Foraging Behaviour and Herbage Intake in the Favourable Tropics/Subtropics

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Key points

1. Herbage intake by animals grazing tropical/sub-tropical pastures is directly related to bite mass, as it is for those grazing temperate pastures.
2. Where these swards have low proportions of stem and dead material (controlled swards), herbage intake follows a similar pattern to that of temperate pasture species, but leaf characteristics, such as lamina length play an important role and influence the short-term rate of intake.
3. Sward structural characteristics and behavioural factors are relatively more important than nutritional factors in terms of herbage intake regulation. The feeding value of the herbage produced is potentially adequate to sustain high levels of beef cattle performance under controlled sward conditions, but relatively limited for dairy cows, since nutrient concentration in the forage is not optimal for high levels of daily milk yield.
4. Sward targets for attaining production objectives are now a feasible management practice on tropical pastures and should be evaluated further.

Keywords: tropical grasslands, animal performance, grazing management

Introduction

Grasslands cover about 3 billion hectares, approximately a fifth of the world's land area of 14.9 billion hectares (Hadley, 1993), with a large proportion concentrated in the tropical and sub-tropical region. Here climatic conditions and the availability of plant and animal resources favour the production of environmentally safe, healthy and low cost animal products, via efficient, competitive and economically viable pastoral systems. However, animal production from pastures in the tropics has consistently been related to low levels of performance, 'explained' by the classical argument that ruminant ingestion and digestion processes are negatively affected by several chemical and physical constraints associated with the available herbage. Recent evidence illustrates these potential limits, but demonstrates that the problem can be minimised by appropriate harvesting of herbage through efficient and well-planned grazing strategies in an environment extremely favourable to the growth of forage species, particularly vigorous C_4 grasses. In fact, there is now enough evidence to support the argument that animal performance can be considerably improved (Andrade, 2003; Martinichen, 2003), and that there exists the opportunity for the development of sustainable-high productivity pastoral systems.

In a scenario characterised by the competing requirements of plants and animals, knowledge about the plant-animal interface is essential. Foraging behaviour is certainly one of the key components for the integration of plant and animal responses in pastures and will be the main objective of this review paper.

The tropical and sub-tropical pastoral environments

The tropical and sub-tropical region is situated between the latitudes 35^o N and 35^o S. The humid tropical climate is characterised by high annual rainfall (> 1000 mm) evenly distributed throughout the year, or with dry periods of 2 to 6 months during the autumn/winter period. Mean annual temperatures vary from 25 to 27^{o}C, with little seasonal variation (< 3^{o}C) and a daily range no bigger than 7 to 14^{o}C. During the coldest month of the year, mean temperatures are higher than 18^{o}C. The sub-tropical climate has a similar total annual rainfall, but dry periods may be concentrated in winter as well as in summer. Annual temperature varies widely, defining clear contrasts between warm and cold seasons. Average summer and winter temperatures vary from 24 to 27^{o}C and 5 to 13^{o}C, respectively, with the possibility of some frosts during the coldest month of the year (Rocha, 1991).

In general, grasslands are subject to distinct moist (usually summer) and dry (usually winter) seasons (Hardy *et al*., 1997), resulting in large fluctuations in quantity and/or quality of the available herbage. Pastures vary from cultivated to non-cultivated and can provide conditions for high levels of animal productivity (25,000 to 30,000 kg milk/ha per year and 1,000 to 1,600 kg LWG/ha per year – Corsi *et al*., 2001), even though average figures for Brazil are low (around 800 to 1000 kg milk/ha per year and 60 to 100 kg LWG/ha per year – Nascimento Jr *et al*., 2003). Cultivated pastures are mainly composed of *Brachiaria* and *Panicum* species - C_4 grasses with high herbage dry matter (DM) yield potential. These swards are very different from most temperate swards with a wide range of plant morphology and structure, varying from prostrate/semi-prostrate to tall-tufted, erect growing plants. Non-cultivated or native pastures are formed by a mixture of plant species varying from herbaceous (grass, legumes and composites) to shrubs and trees varying from predominantly grass stands to mixed grass legume pastures, and open woodland savannas. Examples of non-cultivated pastures are the savannas in the *Cerrado* region (areas of *campo limpo* and *campo sujo* in the central-west part of Brazil), the wetlands of *Pantanal* in central Brazil and the *campo nativo* in Rio Grande do Sul (Brazil), extending to Uruguay and northeast of Argentina (Campos biome - Carvalho, 2002).

