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Daily Forage Intake by Cattle on Natural Grassland: Response to Forage Allowance and Sward Structure☆,☆☆

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ABSTRACT

We investigated the hypothesis that not only forage allowance but also sward structure affects daily forage intake by beef heifers on natural grasslands of the Pampa Biome (southern Brazil). We used data from a long-term experiment, which has been managed by forage allowance levels since 1986. The objective was to investigate sward management targets that maximize daily forage intake. During January and December 2009, we evaluated the effect of forage allowance on forage mass, sward height and tussock frequency, and its consequences on dry matter intake (DMI). The experiment was arranged in a randomized complete block design with two replicates. Treatment was level of daily forage allowance (4, 8, 12, and 16 kg dry matter [DM] per 100 kg of animal body weight [BW]). Data were analyzed using regression, principal component analysis, and descriptive analyses from three-dimensional contour graphs with the data of sward structure, DMI, and DMI rate. Results demonstrated that DMI was positively correlated to forage allowance. However, higher levels of forage allowance can cause lower intake rates of forage and nutrients. We concluded that sward targets which promoted higher DMI and DMI rate were: daily forage allowance of ~12 kg of dry matter per 100 kg of the animal's body weight, forage mass between 1 800 and 2 300 kg DM·ha^{-1}, sward height between 11.5 and 13.4 cm, and tussock frequency lower than 30% of occurrence in the pastures. Within these targets, a high intake of nutrients was obtained, indicating the potential use of sward structure as a tool for managing natural grasslands in order to promote high intake of forage and nutrients by cattle.

Introduction

According to Van Vuuren (1994), forage intake explains between 60% and 90% of the variation in animal performance, and between 10% and 40% of the variation is explained by the concentration of nutrients in the forage consumed. Hence it is important to take into account that predictive models of intake from grazing should consider sward structural characteristics (Baumont et al, 2000; Laca and Demment, 1992). Sward structures that limit bite size and rate, such as low forage mass and/or sward height, cannot be compensated by higher values of forage digestibility (Hodgson, 1990). Thus grazing animals should explore the environment and adapt their feeding strategies to the prevailing conditions in order to meet their nutritional requirements (Bailey, 2005).

Grazing intensity is one of the main drivers of grassland dynamics due to its impact on vegetation growth, sward structure, and nutritive value of the forage (Pavlu et al., 2006). Moreover, it impacts grazing behavior and forage intake, which are important animal responses in the definition of sound grazing environments (Bailey, 2005; Carvalho, 2005). The adjustment in forage allowance is a method used to control grazing intensity (Sollenberger et al., 2005). Forage allowance is the relationship between forage mass and animal body 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). It has been used in several experiments aiming to investigate primary and secondary production potential on natural grasslands in the Pampa

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Biome (Carvalho et al., 2009), the Brazilian portion of the South American Campos Ecosystem (Instituto Brasileiro de Geografia e Estatística [IBGE], 2004; Suttie et al., 2005). This herbaceous vegetation, dominated by grasses from *Andropogon, Aristida*, and *Paspalum* genera, extends along southern Brazil, Uruguay, northeastern Argentina, and part of Paraguay and feeds approximately 65 million domestic ruminants (Berreta, 2001).

Long-term studies focused on grazing management in the Pampa Biome showed the benefits of moderate forage allowances on primary and secondary production, as well as on ecological attributes (Nabinger et al., 2011). Forage allowance is a more useful tool than stocking rate as a parameter to predict animal performance (Sollenberger et al., 2005). However, both result in limited understanding of cause-effect relationships at the plant-animal interface. Some studies have observed relationships between the forage allowance and animal productivity, whereas others have observed no such effect on intake or forage digestibility (Boval and Dixon, 2012). Although we can determine the amount of food available per animal, there is no precise control over how the food is offered and spatially and temporally distributed (Hodgson, 1984); i.e., the sward characteristics are also important, which may limit the use of forage allowance as the only target of grazing management (Carvalho et al., 2001; Da Silva and Carvalho, 2005). Boval et al. (2000) showed studies with tropical grasses in which the forage allowance levels that maximized animal performance ranged widely from 6 to 35 kg DM·100 BW $kg^{-1} \cdot d^{-1}$. This probably reflects forage nutritive value differences, as well as sward structure heterogeneity across the grazing environments studied, in terms of sward height, forage density, morphological composition, and other attributes.

The characterization of sward condition has traditionally been emphasized when studying variables such as above-ground biomass and sward height, as well as botanical, morphological, and chemical composition. This emphasis is based on the assumption that these characteristics, which describe the grazing environment (Carvalho, 2005), have some relevance to forage intake and, consequently, on animal performance (Searle et al., 2007). Moreover, the sward attributes that determine nutrient intake are not only determined by the concentration of nutrients in the forage, but also to the spatial heterogeneity of nutrients and preferred/nonpreferred patches in pastures (Dumont et al., 2007; Laca, 2011). This results from the fact that the sward structure influences the intake rate of nutrients affecting satiety by grazing animals (Provenza et al., 2007). In pastures with low heterogeneity, the animal´s responses are influenced by the vertical sward structure (Carrère et al., 2001), especially in relation to sward height (Armstrong et al., 1995) and bulk density (Benvenutti et al., 2008; Demment et al., 1995; Flores et al., 1993). In the case of pastures with a high degree of heterogeneity, the animals' responses are dependent on the horizontal distribution of preferred patches in the pasture (Roguet et al., 1998). That is, in situations where the limitation is not the forage abundance, but the arrangement of nonpreferred items in space (e.g., tussocks), the animals must make a series of decisions to acquire, in an efficient manner, the nutrients needed to meet their requirements (Carvalho et al., 2013).

