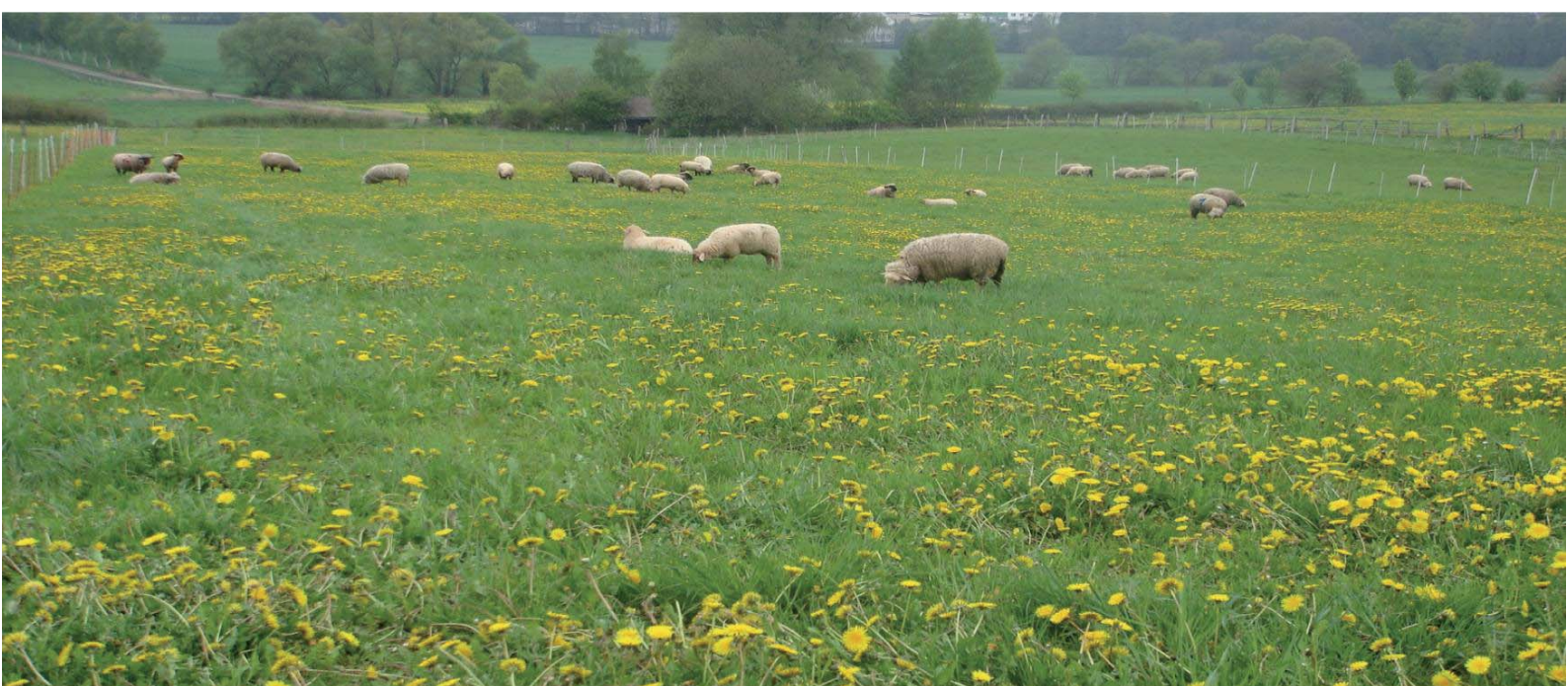




# **GRAZING BEHAVIOR AND FORAGE SELECTIVITY OF CATTLE AND SHEEP GRAZING ALONE OR TOGETHER ON SWARDS DIFFERING IN PLANT SPECIES DIVERSITY**

MARIO CUCHILLO HILARIO



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Grazing behavior and forage selectivity of cattle and sheep grazing alone or together on swards differing in plant species diversity



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together on swards differing in plant species diversity**

Dissertation  
to obtain the Ph. D. degree  
in the Faculty of Agricultural Sciences,  
Georg-August-University Göttingen, Germany

presented by

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## **General introduction**



Conservation of natural resources and wider implementation of biodiversity-targeted production means to facilitate environmental sustainability, are main goals of current farming systems (de Bello et al. 2010). In this regard, grassland greatly contributes to ecological conservation since this area comprises about of forty percent of the earth surface (Lemaire et al. 2005). However, commonly managed high productive grasslands contain a relatively low plant species number. The main focus is on the production of animal feed to achieve a high livestock performance on the expense of other ecosystem services (Sanderson et al. 2007). In contrast, on more diverse grasslands, the herbage production could be generally lower; however, in adverse environments plant diversity may have a production advantage combined with additional ecosystem services (Isbell et al. 2011; Wrage et al. 2011). As farming management influences grassland plant diversity and thereby affecting further complementary ecosystems services, farming practices aiming at the maintenance and enhancement of grassland diversity are to be developed (Dumont et al. 2011; Metera et al. 2010).

An important issue for diversity conservation includes the study of herbivores. Domestic ruminants are able to change botanical composition and structure of the sward by herbage selection, trampling, nutrient recycling and manure deposition (Soder et al. 2009; Dorrough et al. 2007; Rook et al. 2004). Different grazer species may have greater influence than only one herbivore species, i.e. co-grazing of two or more grazer species is expected to have additional effects on swards botanical composition than mono-grazing. In these conditions, grazing may increase rare or endangered plant species and maintain more productive species in stable abundance (Pykälä 2005; Isselstein et al. 2007).

Besides, complementary use of resources by co-grazing might result in improvements in the performance of single animal species or at best even of all species (Benavides et al. 2009; Animut and Goetsch 2008). Therefore, to obtain reasonable herbage productivity and consequently positive animal response; strategies aiming at matching both herbage production and herbivore feed requirements are mandatory.

So far, precise knowledge on potential interactions between sward diversity and co-grazing is not available. A better understanding of how plant and herbivores operate in the grazing process, would allow to design better grazing schemes to augment pasture-animal welfare and productivity. Thus, this study aim at contributing to a better understanding of the behavior patterns and forage selectivity of cattle and sheep, as well as the relationship between plant diversity and herbage-animal responses.

In the **first chapter**, we analyzed the interaction between botanical composition (diverse or grass dominated swards) and animal species [(co-)grazing cattle and sheep], in terms of main (grazing, walking and ruminating) and secondary (bites per minute, steps per minute and bites per step) behavior patterns of cattle and sheep.

In the **second chapter**, the study deals with the intake preferences for six main forage species of (co-)grazing cattle and sheep on diverse or grass dominated swards.

In the **third chapter**, we discuss the relationships between plant diversity and herbage productivity. Later, we explain the viability to use grazing as an instrument to enhance or recover grasslands botanical composition and plant diversity. Further, we underline the importance of interdisciplinary research groups to obtain productive and ecological benefits from grasslands.

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# Chapter 1

## **Behavior patterns of (co-)grazing cattle and sheep on swards differing in plant diversity**

*In preparation*

## **Abstract**

Both botanical composition and the presence of different grazer species may modify the grazing efficiency and ingestive behavior of ruminants. However, at present, precise knowledge on potential interactions between sward diversity and type of grazer is not available. The objective of this study was to evaluate the effect of mono- or co-grazing of sheep and cattle, as well as the influence of sward botanical composition (either diverse or grass-dominated swards) in a fully factorial design on animal behavior patterns. The main behavior (grazing, walking, ruminating) of two core animals per paddock and animal species was recorded in scan samplings every ten minutes from 6 a.m. to 22 p.m. in 2009 and 2010. Four daylight quarters were differentiated. Additionally, bites per minute, bites per step and steps per minute were observed 15 times per core animal and day. There were significant differences between sheep and cattle. Cattle varied their grazing behavior depending on the presence of sheep. However, plant diversity had no effect on cattle behavior. Cattle combined longer grazing periods with longer times for ruminating whereas sheep kept more regular time for grazing and ruminating. For sheep behavior, plant diversity rather than mono or co-grazing management was the determinant factor. Both, cattle and sheep had a tendency to spend more time grazing and less time ruminating towards the end of the day. The ability of sheep to modify grazing behavior at different plant assemblages and cattle to adjust the ingestive behavior differently to co-grazing management, may reinforce their aptitude to maintain plant diversity on both diverse and grass dominated swards in co-grazing schemes.

Keywords: biodiversity, mixed grazing, botanical composition, foraging behavior, grassland

## 1. Introduction

Animal behavior is influenced by a range of factors: environment, weather, temperature, geographical conditions, sward surface height, time at pasture, age, herbage allowance and stock density, among others. Botanical composition is one of these factors. It affects the selectivity, but is also affected by grazer's selectivity, which differs for different animal species (Rutter, 2006; Benavides et al., 2009; Villalba and Provenza, 2009). For instance, in grasslands with high cluster distribution of less preferred forages, intake rate of more palatable forages by cattle increased. Conversely, in swards with more evenly distribution of less preferred species, intake of more palatable forages diminished (Wang et al., 2010). In this sense, spatial distribution of forages and botanical composition of grasslands modify behavior of ruminants (Hejmanová et al., 2009; Lin et al., 2011). Moreover, the time distribution of grazing animals might also vary on diurnal and seasonal timescales, with length of daylight and temperature playing important roles (Dumont et al., 2004; Röver, 2006; Rutter, 2010).

Employing grazing to manage botanical composition of grasslands is a low-cost practice, because it requires only little capital investment. In addition it provides several ecosystem services (Metera et al., 2010; Wrage et al., 2011). To this effect, advantages of grazing implementation include better control of weeds, fire control of grazed pastures, increase plant diversity, avoidance of fodder senescence, increasing seed dispersal, promote the creation of micro-niches within pastures by forage selection, enhance the generation of micro-catchments by trampling and facilitate a more efficient recycling of nutrients by manure deposition (Abaye et al., 1994; Rook et al., 2004; Celaya et al., 2007; Soder et al., 2007; Smith et al., 2010). Moreover, co-grazing of two or more grazer species is expected to have additional benefits than mono-grazing. Complex interactions of intake preferences boost competence for food and lead to wider effects on vegetation than mono-grazing. Besides, complementary use of resources by co-grazing might result in improvements in the performance of single animal species or at best even of all species (Animut and Goetsch, 2008; Benavides et al., 2009).

To this end, studying grazing behavior is seen as an essential source of information to design improved grazing schemes that augment animal productivity and welfare (Gibb, 2006; Utsumi et al., 2009; Lin et al., 2011). Likewise, since the plant-animal-interaction knowledge is considered a useful means to reshape the diversity of grasslands, a better understanding of this relationship is mandatory to maintain or improve grasslands ecosystem services. However, little is known about animal behavior as depending on botanical composition and co-grazing species in open grasslands. The majority of studies in this context have been carried out as cafeteria trials or with few choices of forages at pasture, hindering a natural selection of herbivores. Thus, in this study, we evaluate the animal behavior patterns of cattle and sheep pasturing alone or together at two different plant diversity levels on semi-natural grassland. We hypothesized that 1) the plant diversity (diverse or grass dominated swards) and 2) the type of grazing (mono- or co-grazing), would modify the grazing behavior of cattle or sheep. Results are discussed in relation to implications for animal behavior patterns in terms of grassland diversity and the benefits and constraints of mono and co-grazing managements.

## **2. Material and methods**

### *2.1. Experimental set up*

A trial was carried out on mesotrophic permanent grassland in the Solling Uplands of Lower Saxony, Germany, to identify the animal behavior patterns of cattle and sheep grazing alone or together from May to September of 2009 and 2010. Species diversity of paddocks was manipulated by the use of herbicides [(Starane XL® (Fluroxypyr-1-methylheptyl-ester) and Duplosan® ((2R)-2-(4-chloro-2-methylphenoxy) propanoic acid )] in 2006 and 2009, resulting in grass-dominated swards (7 species per 9 m<sup>2</sup>) in contrast to untreated diverse swards (14 species per 9 m<sup>2</sup>) with grasses, forbs and legumes (Seither, 2011). Each sward type was combined with three grazing treatments: C= cattle mono-grazing; S= sheep mono-grazing and CS= cattle and sheep co-grazing. The six treatments were set up on paddocks of 0.5 ha each, replicated three

times in blocks that were grazed rotationally. In May and June, cattle (German Simmental) and sheep (Black headed and Leine breeds) were stocked as follows: for rotation one and two, grazing pressure was  $12.1 \pm 0.9$  and  $12.7 \pm 0.7$  LU ha<sup>-1</sup>, respectively (Livestock unit = 500 kg of animal live weight). In co-grazing plots, LU contributions of cattle and sheep were each half of the LU of mono-grazed plots. Due to a lower herbage production of the swards, stocking density per plot was reduced from July onwards (third rotation) to  $8.2 \pm 0.5$  LU ha<sup>-1</sup>. Ruminants were moved to the next block when the average compressed sward height had decreased to ca. 6 cm (Castle, 1976).

## *2.2 Animal behavior*

The main (grazing, walking, and ruminating) and secondary (bites per minute, steps per minute and bites per step) behavior patterns of two core animals per mono-grazed paddock were recorded on two blocks (A and B). In co-grazed plots, two animals per species were observed (i.e. two cattle and two sheep). The geographical conditions of block C made it impossible to perform the scans without disturbing the normal behavior of animals. Main and secondary behavior patterns were obtained according to Dumont et al. (2004). Main behavior patterns were obtained by conducting scan sampling every ten minutes from six a.m. to ten p.m. Four day-light quarters (DLQ) of four hours each (DLQ1= from 0600 to 1000 h; DLQ2 = from 1000 to 1400 h; DLQ3= from 1400 to 1800 h and DLQ4= from 1800 to 2200 h) were regarded to better characterize the main behavior patterns along the day (Dumont et al., 2004; Röver, 2006). For the third rotation of 2010, it was not possible to conduct animal observations after nine p.m. Darkness impeded clear scans of animals. Here, the percentage of three observational hours for the last DLQ was taken instead of four hours (from 1800 to 2100 h). Secondary behavior patterns were obtained from 15 measurements per core animal and day. Main and secondary behavior patterns were recorded on five days in 2009 and seven days in 2010 throughout the whole grazing season from May to September.