Foraging behaviour and herbage intake by the grazing animal

General principles

Much of the available evidence on foraging behaviour and herbage intake comes from studies on temperate forage species with domesticated animals under controlled experimental conditions (Gordon & Lascano, 1993; Hodgson *et al*., 1994; Ungar, 1996; Hodgson *et al*., 1997; Illius, 1997; Prache & Peyraud, 2001; Sollenberger & Burns, 2001). In general, these reviews relate to small-scale studies aimed at providing a comprehensive understanding of the mechanics of the grazing process, with particular emphasis on bite dimensions, bite mass and short-term rate of intake. This involves the cropping, mastication and swallowing of herbage, with constraints related to grazing (e.g. time spent feeding, choice of feeding station, activity budget). Digestive processes (e.g. ease of digestion and turnover of digesta in the rumen) are generally dealt with in longer term studies (Fryxell, 1991).

The early work of Allden & Whittaker (1970) defined herbage intake in terms of the components of ingestive behaviour (intake per bite, rate of biting and grazing time). This work provided the basis for understanding the influence of sward structure on bite mass, the reciprocal relationship between intake per bite and rate of biting, and the effect of these on daily herbage intake. With the development of techniques for close control and manipulation of both sward and animals, a detailed knowledge base evolved of the plant-animal interface (Hodgson *et al*., 1994). However, extrapolation to practical grazing conditions has been limited (Taylor, 1993), largely due to spatial and temporal heterogeneity, and so animals need to make choices relating to landscape, vegetation community, patch and bite characteristics (foraging strategy) as well as to aspects related to digestion and time available for grazing (Gordon & Lascano, 1993). Although foraging behaviour is highly scale dependent (time, size and space) (Fryxell *et al*., 2001), it has been argued that the basic parameters of foraging strategy are essentially the same across a range of grazing conditions, suggesting that the understanding developed under controlled conditions can be applied in less controlled environments (Hodgson *et al*., 1997).

Bite mass is the most important determinant of daily herbage intake (Hodgson *et al*., 1994; Illius, 1997) and is primarily influenced by bite depth, since bite area is relatively less sensitive to variation in sward height or herbage mass. Variation in herbage bulk density may contribute independently to bite mass (Hodgson *et al*., 1994), although variation in sward height generates a wider range in intake per bite (Mitchell *et al*., 1991). Bite rate is generally negatively related to intake per bite, a consequence of the larger number of manipulative jaw movements (prehension and chewing) with increasing bite mass. Despite this negative association between bite rate and bite mass, the short-term rate of intake still tends to increase asymptotically with bite mass or sward height.

According to Poppi *et al*. (1987), the ability of the grazing animal to harvest herbage appears to be the most important factor limiting intake when intake is responding steadily with increase in bite mass, i.e. in the middle section of the asymptotic curve. This ability is influenced by sward structure and grazing behaviour (diet selection, grazing time, bite mass and rate of biting), characteristics strongly influenced by grazing management practices. Approaching the asymptote, nutritional factors such as herbage digestibility, the time feed stays in the rumen, and concentration of metabolic products appear to be important in controlling intake, although there is increasing evidence that non-nutritional factors may also operate at this level (Carvalho, 1997). In this context, grazing time is considered the link between the short-term rate of intake and daily forage intake of the grazing animal, since it may be constrained to some extent by rumination (related to diet characteristics) and idling time (related to animal factors such as nutritional status) (Hodgson *et al*., 1997). These general relationships appear to 'hold up' quite well for temperate pasture conditions, where plant size and the stem component of herbage growth are both small in comparison to tropical and sub-tropical forage species. In the tropics and sub-tropics sustainability is an important issue, but the requirement to meet human food needs should not be forgotten, thus an understanding of foraging behaviour and herbage intake should embrace productivity goals.

Cultivated pastures in the favourable tropics/sub-tropics

The pioneer work of Stobbs (1973a,b) and Chacon & Stobbs (1976) with cultivated tropical pastures indicated that the major animal factor influencing herbage intake was bite mass. However, in contrast to temperate pastures where variation in sward height strongly influences intake per bite, the major sward characteristics influencing bite mass and short-term rate of intake of tropical pastures were leaf mass, leaf-to-stem ratio and sward bulk density. These findings suggested that tropical and temperate swards are quite different and that tropical pastures would impose physical (behavioural) as well as chemical (nutritive value) constraints that would severely limit herbage intake and performance of grazing animals (Hardy *et al*., 1997). Little progress was made on the grazing ecology of tropical and sub-tropical pastures during the 1980's and 1990's, and it became generally accepted that tropical pastures only produced stemmy, low density, poor quality herbage, suitable only for low levels of animal performance (Hardy *et al*., 1997; Sollenberger & Burns, 2001).

