

Managing natural grasslands in a changing world : grazing ecology insights to accomplish re-oriented management expectations

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Key points :

1. There is an increasing debate regarding the quality of pastoral environment . More than the production *per se* , a series of multifunctional responsibilities have been attributed to the pastoral ecosystems , that they always had , but have only become imperative as the world natural resources became threatened .
2. The quality of the use of a pastoral ecosystem can be interpreted through signals emitted by their biotic and abiotic components . For example , plants and animals show patterns of behaviour that permit inferences about nutrient acquisition status or nature of the competition being faced . As a result , the prevailing strategies of response in a given environment indicate the selection forces involved that , in turn , determine particular adaptive attributes of plants and animals as a response to them .
3. The objective of this paper is to discuss patterns of behavioural responses of plants and animals based on the most common source of disturbance manipulated by human actions in a pastoral ecosystem , the grazing intensity .
4. It is suggested that the recognition and interpretation of plant functional groups and ingestive behaviour of animals should provide the basis for the invention and planning of re-oriented grazing management strategies to construct pastoral environments in agreement with the new expectations and demands of a changing world .

Key words : biodiversity , ingestive behaviour , plant functional types , Brazilian Pampa , sward structure

Threatened natural grasslands , grazing challenges and opportunities : the Brazilian Pampa example

Natural grasslands have been facing contradictory pressures in developing countries . On one hand , there is a need to produce food and contribute to the country's development . On the other , there is the need to preserve the environment and the ecosystem . This dilemma is reaching a crucial point in Southern Brazil . Pampa is the most southern Brazilian biome and represents 2 .07% (176 496 km²) of the national territory (Carvalho & Batello , 2008) . Its subtropical natural grasslands are the most important forage resource for almost 13 million cattle and 5 million sheep . Recent studies have shown that this natural grassland ecosystem is under threat and disappears at a rate of 410 000 ha per year (Nabinger & Sant'Anna , 2007) , with only 33 8% of its natural vegetation cover still remaining (Hasenack et al . , 2007) . The expansion of agriculture (mainly cash crops , forestation , etc .) , along with overgrazing are the most frequent actions threatening this biome (Carvalho & Batello , 2008) .

Pampa is a complex vegetation comprised mainly of grasses (especially *Andropogonea* and *Panicum*) and herbs (small shrubs and trees are occasionally found) with a great degree of biodiversity as Overbeck et al . (2007) estimated the occurrence of 3000 4000 phanerophytes . Grazed grassland communities are heterogeneous and usually show a short inter-tussock stratum of prostrate species that is intensively grazed , and a taller stratum of plants with a more or less patchy distribution . Tussocks are often comprised of tall-tufted grasses with low forage value and other species that are unattractive to grazing animals (shrubs and thorny species) . Thus managers and animals face a very diverse grazing environment to explore in floristic , functional and structural terms .

Humans and grazing animals respond differently to the challenge of exploiting complex pastoral environments (Carvalho , 2005) . Because humans do not know how to deal with heterogeneous environments , nor manipulate their dynamics , they normally tend to replace complex with simpler systems (e .g . mono specific pastures) as a means of increasing control . The consequence of misunderstanding the complexity of natural pastures is the low animal productivity attained (60 kg LW .ha⁻¹ . year⁻¹) , which does not compete efficiently with other economical alternatives of land use . On the other hand , grazing animals , when allowed , are capable of successfully exploring heterogeneity and even benefit from it (Rook et al . , (2004) , since they evolved in complex environments and developed a series of mechanisms that enables them to survive in such environments (e .g . Villalba & Provenza , 2007) . For example , Cortes et al . (2006) pointed out that diverse grazing environments stimulates animals' intake . However , the most common is to find situations where animals face restrictions to their mobility and selectivity (Bailey , 2005) . By selecting forage , animals increase heterogeneity on the swards by reducing the most palatable species with a concomitant increase in the less palatable . This situation worsens and managers usually react by increasing stocking rate and/ or adopting grazing strategies that restrict animal's choices .