A long-term experiment in the natural grassland of the Pampa Biome, maintained from 1986 to present (Carvalho et al., 2015; Cruz et al., 2010; Da Trindade et al., 2012) under forage allowance levels for cattle resulted in contrasting differences in forage abundance and sward structure (Neves et al., 2009a). Although treatments do not ensure a strict control of the sward structure, this context, specifically due to the legacy effects of grazing intensities, still allows sward targets to be determined on the basis of the main sward characteristics affecting the ingestive behavior of cattle on natural grasslands (Bremm et al., 2012; Da Trindade et al, 2012; Gonçalves et al., 2009): forage mass, sward height, and tussock cover. In order to understand the plant-animal relationships in a complex grazing environment as heterogeneous as natural grasslands, we investigated the hypothesis that not only forage allowance but also the sward structure affects daily forage intake. In continuous stocking, when the forage is abundant and of high nutritive value, the grazing time is reduced (Hodgson, 1990) and daily forage intake is higher. The opposite scenario results in a decline in intake rate, and the daily forage intake will be limited if the reduction in intake rate cannot be compensated by an increase in grazing time. In a previous study (Da Trindade et al., 2012), we found that grazing time could be high even in abundant food conditions, indicating that a selection costs when the grazing environment is heterogeneous and diverse. The objective of this paper was to establish sward management targets that maximize daily forage intake by beef cattle and determine whether such conditions could be associated with high intake rates of forage and nutrients. These findings should contribute to the understanding of animal-sward interaction leading to sustainable management of grasslands of the Pampa Biome.

Methods

Location, Treatments, and Experimental Design

The experiment was performed on the experimental farm of the Federal University of 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 natural grassland representative of the Campos Sulinos phyto-physionomy (IBGE, 2004), which forms part of the Pampa Biome. The climate at the experimental site is subtropical humid (Cfa classification, Köppen), with an annual precipitation of 1 440 mm, well distributed throughout the year; June is the wettest month (168.2 mm), and December is the driest (97.7 mm). Since 1986, the experimental area has been managed under continuous stocking with varying daily forage allowance levels for beef cattle, via the use of the "put-and-take" technique (Mott and Lucas, 1952). Treatments consisted of four forage allowance levels: 4, 8, 12, and 16 kg dry matter (DM) per 100 kg of the animal body weight (BW) per day (kg DM·100 $kg^{-1} \cdot d^{-1}$ or % BW), adjusted every 28 d (for more details on the treatments, see Soares et al., 2005 and Neves et al., 2009a,b). The only anthropic interventions in the experimental units were the management of grazing intensity via adjustments in the forage allowance, so there was no fertilization, irrigation, fire, or mowing.

The experiment was arranged in a randomized complete block design with two replicates (paddocks). Differences in soil type were the determinant for blocking criteria. The paddocks varied from 3.0 to 5.2 ha in area and have a slightly undulating landscape. The 25-yr-use of the area resulted in varying plant functional types (Cruz et al., 2010) and sward structures (Neves et al., 2009a). The vegetation in the paddocks (Fig. 1) is characterized as a bimodal height structure consisting of a mosaic of short (intertussock) and tall (tussock) plants (Côrrea and Maraschin, 1994). In the intertussock areas, the predominant species are *Paspalum, Axonopus, Piptochaetium*, and *Coelorachis* genera. With increasing forage allowance, tussocks were formed mainly by *Aristida, Eryngium, Andropogon, Bacharis*, and *Vernonia* genera.

Animals and Experimental Period

Fifteen-month-old Angus-Hereford crossbred *(Bos taurus taurus)* and Nellore *(Bos taurus indicus)* heifers (196 ± 4 kg BW) were used. The number of animals was based on forage mass (FM) present and daily dry matter accumulation rate (DAR) to achieve the forage allowances required.

The evaluations in this study were conducted in two seasons: summer (from 11 January to 7 March 2009) and spring (from 27 October to 5 December 2009). The heifers were weighed, without fasting, in each season and had a BW of 174 ± 3.9 kg and 206 ± 4.6 kg in summer and spring, respectively. In each season, measurements were performed to characterize the sward structure and animals were dosed with *n*-alkanes to estimate the daily DMI and nutritive value of the forage apparently consumed by heifers.