This seems a rather simplistic generalisation of a complex problem, since the experimental treatments and protocol in Stobbs (1973b) were based on only two forage species (*Setaria anceps* cv Kazungula and *Chloris gayana* cv Pioneer). There was no sward structure control - simply a description of sward components for fixed regrowth periods. The general results presented by Stobbs (1973b) indicate quite clearly that during the time plants were vegetative and/or with little contribution of stem to herbage mass (2 and 4-week regrowth periods), bite mass was influenced by sward height/mass. This trend changed when swards were reproductive and/or stem and dead material altered sward structure significantly (6 and 8-week regrowth periods). Chacon & Stobbs (1976) produced a similar data set, with bite mass being highly correlated with sward height and/or mass at the early stages of the grazing process, when animals consumed mainly leaf. This changed towards the end of the grazing period, when stem and dead components were increasing in the grazing strata.

In all those situations, data sets were analysed with no distinction made between vegetative or reproductive state (Stobbs, 1973b), and/or within phases of the same grazing period (Chacon & Stobbs, 1976). It was concluded that leaf mass, sward bulk density and leaf-to-stem ratio provided a better expression of forage supply than grazing pressure i.e. herbage mass, and better explained variation in bite mass in 'tropical' pastures. However, it can be argued that the process should be studied in two ways: situations where swards are leafy, with low proportions of stem and dead material (e.g. most of the evidence available for temperate pasture conditions), and situations where swards are stemmy, with high proportions of dead material (e.g. reproductive and/or uncontrolled temperate and tropical swards).

Griffiths *et al.* (2003a,b), working with *Lolium perenne* (perennial ryegrass) and studying multiple patch choices offered to cows under controlled conditions, demonstrated that animals, in order to optimise their rate of herbage intake, preferred to graze on tall patches unless tallness reflected greater maturity (e.g. high stem content and/or bite effort). In this situation, preference switched to short immature patches. A similar response was reported by Prache *et al*. (1998) for grazing sheep. This indicates that for temperate pastures the distinction between leafy and stemmy sward conditions is also relevant, and suggests that when considered on an equivalent basis, temperate and tropical pasture species may similarly influence bite mass and herbage intake of grazing animals.

More recent experimental evidence with tropical species seems to support this argument. Sarmento (2003), working with *Brachiaria brizantha* cv. Marandu (a popular semi-prostrate forage species in Brazil) under tight sward state control (sward height maintained at 10, 20, 30 and 40 cm), reported causative relationships between short-term rate of herbage intake and sward height (Figures 1a,b,c &d). However, due to the long leaf laminae on the tallest swards (Table 1), increasing time per bite (Figure 1e) resulted in a reduction in rate of intake (Figure 1f) regardless of the greater bite mass, implying that even when there was no limitation in herbage allowance (Table 1) or chemical composition (85% leaf, 12.5% CP, 61.7% NDF, 65% IVOMD - Andrade, 2003), behavioural factors restricted herbage intake.

