Changes in Defoliation Patterns of Plant Functional Groups under Variable Herbage Allowance in Campos Grasslands

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The XXIV International Grassland Congress / XI International Rangeland Congress (Sustainable Use of Grassland and Rangeland Resources for Improved Livelihoods) takes place virtually from October 25 through October 29, 2021.

Proceedings edited by the National Organizing Committee of 2021 IGC/IRC Congress

Published by the Kenya Agricultural and Livestock Research Organization

Presenter Information
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Key words: grazing probability; intensity of defoliation; grasslands; functional groups

Abstract
Several studies have evaluated separately forage production, botanical composition, leaf traits and animal performance. However, few of them have focused on defoliation patterns at the level of functional groups (FGs) under different and variable herbage allowance (HA), especially in natural, diverse grasslands. The objective was to evaluate the relationship between HA and leaf traits on defoliation patterns of mature beef cows in the autumn, winter and spring. We evaluated the grazing probability (GP), intensity of defoliation (ID), and leaf traits on 14 species that represent more than 80% of total dry matter of the pasture. The experiment at which we evaluated those traits and responses has been managed under High HA (HHA) and Low HA (LHA) (8 and 5 kg dry matter kg live weight^{-1}, respectively). Four plant FGs (A, B, C and D) were defined according to leaf traits, and a selectivity index (SI) was developed for each group (considering the proportion of grazed and ungrazed species). Grazing patterns shifted across seasons. In the autumn, grazing was concentrated on FGs A, B and C groups (GP = 0.417). While for FG D, represented by high-biomass tussocks, the GP was lower (0.075). During winter, when herbage accumulation rate is limited, the average GP was 0.175. FGs C and D were more defoliated in relation to autumn, and during spring the GP shifted to FG B (0.289). The ID was similar to all FGs and seasons (66 % of leaf removed). In autumn and spring, the SI was affected by FGs and HA while in winter were similar between FGs but higher in HHA. Cows behaved differently in the defoliation pattern, modifying mainly the GP on FGs rather than the ID. Variation in HA across season determined changes in defoliation pattern, allowing to express selectivity in autumn and spring.

Introduction
Campos grasslands is a biome composed by a large array of grass and forb species forming a mosaic of tall and short patches as the result of soil types, fertility, botanical composition, topography and grazing management. This spatial heterogeneity, both on vertical and horizontal panes, affects animal intake (Laca, 2008) through mechanisms such selection, defoliation intensity and grazing behavior. The link between the pasture and grazing animals is the defoliation pattern, defined as the frequency and intensity of defoliation (Nabinger and Carvalho, 2009). This affects animal daily intake and diet composition, and, on the pasture side, determines the impact of grazing on vegetation. One approach to assess plant resource utilization strategies, grazing response and defoliation pattern is through plant functional traits (Díaz et al., 2001). This concept allows for a large number of species to be grouped into a small number of functional groups (FGs) through clustering species by values of specific functional traits (Duru et al., 2005). The more common functional traits are specific leaf area (SLA), leaf dry matter content (LDMC), leaf width and leaf tensile strength (LTS) (Garnier et al., 2015). Several studies have evaluated independently forage production, botanical composition, leaf traits and animal performance, but few have studied the fine tuning of those variables and diet selection. Specifically in the Campos, few evaluations considered herbage allowance (HA) or grazing pressure influences on plant functional traits (Cingolani et al., 2005; Cruz et al., 2010; Jaurena et al., 2012). The objective of this study was to further our understanding of the plant-animal interface on native grasslands through evaluating the relationship between HA and plant FGs on the defoliation patterns and selectivity of mature beef cows in three different seasons.

Methods and Study Site
The experiment was carried out at the "Bernardo Rosengurtt" Experimental Station, School of Agronomy, Universidad de la República in northeastern Uruguay. Evaluations were done during three periods: 1st Mar – 15th Apr (autumn), 30th Jul – 26th Aug (winter) and 1st Oct – 15th Nov (spring), 2017. Soils of the experimental area are Hapluderts, Argiudolls, Hapludalfs and Natruaqolls. The layout of the experiment is a complete random design with two treatments [High HA (HHA) and Low HA (LHA)] and two replicates. Treatments HHA and LHA are represented in kg dry matter (DM) kg live weight $^{-1}$(LW) (Sollenberger et al., 2005). Target annual average HA is 8 and 5 kg DM kg LW^{-1}, HHA and LHA respectively, variable in each season. During spring the target level is 12 and 8 kg DM kg LW^{-1}, during summer and autumn is 8 and 4 kg

DM kg LW^{-1}, and during winter 4 and 4 kg DM kg LW^{-1} for HHA and LHA, respectively (Do Carmo et al., 2018). The LHA paddocks have an area of 10 ha per replicate, and HHA 14 ha per replicate, totaling 48 ha. The experimental area was continuously stocked throughout the year, since 2007, with variable stocking rate adjusted monthly using the "put and take" method (Mott and Lucas, 1952). Animals used were multiparous pregnant beef cows (Hereford, Angus and reciprocal Hereford*Angus cross), of 446 ±63 kg of LW.

