Harry Stobbs Memorial Lecture: Can grazing behavior support innovations in grassland management?

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Abstract

Grazing is a fundamental process affecting grassland ecosystem dynamics and functioning. Its behavioral components comprise how animals search for feed, and gather and process plant tissues in different spatio-temporal scales of the grazing process. Nowadays, there is an increasing emphasis on grazing management and the role of the grazing animal on ecosystem services, concomitantly with a decreasing emphasis on grazing management generating animal production outputs. Grazing behavior incorporates both approaches, which are not necessarily dichotomist. It would provide the basis to support innovation in grazing systems. However, it is unclear how the significant knowledge, developed in this research area since the disciplines of Agronomy and Ecology began to interact, have supported creativity in grazing science. It seems there is a current gap in this context, which was a major concern of researcher leaders like Harry Stobbs. This paper pays tribute to him, reviewing recent grazing behavior research and prioritizing those studies originating in the favorable tropics and subtropics. New evidence on how pasture structure limits forage intake in homogeneous and heterogeneous pastures is presented. Pasture management strategies designed to maximize bite mass and forage intake per unit grazing time are assumed to promote both animal production and landscape value. To conclude, a Brazilian case study (PISA) is briefly described to illustrate how grazing behavior research can reach farmers and change their lives by using simple management strategies ("take the best and leave the rest" rule) supported by reductionist approaches applied in holistic frameworks.

Resumen

El pastoreo es un proceso fundamental que afecta la dinámica y el funcionamiento de los ecosistemas de pasturas. Sus componentes comprenden la forma cómo los animales buscan el alimento y lo ingieren y cómo procesan los tejidos de las plantas en diferentes escalas espacio-temporales dentro del proceso de pastoreo. Actualmente existe un énfasis creciente en el manejo del pastoreo y en el papel de los animales en pastoreo respecto a los servicios de ecosistemas, conjuntamente con el descenso del énfasis en el manejo de pastoreo con fines de producción animal. El comportamiento de pastoreo incorpora ambos enfoques, los cuales no necesariamente son dicotómicos; puede proporcionar la base para innovaciones en los sistemas de pastoreo. No obstante no es claro cómo los avances significativos del conocimiento en esta área de investigación, desde que las disciplinas de agronomía y ecología comenzaron a interactuar, han contribuido a la creatividad en la ciencia del pastoreo. Aparentemente existe un vacío en este contexto, y esto fue una de las preocupaciones principales de investigadores líder como Harry Stobbs. En el presente documento se rinde homenaje a este científico y se revisan las investigaciones recientes en comportamiento de pastoreo, priorizando estudios procedentes de zonas favorables del trópico y subtrópico. Se presenta una nueva evidencia de la forma cómo la estructura de una pastura limita el consumo del forraje tanto en pasturas homogéneas como heterogéneas. Se asume que las estrategias de manejo del pastoreo, diseñadas a maximizar el bocado y su ingestión por unidad de tiempo de pastoreo, son dirigidas a promover tanto la producción animal como el valor paisajístico. Para concluir, se presenta un estudio de caso en Brasil (PISA) que ilustra y describe brevemente cómo la investigación en el comportamiento de pastoreo puede llegar a los productores para contribuir a su bienestar solo con la adopción de estrategias sencillas de manejo (la regla del "tome lo mejor y deje el resto"), con el apoyo de enfoques reduccionistas que se aplican en marcos holísticos.

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Introduction

Harry Stobbs had a strong desire that results of scientific research would reach practicing farmers in the field and be adopted. He believed that most scientists worked to solve problems/issues identified by themselves, and that much knowledge generated did not turn into practice. As an outstanding researcher of issues at the plant-animal interface, he passed from this life too early in 1978. He lived during a transition period, where pasture studies, focused on the end product, were being expanded to include an understanding of underlying processes driving grassland ecosystem dynamics. His legacy on grazing behavior research appears to have been embraced more within temperate grassland research than in the tropics, where a knowledge gap still exists (da Silva and Carvalho 2005).

In the late 90s, agronomists and ecologists conducted grazing behavior investigations aimed at understanding plant-herbivore relationships and their influence on the sustainability and equilibrium of grassland ecosystems (Milne and Gordon 2003). Despite this advance, there are no clear examples of how grazing ecology research has produced innovations in pasture management (but see Gregorini 2012).

Nowadays, pasture management is no longer oriented primarily towards secondary productivity from the grassland (animal products), but has a multifunctional focus including the whole pasture ecosystem, i.e. processes involved in pasture production, utilization and sustainability (Lemaire et al. 2011). Kemp and Michalk (2011) stated that desirable outputs of new pastoral farming systems should be minimizing soil erosion from wind or water, delivering clean water into river systems, and maintaining a diversity of plants and associated species. This is the current reality in grassland research in most countries.

Accepting the importance of moving forward in this direction, it is worth mentioning that an interruption in the advancement of grazing behavior investigations appears to have occurred in order to support the emergence of innovations in pasture management, oriented towards secondary productivity. This is of particular concern in developing countries, where grazing livestock is an important provider of income and employment (Herrero et al. 2013). This disrupted continuum, when knowledge generated by research does not translate into technology benefiting farmers in the field, was a major concern for Harry Stobbs.

This review aims to pay tribute to Harry Stobbs by reviewing grazing behavior research that aims to support grazing management and secondary production in the favorable tropical/subtropical areas. A case study (PISA) is presented briefly in order to illustrate how grazing behavior research can be used to improve the lives of farmers in the field.

Grassland Science and the new context for grazing behavior

Grassland Science during the last century was oriented towards production systems, and the maximization of both primary and secondary production of pasture (Humphreys 2007). The main goal was to identify the potential productive boundaries, and the management tools to reach them. Maximizing profits and enhancing efficiencies in animal production on pastures were essential.

In the late 1980s, Grassland Science, in relation to grazing management, evolved from the debate on stocking rate, grazing methods and livestock production to focus on sward structure as a determinant of pasture productivity and the main connecting link between plant composition and animal grazing behavior (Hodgson 1985). Harry Stobbs led this research approach in tropical pastures, but greater advances were made with temperate pastures, because his premature death resulted in a termination of this research endeavor, until recently (see Benvenutti et al. 2008a, 2008b, 2009; da Silva et al. 2012; Fonseca et al. 2012).

This focus on the plant-animal interface required original approaches to understand causal relationships. The concept of ecological hierarchy adapted to grazing ecology introduced the different spatial and temporal scales of the grazing process (Senft et al. 1987). Bailey et al. (1996) functionally defined spatial and temporal scales based on characteristic behaviors that occur at different rates, so grazing behavior was investigated in a continuum from bite up to home range. The underlying relationships between plants and grazing animals have been investigated in relation to variations in behavior over time and space (Bailey and Provenza 2008). Provenza et al. (2013) pointed out that current behaviors are often consequences of past conditions, and that many consequences are delayed in time and distant in space. Those approaches were important to understand landscape utilization by the grazing animal, which is critical for management of rangelands and pastures.

Grazing systems are now being re-designed to link production with environmental management to meet the desired multifunctional aspects of grasslands (Kemp and Michalk 2007; Boval and Dixon 2012). Grazing management has been assessed in terms of reducing the

environmental impact of the most intensive systems, so the multifunctional role of the grassland ecosystem becomes an important component of grazing systems. Doré et al. (2011) presented this paradigm of ecological intensification, based on intensification in the use of the natural functionalities that ecosystems offer. In some way, this demand for a multifunctional role for pastures arose before grazing behavior research became a component of grazing management. Provenza et al. (2013) criticized the "reductionistic control of researchers" and their traditional inability to create innovative practices. In fact, the current grazing behavior research scenario is more complex. Kemp and Michalk (2007) stated that the achievement of desirable outcomes in grassland management that satisfy multiple objectives will require new areas of research that seek viable solutions for farmers and society. Whether grazing ecology can support these new outcomes is not totally clear, but there is evidence that grazing management, which promotes higher individual animal production (e.g. moderate grazing), fosters both environmental parameters (see Carvalho et al. 2011).

The atom of the grazing process: harvesting bites in homogeneous and heterogeneous pastures

Grazing is an essential component of pastoral farming, and affects ecosystem properties and functions (Carvalho et al. 2013). In general, grazing herbivores select plants and morphological components in order to optimize nutrient intake, as well as minimizing energy cost and intake of harmful phytochemicals.