In the Pampa Biome the course of history regarding natural grasslands is the same as for other areas of the world (Suttie et al . , 2005) , and is related to an intensification process of the pastoral systems with significant reduction of biodiversity and

degradation of natural resources . Nevertheless , the debate and awareness of how these natural resources are being misused is increasing (Nabinger & Sant'Anna , 2007) , and maybe it will not be necessary to reach an almost complete deterioration of the ecosystem before important issues like environmental pollution and degradation , biodiversity and extensification start to be seriously addressed (Lemaire et al . , 2005) . In this context , knowledge of the plant-animal relations in such complex environments is important to describe the nature of and generate interest in the interacting processes under those conditions . This would facilitate communication and getting people aware of how dependent they are on the conservation of those resources . In spite of the difficulties of debating issues like this in developing countries , it is essential to encourage public policies and management actions aimed at striking an adequate balance between the conflicting objectives of production and conservation (Carvalho & Batello , 2008) . In South Brazil , preservation of Pampa cannot be separated of their natural vocation , i . e . the economical exploitation of domestic herbivores . As a result , ecological arguments should not be considered without taking into account the need to achieve satisfactory animal productivity . However , there is an opportunity to incorporate ecological variables into the pool of "productive" variables used to guide the actual use and management of such ecosystems , that being the purpose of this paper .

Plant-animal relations in heterogeneous environments : focus on plant strategies

It may seem logical that the necessary characteristics for plants to survive in desert habitats are not the same as those required for humid tropical/sub-tropical habitats . This simplistic observation implies that each habitat determines adaptive characteristics to plants that would allow them to exist . The edaphic and climatic potential of the environment in association with the local floristic diversity and its evolution history with grazing and fire , for example , determine the type of vegetation potentially capable of existing in a given habitat . Even though there is a wide range of possible vegetation types , it is the current characteristics of the habitat that will define the type and structure of the existing vegetation . The fact that ecosystems show variable patterns of making nutrients available to plants , as well as the amount and type of predators inhabiting them , allow for the existence of contrasting strategies of growth and resistance (e . g . , prostrate sward forming or tall-tufted species , short and long life cycle , fast and low growing plants , etc .) . Further , when grazing and other management interventions are considered , there is the definition of a vegetation structure that reflects , at a given point in time , the result of a "local selection" process (Carvalho et al . , 2007) .

Recently , there has been increasing interest in a functional approach for interpreting plant strategies and their impact on ecosystem dynamics (Garnier et al . , 2004) . The description of the floristic composition and identification of individuals is less important (Sosinski Junior & Pillar , 2004) than identifying groups of plants with similar functions in the ecosystem (Gitay & Noble , 1997) . The basic assumption is that the prevailing conditions in a given ecosystem will select the pool of markers (functional types) more correlated with the vital functions of the species (but see Wright et al . , 2004) . In this context , markers are defined as measurable morphological , physiological and/or propagation traits , and can be classified as "response traits" , when they indicate responses of plant communities to variations in their environment , or as "effect traits" , when they indicate the effect of plant communities upon how the ecosystem work (Lavorel & Garnier , 2002) . A list of markers has been evaluated by several authors (e . g . , Pontes , 2006) as a means of studying plant communities in different observational scales . It has been demonstrated that once efficient markers for functional strategies of plants have been identified , they will become important for diagnosing and managing grasslands (Cruz et al . , 2002) . For example , response traits related to high soil fertility are high specific leaf area (SLA) , high nutrient concentration (particularly N) , low leaf dry matter content (LDMC) , short leaf lifespan (LLS) , and high rates of photosynthesis and respiration (Wright et al . , 2005) . Species adapted to such environmental conditions usually show high rates of growth and turnover of plant organs . As a result , leaves are short lived and plants have high nutrient requirements . On the other hand , response traits related to low soil fertility are low SLA , low N content , high LDMC , high proportion of cell wall constituents and high LLS (Westoby et al . , 2002) .