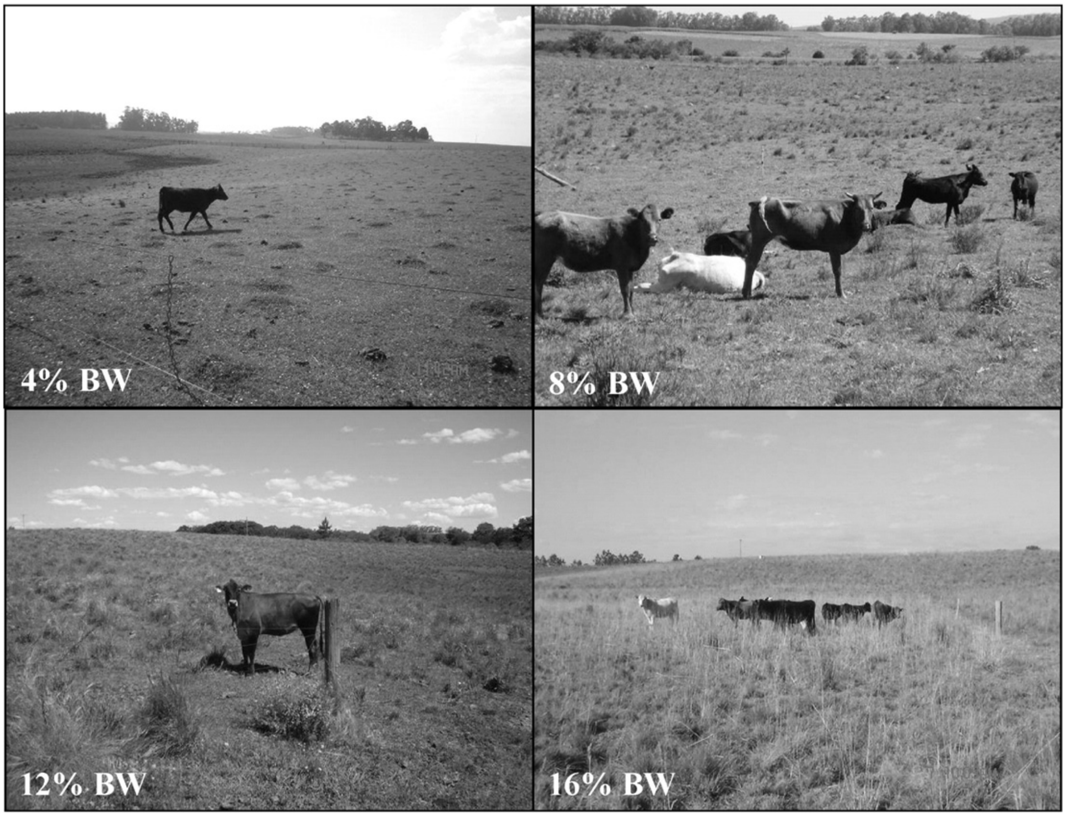

Fig. 1. Typical sward structure of the experimental area as a function of forage allowance on a natural grassland of Pampa Biome. Eldorado do Sul, Rio Grande do Sul, Brazil. Photos by Grazing Ecology Research Group–Federal University of Rio Grande do Sul.

Sward Structure and Calculation of Forage Allowance

The sward structure was evaluated by sampling the vegetation in each paddock. The FM (FM, kg DM·ha^{-1}) and sward height (H, cm) in the intertussock area and the proportion of the area covered by tussocks (%) have been reported as sward conditioning factors affecting behavioral patterns of grazing cattle on natural grasslands of the Pampa Biome (Bremm et al., 2012; Da Trindade et al., 2012; Gonçalves et al., 2009; Mezzalira et al., 2013) and therefore were evaluated in this study. The FM was determined by the double-sampling technique (Wilm et al., 1944), using a calibration of visual estimates with clipped and weighed samples. In the summer, a metal quadrat (0.5 × 0.5 m) was placed in each 200 m^2 (grid 10 × 20 m) in each paddock. In spring, the quadrat was randomly placed to achieve a minimum of 50 random locations in the intertussock area in each paddock. The difference in the number of samples between seasons was due to a concomitant study focusing on a georeferenced botanical description (unpublished) performed on the same sampling quadrat. Despite the difference in sample numbers, sampling sufficiency was achieved on the basis of the database spanning 25 yr in the experimental area. When the vegetation within a metal quadrat was represented by tussocks, the frequency of occurrence (%) was registered on the basis of the ratio between the number of occurrences and the total number of quadrat samples. The FM was visually estimated, and H was measured with a sward stick at five points inside each quadrat.

After sampling to estimate the FM, H, and tussock, 10 samples per paddock of the forage in the intertussock vegetation were clipped at ground 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. The sample weights were used to adjust the visual estimates of FM in each evaluation by regressing the collected FM (y) in the sample on the FM given by each evaluator (x). The selection of the evaluator to be used was based on the highest coefficient of determination (R^2) and the P value ($P < 0.05$).

To verify whether the forage allowances were achieved after stocking adjustments, the actual forage allowance (AFA, % BW) was calculated as: AFA = ([FM/n + DAR]/SR) × 100, where n = the number of days in each period evaluated, DAR = the daily DM accumulation rate in kg DM·ha^{-1}·d^{-1}, and SR = the stocking rate in kg BW^{-1}·ha^{-1}. The DAR used in the equation was estimated with the use of four exclusion cages per paddock according to the method by Klingman et al. (1943).

Dosage of C32-Alkane and Collection of Feces and Forage

Three heifers randomly selected in each paddock (n = 24) were dosed twice daily (at 0800 and 1600 hours) with a cellulose capsule containing 176.5 mg ± 1.82 SE of C32-alkane (97%, Sigma-Aldrich Corp., St. Louis, MO, USA) for 12 uninterrupted days: from 16 February to 27 February 2009 (summer) and from 11 November to 22 November 2009 (spring). From days 7 to 12, fecal samples were collected concomitantly twice daily, per rectum, simultaneously with n-alkane dosing. The samples were identified individually, packed in plastic bags, and frozen at ⁻20°C. At the end of the collection period, the samples from each animal were thawed and homogenized, dried (i.e., 60°C for 72 h), milled to pass through a 1-mm mesh, identified, and stored in plastic bags for subsequent analysis of n-alkanes.

Forage samples were collected to quantify the n-alkane profile and nutritive value. To obtain a sample of forage apparently consumed by the animals, we used the hand-plucking technique (De Vries, 1995) from days 7–10 of the dosage and collection period. Before performing hand plucking, the tester heifers were monitored with global positioning system devices and acoustic recorders, as described by Da Trindade et al. (2012). The aim was to analyze the acoustic recordings (Da Trindade et al., 2011) and to determine the locations of grazing areas in which the animals concentrated grazing activity for collecting samples by hand plucking to simulate grazing. The forage samples were dried (i.e., 60°C for 72 h), milled using a 1-mm mesh, identified, and stored in plastic bags for subsequent analysis of *n*-alkanes.

Laboratory Analyses

The forage samples were analyzed in duplicate for chemical composition: crude protein (AOAC, 1995), neutral and acid detergent fiber (Goering and Van Soest, 1970), and in vitro dry and organic matter digestibility (Tilley and Terry, 1963). Total digestible nutrients were estimated by multiplying the values of organic matter content and in vitro DM digestibility.

The *n*-alkanes' contents of individual samples of forage and feces were analyzed in duplicate according to the method of Dove and Mayes (2006). Identification and quantification of the *n*-alkanes were carried out by gas chromatography, using a SHIMADZU GC-2010 (Shimadzu, Tokyo, Japan), equipped with flame ionization detector, an AOC-20S autosampler, and temperature-programmable AOC-20i autoinjector. The *n*-alkane extracts were injected (1 μL) by on-column Rtx-5 RESTEK (30 m × 0.25 mm × 0.25 μl, absorbent composed of 5% diphenyl and 95% dimethylpolysiloxane). Nitrogen was used as the carrier gas at a constant flow of 30 $mL \cdot min^{-1}$. Gradients of temperature were used for the injector (270°C) and the column (170°C for 1 min; from 30$°C \cdot min^{-1}$ to 215°C for 1 min and 6$°C \cdot min^{-1}$ at 300°C; for a 21-min period). The flame ionization detector was maintained at 340°C.