Laca and Ortega (1996) defined bite as the atom of grazing. The grazing animal gathers thousands of bites throughout the day, which ultimately defines daily dry matter intake and animal performance (Figure 1).

Allden and Whittaker (1970) provided the mechanistic basis to study this process, first defining forage intake as components of grazing behavior, i.e. the product of bite mass, bite rate and grazing time. This classical paper was influential in underpinning the effects of pasture structure on intake, and describing the reciprocal relationship between bite mass and bite rate.

Grazing time was then depicted in terms of meal number and duration (Rook 2000), while daily dry matter intake was a consequence of intake per meal and the number of meals during the day (Gibb 1998).

Shipley (2007) argued the importance of bite scale, as it falls at the very bottom of the foraging hierarchy. Any systematic error grazing animals make in selecting bites will be compounded over days, seasons and lifetimes. With increasing time and spatial scales of the grazing process, the influence of abiotic factors in determining daily dry matter intake increases (Bailey et al. 1996). Therefore, grazing behavior is highly bite scale dependent (Fryxell et al. 2001).
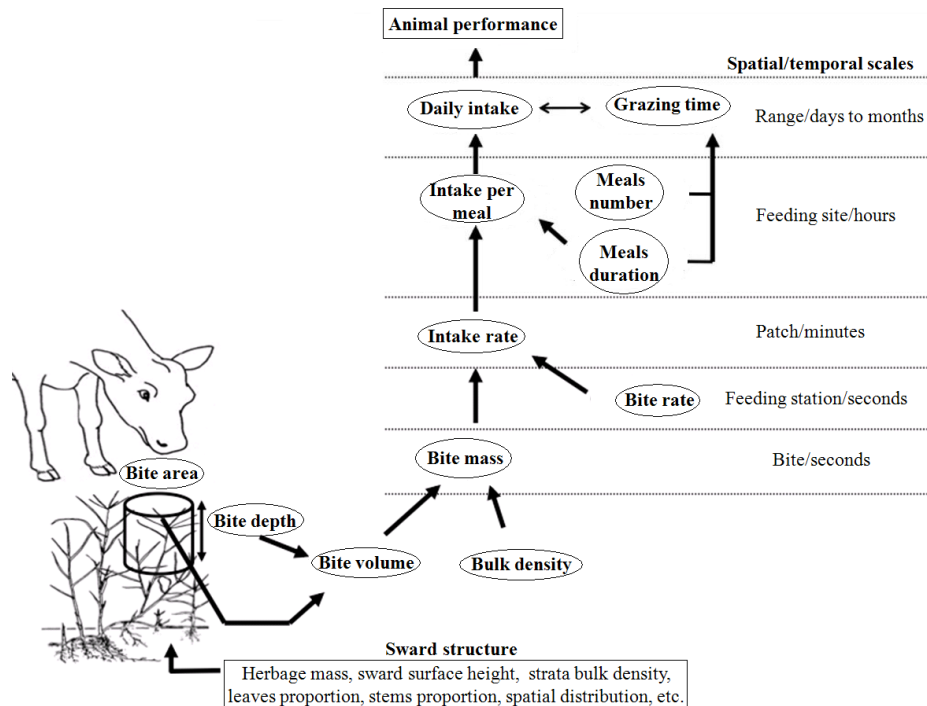

Figure 1. Spatial and temporal scales of grazing (adapted from Bailey et al. 1996; Cangiano et al. 1999; Bailey and Provenza 2008).

Spalinger and Hobbs (1992) developed a mechanistic model depicting intake rate as an asymptotic function of bite mass based on three processes of resource acquisition. Time per bite is described as a function of time committed to sever and process a bite. Bite mass is the only component of the grazing process that directly converts to plant biomass gathered, bite rate and grazing time being related mainly to the time scale (processing rates) of the grazing process.

There is an asymptotic relationship between plant biomass and intake rate in herbaceous grasslands (type II functional response, see Gross et al. 1993), because bite mass is usually correlated with biomass density (Shipley 2007; Hirata et al. 2010; Delagarde et al. 2011). The pioneer work of Stobbs (1973a; 1973b) and Chacón and Stobbs (1976) indicated bite mass was the major parameter influencing daily dry matter intake in tropical pastures. Stobbs (1973a; 1973b) highlighted the influence of bulk density in tropical pastures in imposing behavioral constraints that would severely limit forage intake. There has been little follow-up research on this aspect (but see Carvalho et al. 2001; Benvenutti et al. 2006; Hirata et al. 2010), and the prevailing idea is that lower animal production in tropical pastures is associated with low forage quality. Sollenberger and Burns (2001) reported that tropical pastures produce low-quality forage with high bulk density of pseudostems, and will support only low levels of animal performance. However, da Silva and Carvalho (2005) revisited this discussion and concluded that pasture structure was more important in constraining forage intake than previously supposed. In fact, basing pasture management on degree of canopy light interception and avoiding stem development has supported new management strategies (e.g. Montagner et al. 2012), resulting in unexpected high levels of animal production.

The meta-analysis presented in Figure 2 demonstrates novel evidence of how tropical pasture structure influences forage intake. The results suggest that grazing animals take more time to gather a given bite mass in tropical than in temperate pastures. The intercept of the model refers to the time to prehend the bite, independently of bite mass. The regression coefficient refers to the time to process a bite with increasing bite mass. There are many implications of these models in discussing the functional response of grazing animals, but for the purposes of this paper it is worth noting that tropical pasture structure is time jeopardizing. Consequently, the low daily dry matter intakes registered in animals grazing tropical pastures cannot be a function of only poor forage quality, as previously suggested by da Silva and Carvalho (2005). This is particularly significant when total foraging time cannot compensate for the higher time per bite demanded for biting tropical forages, a condition commonly observed in pastures with low forage masses or high-demanding animals.
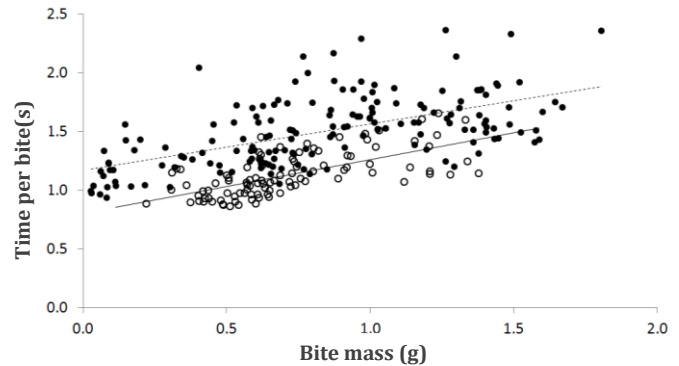

Figure 2. Temperate pastures (○, solid line): 1 – *Lolium multiflorum* (Amaral et al. 2013); 2 – *Avena strigosa* sward under continuous, and 3 – rotational stocking (Mezzalira 2012); 4 – *Lolium multiflorum*, *Avena strigosa* and avena + ryegrass mixture (G.C. Guzatti, pers. comm.). Tropical pastures (●, dotted line): 5 – *Cynodon* sp. under rotational, and 6 – continuous stocking (Mezzalira 2012); 7 – *Sorghum bicolor* under rotational, and 8 – continuous stocking (Fonseca et al. 2013); 9 – *Brachiaria brizantha* under rotational stocking (da Trindade 2007); 10 – natural grassland under continuous stocking (Bremm et al. 2012); 11 – *Pennisetun glaucum* under rotational stocking (Mezzalira et al. 2013a). Regression equations have been generated for each species in each experiment, and then compared by parallelism test and equality of intercepts ($P<0.05$). There are no differences between stocking methods in each group of pastures. Temperate pastures model: $y = 0.457x + 0.800$; $R^2 = 0.724$; $P<0.0001$; s.e. = 0.142; n = 98. Tropical pastures model: $y = 0.395x + 1.166$; $R^2 = 0.489$; $P<0.0001$; s.e. = 0.239; n = 185.

Carvalho et al. (2009) argued that pasture structure is both cause and consequence of the grazing process. Defoliation provokes differential tissue removal, altering vegetation competition and plant growth patterns; thus pasture structure is altered by defoliation. At the same time pasture structure determines defoliation patterns and forage intake, ultimately determining body condition and fitness of animals. In heterogeneous pastures, these cause and consequence relationships are more evident, contrasting structures being built by distinct grazing intensities (Cruz et al. 2010). Regardless of the scale-dependency of this heterogeneity (Laca 2008), a challenging environment results, where grazing animals constantly need to sample to be able to correctly perceive it.

