeatedly from April to October in 2013 and from April to November in 2014, comprising 6 growth periods in 2013 and 7 growth periods in 2014. In both years, the first growth period started before, and the last growth period ended after the grazing season. Before and after each growth period, we measured compressed sward height on two square frames (0.25 m^2 each) within the cage. To predict standing biomass from the measured sward height (Appendix I, Supporting Information S1, Figure S.1), we used a double sampling technique with calibration cuts (Mannetje, 2000). We calculated ANPP as the difference between standing biomass in the cages at the beginning and at the end of each growth period. In a second step, we calculated daily herbage growth rates within each growth period by dividing the standing biomass increment between beginning and end of each growth period by the duration of this growth period. ANPP was then calculated by summing up all positive daily herbage growth rates. We set apparent negative daily herbage growth rates to zero for this calculation.

To quantify the distribution of ANPP within the vegetation period the date by which half of the annual ANPP was produced, $t_{0.5ANPP}$, was calculated for each stocking rate and patch type from the daily herbage growth rates.

Soil sampling

To determine soil nutrient concentrations, we took topsoil (0–10 cm) samples in August 2013 and July/August 2014 (Tonn et al., 2019). We randomly selected five sampling areas per paddock. Within each sampling area, we placed a square frame of 0.25 m^2 within each of the three patch types in a stratified random sampling (135 samples in total). Within each square frame, we took 14 cores with 15 mm in diameter. We obtained concentrations of phosphorus

(P), potassium (K), and magnesium (Mg) as well as pH values of the dried soil samples via calcium acetate-lactate and determined the extract's phosphate concentration and pH photometrically, the potassium concentration spectrometrically via continuous flow analyser.

To determinate bulk density, we took cylindrical (100 cm^3) topsoil samples (5–10 cm) in February 2014, when soil water saturation was adequate, and determined their dry mass after drying them at 105 °C for 24 h. The sampling design was analogous to that of the soil nutrient sampling, with the exception that we chose two instead of five sampling areas per paddock (45 samples in total). Per square frame, we took three repeated measurements. Subsequently, we calculated topsoil (0–10 cm) nutrient stocks by multiplying soil nutrient concentrations (nutrient mass per soil dry mass) by bulk density (dry soil mass per soil volume). For further analysis, we used mean values per paddock and patch type, averaged over sampling areas.

We selected P and K, rather than nitrogen, as indicators for soil nutrient availability, even though nitrogen is the limiting plant nutrient at our experimental site (peak standing crop N:P ratios of 3.9–9.7 and N:K ratios of 0.6–1.9, unpublished data). However, stocks of mineral nitrogen at any one time do not reflect nitrogen supply rates, but rather the current equilibrium between mineralisation, plant uptake, immobilisation, and hence show great variability over time. In contrast, the cycling of phosphorus and potassium through grazing animals is coupled to that of nitrogen. As non-limiting nutrients, phosphorus and potassium can be expected to accumulate within areas of positive net nutrient balance. Thus, any consistent patterns of animal-mediated nutrient redistribution would be reflected in differences in the soil phosphorus and potassium.

Statistical analyses

We carried out all calculations and statistical analyses with R 3.2.3 (R Core Team, 2015). We used linear mixed effects models (R package 'nlme', Pinheiro et al., 2015) to analyse the single, pairwise and three-way interactive effects of patch type (short, medium, tall), stocking rate (moderate, lenient, very lenient) and year (2013, 2014) on the annual ANPP and on $t_{0.5ANPP}$, as well as the single and pairwise interactive effects of patch type and stocking rate on topsoil nutrient stocks (Mg, P, K) and pH. To account for the nested design of the experiment, the random factor 'paddock' was nested in the random factor 'block'. We examined model residuals visually for normality and variance homogeneity of residuals. In case heterogeneous variances occurred, we specified appropriate variance structures. In the model for ANPP, an exponential variance function structure was used that allowed the spread of ANPP to differ per year. In the model for $t_{0.5ANPP}$, variance was permitted to vary between levels of the factors 'year' and 'stocking rate'. We log-transformed soil potassium and magnesium stocks before analysis.

We simplified the full models by choosing the model with the lowest value of the 'Akaike Information Criterion' (AIC, Akaike 1973), determined under maximum likelihood estimation. When marginal Wald tests indicated significant main or interactive fixed effects, we analysed differences between means using Tukey post-hoc tests, implemented in the R package 'lsmeans' (Lenth, 2016).

Results

Aboveground net primary productivity (ANPP)

Patch type and stocking rate interactively affected ANPP (Table 2). Under moderate and lenient grazing, it differed between patch types. Short patches showed the lowest ANPP and were 22.8% less productive than tall patches under LS (Figure 1). Under MS, medium patches had an ANPP that was 50.8% and 35.2% higher than that of short and tall patches, respectively. For the medium patch type, ANPP increased from 371 to 869 g m^{-2} a^{-1} with increasing stocking rate. Across patch types and stocking rates, ANPP was 24.6% higher in 2014 than in 2013.

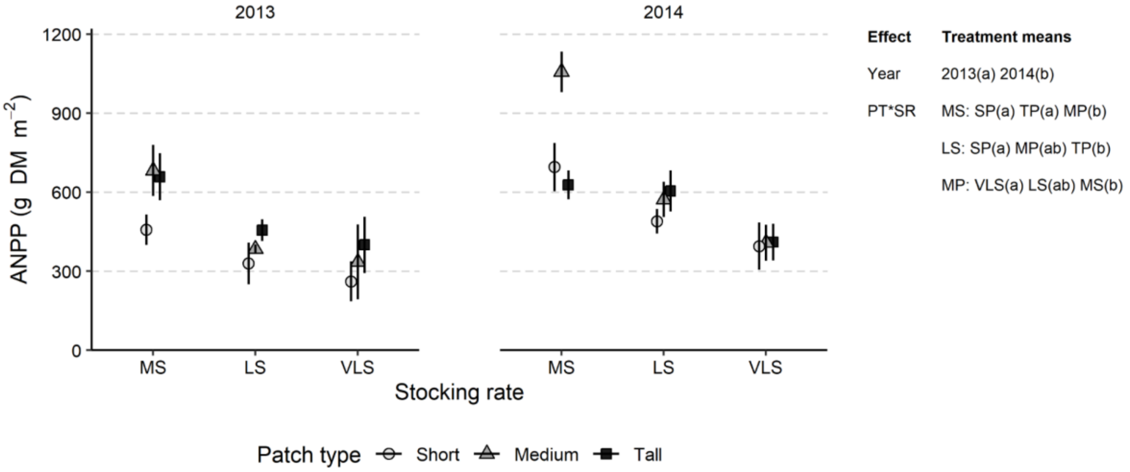


Figure 1. Aboveground net primary productivity of different patch types (short, medium and tall) under different stocking rates (moderate, lenient and very lenient stocking). Shown are means and standard errors (SEM) of three replications. Different letters designate significant differences (method: Tukey, $P < 0.05$) between treatment means of one factor within factor levels of an interacting factor. Abbreviations: MS Moderate stocking, MP Medium patch, LS Lenient stocking, PT Patch type, SR Stocking rate, VLS Very lenient stocking.

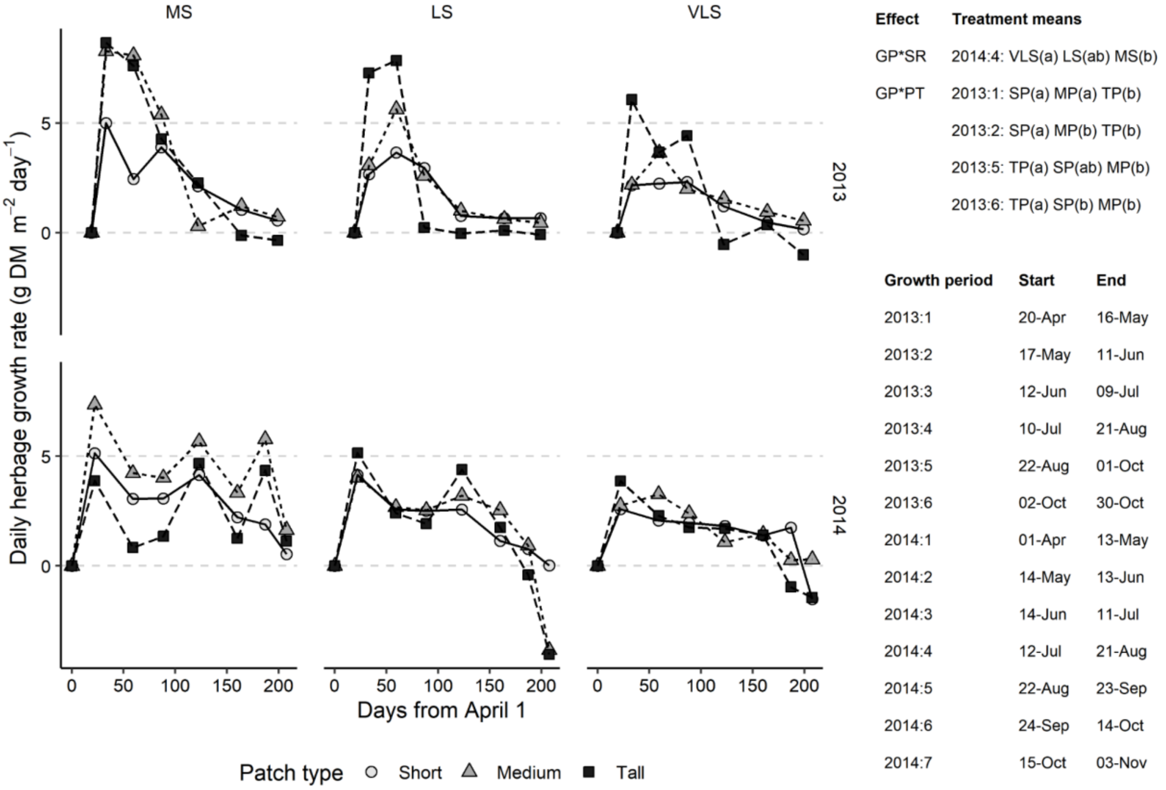
Table 2. Results of marginal Wald tests for the linear mixed effects models for aboveground net primary productivity (ANPP), daily herbage growth rates (DHGR), the date at which half of the annual biomass is produced ($t_{0.5\ ANPP}$), topsoil (0–10 cm) phosphorus (P), potassium (K) and magnesium (Mg) stocks as well as topsoil pH

Response variable	**Predictor**	**Degrees of freedom**		***F* value**	***P* value**
		num	*den*		
ANPP	Y	1	38	51.3	**<0.001**
	PT	2	38	6.2	**0.0046**
	SR	2	4	8.8	**0.0342**
	PT*SR	4	38	2.9	**0.0329**
DHGR	GP	12	280	44.3	**<0.001**
	PT	2	280	1.5	0.2306
	SR	2	4	6.6	0.0538
	GP*PT	24	280	2.4	**<0.001**
	GP*SR	24	280	2.1	**0.0032**
$t_{0.5\ ANPP}$	Y	1	38	10.1	**0.0030**
	PT	2	38	4.2	**0.0229**
	SR	2	4	2.3	0.2168
	Y*PT	2	38	6.3	**0.0043**
	Y*SR	2	38	3.1	0.0557
P	PT	2	12	18.6	**<0.001**
	SR	2	4	1.1	0.4138
	PT*SR	4	12	13.3	**<0.001**
K	PT	2	16	24.7	**<0.001**
	SR	2	4	6.0	0.0625
Mg	Intercept	1	18	1,030.8	**<.0001**
pH	Intercept	1	18	2177.0	**<.0001**

Note Effects and interactions not shown were not retained in the final model. Abbrevations: Y, year; PT, patch type; SR, stocking rate; GP, growth period. Values shown in bold print denote statistical significance at the $p < .05$ level.

Temporal distribution of ANPP

Daily herbage growth rates varied between growth periods in interaction with both patch type and stocking rate (Table 2). In the first two growth periods of 2013, tall patches had more than two times higher daily herbage growth rates than short patches. By contrast, during growth periods five and six in autumn, their daily herbage growth rates were less than those of medium and short patches, respectively (Figure 2). In 2014, patch types did not significantly differ in daily herbage growth rates, but across patch types, MS had significantly higher daily herbage growth rates compared to VLS in late summer (4.8 g $m^{-2}d^{-1}$ versus 1.8 g $m^{-2}d^{-1}$).



Effect	Treatment means
GP*SR	2014:4: VLS(a) LS(ab) MS(b)
GP*PT	2013:1: SP(a) MP(a) TP(b)
	2013:2: SP(a) MP(b) TP(b)
	2013:5: TP(a) SP(ab) MP(b)
	2013:6: TP(a) SP(b) MP(b)

Growth period	Start	End
2013:1	20-Apr	16-May
2013:2	17-May	11-Jun
2013:3	12-Jun	09-Jul
2013:4	10-Jul	21-Aug
2013:5	22-Aug	01-Oct
2013:6	02-Oct	30-Oct
2014:1	01-Apr	13-May
2014:2	14-May	13-Jun
2014:3	14-Jun	11-Jul
2014:4	12-Jul	21-Aug
2014:5	22-Aug	23-Sep
2014:6	24-Sep	14-Oct
2014:7	15-Oct	03-Nov

Figure 2. Daily herbage growth rates of different patch types (short, medium and tall) under different stocking rates (moderate, lenient and very lenient stocking) in 2013 and 2014. Shown are means of three replications. Treatment means for relevant significant effects were compared within a factor level when involved in an interaction (method: Tukey, $P < 0.05$). Significant differences between growth periods are not listed. Abbreviations: MS Moderate stocking, MP Medium patch, LS Lenient stocking, PT Patch type, SP Short patch, SR Stocking rate, TP Tall patch, VLS Very lenient stocking.

Both year and patch type affected $t_{0.5ANPP}$, the mean date at which half of the total biomass was produced (Table 2). This date differed between patch types in 2013, when tall patches reached $t_{0.5ANPP}$ 19 and 14 days earlier than short and medium patches (Figure 3). Both medium and tall patches reached $t_{0.5ANPP}$ 14 and 25 days later in 2014 than in 2013, respectively.

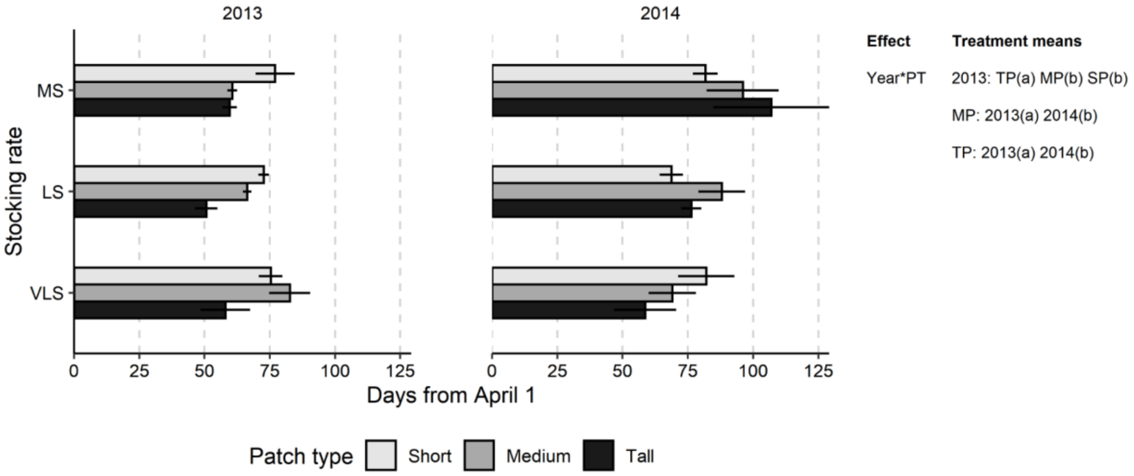
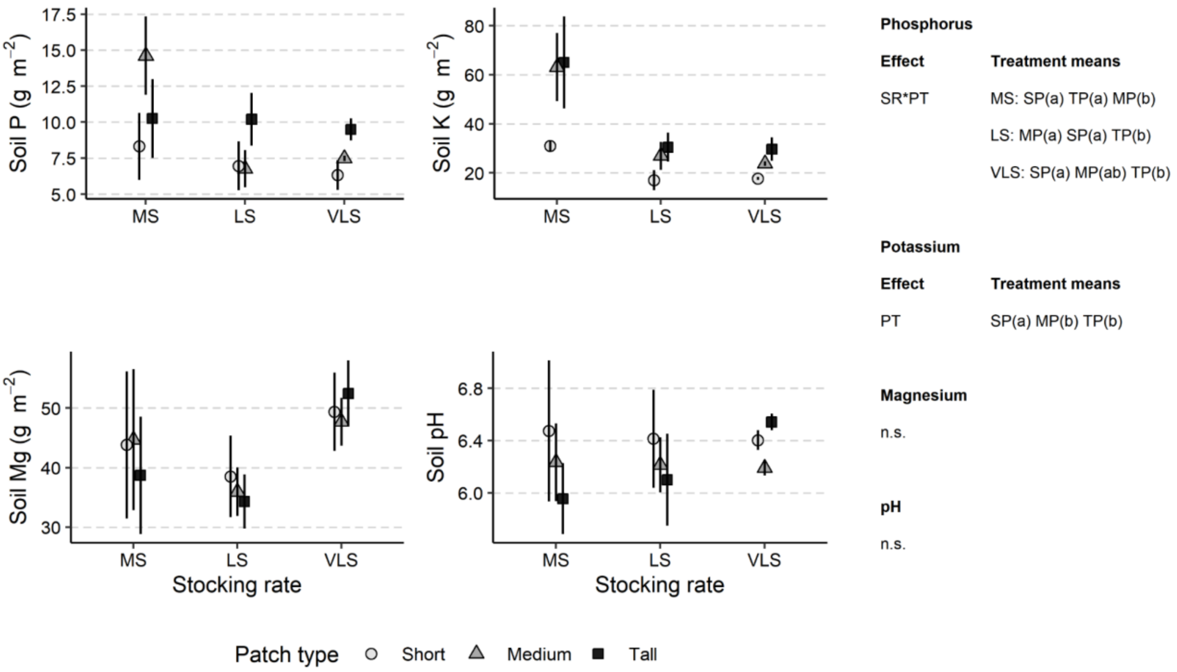


Figure 3. Dates at which half of the annual aboveground net primary productivity of different patch types (short, medium and tall) was reached ($t_{0.5ANPP}$) under different stocking rates (moderate, lenient and very lenient stocking). Shown are means and standard errors (SEM) of three replications. Different letters designate significant differences (method: Tukey, $P < 0.05$) between treatment means of one factor within factor levels of an interacting factor. Abbreviations: MS Moderate stocking, MP Medium patch, LS Lenient stocking, PT Patch type, TP Tall patch, VLS Very lenient stocking.