Gas chromatographic procedures were calibrated with a standard solution containing a mixture of synthetic *n*-alkanes (from C7 to C40) (>99% pure, Sigma-Aldrich Corp., St. Louis, MO, USA) with similar concentrations to those found in the extracts. The response factors for individual *n*-alkanes were calculated from peak areas and the known concentrations. Within the peak areas, *n*-alkane concentrations were determined using the *Shimadzu GC Solution* software, in which the identification of *n*-alkanes is based on comparison to an external standard for the average retention time in each column *n*-alkane. The peaks identified were converted into quantities of *n*-alkanes with reference to the internal standard C34 and expressed in $mg \cdot kg\ DM^{-1}$.

Calculations

The DMI ($kg\ DM \cdot 100\ kg\ BW^{-1} \cdot d^{-1}$, or % BW) was estimated from the ratio of *n*-alkane concentrations found naturally in the forage and dosed *n*-alkane (C_{33}/C_{32}) in forage and feces samples, according to the equation proposed by Mayes et al. (1986):

$$DMI = \frac{\left(\frac{F_{C33} \times \frac{D_{C32}}{F_{C32}}}{H_{C33} - \frac{F_{C33} \times H_{C32}}{F_{C32}}} \right) \times 100}{BW} \quad (1)$$

where D_{c32} is the daily dose (mg) of synthetic alkane C_{32} in cellulose paper, F_{C33} and H_{C33} are respective concentrations ($mg \cdot kg\ DM^{-1}$) of C_{33} in feces and forage, F_{C32} and H_{C32} are respective concentrations ($mg \cdot kg\ DM^{-1}$) of C_{32} in feces and forage, and *BW* is the body weight of animals (kg).

Total digestible nutrient intake and crude protein intake were estimated by multiplying the DMI by concentration of total digestible nutrients and crude protein in the forage, respectively. DMI rate, total digestible nutrients intake rate, and crude protein intake rate were obtained by the ratio between daily intake of these fractions and daily grazing time, being expressed in $mg \cdot min^{-1} \cdot kg\ BW^{-1}$. The methodology and data of daily grazing time are presented in Da Trindade et al. (2012) and refer to the same experimental area and period of this study. The averages of daily grazing time in summer were 624, 534, 626, and 597 min, and in spring they were 710, 510, 573, and 566 min for 4, 8, 12, and 16% BW of forage allowance treatments, respectively.

Statistical Analysis

We tested the mathematical possibility of all models generated using data from two periods ($n = 16$). The Levene Test (v.9 SAS software; SAS Institute Inc., Cary, North Carolina, USA) showed homogeneity of variances between the seasons ($P > 0.05$) for all variables used in the models: actual forage allowance, FM, H, tussock, crude protein, neutral and acid detergent fiber, in vitro dry and organic matter digestibility, DMI, total digestible nutrients and crude protein intake, DM, total digestible nutrients, and crude protein intakes rate. In this way, the variables were analyzed from the complete data set using both seasons ($n = 16$).

The sward characteristics, chemical composition of forage apparently consumed, and the intake variables were analyzed by regression, testing linear and quadratic models. The linear and quadratic model responses for the actual forage allowance were generated with the use of the preset values of forage allowance treatments, whereas the other models that verified the effect of the forage allowance were generated from the values of the actual forage allowance. The regression analyses were performed using SAS v.9 software through the REG procedure. Considering a significant regression coefficient at a level of 5%, the block effect was removed and the models with higher coefficients of determination (R^2) were selected. Principal components analysis was conducted, by taking linear combinations of eigenvectors of the correlation matrix, the relationship between actual forage allowance and mean FM, H, and tussock frequency by reducing the dimensionality for two principal components with the most prominent directions of the total variation. The principal components were derived from an eigenvalue decomposition of the correlation matrix, and points were derived from the eigenvector linear combination of the variables. The Bartlett Test ($P < 0.05$) was performed and indicated on the graph ordination, which shows the results of the homogeneity test to determine if the eigenvalues have the same variance by calculating the Chi-square, degrees of freedom, and the *p* value for the test. The principal components analysis was conducted with the JMP software (v.9; SAS Institute Inc.).

Contour plots were generated using the FM, H, and DM intake variables to verify the pattern of the DMI and daily DMI rate in response to the sward structural configuration. The three-dimensional contour graphs were generated with the use of the 'Graph' option of the JMP software (v.9; SAS Institute Inc.).

Results

The forage allowance levels resulted in a gradient of vegetation abundance, sward structure, and, to a lesser magnitude, nutritional value (Table 1). The actual forage allowance values were numerically lower than the preset values. However, a significant relationship was found with the preset values, resulting in a gradient among the forage allowance levels (3.4–13.4% BW). The values of FM, H, and tussock frequency showed incremental changes when the forage allowance increased from 4% to 16% BW. These results confirmed the sward structure gradients, creating contrasting environments that were essential to investigating the hypothesis. Although there was no relationship of neutral detergent fiber with forage allowance ($P = 0.5647$), the variation in the nutritional quality of forage presented negative responses ($P \leq 0.004$) except for the acid detergent fiber that showed a quadratic response to increasing forage allowance ($P = 0.0265$), showing an increase up to forage allowance values of approximately 10% BW (see Table 1). On average, the structural characteristics had wide variations among the forage allowance levels compared with the nutritional characteristics of forage.