### *2.3 Statistical analysis*

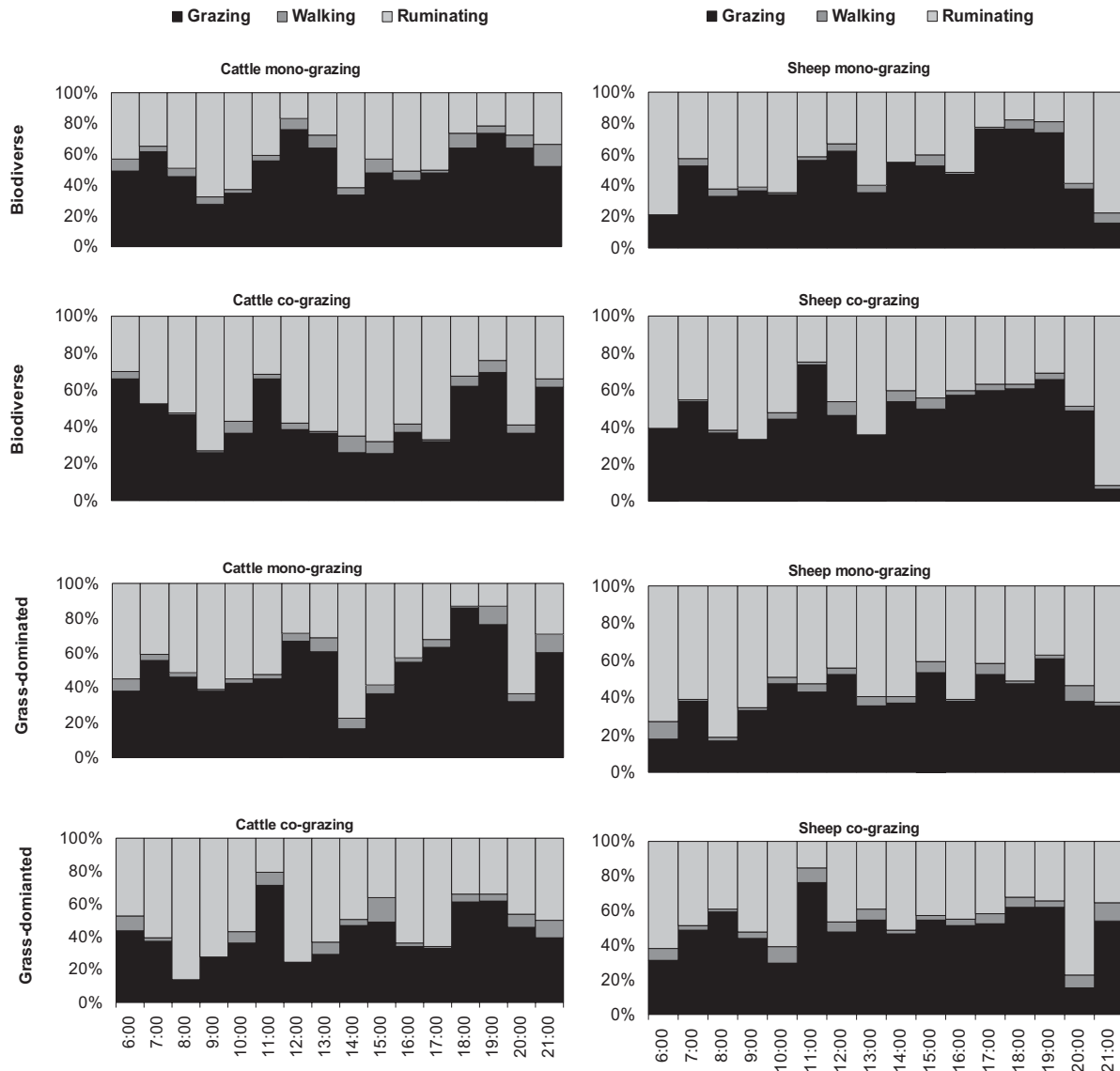
Animal behavior observation was analyzed by ANOVA using the Proc Mixed model of SAS v.9.2 (2009). Plots were considered the statistical unit. All factors were treated as fixed, however, block was considered random. Observations of the same animal were nested. The model employed was  $Y_{ij} = \mu + PD_i + GT_j + PD_i \times GT_{ij} + e_{ij}$ ; where  $Y$  is the target variable,  $\mu$  is the overall mean,  $PD$ = plant diversity treatment (Diverse or grass-dominated swards)  $i$ ,  $GT$ = grazing type (cattle or sheep / mono- or co-grazing)  $j$  and  $e$ = random experimental error. Comparison of the means with a significant difference ( $\alpha= 0.05$ ) was established by Tukey's test using the macro PDMIX612 of SAS (Saxton, 1998).

## **3. Results**

### *3.1. Behavioral patterns across observational days*

Diurnal activities of cattle and sheep are shown in figure 1. Cattle used on average up to 47 % for grazing, 6 % for walking and 47 % for ruminating, whereas sheep spent 49 % for grazing, 4 % for walking and 47 % for ruminating. Both ruminant species had two major grazing periods along the observational days. Peaks of grazing activity were registered at eleven to twelve a.m. and at six to seven p.m. However, an additional peak of grazing activity was observed from six to seven a.m. Cattle combined longer grazing periods with longer times for ruminating after peak grazing events, whereas sheep alternated shorter times for grazing and ruminating.

Figure 1. Distribution time of cattle and sheep spent for grazing, walking or ruminating when grazing alone or together on grass swards differing in plant species diversity (diverse or grass-dominated) along an observation day. Values shown are means of animal observations within the same treatments for the complete grazing seasons of 2009 and 2010.



### 3.2. Effects of plant diversity and type of grazing

Results show that on mono grazed paddocks cattle spent more time grazing (51 and 49 %) than cattle co-grazing (43 and 44 %, for diverse and grass-dominated swards, respectively), albeit this effect not being significant (Table 1). In general, grazing and ruminating behavior of cattle was affected by grazing treatment, i.e. that cattle behavior varied depending on the presence of sheep. In contrast, plant diversity had no effect on cattle behavior. For walking, no

significant differences were observed for cattle neither due to plant diversity ( $P = 0.307$ ) nor to grazing type ( $P = 0.786$ ).

Interestingly, for sheep the time spent grazing on grass-dominated swards was larger (52 and 52 %) than on diverse swards (45 and 49 % for mono and co-grazing, respectively), however, only mono-grazing treatments were significantly different ( $P = 0.010$ ). Sheep grazing on diverse swards tended to spend more time ruminating (51 and 46.1 %) than those grazing on grass-dominated swards (44 and 45 % for mono and co-grazing, respectively). In contrast to cattle, the time spent for walking of sheep was affected by sward diversity, i.e. diverse swards tended to increase the time sheep allocated to walking ( $P = 0.050$ ).

### *3.3 Day-light quarters effect*

Day-light quarters (DLQ) had significant effects on the grazing behavior of cattle and sheep (Table 1). For all swards and grazing treatments there was a consistent effect of time spent for grazing with an increase from dawn to dusk while it was vice versa for ruminating, e.g. cattle mono-grazing on diverse swards spent the smallest amount of time for ruminating in DLQ4 (24 %) and the largest for grazing (69 %). Generally, the time spent walking by cattle tended to increase in all cases from DLQ1 to DLQ4.

For sheep, the time spent grazing also increased from the early morning (DLQ1 and 2) to the evening (DLQ3 and 4). At the same time, the time spent for ruminating decreased. The time spent walking by sheep also tended to increase from DLQ1 to DLQ4.

Table 1. Percentage time of cattle and sheep spent for grazing, walking or ruminating when grazing alone or together on grass swards differing in plant species diversity (diverse or grass-dominated) along an observation day. Values shown are means of animal observations within the same treatments for the complete grazing seasons of 2009 and 2010.

Cattle																	Sheep													
Average										P value							Average							P value						
DLQ		Diverse			Grass-dominated			SEM		PD		GT		PD*GT		Diverse			Grass-dominated			SEM		PD		GT		PD*GT		
		C		CS		C		CS								S		CS		S		CS								
Grazing	1	48.6	37.5	47.8	47.0	0.12	0.209	0.114	1.151	30.5 <sup>b</sup>	42.2 <sup>ab</sup>	45.3 <sup>a</sup>	46.1 <sup>a</sup>	0.05	<b>0.018</b>	0.062	0.090													
	2	52.4	42.7	50.7	41.7	0.07	0.550	<b>0.012</b>	0.872	48.2	51.4	50.1	54.4	0.04	0.424	0.235	0.860													
	3	39.9	48.0	41.0	31.3	0.18	0.075	0.819	0.055	46.0	51.6	54.2	51.9	0.02	<b>0.042</b>	0.317	0.054													
	4	69.0 <sup>a</sup>	45.0 <sup>b</sup>	61.3 <sup>ab</sup>	58.1 <sup>ab</sup>	0.19	0.458	<b>0.013</b>	<b>0.033</b>	61.8	53.2	61.7	54.7	0.16	0.676	<b>0.021</b>	0.671													
	Average	51.3	43.1	49.4	44.4	0.11	0.884	<b>0.036</b>	0.471	45.2 <sup>b</sup>	49.0 <sup>ab</sup>	51.9 <sup>a</sup>	51.5 <sup>a</sup>	0.04	<b>0.013</b>	0.202	0.132													
Walking	1	4.7	3.9	6.5	3.5	0.03	0.461	0.088	0.264	3.6	3.8	3.5	1.8	0.04	0.179	0.332	0.244													
	2	4.9	4.3	6.8	5.7	0.03	0.069	0.266	0.728	4.9	5.8	3.7	3.9	0.02	<b>0.036</b>	0.522	0.360													
	3	4.5	6.3	5.3	6.8	0.03	0.393	0.082	0.810	3.8	4.0	3.0	5.5	0.03	0.773	0.197	0.284													
	4	7.4	9.3	9.0	6.5	0.05	0.524	0.717	0.066	4.7	6.3	6.4	3.9	0.04	0.724	0.507	0.059													
	Average	5.1	5.9	6.7	5.6	0.02	0.307	0.786	0.176	4.2	5.0	4.1	3.5	0.02	<b>0.050</b>	0.763	0.099													
Ruminating	1	47.0	59.9	46.0	50.0	0.08	0.114	<b>0.035</b>	0.168	65.7	53.9	51.1	51.9	0.06	<b>0.033</b>	0.100	0.071													
	2	42.8	53.0	42.6	53.0	0.07	0.943	<b>0.009</b>	0.986	47.0	42.8	46.1	42.0	0.06	0.786	0.235	0.999													
	3	55.6	45.5	53.6	62.0	0.17	0.079	0.791	<b>0.042</b>	50.2 <sup>a</sup>	44.5 <sup>ab</sup>	42.9 <sup>b</sup>	43.6 <sup>b</sup>	0.01	<b>0.016</b>	0.068	<b>0.034</b>													
	4	23.6 <sup>b</sup>	45.8 <sup>a</sup>	29.6 <sup>ab</sup>	35.1 <sup>ab</sup>	0.18	0.494	<b>0.009</b>	0.051	33.8	41.7	32.0	41.6	0.15	0.730	<b>0.015</b>	0.756													
	Average	43.4	50.8	43.8	49.8	0.09	0.881	<b>0.023</b>	0.705	50.6 <sup>a</sup>	46.1 <sup>ab</sup>	44.2 <sup>b</sup>	45.1 <sup>b</sup>	0.03	<b>0.010</b>	0.115	<b>0.033</b>													

DLQ: day-light quarter; C= cattle mono-grazing; S= sheep mono-grazing; CS= Cattle and sheep co-grazing. SEM= standard error of the mean. PD= plant diversity treatment. GT= grazing type. Effects in bold characters are significant at  $P < 0.05$ . Within a row, means without a common superscript differ at  $P < 0.05$

### 3.4 Secondary behavior patterns

Table 2 shows the secondary behavior patterns of cattle and sheep (bites per minute, steps per minute, and bites per step). In general, there were little effects of either sward composition or grazer species. However, an effect of plant diversity ( $P = 0.005$ ), grazer species ( $P = 0.004$ ) and their interaction ( $P = 0.001$ ) was found for bites per step of cattle. Cattle mono-grazing on diverse swards showed the lowest bite rate (57 bites per minute). Sheep co-grazing on diverse swards had an increased step rate ( $P < 0.007$ ).

Table 2. Bites per minute (BPM), steps per minute (SPM) and bites per step (BPS) of cattle and sheep spent for grazing, walking or ruminating when grazing alone or together on grass swards differing in plant species diversity (diverse or grass-dominated) along an observation day. Values shown are means of animal observations within the same treatments for the complete grazing seasons of 2009 and 2010.

		Means				<i>P</i> value			
		Diverse		Grass-dominated		SEM	PD	GT	PD*GT
		Mono grazing	Co-grazing	Mono grazing	Co-grazing				
<b>Cattle</b>	BPM	57.4 <sup>c</sup>	63.4 <sup>a</sup>	63.1 <sup>a</sup>	61.2 <sup>b</sup>	0.00	<b>0.005</b>	<b>0.004</b>	<b>0.001</b>
	SPM	8.5	9.4	9.1	9.2	0.01	0.545	0.174	0.278
	BPS	7.2	7.0	7.1	6.8	0.01	0.710	0.458	0.818
<b>Sheep</b>	BPM	53.1	62.6	53.1	54.6	0.26	0.441	0.309	0.449
	SPM	7.8 <sup>b</sup>	9.0 <sup>a</sup>	8.1 <sup>ab</sup>	8.9 <sup>ab</sup>	0.00	0.805	<b>0.007</b>	0.317
	BPS	7.6	7.3	7.0	6.6	0.03	0.288	0.535	0.996

SEM= standard error of the mean. PD= plant diversity treatment. GT= grazing type. Effects in bold characters are significant at  $P$  value  $< 0.05$ . Within a row, means without a common superscript differ at  $P < 0.05$ .

## 4. Discussion

We hypothesized that the interaction of sward composition and grazing type (mono- or co-grazing) would influence the behavior pattern of cattle and sheep. Different ruminant species are expected to shape and modify plant assemblages of swards by selective grazing in different ways (Fraser et al., 2007; Seither, 2011). With this in mind, the behavior patterns would be expected to differ between swards contrasting in plant diversity. Nevertheless, in our experiment

cattle do not seem to react to plant diversity with changing behavior. This result is in accordance with the findings of Hejmanová et al. (2009), who did not report any variation of cattle behavior under extensive and intensive continuous grazing. A possible explanation for this result is that cattle are limited by their anatomical characteristics to perform acute vertical selection (selection of different plant parts) being less sensible to changes in vegetation than sheep or goats (Abaye et al., 1994; Fraser et al., 2007; Benavides et al., 2009). The higher ingestion rates of cattle compared to small ruminants may help to constrain the selective grazing of large ruminants at pasture (Walker, 1994; Rutter, 2010)

Wang et al. (2010) showed that sheep intake patterns vary when they were fed with a heterogeneous source of feed and with different forage preferences. These results are in line with our findings. Ingestive behavior of sheep was affected by the plant diversity treatment. In a sense, grazing time of small ruminants increased, because of the limited ingestive capacity of the rumen hindered sheep to consume large amount of fibrous forages, seeking for more rapidly degradable forages, further being more selective. In accordance with this assumption, Metera et al. (2010) concluded that the time sheep allocated to grazing can be greatly modified by plant diversity, i.e. small ruminants need to consume dietary energy in small proportion of ingestions, so they have to choose forages with higher nutritive value than cattle.

Hewitson et al. (2005) demonstrated that sheep increased foraging efficiency utilizing short time memories to allocate preferred sources of feed (in more predictable environments) and sampling activity (in conditions with high and more complex variability of food selection). In this sense, sheep avoid unnecessary energy losses seeking for preferred forages, but at the same time performed acute feed selection among available plant species, plant proportions and plant heights (Ginane and Dumont, 2010; Lin et al., 2011). This explains why sheep respond to different plant arrays of grasslands with respect to their behavior, i.e. the larger effects of plant diversity treatment on sheep than on cattle are due to a greater selection activity of sheep (Cuchillo and Isselstein, 2010).

Soder et al. (2009), concluded that the animal-plant relationship causes an equilibrium between grazing time and digestive capacities. Thus, the fine-scale choices performed by sheep changed their time budget and grazing behavior to balance quality and quantity of the ingested feed. This explains why sheep employed more time grazing on low diverse swards compared to high diverse swards (Fraser et al., 2007; Villalba and Provenza, 2009; Metera et al., 2010). The longer time for grazing and shorter time for ruminating in low compared to high diversity swards, denoted also greater flexibility of sheep than cattle to choose higher digestible forages even when forages on offer are mainly of low quality (Fraser et al., 2007; Edouard et al., 2010; Villalba et al., 2010).

Co-grazing influenced the grazing and rumination time of cattle. Cattle modified their activities when they were grazing together with sheep. However, the total time designated to grazing and ruminating can finally result in a similar budget but with different patterns across the day (Abaye et al., 1994; Hejcmanová et al., 2009). This is supported by the observation that grazing time increases at the expense of ruminating. In contrast to grazing and ruminating, co-grazing management did not influence the time of cattle used for walking.

Benavides et al. (2009) noted that cattle, sheep and goats improved their grazing efficiency when they were co-grazing rather than mono-grazing. This demonstrates that complementarity of preferences among animal species can play an important role. However, in longer grazing periods or in overgrazing situations with mono or co-grazing management, intra and inter-specific competition of animal species may arise because of a lower availability of feed resources over time (Rook et al., 2004; Metera et al., 2010). In our study, sheep did not seem to respond with regard to their behavior when other animal species were sharing the grazing areas (with exception in DLQ4 for grazing and ruminating patterns). Rather, it was found that the behavior of sheep is almost exclusively modified by different plant assemblages (Sanderson et al., 2004; Soder et al., 2007)

Cattle showed a tendency to spend more time grazing and less time ruminating in DLQ4 in all treatments. This is in line with previous studies. Hejzmanová et al. (2009) found a similar pattern for cattle in a trial under intensive and extensive grazing. In that study, two grazing intensities were investigated. High temperature during the day resulted in a larger time spent for resting at midday and longer time for grazing during sunset and the ongoing night. In our study, cattle co-grazing on diverse swards increased the time spent grazing from the early morning into the evening. This phenomenon was also reported by Lin et al. (2011) in fat tailed sheep. However, grazing time in that study was strongly influenced by stocking density i.e. grazing time of sheep was longer when stocking density was higher. In contrast, sheep with lower stocking density used shorter time for grazing.