The adaptive strategies of plants to high grazing intensities keep similarities to those related to high soil fertility (Cruz et al . , 2002) . In fact , strategies for high soil fertility conditions can be considered as tolerance mechanisms to grazing , since they involve responses related to high rates of plant growth (Diaz et al . , 2001) . Conversely , the characteristics that favour adaptation of plants to low soil fertility conditions are associated with low herbage quality and , consequently , low intake . SLA is negatively correlated with LLS (Westoby et al . , 2002) that , in turn , is negatively correlated with nutritive value . According to Pontes et al . (2007) , herbage dry matter digestibility has negative correlation with LDMC and positive correlation with SLA , corroborating the propositions of Garnier et al . (2004) , which indicate that SLA and LDMC correspond to central traits to diagnose vegetation types . The application of these markers in pastoral environments would allow characterisation and classification of the existing vegetation in terms of potential productivity and nutritive value (Cruz et al . , 2002) .

The proposition of assessing grasslands through their prevailing plant functional types was tested by Quadros et al . (2006) on a natural pasture in South Brazil . The existing vegetation had been subjected to contrasting grazing intensities (daily herbage allowances of 4 , 8 , 12 and 16 kg DM/100 kg LW) during 17 years (Carvalho et al . , 2007) , and their interaction with different conditions of natural soil fertility generated four large functional groups distinguished by LDMC and SLA of the several plant species in each group (Table 1) .

Table 1 Groups of plant functional types based on leaf area (SLA) in a natural pasture subjected to contrasting grazing intensities during 17 years (Quadros et al., 2006)

Groups	LDMC (mg .g ⁻¹)	SLA (m ² .kg ⁻¹)	Species
A	230	24	<i>Axonopus affinis</i> , <i>Panicum sabulorum</i> , <i>Paspalum paucifolium</i>
B	310	16	<i>Andropogon lateralis</i> G* , <i>Coelorachis selloana</i> , <i>Paspalum paucifolium</i> , <i>Paspalum notatum</i>
C	380	8	<i>Andropogon lateralis</i> T* , <i>Piptochaetium montevidense</i> , <i>Sporobolus indicus</i>
D	500	6	<i>Aristida</i> spp (<i>A . laevis</i> , <i>A . phyllifolia</i> , <i>A . venustula</i>)

* G= grazed ; T= tussock

There was an inverse relationship between LDMC and SLA . Plant species with high SLA and low LDMC could be identified as plants that developed a resource capture strategy (groups A and B) , with ability to compete for nutrients , showing high rates of herbage accumulation and low LLS . Phyllochron values of *P . notatum* and *C . selloana* (group B) were lower (Eggers et al . , 2004) than those of *A . lateralis* (T) and *P . montevidense* (group C) . Plants of the first group were characterised by a stoloniferous growth habit . Groups C and D were characterised by low SLA and high LDMC , suggesting plants with a strategy for resource conservation , with low rates of herbage accumulation and high LLS . These are species that have , in their large majority , a tall-tufted growth habit that , according to Briske & Derner (1998) , permits plants to explore and capture nutrients in a diameter larger than that used to release them , resulting in nutrient accumulation right under the vertical projection of the leaf canopy , a strategy called "resource monopolization" . Quadros et al . (2006) demonstrated that plants types associated with strategies of nutrient conservation occurred on areas where grazing intensity was low . Conversely , plant types associated with strategies of nutrient capture occurred on areas where grazing intensity was high . The authors concluded that the prevailing plant functional type was closely related to grazing management . Halford et al . (2008) studied the same vegetation subjected to contrasting intensities of grazing throughout a 20 year period and confirmed that high long-term grazing intensity significantly modified grassland composition , forming homogeneous overgrazed pastures characterised by a specific species assemblage . On the other hand , lower grazing intensities created more heterogeneous vegetation with grazed and ungrazed areas , but had small impact on floristic composition of grazed areas . Medium grazing intensities increased vegetation heterogeneity by enhancing species richness (Goret , 2005) and creating distinct grazed and ungrazed areas (Halford et al . , 2008) , enhancing primary and secondary productivity , while very high or very low grazing intensities reduced vegetation diversity and promoted abundance of a few adapted species (Soares et al . , 2003) .