The principal components analysis with actual forage allowance and sward structure characteristics showed two significant principal

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

	FA (% BW[1])				Model	*P*	R^2	RSEM
	4	8	12	16				
AFA (% BW)	3.4	6.8	10.5	13.4	AFA = 0.14 + 0.83FA	<0.0001	0.73	0.14
FM[2] (kg DM·ha^{-1})	685	1 523	1 864	2 283	FM = 194.0 + 164.5AFA	<0.0001	0.79	23.6
H[3] (cm)	4.8	8.7	11.2	13.2	H = 2.4 + 0.83AFA	<0.0001	0.78	0.12
T[4] (%)	0.8	19.0	26.4	36.3	T = 0.47 + 2.4AFA	0.0002	0.68	0.50
CP[5] (%)	12.6	11.1	10.6	10.1	CP = 13.3 – 0.25AFA	0.0040	0.49	0.07
TDN (%)	38.7	34.7	31.0	31.3	TDN = 40.9 – 0.82AFA	0.0008	0.61	0.18
NDF[6] (%)	86.7	86.3	84.5	88.4	NDF = 86.5	0.5647	-	-
ADF[7] (%)	40.9	41.0	49.3	42.8	ADF = 29.4 + 3.7AFA-0.19AFA^2	0.0265	0.41	0.07
IVDMD[8] (%)	42.5	38.7	34.9	34.3	IVDMD = 45.3 – 0.91AFA	0.0005	0.64	0.19
IVOMD[9] (%)	42.4	37.5	34.3	33.5	IVOMD = 44.7 – 0.94AFA	0.0004	0.65	0.19

[1] BW = body weight.
[2] FM = forage mass.
[3] H = sward height.
[4] T = tussock frequency.
[5] CP = crude protein.
[6] NDF = neutral detergent fiber.
[7] ADF = acid detergent fiber.
[8] IVDMD = in vitro dry-matter digestibility.
[9] IVOMD = in vitro organic matter digestibility.

components, which accounted for 95.6% of the total variation in the data (Fig. 2). The principal component 1 represented 85.7% of the total variation, and the ordination expressed the contrast and gradient of heterogeneity (i.e., distance between points) and a similar pattern of response, within and between the treatments, with increase in forage allowance levels, independent of season. The loading values of actual forage allowance, FM, and H and directions on the ordination biplot in relation to principal component 1 were similar (see Fig. 2), demonstrating the close relationship between these variables. However, the principal component 2 showed a high loading value (0.53) with tussock. This contributed, especially in the spring, in a greater sward structure variability among experimental units, except for the 4% BW treatment that revealed, beyond virtual absence of tussocks (see Table 1), less heterogeneous conditions among the experimental units and seasons (see Fig. 2).

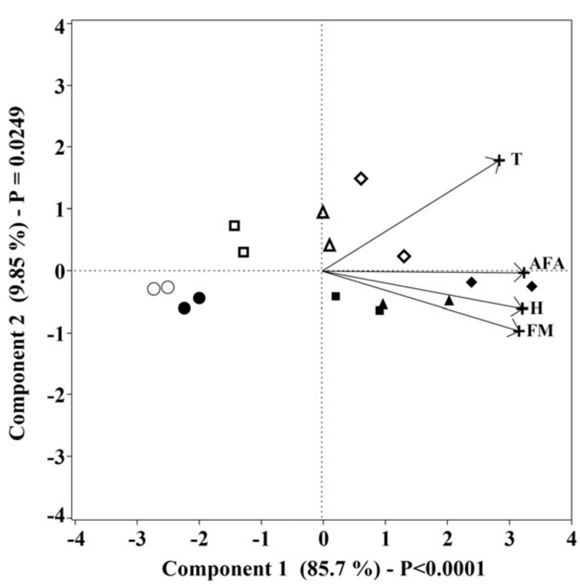

Fig. 2. Principal components analysis ordination diagram of forage allowance and the descriptors of sward structure based on mean by paddock and season on the natural grasslands of the Pampa Biome. AFA indicates actual forage allowance (% BW); FM, forage mass (kg DM·ha^{-1}); H, sward height (cm); and T, tussock frequency (%). The eigenvectors values among AFA, FM, H, and T with the principal component 1 are 0.96, 0.94, 0.95, and 0.84 and with the principal component 2 are –0.01, –0.28, –0.18, and 0.53, respectively. The points correspond to summer: ● = 4% BW, ■ = 8% BW, ▲ = 12% BW, ♦ = 16% BW; spring: ○ = 4% BW, □ = 8% BW, Δ = 12% BW, ◊ = 16% BW.

The three-dimensional contour graphs in Fig. 3 demonstrate the relationships between H and FM with DMI and daily DMI rate. The higher values of DMI occurred when the FM was between 1 620 and 2 800 kg DM·ha^{-1} and the H was between 10.1 and 14.4 cm (Fig. 3a). The higher values of daily DMI rate, above 55 mg DM·min^{-1}·kg BW^{-1}, were recorded in a sward structure characterized with an FM between 1 820 and 2 280 kg DM·ha^{-1} and H between 11.5 and 13.4 cm; when the values were above or below those conditions, heifers reduced daily DMI rate (Fig. 3b). The conditions that promoted the highest values of DMI rate were found in the spring in a single experimental unit of the 16% BW treatment.

Discussion

The grazing intensities determined gradients of conditions of vegetation abundance and sward structure, also creating sward heterogeneity with increase in forage allowance levels. This situation confirms that forage allowance management targets do not result in a strict control of sward structure or its prediction. Although sufficient control existed to adjust the amount of available forage per animal, due to variations in environmental factors, plant functional diversity and its interactions with grazing intensity (Cruz et al., 2010), two managed pastures with the same forage allowance may result in different sward structures. This is true particularly for moderate (i.e., 8% and 12% BW treatments) and low (i.e., 16% BW treatment) grazing intensity levels (see Fig. 2), which resulted in important sward structure variations in the intertussock stratum (or preferred patches) in combination with different levels of tussocks (or nonpreferred patches). The sward heterogeneity complicates the management and may involve complex changes in foraging strategies (Bremm et al., 2012; Cid and Brizuela, 1998; Oom et al., 2008; Roguet et al., 1998) but is a necessary part of the functioning of the ecosystem, allowing the animals to select a different diet of what is offered (Laca, 2011).

