

Forage Allowance as a Target of Grazing Management: Implications on Grazing Time and Forage Searching

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Abstract

This work aimed to evaluate the following hypotheses: 1) the daily grazing time (GT) and 2) forage searching are more associated with the sward structure than with the levels of daily forage allowance (FA). To this end we proposed a model that was tested through an analysis of the sward structure, grazing time, and displacement in grazing by heifers on the natural grassland of the Pampa Biome (southern Brazil), which has been managed by FA levels since 1986. For three seasons, between January 2009 and February 2010, we evaluated the effect of FA on the main descriptors of the sward structure (herbage mass, sward height, and tussocks frequency) and the effect of these on the GT, displacement rate (DR), and daily displacement (D) in grazing. The data were analyzed with the use of regression and descriptive analyses from three-dimensional contour graphs with the data of the sward structure and GT. The DR was not associated with the FA levels or sward structure; however, the DR presented a positive linear relationship with the D and GT. The incremental change in the GT was accompanied by an increase in the D. Lastly, independently of the level of the FA and season evaluated, the lower values of GT were always associated with the following structural configuration: forage mass between 1 400 and 2 200 kg DM · ha⁻¹, sward height between 9 and 13 cm, and tussock levels not exceeding 35%. Outside these limits, a penalty occurred in the GT and displacement patterns of the heifers. We found evidence that a better understanding of the cause–effect relationships between the sward structure and the ingestive behavior of the animals demonstrates the possibility of increasing the performance of domestic herbivores with important economic and ecological consequences.

Resumen

El objetivo del estudio fue evaluar las siguientes hipótesis: (i) si el tiempo de pastoreo diario (TP) y (ii) la búsqueda de forraje están más estrechamente relacionados a la estructura del pasto que a los niveles diarios de oferta de forraje (OF). Con este fin, propusimos un modelo que se puso a prueba en base al análisis de la estructura del pasto, el tiempo de pastoreo y el desplazamiento en pastoreo en terneras sobre un pastizal natural del Bioma Pampa (sur de Brasil) que, desde 1986, se ha manejado con distintos niveles de OF. En tres épocas, entre Ene/2009 y Feb/2010, se evaluó el efecto de la OF sobre los principales descriptores de la estructura del pasto (biomasa de forraje, altura y frecuencia de matas) y el efecto de éstos sobre el tiempo de pastoreo (TP), la tasa de desplazamiento (TD) y el desplazamiento diario (D). Los datos fueron analizados mediante regresión y por análisis descriptivos a partir de gráficos de contorno tridimensionales en base a los datos de estructura del pasto y TP. La TD no tuvo relación con OF ni con la estructura del pasto, pero mostró una relación lineal positiva con D. Incrementos en TP estuvieron asociados a incrementos en D. El estudio demostró la importancia de la estructura del pasto al constatar que, independientemente del nivel de OF y de la época del año evaluada, los valores más bajos de TP siempre estuvieron asociados a estructuras del pasto caracterizadas por una masa de forraje de 1 400 a 2 200 kg MS · ha⁻¹, alturas de 9 a 13 cm y frecuencia de matas en el pastizal menores al 35%. Fuera de estos límites hubo una penalización en el TP y en el patrón de desplazamiento en pastoreo de las vaquillas. Encontramos evidencias de que el mejor entendimiento de las relaciones causa-efecto entre la estructura del pasto y el comportamiento en pastoreo harían posible incrementar el rendimiento de los herbívoros domésticos, con importantes consecuencias económicas y probablemente ecológicas.

Key Words: displacement in grazing, grazing intensity, grazing pressure, ingestive behavior, natural grassland, Pampa Biome

Da Trindade was sponsored by a postdoctoral scholarship from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). CN and PCFC are grantees of CNPq productivity.

At the time of research, Da Trindade had a doctoral scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior.

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Manuscript received 30 October 2011; manuscript accepted 18 February 2012.

INTRODUCTION

Natural grasslands occur on all of the continents of the world, but the success of their utilization and conservation requires the adoption of sustainable management practices (Overbeck et al. 2007), creating dilemmas for the managers (Carvalho and Batello 2009). The utilization of grazing environments neces-

sarily involves the control of livestock grazing. The concept of one adequate grazing environment for livestock production and resource conservation is an emerging concept that must integrate aspects of production with the quality requirements of the production system (Carvalho 2005).

Carvalho et al. (2001) proposed that grazing management is observed as the art of creating and manipulating sward structures to optimize the vegetation growth process and the forage harvested by grazing animals. The main factors of management are those that determine the degree of grazing intensity, which modifies vegetation growth and the behavior and herbage intake of the animals (Nabinger et al. 2009), fundamental variables in the definition of adequate grazing environments (Bailey 2005; Carvalho 2005). The adjustment in the daily forage allowance (FA) is a method to manage the grazing intensity (Nabinger 1998).

The FA is the relationship between the forage mass and animal live weight per unit area of the specific unit of land being grazed at any time, providing an instantaneous measurement of the forage-to-animal relationship (Allen et al. 2011). The FA is the inverse of grazing pressure (see McCartor and Rouquette 1977). This method of managing grazing intensity has been considered a target of grazing management for some time; it is still considered a target, as research to improve the consistency of results when the stocking rates were not considered goals (Mott 1960; Jones and Sandland 1974) but consequences of the FA level. In this context, many experimental protocols were developed to manage and improve vegetation and animal production on natural grasslands in the Pampa Biome (Côrrea and Maraschin 1994; Maraschin et al. 1997; Soares et al. 2005; Pinto et al. 2008).

The southern grasslands (between 24 and 35°S) are an ecosystem that extends along the south of Brazil, Uruguay, northeastern Argentina, and part of Paraguay, with a wide floristic diversity along 500 000 km² of land (Bilenca and Miñarro 2004). Campos place has a type of vegetation composed predominantly of grasses and other herbaceous plants and classified as “steppe” in the phytogeographic international system. This vegetation feeds approximately 65 million domestic ruminants (Berreta 2001). The largest part of Campos Sulinos in the Brazilian area consists of the Pampa Biome (Instituto Brasileiro de Geografia e Estatística [IBGE] 2004), which is located in the southern state of Rio Grande do Sul and represents 90% of the natural grasslands in this state. These natural grasslands are dominated by grasses, especially those belonging to the *Andropogon*, *Aristida*, and *Paspalum* genera, totaling approximately 450 species with approximately 200 species of legumes (Boldrini 2009).

The studies conducted for more than 20 yr in the Pampa Biome showed the benefits of a moderate FA on production and the quality of the grazing environment. However, as a tool of grazing management, the FA does not provide any information about how the forage is offered and spatially and temporally distributed (Hodgson 1984). The architecture, composition and quantity of forage describe aspects of the sward structure that affect the grazing process and forage intake by herbivores (Hodgson 1990) and describe the grazing environment (Carvalho 2005).

There is no doubt that the management of grazing intensity via the FA brought substantial changes in forage and livestock

production when indicated as a management target. However, as the concept of FA was conceived, and considering the aspects highlighted by Hodgson (1984) and Heringer and Carvalho (2002), this way does not ensure the control of the sward structure per se, which limits the use of the FA as a target of grazing management (Carvalho et al. 2001; Da Silva and Carvalho 2005). An experiment in the natural grasslands of the Pampa Biome maintained for 25 yr under FA levels for beef cattle determined real contrasts in the forage abundance and sward structure over this period (Neves et al. 2009). This scenario, singular in its long-term application of treatments, still allows sward targets to be investigated based on what currently is thought to be the main sward characteristics affecting the behavior of beef cattle grazing on natural grasslands (Pinto et al. 2007; Gonçalves et al. 2009a, 2009b; Mezzalana 2010; Bremm 2010): herbage mass, sward height, and tussock frequency. The effect of these variables on livestock production is associated with the ability of the animal to harvest a greater or lesser amount of forage of greater or lesser nutritive value (Heringer and Carvalho 2002).

When grazing, herbivores select sites with sward structures that favor the foraging efficiency (Bailey et al. 1996) and respond to changes in the arrangement of preferred and nonpreferred items (Clarke et al. 1995). One herbivore response is changing the time allocated to grazing activity. In theory, the better the conditions of the feeding environment are, the less time the animal will devote to this activity, as it increases the rate and efficiency of harvesting and consequently animal performance. The herbivore needs time to search the forage to be consumed, achieving a key process of foraging behavior that is time-dependent (Carvalho et al. 2001). During grazing, the animals are faced with the challenge of finding food in this context; the daily displacement associated with this activity expresses, in part, the magnitude of searching in an attempt to find the best pasture sites for feeding.

Based on the importance of the relationship between the characteristics of the sward structure on the ingestive behavior and pattern of forage searching by grazing herbivores, we postulated that 1) the grazing time and 2) forage searching are strictly associated with the sward structure more than with the preset levels of the FA. If these hypotheses are confirmed, possible increases in the performance of ruminants and a better understanding of the cause-effect relationships in natural grasslands may be expected. Moreover, it would imply that the targets of grazing management will be sustained if based on both the FA and also on a more precise control of the sward structure that the grazing animals face. The objective of this study was to test these hypotheses and to propose a model that was tested based on an analysis of the sward structure, daily grazing time, and displacement in the grazing of beef heifers on the natural grasslands of the Pampa Biome, which has been managed by FA levels for 25 years.