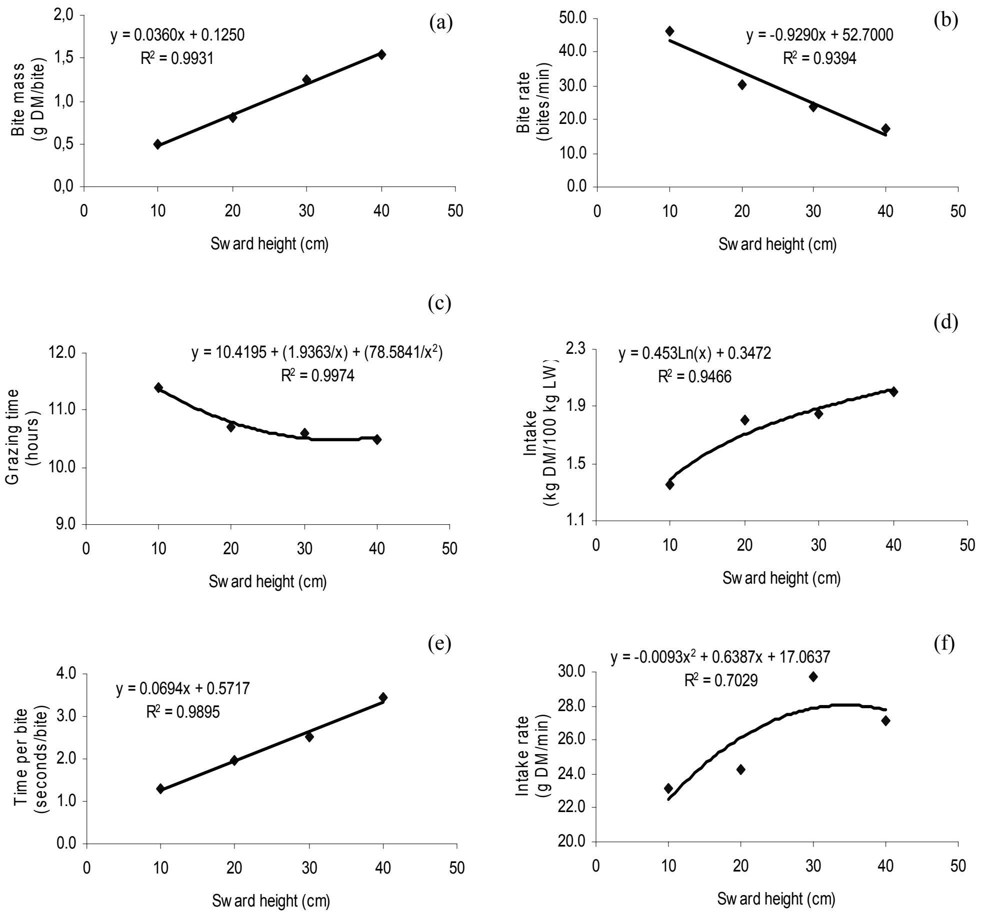

Figure 1 Grazing behaviour and herbage intake of beef cattle heifers grazing *Brachiaria brizantha* cv. Marandu pastures maintained at 10, 20, 30 and 40 cm sward surface height by continuous stocking and variable stocking rate (adapted from Sarmento, 2003)

Table 1 Sward structural characteristics of *Brachiaria brizantha* cv Marandu swards maintained at 10, 20, 30 and 40 cm by continuous stocking and variable stocking rate – summer period (December to March)[1]

Characteristic	Sward surface height (cm)				
	10	20	30	40	SEM[2]
Herbage mass (kg DM/ha)	4630	8210	11920	14420	512
Leaf-to-stem ratio	0.72	0.84	0.78	0.69	0.08
Total bulk density (kg DM/ha per cm)	460	410	400	360	31
Leaf bulk density[3] (kg DM/ha per cm)	150	130	120	90	10
Leaf lamina length[4] (cm)	10.3	14.9	19.1	20.6	0.29

[1]Molan (2004); [2]Standard error of the mean; [3]Top 50% of sward height; [4]Sbrissia (2004);

Animal performance was more related to intake (Table 2) than to the nutritive value of the herbage, since there was no difference in chemical composition of the ingested herbage and animals grazed a relatively constant proportion of sward height (top 33% - Gonçalves, 2002). Under these circumstances, herbage mass increased with increments in sward height, but herbage bulk density decreased (Table 1). However, variation in leaf bulk density (top 50% of sward height) was relatively small (150 to 90 kg DM/ha cm - Molan, 2004), suggesting that variations in bite mass were mainly due to variations in depth of the leaf lamina and/or grazing strata and characteristics of individual leaves (e.g. lamina length, mid rib diameter and shearing force).

Table 2 Daily herbage intake[1] and performance[2] of beef cattle heifers grazing *Brachiaria brizantha* cv Marandu swards maintained at 10, 20, 30 and 40 cm by continuous stocking and variable stocking rate – summer period (December to March)

Variable	Sward surface height (cm)				
	10	20	30	40	SEM[3]
Herbage intake (kg DM/100 kg LW per day)	1.3	1.8	1.8	2.0	0.07
Live weight gain (kg/animal per day)	0.19	0.51	0.75	0.93	0.10

[1]Sarmento (2003); [2]Andrade (2003); [3]Standard error of the mean

Similar evidence has been generated from grazing experiments with *Panicum maximum* cv Mombaça, a tall tussock-forming tropical species. Silva (2004) studied the short-term rate of herbage intake of dairy heifers grazing Mombaça grass pastures, and found that bite mass decreased and bite rate increased with decreasing pre-grazing sward height (Figure 2a,b). Despite the greater bite mass in taller swards, time per bite increased (leaf lamina length around 70 cm) and intake rate decreased (maximum around 100 cm sward height) (Figure 2c,d). Further, as pre-grazing sward height decreased, the number of feeding stations increased and the number of steps between feeding stations decreased (Figure 2e,f), showing the importance of controlling and manipulating sward structure (Table 3).

Table 3 Sward structural characteristics of *Panicum maximum* cv Mombaça pastures intermittently stocked and grazed down from 60, 80, 100, 120 and 140 cm pre-grazing sward surface height by dairy heifers[1]

Characteristic	Sward surface height (cm)					
	60	80	100	120	140	SEM[2]
Herbage mass (kg DM/ha)	7570	9130	11060	13130	17250	1080
Leaf-to-stem ratio	0.48	1.07	1.47	1.06	1.37	0.39
Total bulk density (kg DM/ha per cm)	126	114	110	109	123	13
Leaf bulk density (kg DM/ha per cm)	21	36	43	44	54	5
Leaf lamina length (cm)	22.2	48.8	62.7	65.5	66.5	3.8