Grazing times of eight hours have been reported necessary for herbivores to maintain rumen functioning and sufficient degradation rates of fiber (Gibb, 2006). In the study presented here, cattle and sheep had grazing activity peaks at eleven to twelve a.m. and at six to seven p.m. Obviously, fluctuations of grazing events followed by a ruminating time in cattle were adjusted to achieve organic matter intake without affecting rumen functionality. However, small ruminants showed more homogeneous behavior to maintain their intake rates; i.e. sheep used the noon time to a comparable extent for grazing and for ruminating with a slightly higher grazing activity.

During the day, when sunlight is strong, cattle and sheep obviously consumed lower quantities of fibrous forages with a high digestibility and high rumen passage rates in order to avoid a highly filled rumen (Rutter, 2006; Sauvé et al., 2009; Rutter, 2010). Röver (2006) reported that cattle are able to shift ruminating time to the night to maximize grazing periods during daylight. However, the author correlated lower availability and lower quality of forages at the end of the grazing season that led animals to spend more time grazing during the day.

Other complementary aspects would be that as the day advances, forages have larger concentrations of non-structural carbohydrates than in the morning, furthermore, the digestibility



of the same forages is larger and passage rates are shorter at different stages of the day. So cattle and sheep seek for more palatable forages growing in the same swards in the afternoon and during the early night (Edouard et al., 2010; Villalba et al., 2010).

In addition, the “anti predator theory” states that herbivores are willing to graze at dawn and dusk to avoid a risky grazing in the darkness (Ruckstuhl et al., 2003; Gibb, 2006). Thus, cattle and sheep may be forced to consume higher rates of fibrous forages at dusk to have longer time for digestion during the night.

There were no large changes in secondary behavior patterns due to plant diversity. However, bites per minute (BPM) performed by cattle were influenced by plant diversity as well as grazer species. High bite rate (63 BPM) in co-grazing diverse swards was correlated with shorter time for grazing (43 %) and longer time for ruminating (51 %); i.e. cattle tended to spend less time grazing at high ingestive rates. A different relationship was found for cattle mono grazing on the grass dominated swards. A higher bite rate (63 BPM) was correlated with longer time for grazing (49 %) and shorter time for ruminating (44 %). In line with these results, Utsumi et al. (2009) reported bite rate of 48 and 46 BPM for cattle grazing alfalfa and tall fescue, respectively. Here, a strategy of cattle to increase walking speed between feeding stations and to forage longer times on alfalfa was found. The authors attributed this to the preference for alfalfa since this forage gave larger intake potential per bite than tall fescue. However, Dumont et al. (2007) observed a negative correlation between bite rate and stocking density in cattle grazing mountain grasses in central France. A bite rate of 57, 54 and 51 BPM was reported for high, medium and low stocking rate, respectively. Cattle adjusted the behavior to lower sward heights by increasing BPM and steps per minute. A similar result was found by Röver (2006) who reported that young bulls increased the BPM, when the availability of feed resources diminished; i.e. behavior changed to balance smaller bite sizes and lower intake rates with more time for grazing.

Sheep mono-grazing swards reduced their SPM rate compared to sheep co-grazing swards ( $P = 0.007$ ). Unlike cattle, sheep performed more steps per minute during the grazing period when cattle were on the same plots. Glienke et al. (2010) observed that sward structure modified sheep behavior. Sheep grazing a mixture of *Lolium multiflorum* and *Trifolium pratense* under different scales of defoliation (low, mean, high, and very high) varied the SPM rate (from 27 to 34 SPM) by increasing the number of switches among feeding stations with low number of steps. However, the availability of protein and NDF percentages in the herbage on offer was closely associated to the bite rate, i.e. lower BPM was noticed when the quality of forages decreased (more NDF and less protein).

In contrast, Ruckstuhl et al. (2003) reported that BPM performed by Rocky Mountain bighorn sheep (*Ovis canadensis*) was not correlated to herbage allowance. However, BPM varied according to age, sex and reproductive status, and diminished from the beginning (April) to the end (September) of the grazing season. The authors found that BPM increased generally as follows: non-lactating female sheep > sub adult ram > ram > lactating sheep. Bighorn sheep's vigilance activity against predators was related to high BPM rate; i.e. lactating sheep spent more time in alertness in comparison to rams or non-lactating sheep, increasing BPM rate.

## **5. Conclusions**

Cattle varied their grazing behavior depending on the presence of sheep. However, plant diversity had no effect on cattle behavior. Cattle combined longer grazing periods with longer times for ruminating whereas sheep kept more steady times for grazing and ruminating. Plant diversity was the determinant factor for sheep behavior, rather than mono or co-grazing management. Both cattle and sheep had a tendency to spend more time grazing and less time ruminating at the end of the day. The ability of sheep to modify grazing behavior at different plant assemblages and cattle to adjust the ingestive behavior differently to co-grazing

management, may reinforce their aptitude to maintain plant diversity on both diverse and grass dominated swards in co-grazing schemes.

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## **Chapter 2**

### **Forage selectivity of (co-)grazing cattle and sheep on swards differing in plant diversity**

*In preparation*

## Abstract

Grassland composition and animal species may affect the grazing efficiency and ingestive behavior at pasture. For pasture systems with mixed species grazing, precise knowledge on potential interactions between sward diversity and grazing behavior is not available. The objective of this study was to investigate the effect of either mono grazing of sheep and cattle or co-grazing, as well as the influence of sward botanical composition (either diverse swards or grass dominated swards) on intake choices among six target forage species. The hypothesis was tested that the sward composition and the type of grazing modify intake choices of sheep and cattle. Jacobs' selection index (JSI) was employed to quantify the proportion of preference for single species in relation to its proportion to the sward composition. Results revealed distinct intake preferences of sheep and cattle; especially, sheep were more selective than cattle. To a lesser extent, the sward composition had an effect on intake preferences. *Phleum pratense* was the most preferred forage species (JSI=0.62). *Lolium perenne*, *Taraxacum officinale* and *Trifolium repens* were also highly preferred regardless of sward composition or type of grazing (JSI=0.47, 0.32 and 0.27, respectively). *Dactylis glomerata* and *Festuca pratensis* had a tendency to increase their abundance after grazing in both, diverse and grass-dominated treatments. Co-grazing facilitated a more homogeneous consumption of the main forage species. Co-grazing might have the potential to better serve grassland biodiversity.

Keywords: biodiversity, intake choices, mixed-grazing, botanical composition, grassland

## Introduction

Complex inter-relationships between herbivores and their particular environmental circumstances strongly modify the feed selection of grazers in time and space. The two-fold animal-plant interactions have been described in which both parts are influenced by each other (Rook, *et al.*, 2004; Sanderson, *et al.*, 2007; Mazorra, *et al.*, 2009; Soder, *et al.*, 2009; Metera, *et*

*al.*, 2010). While investigating the various factors involved in these process diverse approaches had been suggested to forecast probable effects of animal feed choices in grasslands (Swain, *et al.*, 2007; Utsumi, *et al.*, 2009; Wang, *et al.*, 2010). Likewise, to understand the determinants of the herbivore selection process and to obtain more reliable and predictable results, several studies have placed attention to the conditioning of ruminants against specific botanical families and plant species, and against post-ingestive effects (Ginane and Dumont, 2006; Favreau, *et al.*, 2010; Ginane and Dumont, 2010; Ginane and Dumont, 2011).

Heterogeneity of swards is one of the main factors involved in the outcome of ruminants' feed selection. The effect of botanical composition redirect animal preferences and intake efficiency of forages (Dumont, *et al.*, 2007a; Fraser, *et al.*, 2007). Therefore, herbivores must deal with preference decisions among available resources to balance their diet with regard to the quality and quantity of the forage (Edouard, *et al.*, 2010; Thomas, *et al.*, 2010; Wang, *et al.*, 2010). In circumstances where botanical composition includes complex choice items and a wide range of well distributed plant arrays, herbivores are particularly challenged to select the most appropriate feed items according to their nutritional value and availability in the sward (Hewitson, *et al.*, 2005; Fraser, *et al.*, 2007; Favreau, *et al.*, 2010). To avoid unnecessary waste of time looking for the most preferred forages, previous experiences of herbivores at pasture are decisive elements of animal feed preference (Utsumi, *et al.*, 2009).

Since farming management influences grassland plant diversity and thereby affecting further complementary ecosystems services, farming practices aiming at the maintenance and enhancement of grassland diversity are to be developed (Metera, *et al.*, 2010; Dumont, *et al.*, 2011). However, commonly managed high productive grasslands contain a relatively low plant species number. The main focus is on the production of animal feed to achieve a high livestock performance on the expense of other ecosystem services. In contrast, on more diverse grasslands, the herbage production could be generally lower; however, in adverse environments plant diversity may have a production advantage combined with additional ecosystem services



(Sanderson, *et al.*, 2007; Wrage, *et al.*, 2011). Similarly, research has shown that the type of grazer also modifies feed selection at pasture. Precise knowledge of advantages of using mixed herds as compared to only one ruminant species to maintain or improve botanical composition of grasslands is not completely clear. However, it is accepted that cattle and sheep adjust their intake preferences if they are grazing in mono or mixed-grazing by competition among species or among peers (Celaya, *et al.*, 2007; Fraser, *et al.*, 2007; Animut and Goetsch, 2008; Fraser, *et al.*, 2009; Celaya, *et al.*, 2011). So far, no information is available on whether vegetation composition and the type of grazer interact in this respect. A deeper knowledge would help to understand how plant diversity affects animal selectivity and intake preferences. Thus, the search for an optimum use of available resources and the best suitable management of pastures to maintain plant diversity and to promote an animal friendly farming is required. This could build the basis for an improved pasture management aiming at the enhancement of animal production while maintaining plant diversity. Thus, a trial was carried out to test the feed preferences of cattle and sheep grazing simultaneously alone or together on a permanent grassland with a varying sward botanical composition.

## **Material and methods**

### **Experimental set up**

A trial was carried out on mesotrophic permanent grassland in the Solling Uplands of Lower Saxony, Germany, to identify the selectivity of feed intake of cattle and sheep grazing alone or together from May to September of 2009 and 2010. Species diversity of paddocks was manipulated by the use of herbicides [(Starane XL® (Fluroxypyr-1-methylheptyl-ester) and Duplosan® ((2R)-2-(4-chloro-2-methylphenoxy) propanoic acid)] in 2006 and 2009, resulting in grass-dominated swards (7 species per 9 m<sup>2</sup>) in contrast to untreated diverse swards (14 species per 9 m<sup>2</sup>) with grasses, forbs and legumes (Seither, 2011). Each sward type was combined with three grazing treatments: C= cattle mono-grazing; S= sheep mono-grazing and CS= cattle and

sheep co-grazing. The six treatments were set up on paddocks of 0.5 ha each, replicated three times in blocks that were grazed rotationally. In May and June, cattle (German Simmental) and sheep (Black headed and Leine breeds) were stocked as follows: for rotation one and two, grazing pressure was  $12.1 \pm 0.9$  and  $12.7 \pm 0.7$  LU ha<sup>-1</sup>, respectively (Livestock unit = 500 kg of animal live weight). In co-grazing plots, LU contributions of cattle and sheep were half of the LU of mono-grazed plots each. Due to a lower herbage production of the swards, stocking density per plot was reduced from July onwards (third rotation) to  $8.2 \pm 0.5$  LU ha<sup>-1</sup>. Ruminants were moved to the next block when the average compressed sward height had decreased to ca. 6 cm. The grazing periods lasted on average 11.0, 6.1 and 12.3 days for the first, second and third rotation, respectively. To determinate the compressed swards height, before and after three days of grazing, four measurements within a 0.5 m<sup>2</sup> in five points (subplots) distributed along a transect on each plot were carried out (Castle, 1976).

### **Forage selectivity**

Measurements of intake choices were done on six forage species widespread over the experimental grassland: *Dactylis glomerata*, *Festuca pratensis*, *Lolium perenne*, *Phleum pratense*, *Taraxacum officinale* and *Trifolium repens*. Throughout the whole season, the percentage mass of the six target species was visually assessed in five 0.5 m<sup>2</sup> subplots per plot immediately before and after a period of three grazing days on a plot. Intake choices were recorded six times in 2009 and seven times in 2010. The target species of this study were selected because they were the most abundant ones. Jacobs' selection index (JSI) was used to quantify the intake preference for single target species in relation to their proportion in the sward (Jacobs, 1974).  $JSI = \frac{ci - ai}{ci + ai - 2ciai}$ ; where  $ci$  = % forage in the diet and  $ai$  = % forage in the pasture. Here,  $ai$  was evaluated by the difference between the percentage mass of each species before and after three days of grazing. Data were transformed to have a Gaussian

distribution by adding 1 and multiply by 0.5; then, values of forage selection ranged between -1.0 (entirely rejected) to +1.0 (exclusively preferred).

### **Nutritive value of herbage**

Five herbage samples were collected on each paddock and rotation before and after three days of grazing. Therefore, herbage was cut on randomly distributed points below the disc of the rising plate meter (diameter = 30 cm) to ground level after to measure the compressed sward height of the pasture. Herbage was dried for 48 hours at 60° C. Dried herbage was ground to a particle size of 1 mm. Crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF) and soluble carbohydrates were determined using near infrared spectroscopy (NIRS), following the recommendations of VDLUFA Qualitätssicherung, Kassel-Germany for grassland herbage. Herbage samples for chemical composition analyses were taken at the same time, as swards height was determined.

### **Statistical analysis**

Results of forage selectivity were analyzed by ANOVA using the Proc Mixed model of SAS v.9.2 (2009). Plots were considered to be the statistical unit. All factors were treated as fixed, however block was considered random. Before further statistical analysis, the average percentage mass of each target species was calculated per plot. Observations in the same plot were nested. Measurements of blocks and rotations were treated as repeated measurements. The model employed was  $Y_{ij} = \mu + PD_i + GT_j + PD_i \times GT_{ij} + e_{ij}$ ; where  $Y$  is the target variable,  $\mu$  is the overall mean,  $PD$  = plant diversity treatment (diverse or grass dominated swards)  $i$ ,  $GT$  = grazing type (cattle or sheep / mono or co-grazing)  $j$  and  $e$  = random experimental error. Comparison of the means with a significant difference ( $\alpha = 0.05$ ) was established by Tukey's test using the macro PDMIX612 of SAS (Saxton, 1998).

## Results

### Compressed sward height and sward composition

The mean value of compressed sward heights differed significantly after grazing on grass dominated swards among the different grazing treatments (Figure 1). Cattle and cattle-sheep co-grazing showed the maximum compressed sward height ( $9.3$  and  $8.8 \pm 3.4$  cm, respectively); whereas swards grazed by sheep, had the lowest height ( $6.7$  cm). For diverse swards, no differences were observed among the grazing treatments ( $P > 0.05$ ), instead a lower variability of sward height was measured ( $7.7 \pm 2.5$  cm).