The available results allow an inference to be made that assessment of plant functional types in a given pastoral environment might be used to understand and interpret the existing driving forces and what their influences on the local vegetation composition are . Based on these , management actions can be thought up which aim at achieving a pre-determined vegetation type and structure necessary for proper animal utilisation in harmony with the objectives planned for that environment .

Plant-animal relations in heterogeneous environments : focus on animal strategies

In natural grasslands subjected to high grazing intensities , it is common that the prevailing plants species have resource capture strategies and avoidance mechanisms to resist grazing . The size and structure of such plants result in little "exposure" of the acquired carbon , making more difficult the process of herbage capture by the grazing animal . Under these conditions , daily grazing time can easily exceed 600 minutes (Pinto et al . , 2007) . Depending on the grazing management , as well as on the floristic composition of the vegetation , this area dominated by a sward forming vegetation can form a mosaic with tussocks varying in frequency , topographic location and in degree of patchiness (Carvalho et al . , 2007) . The influence of double stratum vegetation on the grazing process was discussed by Gordon (2000) . The author reviewed plant-animal relations in communities dominated by *Nardus stricta* and showed how the characteristics of each stratum were inter-related determining intake and diet selection by the grazing animals . In general , the availability of the preferred stratum affects the intensity with which it is used as well as the utilisation of the less preferred stratum , indicating a high degree of complexity that usually limits detailed experimentation and knowledge regarding such ecosystems .

In such heterogeneous environments it has been observed that the grazing process , at its lowest scales of decision , is essentially the same as that in sown temperate swards . For example , Pinto et al . (2007) did not find correlation between grazing time and herbage mass in natural grassland , when herbage mass is estimated on average . However , when only the herbage mass of the inter-tussock vegetation was considered , grazing time increased 67 minutes for each centimetre decrease in sward height . In a pioneer work , Gonçalves (2007) elaborated a reductionist protocol to mimic sward heights of the lower stratum of natural grasslands subjected to decreasing levels of grazing intensity . The author confirmed that the structure of the inter-tussock vegetation affected bite dimensions and intake in a similar manner as reported by sown pastures . The comparison between bite depth of ewes and heifers revealed a linear relationship with sward height and no difference between animal species (Figure 1) .

The constant proportionality of herbage removal was observed, as previously discussed by Hodgson et al. (1994). As sward height decreased, bite mass was more negatively affected for heifers than for ewes. Large animals are more handicapped on short swards where bite mass increases more slowly with body weight than do the energetic requirements. Time per bite increased with increasing bite masses, and lesser for heifers, a likely consequence of the larger capacity of cattle to perform compound chew-bite jaw movements in situations of large bite mass (Ungar et al., 2006). Bite mass was the main determinant of intake rate. The reduction in bite mass and intake rate from around 10.0 and 11.5 cm for ewes and heifers, respectively, indicates that C4 forage species need careful control of sward structure in order to optimise herbage utilisation, as pointed out by Da Silva & Carvalho (2005).

In pastoral environments dominated by prostrate species with resource capture strategies, animals alter their dynamics of herbage acquisition, patterns of movement and use of feeding stations (FS). Mezzalana (unpublished data) showed that under such conditions animals increase total grazing time reducing the number of meals but increasing the duration of each meal.