Regarding the response models of animal and sward structure in relation to forage allowance, a sward structure that allows animals to dedicate less time to grazing activity (FM between 1 400 and 2 200 kg DM·ha^{-1} and an H between 9 and 13 cm, data by Da Trindade et al., 2012) was close to that which provided the higher DM (2 062 kg DM·ha^{-1} and 12.6 cm) and nutrient intake rates (11.5 cm) in this study. Analyzing the values of total digestible nutrients and crude protein intake rates, we can infer that differences in individual weight

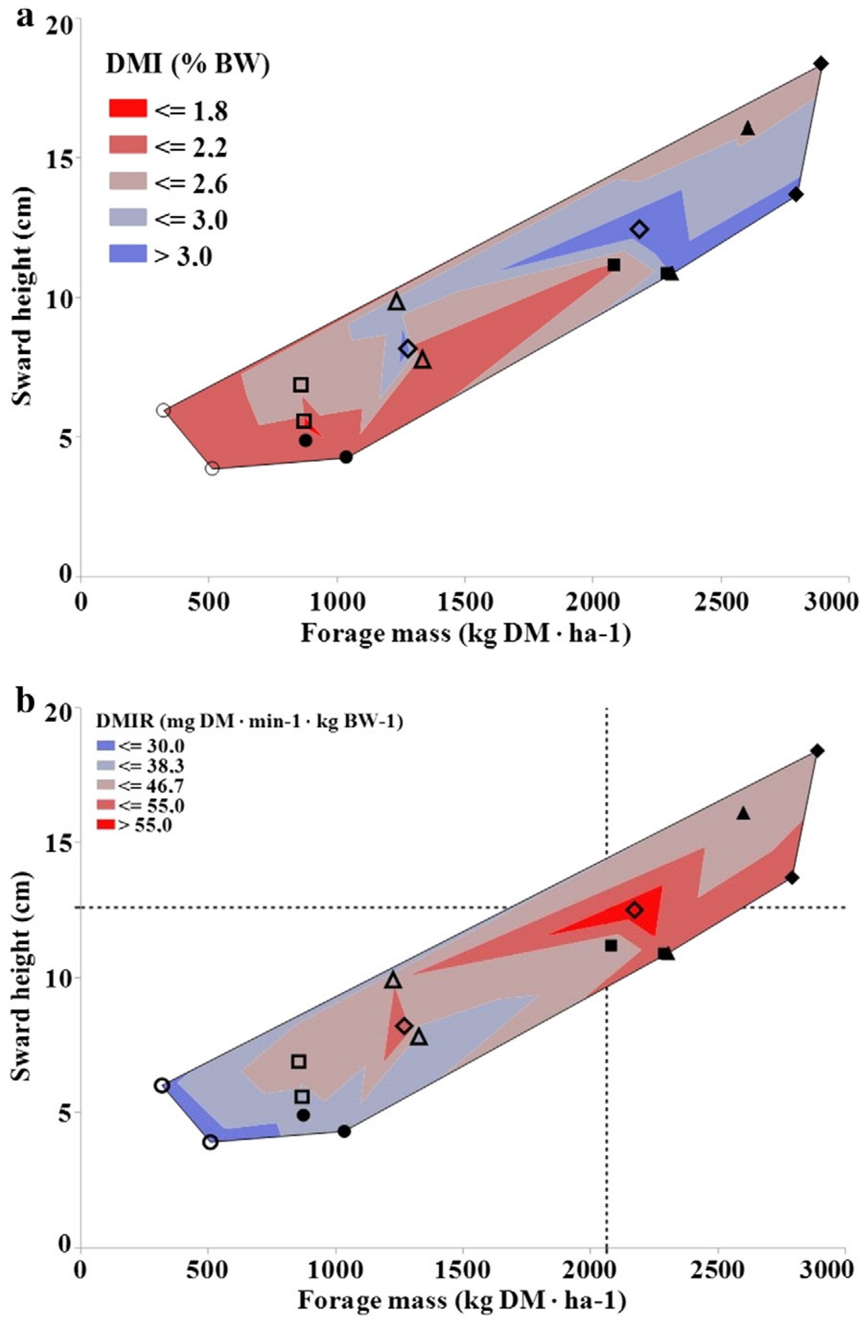

Fig. 3. Three-dimensional relationships (**A**) among FM, H, and daily dry matter intake (DMI, % BW) and (**B**) among FM, H, and daily dry matter intake rate (DMIR, mg DM · min^{-1} · kg BW^{-1}) of beef heifers on the natural grasslands of the Pampa Biome managed with FA levels (% BW). The dotted lines perpendicular to the *x* and *y* axes represent, respectively, the values of FM and H that determined the higher DMIR, verified from the regression models (Table 2). The points correspond to: summer: ● = 4% BW, ■ = 8% BW, ▲ = 12% BW, ♦ = 16% BW; spring: ○ = 4% BW, □ = 8% BW, Δ = 12% BW, ◊ = 16% BW.

gain between 12% and 16% BW of forage allowance, already reported in previous studies in the same experimental area (Mezzalira et al., 2012; Neves et al., 2009b; Soares et al., 2005), are explained by sward structure and its influence on selectivity for higher-quality forage. Lower animal production has been attributed to conditions of high forage allowance due to the low nutritive value of the forage present in the pasture (Maraschin, 2001; Soares, 2002). However, animals can consume a diet of higher nutritional value than the average presented to them (Dumont et al., 2002; Hodgson, 1990), reflecting on their performance (Chapman et al, 2007). With the increase of forage allowance in natural grasslands of the Pampa Biome, some complicating factors for the ingestive process such as low bulk density of available vegetation and high tussock frequency may occur, modifying the sward structure and, consequently, constraining the intake rate (Bremm et al., 2012; Gonçalves et al., 2009). Such factors may require a higher expenditure of time and energy by the animal in foraging and thus lead to a reduction in growth performance (Carvalho et al., 2010).