[1]Silva (2004); [2]Standard error of the mean

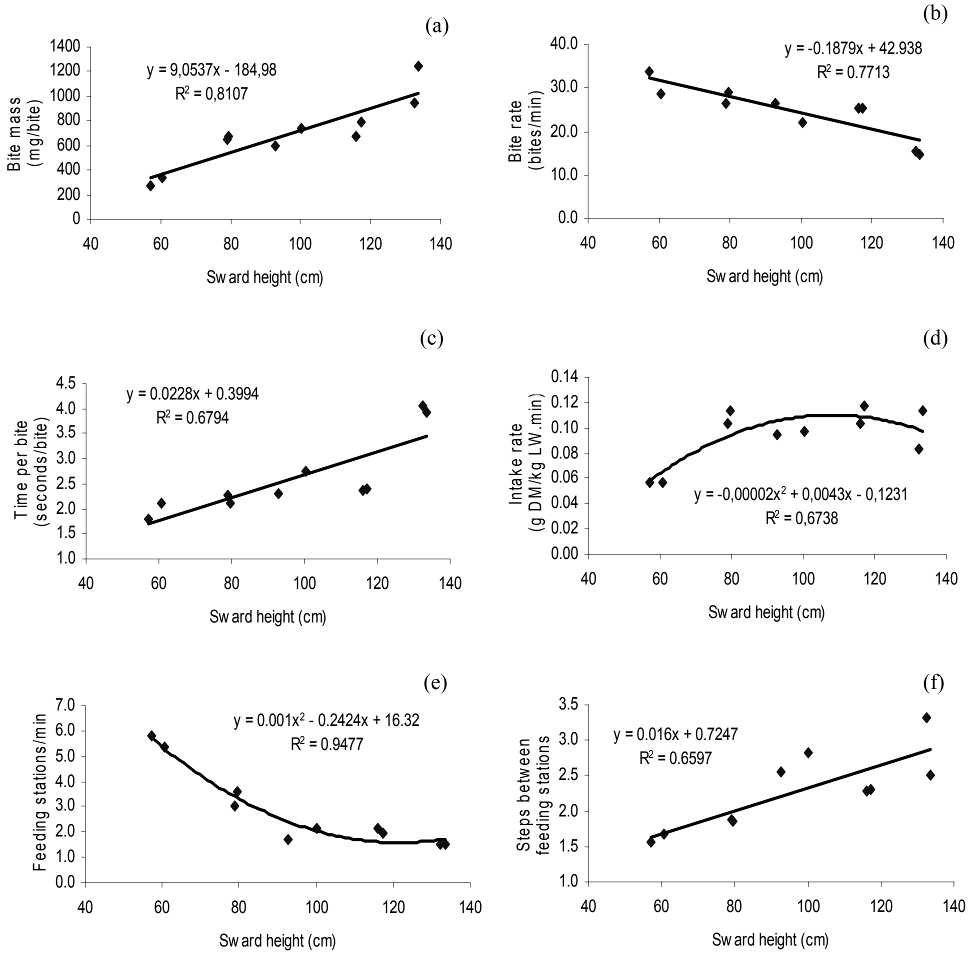

Figure 2 Grazing behaviour and short-term rate of herbage intake of dairy heifers during the grazing down process of intermittently defoliated *Panicum maximum* cv Mombaça pastures (Adapted from Silva, 2004)

The results reported for herbage and leaf bulk densities in these two studies (Tables 1 and 3) are within the range of values for temperate pasture species (Sollenberger & Burns, 2001), and are higher than those from Stobbs (1973b) (14-98 and 12-43 kg DM/ha per cm respectively). This suggests that there may be more similarities than differences between tropical/sub-tropical and temperate pasture species than otherwise implied, the main difference being stem elongation during vegetative development and its contribution to herbage bulk density.

Plant developmental responses have also been found to be closely related to manipulation of sward conditions, indicating the potential use of sward targets as a means of managing animal production on tropical and sub-tropical pastures (Hodgson & Da Silva, 2002). Carnevalli (2003), studying the dynamics of regrowth in Mombaça grass pastures rotationally grazed by dairy cows at either 95 or 100% canopy light interception (LI), found that leaf accumulation was the predominant growth process during the early stages of regrowth, until the canopy intercepted 95% of the incident light (leaf lamina length around 70-80 cm). From this point onwards, leaf accumulation decreased and stem and senescent material accumulation increased (Figure 3), indicating that regrowth in tropical/sub-tropical grass species is a two-stage process, and that control of stem development could be effectively achieved by monitoring and management of sward structure, particularly via grazing frequency. Overall, annual production (26900 kg DM/ha – Carnevalli, 2003) and nutritive value of the herbage produced (11.5% CP and 60% IVOMD – Bueno, 2003) were higher for the 95% LI pre-grazing condition, with losses due to grazing being higher for the 100% LI treatments (25.9% - Carnevalli, 2003). There was a high correlation between light interception and sward height (0.84), with 95% LI being consistently reached at 90 cm (leaf horizon) throughout the year, regardless of the physiological state of plants and post-grazing residues used (30 and 50 cm).