METHODS

Location, Treatments, and Experimental Design

The experiment was performed in the experimental area of the Universidade Federal do Rio Grande do Sul (lat 30°05'S, long 51°40'W and 46 m above sea level [a.s.l.]), Brazil, in an area of

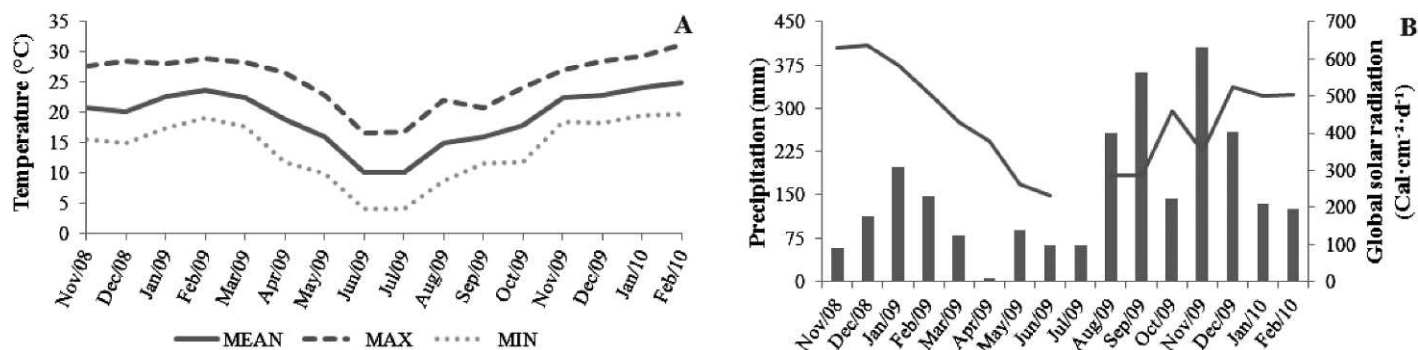


Figure 1. Monthly meteorological data during the experimental period: **A**, mean air temperature (°C; MEAN) maximum (MAX), and minimum (MIN); **B**, rainfall (mm, bars) and global solar radiation (Cal · cm⁻² · d⁻¹, line). Source: meteorological station of the EEA/UFRGS.

natural grassland representative of a Campos phyto-physiomy (Boldrini et al. 2010), which forms part of the Pampa Biome. The climate at the experimental site is humid tropical, with an annual precipitation of 1440 mm, which is well distributed throughout the year; June is the wettest month (168.2 mm), and December is the driest (97.7 mm; Bergamaschi et al. 2003). Since 1986, the experimental area, approximately 31 ha, has been managed under continuous stocking and FA levels for beef cattle. The preset levels of FA were 4, 8, 12, and 16 kg of dry matter (DM) per 100 kg of the animal's live weight (LW) per day (kg DM · 100 kg LW⁻¹ · d⁻¹ or % LW). The levels were adjusted every 28 d with the use of the put-and-take technique (Mott and Lucas, 1952; for more details on the treatments, see Soares et al. 2005 and Neves et al. 2009). Except for the management of the grazing intensity via adjustments in the FA, there were no other anthropic interventions in the experimental units (e.g., fertilization, irrigation, fire, or mowing).

The experiment was arranged in randomized blocks with two replicates. The difference in the soil drainage capacity was the determining factor for the division of the experimental area into blocks. The experimental units (EUs) varied from 3.0 to 5.2 ha in area and presented a slightly undulating relief. The 25-yr-use area with different levels of FA resulted in different floristic compositions (Cruz et al. 2010) and sward structures (Neves et al. 2009). In an EU managed with a low FA (e.g., 4% LW), there is only one stratum of vegetation, which is homogeneous and with a low sward height. The intertussock areas of pasture are predominantly composed of species of the *Paspalum*, *Axonopus*, *Piptochaetium*, and *Coelorachis* genera. With the increase of the FA, tussocks are formed mainly by species of the *Aristida*, *Eryngium*, *Andropogon*, *Baccharis*, and *Vernonia* genera, configured in a bimodal vegetation structure and dispersed in mosaics (Côrrea and Maraschin 1994).

Animals and Experimental Period

The experimental animals were crossbred Angus and Hereford (*Bos taurus taurus*) and Nellore (*Bos taurus indicus*) heifers, 15 mo of age and 152 kg LW ± 4.0 SE when placed in the experimental area on 15 November 2008. The initiation of the experiment occurred after an adjustment period of 153 d in autumn–winter. The animals remained in the experimental area for 174 d until 27 May 2009, when the temperature began to decrease after a period of low precipitation (Fig. 1), compro-

mising the growth and condition of the sward for keeping the animals in the experimental area. For this reason, the animals were removed from the experimental area to an area adjacent to the EUs of natural grassland that was in better condition. The animals remained out of the experimental area until 7 October 2009, when they were returned, and the adjustments to the preset FA levels were repeated. The animals remained in the experimental area until mid-February 2010. The experimental period described above was divided into three periods that were analyzed separately: summer 2009, from early January to late February 2009; spring 2009, evaluated in November 2009; and summer 2010, from early January to mid-February 2010.

Sward Structure and Calculation of FA

The sward structure was evaluated by sampling the vegetation in each EU. An iron frame (0.5 × 0.5 m) was used to take the samples. In the summers of 2009 and 2010, one point in a frame was taken in each 200 m² (grid 10 × 20 m); in spring 2009, the samples were randomly distributed to achieve a minimum of 50 points exclusively in the intertussock stratum. The forage mass (FM) and sward height (H) were estimated only when the intertussock stratum were represented in the frame. The double-sampling technique described by Wilm et al. (1944) was used to estimate the FM, and the H was measured with the use of a sward stick (Barthram 1985) and estimated by five measurements per frame. When the frames were represented by tussocks, the frequency of occurrence was registered (T, %) based on the ratio between the number of occurrences and the total number of sampled points in each EU.

After sampling to estimate the FM, H, and T, 10 samples per EU of the forage in the intertussock vegetation were cut at the litter level after a visual estimation of the FM by trained evaluators. The cut forage was collected in paper bags, oven dried at 65°C for 72 h, and then weighed with the use of a precision balance. The weights of the samples were used to adjust the visual estimates of the FM in each evaluation with the use of linear regression ($y = a + bx$) between the FM given by the evaluator (x) and the collected FM (y) in the sample. The selection of the equations to be used was based on the highest coefficient of determination (R^2) and the P value ($P < 0.05$).

To verify whether the FAs were achieved in each period, the actual forage allowance (AFA, % LW) was calculated according to the following equation: $AFA = ([FM/n + DAR]/$

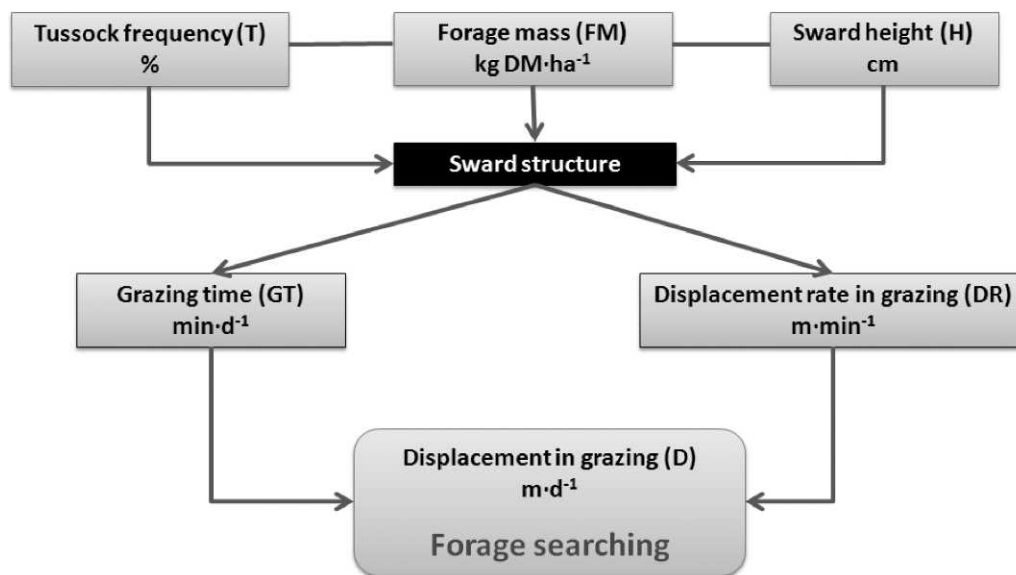


Figure 2. Conceptual model of forage searching by grazing animals as a function of the sward structure.

SR) 100; where n = the number of days in each period evaluated; DAR = the daily dry-matter accumulation rate in $\text{kg DM} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$; and SR = the stocking rate in $\text{kg LW}^{-1} \cdot \text{ha}^{-1}$. The DAR used in the equation was estimated with the use of four exclusion cages per EU according to the method proposed by Klingman et al. (1943).