It is difficult to determine the independent effects of sward structure components on forage intake by animals due to the fact that sward descriptors are highly correlated (Demment and Laca, 1993), as indicated by the principal components analysis (see Fig. 2). This leads to the concept that some sward structural characteristics can be combined in an integrated manner to understand the foraging decisions of grazing ruminants (Da Trindade et al., 2012; Tharmaraj et al., 2003). Below 1 620 kg DM · ha^{-1} and 10.1 cm of H, animals had decreased DMI, which cannot be compensated for by increasing daily grazing time

(Da Trindade et al., 2012), leading to a condition in which the DMIR was almost 75% lower compared with the highest average values found. Under those conditions, the animal strategy was to increase bite rate in the short-term scale (Bremm et al., 2012; Gonçalves et al., 2009), whereas the daily number of total grazing jaw movements was practically constant in the daily scale (Ungar, 1996). In continuous stocking, the increase in bite rate means that the animal is consuming low bite mass, considering that bite depth is often constant and proportional to half of the sward height (Carrère et al., 2001; Gonçalves et al., 2009; Laca et al., 1992; Mezzalira et al., 2014; Ungar et al., 1991). However, the strategy of the animal in devoting a greater number of jaw movements for harvesting cannot compensate for the reduction in intake rate (see Fig. 3A). Therefore to maintain a constant daily intake, the animals need to increase their grazing time (Erlinger et al., 1990; Stobbs, 1975) within the limits that they can achieve.

The results presented here demonstrate that DMI increases when animals are faced with higher sward heights and forage masses. However, grazing time can be higher even in conditions of vegetation abundance (Da Trindade et al., 2012) and high intake, implying that the process of acquiring food is not optimized. Fig. 3 demonstrates this scenario in which, despite the high DMI observed with increases in the food availability per animal, the inefficiency in grazing can lead to a high duration of this activity and increases in the energy expenditure during grazing (Osuji, 1974), potentially limiting increases in animal performance under conditions of higher forage allowances (Mezzalira et al., 2012).

Pinto et al (2007), Da Trindade et al. (2012), and Mezzalira et al. (2012) evaluated the grazing time of heifers in the same experiment and registered a variation from 453 min to 710 min/day, and in an adapted model using data from these studies, Carvalho et al. (2015) found grazing time was significantly affected by intertussock surface height and tussock frequency. The animal uses compensatory strategies when sward structure offers complicating factors to the ingestive process (Laca, 2008). To compensate for the inflection in DMIR, which occurred with 12.1% BW of forage allowance, 2 062 kg DM/ha of FM and 12.6 cm of H, the animal increased grazing time (Da Trindade et al., 2012). However, the total digestible nutrients and crude protein intake rates, due to inflection with H of 11.5 and 11.0 cm, respectively, implies that the animal's strategies to increase grazing time does not compensate for the decrease in intake rate of nutrients, which can result in lower animal performance in those sward conditions (Mezzalira et al., 2012; Soares et al., 2005). In this context, the grazing process may be limited due to the spatial dispersion of food items, either vertically or horizontally in the sward (Carrère et al., 2001). Although we have not found a grazing intensity and sward structure condition that characterizes the maximum DMI, the results showed that high intake rate, of both DM and nutrients, occurred with 11.8 cm of the H.

Gonçalves et al. (2009) performed a reductionist protocol and mimicked the heights of the intertussock stratum in natural grassland similar to what was present in this experiment. The authors found that, despite the narrow relationship with sward height, the bite depth was not able to compensate for the negative effect of the high leaf lamina dispersion (i.e., low bulk density) on the bite mass, which meant that animals harvested less forage per bite. Although bovines can expand the bite area through tongue movements (Demment and Laca, 1994), above 11.4 cm of H the bite mass and, consequently, the intake rate were reduced. This value is close to that found in this study, and both intake rate models showed quadratic responses with H. However, Mezzalira et al. (2014) found a previously undescribed phenomenon whereby the interaction can be destabilized by a reversal of the relationship between sward height and intake rate in tall swards in two contrasting forage species (tropical and temperate). Despite the different scales of time and space that were used in the protocols of Gonçalves et al. (2009) and Mezzalira et al. (2014), the effects observed in the smaller scales have affected the decisions of the animal in the higher scales (Carvalho et al., 2015).

In situations where the forage allowance is increased, there is an increase in heterogeneity of vegetation by the development of some species forming tussocks, in this experiment illustrated by the second principal component analysis shown in Fig. 2, which can be restricting factors for the forage intake process (Bremm et al., 2012; Gordon, 2000; Laca, 2008). In natural grasslands of the Pampa Biome, the vegetation communities contain different plant functional types in moderate and low grazing intensities (Cruz et al., 2010), forming tussock and intertussock areas dispersed in mosaics (Cid and Brizuela, 1998; Côrrea and Maraschin, 1994). The mechanisms that could cause a decrease in the forage intake likely involve, in short-term scale (e.g., bite and feeding station scales), a decreasing mass of cropped forage units and increasing handling efforts per unit forage through selection against low-quality parts of forage (Drescher et al., 2006). Bremm et al. (2012) studied the effect of a nonpreferred tussock, *Eragrostis planna* Nees, on the short-term intake by cattle and sheep in a protocol on the natural grassland of Pampa Biome. With the increase of tussock frequency, the animals must choose between quality and quantity of the forage ingested, and, under high tussock frequencies, the animals give up selection of preferential items over less preferred items, but they can maintain high intake rate, according with the optimal foraging theory (Roguet et al., 1998). Bremm et al. (2012) found an increase in the proportion of bites in tussocks with increasing *E. planna* tussock frequency, due to reducing accessibility of the preferred diet item. In that context, maximizing the use of time, maintaining intake rate by allocating bites in tussocks may have led to a decrease in diet quality (Bergman et al., 2001). However, the heifers reduced the short-term intake rate and bite mass when the percentages of tussock were greater than 34% or 44%, respectively, suggesting that an increase in grazing time with a higher level of tussock can be expected. When animals begin to include the tussocks in the diet, they fail to maximize the intake rate, because this plant type acts as a vertical and horizontal barrier that interferes in the bite formation and, consequently, reduces the bite mass (Bremm et al., 2012). Therefore the grazing intensity, in addition to changing the sward vertical structure affecting the forage intake components (e.g., bite dimensions), creates and alters a horizontal mosaic of patches with tussocks and intertussock stratum, which also interacts with the animals (Marriott and Carrère, 1998) and influences the intake behavior and animal´s displacement during grazing (Da Trindade et al., 2012). In the present study, although the higher values of tussock were only 37% (see Table 1) and animal responses have shown positive linear relationships with the increase of tussock, we found, based on quadratic models presented in Table 2, that 29.5% of tussocks comprise the frequency level that was associated with the forage allowance and sward condition (FM and H) that promoted the highest DMI rate. Adaptive foraging options on patchy heterogeneous sward structure and composition can increase the carrying capacity (Fynn, 2012), but above this value limit of tussocks, which was similar to that found by Bremm et al. (2012), we believe that the combination of factors that occur in the intertussock stratum, as previously reported, with high tussock level play an important role that results in decreases in harvested forage by grazing animals in abundant forage allowances.

