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**MODELING THE DYNAMICS OF HERBAGE PRODUCTION AND INTAKE IN
COMPLEX GRASSLANDS**

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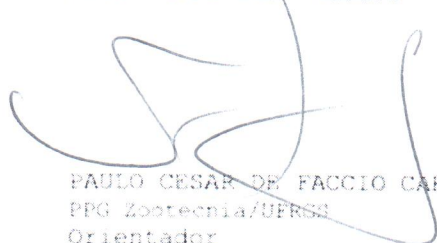
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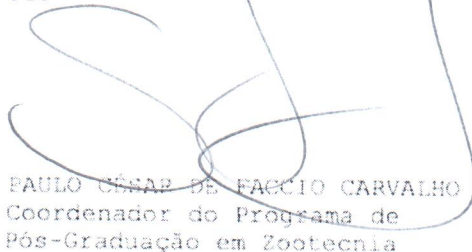
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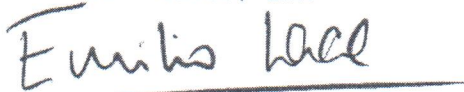
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“Grass is the forgiveness of the nature – her constant benediction. Fields trampled with battle, saturated with blood, thorn with the ruts of cannons, grow green again with grass, and carnage is forgotten. [...] Beleaguered by the sullen hosts of winter, it withdraws into the impregnable fortress of its subterranean vitality, and emerges upon the first solicitation of spring. [...] Its tenacious fibers hold the earth in its place, and prevent its soluble components from washing into the wasting sea.[...] Banished from the thoroughfare and the field, it bides its time to return, and when vigilance is relaxed, or the dynasty has perished, it silently resumes the throne from which it has been expelled, but which it never abdicates.[...]. It yields no fruit in earth or air, and yet should its harvest fail for a single year, famine would depopulate the world.

*John James Ingalls, 1872, Kansas Magazine
In USDA Yearbook of Agriculture 1948*

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People say networking is essential; and in fact it really is. This project took me from the deep prairies of the Campos, from branding calves and pushing cattle, to high-tech California, mediaeval France, and through many places along the way. But it is the people we meet and interact with that makes the journey fascinating. All the new ideas, the new perspectives, and the new views of a changing world. I am very grateful for having an amazing network of people surrounding me, and if I was to acknowledge each and every one who was influential on me during the past years, there would not be enough pages. First of all, my deepest gratitude for the reception Dr. Paulo Carvalho gave me when joining Grazing Ecology Research Group (GPEP), and especially for the opportunities created that allowed me to follow my path. Also, for being understanding of the many parallel projects I had going on, from ranching to controlling feral hogs and taking missions of producers to Canada. All were important parts of my professional formation as well. To Dr. Olivier Bonnet, for instigating me to follow this line of research, posing questions, many times annoying but always with the best of the intentions, that propelled me to go further. Our discussions opened my mind for a different view of the grassland ecosystem, from an ecological perspective.

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Modeling the dynamics of herbage production and intake in complex grasslands¹

Author: Marcelo Osório Wallau

Major professor: Paulo César de Faccio Carvalho

Abstract: Studies in grassland management and ecology have always been challenging because of the large amount and great variation of the entities representing and affecting the system. Despite that, we were able to progress significantly in range experimentation in the Campos, in Southern Brazil. Along past thirty years, a large amount of data and information was generated, from vegetation production to components of intake. In an attempt to integrate the information available, seeking for a deeper understanding of the functioning of native grasslands, we propose adapting a mechanistic vegetation model, aggregated of a spatialized grazing component to create PampaGraze. This model was developed for temperate perennial grasslands, and was adapted and tested for subtropical, C4-dominated grasslands of the Campos of Southern Brazil (Chapter III). Despite the limited capacity of field data for validating, the model was able to relatively well simulate the trends in vegetation production along the year and seasons, while overpredicting herbage production during peak growing season. The structure of the model as it is did not allow for an accurate simulation slow-growing, tussock-forming species. Further, we developed and integrated a grazing model, based on a hybrid approach of the classical mechanistic equations of the prey model (STEPHENS & KREBS, 1986), and experimental data on foraging behaviour measured on native grasslands (Chapter IV). The model was very successful on predicting the components of intake, and responded well to variation of components in relation to changes in vegetation and to selectivity pressures, compared to available literature. Regardless of the limitations on the vegetation model, we were able to further explore the relationships of components of intake, identifying possible major limitations for herbage consumption, thus animal performance, in native grasslands. A significant progress was achieved with this thesis, but still long ways to go with this project. A list of suggestions for further developments can be found in Chapter V. We identified the emergent needs for field studies on parameters and morphogenesis, for improving predictions of the vegetation model, as well as structural points of the model that could be addressed for better representation of natural phenomena. This thesis is the first step towards a more detailed and reliable tool for studying and predicting the behaviour of vegetation dynamics and animal production in sub-tropical grasslands. This can allow us to explore relationships and scenarios beyond our experimental capacity, and investigate the connectivity of the system, as well as each mechanism separately. The stage has been set, awaiting further developments.

Key words: native grasslands, mechanistic modeling, prey model, grazing behaviour

¹ Ph.D. thesis in Animal Science – Faculdade de Agronomia, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil. (140 p.), May, 2017.

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LIST OF ABBREVIATIONS²

d	Day
DM	Dry matter
FG	Functional group
g	Grams
ha	Hectare
HAR	Herbage accumulation rate (kg DM ha ⁻¹ d ⁻¹)
kg	Kilograms
LW	Live weight (kg)
mg	Milligrams
MJ	Mega Joules
PAR	Photosynthetic active radiation (MJ m ⁻² d ⁻¹)
SD	Standard deviation
yr	Year

² A complete list of parameters along with definition and units can be found on Chapter 3, Table 1 (p. 83)

CHAPTER I - INTRODUCTION

1. INTRODUCTION

Grassland ecosystems are characterized by a large number of entities, interacting in several levels of temporal and spatial scales. The degree of complexity is given by the number and heterogeneity of those entities, and especially by how the system is organized (TAINTON et al., 1996; PARSONS & DUMONT, 2003). Those components, however, interact non-linearly, frequently having “response delays and feedback loops” among them, generating emergent properties and unexpected behaviors (WU & MARCEAU, 2002). The identification of the main entities and their interface is fundamental for understanding causes and direction of changes, and the effects of management on the system (FRIEDEL et al., 2000; GORDON, 2000). There are several underlying mechanisms from the interaction of the grazing animal and the pasture that will affect both herbage growth and animal performance (UNGAR, 1996; PARSONS & DUMONT, 2003; LACA, 2008). Besides being very heterogeneous in terms of species composition and distribution, rangelands and native grasslands are also, in many times, climatically marginal environments. Variations in abiotic conditions (especially rainfall) can have a large effect in the equilibrium of the system, and effects can be larger than any change caused by management (FRIEDEL et al., 2000). Therefore, the definition of stability may have to come along a definition of spatial and temporal scales (LACA, 2008).

The Campos in Rio Grande do Sul, Brazil, is a complex pastoral ecosystem, composed of a large diversity of species (and functional groups) interacting with edaphoclimatic conditions and herbivores. Thirty years of experimentation to evaluate the productivity potential of native grasslands under variable management practices shows that moderate herbage allowances have an advantage over high or low stocking rates on gain per area and per animal (MARASCHIN, 1998; SOARES et al., 2005). Reductionist experiments conducted to explore specific mechanisms of animal and vegetation processes determined management rules for achieving high intake rates and help identifying vegetation characteristics for increasing productivity (GONÇALVES et al., 2009a; NEVES et al., 2009; da TRINDADE et al., 2012, 2016; BONNET et al., 2015). Results, however, are disguised by large interannual and seasonal variations, which difficult the understanding of the process related to herbage and grazing dynamics. Besides having a large quantity of data, animal performance and herbage allowance relationships are not as clear as previously thought, and there is still a lot to understand about animal production in our environment.

For advancing in the understanding of this pastoral system, a novel approach is needed, incorporating all information already generated, and identifying future research needs. A recent effort using a deterministic, top-down model for exploring the influence of short-term intake on animal performance indicated that most of the explained variation on animal performance is related to season and inter-tussock canopy height, used as a proxy for bite mass (CARVALHO et al., 2015). We believe that there are other non-linear interactions between vegetation and cattle more difficult to be accounted for, requiring a more detailed spatially-explicit model to be explored. Thus, we

propose the adaptation of a mechanistic dynamic model (JOUVEN et al., 2006a) to study the underlying forces influencing herbage production and cattle grazing behavior in heterogeneous, complex native grasslands in southern Brazil.

The global objectives of this project are to 1) develop a theoretical model for studying the dynamics of vegetation and animal production in multi-specific subtropical grasslands, including the vegetation composition and structure response to variable grazing and environmental conditions; and, from this model to 2) develop a decision support system that allows managers to define stocking rates and predict production indexes based on management characteristics and weather forecast. Here, set the stage by presenting the first step towards that direction. The core of this thesis is based on two main models (the vegetation and the grazing models) which need to incorporate principles of heterogeneity (vertical and horizontal distribution of plant components) and diversity (botanic composition), and their influence on herbage dynamics and grazing behavior, and accommodate to the knowledge, information, and tools available. It integrates mechanistic and empiric equations, both from local and international literature, and from data obtained in 30 years of experimentation in native grasslands in southern Brazil. The vegetation model utilizes the principles of functional groups to describe the vegetation diversity, distributed in space, with functional attributes simulating biomass fluxes and responses to environmental factors and seasonality. The grazing model uses the concept of profitability of bites available per patch, incorporating empirical and mechanistic equations based on optimality principles.

A vast literature was reviewed for achieving the objectives. In the literature review (Chapter 2), I will briefly summarize the most important information studied for each of the models, which will complement what has been written on the two proposed papers (Chapters 3, the vegetation model; and 4, the grazing model), presented in a logical way which led to the origins and development of the ideas behind this project. Chapter 3 brings the adaptations proposed for the original model (which is detailed described in Chapter 2), as well as verification and validation against observed experimental data. The grazing model is proposed on Chapter 4, incorporating observed data on grazing behavior with classical mechanistic equations, held together in the theoretical framework of the “optimal foraging theories”. Both models can be expanded and improved to integrate dynamics of vegetation composition and animal performance, for example. At the end, Chapter 5 brings the general conclusions and main findings of this thesis, as well as personal remarks on how this project was influential on my professional and personal career.

CHAPTER II – LITERATURE REVIEW

2. LITERATURE REVIEW

2.1. Complex grazing environments and animal production – the origins of the ideas

2.1.1. General overview

Complexity in ecosystems science can be described as composed by three main axes: heterogeneity, connectivity and historical contingency (CADENASSO et al., 2006). Heterogeneity *per se* is a multidimensional concept, related to patch richness and configuration, how the pieces of the system are arranged and how they differ from each other (LACA, 2008). Connectivity is regarding the organization and how the pieces interact (TRAITON et al., 1996). Lastly, the historical contingency describes the changes on the system over time (CADENSASSO et al., 2006). While herders many times, empirically, consider those axis together (MEURET & PROVENZA, 2015), historically, natural resources management has been characterized by high efforts on reducing variability for increasing predictability in agroecosystems (FUHLENDORF et al., 2017). From controlled experiments designed to minimize heterogeneity for studying specific mechanisms, to high-intensity grazing and mowing for homogenizing the pastures, our focus has, been on the pieces of the system instead of on its functioning. Those are important steps on the information building process, but knowledge only emerges when putting the pieces together for making sense of the whole. But when adding those components in a system's perspective, in an organized and interactive manner, the results are quite different from expected, and new proprieties emerge (TRAITON et al., 1996; CADENASSO et al., 2006; HIERONYMI, 2013; FUHLENDORF et al., 2017).

Complexity in grazing systems arise from the relationships of plants and environment, the plant-animal interface which are driven by herbivore species and category, and from the management techniques which influence the allocation and use of resources (TRAITON et al., 1996). The relative importance of (a few) specific species of native grasslands on the diet composition and animal performance adds to the complexity of the system and is, many times, the focus of management goals (e.g. reduce proportion of tussocks or increase the proportion of legumes). Heterogeneity is difficult to conceive and generally hard to manage. Naturally, for lack of understanding, we regard it as detrimental. But homogenizing grasslands could be an answer? Heterogeneity is critical for the ecosystem functioning (LACA, 2008; BLOOR & POTTIER, 2014; FUHLENDORF et al., 2017). If we think from an ecological perspective, the diversity of species, or functional diversity (DIAZ & CABIDO, 2002), is essential for providing ecosystem services. From the animal perspective, it can be seen as opportunity for a varied and more complete diet, but, depending on vegetation characteristics, a hindrance on foraging behavior. The question, therefore, is: how can we better utilize heterogeneity?

An example of those complex grassland ecosystems is the Pampa biome, extending from southern Brazil to Uruguay and north-eastern Argentina. It covers an area of approximately 700,000 km², housing 43 million head of cattle and 14 million sheep, along with 400 species of vertebrates exploiting over 4000 native plant species (MODERNEL et al., 2016). This vast botanical

composition is arranged in a mosaic organized in time and space, interacting with edaphic and macro- and micro-climatic conditions, largely influenced by use characteristics, and with specific features depending on local characteristics and scale. The grassland physiognomy of the Campos region, in the northern part of the Pampa (Brazil and Uruguay), is dominated by perennial C4 grasses, but composed by over 450 grass and 200 legume species (BOLDRINI, 2009). Climatic characteristics are determining factor affecting the maintenance and productivity of those grasslands, which are kept by disturbances (White et al., 2000) such as periodic draughts and herbivory, despite actual precipitation levels already be supportive of shrub encroachment and forest expansion (OVERBACK et al., 2007).

2.1.2. A brief scientific history of our long-term experiment in native grasslands

Grazing experiments, especially in native grasslands, can take a long period of time to stabilize. Thus, long-term experiments are important for allowing for a better interpretation of the trajectory of the system and magnitude of changes in components along time (KNAPP et al., 2012; PORENSKI et al., 2015). This facilitates the study of the mechanisms and temporal dynamics of the cause and effect relationships to a greater extent, especially if complemented with side experiments for studying specific questions of the mechanisms of the system (KNAPP et al., 2012).

In 1986, Professor G. E. Maraschin started an experiment to understand the production dynamics of native grasslands in Rio Grande do Sul, at the Federal University's (UFRGS) Agronomic Experimental Station. The objective was to assess the productive capacity of the Campos grasslands for beef cattle by only managing herbage allowance. Four herbage allowance levels were tested, based on the amount of forage (kg) by 100 kg live weight (LW) per day, or % LW d⁻¹: 4, 8, 12 and 16 % LW d⁻¹ offered (MARASCHIN, 1998) based on an estimated ideal intake of 3 % LW d⁻¹ (VAN SOEST, 1994).

In a first moment, it was observed that maintaining herbage allowance between 11 and 13 % LW d⁻¹ (moderate grazing pressure) allowed for gains around 120 kg ha⁻¹ yr⁻¹, while the average for the State was 70 kg ha⁻¹ yr⁻¹, and 0.4 kg LW animal⁻¹ d⁻¹ (MARASCHIN, 1998). Soares et al. (2005) then realized that by attempting to manage vegetation structure it was possible to achieve better animal performance. They imposed three new treatments with variable herbage allowance though out the year: 8 % LW d⁻¹ in the spring, 12 % LW d⁻¹ the rest of the year (8-12 % LW d⁻¹); 12 % LW d⁻¹ in the spring, 8 % LW d⁻¹ the rest of the year; and 16 % LW d⁻¹ in the spring, 12 % LW d⁻¹ the rest of the year. The 8-12 % LW d⁻¹ outperformed the original treatments, and productivity raised to approximately 230 kg LW ha⁻¹ yr⁻¹.

But besides achieving those results, there was no understanding on the mechanisms behind the responses. Herbage allowance brought no information on vegetation structure (UNGAR, 1996) and it's relationships with animal productivity were not as strong as previous thought (MARASCHIN, 1998), proving not being a good predictor of intake and performance (CARVALHO et al., 2015). Mass per unit of area available for the animal to graze is in a two-dimensional plane, while bites are taken in a three-dimensional universe,

regulated by many factors other than just vegetation biomass (UNGAR, 1996; LACA, 2008; VAN LANGEVELDE et al., 2008).

As researches advanced and a better understanding of the production system was achieved, new questionings emerged and along came new hypotheses based on the basic processes of the system's functioning. Thus, a third stage of experimentation began with reductionist essays, focusing on instantaneous and daily intake (GONÇALVES et al., 2009a,b; NEVES et al., 2009; DA TRINDADE et al., 2016), selectivity (TISCHLER, 2014; BONNET et al., 2015) and space utilization patterns (SANTANA, 2015). It was believed that cespitose grasses available and other tussock-forming species, in general, were not part of the cattle's diet composition, because of low nutritive value, secondary metabolites or difficulty in accessing forage (PINTO et al., 2007; CARVALHO et al., 2008; NEVES et al., 2009). However, those species can have a larger than thought importance on vegetation dynamics (BRISKE & DERNER, 1998) and herbage intake (BONNET et al., 2015), but the interaction between upper (tussocks) and lower (lawn) strata, and upper strata and herbage intake are not clear. Some researches already indicate that an important fraction of grazing time and total intake is actually from those tussocks (TISCHLER, 2014; BONNET et al., 2015).

The constant application of herbage allowance levels along time resulted in very particular vegetation characteristics for each treatment, characterized by variable proportions a bimodal structure composed of grazing lawns (lower stratum) of prostrate species intermingled within tall tussocks (upper stratum) of cespitose, less-desired species (BOLDRINI, 1997; SOARES, 2005; NEVES et al., 2009). The most frequent species on the lower stratum are *Paspalum notatum*, *P. pumilum*, *P. paucifolium*, *Axonopus affinis* e *Piptochaetium montevidensis*; while the upper stratum is composed by *Andropogon lateralis*, *Aristida jubata*, *A. laevis* e *Schyzachirium microstachyum*. With increasing herbage allowances, there is an increase in frequency and dominance of tussocks, with significant participation of non-grass species such as *Eryngium horridum*, *Baccharis coridifolia* e *Vernonia nudiflora* (DA TRINDADE et al., 2012). The arrangement and disposition of those other species in the vertical structure of the canopy and on the area, respectively, affect directly animal performance, by influencing factors related to intake, such as bite size and rate, selectivity, and prehension capacity SOLLENBERGER & BURNS, 2001; LACA, 2008).