Grazing Time and Displacement in Grazing

The observation of the daily grazing time (GT, min) was performed on two experimental animals per EU on February 10 and 12, 2009 (summer 2009), November 19 and 21, 2009 (spring 2009), and January 3 and 5, 2010 (summer 2010). On each day, only the EUs of the same experimental block were evaluated. We used a bioacoustic technique proposed by Da Trindade et al. (2011) to estimate the GT. Sounds were recorded during 24 h using microphones protected by Styrofoam and fastened to a halter on the animal's forehead where a digital recorder (ICP-P620; Sony, Manaus, AM, Brazil) was attached. The halters were placed on the animals in the morning and removed the following morning. The sounds were transferred to a computer and converted into the .aif format. To obtain the GT ($\text{min} \cdot \text{d}^{-1}$), the acoustic registers were analyzed, and the activities of grazing were discriminated using the Sound Forge software (v.9; Sony Creative Software Inc., Middleton, WI).

In spring 2009 and summer 2010, the experimental animals were also equipped with global positioning system (GPS) navigation (Etrex; Garmin, Olathe, KS). The GPS devices were attached to the halter and adjusted on the upper neck of the heifers to capture the largest number of satellites and to promote a greater precision of obtained registers. Data tracks were extracted from the GPS Trackmaker Pro software (v.4.7; Geo Studio Tecnologia Ltda., Belo Horizonte, MG, Brazil), considering only the periods when the animals were identified as participating in grazing activity. The daily displacement in grazing (D, $\text{m} \cdot \text{d}^{-1}$) corresponded to the sum of the entire route traveled by the animals and the daily displacement rate in

grazing (DR, $\text{m} \cdot \text{min}^{-1}$) and was expressed as the ratio between the D and GT.

Forage Searching

To address the hypotheses related to forage searching, we proposed the model presented in Figure 2. The model suggests that sward structure is characterized by the interaction between the principal structural variables affecting animal behavior: FM, H, and T. The sward structure, in turn, determines the allocation of daily time for grazing activity and the DR. The D is an indicator of the forage searching on the feeding environment and is affected by the GT and DR.

Data Analysis

The values of the AFA and DAR and the values of the sward characteristics (FM, H, and T) were analyzed with the use of linear and quadratic regression models. The model's responses for the AFA were generated with the use of the preset values of FA, whereas the other models that verified the effect of the FA on the characteristics of the sward structure and on the time and displacement in grazing were generated from the values of the AFA. Consequently, we performed regression analyses to evaluate the relationships between the descriptors of sward structure (FM, H, and T) and the GT and DR and, in turn, their relationships with the variations in the D for spring 2009 and summer 2010 by testing the linear and quadratic models. The regression analyses were performed with the use of SAS® v.9 software through the REG procedure. The block effect was removed and the models with the higher coefficients of determination were selected (R^2) because the regression coefficients were significant at a 10% level.

Contour plots were generated to describe a three-dimensional form (with the FM, H, and T variables) of the sward structure configurations presented to the animals during each period (summer 2009, spring 2009, and summer 2010). The contour plots were also generated with the FM, H, and GT

Table 1. Actual forage allowance and sward structure characteristics managed with forage allowance levels (FA) in the natural grasslands of the Pampa Biome.

	FA (% LW ¹)				Model	P	R ²	RSEM
	4	8	12	16				
Summer 2009								
AFA ² (% LW)	4.2	9.2	11.9	16.0	AFA = 0.8 + 0.9FA	0.0014	0.90	0.15
DAR ³ (kg DM ⁴ · ha ⁻¹ · d ⁻¹)	25.9	29.8	26.1	29.3	DAR = 27.8	NS ⁸	—	3.03
FM ⁵ (kg DM · ha ⁻¹)	955	2 184	2 453	2 842	FM = 568.7 + 149.2AFA	0.0016	0.88	24.2
H ⁶ (cm)	4.6	11.1	13.5	16.1	H = 1.5 + 0.9AFA	0.0007	0.92	0.13
T ⁷ (%)	1.0	19.0	29.5	35.5	T = -7.7 + 2.7AFA	0.0009	0.91	0.38
Spring 2009								
AFA (% LW)	2.5	4.4	9.1	10.5	AFA = -0.6 + 0.7FA	0.0004	0.94	0.08
DAR (kg DM · ha ⁻¹ · d ⁻¹)	11.8	12.6	19.8	15.9	DAR = 15.0	NS	—	1.64
FM (kg DM · ha ⁻¹)	415	861	1 278	1 723	FM = 190.9 + 132.3AFA	0.0214	0.69	40.0
H (cm)	4.9	6.3	8.8	10.4	H = 3.6 + 0.6AFA	0.0037	0.88	0.12
T (%)	1.0	19.1	28.4	37.0	T = -4.2 + 3.8AFA	0.0021	0.88	0.65
Summer 2010								
AFA (% LW)	3.2	6.1	12.3	15.2	AFA = -1.3 + 1.1FA	0.0004	0.93	0.13
DAR (kg DM · ha ⁻¹ · d ⁻¹)	12.4	13.8	14.7	15.0	DAR = 13.7	NS	—	2.09
FM (kg DM · ha ⁻¹)	564	1 034	1 860	1 990	FM = 298.5 + 115.8AFA	0.0011	0.90	17.23
H (cm)	5.9	8.9	12.3	14.8	H = 4.0 + 0.7AFA	< 0.0001	0.97	0.06
T (%)	1.0	19.1	28.4	37.0	T = -2.8 + 2.6AFA	0.0048	0.88	0.44

¹LW = live weight.

²AFA = actual forage allowance.

³DAR = daily dry-matter accumulation rate.

⁴DM = dry matter.

⁵FM = forage mass.

⁶H = sward height.

⁷T = tussock frequency.

⁸NS = not significant.

variables to verify the patterns of the GT in response to the structural configurations. The three-dimensional contour graphs were generated with the use of the ‘Graph’ option of the JMP software (v.9; SAS Institute Inc., Cary, NC).

RESULTS

Sward Structure and Animal Variables in Relation to Forage Allowance

The values of the AFA showed a significant relationship with the preset values, resulting in a gradient among the levels (Table 1), as was needed to test the hypotheses of this study. The values of the AFA were similar to those preset, except in spring 2009, when they were smaller. The highest values of the DAR occurred in summer 2009, but did not show a relationship with the AFA levels. The descriptive variables of the sward structure were affected by the FA (Table 1). The values of the FM, H, and T showed incremental changes when the FA increased from 4% to 16% LW. This confirmed the occurrence of the sward structure gradients between the FA levels, creating contrasting food environments and allowing us to investigate the effect of the sward structure on the animals’ responses, which was also essential to testing the hypotheses. In addition to the contrasting feeding environments produced by the FA management, in the summer of 2009, the values of the FM and H were high compared to the other periods. During this period, except

for the EUs using the 4% LW treatment, the FM and H were higher than 2 000 kg DM · ha⁻¹ and 9 cm, respectively.

In contrast to the response pattern found in the sward variables, the variables of the heifers’ behavior were not affected by the FA levels except in the spring of 2009 (Table 2). During this period, the time dedicated to grazing by the animals in the 4% LW treatment represented 49% of the daytime, whereas this activity represented only 38% in the average of the other treatments. In addition, the quadratic models predicted that the lower values of the GT, DR, and D were obtained when the FA in spring 2009 showed values of 7.1, 6.7, and 7.4% LW, respectively. In the summers of 2009 and 2010, the GT in the 4% LW treatment represented 45% of the daytime, whereas this value was approximately 41% in the other treatments.

Forage Searching Model

In spring 2009 and summer 2010, we verified that the variations in the sward structure did not cause an effect on the DR ($P > 0.10$) but did affect the GT (Figs. 3A and 3B). In spring 2009, we found a close relationship between the T and GT, with lower values of the GT associated with T values between 20% and 30% (Fig. 3A).

During both periods, the GT decreased with increasing FM. In spring 2009, the coefficient of determination of the effect of the FM on the GT was lower, but the effect of the T on the GT

Table 2. Variables of beef heifer behavior on the natural grasslands of the Pampa Biome managed with forage allowance levels (FA).

	FA (% LW)				Model	<i>P</i>	<i>R</i> ²	RSEM
	4	8	12	16				
Summer 2009								
GT ¹ (min d ^{−1})	624	534	626	597	GT = 598.4 − 0.31AFA ²	0.9583	0.02	4.13
Spring 2009								
GT (min d ^{−1})	710	510	573	566	GT = 995 − 131.4AFA + 9.3AFA ²	0.0771	0.65	3.91
DR ³ (m min ^{−1})	6.5	5.4	5.9	6.0	DR = 11.1 − 0.8AFA + 0.06AFA ²	0.0635	0.93	0.023
D ⁴ (m d ^{−1})	4382	2778	2910	2978	D = 8254 − 1108AFA + 74.8AFA ²	0.0396	0.87	24.85
Summer 2010								
GT (min d ^{−1})	670	642	592	582	GT = 692.2 − 7.7AFA	0.1158	0.63	4.05
DR (m min ^{−1})	4.2	4.0	3.8	4.5	DR = 4.2 − 0.008AFA	0.8795	0.30	0.0492
D (m d ^{−1})	2807	2607	2257	2570	D = 2922 − 39.4AFA	0.3277	0.19	36.31

¹GT = grazing time.²AFA = actual forage allowance.³DR = displacement rate.⁴D = daily displacement in grazing.

was high ($R^2 = 0.98$). These results verified that this model was quadratic in the spring of 2009.