**Figure 1** Average compressed height ( $\pm$  standard error of the mean) of diverse and grass dominated swards grazed by cattle and sheep in mono or co-grazing before and after three grazing days for the complete grazing season of 2009 and 2010. C= cattle mono-grazing; M= mixed-grazing. PDT= plant diversity treatment. GT= grazing treatment. Means without a common letter differ at  $P < 0.05$

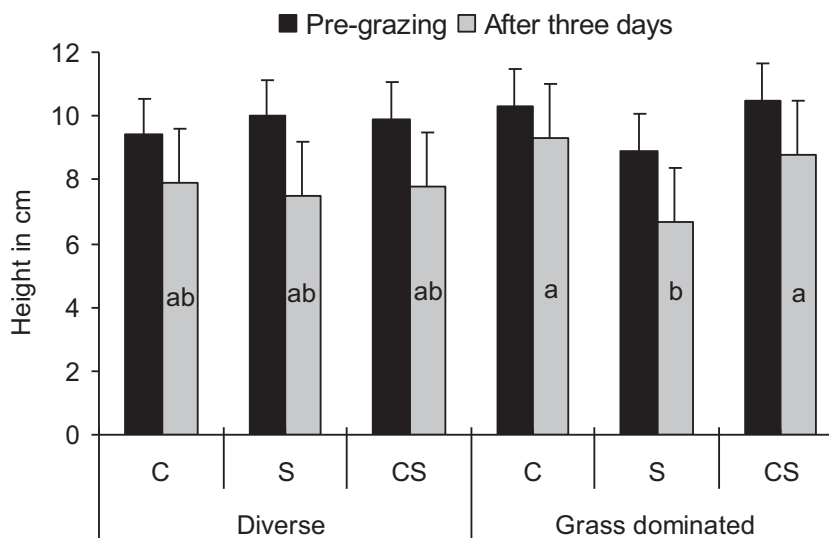
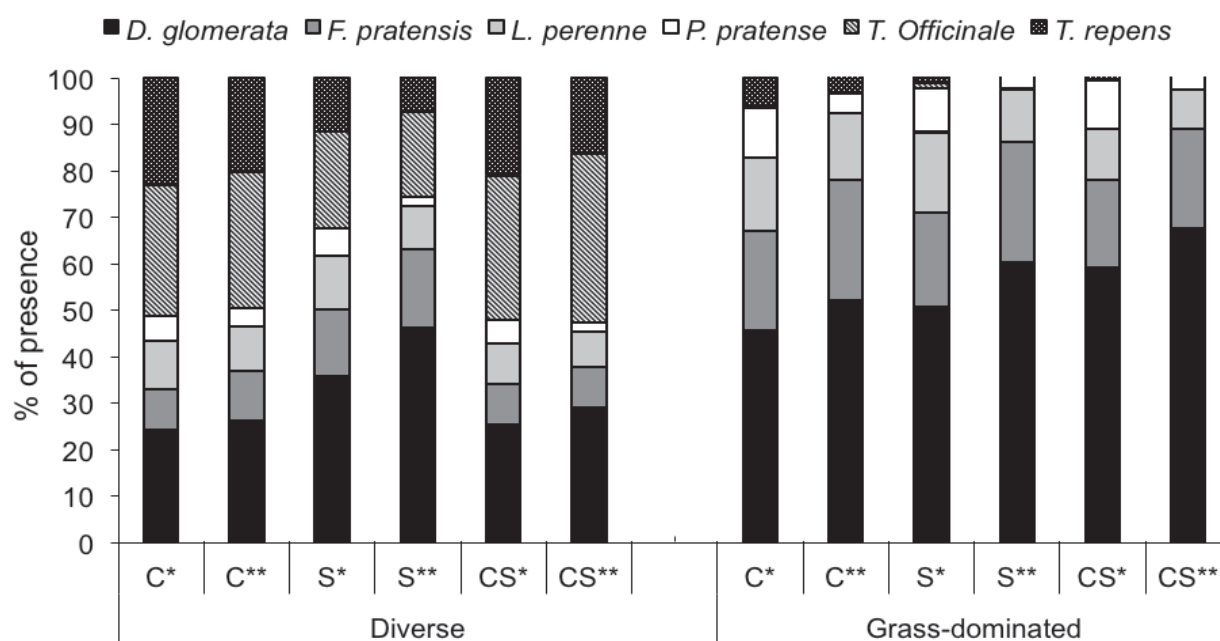


Figure 2 shows the percentage mass of the six main forages encountered on the experimental swards. *D. glomerata* and *F. pratensis* had a tendency to increase their abundance after grazing in both diverse and grass-dominated swards. In contrast, *L. perenne* and *P. pratense* seemed to reduce their post-grazing abundance, however this was stronger on grass dominated than on diverse swards. Likewise, *T. repens* diminished their biomass abundance after three days of grazing. The contribution to total biomass of the six main species studied here did not show any

great differences before (81.2 %) or after grazing (79.6 %), for diverse or for grass dominated swards.

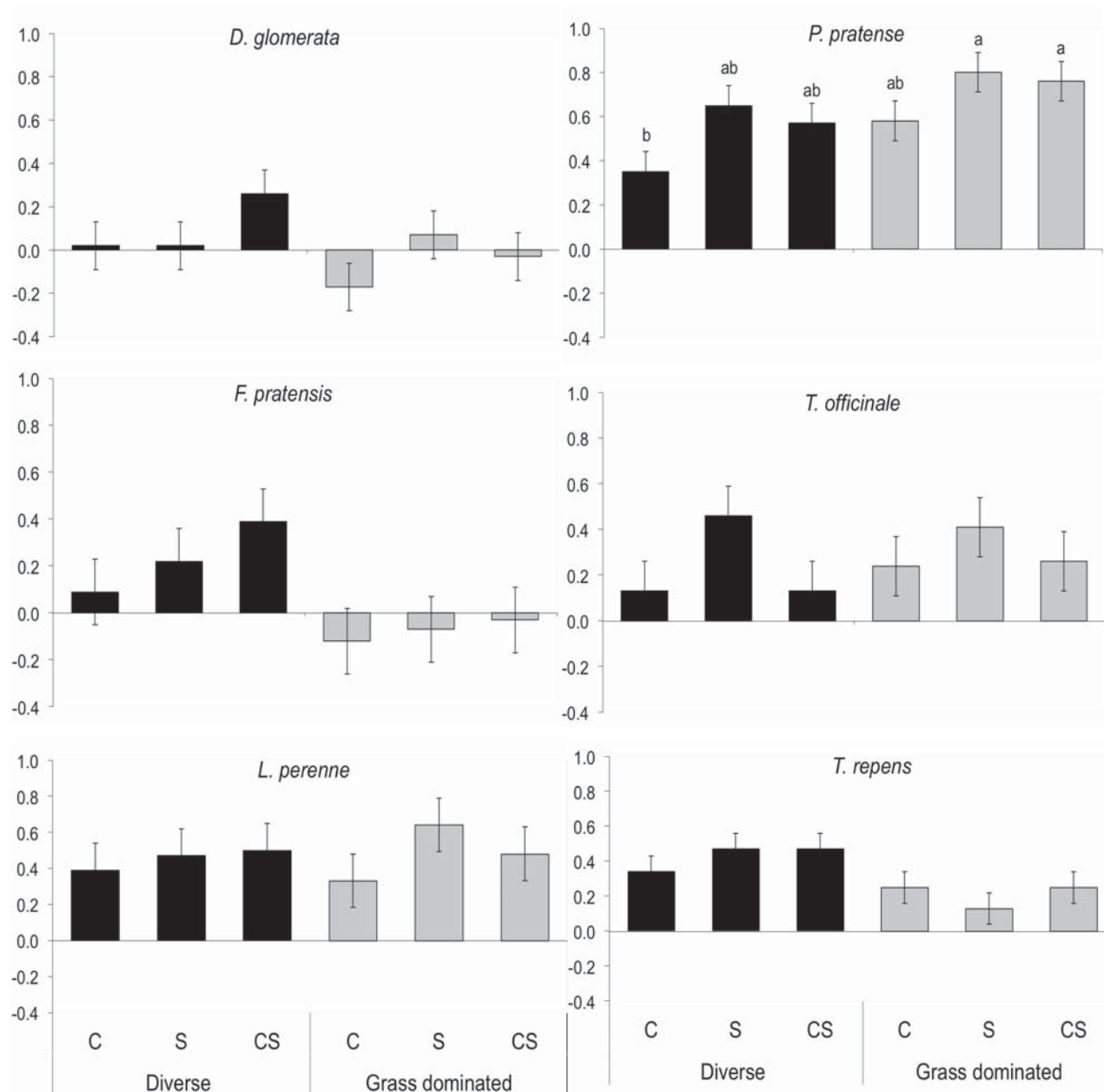
**Figure 2** Dominant plant species encountered on diverse and grass dominated swards grazed by cattle and sheep in mono or co-grazing before and after three grazing days for the complete grazing season of 2009 and 2010. C= cattle mono-grazing; S= sheep mono-grazing; CS= Cattle and sheep co-grazing. \*= pre-grazing; \*\*= after three days of grazing



### Forage selectivity

Results indicate that timothy (*P. pratense*) was the most preferred forage species with a Jacobs's selection index (JSI) of 0.62 on average (Figure 3). Here, the effects of plant diversity ( $P=0.001$ ) and grazer type ( $P=0.010$ ) were significant (Table 1). However, cattle on diverse swards consumed the lowest amount of timothy (JSI=0.35), whereas sheep and cattle-sheep co-grazing grass dominated swards had the highest intake (JSI=0.80 and 0.76, respectively). *L. perenne*, *T. officinale* and *T. repens* were also highly preferred regardless of sward composition or type of grazing (JSI average = 0.47, 0.32 and 0.27, respectively). Likewise, the intake of *T. repens* was influenced by plant diversity ( $P=0.005$ ), however, there was no interaction with type of grazing ( $P=0.375$ ).

**Figure 3** Jacobs' selection index of dominant plant species grazed by cattle and sheep grazing alone or together on grass swards differing in plant species diversity. C= cattle mono-grazing; S= sheep mono-grazing; CS= Cattle and sheep co-grazing. Values shown are least square means ( $\pm$  standard error of the mean) of observations within the same plots treatments for the complete grazing season of 2009 and 2010. Means with different letters indicate significant differences at  $P < 0.05$

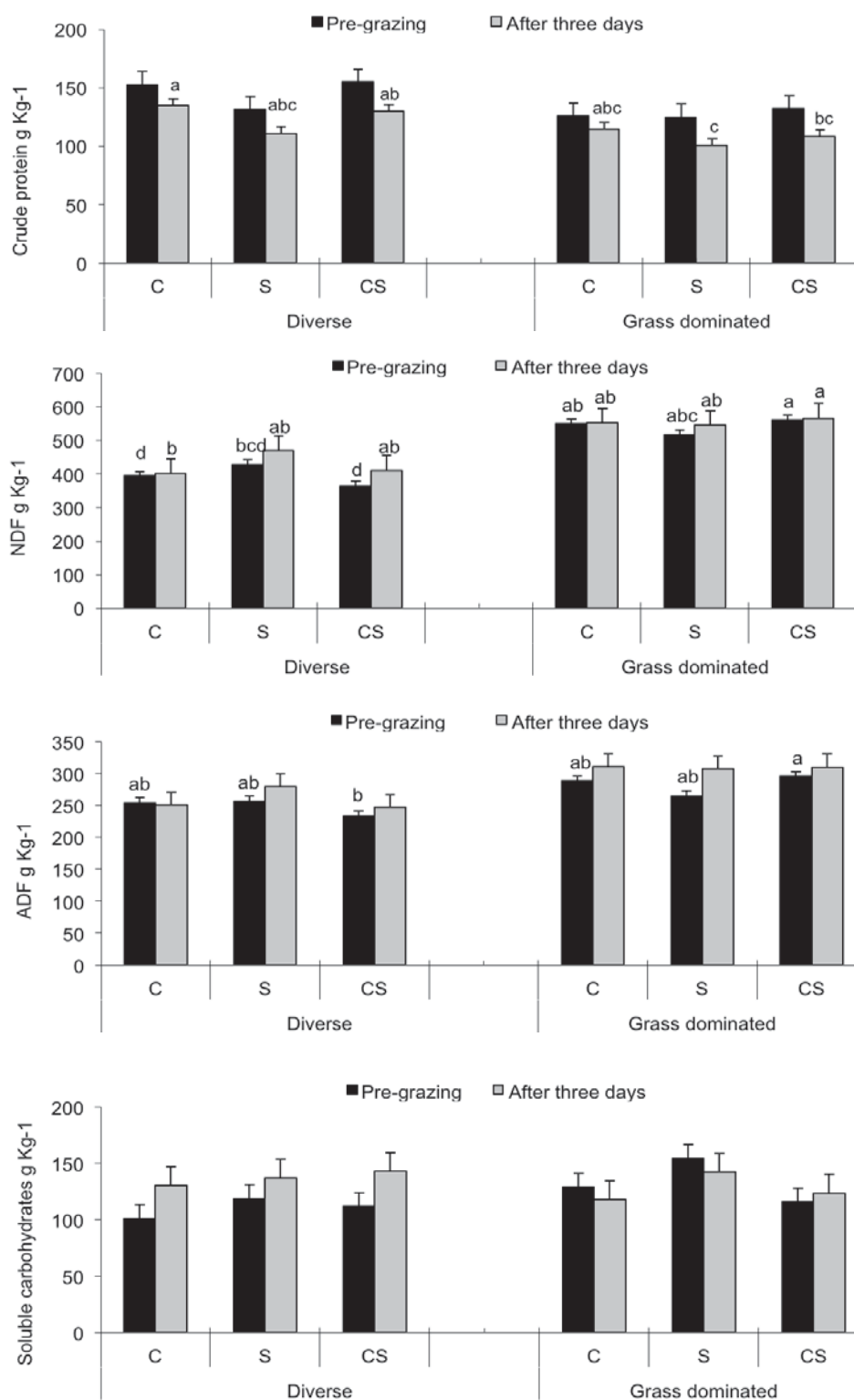


The intake of *F. pratensis* was affected by plant diversity ( $P=0.004$ ) i.e. on diverse swards the consumption was positive for all treatments; in contrast, on grass dominated swards there were negative JSI for both mono and co-grazing. It is important to notice that although the effect of the grazer species was not significant ( $P=0.298$ ), the ingestion of *F. pratensis* diminished with the presence of sheep. The maximum rejection was observed on cattle mono-grazing grass dominated swards (JSI=-0.12), whereas the highest ingestion was found for cattle and sheep co-grazing diverse swards (JSI=0.39). *D. glomerata* was preferred in all grazing treatments on diverse swards. However, the maximum preference was observed on cattle and sheep co-grazing (JSI=0.26). In contrast, on grass dominated swards no consistent results for *D. glomerata* were found. Cattle and cattle-sheep co-grazing almost refused this species (JSI=-0.17 and -0.03.); whereas sheep mono-grazing showed a positive value (JSI=0.07).

**Table 1** Probability values of Jacobs' selection index performed by cattle and sheep grazing alone or together on diverse and grass dominated swards for the complete grazing season of 2009 and 2010. SEM= standard error of the mean. PD= plant diversity treatment. GT= grazing treatment. Effects in bold characters are significant at  $P$  value <0.05.

	SEM	Probability values		
		PD	GT	PD*GT
<i>D. glomerata</i>	0.113	0.125	0.264	0.318
<i>F. pratensis</i>	0.137	<b>0.004</b>	0.298	0.689
<i>L. perenne</i>	0.146	0.676	0.071	0.370
<i>P. pratense</i>	0.091	<b>0.001</b>	<b>0.010</b>	0.930
<i>T. officinale</i>	0.131	0.534	0.102	0.771
<i>T. repens</i>	0.090	<b>0.005</b>	0.696	0.375

**Figure 4** Protein, Neutral Detergent Fiber (NDF), Acid Detergent Fiber (ADF) and soluble carbohydrates ( $\pm$  standard error of the mean) of diverse and grass dominated swards grazed by cattle and sheep in mono or co-grazing before and after three days of grazing for the complete grazing season of 2009 and 2010. C= cattle mono-grazing; S=Sheep mono-grazing; CS= cattle and sheep co-grazing. Means without a common letter differ at  $P < 0.05$





## Nutritive value of herbage

Plant diversity ( $P=0.003$ ) and grazing treatment ( $P=0.016$ ) affected protein content after grazing. Diverse swards grazed by cattle had the highest protein content ( $135 \text{ g kg}^{-1}$ ), whereas sheep mono-grazing grass dominated swards had the lowest value ( $101 \text{ g kg}^{-1}$ ). Plant diversity had a significant effect on NDF and NDF concentration before ( $P=0.002$  and  $P=0.009$ ) and after ( $P=0.001$  and  $P=0.011$ ) grazing (Figure 4).

Diverse swards showed slightly lower NDF and ADF values than grass dominated swards. Interestingly, for soluble carbohydrates, we observed an increase on diverse swards after grazing (plus  $26.3 \text{ g kg}^{-1}$ ); in contrast, on grass dominated swards the value decreased (minus  $12.1 \text{ g kg}^{-1}$ ), except for co-grazing (plus  $7.7 \text{ g kg}^{-1}$ ).