Implications

This study demonstrated that higher levels of forage daily intake were associated with increased vegetation abundance and with sward structure. The management with low levels of forage allowance (*ca* 4% BW) constrained forage intake. On the other hand, high levels of forage allowance (*ca* 16% BW) also resulted in lower intake rates of nutrients. Thus, the average sward conditions that promoted a high daily forage intake, as well as a high nutrient intake rate, by cattle grazing natural grassland of the Pampa Biome occurred around 12.1% BW of forage allowance, characterized by an FM between 1 820 and 2 280 kg DM·ha^{-1} and between 11.5 and 13.4 cm of H, with tussock levels that did not exceed 30%. Those characteristics promote high daily forage intake and intake

Table 2
Regression analysis between actual forage allowance (AFA, % BW) and sward structure characteristics with dependent variables of beef heifers that describe ingestive behavior on the natural grassland of the Pampa Biome managed with forage allowance levels (FA)

Depedent variables (y)	FA (% BW)				Independent variables (x)	P value		Model	R^2	RSEM
	4	8	12	16		L[10]	Q[11]			
DMI[4] (% BW)	1.97	2.24	2.61	3.00	AFA (% BW)	0.0012	0.0926	y = 1.74 + 0.08x	0.65	0.019
					FM[1] (kg DM·ha^{-1})	0.0080	0.1935	y = 1.86 + 3.7e^{-4}x	0.54	1.2e^{-4}
					H[2] (cm)	0.0163	0.0848	y = 1.82 + 0.068x	0.49	0.02
					T[3] (%)	0.0010	0.3211	y = 1.97 + 0.023x	0.66	0.006
CPI[5] (% BW)	0.25	0.25	0.27	0.30	AFA (% BW)	0.2702	0.3992	ND[12]	-	-
					FM (kg DM·ha^{-1})	0.5640	0.4254	ND	-	-
					H (cm)	0.6500	0.1415	ND	-	-
					T (%)	0.1174	0.2496	ND	-	-
TDNI[6] (% BW)	0.67	0.70	0.74	0.88	AFA (% BW)	0.1770	0.4350	ND	-	-
					FM (kg DM·ha^{-1})	0.4634	0.5189	ND	-	-
					H (cm)	0.6005	0.0836	ND	-	-
					T (%)	0.0441	0.0999	y = 0.67 + 0.004x	0.37	0.0020
DMIR[7] (mg·min^{-1}·kg BW^{-1})	29.7	42.8	43.3	51.8	AFA (% BW)	0.0043	0.0267	y = 14.8 + 5.8x − 0.24x^2	0.71	0.086
					FM (kg DM·ha^{-1})	0.0096	0.0192	y = 14.6 + 0.033x − 8.0e^{-6}x^2	0.69	3.0e^{-6}
					H (cm)	0.0280	0.0109	y = −0.69 + 8.3x − 0.33x^2	0.67	0.100
					T (%)	0.0001	0.8335	y = 31.6 + 0.50x	0.73	0.106
TDNIR[8] (mg·min^{-1}·kg BW^{-1})	10.5	13.5	12.3	15.2	AFA (% BW)	0.1645	0.1281	ND	-	-
					FM (kg DM·ha^{-1})	0.2987	0.0805	ND	-	-
					H (cm)	0.5011	0.0057	y = 3.22 + 2.07x − 0.09x^2	0.54	0.029
					T (%)	0.0057	0.8213	y = 10.7 + 0.10x	0.50	0.035
CPIR[9] (mg·min^{-1}·kg BW^{-1})	3.7	4.7	4.6	5.3	AFA (% BW)	0.2003	0.0965	ND	-	-
					FM (kg DM·ha^{-1})	0.3255	0.0506	ND	-	-
					H (cm)	0.4869	0.0126	y = 0.97 + 0.77x − 0.035x^2	0.52	0.0112
					T (%)	0.0153	0.9780	y = 3.9 + 0.03x	0.47	0.014

[1] FM = forage mass.
[2] H = sward height.
[3] T = tussock frequency.
[4] DMI = dry-matter intake.
[5] CPI = crude protein intake.
[6] TDNI = total digestible nutrients intake.
[7] DMIR = dry-matter intake rate.
[8] TDNIR = total digestible nutrients intake rate.
[9] CPIR = crude protein intake rate.
[10] L = linear effect.
[11] Q = quadratic effect.
[12] ND = not done.

rate of DM and nutrients by grazing beef cattle. Besides the importance in the quantity of food per animal, management practices in natural grasslands should also be associated with the control and monitoring of sward structure to build adequate grazing environments that enable high intake of forage and nutrients.

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