The D was affected by the DR and GT in spring 2009 and summer 2010 (Fig. 4). In the spring of 2009, the increase of 1 m · min⁻¹ in the DR resulted in an increase of 635 m · d⁻¹ in the D, whereas the increase of 1 min in the GT resulted in an increase of 7.7 m · d⁻¹ in the D. In the summer of 2010, we adjusted the quadratic model for the effect of the DR on the D, showing an increase in the D up to values of approximately 5 m · min⁻¹. During the same period, an increase of 1 min · d⁻¹ in the GT resulted in half of the increase observed in spring 2009, with a value of 3.6 m · d⁻¹. In general, the values of the DR and D for spring 2009 were high when compared to summer 2010.

Three-Dimensional Analysis: Configuration of Sward Structure and Grazing Time

We found an increase in the FM associated with an increase of the H and T (Fig. 5) independently of the period evaluated and the FA level. Although there were no important modifications

in the values of T between the periods, we verified the opposite response for the FM and H because these vary considerably, creating distinct sward structure configurations between the treatments and EUs of the same FA level. The FAs for the 4% and 8% LW treatments had similar values of FM, H, and T between the EUs and even between periods, whereas we observed major variations in the higher FAs, 12% and 16% LW.

In summer 2009, the lower GT (≤ 550 min · d⁻¹) occurred when the FM was between 1 700 and 2 300 kg DM · ha⁻¹ and the H was between 9 and 12 cm (Fig. 5B). At that time, the EUs of the 8% LW treatment and a single EU of the 12% LW treatment presented conditions that resulted in lower values for the GT. In spring 2009, the lower values of GT occurred when the FM was between 700 and 2 100 kg DM · ha⁻¹ and the H was between 5 and 12 cm (Fig. 5B); these conditions were also detected in the EUs of the 8% LW treatment, a single 12% LW treatment, and a single 16% LW treatment. In summer 2010, lower values of the GT were observed when the FM ranged

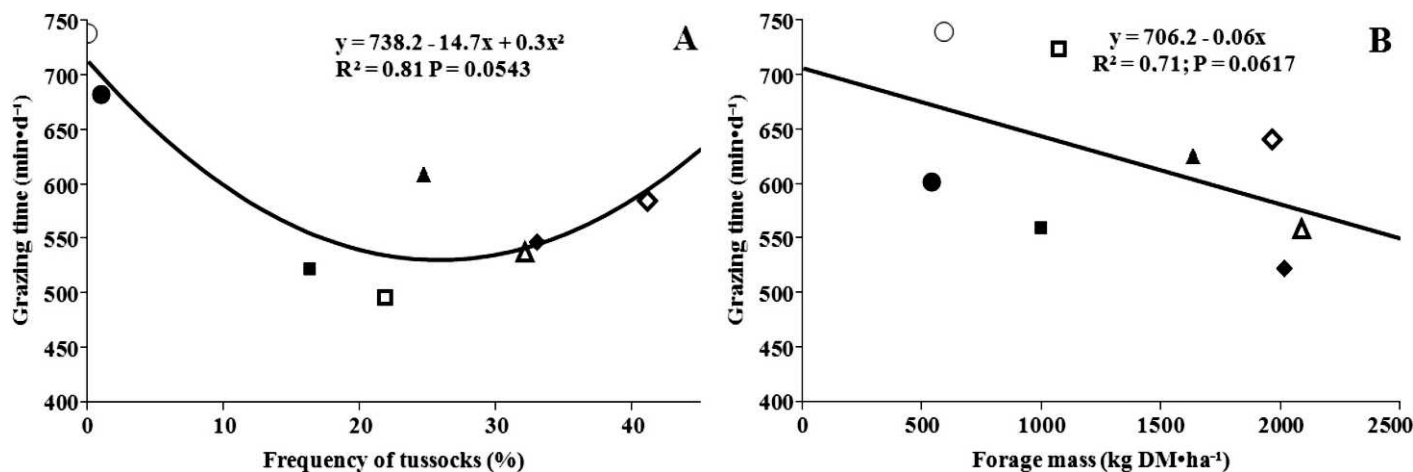


Figure 3. Regression models of grazing time (min · d⁻¹) for beef heifers in relation to the forage mass (kg DM · ha⁻¹) and frequency of tussocks (%) on the natural grasslands of the Pampa Biome managed with FA levels (% LW). **A**, Spring 2009, **B**, summer 2010. The points of models correspond to the following replicates: 4% LW = ● (block 1), ○ (block 2); 8% LW = ■ (b1), □ (b2); 12% LW = ▲ (b1), △ (b2); and 16% LW = ◆ (b1), ◇ (b2).

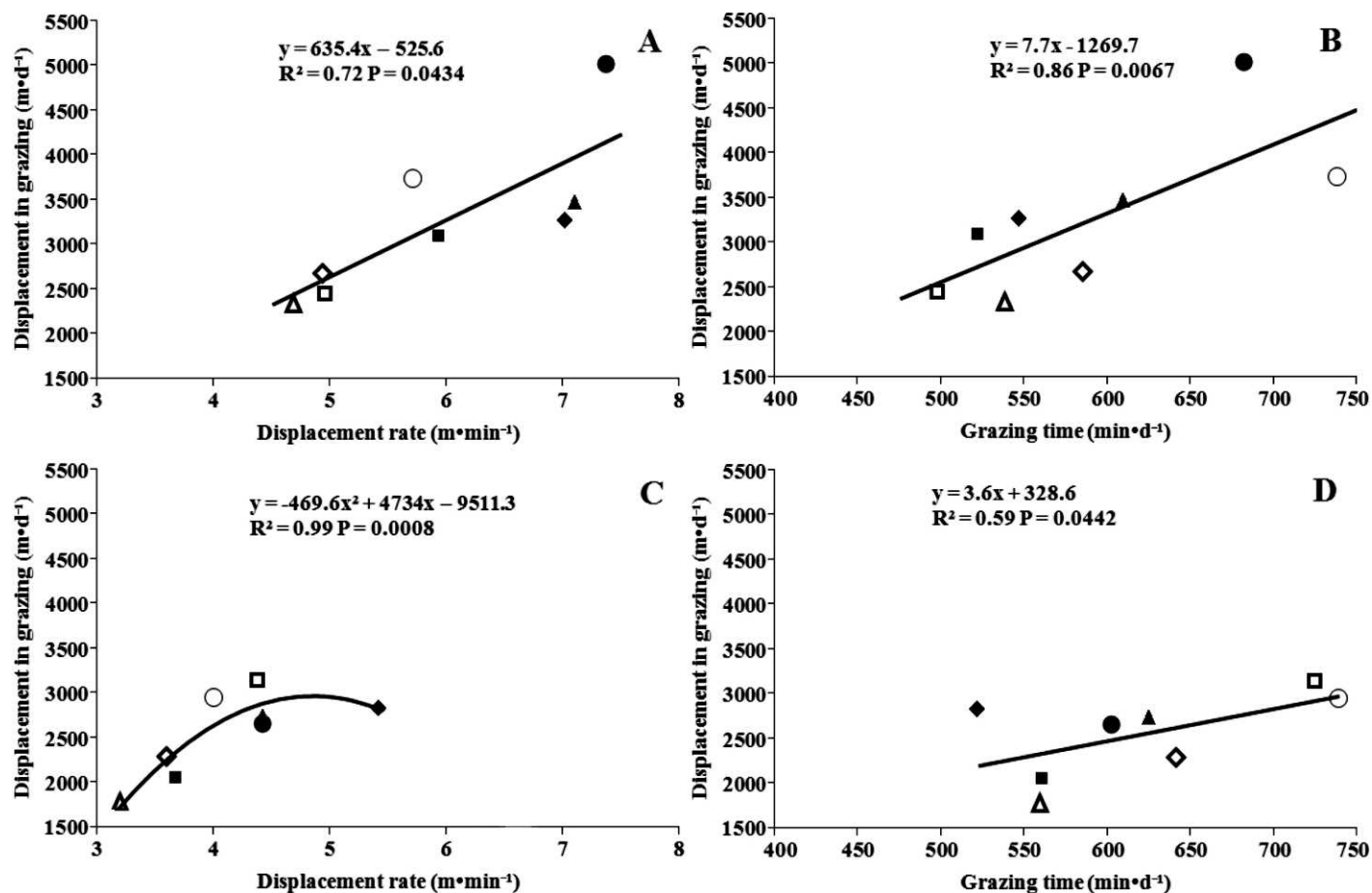


Figure 4. Regression models of the displacement in grazing ($\text{m} \cdot \text{d}^{-1}$) in relation to the displacement rate ($\text{m} \cdot \text{min}^{-1}$) and grazing time ($\text{min} \cdot \text{d}^{-1}$) of beef heifers on the natural grasslands of Pampa Biome managed with FA levels (% LW). **A** and **B**, spring 2009; **C** and **D**, summer 2010. The points of models correspond to following replicates: 4% LW = ● (block 1), ○ (block 2); 8% LW = ■ (b1), □ (b2); 12% LW = ▲ (b1), △ (b2); and 16% LW = ◆ (b1), ◇ (b2).

between 1 900 and 2 100 $\text{kg DM} \cdot \text{ha}^{-1}$ and the H was between 12 and 13 cm (Fig. 5F). These conditions were found in a single EU of the 12% LW treatment and a single 16% LW treatment. In summary, the graphs in Figure 5 show that high values of the GT were always associated with a low FM and H. Nevertheless, when analyzing the graphs together, we also observed a high GT when the values of the FM, H, and T exceeded 2 000 $\text{kg DM} \cdot \text{ha}^{-1}$, 13 cm, and 30%, respectively.