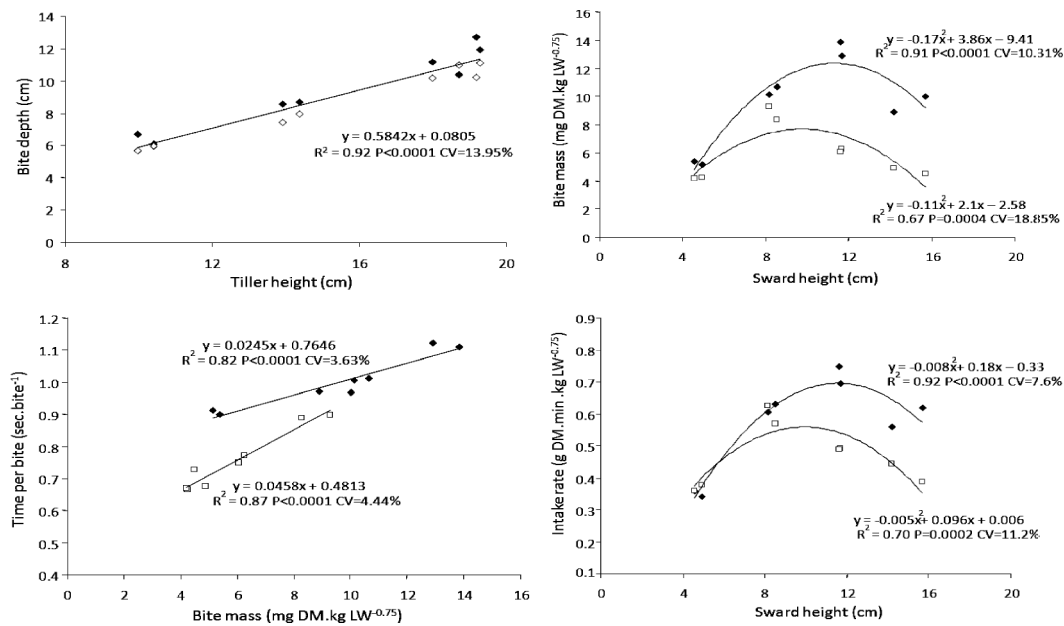


Figure 1 Ingestive behaviour of heifers (◆) and ewes (□) in natural pastures (Gonçalves, 2007).

Modifications in patterns of herbage acquisition were also associated with reduction of the number of inter-meal intervals and the angle of animal's trajectory during grazing. The increase in grazing time is a classic response to situations of low herbage mass, while the reduction of trajectory angle during grazing causes animals to spend less time on a limiting grazing site in an attempt to increase the probability of finding a more appropriate one (Prache et al., 1998). Gonçalves (2007) studied patterns of animal movement and herbage search for cattle and sheep on a natural pasture. Both species showed the same pattern of response, but with different magnitudes (Table 2).

Table 2 Feeding station behaviour of calves and ewes in natural pastures (Gonçalves, 2007).

Variable	Sward height (cm)				Model*	P	R ²	CV (%)
	04	08	12	16				
Feeding station per minute								
Calves	13.7	9.5	7.0	8.7	Q	<0.0001	0.876	10.55
Ewes	19.0	7.5	9.7	11.2	Q	0.0001	0.791	18.58
Steps per feeding station								
Calves	1.1	1.3	1.8	1.2	Q	0.0057	0.498	19.18
Ewes	1.1	2.4	1.6	1.2	Q	0.0009	0.620	22.15
Bites per feeding station								
Calves	4.8	6.4	7.8	7.2	Q	0.0182	0.695	12.35
Ewes	4.6	8.9	8.4	7.8	Q	0.0008	0.712	13.21

Variable	Sward height (cm)				Model*	P	R ²	CV (%)
	04	08	12	16				
Movement rate (steps · minute ⁻¹)								
Calves	14.5	13.0	12.0	10.5	L	0.0023	0.497	12.50
Ewes	20.5	17.7	15.7	14.2	L	0.0003	0.649	10.17
Time per feeding station (seconds)								
Calves	4.3	6.4	8.7	6.9	Q	0.0006	0.788	12.92
Ewes	3.1	7.9	6.4	5.4	Q	0.0002	0.706	17.91

* L= linear ; Q= quadratic

Under intake limiting conditions, both cattle and sheep visit a larger number of FS, harvesting fewer bites and remaining less time on each FS, a behaviour that is in agreement with the Optimum Foraging Theory (Prache et al., 1998). Further, animals move faster, but with fewer steps between FS, indicating an attempt to increasing the rate of encounter with potential FS. Such behaviour is also compatible with the low bite mass obtained in the last bite, taken prior to abandoning the previous FS, which does not allow efficient movement of animals (selection of new FS while processing the last bite harvested). These behavioural responses change in the opposite direction as sward characteristics become more favourable to herbage harvest, reaching a different plateau for each animal species.