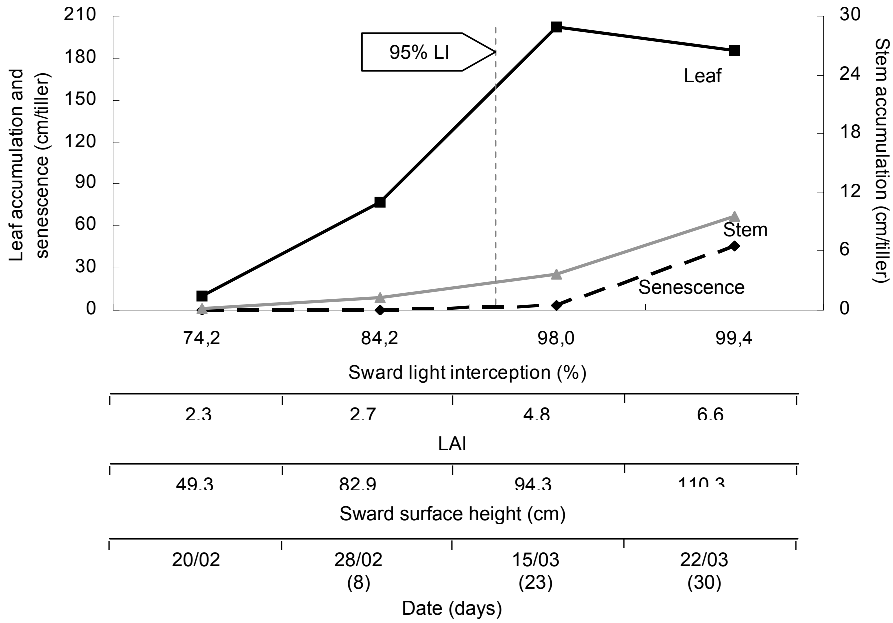

Figure 3 Dynamics of herbage accumulation during regrowth of Mombaça grass grazed at 100% sward light interception and post-grazing residue of 50 cm (from Carnevalli, 2003)

Apparently, the same pre-grazing sward condition that would optimise herbage production and nutritive value would also maximise herbage intake rate for this forage species (Figure 2d). Additionally, such a tall tufted-growing forage species would have high herbage and leaf bulk densities (Table 3), conditions that would likely favour animal performance. The results of Martinichen (2003) support this assumption, since dairy cows grazing Mombaça grass exclusively (and offered the same herbage allowance from sward structures similar to the recommended targets above) produced 13.5 to 15 kg milk/cow per day. In this case there was no difference in total herbage intake but ingestion of leaf varied, indicating that sward structure may operate independently in defining leaf accessibility.

These findings reveal a considerable potential for animal production and highlight the need for reviewing the generally held concept that tropical forages are of low feeding value. They also suggest that non-nutritional factors like leaf size (e.g. lamina length) might operate even in conditions where feed quantity is not limited (e.g. herbage mass, leaf mass, leaf bulk density), and interfere with herbage intake by increasing the need for manipulative jaw movements, and as a consequence, decrease the rate of intake of the grazing animal.

Efforts to describe sward vertical structure are usually made by quantifying each morphological component in 'volumetric layers' on a DM basis (e.g. mg DM/cm^3 or kg DM/ha per cm). The challenge at this scale is how to characterise the sward structure that animals actually respond to (e.g. size, shape and spatial distribution of individual components like leaf and stem). The wide range of herbage mass in *Brachiaria brizantha* (4630 to 14420 kg DM/ha) accounted for differences in leaf bulk density of only 60 kg DM/ha per cm (0.6 mg/cm^3) (Molan, 2004), indicating that the cropping process could not be understood or predicted from sward structure being described only on a DM basis. In short and tall managed *Brachiaria brizantha* and *Pennisetum americanum* (L.) Leeke (pearl millet) pastures, leaf lamina length can be increased two-fold (Sbrissia, 2004), or even five-fold (Castro, 2002). Thus, if the grazing layer does not change significantly in terms of leaf bulk density, the number of grazed leaves will decrease with increasing sward height, and animals will be forced to graze leaves individually when swards are very tall. This was observed with lambs grazing *Pennisetum americanum* (Castro, 2002), hoggets grazing *Panicum maximum* cv Tanzânia (Carvalho *et al*., 2001) and Holstein heifers grazing *Panicum maximum* cv. Mombaça (Silva, 2004). Despite the importance of leaf lamina length to the intake process, the sward condition from which animals would start grazing leaves individually for different tropical grass species remains to be determined.