Grazing animals face potential bites to be harvested in a vegetation continuum. Diet selection, as a result of

internal and external signals perceived by the animal (Gregorini et al. 2009a, 2009b; Villalba et al. 2009), determines which bites will be effectively gathered. The more complex the grazing environment, the greater the difference (beneficial) between the diet selected and the average botanical and chemical composition of the vegetation. Excessive grazing intensities decrease floristic and functional diversity in complex heterogeneous pastures, diminishing the difference between forage offered and selected. In this circumstance, grazing intensity determines that plant species with avoidance strategies are the only successful ones in the vegetation community. In contrast, moderate grazing promotes floristic and functional diversity, because defoliation patterns allow for a diverse community, comprising plant species with both tolerance and avoidance mechanisms (Briske 1999; Skarpe 2001).

The benefits of diversity are well known in terms of primary (Huyghe et al. 2012) and secondary productivity (Dumont and Tallowin 2011) in grassland ecosystems. Grazing animals respond positively to diversity and generally select mixed diets even when a unique diet is possible. This is classically demonstrated by the ryegrass-white clover model and the associated preference studies (Parsons et al. 1994a). However, there are fewer illustrations in natural heterogeneous pastures. In this context, bite diversity and its relationship with grazing management are illustrated by a long-term trial, where pasture structures resulted from various grazing intensities applied over 26 years. Biting behavior was described by visual assessment and classified, generating bite structural types (see Agreil and Meuret 2004, Figure 3).
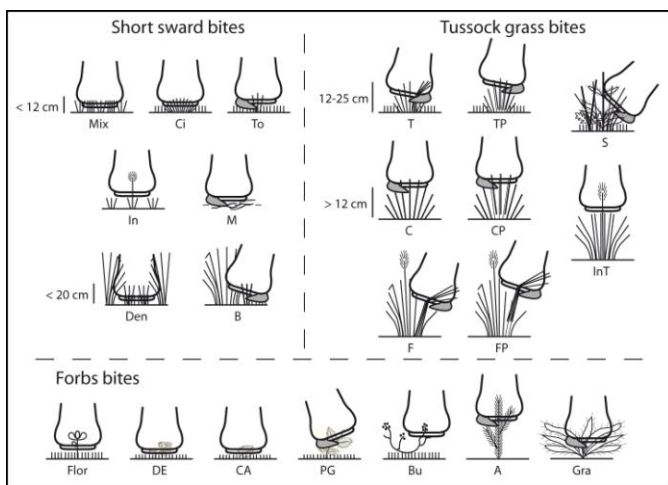

Figure 3. Bite types recorded for heifers grazing native Pampa vegetation in subtropical Brazil. Bite types attempt to separate bites based on the physical structure of the plant part consumed and on biting behavior. The codes for each bite type appear below the drawings and are used again in Figure 4.

The mass of each bite type is estimated by the hand-plucking method (Bonnet et al. 2011), so cumulative forage intake and diet selection can be described visually bite by bite. Figure 4 illustrates bite structural diversity and the associated range in mass observed at high (4% daily forage allowance) and moderate (12% daily forage allowance) grazing intensities.

Characteristics of vegetation communities resulting from grazing management determine the array of bite options potentially available to the grazing animal. At higher grazing intensities, bite diversity is lower (9 bite types among 33 species), as a consequence of decreasing species and vegetation structural diversity by overgrazing.
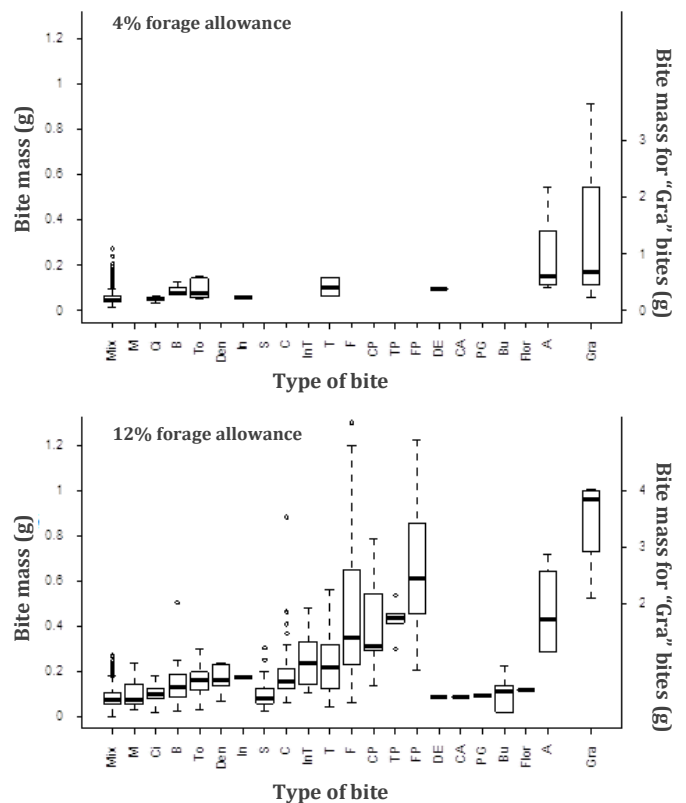

Figure 4. Comparison of the structural diversity of bites gathered by heifers in continuous stocking on native vegetation managed under low (4%, top) or medium (12%, bottom) daily forage allowance (kg dry matter in relation to kg live weight). The codes reported on the X-axis correspond with a classification of observed bites based on the physical structure of the plant part consumed (as illustrated in Figure 3). The Y-axes represent the range in bite mass assessed for each structural type of bite. Horizontal lines are median values; boxes include the central 50% of the bite mass distribution; and vertical dashed lines the smaller between the entire distribution and two standard deviations. The bite type "Gra" is out of scale and follows a different scale for bite mass reported on the right.

In contrast, moderate grazing promotes species and vegetation structural diversity, so grazing animals are able to gather 22 different bite types among more than 60 plant species (bite masses ranging from 0.01 to 4.025 g). Consequently, the possibility of acquiring nutrients and secondary plant compounds in order to consume an optimal combination of nutrients (Revell et al. 2008) is enhanced. Shipley (2007) reported the central role of bite masses offered by plants in determining intake rates within and among patches. Delagarde et al. (2001) reviewed bite masses of growing cattle in homogeneous temperate pastures and reported a maximum of 0.7 g per bite, in comparison with the 3.5 g of "Gra" bite type observed with moderate grazing in this example. It is worth noting that bite masses of the same bite type are higher at moderate grazing, reflecting plant structural benefits (i.e. plant height) by decreasing grazing intensity. Therefore, grazing animals under moderate grazing can gather bites of different types and higher masses. Under similar conditions, da Trindade et al. (2012) registered higher daily dry matter intake, and Carvalho et al. (2011) reported highest animal production, supporting the idea that grazing animals respond positively to the diversity of bite options.

Ingestive behavior generating tools for grazing management: homogeneous pastures

Assuming bite mass is the main determinant of intake rate, which in turn ultimately defines animal production, for purposes of grazing management it seems reasonable to define pasture management targets based on pasture structures that optimize bite mass. This situation applies particularly where output from pastoral farming systems is fundamentally oriented to animal production (but see Carvalho et al. 2013 for potential converging with environmental outputs), and based on homogeneous sown pastures. In this context a question emerges: what would be the best pasture structure to be offered to a grazing animal, assuming that bite mass is the main indicator of this condition? Figure 5 illustrates this reasoning.