Gonçalves et al. (2009a,b), found a linear relationship of bite depth and inter-tussock stratum canopy height, but a quadratic relationship with bite mass because of lower densities of taller canopies. The highest intake rates were observed at canopy heights between 10 and 11 cm. The effects of tussocks was studied by Bremm et al. (2012), which found a decrease in 0.6% in grazing time in the inter-tussock strata for each 1% increase in tussock cover, but intake rates were higher when proportion of tussocks was between 34 and 44%. Thus, as rule of thumb, the "ideal" vegetation structure for native grasslands would be between 1400 to 2200 kg DM ha⁻¹ standing biomass, with < 35% tussock cover, and inter-tussock stratum height between 9 and 13 cm for increasing intake and decreasing grazing time (DA TRINDADE et al., 2012).

The problem, however, is that this sort of structure proved very hard to be maintained by managing grazing only, especially with fixed herbage

allowances. For intermediate herbage allowance, which had the highest productivity, 60 to 70% of grazing patches have heights < 6 cm, considered limited to intake potential (NEVES et al., 2009). Increasing herbage allowance decreases effectively grazed area while increasing grazing intensity reduces tussock cover and inter-tussock canopy height. Despite the high forage availability at high herbage allowance, structure of the canopy (low density) and of the pasture (high frequency of tussocks) limits intake. The arrangement of those tussock-forming species in the area and canopy profile affect directly animal performance, since they are determining factors affecting intake parameters, such as selectivity, bite mass and rate, and easiness of prehension (SOLLENBERGER & BURNS, 2001; LACA, 2008). Hence, managing only based on herbage allowance imposes significant restrictions to animal performance (CARVALHO et al., 2008; Da TRINDADE et al 2012).

Furthermore, the relationship of animal intake, vegetation structure and herbage allowance with animal performance was not clear. Carvalho et al. (2015) performed a general statistical analysis of 10 years of data from this experiment, based on a conceptual model where bite mass (short-term intake rate) was determinant of long-term animal performance across a range of canopy conditions. Around 78% of the variation on live weight gain was explained by the model, but only 35% were related to known fixed effects, being 16% due to season variations and 11% to bite mass (which were simulated based on canopy height). The lack of prediction was attributed to not accounting tussocks on the model, which, as mentioned before can represent a significant proportion of forage intake, thus performance (BONNET et al., 2015).

For evolving on this line of research on native grasslands, there was a need for a different approach, something that could integrate all this information, analyzing in more depth the relationships between herbage production and consumption, the effects of distinct groups of plants, and their interaction with the foraging animals and environment. This scenario led us to the idea of developing a mechanistic model that could represent vegetal species diversity and heterogeneity, be influenced by weather constraints, and allow for selective grazing leading to simulating vegetation dynamics and animal production. To the best of our knowledge, this is the first of such effort in our environment, and still fairly unique across other biomes.

2.2. Modeling grasslands

Empirical and mechanistic models, collectively, have increased considerably our fundamental knowledge and understanding of several aspects and processes of ecosystem functioning and dynamics (DERNER et al., 2012). Although large advance in ecological and agricultural models in recent years (JORGENSEN 2011; and see JONES et al., 2016), few of those explore the effects of spatiotemporal and climatic variability on grassland management (TEAGUE et al., 2009).

Studying the major components of a system in isolation, which it is the focus and design of many of our agricultural field experiments, is not necessarily sufficient to understand the overall systems' functioning (HIERONYMI, 2013; JONES et al., 2016). Adding the components together, in an organized manner, interacting among them and with the external environment creates properties previously unseen, affecting the behavior of the

system within its boundaries and even expanding them (THORNLEY, 2001; JONES et al., 2016). Mechanistic modeling is a tool for adding those components together and exploring their relationships, in a way to study how grazing systems work and identify research needs and opportunities for intervening for maximizing future events (THORNLEY, 2001).

Identifying the main entities and their relationship is fundamental for understanding the causes and direction of changes and the effects of management interferences in the system (FRIEDEL et al., 2000; GORDON, 2000). Many times, the lack of knowledge about those entities and their interaction, or even neglecting for simplifying the studies, limits our interpretation and weakens the analysis of the results. On the other hand, high degree of complexity and large number of variables and parameters does not guarantee higher confidence or representability, especially if parameters are have large estimation errors (uncertainty on parameters – e.g. RYKEL 1995; GAN et al., 2014; SUMNER et al 2012). Thus, knowing how much and when to simplify is essential (THORNLEY, 2001).

First ecological models of grasslands were developed in the late 1960's and 1970's, supported by early developments on ecophysiological process of photosynthesis, resource allocation and herbage production (e.g. BROUGHAM, 1959; DE WIT et al., 1978; PARSONS et al., 1983; and see JONES et al., 2016 for general review on agricultural systems modeling and PETERS 2011 for more specific grassland models). Peters (2011) classify grassland models into five major classes, regarding drivers and key response variables: demographic models, including individual-based models and cellular automata (which is the classification of this project), for simulating processes affected by competition and succession in plant population across landscapes; physiological models, or source-sink models, for simulating carbon assimilation, allocation and growth of plant species; physical models, which are appropriate for simulating soil and water processes and vegetation responses; biogeochemical models, for global carbon, water and nutrient flows; and dynamic global vegetation models, for simulating vegetation functional and structural dynamics at global scale.

The model choice has to take in account many aspects, including, first, objectives of the study, or the question we intend to answer. At the end of the project, what matters is if the model used was adequate for testing the hypothesis and helped us improving the understanding of the process or system being simulated. The scale being simulated is an important factor to be considered both for the representability of the simulation and computing capacities. Generally, the main hurdle modelers face is the availability and quality of the data for parametrizing, and the high variation and difference of measurement techniques across the literature. Considering that most species composing perennial grasslands are poorly or not at all studied, this can seriously impair the quality of simulations since not only parameters, but some processes themselves are not very clear (especially when involving grazing). Finally, the level of detail desired, which is aligned with the objectives, but has to be thoroughly planned considering limitations in assumptions and generalizations. The lack of understanding of the functioning of specific mechanisms, on the other hand, should not be an impediment for modeling, and the chosen model has to be able to consider those limitations. In fact, identifying

those limitations is part of the modeling process and knowledge development, which may guide research needs and evolving on the study of such problems.

2.2.1. Some models and ecological considerations

There is a very broad array of models available for simulating pasture, grassland and rangeland systems, with varied levels of details to fulfill distinct demands. The objective of this section is not making a broad review of the literature on all type models, but to illustrate the path which guided to the choice of model used on this dissertation. More detailed information can be obtained in the referred literature and reviews such as from Bryant and Snow (2008), Peters (2011), Derner et al. (2012), Andrade et al. (2015) and Jones et al. (2016).

2.2.1.1. Developing the ideas for this project

As mentioned in the previous section, there was an eagerness to understand the whole functioning of the Campos grasslands, including the effects of management and environment on herbage and species dynamics, searching for the most appropriate theoretical framework (e.g. Dyksterius, 1949; NOY-MAYER, 1975; WESTOBY et al., 1989; LOCKWOOD & LOCKWOOD 1993). As we started with Noy-Mayer's idea of dynamic equilibrium, the natural line to be followed was the work developed by A. Parsons, I. R. Johnsons and J. H. M. Thornley (JOHNSON & THORNLEY, 1983; JOHNSON & PARSONS, 1985; PARSONS et al., 1994; THORNLEY et al 1994; which are the origins and developments of the Hurley Pasture Model, THORNLEY 1998; and further SWCHINNING & PARSONS, 1996, 1999).

Johnson and Thornley (1983) proposed an herbage growth model based on the leaf area expansion, including leaf age structure and senescence process. Leaf area index (LAI) was considered as independent variable, since distinct canopy structures could yield the same LAI (i.e.: cutting the forage to a specific LAI has a totally different structure than allowing growing to that same LAI). This model was latter complemented with grazing functions (JOHNSON & PARSONS, 1985) where at each time span a proportion of each leaf age compartment (4 compartments, leaf 1 – expanding – to leaf 4 – senescing) was harvested (being grazing considered a continuous and deterministic process). The authors suggested, based on the propositions made by Noy-Meir (1975), that depending on the initial/residual canopy state and on climatic conditions (i.e. season or limitation event such as drought) there could be two vegetation equilibria for a same stocking rate. This was regarded as a discontinuous stability, because the system could move from a stable state of high productivity to a lower stable state of productivity with a small increase in grazing pressure or minor disturbance. Returning to a higher equilibrium would require a large reduction on stocking rates or significant increase in herbage production.

This implies that a continuously stocked pasture would have multiple steady states, but being “discontinuously stable”. The idea was then reviewed by Schwinning and Parsons (1999), with a slight different approach in some of the main aspects of the model. They reduced complexity by narrowing to 1 compartment for herbage growth, without aging function, while altering the conventional logistic equation for growth, adding a factor to consider residual sward state in each grazing interval. They modeled grazing and herbage growth

processes at the bite scale, adding spatial variability by combining discrete and stochastic defoliation process (instead of continuous and deterministic, respectively, as in JOHNSON & PARSONS, 1985). However, considering only one leaf compartment, they lost the differential effect of grazing on leaf compartments, altering significantly the herbage and consumption dynamics. Consumption was a function of sward state and limited by grazing time or by maximum intake. The authors suggested that previous models (NOY-MAIR, 1975; JOHNSONS & PARSONS, 1985) had overemphasized the importance of the dual stability, mainly because they were not considering the stochasticity of the grazing process and spatial heterogeneity of the vegetation.

On the other hand, Schwinning and Parsons (1999) also showed that the dual stability region largely expands when accounting for animal patch selection (rejection of low biomass patches) rather than random consumption. Their model was proposed by mono-specific, temperate grasslands, without environmental restrictions and considering grazing a random process. Grazing activity is not random, but regulated by several factors, including animal characteristics (species, selectivity, foraging history), vegetation characteristics (structure and composition), and habitat (paddock and patch sizes, attractive spots, terrain) (PARSONS & DUMONT, 2003; BONNET et al., 2015). When considering a larger botanical composition (more than one species), animal's selectivity between different plant species or vegetation compartments, especially in natural grasslands, will add heterogeneity to system (Parsons and Dumont, 2003). We believe that not considering grazing as a stochastic process, adding preference guidelines (depending on preference vs. availability) and grazing strategies (gut fill vs. nutrient harvesting, based on the grazing behavior data from direct observations already collected), as well as limiting environmental conditions, we will probably find large discontinuities in the system (NEWMAN et al., 2007).

Moving along with our literature review, some models proposed the use of functional traits to predict herbage growth, nutritive value and management influences on perennial pastures (JOUVEN et al., 2006a; DURU et al., 2009). This approach groups plant species into functional types (groups) of similar response to environmental characteristics and defoliation regimes, assuming that the functional traits incorporate most of the relevant variables needed for modeling the capture and use of resources and tissue flows (JOUVEN et al., 2006a; for a more detailed description of the model functioning and assumption, see following sections). The model was validated (JOUVEN et al., 2006b) and tested over other conditions (HURTADO-URIA et al., 2012; CALANCA et al., 2016), producing reasonable results, being considered appropriate for studying the vegetation and management dynamics in permanent grasslands (JOUVEN et al., 2006b). One of the drawbacks is that the model is sensitive mostly to temperature and seasonal effects (same problem as previous attempts on modelling our experimental data, CARVALHO et al., 2015), and being somehow less sensitive to the actual functional traits. For Hurtado-Uria et al (2012), the model tended to under-predict herbage growth of perennial ryegrass (*Lolium perenne*), with quality of responses dependent on season. Calanca et al. (2016), testing Jouven's et al. (2006a) model for temperate perennial grasslands in Switzerland, found that it adequately simulated drought effects and seasonality on growth, but there was a tendency for overestimating the impacts of moderate water stress. Both authors noted adjustments for

improving accuracy, some of which were already suggested by Jouven et al. (2006b). Similar idea of using functional attributes for simulating perennial grasslands was explored and improved by Duru et al. (2009), with more emphasis given to leaf traits (leaf dry matter content and LAI) and nutrient availability. They adapted a mono-specific grass model to species-rich grassland under cutting regime, using environmental conditions to control the rates of biological processes. Simulated results were tested against two datasets and found good fit for the results, with few discrepancies related probably to the presence of non-grass species.

2.2.1.2. Brief on other grassland and rangeland models

Different lines of models were also considered and studied for this project, and some of them with more relevance will be briefly discussed in this section. Along with the Hurley Pasture Model (THORNLEY, 1996), SAVANNA are two of the most influential models and modeling lines (Jones et al., 2016). SAVANNA was developed by Coughenour (1993) for grazing studies in arid and semi-arid regions of Africa, and further adapted to Australia (e.g. LUDWIG et al., 2011) and western US and Canadian rangelands (e.g. WEISBERG & COUGHNOUR, 2003). It is a spatial model for simulating feedbacks between plants and herbivores (livestock and wildlife), accounting for most key ecosystem components and processes, allowing for simulating multiple ecosystem goods and services, and with practical herd management outputs for stakeholders and policy makers (Bonne et al., 2002). The model is consisted by vegetation, soil and ungulate sub-models, subjected to weather, animal and vegetation management. The level of output details from the SAVANNA allows for a thorough analysis on the historic drivers and spatiotemporal variation on vegetation and landscape, but, on the other hand, is very demanding in terms of computation and parametrization for new locations, requiring practical field expertise and local knowledge for fitting (DERNER et al., 2012).

ALMANAC (KINIRY et al., 1992) has also been used to simulate production of perennial native grasses in the North American Great Plains (KINIRY et al., 2002, 2007, 2013, 2014; KIM et al., 2016) under variable rainfall regimes. Since it was first developed in the base of row-crop weed competition model (an evolution of the EPIC model), ALMANAC is able to simulate inter-species competition for resources, especially water, nutrients and light. It does require significant detailed soil information and potential LAI of the considered species, as well as reduction coefficients for biomass and LAI after anthesis. Despite the intensive parametrization needed, the model was developed to use readily available inputs and has been intensively tested for many crops (including bermudagrass [*Cynodon dactylon* (L.)] and bahiagrass [*Paspalum notatum* Flügge]; KINIRY et al., 2007).

Another line of models have been developed by B.D. Hahn and F.D. Richardson (HAHN et al., 1999, 2005; RICHARDSON & HAHN, 2007a,b; RICHARDSON et al., 2005; 2010; RICHARDSON 2009) for the semi-arid Succulent Karoo in South Africa, for addressing questions from conservation to applied management practices. The models account for changes in vegetation (production and composition) in response to grazing and climate variability, and nutritional conditions and performance of cattle and goats. Despite objectives being similar to ours, their complex models have a high level of details and

parameter requirements, which would be made relatively complicated to be adapted to our grasslands, especially in a spatially-explicit manner.

McCall and Bishop-Hurley (2003) proposed a generalized climate-driven model to evaluate and describe observed data for *Lolium perenne*, further evolved by Romera et al. (2009). The rationale and parts of this model have been considered when implementing Joven's et al. (2006a) ModVege [i.e. $f(W)$, eq. 14-16 and Fig. 4 in following section]. The reasonable simplicity is appealing, but for our purposes it lacks the species diversity would be difficult to parametrize for other species than the more commonly known in the Pampas (e.g. *Paspalum notatum*).

Paruelo et al (2008) presented COIRON, grid-based approach for simulating long-term vegetation dynamics of the Patagonian steppe under stochastic climate and different grazing regimes. The focus on their model is on the effect of those variables on *Festuca pallensis* tussocks distribution and survival, especially for analyzing management influences on desertification process. This model was later upscaled from 0.15 ha to 2500 ha for analyzing regional variations (CIPRIOTTI et al., 2015) using a non-parametric approach with transition matrixes. The model's time step is one year, and, since the focus is on vegetation transition, does not represent the grazing process to the level of detail we need. Grazing is considered as a sequence of events which continue until forage needs are met, available forage reaches a minimum or no suitable cells are found. Defoliation intensity is subject to a grazing probability, which declines with increased accumulation of dead material, but increases with higher stocking rates. Vegetation state transition probability matrix are conditioned to precipitation class and stocking rate, which stored in a previously generated library to facilitate computation.

Simulation models for tropical pastures are somehow more limited and more recent. An effort in that sense has been put to adapt CROPGRO and APSIM to simulate growth of *Brachiaria brizantha* (e.g. PEDREIRA et al., 2011) and *Panicum maximum* (e.g. LARA et al., 2012; ARAUJO et al., 2013) in a large initiative involving research institutions from US, Australia, Brazil and Colombia [see ARAUJO et al. (2016) for more references]. Neither of those models, however, includes a grazing component [but check GRAZPLAN suite for APSIM, in BRYANT & SNOW (2008) for more references].

And the list of available models keeps increasing, as more uses are given and more adaptations are made. From whole rangeland and animal production models, like the SPUR (e.g. CORSON et al., 2006) to empirically-based management simulation model to assess ecological and socioeconomic issues (MÜLLER et al., 2007), to theoretical spatialized models to study heterogeneity in grazing (MARION et al., 2005), or creation and maintenance of structural vegetation patterns (MOUISSIE et al., 2008) and functional responses van Langevelde et al. (2008). Searching for the "right model" is not an easy task, but has to begin with the "right question" and assessment of available tools.

2.2.2. Cellular automata

The use of spatially explicit models on the study of vegetation and herbivore dynamics can be a great tool for investigating of those complex systems, and bring new insights for previously set assumptions (VAN

LANGVELDE et al., 2008; MOUSSIÉ et al., 2008; DERNER et al., 2012; JAKOBY et al., 2015), particularly when non-linear relationships emerge from the interactions between herbage, climate and livestock (COLASANTI et al., 2007). Spatial patterns of vegetation distribution have large impact on resource use by the foragers, affecting movement, intake and selection (PARSONS & DUMONT, 2003; LACA, 2008), creating and maintaining heterogeneity (MOUSSIÉ et al., 2008).

Cellular automata are discrete models in time, space and state, popular on the study of ecosystem dynamics (see BALTZER et al., 1998; DEUSTCH & DORMANN, 2005). A simple cellular automaton is defined by a lattice of cells characterized by a set of elementary states, interacting with a neighborhood template via space- and time-independent transition rules (DEUSTCH & DORMANN, 2005). Shape, size, organization and interaction of the cells are defined by the modeler. A commonly-used lattice is composed by hexagonal cells which interact with the six nearest neighbors (Figure 1), but many other formats and cell arrangements in one- or two-dimensional grids are available (DEUSTCH & DORMANN, 2005). Change in state of each specific cell is given by deterministic or stochastic rules, influenced by the state of the neighbors, in discrete time steps. A general detailed description of the functioning and equations of a cellular automata model can be found on Chapter 4 on DEUSTCH & DORMANN (2005).