DISCUSSION

The sward structure variables showed significant linear relationships with the FA. We observed a relationship between the FA and the time dedicated to grazing and displacement only in spring 2009 when the conditions of the feed environment were more restrictive. During this period, the obtained values for the FA were below the preset values, and the FM and H were less than 1 800 $\text{kg DM} \cdot \text{ha}^{-1}$ and 11 cm, respectively, in all of the EUs. In general, spring is the season with a greater DAR and higher animal performance in the natural grasslands of southern Brazil (Pallarés et al., 2005). However, in spring 2009, we observed a high precipitation associated with a low solar global radiation (Fig. 1), which may have affected the forage

accumulation and the conditions of the FA and sward structure (Table 1).

In experiments that use the FA as a unique variable of control, when the DAR is high and increasing (midspring to late summer), we observe an increase in the FM that coincides with the period of highest animal performance (Maraschin and Jacques 1993). According to Heringer and Carvalho (2002), the accumulation rates decrease as autumn approaches, and the FM also decreases, which confounds the effects of FA management (controlled) and sward structure (variable). This is reflected in the obtained values of the FA, in which the differences between the preset (FA) and observed (AFA) values are associated with variations in the DAR and in the difficulty in achieving the preset levels, particularly during periods of forage accumulation restriction (Table 1).

Despite the distinct conditions of forage availability, the FA appeared to be unimportant in the observed responses of the animals in some periods of the year, as was found in the summers of 2009 and 2010 (Table 2). In this context, the variables that characterize how the food resources are presented to the animals can have considerable importance to understanding the responses in the pastoral environments. Pinto et al. (2007) found no correlation between the GT of beef steers and the FA in the same area of natural grassland used in

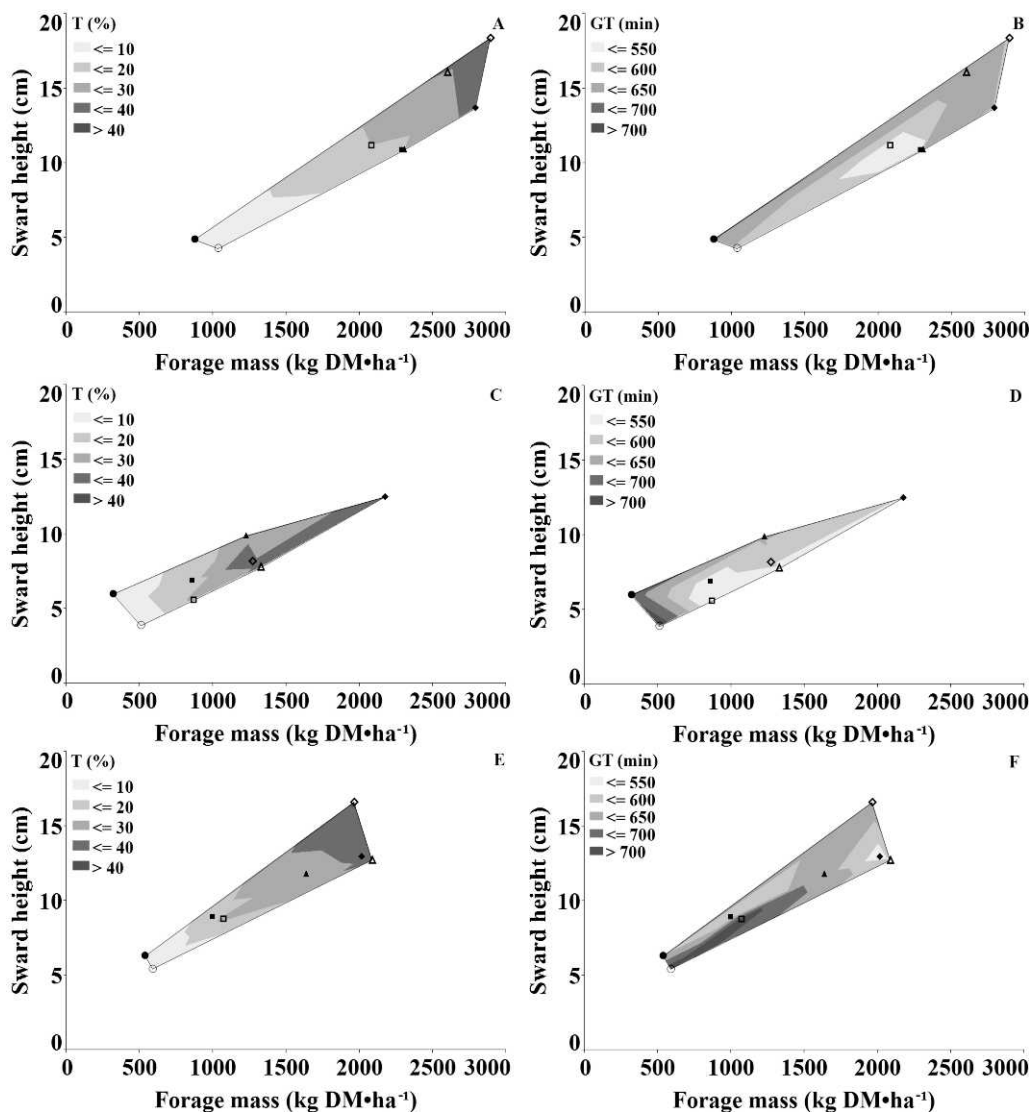


Figure 5. Three-dimensional relationships among the forage mass (FM, kg · DM · ha⁻¹), sward height (H, cm), and frequency of tussocks (%) and among the FM, H, and daily grazing time (GT, min) of beef heifers on the natural grasslands of the Pampa Biome managed with FA levels (% LW). **A** and **B**, summer 2009; **C** and **D**, spring 2009; **E** and **F**, summer 2010. The points correspond to replicates: 4% LW = ● (block 1), ○ (block 2); 8% LW = ■ (b1), □ (b2); 12% LW = ▲ (b1), △ (b2); and 16% LW = ◆ (b1), ◇ (b2).

this work. However, when the GT was correlated with the H, they observed an increase of 67 min in the GT for each centimeter of reduction in H. High correlations between the sward structure and the ingestive behavior and displacement variables were also found by Gonçalves et al. (2009a, 2009b) and Bremm (2010). Therefore, the evidence confirms that both the FA and how the forage is presented to the animals affects their strategies in grazing.

Grazing is a highly complex process that involves the characteristics of the herbivores and the available food in their environment (Prache et al. 1998). In summer 2009, a reduction of 500 kg DM · ha⁻¹ in the FM produced an increase of 30 min · d⁻¹ dedicated to grazing by the heifers (Fig. 3B). Therefore, the results indicate that the FM also seems to be an important conditioning factor for the time spent in grazing, even in pastoral environments as complex as the natural grasslands of the Pampa Biome.

In a strategy to increase the quantity of forage available per animal by increasing the FA, some complicating factors may occur in the tussocks of the sward structure, resulting in major complexity in the understanding of the animals' response in natural grazing environments. The occurrence of tussocks causes an important reduction in the area of the intertussock stratum that is frequently defoliated (Neves et al. 2009) and, depending on the level of occurrence, tussocks can be configured as a physical and nutritional complication for grazing animals (Gordon 2000; Bremm 2010). If grazing animals do not graze randomly (Gibb 2006) but select a diet when their preferred components are less abundant and arranged in mosaics that alternate with nonpreferred items, the animals would have to increase their searching activity during grazing. This study found a close relationship between the GT and T in spring 2009 (Fig. 3B). During this period, the lower values of the GT (approximately 550 min · d⁻¹) were

associated with a T between 20% and 30%; values below or above this range resulted in an increase in the GT. In spring 2009, the forage abundance was compromised, and even in the treatments of a higher FA with a higher T (>35%), the searching activity can become more onerous for the animals because they increase the GT, DR, and D (Table 2) in an attempt to increase the encounter rate of potential bites (Carvalho et al. 1999) to maintain satisfactory levels of forage intake.