The basis of the functional response in grazing herbivores (i.e. the relationship between intake rate and herbage availability) is the response of bite mass to herbage mass, with the asymptotic part of the curve being explained by saturation of the grazing process (Gordon & Lascano, 1993). When focus is concentrated at the leaf lamina level, it becomes clear that not only bite dimensions and dynamics of jaw movements contribute to the functional response, but also the structure of the leaf lamina itself plays an important role. In tropical grasses, as sward height increases, leaf lamina length increases linearly, while increase in leaf mass per unit leaf lamina length is quadratic (Castro, 2002; Silva, 2004). This indicates that (i) the ascending section of the functional response curve is not strictly a function of increasing bite volume; (ii) a progressive decline can be expected in the rate of mass acquisition per unit of bite volume from tall swards, when leaf mass per unit of leaf lamina length reaches a plateau; and (iii) for tropical/sub-tropical species, it is important to describe leaf lamina structure more precisely in order to develop our understanding of the grazing process.

Non-cultivated pastures in the favourable tropics/sub-tropics

Animals grazing non-cultivated pastures face a much more diverse and variable foraging environment. The magnitude of this spatial and temporal variability and the interaction between them usually create a large mosaic of patches that, in turn, vary in time and space (O'Reagain & Schwartz, 1995). Animals deal with this condition by continuously sampling the environment and learning about it (Provenza & Launchbaugh, 1999). In this process they also remember preferred patches (Dumont & Gordon, 2003), and integrate information about their internal state with that of the changing environment (Laca, 2000). In cultivated pastures, heterogeneity is significantly lower and spatial scale seldom extends beyond patch level.

Consequently, cultivated, as opposed to non-cultivated pastures, are better suited to testing hypotheses concerning the grazing process.

Despite the large area occupied by natural grasslands (around 78 million ha) and its importance to animal production in Brazil, there is a paucity of research about the ecosystem and its dynamics. However, studies on *campo nativo* in southern Brazil (Campos biome) are starting to provide knowledge on the ecology and management of native pastures. Vegetation in these areas is highly complex and characterised by the co-existence of more than 30 forage species/m^2 (Boldrini, 1993), differing in structure, quality and metabolic pathway (C_3 and C_4). Herbage intake rate is a function of vertical as well as horizontal heterogeneity in varying scales, integrating biotic and abiotic factors that determine large differences between potential and actual bites and/or in spatial distribution of these bites. In such an environment, tufted grasses increase their abundance according to grazing pressure and can comprise more than 50% of ground cover at low grazing intensities, and less than 5% at high grazing intensities. Tufted grasses may represent a forage resource depending on the availability of preferred species (Soares, 2002), and so the concept of 'forage' itself may be quite variable, and represents an additional challenge to the characterisation of the grazing environment.

The spatial heterogeneity of non-cultivated pastures is known to impact on the grazing process. In a double strata sward structure (typical of certain zones of the Campos biome) grazing time decreased by 66.7 minutes per cm increase in inter-tussock vegetation height (Pinto, *pers. comm.*).. In these circumstances, total pasture herbage mass increased with decreasing grazing pressure, a result of a more pronounced increase in herbage mass of the tussock in relation to the inter-tussock vegetation. This indicates that the usually high correlation found between herbage mass and time spent grazing on a patch in cultivated pastures, is not necessarily applicable to non-cultivated pastures. This is one reason for the lack of accuracy in predicting patch residence time from herbage mass data only (Santos *et al.*, 2003).

Inter-tussock vegetation cover decreases from 100 to 67% when grazing pressure increases from 8.8 to 25 kg LW/kg DM per day, although the actual grazing intensity at the inter-tussock vegetation remains similar (Goret, 2005). This indicates that grazing behaviour depends on the dynamics of the inter-tussock/tussock vegetation cover, and responds predominantly to inter-tussock vegetation characteristics in a similar manner to the model proposed by Gordon (2000) for complex communities dominated by *Nardus stricta*. Consequently, it seems important to establish causative relationships between inter-tussock characteristics and animal responses. Thus Gonçalves (unpublished data) created controlled inter-tussock areas with sward height varying from 3 to 18 cm, and verified that grazing behaviour responses were similar to the classical responses reported for animals grazing cultivated pastures. Under those circumstances bite rate decreased, as did the number of feeding stations visited when inter-tussock sward height increased. Response of short-term rate of intake was quadratic, with a maximum at 13 cm (11.6 g DM/min – heifer beef cattle). At 18 cm, it was reduced to 6.6 g DM/min, a consequence of an increase in reproductive structures and their influence on the grazing process. Although tussock vegetation cover has a minor direct influence on the herbage intake of grazing animals, it represents a dry matter reserve that can be used depending on the type and class of the animals, inter-tussock characteristics, time of the year etc. Moreover tussock vegetation, are areas of high plant diversity (Goret, 2005), and some species only flower when protected by the tussocks.