2.2.3. ModVege description

Our choice of model took in account three important aspects, based on data availability and our long-term objectives with this project. First, we need a model which is fairly simple to adapt and work, based on the limited expertise in the modeling process and programming, and that requires few parameters, considering that some of those would have to be calculated or estimated based on the little available data. Second, a model which allowed for vegetative and reproductive growth, representing heterogeneity of vegetation structure, and that grew year around, regulated by environmental constraints. And finally, a model which allowed us to evaluate the effect of vegetation composition and distribution on the forager's choice, and the impact of the forager's choice on vegetation dynamics including shifts on functional composition.

Jouven et al. (2006a) presented a simple mechanistic, dynamic approach to study "the effects of management (type and intensity) on biomass, structure and quality dynamics" of multi-specific perennial pastures. It is based in the combination of two approaches, functional and structural. Vegetation flows are based on functional attributes of plant groups, which can be used to simulate herbage production under variable composition of functional groups (diversity), environmental conditions (especially N nutrition and water availability) subjected to cutting regime. The structural part is a scheme of four compartments representing both green and dead biomass of vegetative and reproductive growth.

The conceptual base for the Jouven et al. (2006a) model has five main assumptions:

- 1) The functioning of perennial grasslands can be explained by the mean value of functional parameters (biological attributes) of the composing functional groups. Those traits can be associated to production dynamics

in response to environmental conditions and defoliation regimes. Values for the functional attributes are given by the weighted averages of the values for each functional group given the proportion of the group in the community.

- 2) Sward heterogeneity can be described by the relative abundance of structural components, which determines nutritive value and allow for grazing selectivity within the sward. The sward is divided into green vegetative ($_{GV}^3$), green reproductive ($_{GR}$), dead vegetative ($_{DV}$) and dead reproductive ($_{DR}$)(CARRÈRE et al., 2002).
- 3) Growth, senescence and decay⁴ can be described as continuous flows (JOHNSON & PARSONS, 1985), giving that a cohort of leaves which appear on the same day will successively expand, mature and disappear together.
- 4) Shoot growth is regulated by seasonal pattern which accounts for storage and mobilization of carbon reserves. Growth starts with mobilization of reserves in the springs, peaks in late spring and early summer, and decreases from late summer on. This decrease in growth accounts for allocation of reserves to storage or reserves and root growth.
- 5) Nutritive value of green compartments, senescence and decay are determined by compartment aging, and related to the leaf lifespan. Digestibility of green compartments decrease linearly with age (from maximum to minimum digestibility), while it is constant (at minimum digestibility) for the dead compartments. Senescence rate of young vegetative material is low, and increases as the compartment ages, especially when approaching leaf lifespan.

A first set of differential equations are responsible for describing the change in state of the system. A second group is responsible for the flows (growth, senescence and decay) and limitations (environment) of the system. Site is described by nutrient index, soil water availability and functional group.

2.2.3.1. Differential equations

The whole assembly of the model is based on the processes within each of the four structural compartments. Each of the four compartments works separately, and is described by a state variable of standing biomass (BM_c , kg dry matter [DM] ha⁻¹, where “c” designates each of the four compartment). Flows between compartments (senescence and decay) are described by age according to thermal units (AGE_c , degree-days, °C d). As compartment ages, nutritive value (as organic matter digestibility – OMD_c) decreases linearly. A set of differential equations control biomass accumulation and disappearance, and aging dynamics within each compartment, in a daily time step.

The changes in biomass of each green compartment is calculated by

³ Underwritten “c” refers to compartment within cell, and underwritten “i” refers to cell characteristics

⁴ The original model (Jouven et al., 2006) uses the term “abscission”. We chose to change to decay since grasses in general do not have abscission layer, and decay seems more appropriate

$$\frac{dBM_{Gc}}{dt} = GRO_{Gc} - SEN_{Gc} \quad \text{eq. (1)}$$

where BM_{Gc} is the biomass for the specific green compartment, and GRO_{Gc} and SEN_{Gc} are the growth and senescence biomasses, respectively (all in kg DM ha⁻¹). Growth of the green vegetative compartment is given by:

$$GRO_{GV} = GRO \times (1 - REP), \quad \text{eq. (2)}$$

where REP [unitless; eq. (19)] works as a “partitioning” function, which determines if assimilates are driven either to vegetative or reproductive growth. If sum of temperatures (ST) is bellow threshold ST_1 , which is when reproduction starts, then REP is set to zero, therefore $GRO_{GV} = GRO$. Whenever reproduction is active ($ST_1 < ST < ST_2$), then REP function is triggered, and GRO_{GV} reduces. Seasonal function (eq. 18) accounts for mobilization or sotarge of carbon reserves. The growth of the reproductive compartment is given by:

$$GRO_{GR} = GRO \times REP \quad \text{eq. (3)}$$

The biomass for the dead compartments is calculated as the difference between SEN_{Gc} (inflow) and decay (outflow; DEC_{Dc}). The changes in dead biomass are then given by:

$$\frac{dBM_{Dc}}{dt} = (1 - \sigma_{Gc}) \times SEN_{Gc} - DEC_{Dc} \quad \text{eq. (4)}$$

where σ_{Gc} (unitless) is the biomass lost through respiration (Ducroq, 1996) during the senescing process (i.e. does not get into the dead material pool).

Another set of differential equations is responsible for the aging of the residual biomass of each compartment, regulated by the mean daily temperature (T , °C). Age can increase or decrease depending on the amount of in- and outflow of material. The mean age (AGE_c , °C d) is calculated as weighted age average of the residual biomass, and the biomass entering the compartment, which is considered to be zero.

$$\frac{dAGE_{Gc}}{dt} = \frac{BM_{Gc} - SEN_{Gc} - GRZ_{Gc}}{BM_{Gc} - SEN_{Gc} - GRZ_{Gc} + GRO_{Gc}} \times (AGE_{Gc} + T) - AGE_{Gc} \quad \text{eq. (5)}$$

For the dead compartments, aging equation is:

$$\frac{dAGE_{Dc}}{dt} = \frac{BM_{Dc} - DEC_{Dc} - GRZ_{Dc}}{BM_{Dc} - DEC_{Dc} - GRZ_{Dc} + (1 - \sigma_{Gc}) \times SEN_{Gc}} \times (AGE_{Dc} + T) - AGE_{Dc} \quad \text{eq. (6)}$$

2.2.3.2. Growth functions

The growth function (GRO , kg DM ha⁻¹) considers only above-ground biomass, and partitioning between growth and reserves, or reserve mobilization, is accounted for by the seasonal effects (SEA , unitless). This partitioning is different than the one mentioned above, where assimilates either go for vegetative or reproductive growth. GRO is then given by potential growth ($PGRO$, kg DM ha⁻¹), which assumes optimal conditions, and growth-limiting factors, based on environmental limitations (ENV , unitless), and regulated by season.

$$GRO = PGRO \times ENV \times SEA \quad \text{eq. (7)}$$

The $PGRO$ is calculated by the equation after Schapendonk et al. (1998):

$$PGRO = PAR_I \times RUE_{MAX} \times [1 - \exp(-0.6 \times LAI)] \times 10, \quad \text{eq. (8)}$$

where PAR_I is the total incident photosynthetic active radiation at the top of the canopy (in MJ m^{-2}), RUE_{MAX} is the maximum radiation use efficiency (set to 3 g DM MJ^{-1}), 0.6 represents the extinction coefficient that indicates the leaf angle, and LAI is the leaf area index ($\text{m}^2 \text{ m}^{-2}$). The “10” ($\text{kg m}^2 \text{ ha}^{-1} \text{ g}^{-1}$) is a factor to convert units to kg DM ha^{-1} .

The leaf area index can be calculated as:

$$LAI = SLA \times \frac{BM_{GV}}{10} \times LAM, \quad \text{eq. (10)}$$

where SLA is the specific leaf area ($\text{m}^2 \text{ g}^{-1}$), BM_{GV} is actual the biomass for green vegetative compartment, and LAM is the fraction of leaf lamina on total biomass, set to 0.68. The “10” is a factor to convert units to g m^{-2} .

Potential growth is limited by environment (ENV), given by a series of simplified functions which represent physiological responses to environmental stress.

$$ENV = NI \times f(PAR) \times f(T) \times f(W). \quad \text{eq. (11)}$$

Nutrient index (NI) is a site specific parameter that restricts for mineral nutrition deficit, calculated after Bélenger et al. (1992).

The conversion efficiency of absorbed light into assimilates is variable, and dependent on radiation intensity, temperature and water availability (SCHAPENDONK et al., 1998). The three following functions on ENV equation account for those limitations, in the original model as: (i) $f(PAR_I)$ decrease in RUE at radiation intensities (PAR) over 5 MJ m^{-2} [eq. (12); after SCHAPENDONK et al., 1988]; (ii) at the beginning of the season, photosynthesis starts after 10 day moving average temperature (T_{m10} , $^{\circ}\text{C}$) is above T_0 [$f(T)$, eq (13); after SCHAPENDONK et al., 1998]; and (iii) water stress [$f(W)$, eq. (14-16) after MCCALL & BISHOP-HURLEY, 2003]. $f(PAR_I)$ (Figure 1) is given by:

$$f(PAR_I) = \min[1, 1 - 0.0455 \times (PAR_I - 5)] \quad \text{eq. (12)}$$

which means that there is no limitation between PAR_I 0 to 5 MJ m^{-2} , and then it reduces growth at a 0.0455 rate for each MJ m^{-2} increment, to a minimum close to zero at around 27 MJ m^{-2} (Figure 1).

The $f(T)$ (Figure 2) is described by

$$f(T) = \begin{cases} 0, & \text{for } T < T_0 \text{ or } T > T_{max} \\ (T - T_0)/(T_1 - T_0) & \text{for } T_0 < T < T_1 \\ 1 & \text{for } T_1 \leq T \leq T_2 \\ (T_{max} - T)/(T_{max} - T_2) & \text{for } T_2 < T < T_{max} \end{cases} \quad \text{eq. (13)}$$

where T is the average temperature for the day, T_0 is the given basal temperature, below which there is no growth (set to 4°C), T_1 and T_2 represent the temperature range for optimum growth (10 and 20°C , respectively), and

T_{max} is the maximum temperature (set to 42°C) above which photosynthesis shuts down.

Water availability is one of the most restrictive factors in native grassland environments. Photosynthesis is limited by stomatal closure, which reduces plant transpiration and restricts CO₂ uptake. Growth limitation by water stress [$f(W)$; Figure 3] is a function of potential evapotranspiration (PET , mm) and water stress (W) which is calculated as the ratio between water reserves (WR , mm) to soil water holding capacity (WHC , mm; after McCall and Bishop-Hurley, 2003), where the maximum value for the nominator is the WHC . Water reserves are replenished by precipitation (PP , mm) up to WHC , after when runoff starts and is not accounted for. Depletion occurs by actual evapotranspiration (AET , mm), which is considered as being equal to PET at canopy light interception of 95%, when $LAI > 3$ (Johnsons and Parsons, 1985), so

$$W = \frac{\min(WR, WHC)}{WHC}, \quad \text{eq. (14)}$$

where

$$WR_t = \max(0, WR_{t-1} + PP - AET), \quad \text{eq. (15)}$$

and

$$AET = \min\left(PET, PET \times \frac{LAI}{3}\right) \quad \text{eq. (16)}$$

which reduces AET if $LAI < 3$.

Those values are based on work developed by Denmead and Shaw (1962), with corn plants in containers filled with Colo silty clay loam soils, subjected to different water restriction treatments and varying potential transpiration rates. Available for plant growth then depends on rooting depth and soil WHC between wilting point (-15 atm) and field capacity (-0.3 atm). Soil WHC for McCall and Bishop-Hurley (2003) is calculated to a depth of 75 cm, which is divided into top (A) horizon (10 cm) and remaining (B) horizon of 65 cm. To simplify calculations, the Jouven et al. (2006a) model just considers one soil horizon and the same rooting depth for all functional groups.

The season (SEA , unitless; Figure 4) is an empirical function proposed by Jouven et al (2006a) based on information from the literature, especially on N remobilization. Season regulates growth by indicating whether there is mobilization of reserves or storage of assimilates. The function sets season at minimum ($minSEA$) during fall and winter, and increases to maximum ($maxSEA$) after the onset of growth. SEA starts increasing at 200°C d, and $maxSEA$ is when $ST_1 - 200 < ST < ST_1 - 100$. SEA starts decreasing again at ST_1 and levels out in $minSEA$ when reproductive period ends, at ST_2 . $SEA > 1$ indicates above-ground growth is supported also by mobilization of reserves, while if $SEA < 1$ there is allocation of assimilates for storage of reserves. Minimum and maximum SEA values and ST_1 and ST_2 vary depending on the functional group (see parameters on Table 1). More conservative groups (i.e. C and D) are more dependable on mobilization of reserves for growth (Thornton et al., 1993; 1994; Gong et al 2014), thus the lower values for $minSEA$ along with a longer lag time for reaching maximum growth (at a greater $maxSEA$).

The reproductive growth is determined by the *REP* function (from eq. 2), which is given by:

$$REP = \left[GR_{min} + \frac{(1 - GR_{min}) \times (NI - NI_{min})}{1 - NI_{min}} \right] \times CUT, \quad \text{eq. (19)}$$

where GR_{min} and NI_{min} are the minimum growth rate and minimum nutrition index, set to 0.25 and 0.35, respectively (BÉLANGER et al., 1994, for respective values of GR_{min} and NI_{min} ; see JOUVEN et al., 2006b for more references). NI is the actual nutrition index, that is one of the model inputs. CUT is a Boolean function which stops *REP* if herbage is cut (or grazed; $CUT = 0$) between ST_1 and ST_2 .

2.2.3.3. Senescence and decay

Senescence (SEN , kg DM ha⁻¹) is proportional to the BM_{Gc} , mean daily temperature (T , °C) and senescing rates (k_{Gc} , °d⁻¹) proposed after Ducrocq (1996). For $T > T_0$, senescence is stimulated by pool-aging functions (Figure 5), while for temperatures between T_0 and 0 °C, senescence flow stops. When temperature drops below freezing point, senescence is driven by freezing effects. SEN is given by:

$$SEN_{Gc} = K_{Gc} \times BM_{Gc} \times T \times f(AGE_{Gc}), \text{ if } T > T_0 \quad \text{eq. (20)}$$

or

$$SEN_{Gc} = K_{Gc} \times BM_{Gc} \times |T|, \text{ if } T < 0 \quad \text{eq. (21)}$$

The decay of dead tissue (ABS , kg DM ha⁻¹) is a function of the standing biomass in the dead compartment, mean daily temperature and decay rates (Kl , unitless; after Ducrocq, 1996), and is determined by pool-ageing (Figure 5):

$$ABS_{Dc} = Kl_{Dc} \times BM_{Dc} \times T \times f(AGE_{Dc}). \quad \text{eq. (22)}$$

Both $f(AGE_{Gc})$ and $f(AGE_{Dc})$ (Figure 4 in JOUVEN et al., 2006a) are functions of age in relation to leaf lifespan (LLS , °d), for the vegetative compartments, or to the reproductive period ($ST_2 - ST_1$) for the reproductive compartments.

2.2.3.4. Nutritive value

Nutritive value in the Jouven et al (2006) model is represented by organic matter digestibility (OMD , fraction). For both dead compartments (OMD_{Dc} , fraction) it is considered constant at a minimum level (equal to $minOMD$). For the green compartments, digestibility starts at maximum ($maxOM$) and declines linearly with the aging of the compartment to a theoretical minimum ($minOMD$) which corresponds to the leaf life span (LLS , °C d) or to the duration of reproductive growth period (from ST_1 to ST_2 , in °C d). So, for green vegetative compartment the equation is:

$$OMD_{GV} = maxOMD_{GV} - \frac{AGE_{GV} \times (maxOMD_{GV} - minO_{GV})}{LLS} \quad \text{eq. (23)}$$

and for green reproductive

$$OMD_{GV} = maxOMD_{GV} - \frac{AGE_{GV} \times (maxOMD_{GV} - minO_{GV})}{(ST_2 - ST_1)} \quad \text{eq. (24)}$$

2.3. Grazing behavior

2.3.1. From bite to intake

2.3.1.1. Classical approaches

There are many approaches used for studying intake, as noted by Ungar (1996), “partially defined by the balance between management-oriented problem solving, hypothesis-testing, the provision of factual information and the elucidation of causal relationships”. For each approach, a set of methodologies (UNGAR, 1996) and timescale (SHIPLEY et al., 1994) is chosen, depending on the emphasis on descriptive of diet selection (e.g. BONNET., 2015), or on the mechanics of bite formation and behavioral components of intake (e.g. STOBBS, 1973; LACA et al., 1992) in relation to the food environment. Intake and foraging behavior in heterogeneous environments can be affected by non-linearity of response to local and instantaneous conditions, selectivity, and change of functional response due to global conditions (Laca, 2008). Thus, the more complex this food environment is, the more variable the bites are, and the more difficult it is to measure or to simulate intake.

Most of the classical, mechanistic approaches studying grazing behavior have been based on homogenous monocultures or simple mixtures (e.g. STOBBS, 1973), while bite components have been studied using hand-made microswards (e.g. LACA et al., 1994) or cut sods (WALLISDEVRIES et al., 1989). Those experiments provide information on the components of bite formation, time budget and bite dimensions, which can be allometrically extrapolated to different animal and canopy characteristics, resulting in an estimated intake rate (ILLIUS & GORDON, 1987, 1991; LACA et al., 1992; SHIPLEY et al., 1994; UNGAR, 1996, BAUMONT et al., 2004). Arithmetically, intake can be given by mean bite mass multiplied by bite rate over a defined period of time (STOBBS, 1973; BURNS & SOLLENBERGER, 2002). This approach, however, does not bring information on the functional relationship among intake components and grazing behavior (UNGAR, 1996), nor the relationship with the food environment. While in homogenous monocultures this is sufficient, for simulating intake in complex, heterogeneous environments it is rather limiting, since many other factors are involved on diet selection (Bonnet et al., 2015). The mechanics of grazing in heterogeneous environments, where a high diversity of species is available, is relatively different from those aforementioned. There is a strong interaction of species composition, distribution and canopy structure with bite selection (BREMM et al., 2012, DA TRINDADE et al., 2016; CARVALHO et al., in prep;). Thus, we chose an empirical approach based on data collected on our long-term experiment using a continuous bite monitoring evaluation (BONNET et al., 2015 and unpublished data) for being more realistic with the environment being modeled.