In each paddock, fixed 50-m transects (7 in HHA and 5 in LHA per paddock) were delimited according to soil type and topography, totaling 24 transects. In each transect, ten 40*40-cm quadrats were fixed every 5-m and divided in 4 quadrants of 20*20-cm. A total of 960 quadrats were assessed per sampling date (560 in HHA and 400 in LHA). In each quadrant, botanical composition was estimated visually, and during each evaluation period, all quadrants were assessed 4 or 5 times, in 5-7 days intervals, in order to avoid re-grazing at this scale between sampling moments. We evaluated the grazing probability (GP), intensity of defoliation (ID), and leaf traits on 14 species that represent more than 80% of total dry matter of the pasture.

Leaf traits measured were: LDMC, SLA, LTS and leaf width. Measurements were done on 10 leaves per plant species per paddock at the end of each period (Cornelissen et al., 2003). The species were grouped in FGs by cluster analysis using package vegan. Data was standardized and FGs were defined using 'Ward' method and Euclidean distance. In each quadrant a grazing event was recorded by marking the tip of the leaf using a water-marker pen. After defining FGs, was calculated the GP, ID and SI for each FG, in each period and treatment.

The intensity of defoliation (ID) was visually estimated as the percentage of leaf removed per grazing event: 25 % when a quarter of leaf was removed, 50 % half of the leaf removed, 75 % three quarter of leaf removed and 100 % when the whole leaf was removed (Lemaire et al., 2009). The ID for each FG* was calculated averaging the percentage of leaf removed by grazing, considering the whole grazed species corresponding to each FG*. Thus, the prorated average considered different number of records and also grazing events of each species. The GP for FG (FG*) was estimated by the sum of grazing events on species corresponding to FG* and the total records of species corresponding to FG* (1). The selectivity index (SI) for each FG (Cingolani et al. (2005), was calculated considering the number of grazed records of each specie corresponding to FG* and number of ungrazed records of each species corresponding to FG* (2). The index varies between -1 and 1. Values near -1 indicates avoidance, values near 1 indicates maximum selectivity, and 0 indicates indifference.

$$(1)\quad \text{GP (FG*)} = \frac{\text{sum of grazing events on species corresponding to FG*}}{\text{total records of species corresponding to FG*}} \qquad (2)\quad \text{SI (FG*)} = \frac{\text{nGR FG* - nUGR FG*}}{\text{nGR FG* + nUGR FG*}}$$

The GP and ID of each FG were analyzed by ANOVA (P< 0.05) for each period. Once defined the FGs (after the cluster analysis), they were added to the model as fixed effects for the analysis of plant-animal interaction. Also, HA was used as fixed effect, while paddock was used as random effect. Furthermore, the SI was analyzed by ANOVA (P< 0.05) using two models. First model considered HA and FGs as fixed effect and paddock as random effect, while second model considered FG and period as fixed effect and paddock as random effect. Data were analyzed using mixed model in R 3.5.1 with lmerTest package (R Development Core Team, 2018).

Results

Four FGs (A, B, C and D) were defined based on leaf traits. From A to D had an increase in LTS and a decrease in SLA and leaf width. The increase in LDMC just occurred from C to D. LDMC, SLA, width and LTS for each species varied over periods and HA. As a result, the number of species in each group was variable between HA and period.

In autumn the GP was different only between FGs, resulting higher in groups A, B and C (0.417) than group D (0.075). Conversely, in winter the GP was only affected by HA, resulting higher GP for all species in HHA (0.230) than LHA (0.121). During spring, the GP was affected by the interaction FGs*HA. The higher GP occurred in group B in LHA, while the lower values occurred in HHA groups A and D, and in LHA group D. The interaction between FGs*HA affected the ID during autumn. Higher values of leaf removed occurred in LHA group B while the lower values occurred in HHA group C and LHA group D. The average leaf removed in the others groups and HA combinations was 62.9 %. Conversely, no difference was observed in winter ID between HA, FGs and interaction. The average leaf removed value in this period was 69 %. During spring, the ID was constant among HA and FGs, averaging 66%.

In autumn, SI was affected by FGs. The higher SI was observed in FGs A and B, while the lower SI in FG D. During winter the SI was only different between HA, where the high SI occurred in HHA, and the low SI occurred in LHA. In spring, SI was different among HA and FG. The higher SI was observed in FG B in LHA, which differed in HHA with FG A and D, and in LHA with FG D. Comparing the SI within FG across periods we observed that for FGs A, B and C the SI was different between period. For FG A the higher SI was in autumn, while the lower values were in winter and spring. For FG B, the higher value was observed in autumn, intermediate in spring, and lower in winter. As in FG A, the higher SI for FG C was observed in autumn, and the lower in winter and spring. Finally, the SI of FG D was similar in both treatments and period.