The overall response patterns of bite mass and short-term intake rate to pasture height are similar, despite the two contrasting growth habits of the forage species and grazing methods (Mezzalira 2012). Bite mass and short-term intake rate are highly correlated and indicate similar optimal pasture structures. At low pasture heights, bite mass, and so intake rate, is constrained mainly by bite depth, which is well registered in the literature (Laca et al. 1992, 2001; Flores et al. 1993; Gregorini et al. 2011). At higher pasture heights, bite mass and intake rate decrease, a phenomenon less commonly registered.
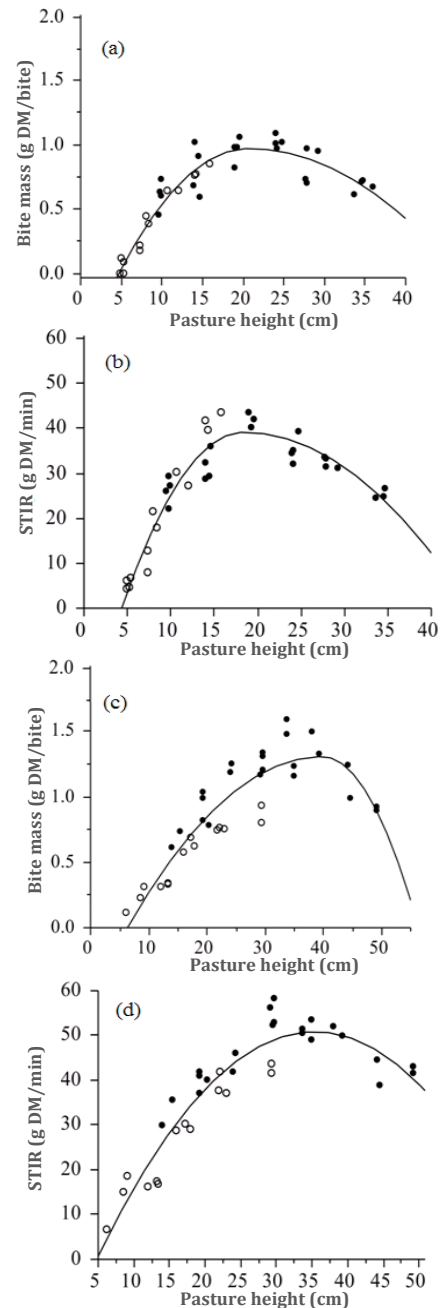

Figure 5. Bite mass and short-term intake rate (STIR) as a function of pasture height in four experiments: (a) and (b) with *Cynodon* sp.; and (c) and (d) with *Avena strigosa* under (o) rotational stocking, or (●) continuous stocking. Models: (a) *Cynodon* sp. – bite mass (mg DM/bite) = $0.97 - 0.003(20.64 - x)^2$, if x<20.64, or $0.001(x - 20.64)^2$, if x>20.64; P<0.0001; R^2 = 0.43; s.e. = 0.2379; n = 36; (b) *Cynodon* sp. – STIR (g DM/min) = $39.16 - 0.20(18.34 - x)^2$, if x<18.34, or $- 0.06(x - 18.34)^2$, if x>18.34; P<0.0001; R^2 = 0.65; s.e. = 6.9358; n = 36; (c) *Avena strigosa* – bite mass (mg DM/bite) = $1.31 - 0.0011(39.84 - x)^2$, if x<39.84, or $0.005 (x - 39.84)^2$, if x>39.84; P<0.0001; R^2 = 0.68; s.e. = 0.2235; n = 36; (d) *Avena strigosa* − STIR (g DM/min) = $50.86 - 0.05(35.39 - x)^2$, if x< 35.39, and $- 0.05(x - 35.39)^2$, if x>35.39; P<0.0001; R^2 = 0.78; s.e. = 6.1943; n = 36. (From Mezzalira 2012).

This fact is related to the increasing time per bite associated with decreasing bulk density in the upper pasture layers.

Stobbs (1973a; 1973b) described this process in tropical pastures, but not the fundamental cause. This phenomenon has been observed with similar response curves in other tropical pastures, e.g. *Panicum maximum* cv. Tanzania (Marçal et al. 2000), *Panicum maximum* cv. Mombaça (Palhano et al. 2007) and *Sorghum bicolor* (Fonseca et al. 2013), in studies aiming to define the optimal pasture structure for grazing animals. In the context of grassland management, this structural indicator defines the optimal pasture structure at the feeding station level for continuous stocking. Theoretically, average pasture height in continuous stocking would be in between the pasture currently being grazed (optimal height) and pasture recently grazed (~50% of optimal height, see above). This optimal average pasture height can be identified by protocols, where different pasture heights are maintained by continuous stocking and regression curves used to determine the optimal average height (e.g. da Silva et al. 2012). However, these types of grazing experiments are delineated at higher spatio-temporal scales and do not define the optimal pasture structure at bite/feeding station level.

In terms of rotational stocking, this optimal structure at bite level can be regarded as a target for pre-grazing structure of pasture. At bite level, there is no difference between grazing methods in the definition of the optimal structure, as shown in Figure 5. This probably indicates that tiller size/number compensation (Sbrissia and da Silva 2008) does not affect dry matter gathered in the same bite volume.

In contrast, with continuous stocking, where animals rarely bite in succeeding layers and there is no direct control of the defoliation interval, a second question emerges: what would be the best pasture structure to be left after a visit by the grazing animal? The underlying question regards the harvest efficiency definition and the characterization of an "optimal post-grazing pasture structure", which is highly correlated with animal production.

When animals enter a new paddock (e.g. strips in rotational stocking), there is a succession of potential bites available in succeeding layers (Ungar 1998; Baumont et al. 2004). Bites are taken progressively from upper layers to the bottom, each succeeding layer constraining bite volume by reducing bite depth and area (Ungar et al. 2001). Nutrient concentration in the bite volume decreases as the layer being grazed approaches the soil surface. This situation is analogous to the gain function, while an animal resides in a patch (see Marginal Value Theorem, Charnov 1976). Departure rules predicted by the model consider the decreasing intake rates experienced by the animal at patch level. This picture is similar to rotational stocking, except for the fact that it is the manager who decides departure time (i.e. change for a new strip). This decision defines post-grazing pasture structure. In general, the manager defines the period of occupation (residence time) and grazing density in order to increase harvest efficiency, so post-grazing masses are commonly very low.

Therefore, an anthropogenic point-of-view defines departure rules based on vegetation indicators under rotational grazing of domestic herbivores in agricultural systems. Carvalho (2005) proposed instead that animal ingestive behavior should define departure rules, mimicking animals' nature. This proposal is exemplified by Figure 6, where short-term intake rate is described along gradients of grazing down in relation to pre-grazing pasture structure (height).
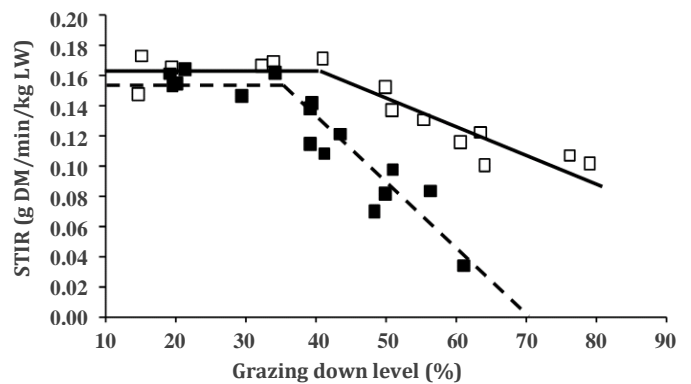

Figure 6. Short-term intake rate during the grazing down (% reduction of initial pasture height) in *Sorghum bicolor* (□; Fonseca et al. 2012) and *Cynodon* sp. (■; Mezzalira 2012). Initial pasture height and models: *Sorghum bicolor* − 50 cm; y = 0.16 + 0.001(40 - x), if x>40, and y = 0.16, if x<40; R^2 = 0.81; P<0.0001; EPM = 0.014; *Cynodon* sp. − 19 cm; y = 0.16, if x<37, and y = 0.16 + 0.006(37 - x), if x>37; R^2 = 0.73; P<0.0001.

Both experiments consider the initial pre-grazing pasture height would maximize bite mass and intake rate. Hence, when animals enter the paddock (beginning of the 'grazing down') and the first bites are taken, pasture structure is considered ideal and intake rate is at a maximum. Despite contrasting pasture structures, the overall response function was similar for the 2 pastures. As 'grazing down' progresses, short-term intake rate is initially constant, and then decreases linearly as forage mass is depleted. Short-term intake rate in *Cynodon* sp. pastures decreases at a faster rate, because succeeding layers are more restricting to bite formation than in *Sorghum bicolor*.

It is worth noting that the constancy in intake rate with the contrasting pasture structures is interrupted at similar depletion heights of the pasture (~40% reduction). This phenomenon is associated with pasture structural changes as a consequence of changing the availability of different plant morphological parts in lower grazing horizons. Preferred leaves become scarce and pseudostem, stem and dead material become predominant in succeeding lower pasture layers (Baumont et al. 2004; Benvenutti et al. 2006; Drescher et al. 2006).