2.3.1.2. Continuous bite monitoring and empirical equations

The continuous bite monitoring (AGREIL & MEURET, 2004; BONNET et al., 2015) is a direct observation method for evaluating the herbivore's interaction with the food environment. It consists of continuous observation of the animal while foraging, recording bite per bite the forage selection and associated behavior for describing in details the diet composition, herbage intake and other behavioral activities (BOLZAN et al., in prep.). Intake is

simulated by mimicking observed bites, hand-plucking the chosen forage by the animal in similar vegetation patch (species and structure). This technique was successfully used to describe diet composition and intake of sheep (AGREIL & MEURET, 2004; O. Bonnet and A. Bolzan, unpublished data), rhino (O. Bonnet, unpublished data), horses (BOLZAN et al., 2017) and beef cattle (TISCHLER, 2014; BONNET et al., 2015). O. Bonnet and A. Bolzan (unpublished data), when validating the continuous bite monitoring for lambs grazing ryegrass against the classical double-weighing technique found a correlation of $r^2 = 0.84$ for short-term intake rate between the two methodologies.

The data used for calculating the empirical equations for bite mass and bite rate were obtained during 2012 and 2013, in our long-term native grassland grazing experiment (TISCHLER, 2014; BONNET et al., 2015; O. Bonnet, unpublished data). The grazing behavior of three animals per experimental unit (see section 2.1.2 for more information regarding treatments) was accessed using the continuous bite monitoring technique, in different seasons of the year. Based on the hand-plucked bite simulation and on frequency of bites, bite mass and bite rates were calculated for each vegetation group or species. Major differences on parameters measured were between vegetation structure, being influenced by treatment and season. Treatment effect was suppressed and vegetation categorized in four functional groups (CRUZ et al., 2010) and divided in “spring” or “other season” (more details on equations, see Chapter 4).

2.3.2. Foraging theories

The optimality approach for simulating and studying diet choices for foragers was originated from the idea of linking economic theories to population biology (MACARTHUR & PIANKA, 1966) by assuming that species evolved through natural selection of individuals which were able to survive and reproduce using more efficiently the available resources, which is related to their fitness (in the Darwinian sense of the number of offspring that survived to reproduce) (STEPHEN & KREBS, 1986; NEWMAN et al., 1995, NEWMAN, 2007). But how does this relate to how animal looks for and selects food? Well, it is not just a matter of whether individuals survive, but how their design is related to that. And, actually, when studying the design, breaking the system down into parts to determine interrelationships, the question is not “how do”, but “how should” animals look for and select food (STEPHEN & KREBS, 1986; GREEN, R.F 1990, unpublished manuscript). If we consider the rather simplistic approach that fitness is dependable on foraging behavior and this behavior is passed on through generations, and that this relationship is known, given by a currency which rate can be maximized for increasing survival, we then have the basic assumptions of the optimal foraging theories (MACARTHUR & PIANKA, 1966; ELMEN, 1966; STEPHENS & KREBS, 1986; PYKE, 1984). This is where biology and mathematics come together for simulating foraging behavior (CHARNOV, 1976).

The optimal foraging theories offer a simple and solid approach for studying the relationships of food environment and diet choices. Despite some of the criticism (e.g. PIERCE & OLLASON, 1987; PROVENZA & CINCOTTA, 1993), there is no ambition on *explaining* the evolution of species or finding a revolutionary way to predict in details what animals are eating. Indeed, it offers a mathematical framework which can help understanding what animals should choose, especially when foraging in heterogeneous food environments, by

maximizing a specific function (STEPHENS & KREBS, 1986; YDENBERG et al, 2007). There are two main lines of models under the foraging theories umbrella (STEPHEN & KREBS, 1986; YDENBERG et al., 2007; NEWMAN et al., 2007) further developed with many different approaches by a series of researchers: the diet and the patch models. The diet model (*aka* prey, contingency or diet breadth) analyses the decision of taking or not taking a food item upon encounter, based on the relative profitability (rate of currency uptake) of that specific item in relation to the food environment, or keep searching. The patch model determines how long the forager should stay in the same patch, given diminishing returns as the patch is exploited in relation to the whole food environment available.

The use of the diet breadth model in this project is to aid on determining the probability of specific items being grazed by determining the proportion of total bites that should be taken at each patch visited. The bulk of the (important) literature on foraging theories is from the 1970's and 80's (PERRY & PIANKA, 1997; OSHANIN ET AL., 2009; VINCENOT Et al., 2015), but the principles are still being used in many areas of research, from herbivores (e.g. THORNLEY et al., 1994) and mollusk-eating shorebirds (Gil et al., 2005), to archeology and neurosciences (HAYDEN et al., 2011; HAYDEN & WALTON, 2014; CODDING & BIRD, 2015), going through a myriad of other uses. The reason of such broad application is because it offers a strong theoretical basis and framework to study behavioral patterns (LACA & DEMMENT, 1996), while being flexible for adapting to new constraints and different scenarios. Here, we do a brief review of some of the principles related to the diet model (*aka*. prey, diet breadth or contingency model), since it will be the focus of this work. Both diet and patch models have similar mathematical solutions, and are well described in Stephen and Krebs (1986) and other literature (CHARNOV, 1976; PYKE, 1984; MCNAMARA & HOUSTON, 1985). More comprehensive documents on the various derivations of foraging theories, comparisons and applications can be find on the cited literature and on recommended papers (also see: WESTOBY, 1974; PYKE et al, 1977; OLLASON, 1980; OWEN-SMITH & NOVELLIE, 1982; BELOVSKY, 1984; MCNAMARA & HOUSTON, 1985; DUMONT, 1995; NEWMAN et al., 1995; FARNSWORTH & ILLUS, 1998; BERGMAN et al 2001; FRYXELL et al., 2004; VAN LANGEVELDE et al., 2008; HENGEVELD et al., 2009).

2.3.2.1. The functioning and application of the diet breadth model

The objective of the foraging theory is maximizing an objective function subject to their constraints (NEWMAN, 2007), assuming that this function is related to the species survival. Many of the classical studies use *net* energy intake as surrogate for evolutionary fitness, while other objective to minimize foraging time. One of the most important steps of the implementation of such models is a clear definition of the constraints (VANDERLIN & WILEY, 1989; BERGAM et al., 2001; NEWMAN, 2007; FRYXEL, 2008). There are three main elements of the foraging models: decision assumptions, which are the base for the forager's choice; currency assumptions, which determine in what the decisions will be based on; and constraint assumptions, which limit animal's feasible choices and limits the pay-off obtained. The decision assumption will determine the best way to make a particular choice, which is the principle of optimization (selection of the best available elements of a specific function).

There are two main problems studied by the foraging models: which items to consume and when to leave a patch. Those questions are the base for the two main branches of forage models, the diet and the patch models. The diet model analyses the decision of taking or not a prey, based on the relative revenue (pay-off) of that specific prey in relation to the food environment. The patch model determines the residency time, how long a forager should stay in the same patch, given diminishing returns as the patch is exploited in relation to the whole food environment available (STEPHEN & KREBS, 1986; NEWMAN, 2007). For both cases, decisions are based on the principles of the marginal value theorem proposed by Charnov (1976), whether is the marginal increase in, for example, net energy intake by adding one more prey item to the diet, or to leave a patch when the marginal capture rate drops to the average rate of the whole food environment.

The currency assumption is regarding the criterion which will be used to compare alternative values of the decision variables. The currency is used to compare all items across the range using a same rate or time parameter, which can be maximized (e.g. net energy or protein intake rate), minimized (e.g. toxin intake rate or time foraging) or stabilized. The constraint assumptions are related to morphological or physiological factors which define limit the relationships between the currency and the decision variables. Constraints can be intrinsic, such as the digestive capacity of the animal or maximum time foraging; or extrinsic, which are the constraints placed by the environment on the animal, such as temperature-limit behaviors. The three basic constraint assumptions are *exclusive search and exploitation*, which states that the forager cannot handle an item while searching for new ones (which is not completely applied for herbivory, see FRANSWORTH & ILLUS, 1996; 1998); *sequential Poisson encounters*, saying that items are encountered in a sequential order, one at the time; and that the forager has *complete information* of the food environment and the rules of the model.

2.3.2.2. The mathematical solution

If we consider that the rate being maximized (R) as being a function of the amount of currency obtained during the period foraging (E_f) by the time foraging (T_f), which can be further broken down in time searching (T_s) and time handling (T_h) the food item, then we have (HOLLING, 1959; STEPHENS & KREBS, 1986):

$$R = \frac{E_f}{T_s + T_h} \quad \text{eq. (26)}$$

Both E_f and T_f are linear functions of T_s . So for a given T_s period of time searching, where certain number of preys were encountered at an average rate of λ , yielding \bar{e} amount of currency at s expense per unit of time searching, and taking an average of \bar{h} amount of time per item handled, then we have that:

$$R = \frac{\lambda T_s \bar{e} - s T_s}{T_s + \lambda T_s \bar{h}} \quad \text{eq. (26)}$$

which can be simplified to (CHARNOV & ORIANI, 1973)

$$R = \frac{\lambda \bar{e} - s}{1 + \lambda \bar{h}} \quad \text{eq. (27)}$$

giving us the rate to be maximized. Considering s as a constant, the long-term rate maximization is

$$R = \frac{\sum_{i=1}^n p_i \lambda_i e_i}{1 + \sum_{i=1}^n p_i \lambda_i h_i} \quad \text{eq. (28)}$$

where underwritten i represents each item in the diet. Given that each prey has a p_i probability of being consumed upon encounter, then

$$R = \frac{p_i \lambda_i e_i + k_i}{c_i + p_i \lambda_i h_i}, \quad \text{eq. (29)}$$

where k_i and c_i are the sum of terms not involving p_i in the numerator and denominator, respectively. When deriving R in relation to p_i , we have

$$\frac{\partial R}{\partial p_i} = \frac{\lambda_i e_i c_i - \lambda_i h_i k_i}{c_i + p_i \lambda_i h_i} \quad \text{eq. (30)}$$

which means that the sign of the derivate of R is independent of p_i (for a more comprehensive explanation on the mathematical development, see Chapter 2 in STEPHEN & KREBS, 1986). For maximizing the rate of currency intake p_i needs to be either the largest ($p_i = 1$) or smallest ($p_i = 0$) possible value, which means either always take or always ignore the food item. This is the base of the “zero-one rule” of the diet model (STEPHEN & KREBS, 1986), and implies that the forager knows the food environment and recognizes the food item immediately upon encounter.

To determine which items should be included in the diet for maximizing the average rate of currency intake, all food items are ranked in decreasing order of profitability (the ratio of currency earned per item by the time it takes for handling it; e_i/t_i) and added to the diet always that the marginal value for including the j^{th+1} item is larger than the item’s profitability [eq. (31)]. Although the marginal value theorem of Charnov (1976) is normally associated to the patch model (diminishing returns), the mathematical solution is similar, and can be further explored on the graphical solution in Figure 6.

$$\frac{\sum_{i=1}^j \lambda_i e_i}{1 + \sum_{i=1}^j \lambda_i h_i} > \frac{e_{j+1}}{t_{j+1}} \quad \text{eq. (31)}$$

Three main results from the diet model are noted by Stephens & Krebs (1986): the zero-one rule, where for maximizing the objective function item should always or never be taken; ranking items, where food items should be added to the diet by order of profitability (largest to lowest e_i/t_i); and independence of inclusion from encounter rate, where the inclusion of an item on the diet depends only on its profitability. Important to note, however, regarding this latest results, is that encounter rates (availability of items) will influence the number of items included in the diet (i.e. if the higher order items are scarce, lower order items have greater probability of being added to the diet).

In a more practical example, if we consider energy as our objective function to be maximized, then each item is classified (ranked) from the greatest to smallest net energy content (amount of energy harvested by the maximum amount of time between cropping or digesting, thus assuming that digestion is one of the main constraints). This is the instantaneous intake rate of the item (slope of the curve). If food items were to be added to the diet in the order of their effective value, the optimal solution is obtained when the maximum

marginal value is reached (i.e. the cumulative net energy obtained when including the i^{th} food item is no longer larger than the set of food items already included in the diet). Whether the item should be included in the diet is then given by comparing the net energy of the specific item to the marginal value.

2.3.2.3. Some general comments

Reading many recent papers and thesis, I realized the misinterpretation of the words “optimal” and “theory”. One student wrote that “the observed behavior of heifers [in a field experiment with variable proportion of tussocks, measuring instantaneous intake rate] was in accordance with *the optimal foraging theory*”. I argued that it should be the opposite: the model should be in accordance (validated) with the results obtained in the field since, at the end of the day, the animal is the one making the choices, and we are just trying to understand those decisions based on our limited knowledge on behavior and mathematical tools. The animal is the standard, not what we think it should eat. In fact, the goal of the optimality strategy is not to test whether the animals are optimal per se, but to aid on identifying the objective function being used and constraints associated to it (MICHELL & VALONE, 1990; DUMONT, 1995; NEWMAN, 2007).

Some very interesting points regarding those misinterpretation are noted by Ydenberg et al (2007) on the first chapter of “Foraging Ecology” (STEPHENS et al., 2007), which could be viewed almost as a sequence to Stephens & Krebs’ 1986 Foraging Theory. First, the “optimality” is just a mathematical procedure used to identify the diet which will give the best marginal return. It does not imply an optimal diet from the animal’s stand point (DUMONT, 1995; NEWMAN, 2007). Furthermore, it is not the only focus of the foraging theory, and the term overemphasizes the wrong aspects of the problem. The word “theory” adds to the confusion. Many take it as an inflexible set of rules, the general principles of a system or behavior, such as the Evolution Theory or the Relativity Theory, for example. In fact, in this case it relates more to the “theoretical approach” than to a body of principles to explain the phenomena. More than a theory, it is a method. The optimal foraging theory is a set of mathematical procedures (or a mathematical approach) used to, in a simple manner, simulate diet decisions taken by the forager. This misinterpretation lead many ecologist to view this “theory” as a “stumbling block” that lead to “[...] a sterile pursuit with little relevance to the rough-and-tumble reality of the field” (YDENBERG et al., 2007; see also NEWMAN, 2007).

Ydenberg et al (2007) finish their chapter saying that “the simplicity of both the diet and the patch models is deceptive”, and for reaching a full understanding of the functioning of the mechanisms involved takes a large effort. One needs to be careful as well, since the literature also contains a variety of misinterpretation and misconceptions, which persist with the published material (e.g. BARKAM & WITHMAN, 1989; *c.f.* SMITH & WINTERHALDER, 1985; NEWMAN, 2007; VINCENOT et al., 2015). Thus, I recommend reading the classical papers (e.g. CHARNOV, 1976; PYKE, 1977; OWEN-SMITH & NOVELLIE, 1982; STEPHENS & KREBS, 1986; FRANSWORTH & ILLIUS, 1998; STEPHENS et al., 2007) for a deeper understanding of the principles of foraging ecology and diet choices.

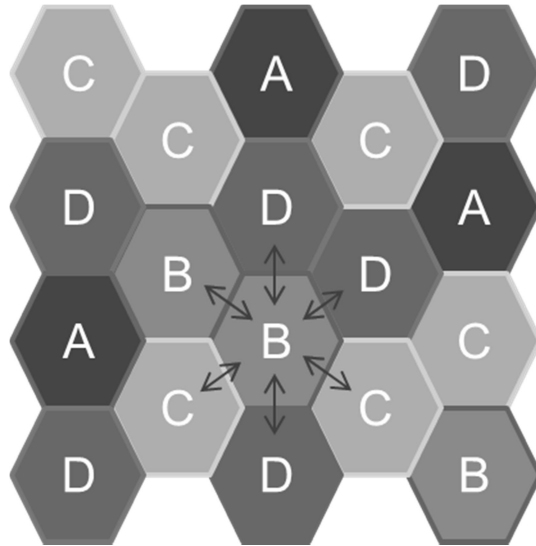


Figure 1. Lattice of hexagonal cells. Arrows represent interaction between cells, and letters represent different states.