The general hypothesis on foraging ecology is that, to improve grazing efficiency when there is an increase in the density of resources, animals increase the tortuosity of displacement and decrease the speed of movement (Viswanathan et al. 1999; Bartumeus et al. 2005). In this work, we found no effect of the sward structure characteristics on the DR. These findings occur more frequently in the context of a smaller space-time scale than found in this study, impacting each choice based on the bite and feeding stations (Griffiths et al. 2003).

We found that the DR and GT affected the D, which ranged between 1.7 and 5.0 km · d⁻¹ (Fig. 4), i.e., with differences greater than 100% between the contrasting feeding environments, which can impact the energy cost by the animals associated with grazing (Ribeiro et al. 1977; DiMarco and Aello 2001) and consequently penalize the animal's performance. The energy required to harvest forage is an insignificant part of the requirements of the animals (Stobbs 1975), but the energy cost of activities associated with grazing (e.g., searching, selection, and manipulation) has been estimated to be between 25% and 50% of their daily energy requirements (Osuji 1974). Therefore, feeding conditions that promote a reduction or modification of grazing activities could result in lower energy costs associated with grazing activity (Krysl and Hess 1993). The evidence found in our model (Fig. 3) suggests that the forage searching was indirectly altered by the sward structure because of its effect on the GT. This fact suggests that the conditions that increase the time spent in the grazing activity are associated with higher daily displacements during the grazing. We measured the highest D in the 4% LW of FA treatment, i.e., a low FA, FM, and H (Table 2).

When faced with changes in sward structure and forage abundance, the animals make numerous behavioral decisions to ensure their success in grazing. Thus, it is important to mention the variations in the patterns of displacement between the seasons of spring 2009 and summer 2010. In spring 2009, the season with the greatest forage restriction (Table 1), the heifers expressed an elevated DR and D in comparison with summer 2010. In a situation of high forage density, Knecht et al. (2007) observed that goats exhibited highly tortuous movements, resulting in a lower net displacement. By doing this, the animals graze in an area with higher food abundance and/or higher nutritional value and have a lower net displacement. With this strategy, animals stay in sites with a high density of resources, increasing the use of these areas (Kareiva and Odell 1987; Turchin 1991; Focardi et al. 1996; Bartumeus et al. 2005; Knecht et al. 2007). When these resources become scarce (e.g., spring 2009), the displacements could become linear (Mezzalana 2010) and faster. In this condition, the linear displacements become more efficient than the highly tortuous displacement because they minimize the chances of revisiting a

site already visited and increase the chance of finding new resources (Turchin 1991; Viswanathan et al. 1999; Bartumeus et al. 2005; Knecht et al. 2007). However, compensatory strategies have limits because, in most cases, they are not associated with success and can imply an energetic balance (harvest vs. searching) that is disadvantageous for grazing animals.

When the forage is abundant and with high nutritive value, the daily grazing time of domestic herbivores is generally reduced (Hodgson 1990). The opposite conditions promote a decline in the short-term intake rate, generating a need to increase their GT to reach the animal's nutritional requirements (Carvalho et al. 2001). However, under the conditions of this study, we would be limited in our ability to identify the isolated effects of the sward structure descriptors on the GT because the sward variables are generally highly correlated even in natural grasslands (Demment and Laca 1993), and there are constant alterations throughout the seasons, as evidenced in this work. The results showed evidence that an integrated analysis of the sward structure variables can provide the best way to understand the animal responses and to propose targets for management on natural grasslands. This leads to the concept that some structural characteristics of the sward can be combined in an integrated way to understand the foraging decisions of grazing ruminants (Tharmaraj et al. 2003, Fig. 5).

The animals' response revealed a similar pattern for their GT in all of the seasons, which is interesting if we consider that the animals were in conditions of high heterogeneity and complex feeding environments. The Pampas grasslands are characterized by a double-stratum sward structure, in which the T increased with the FA level and was positively associated with the FM and H in the intertussock vegetation. Soares et al. (2005) and Pinto et al. (2007) suggested that the animal variables can be related to the intertussock stratum. The results of this study showed that, regardless of the preset level of FA and the season evaluated, the lower values of the GT were always associated with sward structures with an FM between 1 400 and 2 200 kg DM · ha⁻¹ and an H between 9 and 13 cm. The T levels in this structural configuration did not exceed 35%. When the sward did not present this structural configuration, the strategy used by the animals was to increase their GT (Fig. 5). Sward management with the structural configuration that enables low GT also allows animal performances three to four times higher than the usual management (Soares et al. 2005; Pinto et al. 2007). In spring 2009, the season in which even the treatments of a high FA imposed restrictive feeding conditions for the heifers, we verified a compensatory mechanism, i.e., an increase in their GT in response to the decrease of forage abundance. In relation to GT responses, it is clear that changes in the sward structure established new balances in the plant-animal relationship at each moment.

With an emphasis on the intertussock stratum in natural grasslands, Gonçalves et al. (2009a, 2009b) conducted a reductionist protocol of grazing intensity levels by controlling the sward heights. The authors found that the intake and displacement patterns of heifers on natural grasslands are altered by the H levels in the intertussock stratum. The short-term intake rate of the heifers was maximized when the sward height was 11.4 cm, which corresponded to an FM of approximately 2 300 kg DM · ha⁻¹. Surprisingly, the conditions

that promoted less GT in our study are similar to the optimal conditions for the maximum short-term intake rate found by Gonçalves et al. (2009b) in a distinct scale of time, space, and heterogeneity. If the assumptions of Gonçalves et al. (2009b) regarding the best conditions for the short-term intake rate are valid in the scale studied, the structural configuration presented here determined that a reduced GT can be related to the heifers obtaining their nutritional requirements more quickly and with a favorable energetic balance associated with the grazing because a low GT meant a low D. Moreover, the findings from this study corroborate the importance of protocols that reproduce, at smaller scales (e.g., bite, short-term intake rate, and meal) (Gonçalves et al. 2009a, 2009b; Bremm 2010), the situations encountered at larger scales (e.g., GT, daily intake) and that affect the behavior and intake even in environments as complex as natural grasslands.

The GT decreased with the increase in forage abundance, but the GT can be higher even under conditions of food abundance (Fig. 5); in other words it is an optimization function. In the natural grasslands of the Pampa Biome, the increase in the GT can be explained by some complications in the sward structure that emerge when the management is conducted under a low grazing intensity (e.g., a high FA). The grazing process can be limited under these conditions when the forage becomes highly dispersed in the top of the canopy, and consequently, the time dedicated to manipulation and chewing of bites will be greater (Tharmaraj et al. 2003; Gonçalves et al. 2009b), implying a higher time per bite (Hirata et al. 2010). This same complicating factor for grazing related to forage dispersion can also be reflected in the smaller bite mass in response to a decrease in the dry-matter bulk density (Gonçalves et al. 2009b), although cattle have the ability to expand their bite area through movements of their tongue (Demment and Laca 1993).

The occurrence of tussocks is a characteristic present in the natural grasslands of the Pampa Biome when the grasslands are managed at a low grazing intensity (Côrrea and Maraschin 1994). Under these conditions, the herbivores concentrate their grazing on certain preferred areas (Bos 2002), allowing the success of species that form tussocks in areas with a lower frequency of defoliation (Cid and Brizuela 1998; Hester et al. 1999; Oom et al. 2008). Thus, mosaics are created that can act as another complicating agent in the grazing process (Gordon 2000). Mezzalira (2010) verified an increase in the selectivity of feeding stations up to 14% LW of FA, the point at which selectivity decreased, which, according to the author, was detrimental to the high level of tussocks. This FA level was associated with more than 30% of the T. In the current study, we found an increase in the GT ($>600 \text{ min} \cdot \text{d}^{-1}$) when the swards presented this same level of T (Fig. 5). Bremm (2010) built conditions to study the effect of T levels on the ingestive behavior of heifers in a protocol conducted on the natural grasslands of the Pampa Biome that were similar to Gonçalves et al. (2009a, 2009b). Bremm (2010) found that the heifers rejected tussocks of *Eragrostis plana* Nees., and moreover, the short-term intake rate was substantially reduced when the occurrence of tussocks was greater than 34%, suggesting that the animals respond with an increase in their GT on higher levels of T.

The conditions that lowered the GT and D were associated with increased food abundance. However, the excessive increase in FA without controlling the sward structure led to complications in the grazing process, such as the decrease in the bulk density of the DM in the sward, the high frequency of tussocks, and the decrease of areas of the intertussock stratum. This study demonstrated the importance of the sward structure and found that, regardless of the preset level of FA and the season evaluated, the lower values of the GT were always associated with a sward structure with an FM between 1 400 and 2 200 kg DM $\cdot \text{ha}^{-1}$ and an H between 9 and 13 cm, with T levels that did not exceed 35%. Below or above this range of conditions, we found penalization in the GT and displacement patterns of the heifers, reinforcing the observations of Da Silva and Carvalho (2005) that pastures require adequate control of the sward structure. Therefore, a better understanding of the cause-effect relationships between the sward structure and the grazing behavior presents the possibility of increasing the performance of grazing animals in the natural grasslands of the Pampa Biome with important economic and ecological consequences.