Topsoil nutrient stocks and pH

Topsoil phosphorus stocks were interactively affected by patch type and stocking rate (Table 2). Under LS and VLS, soil phosphorus stocks in short patches were 31.8 and 33.4% smaller than those in tall patches, respectively (Figure 4). Under MS, phosphorus stocks in medium patches were 75.7 and 42.5% higher than those of both short and tall patches, respectively. Topsoil potassium stocks differed between patch types (Table 2). Potassium stocks in short patches were 42.4 and 47.6% smaller than those of both medium and tall patches, respectively (Figure 4). Neither topsoil magnesium stocks nor soil pH were influenced by patch type or stocking rate.



Phosphorus

Effect	Treatment means
SR*PT	MS: SP(a) TP(a) MP(b)
	LS: MP(a) SP(a) TP(b)
	VLS: SP(a) MP(ab) TP(b)

Potassium

Effect	Treatment means
PT	SP(a) MP(b) TP(b)

Magnesium

n.s.

pH

n.s.

Figure 4. Stocks of soil phosphorus (P), potassium (K), and magnesium (g m^{-2}, 0-10 cm) as well as pH-values of different patch types (short, medium and tall) under different stocking rates (moderate, lenient and very lenient stocking). Shown are means and standard errors (SEM) of three replications. Different letters designate significant differences (method: Tukey, $P < 0.05$) between treatment means of one factor within factor levels of an interacting factor. Abbreviations: MS Moderate stocking, MP Medium patch, LS Lenient stocking, PT Patch type, SR Stocking rate, TP Tall patch, VLS Very lenient stocking.

Discussion

Effect of patch type on ANPP

Under LS, we found higher ANPP in tall than in short patches confirming hypothesis I, while under MS, both short and tall patches were less productive than medium patches. This contrasts with results from the beginning of this 12-year grazing experiment, when Şahin Demirbağ et al. (2009) found higher ANPP in defoliated short patches compared to non-defoliated tall patches. While defoliation can indeed increase productivity (Hilbert et al., 1981, this depends on a steady soil nutrient uptake by plants for regrowth (Jaramillo & Detling, 1988). Defoliation and resource availability thus interact in their effects on ANPP (Ferraro et al., 2002).

Animal-mediated soil nutrient redistribution may explain why short patches failed to respond with increased productivity to frequent defoliation after long-term low-intensity grazing. We found both soil phosphorus and potassium stocks to be lower in short than in tall patches (Figure 4). By contrast, pH and soil Mg stocks, which are less affected by animal-mediated nutrient cycling, differed neither between patch types nor stocking rates (Table 2, Figure 4). This indicates that the patterns observed in soil phosphorus and potassium stocks result from the expected soil nutrient redistribution from short to tall patches driven by patch grazing over the years. In line with our results, Jewell et al. (2007) and Koch et al. (2018) found that phosphorus was redistributed from grazed to non-grazed areas on heterogeneous mountain pastures because cattle discriminated between areas used for feeding and areas used for ruminating. Uytvanck et al. (2009) likewise found a net nitrogen transport from pasture, the preferred grazing habitat, to forest in a mosaic landscape grazed by cattle. Kohler et al. (2006) moreover observed that defecation mainly appears directly after resting, so that rest areas receive a large amount of excreta, which contributes to the soil nutrient redistribution on pastures (Auerswald et al., 2010; Schnyder et al. 2010). On the other hand, Pavlů et al. (2019) detected no differences in extractable topsoil phosphorus or potassium between short and tall patches in a 15-year-old cattle grazing experiment with pronounced patch-grazing patterns.

Besides soil nutrients, water may be another resource that is less available in short than in tall patches. Due to a comparatively low sward leaf area index and larger proportions of bare ground, evaporation in short patches is increased (Veldhuis et al., 2014), while at the same time frequent defoliation quickly reduces the root growth rates (Evans, 1971) and leads to decreased rooting depth (Schuster, 1964). Moreover, the leaf area index may decrease to a level at which sward photosynthetic capacity is decreased. However, both grazing-induced changes in the plant-soil water balance (Veldhuis et al., 2014) and low leaf area index in short patches can be assumed to have been similarly present in the beginning of the experiment, when ANPP had not been lower than in tall patches.

Finally, differences in defoliation regime and resource availability may lead to diverging floristic development between the patch types, which in turn can affect productivity. Rossignol et al. (2011) described a correlation between the floristic composition of the different sward height patches and their productivity. Under nutrient-rich, humid conditions, short patch vegetation is generally composed of grazing-tolerant plant species with a high shoot to root ratio and a high regrowth capacity (Briske, 1996; Bullock et al., 2001; Evju et al., 2009). Those species are known to show positive responses to defoliation (Milchunas et al., 1988). Under nutrient-poor conditions, grazing often favours defoliation-resistant plant species that avoid tissue loss by structural defences such as a small-statured architecture, unpalatability or increased leaf toughness (Evju et al., 2009; Quétier et al., 2007). Over the long term, a decrease in soil nutrient availability may therefore reduce the proportion of grazing-tolerant species in frequently grazed short patches (Pakeman, 2004; Rossignol et al., 2011). At our experimental site, Perotti et al. (unpublished) compared community weighted means of strategy components according to Grime's triangular CSR model (competitiveness, stress tolerance, ruderality; Grime et al., 2001). They found lower values for competitiveness and higher values for stress tolerance and ruderality in short compared to tall patches. Plant species following a stress-tolerating strategy show comparatively low growth rates but allocate resources to maintenance and defence to survive in unproductive habitats. These are also traits displayed by grazing-avoiding species in response to herbivory at nutrient-limited sites. Thus, we may expect that in the present experiment, the cattle grazing management applied since 2002 has caused permanent stress in the forms of both frequent defoliation and decreasing soil nutrient availability in short patches and has increased the proportion of slow-growing species in short patches, contributing to the comparatively lower ANPP than in earlier years of the experiment.

Seasonal biomass growth in patches

Due to the frequent defoliation in short patches, we expected ANPP to be distributed more evenly over the grazing season in this patch type than in the less frequently defoliated medium and tall patches (hypothesis II). Unexpectedly, this was only the case in 2013 (Figure 3).

In both years, all three patch types showed the highest daily herbage growth rates in spring with lower values in summer and autumn (Figure 2). This pattern is in line with the results from the beginning of this 12-year experiment (Şahin Demirbağ et al., 2009) and is common for temperate pastures. Reproductive growth occurs in spring and early summer. From then on, shoot growth is decreased by reserve storage and root growth (Bausenwein et al., 2001). Besides plant development, resource availability plays a role in shaping the annual herbage growth rate curve, with both water and nutrient availability varying within and between years.

In 2013, precipitation was very low from the middle of June until October (Table 1). Low soil moisture appears to have slowed down herbage growth rates during that time. However, tall patches had been very productive during a relatively short time in spring. Accumulation of senescent plant material (Correll et al., 2003; Şahin Demirbağ et al., 2009) might have further limited ANPP in these patches later in the season by shading the green plant material. Compared to tall patches, medium and short patches had a less pronounced growth peak in spring. This can be explained both by a smaller supply of nutrients caused by nutrient redistribution and by a larger proportion of the stress-tolerance component among the plant species, which is associated with lower overall productivity and may also affect phenology and seasonal distribution of biomass growth. Later in the season, herbage growth rates decreased less strongly than in tall patches, lending support to our hypothesis that frequent defoliation stimulates regrowth throughout the season.

In comparison with 2013, the period of mid-June to end of September 2014 was much wetter, with 2.5 times the precipitation (Table 1). Presumably, this increased water availability permitted relatively high daily herbage growth rates through summer and early autumn, particularly for medium and tall patches. Additionally, the early-season growth peak of tall and medium patches was shorter and less pronounced in 2014 than in 2013, while herbage growth rates of short patches during that season did not differ between years. This shows that patch types do not only differ in ANPP but also react to annual variations of growing conditions in a complex and patch-specific way.

Influence of stocking rate

We hypothesized that accelerated nutrient cycling (Boddey et al., 2004) and more homogeneous nutrient distribution (Peterson and Gerrish, 1996) would lead to an increase of ANPP with increasing stocking rate (hypothesis III). Deviating from this hypothesis, increased stocking enhanced ANPP only in medium patches. Under the highest stocking rate, MS, these patches were also more productive than both short and tall patches.

Interactions of post-defoliation leaf area and soil nutrient availability are likely to have enhanced ANPP in patches of medium sward height under increased stocking. With increasing stocking rate, the proportion of frequently defoliated short patches increases (Cid & Brizuela, 1998; Dumont et al., 2007; Ludvíková et al., 2015; Tonn et al., 2019), and tall patches in our experimental area became less stable (Tonn et al., 2019). It thus becomes more likely that medium patches we sampled represent former tall patches subjected to defoliation when herbage supply becomes limited. Additionally, medium patches may also develop in the vicinity of dung patches that is not yet grazed to the usual biting depth (MacDiarmid & Watkin, 1972; Scheile et al., 2018). As the number of excreta patches also increases with stocking rate, the proportion of such areas among the sampled medium patches might also have increased with stocking rate. This latter would be in line with the fact that under MS, we found the highest phosphorus stocks in the medium, rather than the tall patch type. An intermediate defoliation intensity that decreases mean tissue age and reduces self-shading but leaves sufficient leaf area for optimum light interception, together with comparatively higher nutrient supply, may have enhanced plant productivity in such medium patches.

In addition to increased productivity of medium patches, we found a trend ($p = 0.0625$) towards increased potassium stocks with increased stocking rate, which matches the results of Wrage et al. (2012) from the same experimental site a few years earlier. High amounts of easily plant-available potassium, as well as nitrogen, are returned in urine patches (Haynes & Williams, 1993), indicating that more homogeneous excreta return under increased stocking rate may be responsible for this result.

Consequences and lessons for grassland management

Patch grazing creates sward mosaic structures that are stable over several years (Tonn et al., 2019) and therefore induces changes in soil nutrient distribution (Figure 4) and vegetation composition (Tonn et al., 2019) causing both ecological and agronomic consequences.

In contrast to the beneficial effect of defoliation on plant productivity over the short term, long-term grazing reduces ANPP in short patches (Figure 1), the predominant feeding areas.

Nevertheless, ANPP of such grazing systems may reach a certain equilibrium once the plant species composition in short patches is adapted to prevailing growing conditions, because the higher proportion of stress-tolerator components in the short patch vegetation reduces the risk of a further soil nutrient decline as those species focus on nutrient conservation (Grime, 2001). The stabilization of the mosaic pattern (Tonn et al., 2019) implies that short patch vegetation is composed of palatable plant species that may provide fodder of at least adequate quality. Medium and tall patches, however, can represent an important fodder resource and may become particularly relevant in periods of low sward productivity. The temporal distribution of biomass productivity can be highly variable, which makes it difficult to apply a fixed stocking rate throughout the season.

Conclusions

In our study, results on ANPP and spatial distribution of soil nutrients on low-input cattle pastures revealed long-term processes induced by patch grazing. To gain a better understanding of the underlying mechanisms, we therefore recommend conducting long-term investigations on the relationships between sward heterogeneity, vegetation composition turnover, plant nutrient composition as well as herbage nutritive value in heterogeneous pastures.

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CHAPTER II: HERBAGE PRODUCTION AND UTILIZATION ACROSS A STOCKING RATE GRADIENT AFTER 12 YEARS OF LOW-INTENSITY CATTLE GRAZING

Dorothee Ebeling, Bettina Tonn, Johannes Isselstein

Abstract

Due to their structural heterogeneity, low-input pastures are agroecosystems targeting both agronomic production and ecological benefits. Patch grazing creates and sustains a spatially and temporally stable mosaic of patch types varying in within-paddock grazing intensity. Frequently defoliated short patches are similar or even less productive than tall patches. At the paddock scale, increased stocking enlarges the area of frequently defoliated, less productive patches on the pasture, while at the same time plant growth and herbage quality may benefit from an accelerated soil nutrient cycling. The aim of the present study was to investigate the effect of stocking rate on productivity and utilization of herbage after 12 years of low-intensity, continuous cattle grazing. Results showed that with stocking rate and herbage intake, both herbage production and herbage utilization increased. Patch types contributed differently to total herbage production in paddock as proportions of the different patch types changed with increasing stocking rate. Our results indicate the relevance of stocking rate for herbage productivity of long-term low-input pastures.

Keywords: Low-intensity grazing, herbage production, herbage utilization, patch types, herbage intake

Introduction

Low-input pastures are agro-ecosystems targeting both agronomic production and ecological benefits (Isselstein et al., 2005). Extensive grazing has the potential to reduce biodiversity losses (Marriott *et al.*, 2004; Metera *et al.*, 2010; Rook *et al.*, 2004; Wrage *et al.*, 2011b) as under sufficiently low stocking rates, grazers create a temporally and spatially stable mosaic structure (Tonn *et al.*, 2019; Willms *et al.*, 1988) composed of patches differing in sward height (Adler *et al.*, 2001; Cid & Brizuela, 1998; Parsons & Dumont, 2003).

Patch types represent local areas differing in within-paddock grazing intensity (Tonn et al., 2019). Short patches are maintained by a frequent defoliation of regrowth. Their attractiveness to herbivores is based on the young, high-quality plant material they provide throughout the grazing season (Hempson et al., 2014; WallisDeVries et al., 1999). Tall patches, in contrast, are largely neglected and therefore often reach ceiling yield (Lemaire et al., 2000). They show comparatively high levels of standing biomass (Correll et al., 2003) and litter (Şahin Demirbağ et al., 2008).

Whereas short patches represent the main feeding stations of low-input pastures, tall patches are of minor relevance for the agronomic production of the grazing system, and they may even lower pasture utilization (Chapman et al., 2007). From an ecological point of view, however, biomass productivity in tall patches is of central importance for the system's carbon sequestration potential (Golluscio et al., 2009; Senapati et al., 2014) as the tall-grown vegetation can represent high carbon mass (Smith et al., 2014), and their low-degradable plant biomass has a comparatively long residence time in soil (Rossignol et al., 2011a).

Herbage growth of low-input pastures stays in contrast to that of intensively managed, homogeneous swards (Parsons & Chapman, 2000) as primary productivity differs between the frequently defoliated, short patches and the rarely defoliated, tall patches (Cid et al., 2008), both shortly after grazing introduction (Şahin Demirbağ et al., 2009) as well as after several years of low-intensity grazing (Ebeling et al., 2020). A short-term effect of grazing is the stimulation of herbage growth via defoliation (Hilbert et al., 1981), which is why short patches are known to be more productive than tall patches (Cid et al., 2008; Rossignol et al., 2011b), Şahin Demirbağ *et al.* (2009). However, within the stable sward mosaic the pattern of defoliation, i.e., the pattern of soil nutrient uptake, differs from the pattern of defecation and urination, i.e., the pattern of soil nutrient return (Auerswald et al., 2010). Over the long term, therefore, frequent soil nutrient translocations from defoliated patches to rarely defoliated patches (Ebeling et al., 2020; Schnyder et al., 2010) cause a disparity in soil nutrient status between patch types. Subsequently, short patches become similar or even less productive than tall patches (Ebeling et al., 2020; Rossignol et al., 2011b), where, additionally, shoot plasticity (da Silveira Pontes, Laíse et al., 2010) and shifts in vegetation composition may further lower productivity in short patches (Rossignol et al., 2011b). Thus, at the patch scale, herbage production relevant for agronomic production is reduced, while that for carbon sequestration may be increased.

At the paddock scale, stocking rate maintains the areal proportions of the different patch types (Tonn et al., 2019), where the frequently defoliated area enlarges and the rarely defoliated area decreases with stocking rate (Cid et al., 2008; Dumont et al., 2007; Ludvíková et al., 2015; Peterson & Gerrish, 1996; Rossignol et al., 2011c; Tonn et al., 2019). Consequently, both plant growth for agricultural production and plant growth for carbon sequestration should be reduced under increased stocking. However, on low-input pastures stocking rate is a major driver of soil nutrient cycling as the adjustment of grazers strongly modifies nutrient pathways (Boddey et al., 2004; Haynes & Williams, 1993; Thomas, 1992). With stocking rate, herbage intake per paddock increases (Parsons & Dumont, 2003), and so does the amount of soil nutrients that is pathing the herbivore (Boddey et al., 2004; Thomas, 1992). Therefore, soil nutrient cycling is accelerated, and nutrients become more easily available for plant growth under increased stocking (Auerswald *et al.*, 2010; Haynes & Williams, 1993). Also, both the spatially and temporally utilization of the sward (Hirata, 2002; Ludvíková et al., 2015) as well as the return of nutrients to the soil via excrements occur more homogenously under increased stocking (Haynes & Williams; Peterson & Gerrish, 1996), which results in a more efficient soil nutrient cycling.

Soil fertility sustains a fast regrowth after defoliation (Niu et al., 2016) that are characterized by both large regrowth capacity and high-quality plant tissue, sustaining a comparatively higher herbage quality of the frequently defoliated vegetation than under reduced stocking. On low-input pastures, therefore, comparatively high stocking rates could lead to a ‘win-win’ situation as with increased fodder quality, less biomass is needed to meet each animal’s energy requirements and thus, biomass growth for carbon sequestration increases. On the contrary, however, high-quality litter is more easily degradable (Soussana & Lemaire, 2014), wherefore carbon sequestration within the system may be limited.

Overall, due to the influence of stocking rate on patch formation, soil nutrient cycling and plant-animal interactions, scaling up plant productivity from patch to paddock can be misleading when evaluating the agronomic and ecological potential of a grazing system. We therefore analysed the influence of stocking rate on herbage productivity, herbage intake and herbage utilization on a 12-year low-intensity cattle grazing experiment, answering the following questions: As stocking rate, and therefore herbage intake, increase, does total herbage production decrease or increase? What proportion of herbage is ingested, and what proportion remains on site, over a gradient of stocking rates?

Material and methods

Study site

The experimental pasture was located in Relliehausen, Lower Saxony, Germany (51°46’N, 9°42’E, 250 m a.s.l.). Between 2002-2014, mean annual temperature of the site was 8.8 °C (meteorological station: Moringen-Lutterbeck, , Deutscher Wetterdienst, DWD). Annual accumulated precipitation was 816 mm (meteorological stations: Moringen-Lutterbeck, 2002-2010, Dassel, 2011-2014, DWD). In the experimental years 2013 and 2014 annual precipitation was 673 and 892 mm and mean temperature was 8.4°C and 10.0°C. According to (IUSS Working Group WRB, 2006), the soil is a vertic cambisol. The vegetation is a moderately species-rich, old permanent grassland classified as a *Lolio-Cynosuretum,* with Lolium perenne, Trifolium repens, Taraxacum sect. Ruderale, Dactylis glomerata, Ranunculus repens and Agrostis stolonifera found as main species (Wrage et al., 2012). More detailed information about the study site is published in Isselstein et al. (2007).