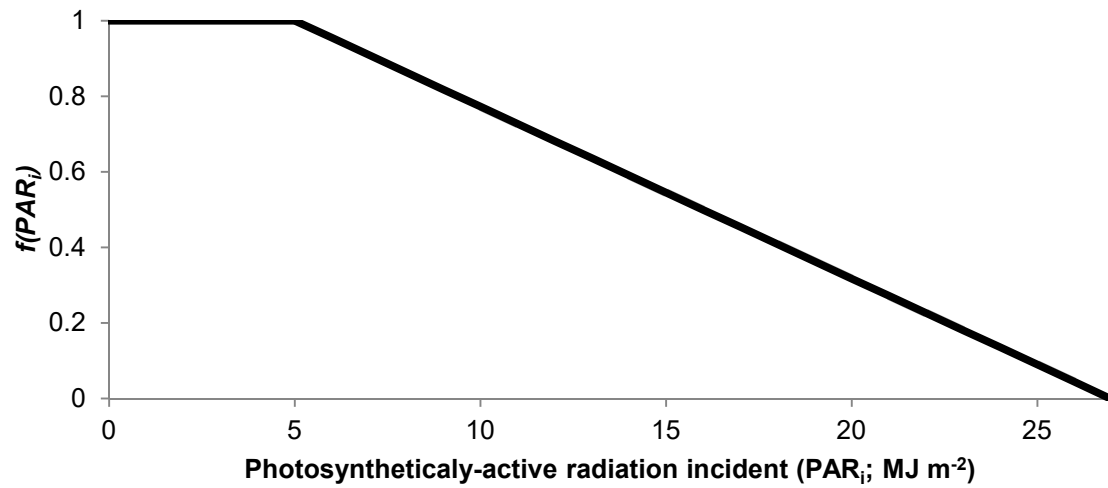


Figure 2. Light saturation threshold function for potential growth limitation as function of photosynthetically-active radiation incident (PAR_i , $MJ\ m^{-2}$; after SHAPENDONK et al., 1988)

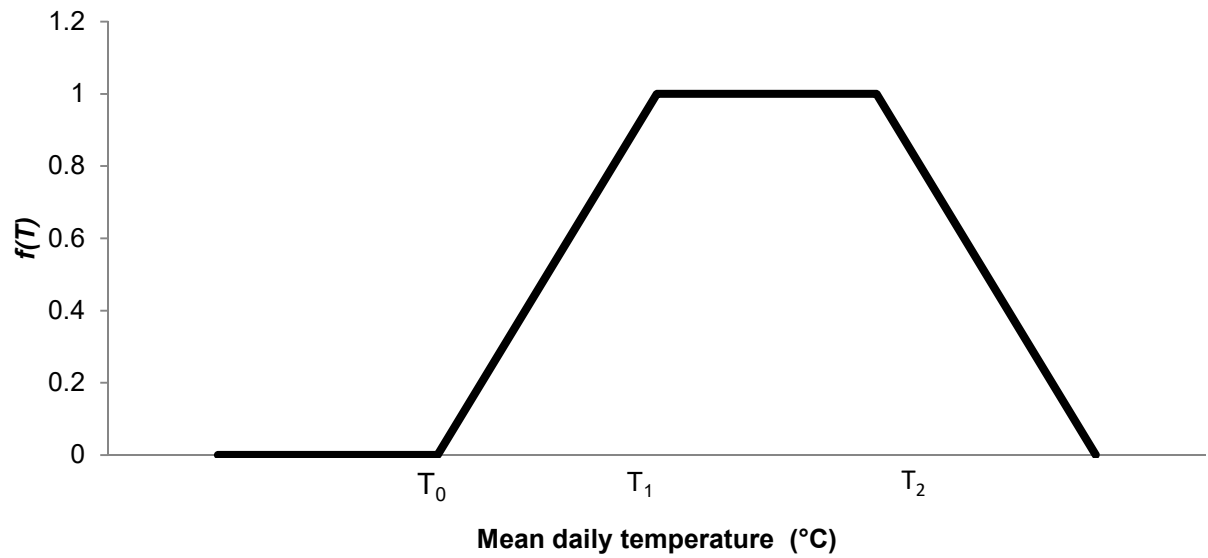


Figure 3: Temperature threshold function for potential growth limitation as function of mean daily temperature (T , °C; after SHAPENDONK et al., 1988)

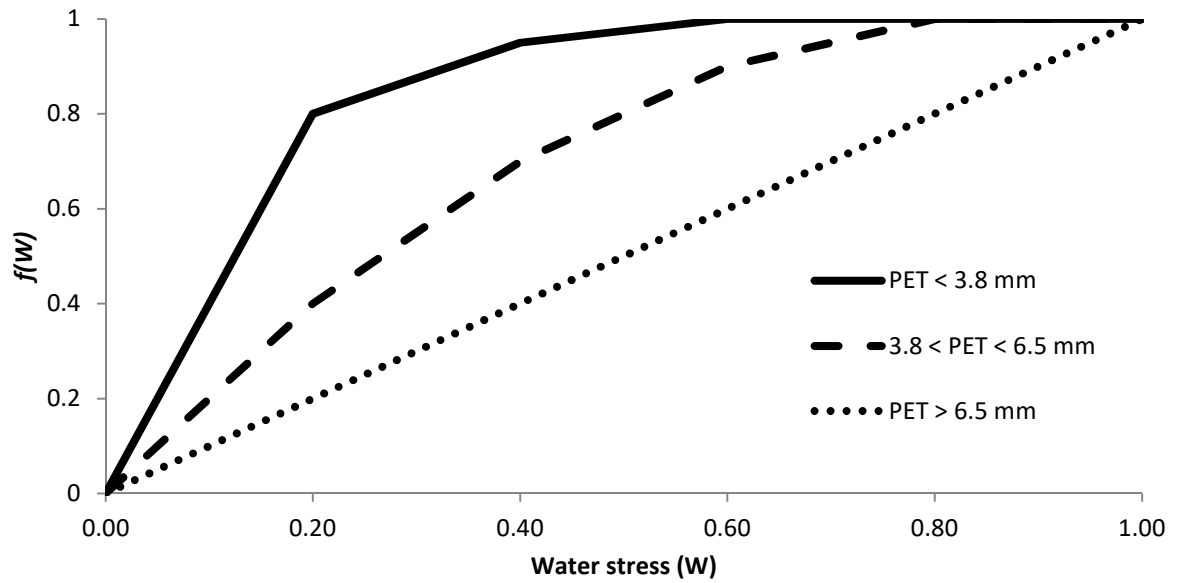


Figure 4: Water threshold function for potential growth limitation as function of water stress (W , unitless; after MCCALL & BISHOP-HURLEY, 2003). Solid line for potential evapotranspiration (PET) < 3.8 mm, dashed line for 3.8 < PET < 6.5 mm, and dotted line for PET > 6.5 mm.

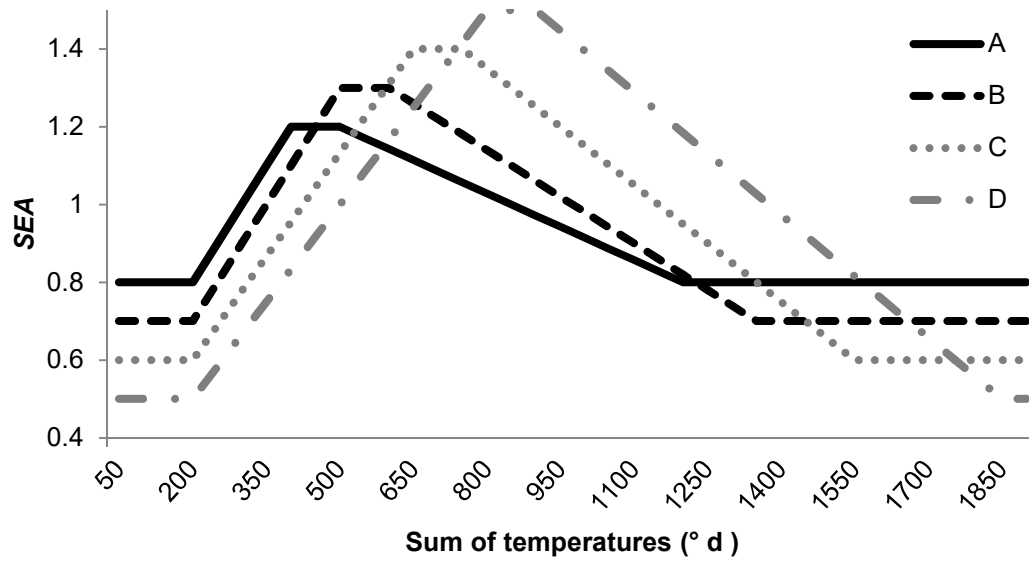


Figure 5: Seasonal effect (SEA) on growth as function of sum of temperatures, per functional group. Solid, black line for functional group A, dashed, black line for functional group B, dotted, grey line for functional group C, and dash-dot, grey line for functional group D. On the original model (for northern hemisphere, season (sum of temperature 0) starts on 1 January. SEA starts decreasing when the reproductive (REP) period begins, and is at minimum at the end of REP.

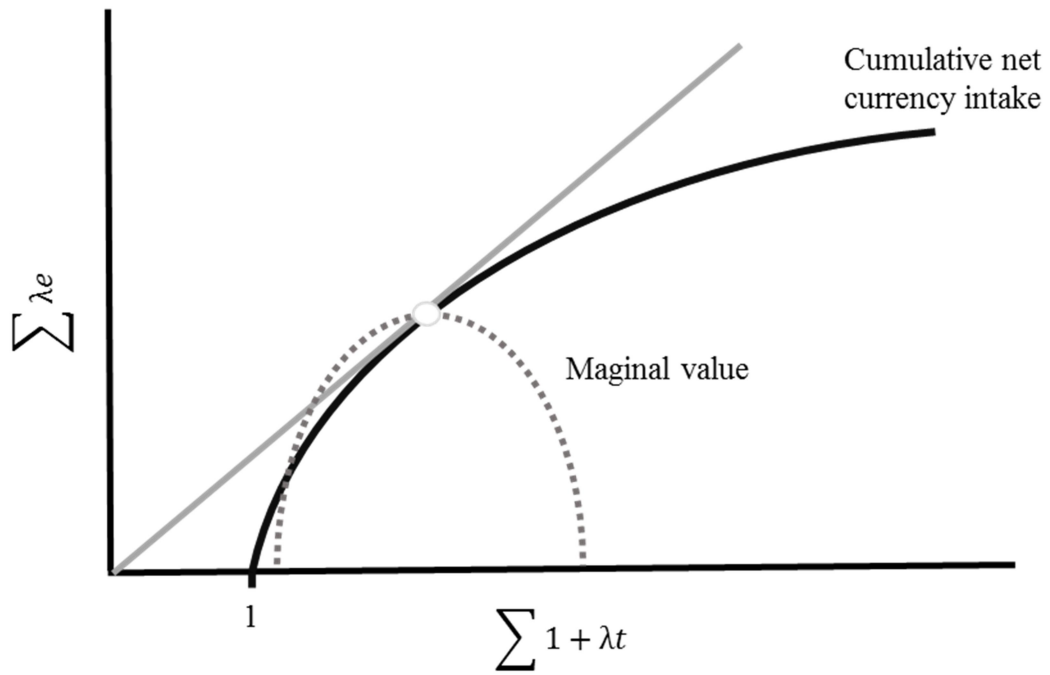


Figure 6. Graphical solution for diet model algorithm. Black line represents the cumulative net currency intake, added in the order of the rank of profitability of individual items; dashed grey line represents the derivate of the currency in respect to time, where the maximum marginal value represents the threshold value (white dot) for items that should be taken (i.e. items with e_i/t_i lower than threshold should not be taken); the solid grey line is the tangent of the maximum marginal value to the origin.

CHAPTER III – THE VEGETATION MODEL

3. ADAPTATION OF A FUNCTIONAL TRAIT-BASED VEGETATION MODEL TO SUBTROPICAL COMPLEX GRASSLANDS

Abstract

Simulation models can be important tools for studying and representing the effects of variable environmental conditions and disturbances in ecosystems. First, from the perspective of decoupling the components of the system in the model's assembling process, allowing for analyzing the functioning and role of each part. Secondly, for exploring responses to a large array of scenarios, manipulating aspects otherwise unviable or impossible under field conditions. In an attempt to study the herbage production dynamics of complex, heterogeneous grasslands, we adapt a mechanistic vegetation model (ModVege; Jouven et al., 2006a) to subtropical, C4 dominated conditions, creating PampaGraze. PampaGraze is based on the concept of functional groups, assuming that functional composition represents diversity, and functional traits of the composing species account for most of the important aspects needed for modeling resources capture and use, and responses to environmental factors and defoliation regimes. We made several changes on parameters and equations for accommodating for the different photosynthetic pathway of the dominant species and for environmental characteristics, later testing the new version of the model against observed data from a long-term grazing experiment in the Southern American Campos region. The validation was very limited by the quality of the observed data, but it was possible to observe a proper general behavior of the model, despite the overall overestimation of herbage production. We simulated scenarios under sequence of dry and wet years, and under various cutting regimes (0, 4, 12 and 24 per year). Herbage growth responded linearly to water limitation, quickly recovering after water reserves were replenished, as was apparently minimally affected by other environmental constraints. Cutting majorly reduced the amount of dead biomass, having basically no influence on herbage growth. The model was not able to simulate herbage production of slow-growing, tussock forming grasses because of some important unaccounted physiological and morphological processes which require a larger alteration of the model's structure to be fixed. For further developments, there is an eminent need on data for parametrizing morphogenesis in response to seasonal patterns, and better quality data for validation. Despite the limited performance, the model is very promising, and properly fixed can be an important tool for studying the dynamics of herbage production in subtropical grasslands.

Key words: simulation model, tussocks, Campos grasslands, functional groups

3.1. Introduction

Native grasslands are complex ecosystems composed by a large quantity of distinct entities coexisting and interacting. The degree of complexity depends on the arrangement and integration of the system components (Tainton et al., 1996), subjected to environmental variation and level of disturbance. Since most biological responses are non-linear in time and space (Parsons and Dumont, 2003), understanding the magnitude and direction of those changes in response to disturbances is fundamental for determining adequate management practices (Friedel et al., 2000; Gordon, 2000). This, however, sometimes requires knowledge not yet available or poorly understood. Conceptual managerial or ecological models (e.g. Dyksterhuis, 1949; Noy-Meyer, 1975; Westoby et al., 1989; and Briske et al., 2003 for a review) can give guidance on the development of the rationale, but without a mathematical framework for the system, discussing those concepts becomes a mere process of accumulating recurring case stories (Lockwood and Lockwood, 1993). In this scenario, mathematical modeling can be an important tool for exploring some of those mechanisms and relationships, helping understanding the complex dynamics of pastoral ecosystems.

Most the grassland models where developed for cultivated, mono-specific or two-species mixed pastures (e.g. Johnson and Thornley, 1983; Schwinning and Parsons, 1996; Hutchings and Gordon, 2001; McCall and Bishop-Hurley, 2003) or require a large amount of detailed information, many times unavailable [e.g. Coughenour et al 1993; Oom et al., 2004; Kiniry et al., 2007; Richardson et al., 2010; see Bryant and Snow (2008) and Andrade et al. (2015) for general review on grassland models]. Whereas there are lots of data on species such as ryegrass and white clover (e.g. Parsons et al., 1983; Chapman and Parsons, 2000; Chapman et al., 2012), the level of understanding of physiological parameters and morphological processes of most species composing native grasslands, is very limited (Duru et al., 2009).

A mechanistic model which simulates vegetation dynamics and spatial heterogeneity, and that realistically incorporates grazing, has not yet been developed for sub-humid, sub-tropical grasslands. The development of such tool can be very useful for exploring the dynamics of herbage production and disappearance under variable environmental conditions, helping improving management practices and conservation guidelines. To study the structural (heterogeneity and botanical composition) response of pastures to grazing and environmental factors, we need a model that represent multiple-species and multiple compartments within plants, accounting for botanical diversity and canopy structure, for determining animal's

selectivity under variable grazing pressures, and shifts in vegetation due to disturbances.

In a first step towards that direction, we propose adapting ModVege (Jouven et al., 2006a), a compartmentalized vegetation model, to represent the herbage dynamics of the Campos grasslands in Southern Brazil. This model uses the concept of functional traits to group species of similar response to environmental characteristics and defoliation regimes (Cruz et al., 2010; Diaz et al., 2004), assuming these traits incorporate most of the relevant variables for modelling the capture and use of resources, biomass allocation and tissue flows (Jouven et al., 2006a; Duru et al., 2009). The use of functional groups for representing vegetation communities is widely recognized approach for accounting and understanding diversity, especially when lacking more detailed data on composing species or when the botanical arrangement of the studied environment is complex or poorly known (Diaz and Cabido, 2001). This method has long been used for describing ecosystem processes, responses, productivity, nutrient cycling and management (Wright et al 2004; Diaz et al., 2004; Ansquer et al., 2009, Cruz et al., 2010). Relatively simple parameters (soft traits), hence, can bring very important information to be considered when modeling vegetation dynamics, and responses to seasonality and disturbances (e.g. rainfall, nutrient availability, grazing).

The objectives of this paper is to report the adaptations made on ModVege for accommodating to sub-tropical conditions, representing a C4, perennial-grass dominated pasture. ModVege has already been validated (Jouven et al., 2006b) and tested for simulating other temperate pastures with different groups of species (Hurtado-urria et al., 2013; Calanca et al., 2016). To validate PampaGraze to the Campos conditions, we compared simulations to data from a long-term grazing experiment (Cruz et al., 2010; da Trindade et al., 2012), from which we dispose of 13 years of detailed data and 17 years of summarized data from published material (e.g. Maraschin, 1998; Moojen and Maraschin, 2002).

3.2. Materials and methods

3.2.1. Model description and adaptations

PampaGraze is a conceptually simple, mechanistic, dynamic model, developed to study “the effects of management (type and intensity) on biomass, structure and quality dynamics” of multi-specific perennial pastures (Jouven et al., 2006a). It uses the concept of functional traits to group species into categories based on vegetative and reproductive traits, diverging, especially, in morphogenesis [leaf

lifespan (*LLS*)] and leaf morphologic characteristics [leaf dry matter content (*LDMC*) and specific leaf area (*SLA*)], resource use, and response to seasonal patterns. Thus, we assume functional traits provide information on most of the relevant variables for simulating herbage dynamics and that will further influence grazing behavior (i.e. diet selection; Pfeifer and Hartnett, 1995; Mingo and Oesterheld, 2004; Duru et al., 2009; Cruz et al., 2010). This approach differs from the traditional sink-source models, where growth rates are determined by the relationships between light interception (and carbon and nitrogen pools; “sources”), and leaf and tiller dynamics (“sinks”; e.g. Shapendonk et al., 1998). Since most species which compose complex grassland ecosystems have not been deeply studied, and there are few morphological and physiological parameters already known (Duru et al., 2009). Therefore, we use a source-driven approach, where biomass is produced from light intercepted and further partitioned into compartments (Jouven et al., 2006a; Duru et al., 2009).

There are five major assumptions adapted from the original model (Jouven et al., 2006a):

- 1) the functioning of perennial, heterogeneous grasslands can be explained by the mean value of functional parameters of the species composing each functional group;
- 2) sward heterogeneity can be described by the relative abundance of structural components, which determines nutritive value and allow for grazing selectivity within the sward;
- 3) growth, senescence and decay can be described as continuous flows;
- 4) shoot growth is regulated by seasonal pattern which accounts for storage and mobilization of carbon reserves;
- 5) nutritive value of green compartments is determined by compartment aging.

In the original model proposed by Jouven et al. (2006a), values for the biological attributes used are weighted averages based on the relative functional composition of the whole pasture. Here, we will analyze the dynamics of each functional group separately, as a preparation for a further spatially-explicit development. Since Modvege was developed for temperate grasslands, we had to make several changes to adapt PampaGraze for sub-tropical, C4-dominated grasslands, especially in the temperature-dependent functions. Equations which were modified will be described below, and other should be referred to in Jouven et al. (2006a) and on item 2.2.3. The model was developed using JAVA (Java SE 8).

3.2.1.1. Differential equations

The whole assembly of the model is based on the processes within each of the four structural compartments. The sward is divided into green vegetative ($_{GV}^5$), green reproductive ($_{GR}$), dead vegetative ($_{DV}$) and dead reproductive ($_{DR}$) compartments (Carrère et al., 2002). Each of the four compartments works separately, and is described by a state variable of standing biomass (BM_c , kg dry matter [DM] ha⁻¹, where underwritten “c” designates each of the four compartment). As compartment ages, nutritive value (as organic matter digestibility – OMD_c) decreases linearly. A set of differential equations control biomass accumulation and disappearance, and aging dynamics within each compartment, in a daily time step.