**Table 2** Probability values Protein, Neutral Detergent Fiber (NDF), Acid Detergent Fiber (ADF) and soluble carbohydrates content by cattle and sheep grazing alone or together on diverse and grass dominated swards before and after three grazing days, for the complete grazing season of 2009 and 2010. SEM= standard error of the mean. PD= plant diversity treatment. GT= grazing treatment. Effects in bold characters are significant at  $P$  value  $<0.05$ .

	SEM	Before grazing			SEM	After three days		
		<i>P</i> value				<i>P</i> value		
		PD	GT	PD*GT		PD	GT	PD*GT
Protein	1.093	0.082	0.412	0.645	0.553	<b>0.003</b>	<b>0.016</b>	0.556
NDF	1.274	<b>0.002</b>	0.718	0.077	3.429	<b>0.001</b>	0.682	0.450
ADF	0.776	<b>0.009</b>	0.467	0.077	2.038	<b>0.011</b>	0.740	0.631
Soluble carbohydrates	1.237	0.073	0.208	0.457	1.658	0.529	0.659	0.748

## Discussion

We hypothesized that the interaction of sward composition (diverse or grass dominated swards) and grazing treatment (cattle, sheep or cattle-sheep co-grazing) would influence the intake preferences of ruminants at pasture. Measurements of the sward heights three days after the start of each grazing rotation showed higher values on grass dominated swards for cattle (9.3 cm) and

cattle-sheep co-grazed (8.8 cm) paddocks, whereas heights of swards grazed by sheep were smaller (6.7 cm). In contrast, diverse swards had a relative homogeneous height throughout grazing treatments and rotations (7.7 cm). Wright *et al.* (2006) evaluated the feasibility to adjust the allowance of forage by controlling the compressed sward height of grasslands, either mono- or co-grazed by cattle and sheep. They found that the daily weight gain of cattle and sheep was higher on taller swards (8-10 cm) compared to smaller ones (4-6 cm). However, mono- or mixed-grazing management did not influence animal performance. In line with this study, Fraser *et al.* (2007) in an experiment with sequential grazing of cattle either grazing alone or together with sheep, found that plots grazed by lambs had slightly lower sward heights than co-grazed plots. However, in the same experiment, authors found that sheep had lower weight gains when swards were previously grazed by sheep than by cattle and sheep co-grazing. Preceding mono- and mixed grazing resulted in different forage selection and varying sward heights, thus, performance of sheep at successive grazing was also affected.

Results of the present study indicate that on diverse swards, all plant species were grazed rather homogeneously on co-grazed pastures, which is in line with earlier findings (Cortes, *et al.*, 2006; Celaya, *et al.*, 2007; Fraser, *et al.*, 2007; Benavides, *et al.*, 2009). Celaya *et al.* (2011) demonstrated that diet overlap among cattle, sheep and goats lead to more uniform consumption and to a more sustainable utilization of diverse swards. The stronger selection performed by sheep and the milder selective intake of cattle encouraged a homogeneous intake of forages, consequently, severe defoliation of preferred species was hindered by complementary competition and diet overlap (Walker, 1994; Benavides, *et al.*, 2009; Wragg, *et al.*, 2011). Thus, a more homogeneous forage intake of plant species by mixed herds may bring positive benefits for sward biodiversity. However, cattle without the presence of sheep can perform a homogeneous intake of forages. Dumont *et al.* (2007b) observed a “homogeneous intake behavior” of cattle when the grasslands consisted of fine-scale heterogeneous plant arrangements that impede forage selection. Thus, decreasing spatial and temporal scales of patches e.g. a

heterogeneous grassland, the stability of botanical composition is improved by affecting the intake rate and to cattle selectivity, i.e. shorter patch size decrease time of residence and intake rate of cattle, whereas shorter distance between patches, diminish the speed of walking among feeding stations but increase total organic matter intake (Utsumi, *et al.*, 2009).

Interrelationships among ruminants in mixed groups may play an important role in their ingestive behavior i.e., herbivore species seem to interact with regard to their intake choice (Benavides, *et al.*, 2009). In this respect, Cuchillo and Isselstein (2010) reported that the ingestive behavior of cattle was modified by the presence of sheep; i.e. cattle spent less time grazing when sheep were co-grazing on the same plots. In contrast, cattle when grazing alone spent more time for grazing with ingestion rates obviously being lower. Sheep behavior was not influenced by the presence of cattle.

Data presented here show that sheep seem to be more selective than cattle. A trend towards a higher consumption of *P. pratense*, *T. officinale* and to a slightly lower extent of *L. perenne* could be seen in sheep. This trend is likely to be related to the higher digestibility of these species as compared to the less preferred *F. pratensis* and *D. glomerata*. Selective grazing by sheep among similar grass species as in our experiment was found by Cortes *et al.* (2006). Sheep preferentially consumed *L. perenne* (78% in the diet) compared to *F. arundinacea* (22 % in the diet), though the herbage on offer at pastures contained only 49% of *L. perenne*.

Several studies have shown that sheep are able to adapt their diet effectively to varying sward botanical composition by selecting items of higher digestibility (Celaya, *et al.*, 2007; Thomas, *et al.*, 2010). Sheep has been shown to select feed items according to the botanical family (Ginane and Dumont, 2010) or even forage species (Ginane and Dumont, 2011). In a heterogeneous sward, sheep would require more time for grazing to find the preferred items, hence decreasing grazing efficiency. However, the aptitude to distinguish preferred species and plant parts within heterogeneous swards would facilitate the ingestion rate of wanted forages,

diminishing the normal time allocated to graze whereas grazing efficiency is enhanced (Hewitson, *et al.*, 2005).

Cattle are generally considered as being less selective when grazing compared to sheep and thus consuming a higher percentage of low digestible forages. This is in part confirmed by our data as – in contrast to sheep – *D. glomerata* and *F. pratensis* were not rejected and even showed positive JSI values on diverse swards. However, on grass dominated swards, their preferences for these grasses changed, i.e. a negative selection index was observed for *D. glomerata* and *F. pratensis*. The results suggest that even cattle with a lower ability of selective grazing, were trying to avoid herbage with a higher fiber content.

On diverse swards, cattle included more digestible forages in their diet, due to increased availability of readily digestible white clover and dandelion, adjusting their intake with the available fodder. Selectivity of grazing is related to the energy requirements of the grazers. Farrugia *et al.* (2006) observed that cattle vary the extent of selective grazing as lactating animals were more selective than dry cattle. The higher the milk production the more selective was the grazing (Farrugia, *et al.*, 2006). In addition, Dumont *et al.* (2007a) found that cattle preferentially consumed vegetative patches of forbs and legumes over taller growing reproductive patches of grass.

Apart from differences between grazer species for the selectivity of grazing and the resulting vegetation dynamics of the sward, the grazing pressure is also quite important. Dumont *et al.* (2011) observed that the stocking rate (high or low) markedly affected the start, the duration and the amount of sward botanical changes. This effect was stronger than that of the grazer species, i.e. when cattle and sheep were compared. After the first and second year of this experiment a low legume and high grass abundance was observed at a high stocking rate. In contrast, grazer species only showed an effect on sward composition after six years of grazing, with sheep grazing resulting in a reduced abundance of legumes and increased presence of

grasses. In our results, the abundance of *T. repens* was also reduced at the expense of the grasses increment.

The theory of nitrogen (N) and carbon (C) balance helps to explain the intake preferences of ruminants at pasture (Rutter, *et al.*, 2004; Rutter, 2010). For an optimum production of microbial protein in the rumen; a steady flow of N and C is required to reach the rumen digesta. Thus, balancing N and C fluxes with different plant parts and plant species seem to be more feasible with multiple feed choices (e.g. a heterogeneous grassland) compared to a restricted offer of feed items (e.g. monocultures of *T. repens* or *L. perenne*). This explains why sheep had a tendency to select more palatable forages and to decrease the protein content of the residual herbage on grass dominated swards. Thus, sheep were seeking more N and less C in their diet.

In contrast, on diverse swards sheep were offered a broader range of highly nutritious forages with low fiber percentages. Given this situation, sheep were obviously searching for more fibrous species with higher C content to avoid elevated amounts of N and readily fermentable carbohydrates. As has been shown by Rutter (2010); ruminants seem to avoid an extra ingestion of N by also ingesting fibrous forages to save the energy cost that would be necessary to metabolize a N surplus.

Our results of the NDF and ADF content of the herbage after the grazing point in the same direction. A higher NDF and ADF content in all treatments suggest that even though cattle are generally less selective than sheep, they were able to choose a diet with a higher digestibility compared to the average digestibility of the herbage on offer. The soluble carbohydrate content was not affected neither by selective grazing nor plant diversity; however, in the diverse sward there was an increase during grazing while on the grass dominated sward the soluble carbohydrate content stayed the same or even decreased. It is likely that on diverse swards the soluble carbohydrates content increases due to a higher preference for legumes and forbs leaving a higher percentage of grasses with a generally higher content of soluble carbohydrates

compared to the dicots. On grass swards, grazers prefer *L. perenne* and *P. pratense*, species that are known for their high soluble carbohydrate content (Bruinenberg, *et al.*, 2002), consequently after grazing, forages became stemier and less digestible. Both behaviors, sheep selecting high quality diets at low ingestion rates and cattle selecting low quality diets but at high ingestion rates, assured daily diet requirements for maintenance and production according to the anatomical and physiological conditions of each species (Walker, 1994; Rutter, 2010).

## Conclusions

The analysis of sward composition and the type of grazing on intake choices revealed differences between cattle and sheep; with sheep being more selective than cattle. To a lower extent, the sward composition showed effects on intake preferences. *Phleum pratense* was the most preferred forage species (JSI= 0.62) followed by *Lolium perenne*, *Taraxacum officinale* and *Trifolium repens* which were also preferred regardless of sward composition or grazer species. *Dactylis glomerata* and *Festuca pratensis* were less preferred irrespective of the grass sward. Co-grazing of cattle and sheep facilitated a more homogeneous consumption of the main forage species. Co-grazing might have the potential to better maintain grassland biodiversity.

## Acknowledgements

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## **Chapter 3**

### **Phytodiversity of temperate permanent grasslands: Ecosystem services for agriculture and livestock management for diversity conservation**

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## **Abstract**

Plant diversity has been reported to increase productivity. Farming practices aiming at conserving or increasing plant diversity are, however, usually less profitable than conventional ones. In this review, we aim to find reasons for this discrepancy, discuss ecosystem services of grassland phytodiversity that are useful for farmers, and ways of livestock management most beneficial for diversity. Under agricultural conditions, a clear effect of species richness on a site's primary or secondary production has not yet been demonstrated. Reasons could be that species numbers in permanent grassland are above the threshold of five species found effective in experimental plots or that the conditions are more in equilibrium with management than in weeded experimental plots. Other diversity effects on production stability, nutrient and water retention or product quality might convince farmers to increase diversity. However, these should be tested in agricultural situations, as most research has again been carried out in experimental plots. To enhance phytodiversity, grazing has been found superior over mowing, as selective grazing, treading and excreta deposition increase the heterogeneity of a sward and thus the niches available. Especially rotational grazing with intermediate intensity may be advantageous for phytodiversity. However, complex interactions between environmental conditions, sward composition, management and livestock behaviour make it difficult to forecast grazing effects. Thus, ecological and agricultural researchers should cooperate more, e.g. either in interdisciplinary projects or by hiring researchers from the respective other profession and thus diversifying research groups, in order to integrate agricultural management into biodiversity research and biodiversity measurements into agricultural research to advance our understanding of how to make conservation and enhancement of grassland phytodiversity both feasible and sustainable.

**Keywords:** grazing; productivity; nutrient and water retention; quality; selectivity; treading; excretion

## **Introduction**

Biodiversity has been increasingly in the focus of scientific and public attention over the past decades, culminating in the United Nations declaring 2010 to be the International Year of

Biodiversity. Concerning the role of phytodiversity in grasslands, positive effects on ecosystem services have repeatedly been pointed out. Thus, increased diversity has been suggested to lead to an enhanced production (Bai et al. 2007; Bullock et al. 2007; Dodd et al. 2004; Hector et al. 1999; van Ruijven and Berendse 2003; Weigelt et al. 2009; Yachi and Loreau 1999) as well as to an improved stability, sustainability and efficiency of grassland production systems (Caldeira et al. 2001; Hooper et al. 2005; Hooper and Vitousek 1998; Kahmen et al. 2006; Luck et al. 2003; Niklaus et al. 2006; Oelmann et al. 2007; Roscher et al. 2004; Roscher et al. 2008; Scherer-Lorenzen et al. 2003; Tilman et al. 2006; Yachi and Loreau 1999).

Despite such promising research results, grassland farming practices aiming at biodiversity conservation are usually regarded as less economically profitable than conventional practices (Pärtel et al. 2005). In temperate regions, grassland is mostly under agricultural management and grassland phytodiversity has developed over centuries in relation to such management (Bender et al. 2005; Isselstein et al. 2005; Moog et al. 2002; Vallentine 2001). Plant communities here are in dynamic equilibrium with utilisation practices. Without management, most temperate grassland would successionaly turn into woodland. A regular utilisation is therefore also required for the protection of species-rich grassland (Moog et al. 2002). However, measures aimed at increasing production have usually led to a decline of biodiversity in grassland areas (Bezák and Halada 2010; Henle et al. 2008; Silvertown et al. 2006).

How can ecologists and farmers come to such diverging views regarding the usefulness of biodiversity for production? Is only one of the views correct? Is phytodiversity not useful in the often fertile situation of agricultural grassland (Schmid 2002)? So far, most of the research on grassland diversity and ecosystem functioning has been carried out in low-input experimental grassland plots sown and weeded to yield different species numbers (e.g. Caldeira et al. 2001; Hector et al. 1999; Tilman et al. 2006). Such artificial experimental conditions make it difficult to draw conclusions for agriculturally managed semi-natural grassland (Caliman et al. 2010; Isselstein 2005). Is this the only explanation for the different views of ecologists and farmers? Is species richness not agriculturally usable?

Here, we want to discuss two central questions: 1) What is the agricultural benefit of biodiversity in livestock production? and 2) How can we manage livestock for biodiversity benefits? To this end, we will summarize results of studies on grassland biodiversity and its ecosystem services like productivity and product quality and discuss implications and applicability for livestock

farming. In the second part, principle interactions between grazers, sward structure and diversity will be outlined. Against this background, the impact of livestock management on diversity will be investigated. In the last part, we will discuss whether and how the diverging views on diversity of ecologists and farmers can be reconciled and what the implications of this are for both livestock management and biodiversity research. Throughout this text, ‘diversity’ will be used synonymously with ‘plant species richness’ unless indicated otherwise.

### **Benefits of grassland phytodiversity for livestock production**

Grassland is needed as the fodder basis for agricultural herbivores. Of importance to the farmer is therefore only at first instance a high primary production efficiency, i.e. large biomass production per unit of input. Essential is that this biomass can then be made available to the animals (Sanderson et al. 2004). To keep the animals adequately performing and healthy, their diet should provide the necessary energy and nutritional components. Especially in meadows, this may not be straightforward as there may be biomass losses and quality impairments during harvest and conversion into silage or hay (Tallowin and Jefferson 1999). Here, broad-leaved herbs have disadvantages as they undergo larger disintegration losses. Because animals have difficulties avoiding poisonous plants in conserved fodder, these should be absent. Therefore, special care has to be taken concerning grassland quality and composition in meadows and mown pastures. However, diversity may also have positive side effects, which will be discussed in the following.

#### *Diversity and productivity*

What can biodiversity of pastures and meadows mean for the farmer who needs biomass for his livestock? Table 1 summarizes results of studies on biodiversity effects on productivity or other ecosystem services. Due to the difficulties involved in transferring results from experimental grassland plots to agricultural situations (Caliman et al. 2010; Isselstein 2005), we will concentrate here mostly on the few studies carried out in agriculturally managed swards.