Grazing experiment

The grazing experiment was set up in spring 2002, comparing three stocking treatments arranged in a randomized block design with three replications comprising nine paddocks of 1 ha each in total. Since 2005, all paddocks have been grazed by non-lactating adult Simmental suckler cows at three different stocking rates.

As stocking rate alters average sward height (Isselstein et al. 2007), mean target sward heights in paddock were used as proxies to define stocking rates: moderate, lenient and very lenient stocking at 6, 12 and 18 cm mean target compressed sward height (CSH, Castle, 1976; Correll et al., 2003). To keep these target heights constant, we performed 50 rising-plate-meter measurements each in a two-week interval and adjusted the animal numbers in a put-and-take system (continuous variable stocking). During the years 2013 and 2014, target sward heights were equivalent to stocking rates of 607 (1.2), 342 (0.7) and 221 (0.4) kg (LU, livestock unit, 500 kg live weight) ha^{-1} a^{-1}. In 2013 and 2014, we used the lower, the middle and the upper third of the biweekly sward height measurements as sward height class thresholds, defining a 'short', a 'medium' and a 'tall' patch type. Mean sward height class thresholds were 5.9 and 8.6 (short to medium) and 11.9 and 14.1 (medium to tall), on average for 2013 and 2014.

In the first two years of the study (2002-2004), the grazing experiment had been run with a moderate and a lenient stocking variant grazed by growing Simmental steers, and another lenient stocking variant grazed by growing German Angus steers (see Isselstein et al., 2007), which in 2005 was turned into the very lenient stocking variant. An overview of stocking data according to mean target sward heights in paddock is published in Jerrentrup et al. (2014). Detailed information about the sward height pattern of the pasture over the long-term is published in Tonn et al. (2019). Before the set-up of the experiment in 2002, the entire pasture area had been treated uniformly with moderate fertilizer applications and stocking rates as well as regular cutting.

Table 1. Stocking rates (kg ha^{-1} a^{-1}) and areal proportions of patch types, on average for 2013 and 2014.

Variant	Stocking rate	Proportion of patch type	
		Short	Tall
Moderate	607	0.60	0.15
Lenient	342	0.31	0.36
Very lenient	220	0.17	0.59

Field sampling

Biomass sampling

To estimate standing biomass, we did calibration cuts in a double-sampling technique. At five dates during the vegetation period (April, May, July, September and October), we randomly chose two randomly located permanent plots (Wrage et al., 2012) per paddock, in whose proximity we selected a short, a medium and a tall patch type, respectively. With a rising-plate meter, we measured compressed sward height (CSH, Castle, 1976; Correll et al., 2003) in a square frame of 0.25 m² in size and subsequently cut the aboveground biomass within the square frame to 1 cm above ground level, respectively. We dried the collected herbage for two days at 60°C and afterwards weighted the dry matter, respectively.

To calculate annually accumulated herbage growth in patch types, we also applied a non-destructive method using replaceable grazing exclusion cages (Şahin Demirbağ et al., 2009). Therefore, we split the vegetation period into growth periods, comprising six periods in 2013 (April to October) and seven periods in 2014 (April to November). The length of each growth period was adapted to the seasonal biomass productivity, i.e., shorter periods in times of high biomass productivity and vice versa. We randomly replaced one exclusion cage per patch type, paddock, and growth period throughout the paddock area, respectively in 2013 and 2014. In both years, we set the first and the last growth period before and after the grazing season. Within the exclusion cage, we measured CSH before and after each growth period at two square frames, each with a size of 0.25 m².

Herbage intake

To calculate herbage dry matter intake, we considered the cattle's energy requirements as well as the metabolizable energy content of the herbage taken in using the dung-N method (Schmidt *et al.*, 1999).

To calculate energy requirements, we weighed each animal before and after the grazing season, respectively in 2013 and 2014. On this basis, we used quadratic regressions to calculate daily live weight gains per cow and per paddock. We calculated the energy requirements per paddock according to Baker (2004) as done in Wrage *et al.*, 2011a.

To obtain herbage quality, we took dung samples at three times during grazing season, respectively in 2013 (June, July, October) and 2014 (May, July, October). Due to the adjustment of animal numbers to seasonal herbage growth, in October 2013 and July 2014 we could take dung samples only from the moderate stocking variant. We dried the dung samples for two days at 60° C, homogenised them via grinding to powder (0.25 mm) and analysed the material for carbon and nitrogen via elemental analysis (weighed portions of 16-18 mg, CN Elemental Analyser, type vario EL, Elementar Analysensysteme GmbH, 63452 Hanau, Germany).

Calculation of herbage productivity

For all calculations, we used R 3.2.3 (R Core Team, 2015). We set up a generalized least squares model fit with restricted maximum likelihood estimation that predicted standing biomass from a given CSH for each combination of sward height, treatment, block and cutting date. We ascertained the optimal random part of the model on regression coefficients of harvested and predicted herbage dry matter and implemented a power variance function structure for CSH to consider the heterogeneity of the data set. We applied 'Akaike Information Criterion' (AIC, Akaike 1973) comparisons with maximum likelihood estimation to simplify the calibration model. The full model included the fixed factors 'CSH', 'cutting date', 'block', 'stocking rate' and their interactions. The final model retained the factors 'CSH' + 'cutting date' + 'block', 'stocking rate' and the interactions 'CSH x cutting date', 'CSH x block x stocking rate' and their marginal effects.

We calculated herbage growth as the difference between standing herbage at the beginning and at the end of each growth period. For one exclusion cage (MG, 2014:6), we had to predict herbage growth via a linear model as the cage was destroyed by cattle.

We calculated daily herbage growth rates for each patch type within growth periods by dividing the amounts of herbage grown by the number of days of each growth period. To assess the accumulation of daily herbage growth for the entire paddock, we set negative daily herbage growth rates of patch types to zero and multiplied daily herbage growth rates in patches with the area percentages of the patch types in paddock.

Statistical analyses

For all calculations and statistical analyses, we used R 3.2.3 (R Core Team, 2015). We applied linear mixed effects models (R package 'nlme', Pinheiro et al., 2015) to analyse the single and interactive effects of stocking rate (moderate, lenient, very lenient) and year (2013, 2014) on the annual herbage productivity, herbage intake, herbage utilization as well as on contributions of herbage productivity of short, medium and tall patches to that of the entire paddock, respectively.

To account for the nested design of the experiment, we set the random factor 'paddock' as nested in the random factor 'block'.

We performed the model selection and validation processes as recommended in Zuur et al. (2009) and used restricted maximum likelihood estimations (REML, package 'nlme', Pinheiro et al., 2015) to set the optimal random model structure, choosing the best model via AIC. We then verified homogeneity via Levene's test and normality via Shapiro–Wilk test. If heterogeneity of residual variance appeared, we implemented variance structures into the model (package 'nlme', Pinheiro et al., 2015).

To set each model's optimal fixed structure, we used maximum likelihood estimation and chose the best model via 'Second-order Akaike Information Criterion' (AICc, package 'MuMIn', Barton, 2016). We then re-fit each final model with REML and validated visually via data exploration. We analysed differences between means via Tukey post-hoc tests (implemented in the R package 'lsmeans'; Lenth, 2016), in case marginal Wald tests indicated significant fixed effects.

The full model for the analysis of herbage intake included a 'varIdent' variance function structure for the group 'stocking rate'. The full model for the analysis of the proportion of herbage taken in included a 'varExp' variance function structure.

Results

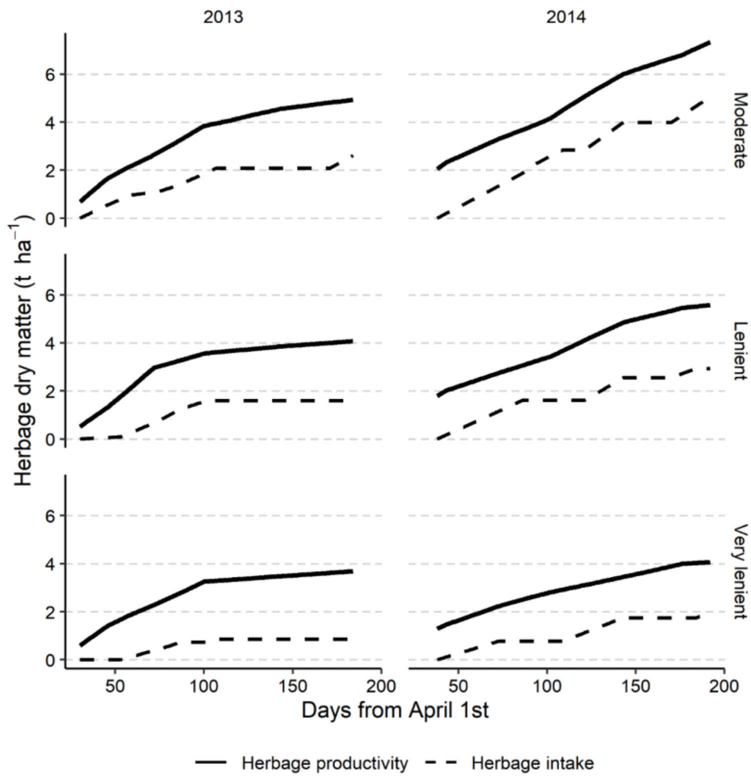
Herbage productivity, intake and utilization

Herbage productivity, herbage intake and herbage utilization differed between stocking rates and years (Table 2, Figure 1). Across years, herbage productivity ± SE was significantly higher under moderate (6.4 ± 0.7 t ha^{-1}) than under very lenient (3.9 ± 0.7 t ha^{-1}) stocking. Lenient stocking had an intermediate position and did not differ from the other two stocking rates (4.9 ± 0.5 t ha^{-1}). Herbage intake differed significantly between all three stocking rates and increased from very lenient (1.4 ± 0.2 t ha^{-1}) to lenient (2.3 ± 0.3 t ha^{-1}) and from lenient to moderate (3.8 ± 0.6 t ha^{-1}) stocking. Herbage utilization was significantly higher under moderate (58.5%) than under lenient (45.8%) or very lenient (39.2%) stocking. Across stocking rates, both herbage productivity (4.3 ± 0.4 vs. 5.8 ± 0.6 t ha^{-1}) and herbage intake (1.7 ± 0.3 vs. 3.3 ± 0.5 t ha^{-1}) were higher in 2014. Pasture utilization also increased from 2013 (39.3%) to 2014 (56.4%).

Table 2. Results of the linear mixed effects models for herbage productivity, herbage intake, and the proportion of herbage utilization in three different patch types and under three different stocking rates in 2013 and 2014.

Response variable	**Predictor**	**Degrees of freedom**		***F* value**	***P* value**
		num	den		
Herbage productivity	SR	2	12	6.7	**0.0110**
	Year	1	12	7.3	**0.0191**
Herbage intake	SR	2	12	84.1	**<0.001**
	Year	1	12	1,440.0	**<0.001**
Herbage utilization	SR	2	4	15.1	**0.0137**
	Year	1	8	50.4	**<0.001**
Contribution of short patch	SR	2	12	33.7	**<0.001**
Productivity to that of paddock	Year	1	12	0.3	0.5851
Contribution of medium patch	SR	2	12	10.1	**0.0026**
productivity to that of paddock	Year	1	12	9.8	**0.0086**
Contribution of tall patch	SR	2	12	127.8	**<0.001**
productivity to that of paddock	Year	1	12	6.2	**0.0282**

Note Fixed effects and their interactions that are not shown were not retained in the final model. Abbreviations: PT Patch type, SR Stocking rate, YD Year*Date (combination of the factors 'year' and 'date'). Values shown in bold print denote statistical significance at the $p < .05$ level.



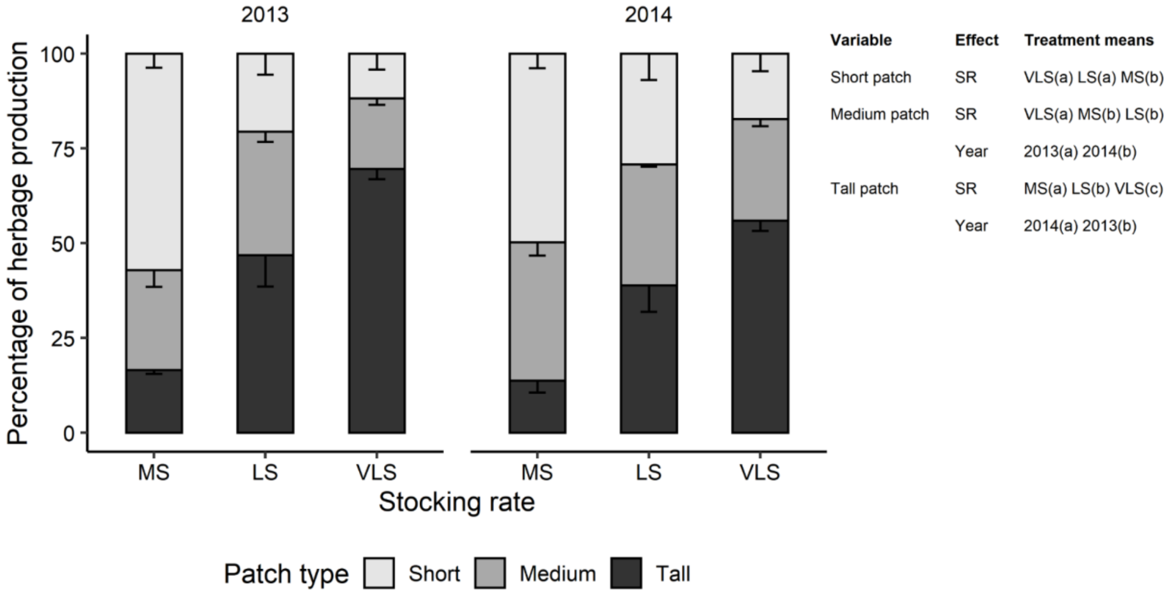
Variable	Effect	Treatment means
Herbage productivity	SR	VLS(a) LS(ab) MS(b)
	Year	2013(a) 2014(b)
Herbage intake	SR	VLS(a) LS(ab) MS(b)
	Year	2013(a) 2014(b)
Herbage utilization	SR	VLS(a) LS(a) MS(b)
	Year	2013(a) 2014(b)

Figure 1. Cumulative herbage growth and cumulative herbage intake by cattle from April 1st in 2013 and 2014 under three different stocking rates (moderate, lenient, very lenient). Sections of cumulative herbage intake without slope illustrate non-grazing periods during the season. Shown are means of three replications.

Contribution of patch productivity to that of paddock

Contributions of patch types to herbage production per paddock was significantly affected by stocking rate for all three patch types. Both contribution of medium patch productivity and contribution of tall patch productivity to that of paddock moreover differed between years (Table 2, Figure 2). Across years, the contribution in short-patch productivity to that of paddock increased from lenient (14.5%) and very lenient stocking (24.8%) to moderate stocking (53.4%), with moderate stocking differing significantly from the other two stocking variants.

The contribution of medium-patch productivity to that of paddock under very lenient stocking (22.6%) differed significantly between that under moderate (31.5%) and lenient stocking (32.3%). The contribution of tall-patch productivity to that of paddock significantly increased from moderate stocking (15.1%) to lenient stocking (42.9%) and from lenient stocking to very lenient stocking (62.8%). Across stocking rates, the contribution of medium patch productivity to that of paddock (25.8 vs. 31.7%) significantly increased from 2013 to 2014, whereas that of the tall patch types (36.2 vs. 44.4%) decreased.



Variable	Effect	Treatment means
Short patch	SR	VLS(a) LS(a) MS(b)
Medium patch	SR	VLS(a) MS(b) LS(b)
	Year	2013(a) 2014(b)
Tall patch	SR	MS(a) LS(b) VLS(c)
	Year	2014(a) 2013(b)

Figure 2. Percentages of herbage production to total annual herbage production per paddock contributed by short, medium and tall patches and herbage utilization under moderate (MS), lenient (LS) and very lenient stocking (VLS) in 2013 and 2014. Shown are means and standard errors of three replications.

Discussion

The aim of the present study was to investigate the effect of stocking rate on the productivity, intake and utilization of herbage after 12 years of continuous, low-intensity cattle grazing.

Herbage production

We asked if total annual herbage production per paddock would increase or decrease with stocking rate and, thus, with herbage intake. The results showed that stocking rates of 0.4 (very lenient stocking), 0.7 (lenient stocking) and 1.2 (moderate stocking) LU ha^{-1} a^{-1} (Table 2) caused the annual herbage intake per paddock to increase by a factor of 2.7 from very lenient stocking up to moderate stocking (Figure 1). By contrast, in consequence, herbage production per paddock was only somewhat more than one and a half times higher under moderate than under very lenient stocking (Figure 1). In consequence, herbage utilisation increased far less than forage intake from very lenient to moderate stocking.

An increase in herbage production with stocking rate on low-input pastures was also found in other studies (Cid et al., 2008; Kassahun et al., 2018; Pavlů et al., 2006). Also Isselstein et al. (2007) and Şahin Demirbağ et al. (2009), who conducted their studies during the initial years of our 12-year experiment, found an increase in herbage productivity with stocking rate.

Stocking rate, up to a certain level, is known to increase herbage production per pasture, because defoliation stimulates plant growth under favourable conditions (Hilbert et al., 1981), while stocking rate enlarges the frequently defoliated proportion of the sward (Cid et al., 2008; Tonn et al., 2019).

Nevertheless, the coincidence of our results with those obtained in earlier years of our long-term experiment is surprising as the initially more productive short patches (Şahin Demirbağ et al., 2009) have become equally or even less productive than the rarely defoliated tall patches (Ebeling et al., 2020). The development is based on the huge stability of the grazing-induced patch pattern. Up to now, the sward mosaic at our experimental site has been spatially stable for more than ten years (Tonn et al., 2019), wherefore grazing induces soil nutrient translocations away from the frequently defoliated short patches (Ebeling et al., 2020). Thus, at the patch scale, the short-term effect of grazing beneficial for herbage production differs from its long-term effect depressing productivity in short patches (Ebeling et al., 2020).

Herbage production per pasture results from the herbage produced in patch types over the course of the vegetation period and the proportions of the sward covered with the different patch types (Table 1). In the present study, the decrease in mean target sward height from 18 to 6 cm CSH resulted in a threefold enlargement of the area covered by short patches. It increased from less than 20% under very lenient stocking up to 60% under moderate stocking, while that of the tall patch type decreased by nearly the same extent (Table 1). Similar results on sward structure changes were reported by Ludvíková et al. (2015).