To the main differential equations which included the flow of biomass from green to dead compartments (i.e. dBM_c/dt and $dAGE_c/dt$) it was added a remobilization factor (α , unitless) for accounting for remobilization of carbohydrates, N and other elements from senescing material back into the green compartment (Cros et al., 2003; Romera et al., 2009; Duru et al., 2009). This number was suggested by M. Duru (unpublished data, on Cros et al., 2003) as being close to 15% of total leaf weight, which is set as 68% of total green biomass in the original model (see eq. [10]). Therefore, α was set to 10.2%.

3.2.1.2. Growth functions

Some major changes were done in the components of the growth function (GRO , kg DM ha⁻¹; eq. 11 in Jouven et al., 2006a). Potential growth ($PGRO$, kg DM ha⁻¹), is still calculated by the same original equation, after Schapendonk et al. (1998; equation 12 in Jouven et al., 2006a), but with some of the parameters altered to better fit the conditions to which this model is being adapted. So,

$$PGRO = PAR_I \times RUE_{MAX} \times [1 - \exp(-k \times LAI)] \times 10, \quad \text{eq. (1)}$$

where PAR_I is the total incident photosynthetic active radiation at the top of the canopy (in MJ m⁻²), considered to be 48% of global incident radiation (Varlet-Grancher et al., 1989). RUE_{MAX} is the maximum radiation use efficiency (g DM MJ⁻¹), k is the extinction coefficient that indicates the leaf angle, and LAI is the leaf area index (m² m⁻²). The “10” (kg m² ha⁻¹ g⁻¹) is a factor to convert units to kg DM ha⁻¹. The original model uses fixed RUE_{MAX} and k for all functional groups. For the extinction coefficient (previously set to 0.6), there are major differences depending on the canopy architecture for each functional group. Group “A” is characterized by prostate grasses, while groups “C” and

⁵ Underwritten “c” refers to compartment within cell, and underwritten “i” refers to cell characteristics

“D” are basically of cespitose, tussock-forming species. For example, k for *Paspalum notatum*, one of the major components of the functional group “B” varies between 1.1 and 1.72 (Kiniry et al., 2007; Barro et al., 2012), values much above to the one assigned in the original equation. For RUE_{MAX} the model uses 3 g DM MJ⁻¹, after Schapendonk et al (1988). Nevertheless, RUE_{MAX} values vary considerably between species and environmental conditions. Radiation use efficiency for *Andropogon gerardii* and *Schizachyrium scoparium* range from 1.0 to 1.6 g DM MJ⁻¹ (average 1.4 g DM MJ⁻¹; Kiniry et al., 1999) and 1.1 to 2.7 g DM MJ⁻¹ of PAR_I (Weiser et al., 1986), while for *Panicum virgatum*, for example, ranges from 1.6 to 4.7 g DM MJ⁻¹, depending on environmental conditions (Kiniry et al., 1999). For *Paspalum notatum* and *P. dilatatum*, Barro (2011) found 1.69 and 2.12 g DM MJ⁻¹, for average between full sunlight, 50% and 80% shading.

The conversion efficiency of absorbed light into assimilates is variable, and dependent on radiation intensity, temperature and water availability (Schapendonk et al., 1998). Light saturation [$f(PAR_I)$] reduces photosynthesis when radiation intensity (PAR_I) reaches over 12.9 MJ m⁻² and virtually stops at 26 MJ m⁻² [eq. (2); after Schapendonk et al., 1988; and parameters calculated from Kiniry et al., 1999].

$$f(PAR_I) = \min[1, 1 - 0.07634 \times (PAR_I - 12.9)] \quad \text{eq. (2)}$$

Maximum growth as function of temperature [$f(T)$ after Schapendonk et al., 1998] is obtained at an optimum temperature range, from T_1 to T_2 (set to 25 and 35 °C, respectively), while growth is null if average temperature of the day (T) is below the basal temperature ($T_0 = 9$ °C; Agnusdei, 1999) or above maximum temperature ($T_{max} = 42$ °C). The $f(T)$ is now described by

$$f(T) = \begin{cases} 0, & \text{for } T < T_0 \text{ or } T > T_{max} \\ (T - T_0)/(T_1 - T_0) & \text{for } T_0 < T < T_1 \\ 1 & \text{for } T_1 \leq T \leq T_2 \\ (T_{max} - T)/(T_{max} - T_2) & \text{for } T_2 < T < T_{max} \end{cases} \quad \text{eq. (3)}$$

Water availability is one of the most restrictive factors in native grassland environments (Friedel et al., 2000). Photosynthesis is limited by of stomatal closure, which reduces plant transpiration and restricts CO₂ uptake. Water stress [$f(W)$; Figure 1] was originally modulated after McCall and Bishop-Hurley (2003). Alternatively we used the framework proposed by Calanca et al. (2016), based on Allen et al. (1998). Despite the authors finding no difference between the methods when testing for C3 grasslands, we believe that McCall and Bishop-Hurley (2003) approach penalized growth too much at higher potential evapotranspiration (PET) levels, especially for C4 species and for an environment where evapotranspiration is frequently above what

they considered the threshold for the maximum level of stress. The same effect was observed by Hurtado-Uria et al. (2013) when testing ModVege for perennial ryegrass (*Lolium perenne* L.), where they stated that the ability of the model to handle water holding capacity and reserves could be over-limiting herbage production, especially under drought conditions. Allen's et al. (1998) method considers that water stress, independently of the *PET* level, reduces growth only after water reserves reach below certain proportion of field capacity (given by a p_5 crop factor). So,

$$f(W) = \text{MIN} \left[1, \frac{W}{1 - (p_5 + 0.04 \times (5 - PET))} \right], \quad \text{eq. (4)}$$

where $p_5 = 0.6$ for pasture and grasslands.

To account for root depth, we determined different soil water available for each functional group, using soil water holding capacity as a proxy. Effective depth to which plants have access to water varies based on soil type and landscape, and access to water depends on below-ground sward architecture, which is distinct between functional groups. Prostrate grasses (i.e. groups A and B) will only have access to shallower depths, compared to cespitose, buchgrasses (i.e. groups C and D), which means that they will suffer earlier from effects of water limitation. Resource utilization strategy and growth rates are tidily linked to some important functional parameters which are being used in this model, such as SLA, LDMC and LLS (Diaz et al., 2004). The resource capture characteristic of the first group, and greater growth rates, will both require more water availability and be more affected by water restrictions than the second group, of resource conserving, slower growing grasses, which are also able to explore a larger volume of soil (Darnier and Briske, 1999; Diaz et al., 2004; Cruz et al., 2010). Nevertheless, soil organic matter immediately beneath tussocks is greater than in vicinity areas, what enhances the soil capacity for accumulating water (Darnier et al., 1997).

The season (*SEA*, unitless; Figure 2) is an empirical function proposed by Jouven et al (2006a) based on information from the literature (Thornton et al., 1993; 1994; Bausenwein et al., 2001), especially on N remobilization. Season regulates growth by indicating whether there is reserve mobilization or storage of assimilates. For cool-season grasses in temperate regions, the first and faster flush of growth starts in the spring, associate with the higher photosynthetic rates of the younger and unshaded tissues during reproductive period (Woledge, 1972; Orr et al., 1988; Duru et al., 2009). For warm-season grasses in sub-tropical regions, the first flush of growth is vegetative, from late-spring to mid-summer, whereas the reproductive period is delayed to mid- to late-summer. Season function was adapted using phenological data from several major

species of the Campos grasslands, further clustered into specific functional groups. The adapted function was based primarily on reproductive status, with *maxSEA* starting mid-spring for representing the peak of growth, which is limited when reproductive growth starts, mid- to late-summer (Rosengurtti et al 1970, Rosengurtti, 1979, Schefer-Basso et al., 2002). The length of the decline from *maxSEA* to *minSEA* represents concentrate flowering (sharp decline) or flowering over a longer period of time (slow decline). Similar approach was used by Kiniry et al. (2002) to reduce radiation use efficiency after anthesis, where a large parameter value simulates a fast, non-linear decrease in biomass accumulation.

Two other parameters were added: ST_0 , which represents the beginning of linear increase of *SEA*, and ST_m , level at which *SEA* is maximum, up to ST_2 . The ST_1 and ST_2 now represents the approximate thermic sum for the month corresponding to the beginning and end of reproductive period for each functional group (Table 1). *SEA* is set to minimum when $ST \leq ST_0$ or $ST \geq ST_2$; to maximum when $ST_m \leq ST \leq ST_1$; increases linearly from *minSEA* to *maxSEA* when $ST_i < ST < ST_m$, and decreases at the same fashion when $ST_1 < ST < ST_2$. Since FG A and B are composed of resource capture species, with greater growth rates, those are able to sustain maximum growth (when not limited by other factors) for a longer period of time than compared to FG D. *SEA* is coordinated by the following set of rules:

$$SEA = \begin{cases} minSEA, & \text{if } ST \leq ST_i \text{ or } ST \geq ST_2 \\ minSEA + (maxSEA - minSEA) \times \frac{ST - ST_i}{ST_m - ST_i} & \text{if } ST_i \leq ST \leq ST_m \\ maxSEA, & \text{if } ST_m \leq ST \leq ST_1 \\ (maxSEA + (minSEA - maxSEA) \times \frac{ST - ST_1}{ST_2 - ST_1}) & \text{if } ST_1 \leq ST \leq ST_2 \end{cases} \quad \text{eq. (5)}$$

3.2.1.3. Senescence and decay functions

In the original model, senescence (SEN , kg DM ha⁻¹) is proportional to the BM_{GC} , mean daily temperature (T , °C) and senescing rates proposed after Ducrocq (1996), and stimulated by pool-aging relative to leaf lifespan (LLS , °d), for the vegetative compartments, or to the reproductive period ($ST_2 - ST_1$), for the reproductive compartments (Figure 4 in Jouven et al., 2006a). Using this approach, values for senescence and decay [as decay in Jouven et al., 2006] were very high, often overcoming growth and resulting in extinction of biomass. The change in terminology (decay to decay) is proposed because grasses in general do not have decay layer on leaves (i.e. leaves do not shed), and it is used as a proxy and simplified manner for

representing microbial and environment-related decay (McCall and Bishop-Hurley, 2003; Tomlinson et al., 2007).

Alternatively, we calculate senescence rates for the green vegetative biomass (K_{GV} , in $^{\circ}\text{C}^{-1}$) from published studies [measured values in Cruz (1998) and Machado et al. (2013)] as function of average temperature for the day and proportional to biomass. Data on senescence rates for reproductive material (K_{GR} , in $^{\circ}\text{C}^{-1}$) for the species being considered is not available. Since turnover of reproductive tissue is slower than for vegetative (Orr et al., 1988), K_{GR} was considered as being half of K_{GV} , and decay rates as half of senescence rates for the respective compartments (same approach as presented in Jouven et al., 2006a). New values for K_{Gc} and Kl_{Dc} are presented on Table 1. The function of age as presented in the original model was removed, since the rapid aging of compartments was excessively increasing senescence and decay, which would soon overcome growth. Adapted the formula for SEN_{Gc} and DEC_{Dc} (formerly ABS_{Dc}) are:

$$SEN_{Gc} = K_{Gc} \times BM_{Gc} \times T \quad \text{eq. (6)}$$

$$DEC_{Dc} = Kl_{Dc} \times BM_{Dc} \times T \quad \text{eq. (7)}$$

3.2.2. Parametrization

Parameters (Table 1) were obtained from literature on native grasslands from the Campos or similar genera in equivalent environments, while other (e.g respiration) were kept as proposed by Jouven et al. (2006a). Parameters not directly available (e.g. senescence and decay rates) were estimated from data presented in the literature. The lack of pattern on methodology for measuring and units for representing physiological parameters, especially those related to rate efficiencies and biomass flows makes combining data challenging and misleading. Those aspects were carefully accounted for when considering and calculating the parameters used, and further tested within each equation to assure reasonable values were obtained. For the functional group classification we use information presented by Cruz et al. (2010).

3.2.3. Verification, validation and model evaluation

The original ModVege has already been validated against diverse temperate grasslands, with distinct botanical composition and submitted to variable water and nutrient regimes (Jouven et al., 2006b; Hurtado-Uria et al., 2013; Calanca et al., 2016). It has accurately simulated herbage dynamics, structure and digestibility (Jouven et al., 2006a), and proved to be a functional and robust model for studies at multiple scales, with minimum need for parametrization (Calanca et al., 2016). For testing our

adaptations, multistage validation procedure (Rykiel, 1996) was performed at several phases of the model development. Adaptations were done based on theoretical and empirical (expert) knowledge. Each equation and group of equations was tested analytically, to verify correctness of the mathematical solution, unit preservation, and biological meaning of the range of values obtained. The internal logic was tested by checking energy flow maintenance between sections and general behavior of the model. To check the implementation and general functioning, the model was tested empirically, using real input data to verify outputs. At a later stage, the simulation outputs were compared to experimental data for statistical validation (Rykiel, 1996; Willmott et al., 2012, Bennett et al, 2013; Yang et al., 2014).

3.2.3.1. Data source

For the validation procedure, we utilized data on herbage accumulation rate (*HAR*; kg DM ha⁻¹ d⁻¹) of native grasses from a long-term grazing experiment on the Campos Grasslands in the Central Depression region of Rio Grande do Sul, Brazil. The experiment is located at the Agricultural Experimental Station of the Federal University of Rio Grande do Sul (EEA-UGRFS) in Eldorado do Sul (30°05'S; 51°40'W), Brazil. It consists of seven herbage allowance levels, fixed or variable along seasons, ranging from 1 to 4 kg DM kg LW⁻¹ (animal live weight), replicated twice in space. Monthly, herbage accumulation and standing biomass are evaluated for adjusting stocking rates for maintaining constant herbage allowance. Herbage accumulation was measured using three to four exclusion cages per paddock, using a double-sampling technique (Haydock and Shaw, 1975), and *HAR* was assessed by dividing the herbage accumulated in the cages by the period of time between evaluations. For more details on experimental design and procedures, refer to Soares et al. (2005) and da Trindade et al. (2012).

The Campos Grasslands are composed by a large diversity of plant species, dominated by C4 perennial grasses, and forming a mosaic of slow-growing, tall bunch-grasses (functional groups C and D) interspersed with faster-growing prostrate grasses (functional groups A and B). The botanical composition and spatial (horizontal and vertical) arrangement of those pastures depend mainly on management (e.g. grazing pressure) and soil characteristics (e.g. type and *WHC*). Because of the evaluation protocol, only data from functional groups A and B are available, and not discriminated. Main composing species of group A are *Axonopus affinis* and *Panicum sabulorum*, and *Coelorachis selloana*, *Paspalum paucifolium*, *Paspalum notatum* and grazed *Andropogon lateralis* on group B. Because of high plasticity on morphological (height)

and leaf (*LDMC* and *SLA*) traits, *A. lateralis* can be classified as both functional group B or C, depending if grazed shortly or forming tussocks, respectively (Cruz et al., 2010).

Herbage accumulation rate data was divided in two pools: from 1986 to 2003, where only averages per treatment per season were compiled from published thesis and scientific articles; and from 2004 to 2013, when more detailed information on both herbage accumulation per plot per period and weather were available. Because of the experimental protocol, we only have data for FG A and B, and not discriminated (i.e. samples include both FG in distinct proportions, depending on treatment and on site in the landscape). Since differences in *HAR* between the original treatments of the experiment were, most of the times, not significant, the treatment effect was not considered in the analysis. Data from the lowest herbage allowance treatment (1 kg DM kg LW⁻¹), however, were not used, since close grazing could affect herbage growth. A total of 62 evaluation periods were available for 12 plots. Data was then aggregated by month and by season for comparisons. Due to the characteristic of the field evaluation methodology (exclusion cages), interannual variability, and several changes on personnel involved on the experiment, the variability of the data is very large, which imposes severe limitations to the validation procedure.

For the simulations, 25 years (Aug-1988 to Jul-2013) of weather data were obtained from a local automated meteorological station. Figure 3 shows average and deviations for precipitation, temperature, rainfall and evapotranspiration. Average rainfall over the 25-year period was 1563 ± 237 mm, relatively well distributed, with monthly average ranging between 104 ± 67 mm in May to 166 ± 80 mm in September. For direct monthly comparisons with observed *HAR*, only the period from 2004 to 2013 was used. Simulated *HAR* was computed as the difference in total biomass (from all compartments) between two dates matching exactly the field evaluations, divided by the period, in days, between evaluations. We did not use the output for the growth function because it does not account for senescence and decay, and would not be comparable to the field data. *HAR* data was then aggregated in months and seasons for comparisons. For general model behavior and comparisons of simulated to observed seasonal averages, 25-year simulations were run.

For observing the behavior of the model in contrasting conditions (i.e. dry vs. wet years), growing seasons (i.e. Aug-1 to Jul-31) were separated into dry, normal and wet, based on the sum of $f(W)$, which represents the cumulative water stress. Years with $\sum f(W)$ lower than one standard deviation below average years were considered Dry (seasons starting in August 1988, 1990, 1995, 1998 and 2005), whereas one standard deviation above or more were considered Wet (seasons starting in 1997,

2000, 2001, 2002 and 2009). For comparison, normal years (1991, 1992, 1993, 1994, 2003, 2006 and 2007) were considered as being within 0.5 standard deviations from the average of $\sum f(W)$. Since the parameter used is one-dimensional, a graphical analysis was performed to check if the magnitude and extent of water limitation condition for selected years was in accordance with the classification. Each year was simulated independently and then pooled for data analysis, to avoid cumulative effect of subsequent years. For standardizing the comparisons, initial biomass for each compartment for each simulation was set as average biomass simulated for end of the season (Jul-31) for normal years. Since no grazing submodel has been implemented yet, we will use the original cut management (Jouven et al., 2006a,b) to impose defoliation regimes to test our adaptations. Cut is fixed to a stubble of 5 cm, independent of canopy height or biomass. Height is calculated bases on bulk density of each compartment.