Fonseca et al. (2013) demonstrated that the number of grazing jaw movements per unit dry matter ingested started to increase from the same point where intake rate started to fall (Figure 7). The results illustrate that animals encounter increasing difficulty in gathering bites as the residence time imposed by the manager in a pasture increases. After a forage depletion of ~40% of the initial pasture height, the efficiency of nutrient harvesting per unit time of bite formation decreases sharply.
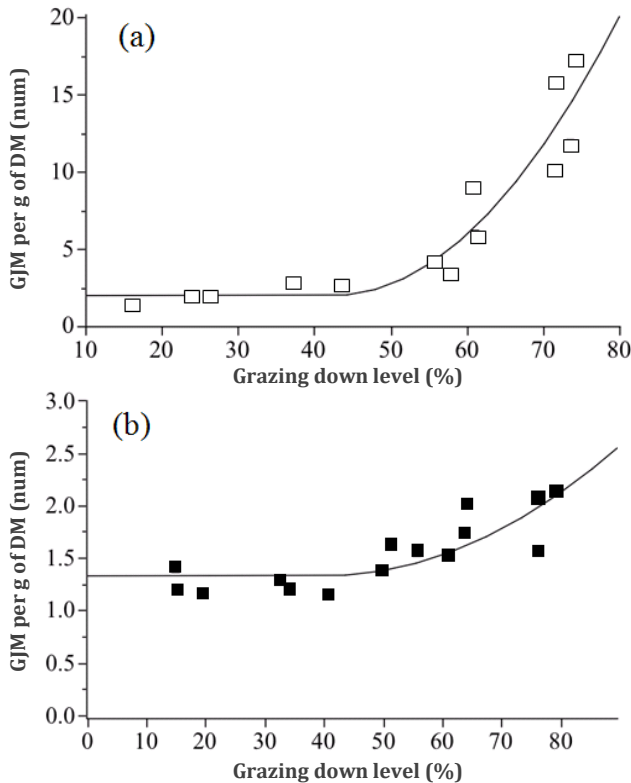

Figure 7. Grazing jaw movements (GJM) per g of dry matter (DM) during grazing down (% reduction of the initial pasture height) in: (a) *Cynodon* sp. (□; Mezzalira 2012); and (b) *Sorghum bicolor* (■; Fonseca et al. 2013). Initial sward surface height and models: *Sorghum bicolor* − 50 cm; y = 1.32, if x<40, and y = 1.32 + 0.0005(40 - x)^2, if x>40; R^2 = 0.636; P = 0.0004; s.e. = 0.20; n = 15; and *Cynodon* sp. − 19 cm; y = 1.97, if x<42.5, and y = 1.97 + 0.013(42.5 - x)^2, if x>42.5; R^2 = 0.898; P<0.0001; s.e. = 1.82; n = 13.

In general, the residence time of the animals is extended beyond this point in order to reach maximum harvesting efficiency levels (Figure 8), forcing animals to consume structural non-preferred items (Ginnett et al. 1999; Benvenutti et al. 2006; Drescher et al. 2006). A green leafy pasture regrowth is also mentioned as justification for this common management practice.
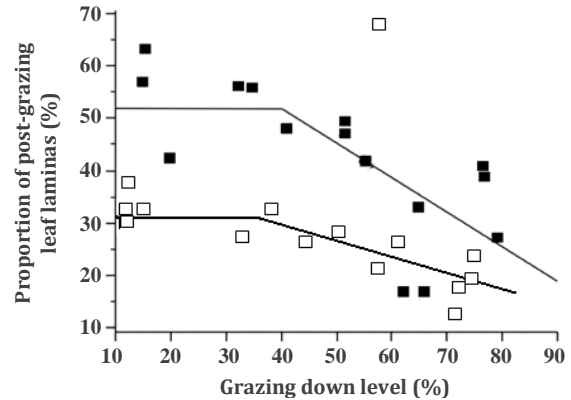

Figure 8. Proportion of leaf laminas in different proportions of grazing down in: *Sorghum bicolor* (■; Fonseca *et al*. 2012b); and *Cynodon* sp. sward (□; Mezzalira 2012). Models: *Sorghum bicolor* − 50 cm; y = 51.87 + 0.33(40 - x), if x>40, and y = 51.87, if x<40; R^2 = 0.50; P = 0.0044; s.e. = 10.55; n = 15; and *Cynodon* sp. − 19 cm; y = 31.93 + 0.45(31 - x), if x>31, and y = 31.93, if x<31; R^2 = 0.71; P = 0.0002; s.e. = 5.53; n = 14.

The issue of how many grazing horizons would be exploited is a matter associated only with rotational stocking, as animals rarely exploit succeeding grazing horizons in a grazing patch in continuous stocking, as previously mentioned. However, this discussion deserves attention, because rotational stocking is a grazing method where the managers mostly control the defoliation process. To address the dynamics and boundaries of the succeeding grazing horizons, it is necessary to refer to the defoliation process at tiller level.

Wade (1991) first demonstrated that animals defoliate tillers to a constant proportion of their height, which was verified by several authors (e.g. Laca et al. 1992; Cangiano et al. 2002), although Griffths et al. (2003) and Benvenutti et al. (2008a) found different responses under specific conditions. Figure 9 illustrates this phenomenon with different animal species grazing different pasture structures. Hodgson et al. (1994) referred to this singularity as the "concept of a constant proportionality of herbage removal". The mechanistic bases of this constancy are not totally understood, but probably are related to forces required to fracture stems (Griffiths and Gordon 2003; Benvenutti et al. 2008b).
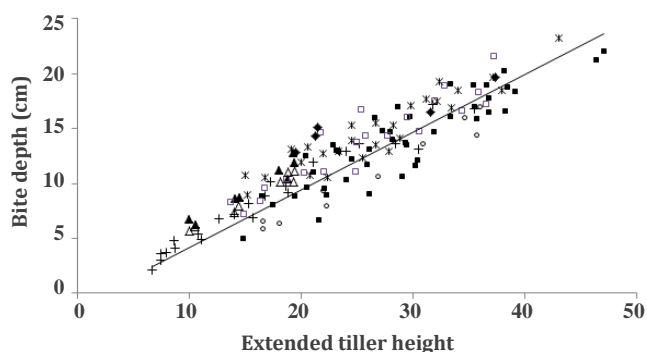
Figure 9. Relationship between bite depth and extended tiller height in: (Δ) sheep and (▲) beef heifers grazing natural grassland (Gonçalves et al. 2009); (♦) beef heifers grazing *Avena strigosa* (Mezzalira 2012); (■) beef heifers grazing *Brachiaria brizantha* (da Trindade 2007); (+) sheep grazing *Festuca arundinacea* and *Dactylis glomerata* (Carvalho et al. 1998); (○) horses in five cvv. of *Cynodon* sp. (Dittrich et al. 2005); (ж) ponies in *Cynodon* sp. and *Paspalum paniculatum* (Dittrich et al. 2007); (□) dairy cows in *Avena strigosa* (Lesama et al. 1999); (y = 1.1 + 0.52x; R^2 = 0.8391; s.e. = 1.9; P<0.0001; n = 203).

This particular biting behavior suggests the existence of grazing horizons, which was proposed by Carvalho (1997). According to Palhano et al. (2006), the highest grazing probability of the uppermost horizons is not a passive preference only. Bite mass is maximized in taller pastures as demonstrated by Laca et al. (1994). Thus pastures can be viewed as sets of superimposed grazing horizons (compartments of bites), with the probability of grazing the lowest horizons increasing as the uppermost layers are progressively grazed (Ungar and Ravid 1999; Baumont et al. 2004). Ungar et al. (2001) described this scenario by observing heifers taking bites from the uppermost grazing horizon, almost exclusively, until approximately three-quarters of its surface area had been removed. Fonseca et al. (2013) registered similar horizon use patterns with different pasture structures under field conditions. Figure 10 presents the changes in the short-term intake rate of grazing animals with the progressive diminution of residual non-grazed surface area during grazing down of pastures.