Due to the large proportion, more than half of the total annual herbage production under moderate stocking was contributed by short patches, while short and medium patches together contributed even more than 80% to total annual herbage production per paddock under this stocking treatment (Figure 2). In contrast to the varying small and large proportions of both short and tall patches related to stocking rate, the proportion covered by medium patches was similar for all three stocking treatments with about one third each (Table 1), while their importance for total annual herbage production per paddock increased with stocking rate (Figure 3). This may be explained by patch-specific herbage productivity in medium patches sensitive to stocking rate (Ebeling et al., 2020). Likewise, herbage production in short patches may have benefitted from a better soil nutrient availability under increased stocking as nitrogen, phosphorus and potassium are redistributed by the grazing animals to a great extent, while simultaneously, the more homogeneous excrement deposition (Peterson & Gerrish, 1996) generates an efficient cycling of the soil nutrients within the system (Haynes & Williams, 1993). Tall patches, in contrast, were of less relevance for herbage production under moderate stocking, primarily due to their small areal proportion under this stocking treatment. However, due to their large proportion, tall patches predominantly contributed herbage growth under very lenient stocking, whereas herbage growth contributed by short patches was marginal both due to their reduced proportion and comparatively low productivity (Ebeling et al., 2020).

Both total annual herbage production per paddock and the contribution of the different patch types to total herbage production differed between years. Years differed in precipitation amount and distribution. Presumably, the increased water availability in 2014 compared to 2013 lead to increased biomass growth in medium patches in 2014, where interactions of post-defoliation leaf area and soil nutrient availability may have stimulated biomass growth.

Herbage utilization

We asked, what proportion of herbage is ingested, and what proportion remains on site, over a gradient of stocking rates. The results showed that herbage utilization under lenient and very lenient stocking was similar, where it varied between 39-46%, but increased up to 60% under moderate stocking (Figure 1).

Herbage utilization can reach up to 90%, depending on the intensity and type of the grazing system (Haynes & Williams, 1993). However, to ensure the accumulation and carryover of plant biomass maintaining ecological functions, low-intensity grazing systems show a reduced level of herbage utilization (Adams et al., 2013).

According to the ‘forage maturation hypothesis’ (Fryxell, 1991), herbivores trade-off herbage intake against diet quality (Dumont et al., 1995). Patch grazing, thus, is an energy intake-maximizing practice (de Vries, Michiel F. Wallis & Daleboudt, 1994) by which herbivores respond to the heterogeneity in spatial distribution of forage resources. Generally, cattle visit easily accessible patches that provide forage of at least adequate attractiveness (Griffiths et al., 2003), i.e., plant material with comparatively high nutrient and low fibre contents (Garibaldi et al., 2007). Due to this selective feeding behaviour and the opportunity to balance intake by adjusting grazing time related to herbage quality (Hejcmanová et al., 2009), cattle diet can be independent of stocking rate (Dumont et al., 2007).

Both availability and quality of herbage on offer vary with stocking rate (Dumont et al., 2007). Under increased stocking, cattle tend to apply a ‘lawnmower-kind tactic’ (Dumont et al., 2007), i.e., they feed less selectively, wherefore they consume more uniform amounts of herbage (Hirata, 2002). In consequence, the sward structure becomes more homogenous (Ludvíková et al., 2015; Şahin Demirbağ et al., 2009) and the vegetation shows a lowered age structure (Cid et al., 2008). This, in turn, enhances herbage acceptance (Dumont et al., 2007).

As mentioned, with an area proportion of about 60% (Table 1), short patches contributed the majority to total herbage production in paddock under moderate stocking. Therefore, grazing breaks in summer were comparatively short (Figure 1) and cattle could graze the moderately grazed pastures in autumn.

Pasture utilization was higher in 2013 (39.3%) than in 2014 (56.4%), which documents the strong effect that water availability has on plant growth (Burke et al., 1998). Under very lenient stocking, nearly twice as much herbage had been ingested in 2014 than in 2013. Water limitation thus might be especially consequential for biomass production under low stocking rates since the proportion of the frequently grazed area used as feeding station is comparatively small (Table 2).

Conclusions

The aim of the present study was to investigate the effect of stocking rate on the productivity, utilization and quality of herbage after 12 years of continuous, low-intensity cattle grazing. Herbage intake influenced herbage production, and herbage utilization increased with herbage intake. Classes of sward height contributed differently to total annual herbage production per paddock. Our results indicate the relevance of stocking rate for herbage productivity of long-term low-input pastures.

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CHAPTER III: GRAZING INDUCED PATCH PATTERN CONTROLS PLANT BIOMASS AND C:N RATIO DYNAMICS OF LOW-INPUT CATTLE PASTURES

Dorothee Ebeling, Bettina Tonn, Johannes Isselstein

Abstract

Low-intensity grazing leads to a mosaic of frequently defoliated short patches and rarely defoliated tall patches. As short patches represent the main feeding stations on the pasture, their productivity decreases in long-term grazing systems due to animal-mediated soil nutrient translocations from short to tall patches. Tall patches, in contrast, are productive and accumulate high amounts of low-quality biomass and litter, potentially relevant for carbon storage. Stocking rate plays a key role for soil nutrient cycling, increasing overall biomass productivity and quality. Besides the amount of biomass returned, litter quality also affects carbon storage in pasture soils. So far, grazing effects on carbon cycling have predominantly been studied by comparing grazed with ungrazed grasslands. We therefore analysed the effect of stocking rate on the seasonal dynamics of live, dead and belowground biomass as well as on the C:N ratio of the plant biomass in varying sward height patches in 12-year low-input cattle grazing experiment. We assumed that the amount as well as the seasonal dynamics of C:N ratio of the live, dead and belowground plant biomass differs between patch types at all stocking rates, and that the C:N ratio decreases with stocking rate. Both live and dead aboveground biomass increased from short to tall patches at all stocking rates and dates. Aboveground biomass ranged from less than 55 (live) and 25 (dead) g DM m^{-2} in short patches up to more than 160 (live) and 170 (dead) g DM m^{-2} in tall patches. Belowground biomass, in contrast, remained uninfluenced by patch type but seemed to be controlled by several factors including the availability of soil resources. C:N ratio of both live and dead aboveground biomass were interactively influenced by patch type and date. The C:N ratio of the live aboveground biomass was lower in tall than short patches in spring, but lower in short than tall patches during summer. In the drier year 2013, the C:N ratio of the dead aboveground biomass was higher, with values between 30 and 50, in tall than in short patches from July on. In 2014, it differed between short and tall patches only in late autumn, presumably due to the likewise high C:N ratio of the dead aboveground biomass in short patches in that year. C:N ratio of the belowground biomass was interactively influenced by patch type and stocking rate, showing a decreasing C:N ratio with stocking rate in both short and medium patches, presumably due to the effect of defoliation in these patch types. Stocking rate also had a decreasing effect on the C:N ratio of the live aboveground biomass in both short and medium patches, whereas the C:N ratio of the dead aboveground biomass was lower under moderate stocking than under lenient or very lenient stocking, independently of patch type. The results showed that long-term low-intensity grazing creates great heterogeneity in the abundance and C:N ratio of the live, dead and belowground plant biomass on pasture. We conclude that the accumulation of high amounts of low-quality litter in tall patches may ensure a comparatively long residence time of carbon within the system, while short patches provide forage of at least adequate quality throughout the season.

Keywords: Patch grazing, standing biomass, C:N ratio, nitrogen cycling, spatial heterogeneity

Introduction

Grassland is a global resource that provides multiple ecosystem services, both agricultural and non-agricultural. European managed grasslands are recognized for their high productivity and provision of high-quality forage. Moreover, their potential as a carbon sink is considered large (Pol-van Dasselaar, A. van den et al., 2018). Ecological problems, however, often occur under intensive management focussing primarily on high agronomic output. In recent years, therefore, trade-offs and synergies between management intensity and ecosystem services have increasingly gained attention also in agricultural systems (Hopkins & Holz, 2006).

There is evidence that the relationship between agronomy and ecology can be improved by reducing management intensity (Jerrentrup et al., 2020; Tonn et al., 2019), and that many ecosystem services depend on biodiversity (Vira & Adams, 2009). Low-intensity grazing has become well known as a tool for grassland biodiversity management (Dumont et al., 2012; Jerrentrup et al., 2014; Klimek et al., 2007; Marion et al., 2015; Metera et al., 2010; Rook & Tallowin, 2003; Tonn et al., 2019; Wallis De Vries et al., 2007; Wrage et al., 2012), and it may moreover have the potential to beneficially modulate carbon storage in pasture soils as the cycling of soil elements on pasture is linked to management intensity (He et al., 2019). The storage of carbon in soils is maintained by several abiotic and biotic factors (Jackson et al., 2017) driving complex interactions at the plant-soil-microbe interface. Among others, it depends on the quantity and quality of litter returned to the system (Abdalla et al., 2018).

A key characteristic of low-intensity grazing is the creation and maintenance of a structurally heterogeneous sward structure (Rook et al., 2004). Under the condition of free dietary choice given on low-stocked pastures, animals pursue their preference for palatable, high-quality fodder (Dumont, 1997), and in this way they create a mosaic of varying sward height patches related to differences in defoliation frequency (Cid & Brizuela, 1998). The phenomenon is well known called 'patch grazing' as described by Adler et al. (2001).

Within the frequently defoliated short patches, grazers keep the vegetation in an early phenological stage, so that short patches provide young regrowth throughout the season. The surplus in herbage production results in tall-grown patches that are largely ignored (Strodthoff & Isselstein, 2001) and potentially reach ceiling yield (Lemaire et al., 2000). Tall patches provide herbage of lower quality and are characterized by comparatively high amounts of standing biomass and litter (Correll et al., 2003). In the agroecological-targeted grazing system, thus, biomass growth in short patches ensures fodder production, while that in tall patches forms a carbon pool potentially playing a critical role in soil carbon storage of low-input pastures.

Biomass growth of low-input pastures is strongly heterogenous as short and tall patches differ not only in the proportion of herbage removed by the grazing animals, but also in their productivity (Cid et al., 2008). (Şahin Demirbağ et al., 2009) found frequently defoliated short patches to be more productive than the rarely defoliated tall patches, presumably due to stimulation of biomass growth by defoliation.

On long-term low-input pastures, nevertheless, the initially more productive short patches (Şahin Demirbağ et al., 2009) become less productive than the rarely defoliated tall patches with time (Ebeling et al., 2020) as due to the spatial and temporal stability of the sward mosaic (Dumont et al., 2012; Tonn et al., 2019; van den Bos & Bakker, 1990; Willms et al., 1988), patch types come to differ in soil nutrient status (Ebeling et al., 2020). This development is driven by a disparity between the spatially and temporally heterogeneous pattern of herbage removal and the likewise heterogeneous pattern of nutrient return via excrements, wherefore soil nutrients are frequently translocated from short to tall patches (Ebeling et al., 2020).

The proportions of the different patch types within a pasture are maintained by the stocking rate. An increase in stocking rate enlarges the area of the frequently defoliated short patches, while it reduces the area of rarely defoliated tall patches, and vice versa (Ludvíková et al., 2015; Şahin Demirbağ et al., 2009; Tonn et al., 2019). Therefore, stocking rate has a major impact on biomass dynamics, and it moreover plays a key role for soil nutrient cycling (Boddey et al., 2004) and herbage growth (Pavlů et al., 2006). Because the major part of the soil nutrients consumed is returned to the pasture via excrements (Haynes & Williams, 1993a), an increase in stocking rate speeds up soil nutrient cycling (Boddey et al., 2004), consequently enhancing biomass productivity (Ludvíková et al., 2015) and turnover of both plant biomass (Dubeux et al., 2006). While higher stocking rates reduce the proportion of tall patches (Tonn et al., 2019), whose biomass is predominantly returned to the soil as litter, a greater biomass productivity under increased stocking may offset this effect in terms of total carbon flow from the atmosphere to the soil.

Besides the amount of biomass returned, litter quality also affects carbon storage in pasture soils (He et al., 2019). While many different aspects of litter chemical composition affect soil carbon and nutrient dynamics, stoichiometry of the critical elements is stated as a good indicator for ecological processes (He et al., 2019). The mineralization by microorganisms, for example, is negatively correlated to C:N ratio in plant biomass (Palm & Rowland, 1997).

Differences in forage nutritive value between short and tall patches, which are mainly a result from the different maturity of standing live biomass, do not necessarily correspond with similar differences in C:N ratio of litter (Garibaldi et al., 2007). However, higher soil nutrient availability found in tall patches may increase plant nitrogen content (Olofsson & Oksanen, 2002) and moreover benefit productive plant species that produce litter more easily degradable by microorganisms (Güsewell et al., 2005).

So far, grazing effects on carbon cycling have predominantly been studied by comparing grazed with ungrazed grasslands. The effect of stocking rate on the spatial pattern and temporal dynamics of the abundance of live and dead plant biomass and C:N ratio of the biomass on low-input pastures remains unclear. Understanding these dynamics is crucial to evaluate stocking rate effects on grassland carbon storage.

We collected data in a long-term, low-input cattle grazing experiment focusing on the influence of stocking rate on the seasonal dynamics of live, dead and belowground biomass as well as the C:N ratio in different sward height patches. We expected that the amount (hypothesis I) and seasonal dynamics of C:N ratio (hypothesis II) of the live, dead and belowground plant biomass differs between patch types at all stocking rates. The C:N ratio decreases with stocking rate (hypothesis III).

Material and methods

Location and grazing experiment

We conducted the study on a 12-year, low-input cattle grazing experiment at the experimental farm Relliehausen of the University of Göttingen. The nine-hectare area is old permanent grassland located in the Solling Uplands, Lower Saxony, Germany (51°46′N, 9°42′E) and ranges between 265 and 340 m above sea level. The soil is classified as a Vertic Cambisol (IUSS Working Group WRB, 2006) with a clayey/silty loam texture. The vegetation type corresponds to a Lolio-Cynosuretum with the main species Lolium perenne, Trifolium repens, Taraxacum sect. Ruderale, Dactylis glomerata, Ranunculus repens and Agrostis stolonifera (Wrage et al., 2012). Mean annual temperature between 2002 and 2014 was 8.8 °C (meteorological station: Moringen-Lutterbeck, Deutscher Wetterdienst, DWD). Annual precipitation during this period was 816 mm (meteorological stations: Moringen-Lutterbeck (2002 to 2010) and Dassel (2011 to 2014), DWD). Annual precipitation in the experimental years 2013 and 2014 was 673 mm and 892 mm, and mean temperature was 8.4 °C and 10.0 °C. Neither fertilizer nor herbicide have been applied to this experimental pasture during the last 20 years. Shrubs have been removed by hand whenever necessary. More detailed information about the experimental site is published in Isselstein et al. (2007). Long-term data about the structure of the sward are published in Tonn et al. (2019).

Study design

Since 2005, the pasture has been grazed by adult Simmental suckler cows at three different stocking rates defined by target sward heights in the paddock: 6 cm (moderate), 12 cm (lenient) and 18 cm (very lenient) mean compressed sward height (CSH, CASTLE, 1976). The experiment was arranged in a randomized block design with three replications, resulting in a total of 9 paddocks à 1 ha each. The grazing experiment had originally established in 2002 to compare three slightly different stocking treatments: a moderate stocking treatment grazed by growing Simmental steers to a target sward height of 6 cm CSH, and two lenient stocking treatments (12 cm target sward height), one of them grazed by growing Simmental steers and the other one grazed by growing German Angus steers. In 2005, the latter was converted into today’s very lenient stocking treatment grazed by Simmental suckler cows.

Throughout the season in 2013 and 2014, we fortnightly took 50 CSH measurements per paddock, resulting in a total of 450 CSH measurements per date. Immediately after each measurement date, we adjusted the animal numbers to keep the sward heights close to the target values (put-and-take system). Averaged over 2013 and 2014, the stocking rates applied to maintain target sward heights were equivalent to 607, 342 and 221 kg live weight per ha and year, under moderate, lenient and very lenient stocking, respectively.

We moreover used the fortnightly CSH measurements to define patch types differing in sward height (short, medium tall). Therefore, we took the lower and upper tercile of each 450 CSH measurements as thresholds (short to medium, medium to tall). In 2013 and 2014, the average classification thresholds across dates were 5.9 cm and 8.6 cm CSH between short and medium patches, and 11.9 cm and 14.1 cm CSH between medium and tall patches.

Field sampling

In 2013 and 2014, we harvested aboveground biomass at five dates per vegetation period (April, May, July, September, October). Of the ten randomly distributed permanent plots per paddock (Wrage et al., 2012), we randomly chose two per date and selected the closest short, medium and tall patch with a minimum size of 0.25 m² in the vicinity of each. In each patch, we measured compressed sward height within a square frame of 0.25 m² to verify that it belonged to the intended patch type and cut the aboveground biomass to 1 cm above ground level. We sorted each sample into live and dead biomass, dried (60°C, 48 h) and weighted it afterwards. In May and October of 2013 and 2014, we additionally collected root samples after harvesting aboveground biomass, comprising 72 plots in total. Within each 0.25 m² square frame , we took eight soil cores with a diameter of 1.64 cm each to a soil depth of 20 cm. Roots were washed, dried (60°C, 48 h) and weighed afterwards to determine belowground dry mass. We ground the plant material to pass a 0.25-mm sieve and analysed it for carbon and nitrogen via elemental analysis (16-18 mg per sample, CN Elemental Analyser, type vario EL, Elementar Analysensysteme GmbH, 63452 Hanau, Germany).

Statistical analyses

We analysed the effects of stocking rate (moderate, lenient, very lenient), patch type (short, medium, tall) and date on the amount and C:N ratio of the aboveground live and dead plant biomass (April, May, July, September, October of 2013 and 2014, respectively) as well as on the amount and C:N ratio of the belowground plant biomass (May and October of 2013 and 2014, respectively). For the statistical analyses, we created a factor combination out of 'year' and 'date within year', which we refer to as 'date'.

All calculations and statistical analyses were carried out with R version 3.6.3 (R Core Team, 2020). As the grazing experiment is set up in a nested design, we applied linear mixed effects models in all statistical data analyses (R package 'nlme', Pinheiro et al., 2020), with 'permanent plot' nested in 'paddock'. We selected and validated the statistical models as recommended in Zuur et al. (2009). In all analyses, the full model contained as many explanatory variables and their interactions as possible as we included stocking rate, patch type, date and their two-way and three-way interactions as well as block as fixed effects. To verify homogeneity of the residual variance and normality, we checked model residuals visually. Additionally, we applied Levene's test to verify homogeneity of the residual variance, and we applied Shapiro-Wilk test to verify normality of the residual variance. In case heterogeneity occurred, we fit variance structures to the model (package 'nlme', Pinheiro et al., 2020). We simplified each initial full model by determining, choosing the model with the lowest second-order Akaike Information Criterion as the final model. Finally, we fit each final model with restricted maximum likelihood estimation and validated the data visually. We applied Tukey's post-hoc tests for pairwise comparisons of means (package 'emmeans', Lenth, 2020) when marginal Wald tests indicated significant main or interactive fixed effects.