**Table 1.-** Results from studies of biodiversity effects on production and further ecosystem services in grassland with some form of agricultural management

Management	Country	Plant diversity	Production	Further ecosystem services	Reference
Rotational grazing (dairy cows), no fertiliser, clipping of excessive ungrazed forage	Pennsylvania, USA	2 to 9 sown species	0 (herbage intake, milk production)	+ (higher conjugated linoleic acid content of milk with more species)	Soder et al. (2006)
Rotational grazing (beef cattle)	Illinois, USA	3 to 8 sown species	0 (stocking rate, average daily gain, despite initially higher herbage mass in more diverse plots before grazing)	n.d.	Tracy and Faulkner (2006)
Rotational grazing (to different target heights), mowing	Pennsylvania, USA	1 to 7 sown species	0 (in favourable years higher yields in fertilised monocultures)	+ (more consistent yields in diverging weather conditions, improved CP and IVTDMD at first harvest, more stable quality of complex mixtures over season)	Deak et al. (2009)
Montane semi-natural grassland (78 plots under agricultural management, grazed or cut)	Germany	8 to 33 species; average of 20 species	0 (for species richness as well as effective diversity and Camargo's evenness) plant community composition explained productivity	n.d.	Kahmen et al. (2005)
Park Grass Experiment, different fertilisation treatments since 1856 with N, P or K, two cuts (initially one cut followed by grazing)	England	3 to 44 species per 200 m <sup>2</sup>	- (less species numbers with more production)	+ (stability of hay biomass was positively correlated with species number, albeit weakly)	Silvertown et al. (2006)
Experimental restoration sites (sown on arable land, no weeding), late cut with autumn and winter sheep-grazing	England	Mixtures with 6 to 17 or 25 to 41 species (species-poor and -rich, respectively)	+ (linear relationship between difference in species number among treatments and increase in hay yield)	0 (no effect on fodder quality)	Bullock et al. (2001)

Experimental plots, no weeding, one cut/year, followed over 9 years	The Netherlands	0 to 15 sown species, on average 10 to 14 species in total	+ (productivity increased with number of sown species) However, if total species number was considered, there was no clear relationship	+ (stability increased with sown species number, but not with total species number)	Bezemer and van der Putten (2007)
Experimental plots, rotational or continuous grazing, initial weeding during establishment	New Zealand	0 to 8 functional groups	+ (for sown species in spring) 0 (for total species production in spring as well as total and sown species production in autumn)	+ (resistance to invasion, resilience to disturbance)	Dodd et al. (2004)
Indoor cafeteria experiment with sheep	China	1 to 11 species	+ (more voluntary average daily intake of sheep with higher diversity)	n.d.	Wang et al. (2010)
854 steppe sites, hay fields or grazed	Inner Mongolia, China	Observational study, up to 36 species per m <sup>2</sup>	+ (at all scales; at regional scale, this correlated with annual rainfall and soil nitrogen; grazing did not affect form of relationship)	n.d.	Bai et al. (2007)
Experimental plots (cut) as well as survey on 37 pastures	Pennsylvania, USA	1 to 15 sown species in experimental plots; up to 11 species in surveys	+ (often more production in more diverse pastures)	+ (less weed invasion)	Tracy and Sanderson (2004)
Experimental plots as well as preexisting vegetation invaded by exotic species at four locations, one cut/year	North Dakota, USA	2 to 32 sown species	Mostly + (in experimental plots) 0 (in preexisting vegetation) Changing relationships over time and sites	n.d.	Guo et al. (2006)
Experimental plots, cutting (1-4 times/year), fertilisation (0-200 kg N ha <sup>-1</sup> a <sup>-1</sup> ), regular weeding	Germany	1 to 16 sown species	+ (plant production)	n.d.	Weigelt et al. (2009)
Experimental plots, cut twice/year, regular weeding	Germany	1 to 60 sown species	n.d.	+ (increased carbon storage in soil)	Steinbeiss et al. (2008)
Experimental plots, regular weeding	Portugal	1 to 14 sown species	+ (plant biomass)	+ (water use)	Caldeira et al. (2001)

Gradient from forest edge to abandoned pasture	Québec, Canada	Observational study, up to 16 species per 0.75 m <sup>2</sup>	Different relationships determined by limiting resources affecting productivity; if pooled together: humped relation; however, this may confound determining environmental variables	n.d.	De Lafontaine and Houle (2007)
Microcosm experiment, four harvests from December to May	New Zealand	1 to 9 sown species	n.d.	+ (less potential nitrification and nitrous oxide production with more species, especially with legumes in mixture), 0 (no effect on methane uptake)	Niklaus et al. (2006)
Microcosm experiment with heat/drought stress	Belgium	1 to 8 sown species	+ (more plant biomass with more species before drought stress)	+ (better water acquisition with more species), - (less survival of plants in mixtures)	Van Peer et al. (2004)
Meta-analysis of data from 171 studies	n.a.	No range given; local scale (< 20 km)	Mostly humped, followed by 0, -, +	n.d.	Mittelbach et al. (2001)
Meta-analysis of data from 1339 plots in 12 natural grassland systems	USA (9 systems), Tanzania, India, Finland	0 to 59 species	- (nonlinear structural equation modelling indicated competitive effects, but no positive effect of species richness on production)	n.d.	Grace et al. (2007)
Meta-analysis of data from 163 studies	n.a.	No range given	Mainly unimodal in temperate zone Mainly + in tropics in total: 60: 0, 46: +, 37 humped, 20: -	n.d.	Pärtel et al. (2007)

0' no clear effect, '+' positive effect, '-' negative effect, 'n.d.' not determined, 'n.a.' not applicable, CP crude protein, IVTDMD in vitro true dry matter digestibility



Results from these studies are conflicting: while some experimental studies found no consistent effect of biodiversity on primary production (de Lafontaine and Houle 2007; Deak et al. 2009; Kahmen et al. 2005; Soder et al. 2006; Tracy and Faulkner 2006), others, both observational (Bai et al. 2007) and experimental (Caldeira et al. 2001; Tracy and Sanderson 2004; van Peer et al. 2004; Weigelt et al. 2009), found a positive effect (Table 1). Despite initially positive impacts on plant production, Tracy and Faulkner (2006) did not measure increased daily liveweight gains of cattle nor could they increase stocking rates in more diverse pastures. Also Soder et al. (2006) found no effects on herbage intake or milk production of dairy cattle with increased plant diversity. In a survey of 854 meadows and pastures in Inner Mongolia, Bai et al. (2007) observed increased primary production with increased plant diversity. However, the authors pointed out that this coincided with patterns of annual rainfall and soil nitrogen. Furthermore, conditions in this area were representative of those in the Eurasian steppe, but not necessarily directly comparable with managed temperate grassland. The voluntary daily dry matter intake of sheep has been found to increase with species richness up to eight species out of eleven in an indoor cafeteria trial (Wang et al. 2010). This should translate into weight gains of the animal, which were however not determined. In a field experiment, no difference in intake was observed between fields with four to six and with more than eight plant species. The authors discuss that this might be due to supplementary corn offered in the field (Wang et al. 2010). Interestingly, the studies finding positive effects were mainly carried out in experimental plots, not in agricultural grassland (Caldeira et al. 2001; Tracy and Sanderson 2004; van Peer et al. 2004; Weigelt et al. 2009). In other studies of experimental plots, positive effects on production were found when the number of sown species was considered. However, based on the total number of species present (i.e. including weeds), no consistent effects were found (Bezemer and van der Putten 2007; Dodd et al. 2004).

It has been a principle of ecological theory that the assembly of species in a given habitat depends on the niches present. Therefore, within the limits of historical influences and site accessibility for propagules, the available resources determine phytodiversity in the first place. Here, diversity has been found to be maximal at intermediate resource availability (Critchley et al. 2002; Janssens et al. 1998; Schmid 2002). Hautier et al. (2009) could show that a negative effect of fertilisation on phytodiversity of fertilised grassland communities was mainly due to increased competition for light and restriction of light reaching the lower layers of vegetation. In contrast to this, Rajaniemi (2002) did not find an effect of shading on species richness or

diversity in an unproductive former field and concluded that the observed significant effects of fertilisation were due to increased total above- and belowground competition. The importance of belowground competition in such a system where light is not limiting could later be confirmed (Rajaniemi et al. 2003).

In agricultural grassland, this initial diversity determined by the available niches is manipulated by management. A new situation develops where species richness is in dynamic equilibrium with the management, if this is constant. In contrast to this, the experimental grassland plots used for biodiversity – productivity research have usually been weeded intensively, inhibiting the establishment of such a dynamic equilibrium. If weeding was terminated, similar species richness developed within two years in all plots of initially different richness (Pfisterer et al. 2004).

Taking a closer look at the results from experimental grassland studies, it becomes obvious that observed diversity effects were most pronounced with species numbers increasing from one to two or four. Many studies found that 90% of the productivity effect was reached with five plant species (Roy 2001). In permanent grassland, the plant diversity is usually larger. For example, Sanderson et al. (2004) summarized that American grazing lands comprised between nine to 50 species per 1000 m<sup>2</sup> and European grasslands between 10 and 60 species per 100 m<sup>2</sup>, depending on management intensity. Thus, species richness may usually be too large in permanent grassland to find effects of diversity on productivity.

Several studies have pointed out the larger impact of species identity (Hooper and Vitousek 1997) or functional diversity (Díaz and Cabido 2001) than species number on primary production. Here, functional diversity is not necessarily only the presence or absence of legumes, but can encompass the range of traits like leaf sizes, canopy heights, or rooting depths (Díaz and Cabido 2001). These findings should have implications for the assembly of seed mixtures for grassland renovation, where the species number is furthermore usually in the range where species richness-productivity effects have been found. In practice, this principle has already been used and the long-term experience of seed companies and farmers has been found to deliver a superior product to experimental mixtures in Switzerland (Suter et al. 2010).

To sum up, a clear effect of species number on primary or secondary production of grassland under agricultural conditions could not yet be demonstrated. This may be due to primary effects

not translating into animal production, vegetation composition developing a dynamic equilibrium with management conditions or higher species richness in permanent pastures than found effective in experimental grassland. If fertilisation was also manipulated in permanent grassland experiments, its effect on biomass production outreached that of diversity (Crawley et al. 2005; Silvertown et al. 2006; but see also Weigelt et al. 2009 for results in weeded experimental grassland). Thus, a potential production benefit may not convince farmers to protect diversity in their grasslands.

#### *Diversity and other services for livestock production*

Despite an unclear productivity effect, increased diversity can still have benefits for livestock farming. First of all, the production stability has been found to increase, granting good harvests also in years with adverse weather conditions (Deak et al. 2009; Silvertown et al. 2006; Tilman et al. 2006). However, in a comparison of stability of biomass production of plots sown with 0, 4 or 15 different species and not weeded, Bezemer and van der Putten (2007) found a positive relation with sown species number, but not with actual species richness and concluded that the relationship is context-dependent.

Nutrient losses may be smaller under diverse grassland (Mulder et al. 2002; Niklaus et al. 2006), probably due to resource complementarity and a better use of the soil space (Harrison et al. 2007; Weigelt et al. 2005). This can also cause a better water use efficiency of more diverse systems (Caldeira et al. 2001; van Peer et al. 2004). So far, most studies looking at these relationships have been carried out in experimental grassland plots. Research on long-term grassland, where root structures have developed over long time periods, is needed.

Important effects of phytodiversity on product quality and animal health have been found, which will now be discussed in more detail. Grazing, as compared to indoor fattening, results in a different fatty acid composition (higher proportions of linoleic and linolenic acid), darker and redder meat with better sensory qualities and an increased shelf-life (Dieguez et al. 2006; Farruggia et al. 2008; Fraser et al. 2009; Hocquette et al. 2007). Fraser et al. (2009) conducted grazing experiments with different breeds on improved permanent pasture (ryegrass/clover) and semi-natural rough grazing on *Molinia caerulea* dominated swards. Their results indicated a greater influence of the sward type on animal performance, grazing behaviour and meat quality than the breed when beef cattle are produced in less favoured areas. Under rough grazing, loin steaks contained more vitamin E and had a lower lipid oxidation (Fraser et al. 2009).

Some recent studies have demonstrated that dairy products from grazing ruminants have a composition thought to be beneficial to human health, compared to that from animals fed concentrate diets; the content of unsaturated fatty acids in milk, for example, increases with grazing (Cuchillo et al. 2010b; Elgersma et al. 2006). Milk yields and animal productivity are limited by genetic potential, botanical composition and trophic status of the pasture, which needs to meet basic requirements to ensure a sustainable system (Osoro et al. 2007). Extensive grazing on bio-diverse swards for milk production is often characterized by smaller milk yields but more solid contents (Farruggia et al. 2008). Moloney et al. (2008) concluded from a review of several experiments that more phytodiverse pastures produced milk with increased C18:3n-3 and polyunsaturated fatty acid concentrations whereas the saturated fatty acid concentrations were in most cases reduced. Leiber et al. (2005) discussed that changes in the ruminal ecosystem due to energy shortage or specific secondary plant metabolites may be possible causes for the high C18:3n-3 concentrations in alpine milk.

Animals mix plant and biochemical diversity to enhance the nutritive value of the diet as well as to maintain possible toxic concentrations of plants below critical levels (Provenza and Villalba 2010). Certain plants can also have health benefits for the animals. For example, legumes contain condensed tannins that may cause increased production of milk and wool, improve the lambing percentage and reduce bloating risk as well as intestinal parasites (Min et al. 2003). In addition, Martin et al. (2010) point out that adding tannin-rich legumes to animal diets may decrease rumen methanogenesis and thus the production of the greenhouse gas methane. As reducing methane production during rumination also means decreasing energy losses by the animals, this is interesting from a production point of view as well. So far, the importance of diverse grasslands in this respect is not completely understood.

Thus, despite unclear productivity effects, plant richness may have positive effects on product quality, animal health, nutrient and water retention as well as production stability. The latter may be especially important for sustainable production under changing climatic conditions, but has so far mainly been studied in experimental plots.

### **Livestock management to enhance grassland phytodiversity**

Extensive grazing has been suggested to be a good means for enhancing and protecting grassland diversity (Dumont et al. 2007; Hart 2001; Loucougaray et al. 2004; Pykälä 2003; Rook et al.

2004; Scimone et al. 2007; Tallowin et al. 2005). What is the advantage of grazers over mowing? How do the animals influence diversity over time and space?

Grazing animals affect the distribution and occurrence of plants in several ways. Besides directly influencing competition between species, they also introduce more heterogeneity into the sward. The main mechanisms in this respect are selective grazing, nutrient redistribution, treading and seed distribution. As the complex actions of biting/defoliation/selection play the most important role in this process (Illius and Hodgson 1996), we will first concentrate on these before discussing the influences of treading and excreta deposition and bringing this together in a discussion of livestock management for biodiversity.

### *Selective grazing*

Selectively grazing animals preferably feed on certain pasture areas (horizontal selection) or plant parts (vertical selection) (Arnold and Dudzinski 1978; Elsässer 2000). Given a free choice, they select a mixed diet rather than choosing one fodder species only (Villalba and Provenza 2009). The chosen biomass usually has higher concentrations of nitrogen, phosphorus and energy than avoided material (Wales et al. 1998). Despite the variability in quality and digestibility of herbage on offer in time and space, ruminants aim to select herbage with fairly constant digestibility (Fulkerson et al. 2007; Garcia et al. 2003). Therefore, the degree of selectivity changes with the quality of the herbage on offer. The animals have to resolve the trade-off between feeding on preferred food and the energy required to forage for that food (Rook et al. 2004; Utsumi et al. 2009). A higher selectivity has been found when preferred patches were aggregated (Dumont et al. 2002).

The intensity of vertical selectivity differs between animal species and is related to the actual mechanical way of fodder uptake. Cattle take up plant material with their prehensile tongue into the mouth where it is pressed against the dental plate of the upper jaw and torn off with a move of the head. They can graze tall herbage more easily than sheep because of their physical size (Hodgson 1990; Wilmshurst et al. 2000). Cattle might select separate leaves merely from tall plants, while sheep and goats with their narrower and more pointed muzzles graze more fastidiously and readily select individual leaves and other plant parts (Animut and Goetsch 2008; Arnold and Dudzinski 1978; Dumont 1997).