Data presented show intake rate is constant until two-thirds of the uppermost surface layer is grazed. It is assumed that the initial constancy in intake rate reflects animals gathering the maximum bite masses available in the uppermost layer (where higher bite depths are experienced). As grazing down progresses, average pasture height decreases, but animals continue to gather bites in previously ungrazed areas (bite mass almost constant), so intake rate remains constant despite pasture depletion (Carvalho et al. 2001). This situation persists until two-thirds of the first layer is harvested. At this point, it
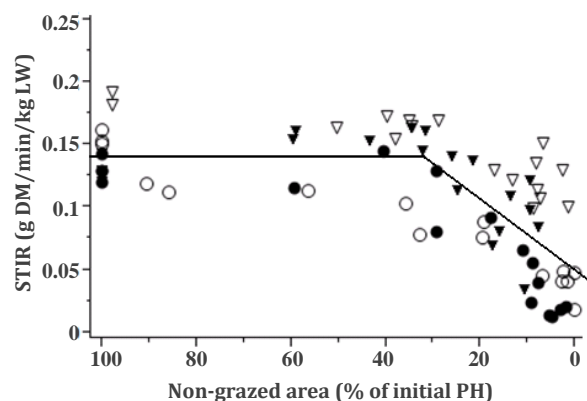

Figure 10. Changes in short-term herbage intake rate (STIR) with reduction in the proportion of non-grazed area [% of initial pasture height (PH), L. Fonseca, pers. comm.]: (●) dairy heifers in *Cynodon* sp. sward under continuous stocking; (○) beef heifers in *Avena strigosa* sward under continuous stocking; (▼) dairy heifers in *Cynodon* sp. sward under rotational stocking; and (Δ) beef heifers in *Sorghum bicolor* swards under rotational stocking. Model: y = 0.143, if x>31, and y = 0.143 - 0.003 (31 - x), if x<31; R^2 = 0.5566; s.e. = 0.03; P<0.0001; n = 71.

seems that the search for preferred ungrazed areas becomes unrewarding (searching costs sensu Parsons et al. 1994b), and grazing of the lower grazing horizon commences as its relative preference increases, as predicted by Baumont et al. (2004). The progression by animals to exploit different grazing horizons is probably not abrupt, but the large decrease in short-term intake rate after two-thirds of initial pasture height is depleted illustrates the huge decline in potential intake rates with succeeding grazing horizons.

The grazing management aspect that emerges from this discussion is: how long should animals stay on a pasture when the manager controls the departure rules? The earlier they are moved to a new strip, the higher is individual dry matter intake per unit time, but the lower is total dry matter intake per unit area. The longer they stay, the lesser the individual dry matter intake but the amount of forage harvested per unit area is greater. These contrasting goals of maximizing animal dry matter intake and pasture harvest efficiency highlight the fundamental ecological dilemma encountered in pastoral farming systems: the incapacity to reach both purposes of optimization simultaneously (Briske and Heitschmidt 1991). Consequently, for a manager to determine the optimal time when animals should depart from a strip under rotational stocking, which rule does the manager respect? In other words, do only pasture utilization goals define these management strategies?

The context presented here suggests ingestive behavior must be taken into account in defining grazing management, whether or not intake maximization is a

goal. However, it is important to remember that secondary productivity in pastoral systems ultimately supplies the income and not pasture harvested per se.

If one considers the statements of the Foraging Theory (Stephens and Krebs 1986) in relation to the natural behavior of grazing animals, optimizing nutrient consumption per unit time is a prime factor in animal behavior. In this sense, it seems reasonable to aim at mimicking natural behavior in order to optimize animal production in agricultural systems. However, optimizing individual animal intake has effects on post-grazing mass dynamics that need to be addressed.

Ingestive behavior generating tools for grazing management: heterogeneous pastures

Grazing behavior can provide behavioral indicators as a tool to quantify the value of "foodscapes" (sensu Searle et al. 2007). Among proposed behavioral indicators, bite formation and foraging velocity were described as animals' decisions directly determining intake rate, which in turn influence daily dry matter intake. Despite Searle et al. (2007) suggesting there were limitations in using vegetation indicators to assess landscape value, as herbivore species perceive the same parameters (e.g. forage mass) differently, Carvalho et al. (2008) argued that plant functional characteristics could provide an adjunct to behavioral indicators as bases for assessing landscape condition and management. Plant functional types and bite structural diversity are closely linked. For example, Cruz et al. (2010) demonstrated how leaf dry matter content and specific leaf area were indicators of overgrazing. In considering potential indicators for functional assessments in pastoral ecosystems, and assuming pasture structure is simultaneously both cause and consequence in the grazing process, ingestive behavior would be considered a short-term indicator, while sward structure behaves as a long-term indicator of landscape value and ecosystem functioning (Carvalho et al. 2008).

Under continuous stocking, animals spend more time in grazing activities when pasture structure constrains intake (Pinto et al. 2007; Thurow et al. 2009). Animals generally increase their grazing time by decreasing the number of grazing meals and increasing the duration of each meal (Mezzalira et al. 2012a). Since meal duration is reciprocal to meal duration interval, low forage allowance provokes a decrease in the interval between meals. At very low forage allowances, Mezzalira et al. (2012a) reported only 3 daily meals, each one lasting on average 190 minutes, for heifers grazing heterogeneous natural pastures.

During a meal, animals adapt their grazing behavior in order to allocate more or less time to harvesting and searching for forage. Mezzalira et al. (2012a) reported that, at low forage allowances, 510 minutes were devoted to forage harvesting (83% of total grazing time), while at high forage allowances this activity was restricted to 271 minutes (57% of total grazing time). In contrast, the time devoted to searching for forage was restricted to 107 minutes at low herbage allowances (17% of daily grazing time), and more than 180 minutes (43% of daily grazing time) at higher herbage allowances. Studies by C.E. Pinto (pers. comm.), using GPS collars, indicate that in natural pastures being grazed at high grazing intensities (5 cm sward height), animals can walk 3.2 km compared with 1.7 km at moderate grazing intensity (19.4 cm sward height). It was estimated that animals might increase their energetic requirements by more than 25% in such a situation.

In response to different pasture structures, animals alter their dynamics of herbage acquisition, patterns of movement and use of feeding stations. Gonçalves et al. (2009) demonstrated bite mass was the main determinant of intake rate in natural grasslands. Considering the preferred inter-tussock strata, intake rate is maximized at heights around 10.0 and 11.5 cm for ewes and heifers, respectively (Figure 11). The authors reported that under intake-limiting conditions, both cattle and sheep visit a larger number of feeding stations, harvesting fewer bites and remaining less time at each feeding station, a behavior that is in agreement with the Optimum Foraging Theory (see Prache et al. 1998).

Further, animals move faster, but with fewer steps between feeding stations, indicating an attempt to increase the rate of encountering potential feeding stations. These behavioral responses change in the opposite direction as pasture characteristics become more favorable to herbage harvesting, reaching a similar plateau for each animal species.

These results indicate short-term intake rate is maximized at intermediate pasture heights. Thus, a question arises regarding vegetation dynamics in complex heterogeneous pastures, because intermediate levels of grazing intensity increase the frequency of less preferable plants and/or structures. Consequently, the frequency and distribution of non-preferred items in pastures can present a challenge to the grazing animal. Mezzalira et al. (2013b) reported that increasing forage allowance allows greater selectivity, and therefore an increase in non-preferred area (tussock frequency in Figure 12).