Results

Amount of live, dead and belowground biomass

Mean amounts of live, dead and belowground biomass in patch types under different stocking rates are shown in Figure 1. Results of marginal Wald tests for the fixed effects models for the amounts of live, dead and belowground biomass are shown in Table 1.

Live aboveground biomass

Live aboveground biomass was significantly affected by patch type and date as well as by the two-way interactions between stocking rate, patch type and date.

It increased from short to medium and from medium to tall patches at all stocking rates. On average, live aboveground biomass in short patches was 32.1% and that in medium patches 63.3% of that in tall patches. Across stocking rates, it was lower in short than in tall patches at all dates. Medium patches were in intermediate position and differed from short and tall patches except for April 2013 and September 2013, when it was similar in medium and tall patches.

Stocking rate had no significant effect on the amount of live aboveground biomass except for May 2014, where it was 28.6% less under very lenient stocking than under moderate stocking, averaged over patch types.

Dead aboveground biomass

The amount of dead aboveground biomass was affected by stocking rate, patch type and date as well as by two-way interactions of stocking rate and patch type and patch type and date. It increased from short to medium and from medium to tall patches at all stocking rates and at all dates. Compared to short patches, the amount of dead aboveground biomass was 3.7 times larger in medium patches and 7.3 times larger in tall patches, averaged over all stocking rates and dates.

Stocking rate affected the dead aboveground biomass in tall patches, where it decreased by 23.1% from very lenient stocking to moderate stocking.

For all patch types, the amount of dead aboveground biomass peaked in September in 2013, and it peaked in July in 2014, across stocking rates. In short patches, it was lowest in October 2013 and April 2014, where it was 68.5% and 74.1% less than that in September 2013 and July 2014, respectively. In medium patches, the dead aboveground biomass lowest in May 2014 and April 2014, increasing to September 2013 and July 2014 by 145.1% and 210.4%, respectively. In both May 2013 and May 2014 that in tall patches was 42.1% and 54.3% from that in September 2013 and July 2014, respectively.

Belowground biomass

Belowground biomass was affected by date. It increased significantly, by 32.4%, from October to May in 2014, but did not differ between May and October in 2013. Belowground biomass was 1.9 times larger in October 2013 than in October 2014. Also, it was 1.8 times larger in May 2013 than in May 2014.

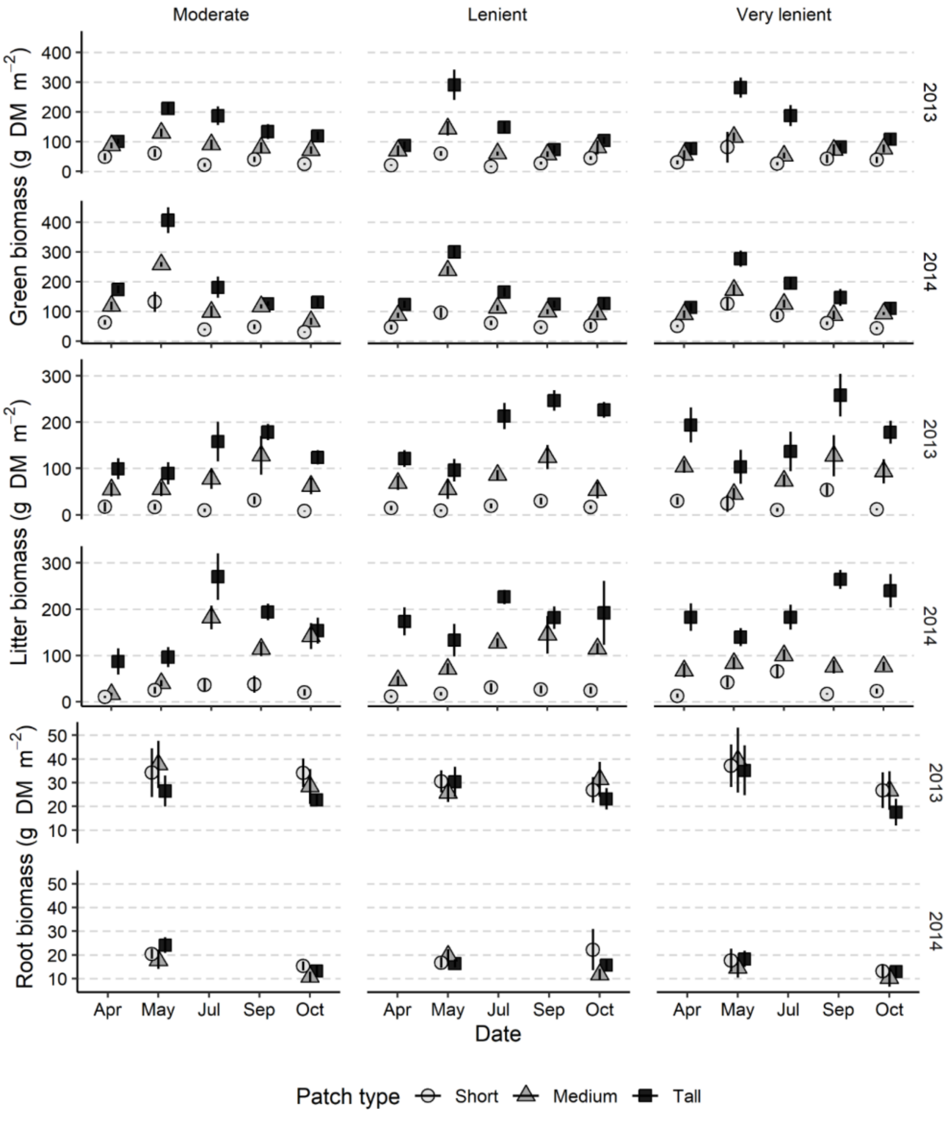

Figure 1. Amount of live and dead aboveground biomass at five annual dates (April, May, July, September, October) as well as of belowground biomass at two annual dates (May, October) in short, medium and tall patches under moderate, lenient and very lenient stocking in 2013 and 2014. Shown are means and standard errors of three replications.

C:N ratio of live, dead and belowground biomass

Mean C:N ratios of live, dead and belowground plant biomass are shown in Figure 2. Results of marginal Wald tests for the fixed effects models for the C:N ratios of live, dead and belowground biomass are shown in Table 1.

C:N ratio of live aboveground biomass

The C:N ratio of the live aboveground biomass was affected by stocking rate, patch type and date as well as by their two-way interactions, respectively. Averaged over dates, C:N ratio of the live aboveground biomass differed between all three patch types under moderate stocking, increasing from short to medium patches by 7.5% and from medium to tall patches by 5.8%. Under lenient stocking, it was 10.2% and 7.5% less in short patches than in medium and tall patches, respectively.

Averaged over dates, C:N ratio of the live aboveground biomass in both short and medium patches increased from moderate stocking to very lenient stocking by 20.2% and 13.7%, with lenient stocking in intermediate position, respectively.

Averaged over stocking rates, in both years 2013 and 2014 C:N ratio of the live aboveground biomass in April was lowest in tall patches, where it was 83.1 and 84.1% (2013) and 90.7 and 90.0% (2014) from that in short and medium patches. Contrary, in July it increased from short to tall patches by 81.5% and 15.5%, with medium patches in intermediate position, respectively in 2013 and 2014. Likewise, it was lowest in short patches in May 2013, increasing by 18.9% and 13.3% to that in medium and tall patches, respectively.

Averaged over patch types, both in July 2014 and October 2014 C:N ratio of the live aboveground biomass increased from both moderate stocking and lenient stocking up to very lenient stocking by 24.2% and 18.4% (July) and 31.3% and 22.2% (October), respectively. In May 2013, that under moderate stocking was 21.2% and 6.9% less than that under lenient stocking and very lenient stocking, respectively.

C:N ratio of dead aboveground biomass

C:N ratio of the dead aboveground biomass was affected by stocking rate, patch type and date as well as by an interaction of patch type and date. Across stocking rates, C:N ratio of the dead aboveground biomass was 22.6% and 18.4%, 15.7% and 18.9% as well as 20.9% and 22.4% lower in short than in medium and tall patches in July, September and October 2013, respectively. Contrarily, in October 2014 it increased from tall to short patches by 24.3%, with medium patches in intermediate position. Averaged over patch types and dates, it was 12.7% and 17.7% lower under moderate than under lenient and very lenient stocking, respectively.

C:N ratio of belowground biomass

C:N ratio of the belowground biomass was significantly influenced by stocking rate, patch type and date as well as by an interaction of stocking rate and patch type.

Averaged over dates, C:N ratio of the belowground biomass under very lenient stocking was 10.5% less in tall than in medium patches, with short patches in intermediate position. Under lenient stocking, that in short patches was reduced by 15.3% and 14.1% from that in medium and tall patches, respectively. Stocking rate affected the C:N ratio of the belowground biomass in short and in medium patches. In short patches, it was 17.1% lower under lenient stocking than under very lenient stocking, with moderate stocking in intermediate position. In medium patches, C:N ratio of the belowground biomass increased from moderate stocking to very lenient stocking by 14%, with lenient stocking in intermediate position. Averaged over both patch types and stocking rates, C:N ratio of the belowground biomass in October 2014 was 13.7% and 9.5% higher than that in October 2013 and May 2014, respectively, with May 2013 in intermediate position.

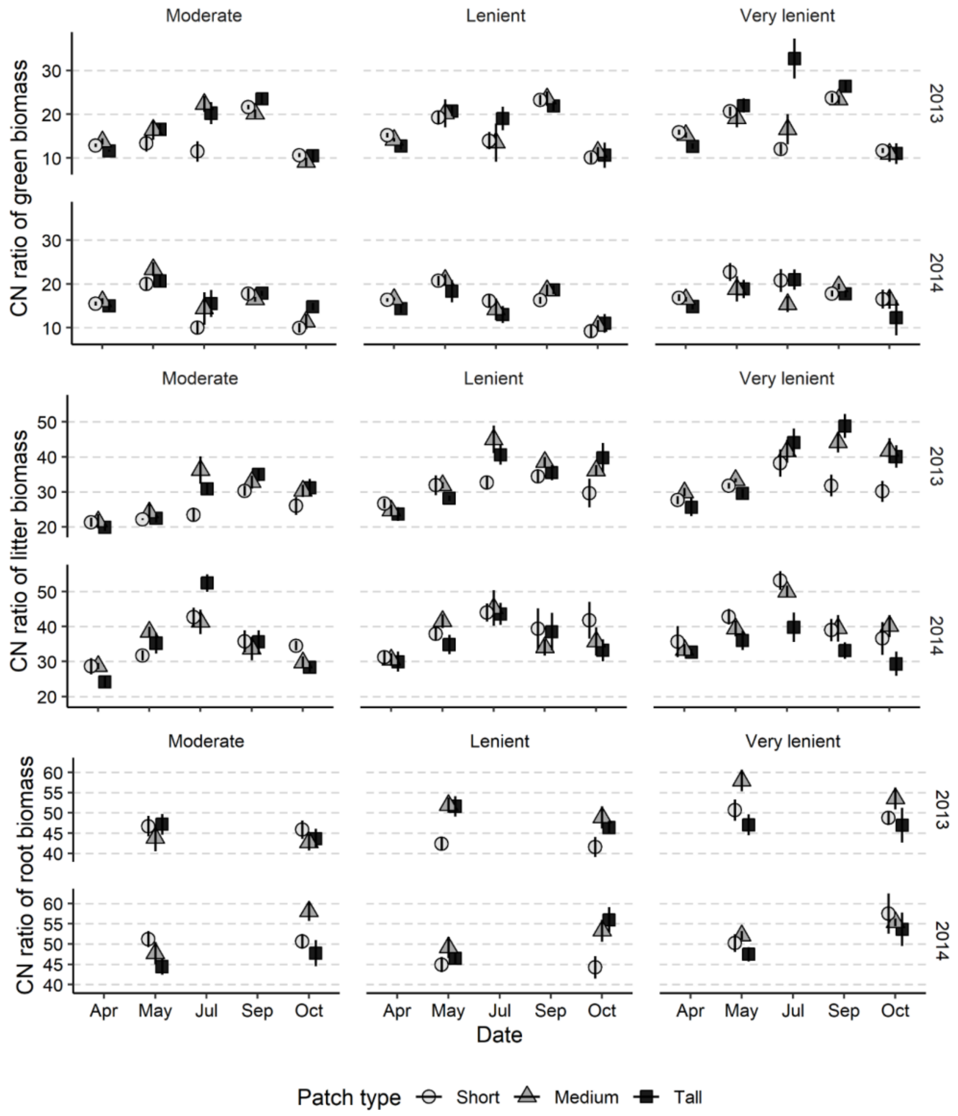

Figure 2. C:N ratio of the live and dead aboveground biomass at five dates (April, May, July, September, October) as well as of root belowground at two dates (May, October) in short, medium and tall patches under moderate, lenient and very lenient stocking in 2013 and 2014, respectively. Shown are means and standard errors of three replications.

Table 1. Results of marginal Wald tests for the linear mixed effects models for amount and C:N ratio of the live, dead and root biomass in three different patch types and under three different stocking rates in 2013 and 2014, respectively.

Response variable	**Predictor**	**Degrees of freedom**		***F* value**	***P* value**
		num	den		
Live aboveground	SR	2	4	4.8	0.085
biomass	PT	2	390	18.5	**<0.001**
	D	9	390	18.3	**<0.001**
	B	2	4	0.4	0.685
	SR*PT	4	390	5.0	**<0.001**
	SR*D	18	390	4.1	**<0.001**
	PT*D	18	390	4.7	**<0.001**
Dead aboveground	SR	2	4	11.3	**0.023**
biomass	PT	2	408	388.0	**<0.001**
	D	9	408	12.7	**<0.001**
	B	2	4	0.9	0.481
	SR*PT	4	408	5.0	**<0.001**
	PT*D	18	408	4.5	**<0.001**
Belowground biomass	D	3	155	23.6	**<0.001**
	B	2	6	12.3	**0.0075**

(Continuation of Table 1)

C:N ratio of live	SR	2	4	18.8	**0.0092**
aboveground biomass	PT	2	391	18.2	**<0.001**
	D	9	391	148.9	**<0.001**
	B	2	4	3.8	0.1207
	SR*PT	4	391	2.8	**0.0254**
	SR*D	18	391	3.5	**<0.001**
	PT*D	18	391	6.6	**<0.001**
C:N ratio of dead	SR	2	4	35.0	**0.0029**
aboveground biomass	PT	2	409	4.1	**0.0179**
	D	9	409	53.9	**<0.001**
	B	2	4	4.1	0.1073
	PT*D	18	409	3.4	**<0.001**
C:N ratio of	SR	2	4	8.3	**0.0378**
belowground biomass	PT	2	143	5.6	**0.0044**
	D	3	143	6.4	**<0.001**
	Bl	2	4	1.5	0.3193
	SR*PT	4	143	6.0	**<0.001**

Note Fixed effects and their interactions that are not shown were not retained in the final model. Abbrevations: SR, stocking rate; PT, patch type; B, block; D, date (combination of ‘year’ and ‘date within year’). Values shown in bold print denote statistical significance at the p < .05 level.

Discussion

On low-input pastures, the grazing animals create and maintain mosaics of sward height patches (Adler et al., 2001) spatially and temporally stable over multiple years (Tonn et al., 2019b). In the present study, we analysed the effect of stocking rate on the seasonal dynamics of live, dead and belowground biomass as well as on the C:N ratio of the plant biomass in varying sward height patches on 12-year low-input cattle pastures.

Effect of patch type on live, dead and belowground biomass

We expected the amount of the live, dead and belowground plant biomass to differ between patch types at all stocking rates (hypothesis I). Results partly confirmed this hypothesis, as both live and dead aboveground biomass increased from short to tall patches at all stocking rates and dates. Belowground biomass, however, was only affected by date and, thus, remained uninfluenced by patch type.

Despite some seasonal variation, there is a linear relationship between sward height and standing aboveground biomass on structurally heterogeneous pastures (Correll et al., 2003; Ebeling et al., 2020). Our results agree with those of previous studies on standing aboveground biomass in patch types of varying sward height (Cid & Brizuela, 1998; Cid et al., 2008; Hirata, 2000). Aboveground biomass on pasture results from the difference between biomass production and biomass removal. Therefore, it is constantly changing as shown by the present results for both live and dead aboveground biomass (Figure 2). The abundance of live aboveground biomass followed the seasonal distribution of biomass productivity typical for this region (Ebeling et al., 2020; Şahin Demirbağ et al., 2009). It peaked in May, i.e., during the period of highest biomass growth, and declined afterwards in all patch types. Dead aboveground biomass, in contrast, followed a reverse trend. While it was lowest during the period of highest biomass growth in spring, it accumulated afterwards and peaked between July and September.

Grazing affects aboveground biomass (McIntire & Hik, 2005; Zhou et al., 2017), both directly through defoliation (Distel et al., 1995; Dumont et al., 2007) and indirectly through both short- and long-term effects of grazing on biomass productivity (Ebeling et al., 2020; Şahin Demirbağ et al., 2009) and senescence rates (Agnusdei et al., 2007). Presumably due to the difference in herbage utilization between patch types (Dumont et al., 2007), seasonal variation in both live and dead aboveground biomass was less in short than in tall patches in the present experiment.

Because short patches constitute the main feeding stations on pasture (WallisDeVries et al., 1998), biomass removal through the grazing animals is high. The abundance of live aboveground biomass in short patches is therefore a function of productivity, senescence and biomass removal by grazers. In short patches, grazers kept the vegetation at low levels of standing biomass throughout the season. Due to the stimulating effect of defoliation on plant growth (Hilbert et al., 1981), short patches provide season-long biomass growth (Ebeling et al., 2020). We may therefore assume that within these highly utilized areas, biomass removal is equal to biomass production, independently of biomass productivity (Gastal & Lemaire, 2015). Constantly lower sward heights in short than in tall patches, and, presumably, lower standing aboveground biomass in short than in tall patches, was also reported by Cid & Brizuela (1998) and Gibb & Ridout (1986) as biomass produced was frequently removed by the grazing animals. In short patches, both old and new leaves are removed to a great extent via defoliation, so that young leaves predominate in the re-growing sward and levels of dead aboveground biomass remain low throughout the season.