In the Pantanal, a biome situated in central-west Brazil and characterised by periodical floods, Santos *et al.* (2003) evaluated the grazing behaviour of beef cows from bite- to home range scale studies. She concluded that animals tended to maximise herbage intake rate by selecting patches containing preferred species with the highest crude protein and the lowest neutral detergent fibre content. Similarly Boggiano (1995) demonstrated that in Campos, steers show preference for plants that can be easily accessed or prehended. The main characteristics associated with preference were: (1) leaves with low resistance to fracture, (2) herbaceous texture, (3) leaves with medium width, and (4) leaf laminae with a flat ('open') cross-section, as opposed to those that are folded or rolled around the mid-rib. *Paspalum notatum* and *Paspalum plicatulum* (typical inter-tussock species) were preferred against *Aristida jubata* (typical tall tussock species). However, the possibility of diet selection, even in heterogeneous native pastures, depends on herbage availability, being increased with increasing herbage allowance (Boggiano, 1995; Piaggio, 1994).

Sheep and cattle consistently select a better quality diet than that of the herbage available (Montossi *et al*., 1998). Generous allowances however, are not necessarily related to high rates of herbage intake. Piaggio (1994) showed a decrease in herbage intake rate from 590 to 370 g OM/steer per hour with increasing herbage allowance, probably due to the significant increase in pasture heterogeneity as a consequence of the too generous allowances used. This illustrates the difficulty in determining available herbage in such a diverse natural pasture, and makes predictions from models developed for simple swards difficult. Further, it highlights the need for specific, planned efforts to generate knowledge and understanding relating to the ecosystem, and its potential development for sustainable pastoral systems.

Implications and perspectives

The tropical/sub-tropical environment is unique, requiring creative and site-specific solutions to overcome production constraints in order to realise its potential. The range of plant species, their varying size, morphology and physiology highlights the need to review some of the concepts and general views relating to animal performance from these pastures. Recent experimental work on pasture ecophysiology and grazing ecology in Brazil has been conceived under the conviction that control, monitoring and manipulation of sward state is an important feature for the establishment of meaningful cause and effect relationships to understand plant, animal and plant-animal responses to grazing management. This is very different from the traditional and simplistic view of production, in which control of the grazing process is made by means of fixed stocking rates, herbage allowances, grazing intervals and grazing method (Carvalho, 1997; Nascimento Jr *et al*., 2003), and allows for significant variation in sward state and/or structure.

Although limited, evidence generated under these conditions clearly demonstrates that tropical/sub-tropical forage species can support high stocking rates during spring and summer (seasonality of production), and produce herbage of sufficiently high quality to ensure satisfactory animal performance throughout the year. Low quality herbage during the winter period (Hardy *et al.*, 1997) can be a result of inefficient harvest during previous favourable growing seasons and is not necessarily an intrinsic characteristic of the herbage produced. Additionally, non-nutritional factors have a greater relative importance than nutritional factors regulating herbage intake of grazing animals.

In general, pastures need to be grazed more frequently than traditionally in order to generate sward control and optimise herbage production and nutritive value (quantitative restriction). At the lower end of the herbage abundance scale (controlled swards) the response of short-term rate of intake to variation in sward conditions follow a similar pattern to that of temperate pasture species, but with one significant difference - long leaf laminae can result in a reduction in herbage intake rate. However, when the main objective is animal performance and high herbage allowances are used (upper end of the herbage abundance), utilisation is low and stemmy and dead material accumulate. In this situation, herbage intake/performance responses are related to sward leaf mass and leaf-to-stem ratio.

In this context, aspects relating to plant size, morphology, structure and distribution play an important role in determining time per bite, bite effort, the search for grazing patches and stations, and grazing time, indicating that careful control, monitoring and description of sward conditions should be essential features of experiments with tropical/sub-tropical forage species. Further, foraging behaviour variables should be considered as a family of interactive factors governing herbage intake and performance of animals grazing either tropical/subtropical or temperate pasture species. Hence a new window of opportunity is created for improving animal production from the available pasture-forming species, augmenting the benefits from breeding and the introduction of new, more productive and resilient forage species.

Animal production systems for tropical/sub-tropical pastures have an additional and significant constraint, i.e. the pronounced seasonality of herbage production. This generates variation in the feed supply-demand balance of the system between and within seasons of the year, which must be managed if sward control is to be achieved effectively. During periods of feed surplus, increasing stocking rate or conservation cuts is the most feasible action to take. Conversely, during periods of feed deficit, reduction in stocking rate and use of supplementary feeds are necessary. Either way, manipulation of stocking rate is a means of achieving sward control. Management practices like these have direct and indirect impacts on sward control, structure and animal performance that need to be known in order to allow for the correct planning and decision making process on a farm scale. In summary, management of tropical/sub-tropical grasslands should be based on the careful control and planning of sward state, with the objective of providing conditions for the construction of ecologically sound pastoral environments to optimise the harvest of nutrients through grazing and favour animal production.

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