Finally, we found that the long-term grazing process of the heifers reproduced responses that were similar to those obtained in experiments investigating the harvesting and searching processes on short scales (e.g., bite, feeding station, meal, and intake rate). This is an important result for those investigating plant-animal relationships in the pastoral environments of the Pampa Biome because of the highly heterogeneous characteristics of these environments.

ACKNOWLEDGMENTS

The authors thank everyone who helped to maintain this long-term experiment, which allowed us to evaluate the effects of herbivory and grazing intensity in the Pampa Biome (Brazil), and to the undergraduate students of Universidade Federal do Rio Grande do Sul (UFRGS), who were essential in conducting the field experiments.

LITERATURE CITED

- ALLEN, V. G., C. BATELLO, E. J. BERRETTA, J. HODGSON, M. KOTHMANN, X. LI, J. McIVOR, J. MILNE, C. MORRIS, A. PEETERS, AND M. SANDERSON. 2011. An international terminology for grazing lands and grazing animals. *Grass and Forage Science* 66:2–28.
- BAILEY, D. W. 2005. Identification and creation of optimum habitat conditions for livestock. *Rangeland Ecology & Management* 58:109–118.
- BAILEY, D. W., J. E. GROSS, E. A. LACA, L. R. RITTENHOUSE, M. B. COUGHENOUR, D. M. SWIFT, AND P. L. SIMS. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49:386–400.
- BARTHAM, G. T. 1985. Experimental techniques: the HFRO sward stick. In: The Hill Farming Research Organization biennial report 1984/1985. Penicuik, UK: Hill Farming Research Organization. p. 29–30.
- BARTUMEUS, F., M. G. E. LUZ, G. M. VISWANATHAN, AND J. CATALAN. 2005. Animal search strategies: a quantitative random-walk analysis. *Ecology* 86:3078–3087.
- BERGAMASCHI, H., M. R. GUADANIN, L. S. CARDOSO, AND M. I. G. SILVA. 2003. Clima da Estação Experimental da UFRGS (e Região de Abrangência). Porto Alegre, Rio Grande do Sul, Brazil: UFRGS. 78 p. (in Portuguese)
- BERRETTA, E. 2001. Ecophysiology and management response of the subtropical grasslands of Southern America. In: J. A. Gomide, W. R. S. Mattos, and S. C.

- Da Silva [EDS.]. Proceedings of the 19th International Grassland Congress; 11–21 February 2001; São Pedro, São Paulo, Brazil. Piracicaba, São Paulo, Brazil: Fealq. p. 939–946.
- BILENCA, D., AND F. MIÑARRO. 2004. Identificación de áreas valiosas de pastizal en las Pampas y Campos de Argentina, Uruguay y Sur de Brasil. Buenos Aires, Argentina: Fundación Vida Silvestre. 352 p. (in Spanish)
- BOLDRINI, I. I. 2009. A flora dos Campos do Rio Grande do Sul. In: V. P. Pillar, S. C. Muller, Z. M. Z. Castilhos, and A. V. A. Jacques [EDS.]. Campos sulinos: conservação e uso sustentável da biodiversidade. Brasília, Brazil: Ministério do Meio Ambiente. p. 63–77. (in Portuguese)
- BOLDRINI, I. I., P. P. A. FERREIRA, B. O. ANDRADE, A. A. SCHNEIDER, R. B. SETUBAL, R. TREVISAN, AND E. M. FREITAS. 2010. Bioma Pampa: diversidade florística e fisionômica. Porto Alegre, Rio Grande do Sul, Brazil: Pallotti. 64 p. (in Portuguese)
- BOS, D. 2002. Grazing in coastal grasslands: Brent geese and facilitation by herbivory [thesis]. Groningen, The Netherlands: Groningen University. 223 p.
- BREMM, C. 2010. Foraging and movement patterns of cattle and sheep in complex pastoral environments [thesis]. Porto Alegre, Rio Grande do Sul, Brazil: Universidade Federal do Rio Grande do Sul. 182 p. (in Portuguese)
- CARVALHO, P. C. F. 2005. O manejo da pastagem como gerador de ambientes pastoris adequados à produção animal. In: C. G. S. Pedreira, J. C. Moura, S. C. Da Silva, and V. P. de Faria [EDS.]. Teoria e prática da produção animal em pastagens. Piracicaba, Brazil: Fealq. p. 7–32. (in Portuguese)
- CARVALHO, P. C. F., AND C. BATELLO. 2009. Access to land, livestock production and ecosystem conservation in the Brazilian Campos biome: the natural grasslands dilemma. *Livestock Science* 120:158–162.
- CARVALHO, P. C. F., S. PRACHE, AND J. C. DAMASCENO. 1999. O processo de pastejo: desafios da procura e apreensão da forragem pelo herbívoro. In: Anais 36th Reunião Anual da Sociedade Brasileira de Zootecnia; July 1999; Porto Alegre, Rio Grande do Sul, Brazil. Porto Alegre, Rio Grande do Sul, Brazil: Gnoisis/SBZ. p. 253–268. (in Portuguese)
- CARVALHO, P. C. F., H. M. N. RIBEIRO FILHO, C. H. E. C. POLI, A. MORAES, AND R. DELAGARDE. 2001. Importância da estrutura da pastagem na ingestão e seleção de dietas pelo animal em pastejo. In: W. R. S. Mattos [ED.]. A produção animal na visão dos Brasileiros: Reunião Anual da Sociedade Brasileira de Zootecnia. Piracicaba, Brazil: Fealq. p. 853–871. (in Portuguese)
- CID, M. S., AND M. A. BRIZUELA. 1998. Heterogeneity in tall fescue pastures created and sustained by cattle grazing. *Journal of Range Management* 51:644–649.
- CLARKE, J. L., D. WELCH, AND I. J. GORDON. 1995. The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep. 1. The location of animals on grass heather mosaics. *Journal of Applied Ecology* 32:166–176.
- CÔRREA, F. L., AND G. E. MARASCHIN. 1994. Growth and disappearance in a natural pasture under four levels of forage on offer. *Brazilian Journal of Agricultural Research* 29:1617–1623. (in Portuguese)
- CRUZ, P., F. L. P. DE QUADROS, J. P. THEAU, A. FRIZZO, C. JOUANY, M. DURU, AND P. C. F. CARVALHO. 2010. Leaf traits as functional descriptors of the intensity of continuous grazing in native grasslands in the South of Brazil. *Rangeland Ecology & Management* 63:350–358.
- DA SILVA, S. C., AND P. C. F. CARVALHO. 2005. Foraging behaviour and herbage intake in the favourable tropics/sub-tropics. In: D. A. McGilloway [ED.]. Grassland: a global resource. Dublin, Ireland: Wageningen Academic. p. 81–95.
- DA TRINDADE, J. K., P. C. F. CARVALHO, F. P. NEVES, C. E. PINTO, H. L. GONDA, L. B. NADIN, AND L. H. S. CORREIA. 2011. Potential of an acoustic method for quantifying the activities of grazing cattle. *Brazilian Journal of Agricultural Research* 46:965–968.
- DEMMENT, M. W., AND E. A. LACA. 1993. The grazing ruminant: models and experimental techniques to relate sward structure and intake. In: Proceedings of the 5th World Conference on Animal Production; 28 June–2 July 1993; Edmonton, Canada. Edmonton, Canada: Keeling & Mundi. p. 439–460.
- DI MARCO, O. N., AND M. S. AELLO. 2001. Energy expenditure due to forage intake and walking of grazing cattle. *Brazilian Journal of Veterinary and Animal Sciences* 53:105–110.
- FOCARDI, S., P. MARCELLINI, AND P. MONTANARO. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. *Journal of Animal Ecology* 65:606–620.
- GIBB, M. 2006. Grassland management with emphasis on grazing behaviour. In: A. Elgersma, J. Dijkstra, and S. Tamminga [EDS.]. Fresh herbage for dairy cattle: the key to a sustainable food chain. Wageningen, The Netherlands: Springer. p. 141–157.
- GONÇALVES, E. N., P. F. C. CARVALHO, T. DEVINCENZI, M. L. T. LOPES, F. K. FREITAS, AND A. V. A. JACQUES. 2009a. Plant–animal relationships in a heterogeneous pastoral environment: displacement patterns and feeding station use. *Brazilian Journal of Animal Science* 38:2121–2126. (in Portuguese)
- GONÇALVES, E. N., P. C. F. CARVALHO, T. R. KUNRATH, I. J. CARASSAI, C. BREMM, AND V. FISCHER. 2009b. Plant–animal relationships in pastoral heterogeneous environment: process of herbage intake. *Brazilian Journal of Animal Science* 38:1655–1662. (in Portuguese)
- GORDON, I. J. 2000. Plant–animal interactions in complex plant communities: from mechanism to modelling. In: G. Lemaire, J. Hodgson, A. Moraes, P. C. F. Carvalho, and C. Nabinger [EDS.]. Grassland ecophysiology and grazing ecology. Cambridge, UK: CAB International. p. 191–207.
- GRIFFITHS, W. M., J. HODGSON, AND G. C. ARNOLD. 2003. The influence of sward canopy structure on foraging decisions by grazing cattle. I. Patch selection. *Grass and Forage Science* 58:112–124.
- HERINGER, I., AND P. C. F. CARVALHO. 2002. Stocking rate adjustment in grazing experiments: a new approach. *Ciência Rural* 32:675–679.
- HESTER, A. J., I. J. GORDON, G. J. BAILLIE, AND E. TAPPIN. 1999. Foraging behaviour of sheep and red deer within natural heather/grass mosaics. *Journal Applied Ecology* 36:133–146.
- HIRATA, M., E. KUNIEDA, AND M. TOBISA. 2010. Short-term ingestive behaviour of cattle grazing tropical stoloniferous grasses with contrasting growth forms. *Journal of Agriculture Science* 148:615–624.
- HODGSON, J. 1984. Sward conditions, herbage allowance and animal production: an evaluation of research results. *Proceedings of the New Zealand Society of Animal Production* 44:99–104.
- HODGSON, J. 1990. Grazing management: science into practice. London, UK: Longman Group. 200 p.
- [IBGE] INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA. 2004. Mapa da vegetação do Brasil e Mapa de Biomas do Brasil. Available at: http://www.ibge.gov.br/home/presidencia/noticias/noticia_visualiza.php?id_noticia=169. Accessed 18 September 2011.
- JONES, R. J., AND R. L. SANDLAND. 1974. The relation between animal gain and stocking rate. *Journal of Agricultural Science* 83:606–611.
- KAREIVA, P. M., AND G. ODELL. 1987. Swarms of predators exhibit “prey taxis” if individual predators use area-restricted search. *The American Naturalist* 130:233–270.
- KLINGMAN, D. L., S. R. MILES, AND G. O. MOTT. 1943. The cage method for determining consumption and yield of pasture herbage. *Journal of Society Agronomy* 35:739–746.
- KNEGT, H. J., G. M. HENGVELD, F. W. VAN LANGEVELDE, F. BOER, AND K. P. KIRKMAN. 2007. Patch density determines movement patterns and foraging efficiency of large herbivores. *Behavioral Ecology* 18:1065–1072.
- KRYSL, L. J., AND B. W. HESS. 1993. Influence of supplementation on behavior of grazing cattle. *Journal of Animal Science* 71:2546–2555.
- MARASCHIN, G. E., AND A. V. A. JACQUES. 1993. Grassland opportunities in the subtropical region of South America. In: Proceedings of the 17th International Grassland Congress; 8–21 February 1993; Palmerston North, New Zealand. Palmerston North, New Zealand: Keeling & Mundi. p. 1977–1981.
- MARASCHIN, G. E., E. L. MOOJEN, C. M. D. ESCOSTEGUY, F. L. CÔRREA, E. S. APEZTEGUIA, I. I. BOLDRINI, AND J. RIBOLDI. 1997. Native pasture, forage on offer and animal response. In: Proceedings of the 18th International Grassland Congress. 8–19 June 1997; Saskatoon, SK, Canada. Winnipeg, MB, Canada: IGC. p. 26–27.
- MCCARTOR, M. M., AND F. M. ROUQUETTE, JR. 1977. Grazing pressures and animal performance from pearl millet. *Agronomy Journal* 69:983–987.
- MEZZALURA, J. C. 2010. The management of grazing in heterogeneous pastoral environments: ingestive behavior and animal production in different herbage allowances [dissertation]. Porto Alegre, Rio Grande do Sul, Brazil: Universidade Federal do Rio Grande do Sul. 159 p. (in Portuguese)
- MOTT, G. O. 1960. Grazing pressure and the measurement of pasture production. In: Proceedings of the 8th International Grassland Congress; 11–21 July 1960; University of Reading, UK. Oxford UK: Alden. p. 606–611.