In contrast to short patches, where biomass removal through the grazing animals is the main determinant of both live and dead aboveground biomass, tall patches remain largely ungrazed. In tall patches, thus, productivity, senescence and decomposition (Coleman, 1992) play major roles for the abundance of aboveground biomass. Productivity in tall patches differs from that in short patches (Ebeling et al., 2020; Rossignol et al., 2011; Şahin Demirbağ et al., 2009), concerning both the amount of annually produced biomass and the seasonal distribution of biomass growth (Ebeling et al., 2020; Şahin Demirbağ et al., 2009). Generally, it is related to peak standing crop (Chanteloup & Bonis, 2013). In our 12-year cattle grazing experiment, sward mosaics remained spatially stable over multiple years (Tonn et al., 2019b), so that animal-mediated soil nutrient translocations from short to tall patches decreased biomass productivity in short patches, while potentially increasing it in tall patches (Ebeling et al., 2020). Nevertheless, biomass growth in these highly productive areas of the pasture is distributed very unevenly throughout the season. As net herbage accumulation rate maximizes at a LAI between 3-5 (Gastal & Lemaire, 2015), the majority of the annually produced biomass grows in spring (Ebeling et al., 2020). Consequently, there was high variation in both live and dead aboveground biomass in tall patches in the present experiment (Figure 2). We found a remarkable increase (more than doubled) in live standing aboveground biomass in tall patches from April to May at all stocking rates as well as a huge decline afterwards. The latter is based on both seasonal effects and a lack of defoliation. Productivity strongly declines during the course of the vegetation period, with growth rates often reaching zero from ceiling yield on, whereas senescence rates increase (Agnusdei et al., 2007). The maturing of the tall-grown vegetation results in large amounts of standing dead biomass as shown by the results of the present study from July on. The decomposition of the dead biomass leads to a loss of total standing aboveground biomass in tall patches (Şahin Demirbağ et al., 2009).

Among others, both light availability and soil nutrient supply influence belowground biomass allocation (Shipley & Meziane, 2002). In the present study, belowground biomass accumulated independently from patch type. This result is insofar surprising as short and tall patches strongly differ in defoliation frequency and, thus, light availability. Generally, defoliation is known to decrease above- and belowground biomass (Ferraro & Oesterheld, 2002).

Consequently, belowground biomass would be lower in frequently defoliated short patches compared to rarely defoliated tall patches. However, plants allocate biomass to increase capture of growth-limiting external resources (Cleland et al., 2019; Poorter et al., 2012). Belowground biomass in the present experiment may thus be interactively affected by patch-specific determinants, some of which may have opposing effects on the accumulation of belowground biomass. Besides defoliation frequency, in a previous study we found patch types to differ in soil nutrient availability in this 12-year experiment (Ebeling et al., 2020).

While frequent defoliation in short patches would lead to decreased belowground biomass, lower soil nutrient availability in short patches (Ebeling et al., 2020), potentially inducing increased biomass allocation to belowground biomass, may counteract the effect of defoliation. Furthermore, water may also be a resource that less available in short than in tall patches, which again would have an opposing effect towards increased belowground biomass. In contrast, high amounts of aboveground biomass and comparatively high productivity in tall patches should positively affect belowground biomass, while due to a sufficient soil nutrient availability there is a reduced need for belowground biomass allocation.

Overall, soil nutrient availability on pasture increases with stocking rate (Haynes & Williams, 1993a; Peterson & Gerrish, 1996). Under increased soil nutrient availability, as we may assume under moderate stocking in our experiment, belowground biomass in short patches may be primarily determined by frequent defoliation, which reduces both standing above- and belowground biomass and counteracts the potential increasing effect of higher stocking rates on productivity that follows from both increased soil nutrient availability and floristic changes (Tonn et al., 2019a). There might be a similar situation in tall patches under increased stocking, where both high productivity and large amounts of standing aboveground biomass (Shipley & Meziane, 2002) would lead to comparatively higher amounts of belowground biomass than in short patches, while at the same time competition for light is high (Wrage et al., 2012) and soil nutrient supply may be adequate for plant growth.

We may assume that belowground biomass was further affected by the amount of precipitation, i.e., water availability, as it was nearly halved from 2013 to 2014, the latter showing adequate precipitation both in amount and distribution. Presumably as a consequence of varying water availability between the two experimental years, belowground biomass in 2014 decreased from spring to autumn, in line with seasonal aboveground biomass productivity, whereas in the drier year 2013, it remained stable as drought stress strongly limited biomass growth from early summer on (Ebeling et al., 2020).

Effect of patch type on the dynamics of C:N ratio of live, dead and belowground biomass

We expected the seasonal dynamics of C:N ratio of the live, dead and belowground plant biomass to differ between patch types at all stocking rates. Results on both C:N ratio of the live and dead aboveground biomass confirmed our hypothesis as they both were interactively influenced by patch type and date. C:N ratio of the live aboveground biomass was lower in tall patches than in both short and medium patches in early spring, but lower in short patches during summer. That of the dead aboveground biomass was higher in tall than in short patches from July on in 2013 but was less than that in short patches in October 2014. C:N ratio of the belowground biomass, in contrast, showed no seasonal variation that related to patch type.

The C:N ratio of plant biomass on pastures is influenced by several factors. Among others, it depends on the phenological stage of the vegetation (Zhang et al., 2013), the current biomass growth (Jaramillo & Detling, 1988) as well as on the species composition (Rossignol et al., 2011). Grazing maintains vegetation in patch types directly through frequent defoliation (or no defoliation) as well as through long-term effects, including shifts in soil nutrient availability (Ebeling et al., 2020) or vegetation composition (Rossignol et al., 2011). At our experimental site, patch types differ in defoliation frequency, productivity and soil nutrient availability, where the frequently defoliated short patches show lower soil nutrient stocks and therefore are less productive than the rarely defoliated tall patches (Ebeling et al., 2020).

Vegetation in short patches is found to show higher nitrogen concentration than that in tall patches (Cid & Brizuela, 1998; Rossignol et al., 2011). Plants growing in short patches are kept at an early phenological stage throughout the grazing season and the vegetation is characterized by an increased proportion of young leaves showing lower C:N ratios compared to older leaves (Zhang et al., 2013). Moreover, the leaf percentage in frequently defoliated swards increases. During regrowth, the demand for soil nutrients is increased (Zhang et al., 2013), wherefore defoliation enhances both uptake of soil nitrogen and allocation of nitrogen to leaves (Jaramillo & Detling, 1988; Milchunas et al., 1995; Polley & Detling, 1989). Moreover, over the longer term, frequent defoliation may promote species characterized by a more easily degradable biomass (Olofsson & Oksanen, 2002; Rossignol et al., 2011). In tall patches, in contrast, plants show reproductive growth in spring and early summer and from then on promote the storage of reserves. Due to the lack of defoliation, they show high proportions of older leaves and litter with comparatively high C:N ratios of both the live and dead aboveground biomass.

However, due to the preferred grazing of short compared to tall patches, tall patches, in which nutrients are returned to the soil as litter, represent areas of net nutrient import. We therefore may assume that especially in early spring, soil nutrient availability in tall patches is higher than in short patches. During this period, biomass growth and demand for soil nitrogen needed for plant growth is high, while the vegetation still is at an early phenological stage. This may explain the lower C:N ratio of the live aboveground biomass in tall patches compared to that in short patches in April in the present experiment.

In our study, summer, and autumn in 2014 were much wetter than in 2013, which enabled an increased biomass growth in early autumn, especially in tall patches (Ebeling et al., 2020). This biomass growth in tall patches in the end of the season could explain the lower C:N ratio of the dead aboveground biomass in tall than in short patches as precipitation might have mobilized soil nutrients in tall patches, making them available for plant growth.

Effect of stocking rate on C:N ratio of live, dead and belowground biomass

We expected the C:N ratio of the live, dead and belowground biomass to decrease with stocking rate. Our results partly confirmed this hypothesis as C:N ratio of the dead aboveground biomass decreased with stocking rates across all patch types. Further, stocking rate decreased the C:N ratio of the live biomass in short and medium patches, but not in tall patches. Moreover, stocking rate affected the C:N ratio of the live aboveground biomass in interaction with date, decreased it in May 2013 as well as in July and October of 2014. The C:N ratio of belowground biomass was interactively affected by stocking rate and patch type but without showing a straight direction.

These variable responses of biomass C:N ratio in patch types according to stocking rate in the present experiment coincides with findings of (Rossignol et al., 2011), who reported varying responses of C:N ratio to within-paddock grazing intensity in a wet grassland in France. Management intensity affects the pathway of soil nutrient return on pastures. With increased stocking rate, a larger part of the soil nutrients is returned through the herbivore instead through the litter pathway, making nutrients more easily available for plant growth (Haynes & Williams, 1993b). An increase in stocking rate from very lenient stocking to moderate stocking in the present experiment can be assumed to have increased overall soil nutrient availability (Haynes & Williams, 1993a; Peterson & Gerrish, 1996), because stocking rate accelerates soil nutrient cycling (Boddey et al., 2004) and leads to a more homogeneous redistribution of the soil nutrients throughout the pasture (Peterson & Gerrish, 1996).

However, vegetation especially in short and medium patches may have benefitted from this increase in soil nutrient availability under moderate stocking as plant growth in frequently defoliated patches is limited by soil nitrogen availability at our site (Ebeling et al., 2020). On fertile sites with adequate below-ground reserves, the frequent removal of plant tissue stimulates biomass productivity (Hilbert et al., 1981) and this way increases soil nutrient uptake by plants needed for regrowth after defoliation. It is moreover likely that in frequently defoliated patches under increased stocking, the proportion of productive, grazing-tolerant species showing higher tissue quality and an increased demand for soil nutrients is increased compared to reduced stocking.

Conclusions

The results showed that long-term low-intensity grazing creates great heterogeneity in the abundance and C:N ratio of the live, dead and belowground plant biomass on pasture. While defoliation in short patches leads to low amounts of both live and dead aboveground biomass, the accumulation of high amounts of low-quality litter (C:N >30:1) in tall patches may ensure a comparatively long residence time of carbon within the system, even under moderate stocking. Potentially, the decrease in C:N ratio of the live aboveground biomass in both short and medium patches may indicate an increased nutritive value of the plant biomass under increased stocking in long-term low-intensity grazing systems. However, results on belowground biomass and C:N ratio showed that belowground responses to grazing may differ from the aboveground responses. As carbon input through belowground biomass is an important driver for carbon storage in soils (Rasse et al., 2005), future research should focus on plant allocation to roots.

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GENERAL DISCUSSION

Due to the creation of structurally divers swards, low-intensity grazing may improve the relationship between agronomy and ecology in grasslands. The aim of the present study was to evaluate the role of stable sward height patches for the productivity, herbage intake and nitrogen cycling of long-term low-intensity cattle pastures differing in stocking rate.

We conducted our study on a permanent low-input cattle pasture with a continuous stocking system. The long-term cattle grazing experiment was established in 2002. We revisited this experiment initially investigated in 2004 Şahin Demirbağ et al. (2009), focussing on the effect of stocking rate on the aboveground net primary productivity in patch types differing in sward height after 12 years of low-intensity cattle grazing (Chapter I). To evaluate the agronomic and ecological potential of the grazing systems varying in stocking rate, we collected data on herbage productivity, intake and utilization at the paddock scale (Chapter II). Moreover, we focussed on the seasonal dynamics of live, dead and belowground biomass as well as the C:N ratio of the plant biomass grown in the different sward height patches under varying stocking rates to analyse the dynamics of carbon pools on long-term low-input pastures (Chapter III).

In the long-term experiment, target sward heights in paddock were used as proxies to define stocking rates: moderate, lenient and very lenient stocking at 6, 12 and 18 cm mean target compressed sward height (CSH, Correll et al., 2003). We frequently re-defined sward height class thresholds according to current mean sward height of all nine paddocks (0.33 quantile and 0.67 quantile out of the 450 CSH measurements taken at each date). During 2013 and 2014, target sward heights were equivalent to stocking rates of 607 (moderate), 342 (lenient) and 221 (very lenient) kg ha^{-1} a^{-1}. Mean sward height class thresholds during these two years were 5.9 and 8.6 (short to medium) and 11.9 and 14.1 (medium to tall) cm CSH.

We combined a double sampling technique (Mannetje, 2000) with an exclosure method and calculated the aboveground net primary productivity in the different patch types. Additionally, we calculated soil phosphorus (P), potassium (K) and magnesium (Mg) stocks as well as pH in patch types, using P and K as indicators for soil nutrient availability. We calculated the proportion of each patch type and, based on these data, calculated the aboveground net primary productivity of the grazing systems. We further analysed herbage intake, and we sampled biomass in patch types and analysed its carbon and nitrogen content.

In our study, we found that aboveground net primary productivity (Chapter I) was interactively affected by patch type and stocking rate after 12 years of low-intensity cattle grazing. In contrast to observations at the start of the experiment (Şahin Demirbağ et al., 2009), ANPP in short patches was similar to or less than that in medium and tall patches. Our result moreover stays in contrast to the findings of (Hilbert et al., 1981), who reported that defoliation may increase biomass growth rates due to the compensation of the lost plant tissue. Results on topsoil phosphorus and potassium stocks in the present study, which likewise were interactively affected by patch type and stocking rate, indicated a long-term redistribution of nutrients by the grazing animals as they were lower in short than in tall patches. Patch grazing creates sward mosaic structures that are stable over multiple years (Tonn et al., 2019), where the heterogeneous pattern of defoliation differs from the likewise heterogenous pattern of excrement placement, i.e., soil nutrient return (Auerswald et al., 2010). Consequently, soil nutrients are redistributed away from short patches. Soil nutrient limitation in short patches could explain their lower aboveground net primary productivity. Moreover, frequent defoliation and reduced soil nutrient availability may have reduced the proportion of productive, grazing-tolerant species in frequently grazed short patches (Perotti et al., unpublished; Rossignol et al., 2011), which can affect productivity. Nevertheless, productivity in short patches may reach a certain equilibrium once the plant species composition is adapted to prevailing growing conditions, providing whole-season biomass growth as due to the effect of defoliation, biomass productivity is distributed more evenly throughout the season as shown in the present experiment. Stocking rate plays a key role for soil nutrient cycling (Haynes & Williams, 1993) and biomass growth (Ludvíková et al., 2015) of low-input pastures as it strongly changes nutrient pathways (Boddey et al., 2004; Haynes & Williams, 1993; Thomas, 1992). In our study, productivity of medium patches increased with stocking rate, while soil potassium concentration showed a similar trend. This result points towards enhanced nutrient cycling under more intensive stocking as also reported in other studies (Boddey et al., 2004; Li et al., 2009).

At the paddock scale (Chapter II), stocking rate maintains the proportions of the different patch types on the pasture. With stocking rate, the frequently defoliated area enlarges, and the rarely defoliated area decreases (Cid et al., 2008; Tonn et al., 2019). Our results showed that with stocking rate and, thus, herbage intake (Dumont et al., 2007; Parsons & Dumont, 2003) both production and utilization of the produced biomass increased. Classes of sward height contributed differently to total annual herbage production per paddock, which was mainly a result of the varying proportions of the patch types according to stocking rate. Our results indicate the relevance of stocking rate for herbage productivity of long-term low-input pastures.

The results showed that long-term low-intensity grazing creates great heterogeneity in the abundance and C:N ratio of the live, dead and belowground plant biomass on pasture (Chapter III). Although C:N ratio of the dead aboveground biomass decreases with stocking rate, from summer on (when litter accumulates) values do not fall below 30, even under moderate stocking. Simultaneously, stocking rate beneficially affects C:N ratio of the live aboveground biomass. The accumulation of high amounts of low-quality litter in tall patches may ensure a comparatively long residence time of carbon within the system.

Our results show the presence of large heterogeneity in nutrient cycling and productivity in long-term low-input pastures. The animal-mediated redistribution of soil nutrients away from short patches leads to a reduced herbage productivity in these frequently defoliated short patches. Nevertheless, those grazing systems may reach a certain equilibrium, as the high temporal and spatial stability of the mosaic structures demonstrates that short patches are still attractive and thus are still used as main feeding stations. Also, productive tall patches accumulate high amounts of low-quality plant litter, potentially increasing the grazing system's carbon sequestration potential. Several interactions between stocking rate and patch type indicate the large influence of stocking rate on soil nutrient cycling.

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SUMMARY

Extensively managed grasslands are multifunctional. Especially low-intensity grazing is known to be beneficial for biodiversity outcomes as well as for numerous other ecosystem services, such as carbon sequestration. The selective feeding behavior of herbivores, the so-called 'patch grazing', leads to the formation of spatially and temporally stable mosaic structures composed of patches differing in sward height. Short patches are frequently defoliated, whereas tall patches are rarely defoliated. The attractiveness of the short patches is based on the comparatively higher quality and palatability of the re-growing plant material. Within the paddock, patch types thus are treated with varying grazing intensities, wherefore they differ in biomass productivity. Short patches are known to be more productive than tall patches, which has been reported in several studies. The herbage growth of short patches is of particular relevance for the agronomic production of low-input grazing systems. The initially formed mosaic structures are stable over the short as well as over the long-term (>10 years), especially on productive sites. Due to frequent defoliation, soil nutrients are taken from short patches and heterogeneously returned to the pasture via excrements. It must be assumed that soil nutrients are re-translocated from short to tall patches. Nevertheless, grazing accelerates soil nutrient cycling as via dung and urine, nutrients become highly available for plant growth. Over the longer term, these processes influence the vegetation composition, and should moreover affect biomass productivity, which must be assumed to be reduced within short patches and, in contrast, should be increased in tall patches. Grazing systems must be regarded at the patch scale as well as at paddock scale. Stocking rate maintains the proportions of the different patch types on the pasture, which thus depend on the biomass consumed. Stocking rate has a determining influence on the temporally and spatially cycling of soil nutrients as well as on the nutrient availability for plant growth. With increasing stocking rate, the share of short patches enlarges, while at the same time, a large part of the soil nutrients is cycling through the herbivore pathway and increasingly is recycled more homogeneously throughout the pasture. Especially productive grasses may benefit from an increased soil nutrient supply resulting from increased stocking. The relationship between stocking rate, spatial heterogeneity in sward structure and nutrient cycling is characterized by a seasonal variability as well as by complex interactions, whose agronomical and ecological consequences are still not sufficiently understood.

The aim of our experiment was to study the effects of grazing intensity on the primary productivity of different patch types, the productivity of the entire grazing system as well as on nutrient cycling throughout the season and therefore to enhance understanding of the underlying processes and seasonal dynamics of primary production of long-term low-input grazing systems both at patch and at paddock scale. In the long-term grazing system, we assumed short patches to be less productive than tall patches, but with biomass production being distributed more evenly over the season. Moreover, we expected herbage productivity

to increase with stocking rate. According to this hypothesis, we asked if total herbage production would increase or decrease as stocking rate, and thus the proportion of the short the patch type, increases. We also asked what proportion of herbage is ingested, and what proportion remains on site, over a gradient of stocking rates. Furthermore, we expected patch types to vary in standing biomass and CN ratio of above- and belowground biomass and assumed that the magnitude of these differences varies with stocking rate as well as seasonally.