The number of non-tussock feeding stations decreases linearly with the increase in herbage allowance due to
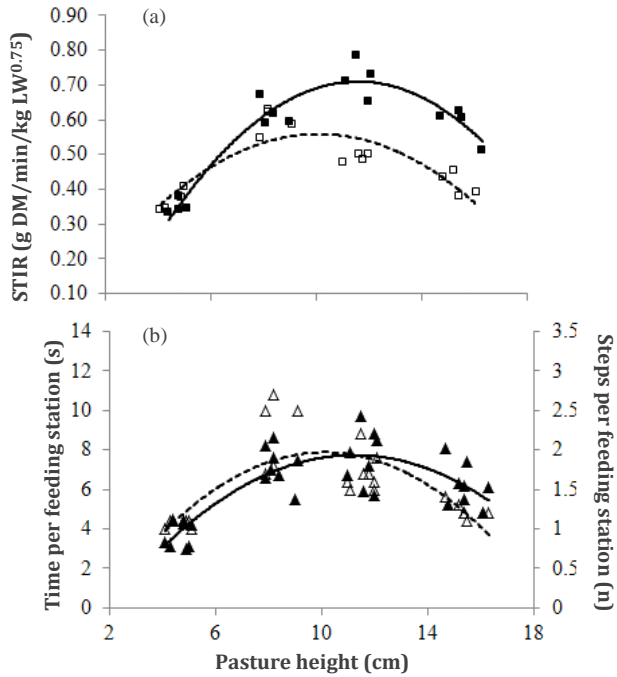
Figure 11. Short-term intake rate: (a) by heifers (■; Y = - 0.326 + 0.178x - 0.0077x^2; R^2 = 0.9229; SD = 0.04; P<0.001), and sheep (□; Y = - 0.016 + 0.113x - 0.0056x^2; R^2 = 0.7342; SD = 0.05; P<0.001); and (b) time per feeding station (▲; Y = 3.95 + 2.1x - 0.09x^2; R^2 = 0.6995; s.e. = 1.1; P<0.0001); and steps per feeding station (△; Y = -0.83 + 0.55x - 0.03x^2; R^2 = 0.6191; s.e. = 0.3; P<0.0001) by heifers and sheep in natural grasslands under different pasture heights (adapted from Gonçalves et al. 2009).
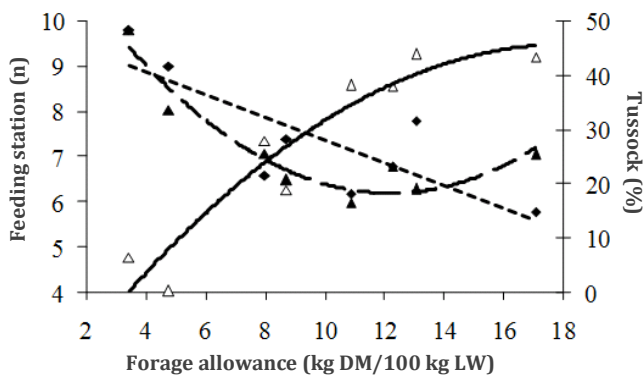

Figure 12. Frequency of tussocks (△) y = 28.6 + 8.71x - 0.279x^2; R^2 = 0.924; SD = 5.1; P = 0.036; number of feeding stations effectively grazed every 10 steps (▲) y = 12.38 - 1.003x + 0.041x^2; R^2 = 0.906; SD = 0.4; P = 0.005; and potential encounter rate of non-tussock feeding stations (♦) y = 9.85 - 0.248x; R^2 = 0.641; SD = 0.9; P = 0.017; of heifers grazing in natural grassland under distinct forage allowances (Mezzalira et al. 2013b).

an increase in tussock frequency. Initially, at lowest forage allowances, the number of effectively grazed feeding stations is similar to the number of encountered feeding stations, with practically no rejected feeding stations. With the increase in forage allowance, the proportion of feeding stations effectively grazed decreases, indicating that animals express higher selectivity in the choice of the feeding stations they used. Furthermore, the fact that the proportion of feeding stations effectively grazed decreases more rapidly than the potential encounter rate of non-tussock feeding stations (distance between the two dotted declining lines in Figure 12) reflects the additional cost for the animal of searching for preferred feeding stations during the selection process.

A slight increase in the proportion of effectively grazed feeding stations is noticed when forage allowance reaches 11%, which corresponds to a 6 cm pasture height. Then, a strong inversion occurs in those processes, until most of the feeding stations found along the path of displacement are used at 14% forage allowance (7.5 cm sward height), interpreted as a reduction in selectivity.

Mezzalira et al. (2013b) suggest this may be associated with the increasing percentage of tussocks, which is close to 40% at 14% herbage allowance. In fact, animal performance reaches a maximum at forage allowances of 12% (Pinto et al. 2008; Nabinger et al. 2011; Mezzalira et al. 2012b), and data from Bremm et al. (2012) support the conclusion that at tussock frequency above ~35%, intake rate of animals is decreased by the costs related to the time spent avoiding tussocks when searching for better feeding stations. However, this impact depends on the animal species, as evidence suggests that, for each 1% increase in frequency of tussocks, time spent grazing on the inter-tussock areas by heifers reduces by 0.6%, while the reduction by ewes is only 0.36% (Bremm et al. 2012).

The effect of frequency distribution of non-preferred food items upon the accessibility of the preferred diet item for grazing animals was studied by Bremm et al. (2012). Ewes adjusted their foraging strategies and maintained a constant short-term intake rate regardless of percentage of tussock cover. Beef heifers exhibited the highest short-term intake rate with 34% tussock cover (Figure 13).

Bite mass of beef heifers decreased when tussock cover increased above 44%, whereas no trend was detected for ewes. Data demonstrated that non-preferred items might act as a vertical and/or horizontal barrier, interfering with the process of bite formation and affecting bite mass of beef heifers.
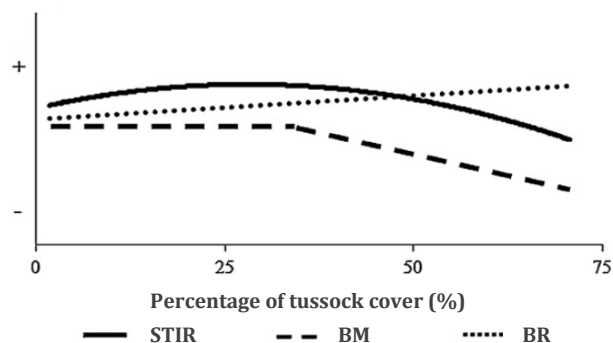
Figure 13. Grazing behavior patterns (STIR – short-term intake rate, BM – bite mass, BR – bite rate) of beef heifers grazing a natural grassland with distinct percentages of tussock cover of *Eragrostis plana*, assumed as the non-preferred food item (Bremm et al. 2012).

Considering the influence of pasture height of tussocks (non-preferred) and inter-tussock areas (preferred) in determining ingestive behavior in heterogeneous pastures, Figure 14 explores boundaries of pasture targets for continuous stocking and its impact on short-term intake rate.
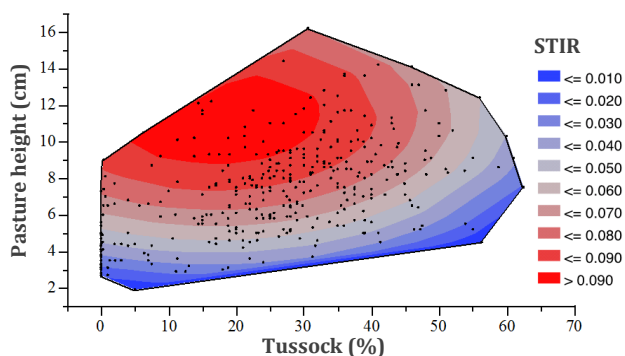

Figure 14. Relationship between tussock frequency (%) and inter-tussock pasture height (cm) in determining dry matter intake rate (STIR, mg DM/min/kg LW) of beef cattle grazing natural grasslands in southern Brazil. Data calculated from Goncalves et al. (2009) and Bremm et al. (2012).

It is assumed that short-term intake rate is well correlated with animal performance, and the frequency of tussocks and the inter-tussock pasture height as a model of the balance between non-preferred and preferred items, respectively. Response curves in Figure 14 show intake rate is depressed when pasture height is lower than 10 cm or tussock frequency is higher than 35%, with pasture height affecting intake rate proportionately in a more pronounceable form.

These boundaries are subsiding recommendations and support new management targets for natural grasslands

in southern Brazil. Formerly, tussocks were viewed only as undesirable components of natural grassland ecosystems.

Recent grazing behavior experiments have demonstrated that grazing animals use tussocks in order to gather strategic high bite masses throughout the day (see Figure 4), contributing to a diverse diet. Tussocks are good indicators of grazing intensity management, because they are normally associated with higher grazing intervals (allowing plant strategies for resource conservation typical of tussock plants, with low rates of herbage accumulation and high leaf life span). Hence, if moderate grazing is being recommended to foster both animal production and ecosystem services (Carvalho et al. 2011), it is inevitable there will be low levels of less preferred items. Formerly, farmers tended to cut tussocks in order to recover presumed wasted areas, regardless of tussock frequency levels. Nowadays, they are requested to interfere only when tussock frequency exceeds 35%, when there is a probability that animal production will decline.