- MOTT, G. O., AND H. L. LUCAS. 1952. The design, conduct, and interpretation of grazing trials on cultivated and improved pastures. *In: Proceedings of the 6th International Grassland Congress*; 17–23 August 1952; Pennsylvania State College, State College, PA, USA. Hershey, PA, USA: Pennsylvania State College. p. 1380–1385.
- NABINGER, C. 1998. Princípios de Manejo e produtividade das pastagens. *In: C. S. Gottschall, J. L. S. Silva, and N. C. Rodrigues. Ciclo de palestras em produção e manejo de bovinos de corte: manejo e utilização sustentável de pastagens. Canoas, Brazil: ULBRA.* p. 54–107. (in Portuguese)
- NABINGER, C., E. T. FERREIRA, A. K. FREITAS, P. C. F. CARVALHO, AND D. M. SANT'ANNA. 2009. Produção animal em campo nativo: aplicações de resultados de pesquisa. *In: V. P. Pillar, S. C. Muller, Z. M. Z. Castilhos, and A. V. A. Jacques [EDS.]. Campos sulinos: conservação e uso sustentável da biodiversidade. Brasília, Brazil: Ministério do Meio Ambiente.* p. 175–198. (in Portuguese)
- NEVES, F. P., P. C. F. CARVALHO, C. NABINGER, A. V. A. JACQUES, I. J. CARASSAI, AND F. TENTARDINI. 2009. Herbage allowance management strategies to raise beef heifers on natural pastures. *Brazilian Journal of Animal Science* 38:1532–1542. (in Portuguese)
- OOM, S. P., A. M. SIBBALD, A. J. HESTER, D. R. MILLER, AND C. J. LEGG. 2008. Impacts of sheep grazing a complex vegetation mosaic: relating behaviour to vegetation change. *Agriculture, Ecosystems and Environment* 124:219–228.
- OSUJI, P. I. 1974. The physiology of eating and the energy expenditure of the ruminant at pasture. *Journal of Range Management* 27:437–43.
- OVERBECK, G. E., S. C. MÜLLER, A. FIDELIS, J. PFADENHAUER, V. D. PILLAR, C. C. BLANCO, I. I. BOLDRINI, R. BOTH, AND E. D. FORNECK. 2007. Brazil's neglected biome: the south Brazilian Campos. *Perspectives in Plant Ecology, Evolution and Systematics* 9:101–116.
- PALLARÉS, O. R., E. J. BERRETTA, AND G. E. MARASCHIN. 2005. The South American Campos ecosystem. *In: J. Suttie, S. G. Reynolds, and C. Batello [EDS.]. Grasslands of the world. Rome, Italy: FAO.* p. 171–219.
- PINTO, C. E., P. C. F. CARVALHO, AND A. FRIZZO, J. A. S. FONTOURA JÚNIOR, C. NABINGER, AND R. ROCHA. 2007. Ingestive behaviour of steers on natural grasslands of Rio Grande do Sul. *Brazilian Journal of Animal Science* 36:319–327. (in Portuguese)
- PINTO, C. E., J. A. S. FONTOURA JÚNIOR, A. FRIZZO, T. M. S. FREITAS, C. NABINGER, AND P. C. F. CARVALHO. 2008. Primary and secondary production in a natural pasture submitted to different herbage allowances at the "Depressão Central," Rio Grande do Sul. *Brazilian Journal of Animal Science* 37:1737–1741. (in Portuguese)
- PRACHE, S., I. J. GORDON, AND A. J. ROOK. 1998. Foraging behaviour and diet selection in domestic herbivores. *Annales de Zootechnique* 47:335–345.
- RIBEIRO, J. M. C. R., J. M. BROCKWAY, AND A. J. R. WEBSTER. 1977. A note on the energy cost of walking in cattle. *Animal Production* 25:107–110.
- SOARES, A. B., P. C. F. CARVALHO, C. NABINGER, C. SEMMELMANN, J. K. DA TRINDADE, E. GUERRA, T. S. FREITAS, C. E. PINTO, J. A. FONTOURA JÚNIOR, AND A. FRIZZO. 2005. Animal and forage production on native pasture under different herbage allowance. *Ciência Rural* 35:1148–1154. (in Portuguese)
- STOBBS, T. H. 1975. A comparison of zulu sorghum, bulrush millet and white panicum in terms of yield, forage quality and milk production. *Australian Journal of Experimental Agriculture and Animal Husbandry* 15:211–218.
- THARMARAJ, J., W. J. WALES, D. F. CHAPMAN, AND A. R. EGAN. 2003. Defoliation pattern, foraging behaviour and diet selection by lactating dairy cows in response to sward height and herbage allowance of a ryegrass-dominated pasture. *Grass and Forage Science* 58:225–238.
- TURCHIN, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* 72:1253–1266.
- VISWANATHAN, G. M., S. V. BULDRYREV, S. HAVLIN, M. G. E. LUZ, E. P. RAPOSO, AND H. E. STANLEY. 1999. Optimizing the success of random searches. *Nature* 401:911–914.
- WILM, H. G., D. F. COSTELLO, AND G. E. KLIPPLE. 1944. Estimating forage yield by the double sampling method. *Journal of American Society of Agronomy* 36:194–203.