We conducted the current study on a low-input continuous cattle pasture located at the experimental farm Relliehausen of the University of Göttingen. The low-input pasture was established in 2002. Since 2005, pastures have been grazed at three different stocking rates (moderate, lenient and very lenient stocking), defined by mean target sward heights in paddock (6, 12 and 18 cm). The experiment was arranged in a randomized block design and included three replications (9 paddocks with 1 ha each in total). During 2013 and 2014, we defined three patch types (short, medium, tall) using thresholds of biweekly sward height measurements (the lower, the middle and the upper third of 50 sward height measurements per paddock at each date). To calculate the annual herbage accumulation in patch types, we used grazing exclusion cages which we have re-placed frequently throughout the vegetation period. Before and after each growth period (cage-replacement), we measured the sward height in order to calculated herbage growth rates. A calibration model predicted standing biomass for a given sward height for each combination of block and date. To set up this calibration model, we did calibration cuts in a double-sampling technique at five dates during the vegetation period, respectively in 2013 and 2014. We moreover analysed these samples for carbon and nitrogen. Including the aerial proportions of the different patch types, we were able to calculate the herbage productivity of the entire paddock, respectively. Due to the energy need of the cattle and the quality of the ingested fodder, we calculated total annual accumulated herbage per paddock.

Patch types differed in herbage productivity, with tall patches being more productive than short patches. Biomass growth in tall patches was concentrated in spring, while that of short patches was more evenly distributed throughout the season. Although the areal proportion of the short patch type was larger under moderate stocking, herbage production of this stocking variant was significantly higher than that under very lenient stocking. Patch types contributed differentially to herbage production of the entire paddock, with an increasing contribution by short patches and, in turn, a decreasing contribution by tall patches with increasing stocking rate. According to the stocking rates applied, herbage intake was higher under increased stocking and also the proportion of the herbage taken to that grown was larger under increased stocking. Herbage utilization differed significantly between moderate stocking and the two more extensive stocking variants.

Standing biomass was lower in short patches than in tall patches. Both, green and dead aboveground biomass were affected by interactions of patch type and stocking rate, as well as by date. Stocking variants differed in green biomass only in spring of the second experimental year. Within the tall patch type, however, the dead aboveground biomass increased with decreased stocking rate. There was no effect of patch type or stocking rate on root biomass, but they interactively influenced root CN content. While under lenient stocking, roots of short patches showed the lowest CN ratio, it did not differ from those of tall patches under very lenient stocking. In short and medium patches, root CN ratios were highest under very lenient stocking. Across patch types, CN ratios of green and dead aboveground biomass increased with decreased stocking. The effect of patch type on CN ratios of green and dead aboveground biomass was linked with an interaction with harvest date, with lower CN ratios in short patches in spring and autumn and higher CN rations in summer. The two experimental years differed in precipitation amount and distribution, which was reflected by the results on patch- and paddock productivity as well as by the results on quality parameters, both being affected by several interactions.

Our results confirm the presence of large heterogeneity in nutrient cycling and productivity. In long-term low-intensity pastures, the re-translocation of soil nutrients from short to tall patches leads to a reduced herbage productivity in frequently defoliated short patches and, in turn, to an increased herbage productivity in rarely defoliated tall patches. The adaption of vegetation composition to a specific regime of defoliation under a given soil nutrient availability indicates a trade-off between biomass productivity and the high floristic diversity known for long-term low-input pastures. Nevertheless, those grazing systems may reach a certain equilibrium, as the high temporal and spatial stability of the mosaic structures demonstrates that short patches are still attractive and thus are still used as main feeding stations. Also, the increased productivity in tall patches increases the grazing system’s carbon sequestration potential. Several interactions between stocking rate and patch type indicate the large influence of stocking rate on soil nutrient cycling. In our study, the lenient, middle-position stocking variant seemed to be the optimal choice to combine agronomical and ecological benefits, as CN ratios of the aboveground biomass were between those of the other two stocking variants, while herbage productivity was maintained at an adequate level.

ZUSAMMENFASSUNG

Extensiv bewirtschaftetes Dauergrünland ist multifunktional. Besonders die extensive bis moderate Beweidung ist förderlich für die Biodiversität sowie zahlreiche weitere Ökosystemfunktionen, darunter auch die Kohlenstoffspeicherung. Das selektive Futteraufnahmeverhalten der Weidetiere, das sogenannte „Patch grazing“, führt zur Ausbildung eines zeitlich und räumlich stabilen Mosaiks aus kurzen, häufig entblätterten sowie langen, selten entblätterten Grasnarbenhöhenbereichen (Patch-Typen). Die besondere Attraktivität der niedrigen Patches gegenüber den hohen Patches liegt in der höheren Futterqualität des Aufwuchses. Innerhalb einer Weidefläche unterliegen die Patch-Typen damit unterschiedlichen Beweidungsintensitäten, und unterscheiden sich infolgedessen in ihrer Produktivität. Niedrige Patches sind im Gegensatz zu hohen Patches zur Biomasseproduktion angeregt und haben sich in verschiedenen Studien als vergleichsweise produktiver erwiesen. Sie leisten den agronomisch relevanten Beitrag im Agrarökosystem Weide. Auch im langjährigen extensiven Weidesystem zeigen sich die initial durch die Präferenzen der Weidetiere entstandenen Mosaikstrukturen zeitlich und räumlich stabil (>10 Jahre), was in besonderem Maße auf produktive Standorte zutrifft. Wiederkehrend werden durch die Futteraufnahme Bodennährstoffe aus den kurzen Patch-Typen entzogen und der Weidefläche im Zuge der Exkrementabsetzung zeitlich und räumlich heterogen rückgeführt. Es muss daher davon ausgegangen werden, dass eine Umverteilung der Bodennährstoffe aus den niedrigen Patches in die hohen Patches stattfindet. Gleichzeitig beschleunigt die Futteraufnahme und Rückführung der Bodennährstoffe in Form von Dung und Urin den Nährstoffkreislauf. Diese Prozesse beeinflussen langfristig die Vegetationszusammensetzung und sollten ebenso Einfluss auf die Produktivität der Patch-Typen haben, wobei von einer zurückgehenden Primärproduktion in den niedrigen Patches und einer steigenden Primärproduktion in den hohen Patches auszugehen ist. Die Weidesysteme müssen sowohl auf der Patch- als auch auf der Weideflächenebene betrachtet werden. Die flächenmäßigen Anteile der Patch-Typen werden von der Beweidungsintensität und damit über die von den Weidetieren konsumierte Biomasse bestimmt. Die Beweidungsintensität beeinflusst die zeitliche und räumliche Umsetzung sowie die Verfügbarkeit der Bodennährstoffe für das Pflanzenwachstum maßgeblich. So nimmt mit steigender Beweidungsintensität der Anteil kurzer Patches auf der Weidefläche zu, gleichzeitig aber wird ein Großteil der Bodennährstoffe über den Weidetier-Zyklus zunehmend homogener und leichtverfügbar rückverteilt, wovon vor allem produktive Grasarten profitieren könnten. Die Beziehung zwischen Beweidungsintensität, räumlicher Heterogenität der Grasnarbenstruktur und Nährstoffumsatz ist durch saisonale Variabilität sowie komplexe Interaktionen gekennzeichnet, deren Auswirkungen auf die agronomische wie ökologische Leistung langjähriger extensiver Weidesysteme bisher nicht hinreichend untersucht worden sind.

Ziel der vorliegenden Studie war es, den Einfluss der Beweidungsintensität auf die Primärproduktion verschiedener Patch-Typen, die Produktivität langjähriger extensiver

Weidesysteme sowie die Nährstoffdynamik über die Saison zu untersuchen und so ein besseres Verständnis über die ablaufenden Prozesse und die saisonalen Dynamiken der Primärproduktion auf Patch- wie auf Weideflächenebene zu erlangen. Wir haben angenommen, dass im langjährigen Weidesystem niedrige Patches generell weniger produktiv sind als hohe Patches, jedoch die Verteilung der oberirischen Biomasseproduktion über die Saison hinweg in den niedrigen Patches gleichmäßiger ist. Zudem sollte eine höhere Beweidungsintensität in kurzen wie in hohen Patches mit einer gesteigerten Produktivität einhergehen. An diese Hypothese angeknüpft haben wir uns die Frage gestellt, ob die Biomasseproduktion bei einer flächenmäßigen Ausdehnung des kurzen Patch-Typs auf der Weidefläche mit steigender Beweidungsintensität insgesamt zu- oder abnimmt, und wie groß der vom Tier gefressene Anteil bzw. der vom Tier zurückgelassene Anteil des Aufwuchses auf der Fläche ist. Weiter sind wir davon ausgegangen, dass sich die Patch-Typen in der stehenden Biomasse, in der Futterqualität und im C/N-Verhältnis von oberirdischer lebender und toter sowie unterirdischer Biomasse unterscheiden und dass diese Unterschiede mit der Beweidungsintensität sowie saisonal variieren.

Wir haben das Experiment auf einer im Jahr 2002 etablierten, extensiven Rinderstandweide des Versuchsguts Relliehausen der Georg-August-Universität Göttingen durchgeführt. Die Beweidung erfolgte seit dem Jahr 2005 in drei unterschiedlichen Beweidungsintensitäten, die über mittlere Zielnarbenhöhen definiert waren (6, 12 und 18 cm – moderate, extensive und sehr extensive Beweidung). Der Versuch war in einem randomisierten Blockdesign angelegt und beinhaltete drei Wiederholungen (in Summe 9 Parzellen à 1 ha). In den Jahren 2013 und 2014 ermittelten wir drei Patch-Typen (kurz, mittel, lang), deren Klassifizierung wir über zweiwöchentliche Grasnarbenhöhenmessungen festgemacht haben (unteres, mittleres und oberes Drittel von 50 Messungen pro Parzelle am jeweiligen Termin). Für die Ermittlung des gesamtjährlichen Biomassewachstums in den Patch-Typen in den Jahren 2013 und 2014 nutzten wir Weidekörbe, die wir wiederholt räumlich versetzten. Jeweils vor Beginn und nach Ende der so entstandenen Wachstumsperioden maßen wir die Narbenhöhe, woraus wir schließlich Wachstumsraten ermittelten. Ein Kalibrationsmodell machte dabei Vorhersagen stehender Biomasse bei gegebener Grasnarbenhöhe für jede Kombination von Block und Messzeitpunkt. Für die Erstellung des Kalibrationsmodells haben wir in den Jahren 2013 und 2014 an fünf Terminen über die Saison im Doppelstichprobenverfahren stehende Biomasse nach Ermittlung der Grasnarbenhöhe geerntet. Das Material dieser Ernten wurde weiter auf seinen Kohlenstoff- und Stickstoffgehalt hin untersucht. Über den Flächenanteil der Patch-Typen an der Gesamtfläche der Parzellen haben wir den Biomassezuwachs auf Parzellenebene berechnet. Über den Energiebedarf der Tiere und die Qualität des aufgenommenen Futters konnten wir die akkumuliert aufgenommene Biomasse bestimmen.

Verschiedene Patch-Typen zeigten sich unterschiedlich produktiv. Dabei waren hohe Patches produktiver als niedrige Patches, wobei sich die Biomasseproduktion in den hohen Patches vor allem auf das Frühjahr konzentrierte und die Biomasseproduktion in den kurzen Bereichen gleichmäßiger über die Saison verteilt war. Trotz des überwiegenden Flächenanteils des kurzen, weniger produktiven Patch-Typs in der moderaten Beweidungsvariante, war die pro Weideparzelle produzierte, gesamtjährlich akkumulierte Biomasse signifikant höher als in der sehr extensiven Beweidungsvariante. Die Patch-Typen steuerten unterschiedlich viel zum Gesamtaufwuchs der Parzellen bei, wobei der Anteil, der in den niedrigen Patches produziert wurde, mit steigender Beweidungsintensität zunahm, und der der hohen Patches abnahm. Entsprechend der Beweidungsintensitäten war die aufgenommene Futtermenge umso höher, je intensiver beweidet wurde. Der gefressene Anteil des aufgewachsenen Futters nahm dabei mit zunehmender Beweidungsintensität zu. Die moderate Beweidungsvariante wies gegenüber den beiden extensiveren Varianten eine signifikant höhere Ausnutzung des Aufwuchses durch das Weidetier auf. Die stehende Biomasse war in niedrigen Patches niedriger als in hohen Patches. Grüne und tote oberirische Biomassen wurden von Interaktionen aus Patch-Typ und Beweidungsintensität sowie dem Erntezeitpunkt beeinflusst. So unterschieden sich die Beweidungsvarianten hinsichtlich der grünen oberirischen Biomasse über alle Patch-Typen hinweg nur im Frühjahr des zweiten Versuchsjahres. Innerhalb der hohen Patches aber erhöhte sich die tote Biomasse mit steigender Beweidungsintensität. Einen Einfluss von Patch-Typ oder Beweidungsintensität auf die Wurzelmassen gab es nicht, jedoch beeinflussten beiden Faktoren den Wurzel-C/N-Gehalt interaktiv. Während unter der extensiven Beweidung die Wurzeln in den niedrigen Patches die geringsten C/N-Verhältnisse aufwiesen, unterschieden sich diese unter sehr extensiver Beweidung nicht von denen der hohen Patches. In kurzen und mittleren Patch-Typen waren die C/N-Verhältnisse der Wurzeln unter der sehr extensiven Variante am höchsten. Über alle Patch-Typen hinweg fielen die C/N-Verhältnisse des grünen und toten Pflanzenmaterials mit abnehmender Beweidungsintensität höher aus. Der Einfluss des Patch-Typs auf die C/N-Verhältnisse in grünem und totem Pflanzenmaterial war an in eine Interaktion mit dem Erntezeitpunkt gebunden, mit in niedrigen Patches geringeren C/N-Verhältnissen in Frühjahr und Herbst, und höheren C/N-Verhältnissen im Sommer. Die beiden Versuchsjahre unterschieden sich in der Niederschlagsmenge- und Verteilung, was sowohl in der Produktivität auf Patch- und Weideflächeneben als auch bei den Ergebnissen der untersuchten Qualitätsparameter durch verschiedene Interaktionen sichtbar wurde.

Unsere Ergebnisse bestätigen, dass in extensiven Weidesystemen eine große Heterogenität des Nährstoffumsatzes und der Produktivität vorhanden ist. In langjährigen Weidesystemen führt die Umverteilung der Bodennährstoffe zu einer reduzierten Primärproduktion in den häufig entblätterten niedrigen Patches und einer höheren Primärproduktion in den selten bis nicht entblätterten hohen Patches. Eine Anpassung der Vegetation an die Entblätterungstiefe und -häufigkeit unter einer gegebenen Verfügbarkeit an Bodennährstoffen kann einen Trade-Off zwischen einer erhöhten Biodiversität und der reduzierten Produktivität des langjährigen Weidesystems bedeuten. Die stabilen Mosaikstrukturen weisen jedoch darauf hin, dass niedrige Patches weiterhin für das Weidetier attraktiv bleiben und das Weidesystem ein Gleichgewicht erreicht. Gleichzeitig erhöht eine gesteigerte Produktivität in den hohen Patches das Potenzial der Kohlenstoffbindung langjähriger Weiden. Diverse Interaktionen zwischen Beweidungsintensität und Patch-Typ verdeutlichen den bedeutenden Einfluss der Beweidungsintensität auf die Nährstoffumsetzung. In unserem Versuch zeigte sich die mittlere, extensive Beweidungsvariante durch zwischen den anderen Beweidungsintensitäten liegende C/N-Gehalte in der oberirdischen Biomasse und einer mittleren Weideleistung bei gleichzeitiger Aufrechterhaltung der Mosaikstruktur als optimal, um sowohl agronomische und als auch ökologische Ziele zu erreichen.

APPENDIX

Appendix I	Supporting information for Chapter I
Appendix II	Figure of compressed sward heights and classification thresholds for patch types
Appendix III	Figures of herbage metabolizable energy content and herbage acid detergent fibre content of hand-plucked herbage samples

Appendix I

Supporting Information for:

Ebeling, D., Tonn, B., & Isselstein, J. (2020). Primary productivity in patches of heterogeneous swards after 12 years of low-intensity cattle grazing. Grass and Forage Science, 75, 398–408. https://doi.org/10.1111/gfs.12505

Published online in the Supporting Information section.

S1 Supplementary methods

We assessed standing biomass in exclusion cages at the beginning and end of each growth period with a double sampling method that relies on a calibration model predicting standing biomass from compressed sward height (CSH; Figure S.1.). This method allows to determine standing biomass in a non-destructive way, permitting measurements at the beginning and end of the growth period to be taken at the same location, which is important in a heterogeneous grass sward.

To parameterise the calibration model, biomass cuts were taken at five dates during the vegetation period (April, May, July, September and October) during 2013 and 2014, resulting in a total of ten cutting dates. Two sampling areas per paddock were randomly chosen. Within each sampling area, short, medium and tall patches were located. Herbage of two 0.25 m^2 square frames per sampling area and patch type were cut to 1 cm above ground level after taking four CSH measurements within each square frame.

A generalized least squares model including the single and interactive effects of CSH, stocking rate and cutting and block was fit to predict standing biomass of the calibration cuts. To address the heterogeneity of the data set, variance was modelled as a power function of CSH.

After model simplification based on AIC, the final model retained the effects of CSH, cutting date, block, and stocking rate, as well as the two-way interactions of CSH and cutting date and the three-way interaction of CSH, stocking rate and block. Dividing the residual variance of the calibration model by the total variance of the standing biomass data showed an average coefficient of determination of $R^2 = 0.80$.

The final model was used to predict standing biomass from the CSH measurements taken in exclusion cages as the basis for calculating daily growth rates.

In September/October 2014 (growth period 2014:6), animals removed one cage located in tall patches under moderate stocking, so that standing biomass at the end of this growth period was unavailable. This data point was filled in by fitting a linear model containing the interactive effects of growth period, patch type, grazing intensity and block.