The consequence of animals spending more or less time grazing and using a larger or lesser number of FS is that a horizontal structure is created over time, where some patches are grazed more often than others (Laca, 2000). Under continuous stocking, animals are particularly attracted by areas where nutrient concentration is high, being able to memorise and use them more frequently than others (Launchbaugh & Howery, 2005). Thus, a heterogeneous mosaic condition is established. When stocking rate is high in relation to the herbage available on the preferred sites, there is an overgrazing of the preferred species on pastures of complex floristic composition and some high nutritive value species run into the risk of disappearing (Eggers et al., 2004). This is often wrongly interpreted as being a restriction of the grazing method used; generating the general impression that continuous stocking is associated with low productivity, a subjective interpretation that supports the inconsistent paradigm regarding rotational stocking as the best grazing method" (see discussion about perception *versus* experimental evidence in Briske et al., 2008). In this context Carvalho (2005) stated that overgrazing on certain areas would rather be consequence of low opportunity for selection. While an instantaneous high herbage allowance would create heterogeneity, frequent use of the preferred areas and rejection of the less preferred areas creates, in the long term, a condition of high herbage allowance on the total area, but limited on the sites effectively used (Neves, 2008). Since they cannot explore other areas as any other herbivore in a natural environment would, animals have no other alternative than overuse preferred sites. This corroborates the statement of Bailey (2005) that the large majority of problems regarding grazing management derive from an inadequate distribution of grazing and not of the use of incorrect stocking rates.

In fact, Neves (2008) indicated that variations in stocking rate slightly modified the characteristics of the inter-tussock stratum, whose magnitude is smaller than the variations suggested by varying grazing intensities. Regardless of the several combinations of grazing intensity studied, the frequency of FS with optimum structure for herbage capture was inferior to 10% of the total surface of inter-tussock vegetation. Carvalho et al. (2007) described this phenomenon as "structural collapse", where the decrease of grazing intensity in plant communities dominated by prostrate growing species with resource capture strategies increase the contribution of such species in terms of herbage mass and height until a certain point, from which the patterns of defoliation and the nature of the competition process change so much that the community starts to give place to another one, usually comprised of tall-tufted species with resource conservation strategies. This indicates that simple manipulation of grazing intensity under those circumstances is not enough to manage the inter-tussock stratum and generate adequate conditions for grazing. Therefore, construction of adequate sward structures for grazing cannot be achieved only through variable stocking, but it needs other management strategies with the objective to construct pastoral environments where diversity of plant functional types and structures would be compatible with production targets.

Thus, as previously discussed for plants, animals also present grazing behavioural signals which could provide a basis for interpreting the richness of a particular pastoral environment and orientate management actions. In this sense, it has been proposed (Gordon & Benvenuti, 2006) that further improvement of animal production from grasslands will need to be associated with the identification and manipulation of animal behavioural responses, favouring the expression of their grazing abilities rather than inhibiting them as it is often the case for antropic interventions.

Concluding remarks

Grazing ecology is rarely treated in a systems context associated with management actions aimed at economical benefits (Soder et al., 2007). In this context, for some natural ecosystems it is important not only to understand how they work and what the mechanisms involved in the grazing process are, but also to evaluate their direct impact on the production and quality of animal

products . Consumers demand production systems that respect not only productivity targets , but also exercise environmental responsibility and animal ethics . Kemp & Michalk (2005) outlined the need to redefine the frameworks within which management decisions are made to enhance the overall environmental values of grasslands . In this sense , the interpretation of the pastoral environment quality using plant and animal behavioural responses as well as indicators of soil chemical , physical and biological fitness is of major relevance to orientate management practices that are coherent with the new expectations and demands of a changing world . In this sense , intensity and distribution of grazing have assumed a new dimension , according to which grazing management must be seen as a means to construct adequate and ecologically sound pastoral environments that allow animals to express their wisdom in harvesting nutrients (Provenza et al . , 2007) and self-medicate themselves by selecting phytochemicals (Revell et al . , 2008) while minimising the energy costs of grazing (Baumont et al . , 2005) , without jeopardising environmental and production system sustainability . In ecosystems where the conservation of natural resources is achieved through their economical use , the importance of the pastoral environment has to be imposed by means of competitive productive indexes and products with high aggregated value .

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