Innovations in grazing management: From bites to farmers

According to van den Pol-van Dasselaar (2012), the popularity of pastoral farming systems based on grazing is declining in Europe. Labor is an important factor to consider, as average herd size is increasing, and large herds are difficult to manage. This explains why continuous stocking is attracting new interest in Europe, and at the same time illustrates the lack of innovation in grazing management.

Carvalho et al. (2013) reported a contrasting situation in the favorable tropics (i.e. Brazil), where new understanding of underlying processes at the plant-animal interface has resulted in recent improvements in animal production from grasslands. Da Silva and Nascimento Jr (2007) reviewed trends in grassland management towards the planning of sound and efficient management practices, and concluded that targets developed for tropical pastures based on pasture structure are changing paradigms related to grassland management. Canopy light interception and dynamics of forage accumulation are being linked with pasture targets and supporting new management strategies for both continuous and rotational stocking methods (e.g. da Silva et al. 2012; Montagner et al. 2012), so old forage cultivars are reaching new unexperienced animal production levels.

Besides, animal-based pasture targets oriented to maximize instantaneous intake rate for grazing dairy cows are being proposed to support new rotational stock-

ing strategies aiming to maximize the intake of herbage per unit grazing time (Fonseca et al. 2012). As presented earlier, grazing behavior research indicated pre-grazing pasture targets in order to optimize intake rate, which is maintained at a high level if pasture is not depleted more than ~40% of the initial pre-grazing pasture height ("take the best and leave the rest" rule, concept adapted from Provenza et al. 2003). In order to illustrate how these insights can support pasture management at a farm level, a successful extension program named PISA (Produção Integrada de Sistemas Agropecuários[1]), currently being applied in Brazil, is briefly described.

PISA is a sustainable intensification production model oriented to increase food production at farm and landscape levels, based on sustainable pillars as no-till conservation agriculture, animal welfare, integrated crop-livestock systems, traceability and certification of farm products, among other good farming practices. It is not oriented to any specific agricultural sector, and its ambition is to diminish environmental impacts, while enhancing food security in the context of sustainable intensification.

In southern Brazil it involves mainly small-scale dairy operations, encompassing presently 575 families in 25 municipalities, which are the dominant farm type. In general dairy cows are fed maize silage + concentrate (60−70% of the diet) and annual temperate (mainly *Lolium multiflorum* and *Avena strigosa*) or tropical (mainly *Sorghum bicolor*, *Pennisetum glaucum* and *Cynodon* sp.) pastures (30−40% of the diet). On average, farmers milk 14 cows, for a total daily milk production of approximately 150 liters.

Many management interventions have been implemented during the 3-year duration of PISA, but modifications in grazing management have produced the most important short-term effects. In general, pastures are managed under rotational systems, with fixed resting periods designed to favor biomass accumulation. The period of occupation and stocking density are oriented to maximize forage harvest efficiency so as to use all forage accumulated. Post-grazing forage mass is viewed as waste. Two daily milking periods, occurring prior to dawn and to dusk, restrict grazing time (see consequences in Chilibroste et al. 2007; Mattiauda et al. 2013).

PISA modifies the prevailing production pattern and aims to make pastures the main nutrient source for animals. Grazing management is modified in order to enhance animal nutrient consumption per unit time. The basis for this strategy is ingestive behavior (pasture structure that maximizes bite mass), as mentioned earlier. Pasture management targets are defined to optimize dry matter intake rate, assuming that nutrient consumption is optimized at the same time. Pre-grazing and post-grazing pasture heights are defined so cows can always ingest forage at the highest intake rates, making maximum use of the few hours animals can devote to grazing. This is particularly important in dairy systems, where cows have a limited period to gather forage by grazing. Table 1 shows proposed pasture targets based on grazing behavior and bite mass maximization being applied at farm level.

The layout of pastures rotationally stocked using this management concept changes to the use of fewer subdivisions of larger size. Farmers appreciate this, because it results in lower labor requirement. Post-grazing pasture mass is high, so overall pasture structure equates with that of continuously stocked pasture moderately grazed. Accordingly, this proposed "take the best and leave the rest rule" is colloquially named "rotatinuous stocking". Resting periods are flexible due to typical fluctuations in pasture growth, and are usually one-third of resting periods previously applied. Post-grazing pasture mass is high, but as resting period is very low (usually less than a week for tropical and annual temperate pastures), senescence and tiller recruitment are apparently maintained at reasonable levels, again similar to continuous stocking at moderate grazing. Finally, post-grazing pasture structure does not deteriorate during the grazing period, and pasture growth seems to be continuously located at the linear phase of the classical sigmoid model of pasture accumulation (see Parsons and Chapman 2000). At the moment, part of this process is empirically described, but there is current research quantifying those fluxes. The rapid increase in soil organic matter measured in PISA farms indicates high carbon sequestration promoted by pasture growth, and supports the hypothesis of almost uninterrupted pasture growth with "rotatinuous stocking" strategy.

Since the lactating cows graze only the upper parts of the plants, the contribution of pasture dry matter in the total diet is increased, decreasing silage and concentrate consumption by almost half. On average, milk yield per cow rose by 30%, reducing feeding costs by 20% at the end of the first year of the PISA program. The number of lactating cows per farm expanded from 14 to 19 in the first year, reflecting increases in pasture production due to the constancy of leaf area able to intercept light and capture solar energy. Consequently, annual milk yield per farm increased from 4800 to 11 250 kg/ha.

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[1] PISA is a public-private initiative led by MAPA (Brazilian Ministry of Agriculture). Farmers apply voluntarily to the program, and the Universities are responsible for proposed technologies. The Program is funded by SEBRAE/SENAR/FARSUL, a public-private partnership, and technologies are applied at farm level by SIA private consultants capacitated in PISA.

Table 1. Pasture targets based on grazing behavior and bite mass maximization being applied at farm level.

Forage species	Pasture target* (cm)	Reference
Sorghum bicolor	50	Fonseca et al. 2012
Pennisetum glaucum	60	Mezzalira et al. 2013a
Cynodon sp.	19	Mezzalira 2012
Native grassland (mainly *Paspalum notatum*, *Axonopus affinis*, *Desmodium incanum* and *Paspalum plicatulum*)	11.5	Gonçalves et al. 2009
Panicum maximum cv. Aruana	30	Zanini et al. 2012
Panicum maximum cv. Mombaça	95	Palhano et al. 2006
Avena strigosa	29	Mezzalira 2012
Lolium multiflorum	19	D.F.F. Silva, pers. comm.

*Pasture targets are considered the pasture structure where bite mass is maximized. In rotational stocking pasture, target refers to pre-grazing pasture height. Post-grazing pasture height should not exceed 40−50% of the pre-grazing height. In continuous stocking, it refers to optimal pasture height at the patch being grazed (average pasture height being lower).

There are a few farmers with more than 3 years in PISA, and these have reached more than 17 000 kg/ha. The social impact in those communities has been quite significant.

The overall technological packages and the way they are applied at farm level are more complex than described here. However, it is worth noting that "rotatinuous stocking" based on grazing behavior insights is the pathway in the short-term by which other technologies can ultimately be applied (e.g. no-till or diversity in crop rotations). In contrast with many other technologies (e.g. no-till to increase soil carbon stocks), increased milk production derived from changes in grazing management is "a week time scale response", so farmers became confident to accept additional structural changes in their activities. It is exciting to monitor farmers' responses throughout this process, how they are initially reactive to change for a new grazing management orientation, how they overestimate the role of silage (apprehension to not have enough feed for cows), and how they rapidly become adapted to looking at pasture structure, and not only cow body condition.

Concluding remarks

Building multifunctional pastoral farming systems requires that managers cannot dictate grassland management only by their anthropogenic assessment. Mimicking nature increases the possibility of creating sound production systems and promoting sustainable intensification. In this context, managers would learn with grazing animals in order to reproduce their behavioral requirements in commercial operations. An understanding of grazing behavior is essential to support grassland management and innovative grazing systems, as demonstrated by the PISA case study based on the "rotatinuous grazing" strategy.

Appropriate use of grazing behavior can support innovations in grassland management, but this is not the current trend, because the anthropogenic way of thinking determines management actions based on human goals (e.g. forage harvest efficiency), that rarely correspond with animal goals. Reconciliation is needed for all agricultural systems that suffer from side-effects originating from human pre-potency. In this sense, there is huge potential to include consideration of grazing behavior when making primary management decisions in grassland ecosystems, as the visionary Harry Stobbs identified so many years ago.

Acknowledgments

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