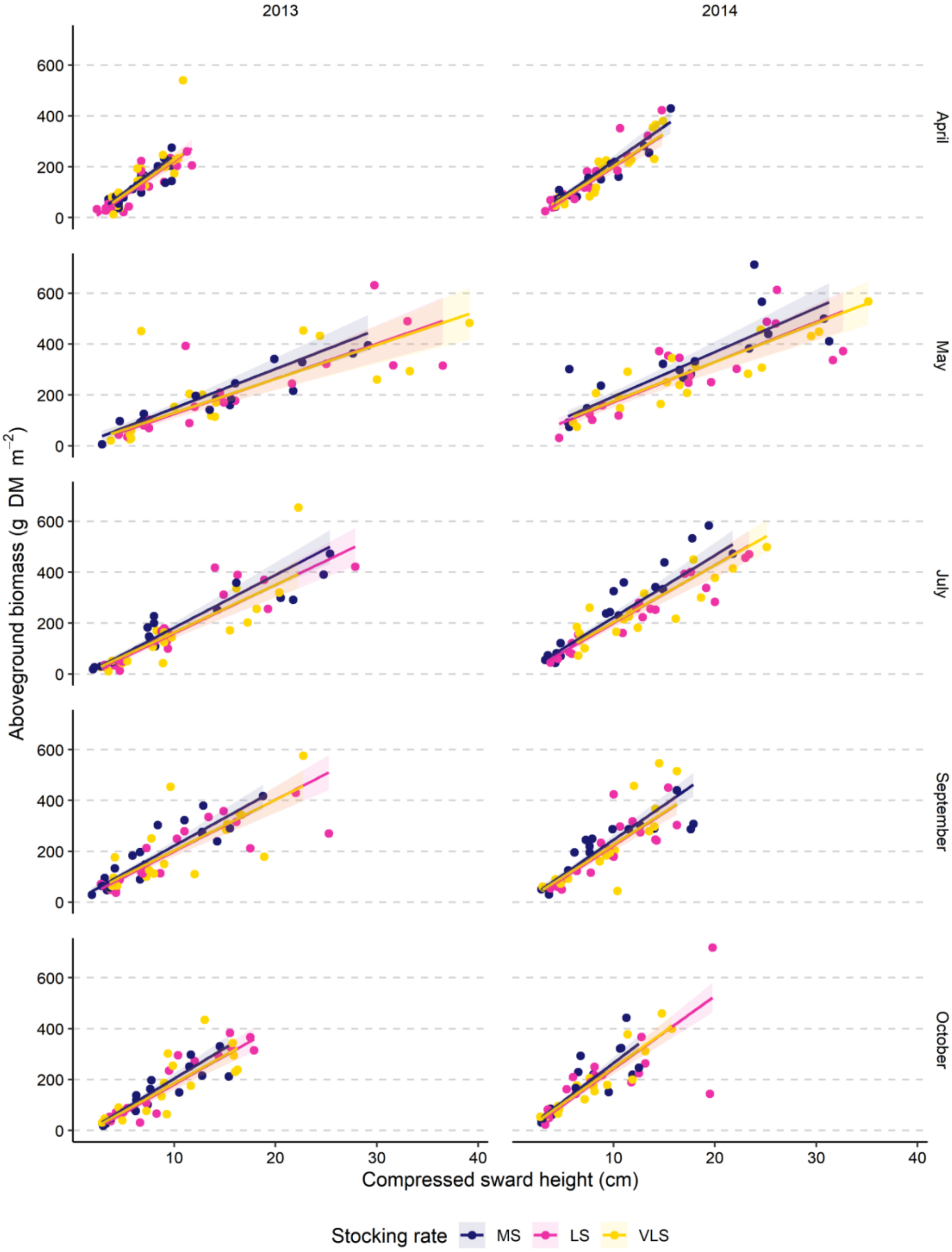


Figure S.1. Regression of standing aboveground biomass and compressed sward height (CSH) under three stocking rates (moderate, lenient and very lenient stocking) at five dates (April, May, July, September, October) in 2013 and 2014. Shown are means of three replications.

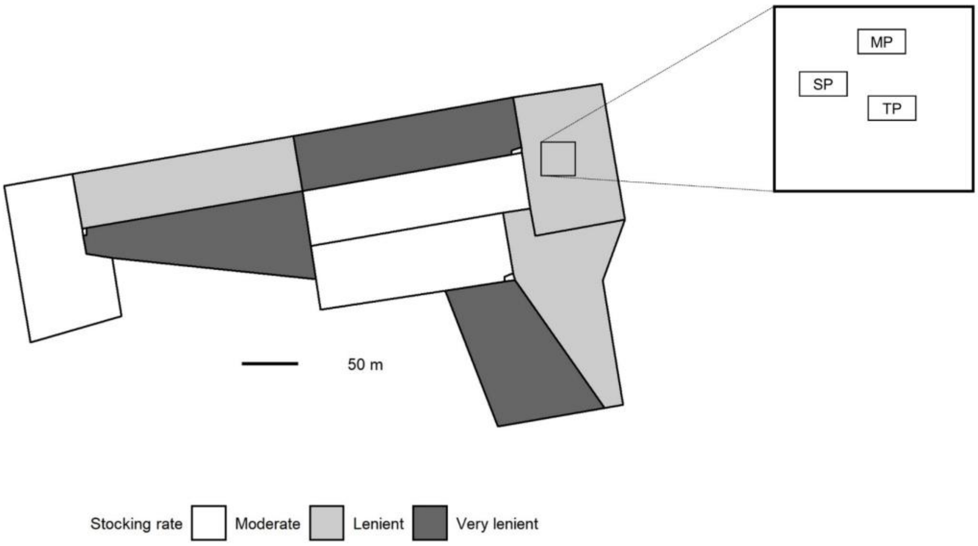


Figure S.2. Experimental area and scheme of exclusion cages placed in different patch types (short, medium, tall). Shown are nine paddocks grazed by cattle at three different stocking intensities (moderate, lenient and very lenient stocking). Per patch type and paddock, one exclusion cage (2 m × 1 m) was repeatedly re-placed. Abbreviations: MP Medium patch, SP Short patch, TP Tall patch.

Appendix II

Figure of compressed sward heights and classification thresholds for patch types

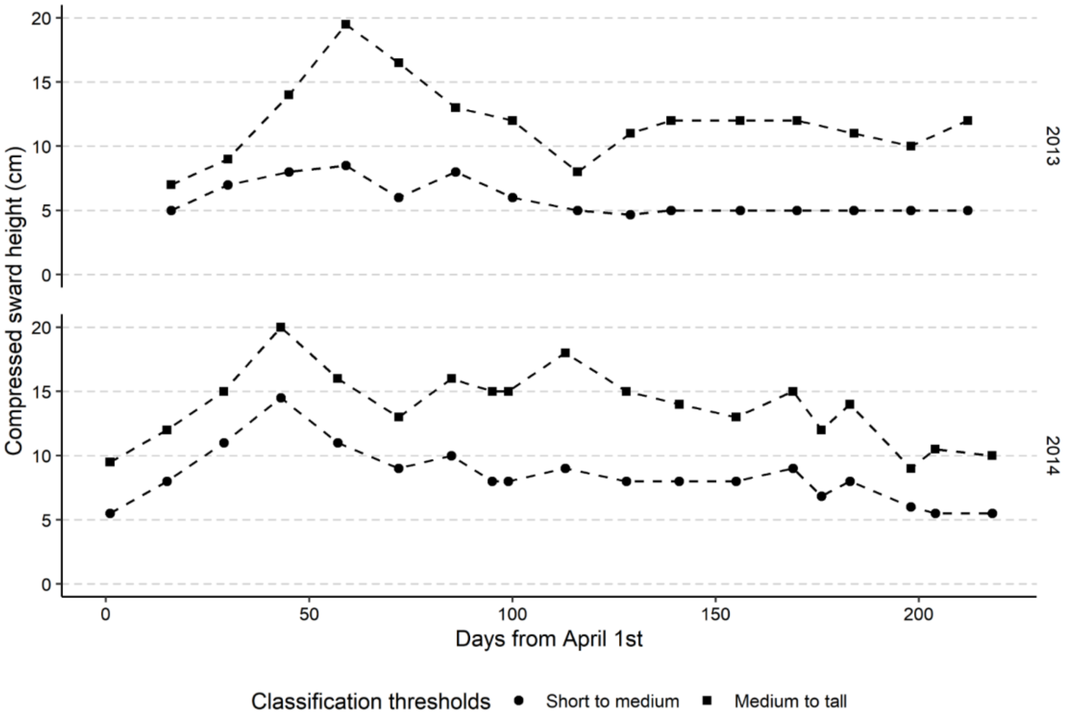
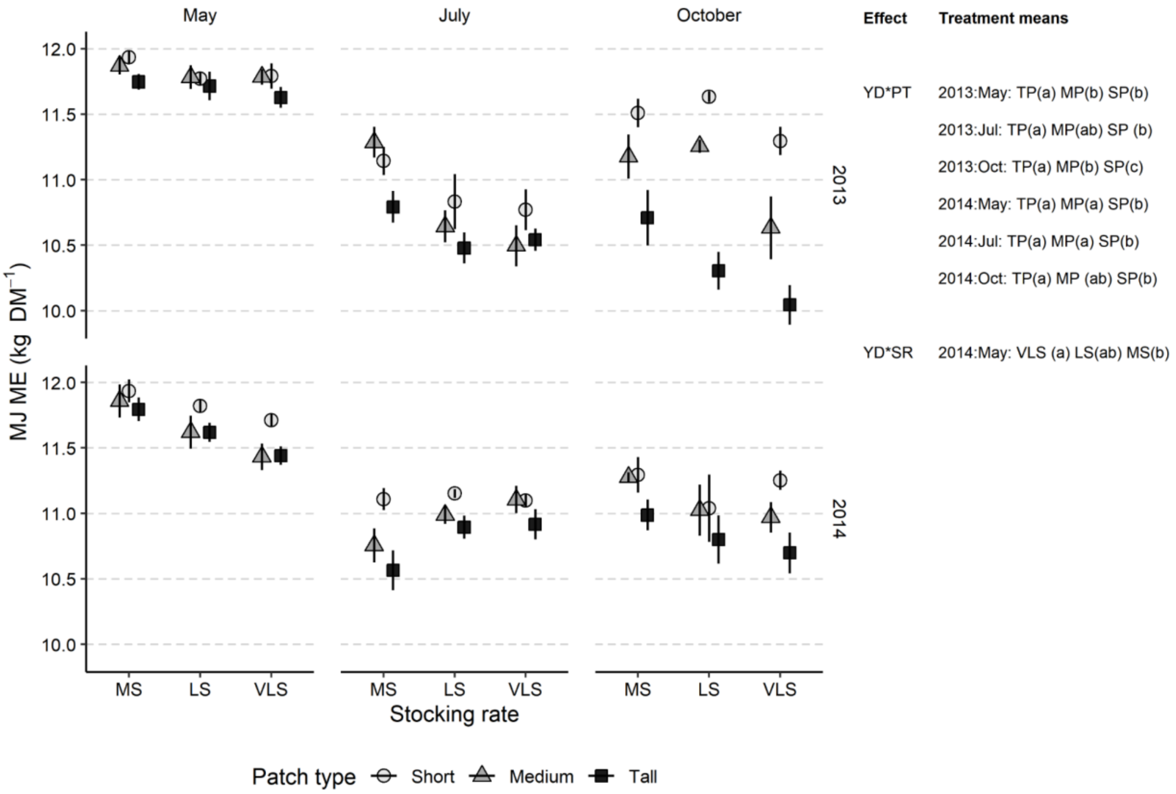


Figure AII-1. Compressed sward heights (cm) and classification thresholds (short to medium and medium to tall) for patch types differing in sward height from April 1st in 2013 and 2014. Mean sward height class thresholds were 5.9 and 8.6 (short to medium) and 11.9 and 14.1 (medium to tall), on average for 2013 and 2014.

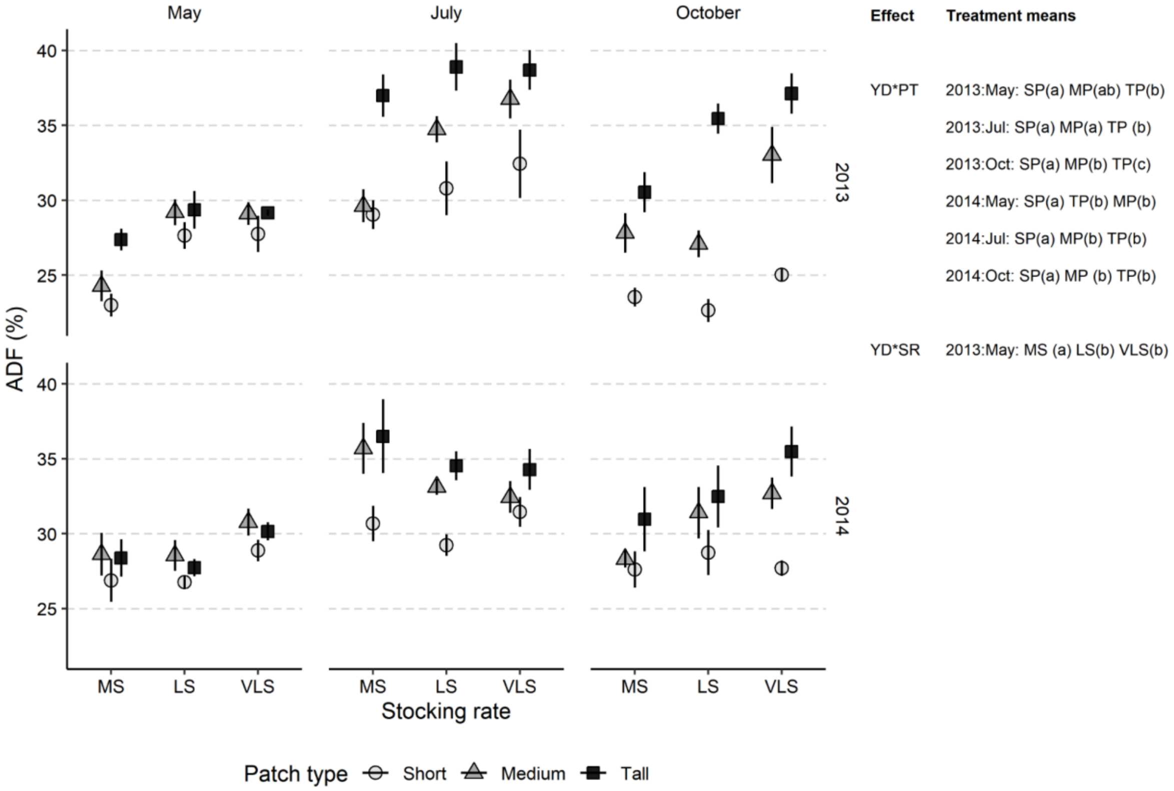
Appendix III

Figures of herbage metabolizable energy content and herbage acid detergent fibre content of hand-plucked herbage samples of short, medium and tall patches under moderate, lenient and very lenient stocking in May, July and October of 2013 and 2014.



Effect	Treatment means
YD*PT	2013:May: TP(a) MP(b) SP(b) 2013:Jul: TP(a) MP(ab) SP (b) 2013:Oct: TP(a) MP(b) SP(c) 2014:May: TP(a) MP(a) SP(b) 2014:Jul: TP(a) MP(a) SP(b) 2014:Oct: TP(a) MP (ab) SP(b)
YD*SR	2014:May: VLS (a) LS(ab) MS(b)

Figure AIII-1. Metabolizable energy content of hand-plucked herbage samples of short, medium and tall patches under moderate, lenient and very lenient stocking in May, July and October of 2013 and 2014. Shown are means and standard errors of three replications. Treatment means were compared within factor levels when involved in an interaction (method: Tukey, $P < 0.05$). Abbreviations: ME Metabolizable energy content, MS Moderate stocking, MP Medium patch, LS Lenient stocking, SP Short patch, SR Stocking rate, TP Tall patch, VLS Very lenient stocking, YD Year*Date (combination of the factors ‘year’ and ‘date’).



Effect	Treatment means
YD*PT	2013:May: SP(a) MP(ab) TP(b)
	2013:Jul: SP(a) MP(a) TP (b)
	2013:Oct: SP(a) MP(b) TP(c)
	2014:May: SP(a) TP(b) MP(b)
	2014:Jul: SP(a) MP(b) TP(b)
	2014:Oct: SP(a) MP (b) TP(b)
YD*SR	2013:May: MS (a) LS(b) VLS(b)

Figure AIII-2. Acid detergent fibre content of hand-plucked herbage samples of short, medium and tall patches under moderate, lenient and very lenient stocking in May, July and October of 2013 and 2014. Shown are means and standard errors of three replications (LS May 2013 and MS Oct 2014: 2 replications). Treatment means were compared within factor levels when involved in an interaction (method: Tukey, $P < 0.05$). Abbreviations: ADF Acid detergent fibre, MS Moderate stocking, MP Medium patch, LS Lenient stocking, SP Short patch, SR Stocking rate, TP Tall patch, VLS Very lenient stocking, YD Year*Date (combination of the factors ‘year’ and ‘date’).

DECLARATIONS

I, hereby, declare that this Ph.D. dissertation has not been presented to any other examining body either in its present or a similar form.

Furthermore, I also affirm that I have not applied for a Ph.D. at any other higher school of education.

Göttingen, 22 June 2020 Dorothee Ebeling

I, hereby, solemnly declare that this dissertation was undertaken independently and without any unauthorized aid.

Göttingen, 22 June 2020 Dorothee Ebeling

LIST OF PUBLICATIONS

Peer-reviewed journal articles

Ebeling, D., Tonn, B., & Isselstein, J. (2020). Primary productivity in patches of heterogeneous swards after 12 years of low-intensity cattle grazing. Grass and Forage Science, 75, 398–408. https://doi.org/10.1111/gfs.12505

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Conference publications

Refereed conference papers

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Köhler, J., Ebeling, D., Tonn, B. , & Isselstein, J. (2016). Root mass of differentially defoliated patches on a long-term grazing experiment. Grassland Science in Europe 21, 711-713. ISBN 978-82-17-01677-9

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Ebeling, D., Tonn, B. , & Isselstein, J. (2015) Wieviel Futteraufwuchs „geht am Rindermaul vorbei"? Brutto- und Nettoweideleistung einer extensiven Rinderstandweide unter verschiedenen Beweidungsintensitäten. 59. Jahrestagung der AGGF „Grünland effizient und umweltschonend nutzen", 27 – 29 August 2015, Aulendorf, Germany.

Awarded Posters

Ebeling, D., Tonn, B. , & Isselstein, J. (2014) Produktivität verschiedener Grasnarbenhöhenbereiche (Patches) auf extensiven Rinderstandweiden unter dem Einfluss von unterschiedlichen Beweidungsintensitäten. 58. Jahrestagung der Arbeitsgemeinschaft Grünland und Futterbau der Gesellschaft Pflanzenbauwissenschaften e.V., 28-30 August 2014, Arnstadt, Germany. (1 place)

Ebeling, D., Köhler, J., Breitsameter, L. , & Isselstein, J. (2013) Regenerationsfähigkeit verschiedener Rasengräser nach Trockenstresseinwirkung. 57. Jahrestagung der Arbeitsgemeinschaft Grünland und Futterbau der Gesellschaft für Pflanzenbauwissenschaften e.V., 29-31 August 2013, Triesdorf, Germany. (3 place)

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