Besides determining the potential bite selection of an animal, the body size also influences the size of a feeding station, i.e. the area a standing grazer can reach with its head (Table 2). A cluster of feeding stations with the same intake rate is defined as a grazing patch. The size of this feeding patch depends on the size of the animal as well as the heterogeneity, biomass and quality of fodder available. Thus, the size and selectivity of the animal in interactions with the heterogeneity of the sward will lead to a mosaic of areas with different spatial and temporal dimensions of defoliation (Table 2).

**Table 2.-** Spatial dimensions of the grazing animal/sward system, following Laca & Ortega (1996) and Vallentine (2001).

<b>Spatial dimension</b>	<b>Description</b>	<b>Unit involved</b>	<b>Temporal dimension</b>
Bite	Area of a bite	Individual (head)	1–2 sec
Feeding station	Total of bites of a standing grazer (circular arc of the head)	Individual	5–100 sec
Grazing patch	Cluster of feeding stations of the same intake rate	Few individuals	1–30 min.
Feeding site	Collection of grazing patches during a grazing interval	Sub-herd	1–4 h
Pasture, habitat/camp	Pasture – in the open landscape related to a central resting and watering place	Herd	1–4 weeks
Habitat/home range	All habitats in an open landscape	Population	1–12 months

Sight helps the grazing animal to position itself towards the other animals and the environment, but is less important in selecting the diet. In experiments, sheep with their eyes bandaged selected a diet similar to that of sheep allowed to see. However, the preference for certain grassland plants changed when touch, smell and taste were impaired (Arnold and Dudzinski 1978). Animals familiar with a sward or forage were quicker in finding their preferred feeding patches (Bailey and Sims 1998) and using the available forage (Flores et al. 1989a; Flores et al. 1989b), suggesting an influence of learning in patch selection (Dumont 1997).

Besides a spatial and qualitative dimension of selective grazing, there is also a temporal dimension that influences the structure of the sward and helps to establish a mosaic of more or less frequently defoliated patches. Thus, the previous meal an animal had seems to have an influence on the preference for the next one (Dumont 1997; Mote et al. 2008). From experiments

on extensive grazing it was concluded that there was a strong diurnal pattern of selectivity: Dumont et al. (2007) found a marked preference of cattle for short, highly digestible bites in the morning and an increased consumption of bite types requiring a greater rumination effort during the second half of the day. Bites of short mixed vegetation consisting of grasses and herbs were generally grazed preferentially, regardless of the offer and time of day (Dumont et al. 2007).

Plant species on a pasture usually exhibit two defence strategies: resistance to (avoidance) and tolerance of herbivory (Briske 1996). Resistance refers to the ability of a plant to reduce the amount of damage. This means reducing the probability and intensity of defoliation by morphological traits like thick hair, sharp leaf blades (silica) and chemical defences. This group is classified as facultative weeds and weed grasses if they are potentially edible (Opitz von Boberfeld 1994). Among these are *Holcus lanatus*, *Deschampsia caespitosa* and *Ranunculus repens*. Also unwanted poisonous and non-edible plants like *Equisetum palustre*, *Cirsium palustre* or *Juncus effusus* show this defence mechanism and may compete successfully for space and nutrients if no agronomic measures are taken (Moretto and Distel 1997; Moretto and Distel 1999). Tolerance is the ability of a plant to react to defoliation by rapid regrowth and recovery without a reduction in fitness. In this case, growing points for regeneration are located below the grazing level at the shoot basis or along stolons and storage roots may contribute to survival after intense defoliation (Herben and Huber-Sannwald 2002).

Disturbances by the grazer can shift the competition conditions among plants, as varying defoliation frequencies lead to different optima in adaptation to grazing. Generally, intensive grazing will induce the formation of a dense, well-tillered sward (Frame 1992; Matthew et al. 2000; Nelson 2000). As a result, the vegetation composition usually differs between tall and short sward areas (e.g. Correll et al. 2003) and indicator species for the extremes in grazing, i.e. selective undergrazing and selective overgrazing, can be determined (Opitz von Boberfeld 1994).

### *Treading*

The treading of grazing animals can have two effects: it may cause compaction of the topsoil and it can create open gaps without vegetation cover. According to Jacob (1987), the tread of a cattle of 600 kg causes a pressure of 4–5 kg cm<sup>-2</sup> on the topsoil. The resulting compaction may lead to retarded water infiltration and gas diffusion, increasing the risk of surface runoff and elevated emissions of gases like the greenhouse gas nitrous oxide (Menneer et al. 2005; Mulholland and Fullen 1991; Oenema et al. 1997; van Groenigen et al. 2005). However, compaction can also



have positive effects: It is expected that treading might compensate for the prohibition of rolling in spring on nature protected grassland (Benke and Isselstein 2001).

Damages of the vegetation leading to patches of bare soil may offer space for propagation of seeds from the seed bank and invasion by other species. This can be desirable, but can also promote the growth of unwanted species. Kohler et al. (2006) found that gaps were colonized by species with small seeds, unspecialized seed dispersal, a persistent seed bank and high vegetation spread. The role of other grazing effects (feeding, dung deposition and trampling) on the recolonisation was only secondary, modifying the competition between recolonisers.

Plant species react differently to treading. Jacob (1987) found that *Poa annua* had increasing yield proportions at heavily frequented pasture gate areas while proportions of *Holcus lanatus* decreased. In line with this, Graf Bothmer (1953) ascribed a community at a zone close to pasture gates of permanent pastures showing highest frequency and dominance of *Poa annua*, *Polygonum aviculare*, *Plantago major* and *Lolium perenne* to larger influences of treading in these areas.

#### *Excreta deposition*

The grazing animal transforms vegetation biomass into animal biomass and performance; however, with considerable losses and a rather low efficiency. In cattle, about 75–95% of the ingested N is returned via excreta (Whitehead 1995). In this transformation, nutrients are redistributed from relatively large areas where the animals feed to small excreta patches. These excreta patches have high input of nutrients, but also experience a grazing pattern different to the rest of the pasture area.

Dung patches might cover 5–10% of the grazed area each year in dairy farming, but the affected area can be much greater and, depending on weather conditions, be one to six times the covered area (Bao et al. 1998; Bastiman and van Dijk 1975; Haynes and Williams 1993). Herbage growing in the vicinity of dung patches is unattractive to stock, also due to the dung smell, and is avoided unless the grazing pressure is very high (Frame 1992; Gillet et al. 2010). This behaviour is explained by hygienical/sanitary advantages of avoidance (Hutchings et al. 1998). As a result, micro-areas with a tall sward develop, especially under extensive grazing.

Urine patches can cover up to 24% (at 700 cow-days ha<sup>-1</sup>) of the pasture and the area affected may be up to double that size (Haynes and Williams 1993; Whitehead 2000). The vegetation at



urine patches may be grazed preferentially (Day and Detling 1990; Steinauer and Collins 2001), probably due to high concentrations of minerals in the herbage.

The nutrient return with excreta is large. It is unevenly distributed within the pasture and often accumulates at feeding, rest and water places (König 2002; Owens et al. 2003). This results in further differentiation in sward structure and soil conditions. In the process of grazing and excretion, a decoupling of major plant nutrients takes place. Usually, more K is excreted in urine than in dung (Whitehead 2000); while P is mainly excreted in dung. A certain amount of N is excreted with dung, the rest with urine (e.g. Schellberg et al. 2007). Thus, the more N cattle take up, the higher the ratio of N in urine versus N in dung (Whitehead 1995).

On urine patches, legumes are especially negatively affected. White clover competes only poorly for mineral N with grasses and is more susceptible to scorch. N<sub>2</sub> fixation can be markedly depressed in the urine patch (Ball et al. 1979; Ledgard et al. 2001). Therefore, urine patches become grass dominated (Ledgard et al. 1982), but the degree of clover reduction and N<sub>2</sub> fixation is dependent on the time of urine application as well as the clover content of the sward (Ball et al. 1979; Ledgard et al. 1982). Thus, Norman and Green (1958) did not find an effect of a single urine application on the botanical composition of a pasture.

Dung patches may lead to an increase in the total yield of grasses around the pats (MacDiarmid and Watkin 1971; Norman and Green 1958). This effect was shown to be stronger when the excretion was combined with defoliation. Underneath the cow pat, the vegetation died (MacDiarmid and Watkin 1971). Dung patches were found to decrease species turnover and thus have a stabilizing effect on plant composition in their direct surroundings in mountain pastures (Gillet et al. 2010).

#### *Grazing management and diversity*

The development of a specific sward structure is induced by the behaviour of the grazing animal as discussed above and by agricultural management (pasture maintenance) on a background of site characteristics. Important with respect to grazing management is the grazing intensity, grazing system and the type and breed of grazing animal. The effects of grazing are further modified and partly determined by the level of nutrient input (fertilization; additional feeding), and the intensity of intermittent management like cutting or topping, rolling and harrowing,

usually intended to decrease grazing effects. However, these secondary management effects will not be considered in more depth here.

High grazing intensity has often been blamed for negative effects on diversity (Dumont et al. 2009; Henle et al. 2008; Plantureux et al. 2005; Vallentine 2001). With increasing intensity, animals become less selective in the choice of their diet in order to obtain sufficient intake (Dumont et al. 2007). Thus, defoliation will be more homogeneous than on less intensively grazed paddocks, creating less diverse niches. Furthermore, the frequency of defoliation will be high, allowing only pasture plants adapted to this to survive. With very high grazing pressure, animals may harm vegetation points by removing too much biomass, especially from preferred plant species. This happens more easily by animals being able to remove biomass close to the soil, such as horses, sheep or goats rather than cattle (Animut and Goetsch 2008; Benavides et al. 2009; Menard et al. 2002). With high grazing intensity, effects due to treading and gap creation will also be more serious. In contrast to selective grazing, gap creation and compaction will not be maximal at low grazing pressures, but increase with increasing intensity. However, colonisation of new gaps will be retarded with high grazing intensity due to frequent disturbances of newly emerging propagules. Excreta patches will affect larger pasture areas (White et al. 2001) and more nutrients can be lost by run-off, leaching or gaseous losses. However, increased grazing pressure decreases the size of dung pats as the animals tend to feed closer to and sooner after an excretion event.

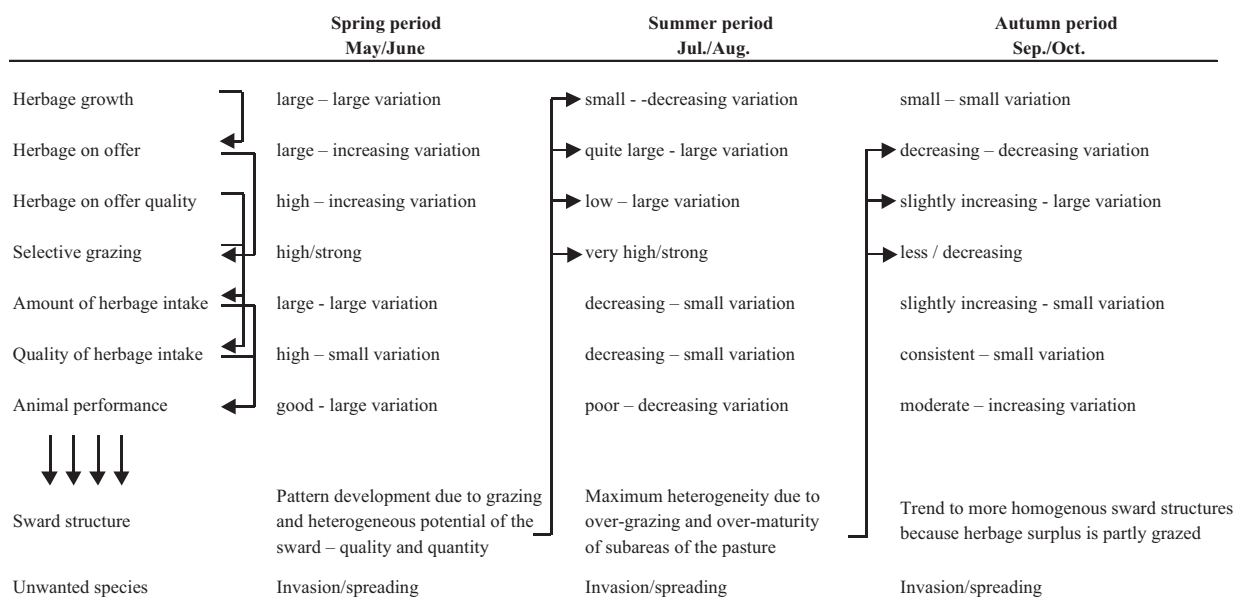
The grazing system may have large effects on diversity, even if the annual stocking density is the same for different systems. Most important in this respect are rotational grazing and permanently stocked pasture. Permanently stocked pasture requires less work from the farmer, as the animals are put on the pasture in spring and removed at the end of the grazing season. In rotational grazing, animals have less space per unit of time, but are transferred to a new paddock at regular time intervals. Thus, at a given time, the stocking density is higher with rotational grazing, but the vegetation is then allowed time to recover until the animals rotate back to the same paddock. Therefore, the pressure on preferred species is less intense than in permanently stocked pastures (Pavlu et al. 2003). It has been found that grazing at intermediate intensity may allow more plants to get to the flowering stage (Correll et al. 2003; Sahin Demirbag et al. 2009) and may thus have positive effects on the vegetation, but also on the abundance of insects (Dumont et al. 2009; Kruess and Tschardt 2002).

As permanently stocked pastures can only be grazed with relatively few animals to allow them to find enough fodder even in times of little vegetation growth, different areas develop with very different frequency of use. The seasonal vegetation development of a continuously grazed pasture (set stocking) in temperate areas can be divided into three parts, namely the spring/early summer period, the summer, and the late summer/autumn period based on the development of herbage mass (Jacob 1987). Fig. 1 gives an overview of the interactions of grazing cattle and sward structure during a grazing period. The spring/early summer period is characterized by a surplus of herbage mass of good quality allowing a high performance of livestock. As grazers initially use only relatively small areas on continuously grazed pastures with set stocking, other areas develop into a generative state where feed quality deteriorates. During the summer period, grazing cattle therefore have to invest time to select herbage and are also forced to use overripe parts of the pasture. As a result, performance of the individual animal decreases (Baumont et al. 2000). Towards the end of the grazing period, in late summer/autumn, the relation between herbage on offer (standing crop) and intake by the grazing cattle synchronizes again. At this time, the variability in quality and sward height is reduced, causing less need for the animal to select. This will allow, weather conditions permitting, a moderate increase in animal performance during that period. Overall, preferred patches are defoliated very frequently and experience the same pressure as on pastures with high grazing intensity. However, other pasture areas are hardly influenced by the animals during long parts of the grazing season. Here, competition between species will drive diversity development. Usually, farmers would choose to cut or mulch surplus vegetation at the end of a grazing season.

The type of grazing animal has important implications for phytodiversity, especially due to different feeding preferences. The mechanical prerequisites for selective grazing and their differences between animal species have already been discussed above. Requirements of the animals for energy and quality further determine their influence on the vegetation. Impacts due to treading and excretion vary between species. Treading is especially important where a lot of weight is carried on a small area or where animals are very mobile. Apart from small differences in nutrient retention between animal species, excretion mainly differs with respect to the amounts excreted at a given time and the distribution of excreta patches. Thus, depending on the size of the pasture, horses may show latrine behaviour, excreting always at the same points (Lamoot et al. 2004), while cattle may distribute excreta more evenly over the pasture area

(White et al. 2001). This has implications for the nutrient return to the plants and mining of nutrients versus accumulation at other places.

**Fig. 1.-** Schematic overview of the phases of developments and of the interactions of grazing cattle and sward structure under conditions of selective grazing on extensively grazed grassland.



Interestingly, the choice of the breed, apart from size and weight restrictions, seems generally to be of less importance in cattle (Fraser et al. 2007; Isselstein et al. 2007), but effects have been reported for sheep and goats (Osoro et al. 2007; Osoro et al. 2002). Larger breeds might achieve better performance rates but have higher requirements for maintenance (protein, energy, minerals etc.).