3.2.3.2. Statistical procedures

Whole-model statistics were computed for comparisons between simulated and observed *HAR*. Mean error (E) is a simple statistics for assessing the predictive bias of the simulated values to over- or underestimate observed data (Power, 1993). The residual variance between simulated and observed was measured using the *RMSE* (Yang et al., 2014). Mean absolute error was used for reducing bias towards large events (Bennett et al., 2013). The modeling efficiency [EF , Eq. (8); Nash and Sutcliffe, 1970; Yang et al., 2014] determines the relative magnitude of residual variance (difference between simulated and observed) compared to the variance on the measured data. The magnitude of difference between simulated and observed deviations about the observed mean, the refined index of agreement [d_r , Eq. (9); Willmott et al., 2012] was calculated as presented in Yang et al. (2014). For a direct comparison, the coefficient of determination (r^2) was calculated (Yang et al., 2014).

$$EF = 1 - \frac{\sum(y_i - x_i)^2}{\sum(x_i - \bar{x})^2}, \quad \text{Eq. (8)}$$

$$d_r = 1 - \frac{\sum |y_i - x_i|}{2 \sum |x_i - \bar{x}|} \quad \text{Eq. (9)}$$

Since this is a deterministic model, outputs are the same for each set of variables input. The exploration of the model in the 25-year simulations and different weather scenarios (Dry and Wet) was done primarily by graphical analysis and measures of dispersion, represented by averages by month or raw data for the whole simulation length. Statistical significance tests for interpreting simulation results is

discouraged for this type of model, since lower and lower significance levels will be achieved as more simulation runs are added (White et al., 2014).

3.3. Results and discussion

3.3.1. Verification and validation against experimental data

We have two set of validation, for each FG A and B: the first simulation without biomass removal; a second set of simulations was performed with monthly cuts to 5-cm stubble to account for grazing, since all *HAR* data available are from grazed areas. Because of the large variation on observed data, the whole-model statistics (Table 2) were also poor and will be just briefly discussed. Overall average for observed *HAR* was 11 kg DM ha⁻¹ d⁻¹ (SD = 12 DM ha⁻¹ d⁻¹), being the most productive in Nov and Feb (27 and 18 kg DM ha⁻¹ d⁻¹) and most variable in Nov and Jan (18 and 17 kg DM ha⁻¹ d⁻¹; boxplot on Figure 4). The simulations were more variable in Dec and Jan, which correspond to most sensitive months in dry years because of the very large evapotranspiration. When looking at the annual average *HAR* for uncut simulations, it approached zero, since the system is close to equilibrium. This means that growth during the spring and summer months, followed by an increased proportion of dead material, is compensated by a negative accumulation (decay) during fall and winter. When cut was applied, *HAR* increased to 26 and 30 kg DM ha⁻¹ d⁻¹ (SD = 20 and 23 kg DM ha⁻¹ d⁻¹, for FG A and B, respectively) because of the drastic reduction in the amount of dead material, which reduced decay (this effect will be discussed in more depth in following sections). Cutting caused an overestimation of biomass accumulation during the summer months, while matching average winter production.

Added to the variation in both observed and predicted, *RMSE* was also significantly large, especially for cut simulations, because of the larger-magnitude overestimations of *HAR* between Nov and Mar, in comparison to the underestimation of uncut *HAR* during fall and winter (Error and Mean Absolute Error; Table 3). This affected negatively the *EF* and *d_r*, especially under cutting regime. For the test statistics, the coefficient of determination (*r*²) was between 0.24 and 0.26 for all combinations. Statistics were also calculated per month and per season, without significant improvement (data not shown). The reduced variation of simulated *HAR* during winter months is related to the lower availability of observed data for the respective period, since the comparisons considered matching dates. While field observations consist of up to 12 plots per evaluation, simulation has only one value per date.

The significance of those statistics, however, is questionable, since the original observed data itself has a very large variation, which can be expected when working with ecological experiments and models. But not having reliable data to validate does not make the model useless or even invalid (Mateus, 2017). Thus, we rely on qualitative evaluation, based graphical analysis for interpreting the general behavior of the responses and average values of predictions compared to empirical knowledge and literature available (Bennett et al., 2013).

Despite the disparity between specific observed and simulated points, the monthly average and variation range of the simulated values is very close to the observed (Figure 4). While simulated averages for HAR without cut were very similar to observed HAR during spring and summer month, cutting sharply increased HAR during those seasons, and neared the estimations for fall and winter, which were underestimated when no cut was applied. The differences in response is both a feature of the method using for calculating simulated HAR and of the biomass flows, especially related to the proportion of dead material. During summer, the more favorable light conditions and increased growth due to *maxSEA*, results in a high herbage accumulation (biomass into the system). On the other hand, the higher temperatures increase senescence and decay flows (where decay represents biomass out of the system), and the difference between GRO and decay is what is being considered HAR. When cut is applied, it reduces the amount of dead material because of a feature of the cutting function (see section 3.2.2.2). This way, decay decreases, at the same time that biomass harvested, besides being a flow out of the system, is not accounted on the HAR calculation, substantially increasing it when cuts are applied. During winter time, when biomass flows are reduced, this effect is diluted, but still present. This under- and overpredictions are captured by the negative and positive Error for no cut and cutting regimes (Table 2). Note that the magnitude of change for Error parameter between the two cutting regimes (0 or 12) is very large, which denotes an important effect of the management practice on the results.

Although the effects of cutting on biomass growth are much different than grazing, it gives a more realistic scenario and better comparison to observed data. Despite the larger differences between predicted and observed HAR during spring and summer months, and the fact that the way cut is applied is influencing the response, the average total biomass per month for the cut simulations (ranging from 995 to 1943 kg DM ha⁻¹ for FG A, and 1426 to 2595 kg DM ha⁻¹ for FG B) was similar to average standing biomass observed in the field experiment (e.g. Neves et al., 2009). Apparently, the model is indeed overestimating growth during the summer. If we

consider that during growing season (especially spring) most of the biomass in the pasture, under grazing management, is composed by green vegetative vegetation (therefore decay should be minimal), GRO would basically represent most of HAR. Then, when comparing simulated GRO, ranging from around 50 to 80 kg DM ha⁻¹ d⁻¹, to observed HAR for summer and spring, GRO would be 2 to 5 times greater. Guido et al. (2014) analyzed the inter-annual variability of above-ground net primary production (ANPP) of Uruguayan grasslands using remote sensing data. Average ANPP values for the corresponding period were between 15 and 20 kg DM ha⁻¹ d⁻¹, also peaking in Oct and Nov, before dropping to a lower plateau (~13 kg DM ha⁻¹ d⁻¹) during summer. Those are more reasonable values, and very similar to averages observed in our experiment.

Seasonal averages for simulated *HAR* were also similar to the early reports for this experiment (years 1989 to 2003; Correa and Maraschin, 1994; Setelich, 1994, Gomes, 1996, Moojen and Maraschin, 2002, Aguinaga, 2004; Soares et al., 2005). Literature averages for HAR for spring, summer, fall and winter were 19, 22, 9, and 3 kg DM ha⁻¹ d⁻¹ (SD = 8 kg DM ha⁻¹ d⁻¹ for summer and spring, and 6 and 1 kg DM ha⁻¹ d⁻¹ for fall and winter, respectively), while mean simulated *HAR* without cut for both functional groups was 17, 8, -14, and -8 kg DM ha⁻¹ d⁻¹ (SD = 13, 19, 5 and 7 kg DM ha⁻¹ d⁻¹) for the corresponding seasons. Negative values indicate that senescence and decay are higher than growth, and, under uncut regime, balance out the positive accumulation during growing season. When including cutting, simulated HAR increased, matching literature data during fall and winter (10 and 9 kg DM ha⁻¹ d⁻¹) but topping by around two fold spring and summer literature HAR (48 and 38 kg DM ha⁻¹ d⁻¹).

3.3.2. Exploring the model

A series of simulation runs were done to evaluate the performance and behavior of the model, including different sets of years and cutting frequency, checking for malfunctioning and extreme behaviors (i.e. extinguish or abnormally large biomass production). First, we consider a 25-year (1988 to 2013) period comparing the productivity and responses of all four FG, to zero and 2 cuts per year (at the peak of growing season and late season for FG A and B). Then, selected Dry and Wet years are tested under 0, 4, 12, and 24 cuts per year, evenly spaced, simulating sequences of 5 years of drought (i.e. 5 selected dry years in a row), or with excessive rainfall. A third section is dedicated to discuss the functioning of the model for FG C and D.

3.3.2.1. 25-year simulations

When simulating the 25 years without cut, it is possible to see that the model correctly captures the variation in total biomass across years for FG A and B (Figure 5a). The system reaches an equilibrium fluctuation, what can be neatly seen by the balance between positive and negative HAR (Figure 5a). The magnitude of the total biomass values are apparently too high for FG B, but considering all our data for comparison include either grazing or cutting, this is not a conclusive statement. The reason for this ca. 50% greater total biomass of FG B compared to A is a combined effect of higher light interception by the higher k , increasing potential growth, and lower senescence rates, thus lower decay. Finally, the larger biomass also results in a larger LAI, since it is calculated based on SLA and BM_{GV} . Despite the magnitude of the values, the behavior of what represent the two lines is very similar, including notable drops in production during dry years (growing seasons of 1990, 1998 and 2005), and a possible cumulative effect of drought on seasons of 1999 and 2006, which were not sorted as dry by our water stress index. The opposite can be seen for wet years (e.g. 2009), but not much difference appears for the other Wet years (i.e. 1997 and from 2000 to 2003), since most of the increase precipitation compared to Normal years was during the off-season (fall and winter).

Observing HAR, it is slightly larger for FG B for late spring (higher peaks), which correspond to the period of maxSEA (larger for B than for A). Herbage accumulation rate seems to be less responsive to restricted years than total biomass, as mentioned above. The peaks of HAR were maintained, although the width (length or period) which HAR was high was reduced. Again, as explained in the previous section, HAR is offset throughout the year, and the higher peak of accumulation in late-spring for B is counterbalanced by a slighter negative HAR during fall and early winter. Despite that, however, there was no important change in the proportion of each compartment composing biomass across years (i.e. the same response-shape for compartment proportion was independent of weather conditions), which explains the even response.

When applying cut to FG A and B, it is possible to see that HAR (Figure 5b) now becomes more positive, since proportion of dead material, and, therefore, decay, was reduced by cutting. The effects of dry years also became more pronounced, since GRO becomes a large part of HAR (i.e. decay is reduced), and it responds linearly to water stress (while rate of decay is not be affected). Those changes became more apparent now because the large amount of total biomass buffers those fluctuations in uncut simulations (i.e. the relative value of GRO to total biomass is much larger when

cut is applied, because reduction in total biomass). The average difference in total biomass between FG A and B dropped to 21% in response to cutting (bottom lines in Figure 5b). This is an effect of a larger reduction in light interception at lower biomass (non-linear response) for B than for A, since at residual biomass (750 and 1000 kg ha⁻¹ for A and B, respectively), LAI is equal (1.22). The more accentuated increase in total biomass under cutting (i.e. higher HAR) is also an effect of the reduced proportion of dead biomass, and decay not offsetting actual growth. Despite being physiologically coherent (Korte et al., 1982; Parsons and Chapman, 2000), this, however, is a purely mechanistic effect of the model structure, and not an intended physiological representation (see next section).

This is an important aspect that should be addressed in future versions of the model, especially related to the LAI calculation. Specific leaf area is a very plastic parameter, varying with grazing management (e.g. Cruz et al., 2010) and fertilization (e.g. Knops and Reinhart, 2000), and straight relationship with LAI is questionable. Furthermore, the relationship of biomass and LAI itself is unstable, and does not account for canopy characteristic which will have large influence on regrowth (Korte et al., 1982; Johnsons and Parsons, 1985; McCall and Bishop-Hurley, 2003). Other modeling approaches, such as the one used in ALMANAC (Kiniry et al., 1992) uses a sigmoid function based on maximum LAI to simulate actual LAI, and can be affected by chosen variables, such as competition (density of plant community) and timing (heat units). This approach could be an interesting alternative, since is more flexible in representing LAI, especially considering, for example, denser canopies with lenient cutting at high frequency, or reduced LAI after mowing long-grown canopies, because of stem elongation (Parsons and Chapman 2000). This, however, would require a considerable effort on measuring maximum LAI for the chosen species.

Regarding the magnitude of the values, a compendium of works in the same ecophysiological region (Rio de la Plata Basin), analyzed by Paruelo et al. (2010), showed average annual ANPP for native pastures mostly ranging between 3,000 and 5,000 kg ha⁻¹ yr⁻¹. Similar results were obtained by Neves et al. (2009), which also registered average standing biomass ranging from 1170 to 2050 kg DM ha⁻¹ in grazed paddocks with fixed herbage allowance (2 to 4 kg DM kg LW⁻¹). Those values are well below the 6,000 to 12,000 kg ha⁻¹ of standing biomass in the absence of cutting, or 8,000 to 11,000 kg ha⁻¹ cumulated harvested biomass our model predicted (although, as mentioned in the previous section, simulated average standing biomass under monthly cuts is very similar to values reported by Neves et al., 2009). Along with that, simulated (daily) ANPP using remote sensing tools ranged from 5 to 30 kg ha⁻¹ d⁻¹

(Paruelo et al., 2010; Guido et al., 2014), which reinforces the conclusion ModVege is indeed overestimating by at least twice the amount of biomass produced. Nevertheless, seasonal trends reported in both works were similar to the response-shape simulated by our model.

When simulating tussock-forming FG C and D, however, biomass was basically extinguished within the first 3 years for group D, while it fluctuated at very low values for FG C, composed basically of BM_{GV} . Apparently, one of the main reasons for this effect is the very low LAI, related to the low SLA of those species. The reproductive phase was not captured, probably by the insufficient allocation of GRO towards reproduction, or too small of an increase in photosynthesis efficiency during the period (i.e. too sharp decline in SEA). This could be partially adjusted increasing the relative weight of the reproductive function [Eq. (15) in Jouven et al., 2006a), for example. Reproductive growth (REP) is a partition of total GRO, determined by the nitrogen index, and was set to 0.74 (i.e. for determinate growth, REP approaches 1). Notwithstanding, there is no information about photoperiod sensitivity of those plants (determinate or indeterminate growth after flowering), which is very influential on representing growth (Mitchell et al., 1998). We explored different parameters within realistic values without success on simulating biomass growth, especially reproductive. Physiological and architectural characteristics of plants composing those two functional groups are very distinct from the original development of the model, and maybe some important features are not being well represented in our equations. The mechanical causes of this effect (i.e. biomass extinguishment) in comparison to the physiological processes of slow-growing, clonal bunchgrasses and other representation alternatives will be further explored in section 3.3.2.3.

3.3.2.2. Response to contrasting weather conditions and cutting regimes

When separating the years by weather condition (Dry, Normal and Wet) and applying cutting regimes (0, 4, 12 or 24 cuts per year), there was no difference in response between FG A and B. Since FG B is more abundant in our environment, graphs shown will be related to this group only otherwise mentioned. The major difference in cumulative monthly rainfall for the simulated scenarios was between Nov and Mar, where Dry years not only had a lower precipitation, but also increased *PET* in relation to Normal and Wet. While on Wet years the water balance was slightly negative only in Jan, it was below zero for the whole spring and summer periods during Dry. The number of rainy days (with rainfall > 1 mm) was also 30 – 40% lower for Dry in relation to Wet years, but for the month of Jan, were water balance tended to be

recovered to some extent what reflected on biomass production of the following month. It is important to note that cumulative rainfall in selected dry years could have been inflated by heavy rain events, which will not over-influence the water stress status, since water reserves can only be as high as soil water holding capacity [$f(W) = 1$]. However, the choice of methodology [$\Sigma f(W)$] could have influenced on the outcome, since, despite the graphical analysis also performed, it may not have identify sequences of dry days (extent of drought) to a finer scale, which can have a larger effect than the magnitude of drought itself.

Water balance for Normal years was mostly not limiting, therefore there was very little difference in response between those and Wet years. For simplicity, most charts only represented comparisons between Dry and Wet years. Average daily green biomass growth (*GRO*) was reduced for November to March on Dry compared to Wet years, and more significantly in Nov and Dec, when *GRO* dropped around 30% due to more severe water restriction (Figure 6). There was basically no difference in response between FG, but for a longer maximum growth towards mid-summer for FG A, which is a function of a longer maxSEA phase. Growth in Dry years was recovered Feb, which is probably a carryover effect from increased rainfall (and water balance) late Jan, increasing amount of green biomass and, consequently, *GRO*. Water is the most limiting factor for biomass production in climate-marginal grasslands (Friedel et al., 2000), but distribution and soil characteristic can be more influential than total amount, and carryover effects can be observed in following seasons or years (Guido et al., 2014).

The cumulative effect of lower growth rates during spring and summer in Dry years on total biomass (Figures 7 and 8) persisted along the subsequent months, maintaining a relatively steady difference between 22 and 28%. This was apparently unaffected by other constrains, and can be seen by the equidistance and similar decreasing behavior of both lines on Figure 8a towards the end of the growing season. It indicates a linear influence of water stress on herbage accumulation, also noted by Calanca et al. (2016), without any carryover effect of the dry period. This effect, however, is different than the arguments used for changing the original water stress function (see Materials and Methods section; Allen et al., 1998; Calanca et al., 2016), where it was debated that the field capacity which would determine restriction in growth should be altered, independent of PET. Under water limited conditions, would be expected a more significant drop on growth, because of greater partitioning of nutrients to roots under stress (Irvin, 2015), and a lag time on recover (Kochsiek et al., 2006) because of increases senescence and reduced decay, resulting in an accumulation of

dead material (Ong, 1978; McCall and Bishop-Hurley, 2003). This fluctuation in the relative proportion of compartments was also not noted (Figure 9), despite the reduction on peak biomass for both green compartments in Dry years. The model lacks a more detailed representation on physiological process under water restriction, especially on the recovery phase. Part of this was addressed by McCall and Bishop-Hurley (2003) with the introduction of an increased senescence coefficient when water stress index dropped below 0.2, and linear reduced of decay with decreased top-layer soil water reserves, both aspects favoring the increase in proportion of dead material.