Discussion

The GP of each FG in autumn was associated to their leaf traits (increasing from D to A) rather than their specific contribution to HM. Cows defoliated the same proportion of groups A, B and C regardless the specific contribution, and the SI was the same between FG A, B and C (Table 2), and avoided group D, which correspond to higher LTS and LDCM. However, the higher GP of FG C (high nutritive value than FG D but lower than A and B) showed that cows selected forage quality but also forage quantity, mainly in LHA, similar results that obtained Bonnet et al. (2015). The difference in SI between treatments in FG C could be explained by the higher herbage mass in HHA (3681 kg DM ha^{-1} vs 2379 kg DM ha^{-1}), which allowed to express more selectivity between FGs. In this condition, cows could select species of FG A and B in HHA, while in LHA, cows grazed FG A, B and C. The winter GP was only different between HA. Even though HM and HA were not different, pasture structure and mainly the body condition of cows could explain a better exploration and selectivity in HHA. This could be a carry effect of HM, HAR and mainly HA, from autumn to winter. The GP in this period was lower than autumn, explained by a lesser HM, HAR and HA. Lemaire et al. (2009) showed that the probability of leaf defoliation decreases with lower HAR, as found in this work, determining the lower GP and lower selectivity. FGs were grazed similarly regardless of the nutritive value and the specific contribution. It could be assumed that cows oriented the foraging strategy to energy intake, rather than forage quality. Furthermore, the SI was not different between FGs, contrary to autumn. The GP was higher in HHA than LHA, possibly associated to the number of animals in each treatment, determining an increase kg LW ha^{-1}, as showed by Lemaire et al. (2009), but also, by an increase in animals/ha to reach the target HA (1.43 cows ha^{-1} vs 0.85 cows ha^{-1}). In spring the group D was the least grazed due to the lower quality of the component species rather than the lower specific contribution. Cows avoided these groups, determining the lower SI. The higher GP observed in FG A in LHA than HHA was due to the presence of *Paspalum dilatatum* in LHA, a desirable specie, while in HHA, FG A was only conformed by *S. microstachyum*, a less desirable species (Rosengurtt, 1979). Comparing to winter, a difference in GP and SI between FGs was observed. In terms of HM was lower but HAR was higher than winter. Also, the number of cows was lower. Therefore, the higher selective capacity showed by cows was explained by high HAR and lower number of animals.

In all periods, the average of ID was 60 - 70%, barely higher value than expressed by Lemaire et al. (2009). This could be caused by a higher capacity of cows to graze intensively, regardless the nutritive value and leaf traits. In this condition, cows modified the GP of each FG rather than the ID. The fact that the ID was similar in FGs could be by a little variation in traits in this section of the lamina. The defoliation pattern on FGs was differently explained by the GP. In this heterogeneous pasture, cows adjust the defoliation pattern by adjusting the proportion of grazed species, regardless the specific contribution of each FG. The ID remained constant in many different situations.

Acknowledgements

To ANII which contributed with financial support.

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Table 1 Effect of functional groups (A, B, C and D) and herbage allowance (HHA and LHA) on specific contribution (%), grazing probability and leaf intensity defoliation in autumn, winter and spring

Period			Functional Groups				Probability values		
			A	B	C	D	FGs	HA	FGs*HA
Autumn	GP	HHA	0.461	0.382	0.283	0.052	**0.011**	0.278	0.897
		LHA	0.454	0.489	0.431	0.098			
	ID %	HHA	59.9 ab	63.0 ab	57.6 b	61.3 ab	**0.035**	0.128	**0.048**
		LHA	64.3 ab	73.7 a	66.4 ab	52.1 b			
Winter	GP	HHA	0.225	0.244	0.210	0.239	0.935	**0.003**	0.769
		LHA	0.147	0.104	0.126	0.105			
	ID %	HHA	73.0	66.7	62.8	76.7	0.168	0.612	0.142
		LHA	62.7	66.1	76.8	67.2			
Spring	GP	HHA	0.035 b	0.221 ab	0.214 ab	0.106 b	**0.017**	**0.023**	**0.045**
		LHA	0.272 ab	0.357 a	0.173 ab	0.119 b			
	ID %	HHA	62.5	67.2	60.1	66.1	0.795	0.198	0.802
		LHA	65.6	68.2	71.8	73.7			

Different letters following means in rows indicate statistical significance at $P < 0.05$.

Table 2 Selectivity index for each functional group, period and treatment, and probability values for herbage allowance (HA), functional group (FG), period, and simple interaction (HA*FG, HA*period)

		Functional Groups				Probability values		
Period	Treatment	A	B	C	D	FGs	HA	FGs*HA
Autumn	HHA	-0,08	-0,24	-0,43	-0,90	**0.011**	0.277	0.897
	LHA	-0,09	-0,02	-0,14	-0,80			
Winter	HHA	-0,55	-0,51	-0,58	-0,52	0.934	**0.002**	0.767
	LHA	-0,71	-0,79	-0,75	-0,79			
Spring	HHA	-0,93 b	-0,56 ab	-0,57 ab	-0,79 b	**0.017**	**0.022**	**0.045**
	LHA	-0,46 ab	-0,29 a	-0,65 ab	-0,76 b			
Probability values	HA	0.446	0.632	0.838	0.365			
	period	**0.036**	**0.033**	**0.013**	**0.082**			
	HA*period	0.273	0.216	0.095	0.084			

Different letters following means in rows indicate statistical significance at $P < 0.05$.