Different effects of grazers on swards are sometimes utilized in co-grazing. Thus, grazing by goats has been found to have positive effects on following sheep grazing, as the proportion of clover in the pasture increased (del Pozo et al. 1998). Sheep may feed on dung pats of cattle and vice versa, decreasing the amount of nutrient and pasture space lost (Abaye et al. 1994; Forbes and Hodgson 1985; Fraser et al. 2007). Co-grazing may also lead to increased daily liveweight gains of both animal species involved (Nolan and Connolly 1989). A combination of species in co-grazing may lead to the development of a more uniform sward with respect to height. However, due to the distinct effects on plant species by selective grazing, treading and excretion,

the underlying heterogeneity might be larger with co-grazing, allowing the creation of more diverse niches.

To sum up, grazing is regarded as a most efficient way of utilizing and maintaining less intensive and semi-natural grasslands. However, the interactions of soil and site characteristics, hydrology, plant communities, and grazing management are complex and the situation is often further complicated by restrictions in grazing time, nutrient return and market demands. A thorough understanding of the grazing process will help to properly address the problems arising in a specific environmental/agricultural/socio-cultural context and to combine benefits of extensive grazing concepts for improved or maintained biodiversity, landscape scenery, soil protection and farm income (Soder et al. 2007). In order to achieve these tasks, it is likely that management restrictions need to be adapted to local conditions, especially by adjusting grazing intensity to productivity, by allowing some form of nutrient return or by mulching, to avoid cases where the process of selective grazing might lead to abandonment of parts of the pasture. In a complex situation like extensive grazing what may be beneficial for one objective may have damaging consequences for another (Mills et al. 2007).

## **Discussion**

Farmers and ecologists have contrasting ideas about the usefulness of biodiversity for grassland production. As outlined above, these seem to be based on contrasting experiences in different environments: Experiments have often been conducted in experimental grassland plots or newly sown grassland where the vegetation composition is not (yet) in equilibrium with the resources, where management and harvests are rarely comparable with agricultural situations and where the focus is on primary production. In contrast, in low to moderate management situations the farmer is dealing with permanent grasslands comprising species numbers that are in dynamic equilibrium with the environment and is engaged in the sometimes difficult task of matching primary production with the needs of the animals.

Results from experimental grassland plots may still have implications for agricultural systems managed in a way similar to these plots, e.g. in ley farming. Here, the growing of cash crops is alternated with legume or grass pastures. The grassland species are sown in and the pasture is kept for a few years to increase soil fertility and disrupt pest cycles before it is ploughed for another round of cash crops. This system may be improved by using more diverse species

mixtures. Research is needed to investigate the transferability of results on impacts of diversity on productivity and other services from experimental studies to ley farming conditions.

To make results applicable for more permanent grassland use, research should focus on established grasslands with species numbers and management comparable to agricultural situations. Next to primary production, the nutritional quality of the biomass should be considered as well as harvest losses in case of meadows. The selectivity of grazers has to be investigated in permanent pastures comprising more than just one or two species. Here, further research has to focus on animal-sward interactions and on the effects of breed, physiological stage and grazing experience on the process of selective grazing. By grazing at different densities, the plant species richness can be - at least partly - determined, but little is known about the potential to create and maintain structurally varying grasslands (Adler et al. 2001; van Wieren and Bakker 1998). Furthermore, a closer look needs to be taken at soil biology and interactions between above- and belowground diversity. In this context, the consideration of organic livestock systems may be interesting, as these may have a higher plant diversity and rely more on services of diversity than conventional systems (Hole et al. 2005; Rundlöf et al. 2010).

For grassland farming, diversity can still have advantages, albeit maybe not the desired production effect. Several other services of biodiversity are also of importance to farmers, e.g. increased stability of production, resilience to changes, improved use of nutrients and water, or influences on product quality. Here as well, more research is needed under more realistic agricultural conditions to better understand the magnitude of these effects. Although in experimental plots more species have been found to be necessary for multiple ecosystem services (Hector and Bagchi 2007), species numbers in permanent grassland might already be high enough to allow such multifunctionality.

For biodiversity conservation, agricultural management is important in temperate grasslands as diversity has developed over the last centuries in line with management. Here, grazing systems with intermediate stocking densities seem to have the largest potential for recreation of diversity. Grazing creates a more heterogeneous sward than mowing as the animals affect sward composition by a mixture of selective grazing, treading and excretion.

Generally, biodiversity-adapted grazing systems might only be economically viable if the costs for maintenance, fertilizer and leasing, especially, can be kept to a minimum. In other cases, the

potential of the pasture needs to be utilized better to be profitable. Animal performance is a result of herbage intake and quality. Due to selective grazing, animals might select diets of a better quality than the mean of the herbage on offer (Rook et al. 2004; Wales et al. 1998). Therefore, with reduced stocking, even less productive grassland might be used for efficient livestock farming (Isselstein et al. 2007). In investigations on extensive grazing with oxen on fen grassland in northwest Germany, Benke & Isselstein (2001) found relatively high individual daily live weight gains of 418–871 g head<sup>-1</sup> with an average of 699 g head<sup>-1</sup> during 1993–2000. The potential gross biomass growth was about 80 GJ NEL ha<sup>-1</sup>, while the net pasture performance amounted to 14.3 GJ NEL ha<sup>-1</sup> in 1999 and 21.3 GJ NEL ha<sup>-1</sup> in 2000. Thus, the grass leavings of about 80% in 1999 and 73% in 2000 were very high. The farmer has to decide whether he wants to maximize production per animal, which is usually largest on extensively used pastures, or production per area, which increases with increasing intensity up to the carrying capacity.

Production of milk and meat from extensive grazing on more bio-diverse pastures is naturally limited and the economic success usually depending on some form of subsidies for conservation of biodiversity, bird breeding, landscape conservation, tourism, and cultural heritage among others (Kemp and Michalk 2007). Ideally, the products can be marketed through special brands and secure premium prices for milk and meat (Mills et al. 2007; Traill et al. 2008). Bermingham et al. (2008) found that products from pastoral production with properties or constituents related to human health were well accepted by the consumer, a promising fact for extensive grazing enterprises. However, sufficient information on production, regional origin and processing is demanded by the consumer. Generally, the positive influence of botanically diverse swards on grazing animals goes beyond grazing as a means of animal welfare and being a natural process, but includes side effects of antiparasitism and antioxidant activity by phytochemicals transmitted from plant to animal (Cuchillo et al. 2010a; Farruggia et al. 2008; Moloney et al. 2008). Moloney et al. (2008) have reviewed the implications of botanically diverse forage-based rations for cattle on product composition, product quality and consumer health. They conclude that, as information accumulates on the effect of individual plant species on milk and meat quality, opportunities will arise to maintain and develop biodiverse pastures. Furthermore, other ecosystem functions that could not be covered in this review, like landscape beauty, meadow bird breeding, soil protection, or abundance of pollinators, have to be taken into account when deciding on the fate of phytodiverse grassland.



## **Conclusions**

Biodiversity in pastures has developed over a long time in line with agricultural management. Therefore, the potential of using grazers for biodiversity enhancement of pastures seems good. However, by modern standards, agricultural management has to be adapted, usually extensified to increase diversity. Diversity does not seem to have the often acclaimed production increasing effect on permanent pastures. Although there can still be other advantages for farmers, like production stability and better use of nutrients and water, farmers still need to be compensated for production losses due to extensification measures. To be able to make full use of biodiversity in agriculture, it is of foremost importance to integrate agricultural management into biodiversity research and to understand the focus and interests of farmers. This may be done by close cooperation between agriculturalists and ecologists, either in interdisciplinary projects or by diversification within working groups through hiring of scientists originally from the respective other discipline. Here, rangeland science may serve as an example where such cooperation seems more common, maybe due to the larger impact of natural processes on production in these usually larger-scale and less intensively managed systems, compared to temperate permanent grassland systems.

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## **General Discussion**

The aim of this study was to contribute to better understand the interaction of botanical composition (diverse or grass dominated swards) and herbivore species on animal behavior patterns and forage selectivity of cattle and sheep grazing alone or together.

For behavior patterns (first chapter), there were important differences between sheep and cattle. Cattle varied their time budget and grazing behavior depending on the presence of sheep. However, plant diversity had no effect on cattle behavior. In contrast, for sheep behavior, plant diversity rather than mono or co-grazing management was the determinant factor. This result is in accordance with the findings of several authors that have reported that cows are less sensitive to the vegetation changes than sheep. Some of the reasons are that their anatomy limits vertical selection (selection of different plant parts) and their higher ingestion rates compared to small ruminants, constrain the selection activity (Fraser et al. 2007; Abaye et al. 1994; Benavides et al. 2009).

In contrast, for small ruminants, grazing time increased, because of the limited ingestive capacity of the rumen hindered sheep to consume large amount of fibrous forages, seeking for more rapidly degradable forages, further being more selective. In accordance with this assumption, Metera et al. (2010) concluded that the time sheep allocated to grazing can be greatly modified by plant diversity, i.e. small ruminants need to consume dietary energy in small proportion of ingestions, so they have to choose forages with higher nutritive value than cattle.

In this sense, sheep avoid unnecessary energy losses seeking for preferred forages, but at the same time performed acute feed selection among available plant species, plant proportions and plant heights (Ginane and Dumont 2010; Lin et al. 2011). This explains why sheep respond to different plant arrays of grasslands with respect to their behavior, i.e. the larger effects of plant diversity treatment on sheep than in cattle are due to a greater selection activity of sheep (Cuchillo and Isselstein 2010).

Soder et al. (2009), concluded that the animal-plant relationship causes an equilibrium between grazing time and digestive capacities. Thus, the fine-scale choices performed by sheep changed their time budget and grazing behavior to balance quality and quantity of the ingested feed. This explains why sheep employed more time grazing on low diverse swards compared to high diverse swards (Metera et al. 2010; Villalba and Provenza 2009; Fraser et al. 2007).

Both cattle and sheep had a tendency to spend more time grazing and less time ruminating towards the end of the day. This is in line with previous studies. Hejmanová et al. (2009) found

a similar pattern for cattle in a trial under intensive and extensive grazing. In that study, two grazing intensities were investigated. High temperature during the day resulted in a larger time spent for resting at midday and longer time for grazing during sunset and the ongoing night. In our study, cattle co-grazing on diverse swards increased the time spent grazing from the early morning into the evening. This phenomenon was also reported by Lin et al. (2011) in fat tailed sheep. However, grazing time in that study was strongly influenced by stocking density i.e. grazing time of sheep was longer when stocking density was higher. In contrast, sheep with lower stocking density used shorter time for grazing.

The ability of cattle to adjust the ingestive behavior differently to co-grazing management, and sheep to adapt grazing behavior at different plant assemblages, may reinforce the aptitude of both domestic ruminants species to maintain plant diversity on diverse and grass dominated swards in co-grazing schemes.

For forage selectivity (second chapter), results indicate that on diverse swards, all plant species were grazed rather homogeneously on co-grazed pastures, which is in line with earlier findings (Benavides et al. 2009; Fraser et al. 2007; Cortes et al. 2006; Celaya et al. 2007). Celaya et al. (2011) demonstrated that diet overlap among cattle, sheep and goats lead to more uniform consumption and more sustainable utilization of available plant diversity. The complementary preferences of ruminant species encouraged a homogeneous intake of forages, consequently, severe defoliation of preferred species was hampered by competition and diet overlap (Wrage et al. 2011; Benavides et al. 2009; Walker 1994).

The analysis of target species, revealed a trend towards a higher consumption of *P. pratense*, *T. officinale* and to a slightly lower extent of *L. perenne* could be seen in sheep. This trend is likely to be related to the higher digestibility of these species as compared to the less preferred *F. pratensis* and *D. glomerata*. Selective grazing by sheep among similar grass species as in our experiment was found by Cortes et al. (2006). Sheep preferentially consumed *L. perenne* (78% in the diet) compared to *F. arundinacea* (22 % in the diet), though the herbage on offer at pastures contained only 49% of *L. perenne*.

Both behaviors, sheep selecting high quality diets at low ingestion rates and cattle selecting low quality diets but at high ingestion rates, assured daily diet requirements for maintenance and production according to the anatomical and physiological conditions of each species (Rutter



2010; Walker 1994). Co-grazing of cattle and sheep facilitated a more homogeneous consumption of the main forage species. Therefore, co-grazing might have the potential to better maintain grassland biodiversity.

For the third chapter (plant diversity and herbage-animal responses), the study revealed that the number of plant species of grasslands does not mean higher biomass production. Though there is evidence on experimental plots that species richness enhances herbage productivity (Tilman et al. 2001) in non-experimental grasslands there are inconsistent results (Henle et al. 2008; Isselstein et al. 2005; Tracy and Sanderson 2004; Hector et al. 1999). Reasons could be that species numbers in permanent grassland are above the maximum number of species to be effective as in experimental plots.

However, complementary benefits of phytodiverse grasslands are reflected on production stability, nutrient and water retention and animal product quality that might convince farmers to increase diversity of grasslands (Farruggia et al. 2008; Elgersma et al. 2006; Sanderson et al. 2004). To enhance plant diversity of grasslands, grazing has a good potential to increase heterogeneity (Dumont et al. 2007; Pykälä 2005).

The study argues that ecological and agricultural researchers should cooperate more to integrate agricultural management into biodiversity research and biodiversity measurements into agricultural research for an enhancement of grassland phytodiversity.

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## SUMMARY

Grassland composition and animal species may modify the grazing efficiency and ingestive behavior at pasture. However, precise knowledge on potential interactions between sward diversity and co-grazing is not available. Thus, a trial was conducted to evaluate the behavior patterns and forage selectivity of cattle and sheep grazing alone or together on grass swards differing in botanical composition. The experiment was carried out on mesotrophic permanent grassland in the Solling Uplands of Lower Saxony, Germany from May to September of 2009 and 2010. Species diversity of paddocks was manipulated by the use of herbicides resulting in grass-dominated swards (7 species per 9 m<sup>2</sup>) in contrast to untreated diverse swards (14 species per 9 m<sup>2</sup>) with grasses, forbs and legumes. Each sward type was combined with three grazing treatments: C= cattle mono-grazing; S= sheep mono-grazing and CS= cattle and sheep co-grazing. The six treatments were set up on paddocks of 0.5 ha each, replicated three times in blocks that were grazed rotationally. The main behavior patterns (grazing, walking, and ruminating) were recorded by conducting scan sampling every ten minutes from six a.m. to ten p.m. Secondary patterns (bites per minute, steps per minute, and bites per step) were obtained per core animal and observation day. Intake choices of *Dactylis glomerata*, *Festuca pratensis*, *Lolium perenne*, *Phleum pratense*, *Taraxacum officinale*, and *Trifolium repens* were obtained as follows: species were visually assessed in five 0.5 m<sup>2</sup> subplots per plot immediately before and after a period of three days grazing on a plot. Jacobs' selection index (JSI) was used to quantify the intake preference for single target species in relation to their proportion in the sward.  $JSI = ci - ai / ci + ai - 2ciai$ ; where  $ci$  = % forage in the diet and  $ai$  = % forage in the pasture. Here,  $ai$  was evaluated by the difference between the percentage mass of each species before and after three days of grazing. For behavior patterns, there were important differences between sheep and cattle. Cattle varied their time budget and grazing behavior depending on the presence of sheep. However, plant diversity had no effect on cattle behavior. For sheep behavior, plant diversity rather than mono or co-grazing management was the determinant factor. Cattle mono-grazing on diverse swards spent more time grazing at lower ingestive rates. *P. pratense* was the most preferred forage species (JSI=0.62). *L. perenne*, *T. officinale* and *T. repens* were also highly preferred regardless of sward composition or type of grazer (JSI = 0.47, 0.32 and 0.27, respectively). Co-grazing facilitated a more homogeneous consumption of the main forage species. Co-grazing might have the potential to better maintain grassland biodiversity.

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## PUBLICATIONS

- 5) Cuchillo, H.M., Wrage, N., Isselstein, J. Forage selectivity of (co-)grazing cattle and sheep on swards differing in plant diversity. *In preparation*.
- 4) Cuchillo, H.M., Wrage, N., Isselstein, J. Behavior patterns of (co-)grazing cattle and sheep on swards differing in plant diversity. *In preparation*.
- 3) Wrage, N., Strodthoff, J., Cuchillo, H.M., Isselstein, J. and Kayser, M. 2011. Phytodiversity of temperate permanent grasslands: Ecosystem services for agriculture and livestock management for diversity conservation. *Biodiversity and Conservation*. 20(14): 3317–3339.
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