There was no effect of cutting on many of the variables analyzed, including *GRO* and harvested biomass. When cut monthly cuts were added (Figures 7 to 9), there was a very noticeable decrease in both dead compartments, and in green reproductive (Figure 9). The effect of weather condition on the general behavior of the curves under cut was minimal, other than the dent in green vegetative during December, restricting the peak of growth. This is just a virtual effect of the reduced total biomass, making changes more noticeable, as commented before, since *GRO* was not altered by grazing frequency grazing. This can be clearly seen on Figure 8: while no cut was applied (Figure 8a), the reduction in the relative difference to Normal years was diluted in a much larger biomass, making changes appear smoother; when monthly cuttings were applied (Figure 8b), the base biomass for comparison is much lower, so an 30% increase in *GRO* have a larger relative representation, approximating total biomass for all conditions in Feb. Plants under frequent cutting and water stress would tend to reduce production very significantly (Kochsiek et al., 2006), what was not noted on the model outputs, once more due to the lack of more detailed physiological responses. On the other hand, given the high bulk density of green vegetative compartments and that the model does not consider the vegetation structure (i.e. tillers), a 5-cm stubble would still hold considerable “leaf area” to sustain high levels of growth. Considering the given bulk density for the green compartments for FG A and B (1.5 and 2 kg DM m⁻³), a 5-cm stubble represents 750 and 1000 kg DM ha⁻¹ of photosynthetically-active residual biomass, which results in an *LAI* of 1.22 for both FG. Since *k* is also large (1.13 and 1.36), total light intercepted by residual vegetation is also high, yielding a high potential growth (e.g. 360 and 389 kg ha⁻¹ d⁻¹ at $PAR_i = 12 \text{ MJ m}^{-2}$). Thus, the cutting per se had little effect on growth, and the reductions on potential growth are majorly due to environmental effects.

One important consideration made by Johnsons and Parsons (1983) is that the structure of a canopy cut to a specific *LAI* is much different form a canopy that grew to that same *LAI*. Although this may not have an important difference in more closely

grazed or frequently cut pastures, it would be expected a significant impact on pastures managed more leniently, were plants are allowed to grow beyond the point of self-shading, increasing tiller production (Korte et al., 1982; Parsons and Chapman, 2000). This would definitely have an important impact on photosynthetic rates, since a 5-cm stubble of a long-grown pasture would be composed majorly by tillers and dead tissue.

As commented in the previous section, the apparent effect of cutting on GRO and HAR is related to a very drastic reduction in dead compartments, and a feature of the mechanical structure of the model rather than an intended effect of cutting per se. Herbage harvested per compartment is given by the difference between total biomass and residual biomass on a 5-cm stubble, calculated based on the bulk density of each compartment. The result is that the lower-density dead vegetation is virtually taller than the green vegetation and more accessible to cut. Thus, has a larger proportion of its mass is harvested. The same happens to the reproductive compartment, but to a smaller extent, because the difference in bulk density from green vegetative to green reproductive is not as large as from green to dead compartments. This is not completely realistic, because while for tussocks tillers and hard leaves may still be standing after senesced, dead material especially in prostrate grasses tend to be in the inferior parts of the canopy, more difficult to be harvested but also more susceptible to decay.

3.3.2.3. Tussock growth

When simulating biomass accumulation for the slow-growing, bunchgrasses of groups C and D, however, independent of initial biomass set, the vegetation would soon get extinguished (Figure 5c). Tracing back the equations, we realized that potential growth was indeed very low, while senescence was overcoming it, but with reasonable values. Despite the large photosynthetic capacity (high RUE_{max} and large LDMC), because of the narrow (low SLA), upright leaves (low k), the actual capture of radiation is limited, and an important proportion of it is captured by old or senesced leaves with little or no influence on carbon fixation. Assuming the parameters used for calculating growth (RUE_{max} , SLA and k) and senescence (K_{GV} and K_{GR}) are appropriate since are measured values, why are we not able to simulate tussock growth? Similar challenge has been noted by Derner et al. (2012), referring to the limited applicability of physiological models to simulate tussock grasses.

Those plants highly invest on leaf structure producing thick mesophylls and palisade parenchyma (high LDMC, consequently low SLA; Wright et al., 2004, Reich, 2014), thus, having a large photosynthetic capacity (expressed by the large RUE_{max}).

This results in high amounts of expensive components (such as lipids and lignin; Wright et al., 2004), which will determine a long *LLS*, slow leaf turnover, high accumulation of old and dead tissues (Cruz et al., 2010), and, subsequently, low photosynthesis per unit of mass and slower response to environmental shifts (Wright et al., 2004). This strategy is related to slow-growing species that can overcome competition and environmental stress by accumulating resources and outcompeting neighbors by its taller canopies (which needs more structural components). Leaf thickness, tissue density, and accumulation of dead material are also strategies associated to herbivory avoidance by increasing components of mechanical resistance (Pfeifer and Hartnett, 1995; Mingo and Oesterheld, 2004), also helping protecting high and possibly exposed meristems.

Hence, this leads us to think that there are missing or miss-represented important physiological mechanism in our model that should account for this difference in growth strategy between faster growing prostrate grasses and slow-growing, tussocks-forming grasses. *Aristida* species, for example, are equipped with an extra layer of bundle sheath cells, densely packed with starch, constituting the main site for reserve storage on leaves (Voznesenskaya et al., 2005), which can help explaining the high adaptation of those species to harsh environments. This readily-available source of non-structural carbohydrates could be an important source of energy for sustaining new growth. But in spite of the speculations towards higher remobilization rates, there are no numbers in the searched literature that allow us to represent it with confidence.

Clonal bunchgrasses also have very distinct growth characteristics, with strong interactions between canopy architecture and resource allocation, affecting the use and recycle of nutrients within its own boundaries (i.e. inter-tiller; Tomlinson et al., 2007). Reallocation of resources from old to new tillers, for instance, has already been identified as important source of carbon for supporting juvenile growth for anatomically-connected subunits in *Schizachyrium scoparium* (Welker et al., 1991). Tussocks tend to capitalize when resources are available (e.g. pulses of soil mineralizable N) by upscaling root and shoot growth, accumulating nutrients in dead biomass (especially below-ground; Briske and Derner, 1998). Those particular characteristic are important strategies for overcoming periods of environmental stress, and also have a deep effect on partitioning of photosynthates and, therefore, on growth. Functional models which base herbage growth on biomass pools, considering only intercepted radiation and efficiency of radiation use, may not be appropriate for realistically simulating tussock growth (Tomlinson et al., 2007). Structural models (e.g. Tomlinson et al., 2007), on the other hand, are able to consider meristem behavior (tiller recruitment and patterns of

survival), and capture and allocation of resources. Despite being more complex, they are able to simulate more accurately seasonal trends and responses to environmental effects, and intra annual dynamics, since life cycle can extend over one year (Briske and Derner, 1998, Tomlinson et al., 2007; Derner et al., 2012). The challenge is, in a simple way, to incorporate both concepts, considering that physiological and structural properties have to be integrated in an interactive way, responding to environmental constraints, season effects and year variations.

3.4. Conclusions

Although models are great tools for studying ecosystem and predicting responses, modeling complexity in a simple way with limited amount of resources (i.e. data, parameters and specific knowledge about processes) is a great challenge faced by the scientific community. Here we attempt to adapt, validate and explore a simple mechanistic model developed to temperate species, based on functional traits, to subtropical grasslands perennial grasslands. The approach is appealing, since functional traits can summarize and represent many aspects related to the capture and use of resources, and responses to disturbances (management and stress). However, the same reason why we want a unifying, easily measured (soft) trait to represent our grasslands (i.e. lack of knowledge on many other “hard traits”) is the same cause for several of the short comes on the understanding of the ecosystem dynamics and on the development of simulation models. The failure to validate and many hindrances encountered on the way of exploring the model, though, should not be seen as detrimental, because they lead to important discussion of many aspects otherwise taken for granted.

“Complexity in grassland simulation models can easily outpace available validation data” (Kiniry et al., 2002). In our case, variability on observed data was the limiting factor, and, because that inconsistency, the validation was not conclusive. Even though, we were able to explore many aspects of the model, comparing distinct scenarios and identifying possible improvements for future versions. Despite the large variation in observed data, averages and variation range for herbage accumulation rate were similar to those observed in the field experiment, although there was a tendency to underestimate HAR during fall and winter, if no cutting management is applied, and overestimating production under cutting regimes. Despite the difference in the magnitude of the values compared to observed data and to the literature, the model realistically represented the behavior of herbage production across seasons. On the other hand, some expected responses to water restriction were not observed. The general functioning of the model is very clear and some of the short comes mentioned

in the discussion are relatively simple to fix. Before any attempts to improve the mechanics of the model, there are major needs for collecting field data for parametrization, especially for the season function (observations on phenological stages and carbon storage-remobilization dynamics) and biomass flows (senescence and decay). More reliable data for validation could lead future developments. Especial attention should be posed on tussock grasses, because they represent an important part of the ecosystem services, including resilience to environmental effects and nutrient cycling, and are significant part of cattle's diet composition.

The scientific contribution of the model is independent of validation (Caswell, 1988; Rykiel, 1996). The primary goal of this modeling project is not only getting an accurate output, but principally help understanding the processes involved on the functioning of the system, and identifying needs for future research. The adaptation of this model guide us though an important idea-developing process, which will be beneficial for the understanding of our and other related systems.

3.5. References

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Table 1. List of functional traits and other parameters used on the simulations for each functional group.

Functional trait	Definition	Unit	Functional group				Reference
			A	B	C	D	
σ_{gv}	Respiration of GV	unitless	0.4	0.4	0.4	0.4	Ducrocq, 1996
σ_{gr}	Respiration of GR	unitless	0.2	0.2	0.2	0.2	
SLA	Specific leaf area	$m^2 g^{-1} DM$	0.024	0.018	0.008	0.006	Cruz et al., 2010; Barro 2011
T_0	Basal temperature	$^{\circ}C$	9	9	9	9	Agnusdei, 1999
T_1	Minimum temperature for maximum growth range	$^{\circ}C$	25	25	25	25	Kakani et al., 2008
T_2	Maximum temperature for maximum growth range	$^{\circ}C$	35	35	35	35	
ST_0	Sum of temperature for beginning of linear increase in SEA	$^{\circ} d$	426	426	900	900	Rosengurtti et al 1970, Rosengurtti, 1979, Schefer-Basso et al., 2002
ST_m	Sum of temperature for maxSea	$^{\circ} d$	900	900	1500	1500	
ST_1	Sum of temperature for the beginning of reproductive period	$^{\circ} d$	2635	2126	2635	2126	
ST_2	Sum of temperature for the end of reproductive period	$^{\circ} d$	4750	4050	5307	2635	
maxSEA	Maximum season	unitless	1.2	1.3	1.4	1.5	
minSEA	Minimum season	unitless	0.8	0.7	0.6	0.5	
K_{gv}	Senescence of GV	$^{\circ}C^{-1}$	$8.81E^{-4}$	$6.05E^{-4}$	$8.91E^{-4}$	$9.10E^{-4}$	Cruz, 1988; Machado et al., 2013
K_{gr}	Senescence of GR	$^{\circ}C^{-1}$	$4.40 E^{-4}$	$3.25 E^{-4}$	$4.45E^{-4}$	$4.55E^{-4}$	
KI_{dv}	Abscission of DV	$^{\circ}C^{-1}$	$4.40 E^{-4}$	$3.03 E^{-4}$	$4.45E^{-4}$	$4.55E^{-4}$	
KI_{dr}	Abscission of DR	$^{\circ}C^{-1}$	$2.20 E^{-4}$	$1.51 E^{-4}$	$2.23E^{-4}$	$2.28E^{-4}$	
LLS	Leaf life span	$^{\circ} d$	400	500	700	1000	Cruz et al., 2010; Machado et al., 2013, Santos et al., 2014
maxOMD _{gv}	maximum OMD GV	fraction	0.8	0.7	0.6	0.5	Santos, 2012
minOMD _{gv}	minimum OMD GV	fraction	0.6	0.5	0.4	0.4	
maxOMD _{gr}	maximum OMD GR	fraction	0.8	0.7	0.4	0.3	
minOMD _{ge}	minimum OMD GR	fraction	0.5	0.45	0.2	0.2	
BD _{gv}	bulk density of GV	$kg DM m^{-3}$	1.5	2	2.5	1.5	
BD _{gr}	bulk density of GR	$kg DM m^{-3}$	1	1.5	2	2.5	
BD _{dv}	bulk density of DV	$kg DM m^{-3}$	0.3	0.3	0.4	0.5	
BD _{dr}	bulk density of DR	$kg DM m^{-3}$	0.15	0.15	0.3	0.45	
k	Extinction coefficient	Unitless	1.13	1.36	0.34	0.35	Kiniry et al., 1999; 2007; Barro 2011
RUE	Radiation use efficiency	$g DM MJ^{-1}$	1.8	1.9	3.2	4.1	
%LAM	Proportion of leaves for calculating LAI	Unitless	0.68	0.68	0.90	0.95	Cruz, 1998
α	remobilization parameter	unitless	0.102	0.102	0.102	0.102	M. Duru, in Cros et al., 2003

Table 2: Error (E), random mean square error (RMSE), mean absolute error (MAE), modeling efficiency (EF), refined index of agreement (d_r) and correlation coefficient (r^2) for validation of herbage accumulation rate simulated for functional groups (FG) A and B, under 0 or monthly cuts.

Statistic	No cut		Monthly cut	
	FG A	FG B	FG A	FG B
E	-8.8	-8.9	14.1	17.8
RMSE	16.7	18.1	22.6	26.7
MAE	13.31	14.37	17.11	20.11
EF	0.17	0.21	0.16	0.17
d_r	0.3	0.25	0.11	-0.05
r^2	0.26	0.26	0.24	0.24

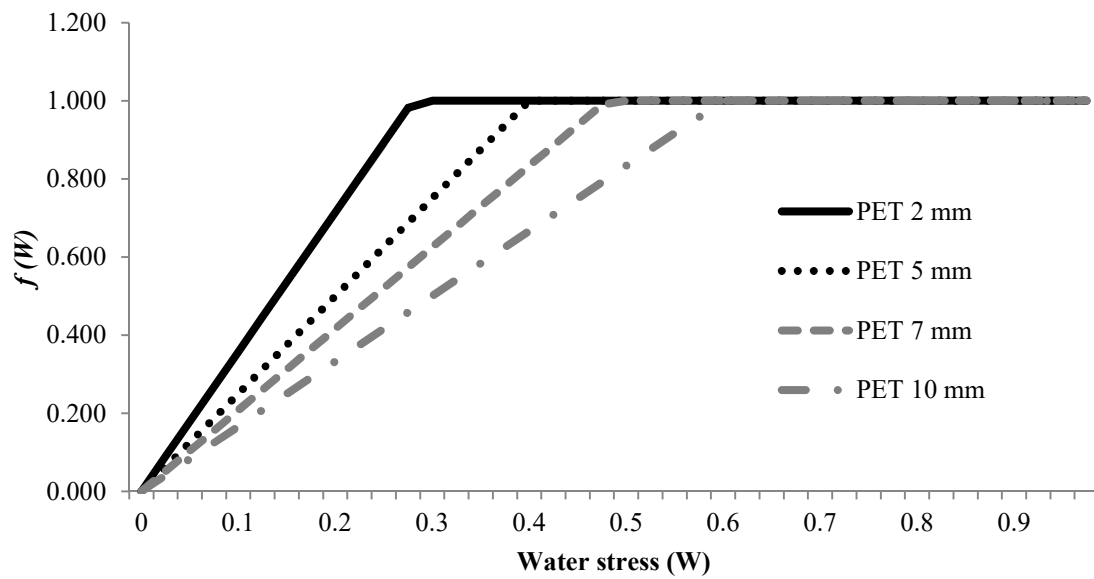


Figure 1. $f(W)$ as function of water stress and potential evapotranspiration [PET; adapted from McCall and Bishop-Hurley (2003) as proposed by Calanca et al. (2016) based on Allen et al. (1998)]

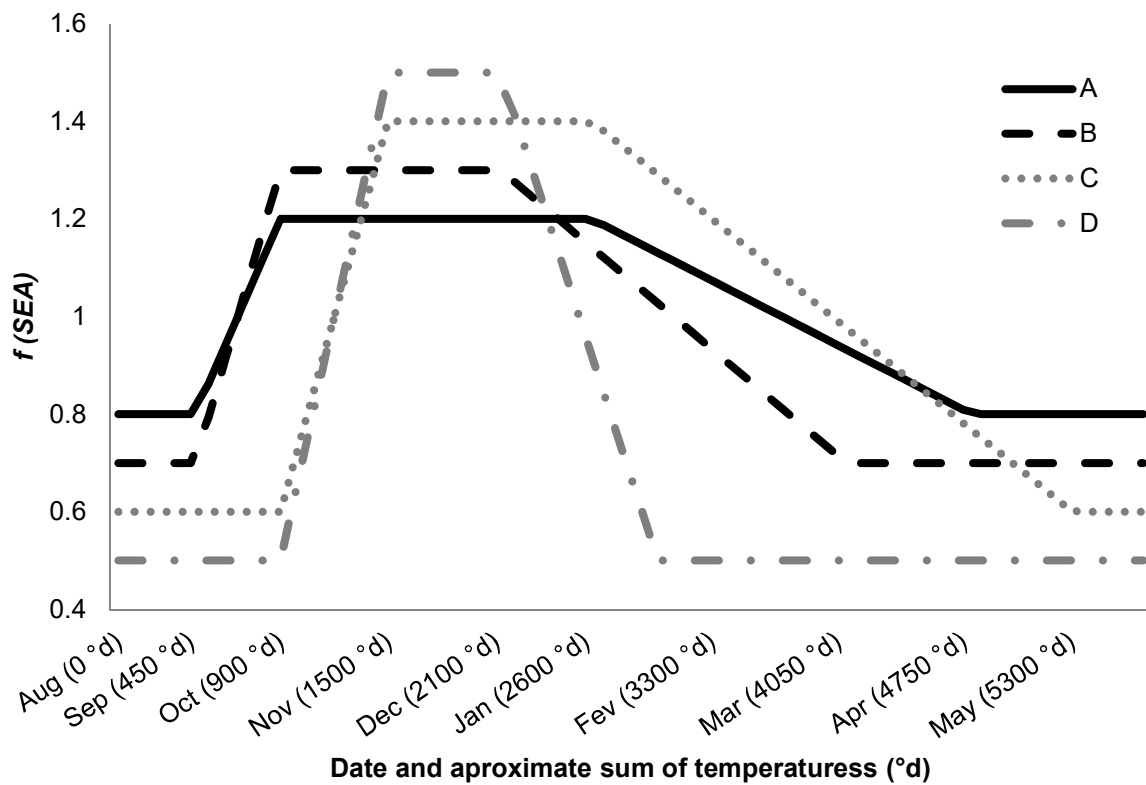


Figure 2: Seasonal effect (SEA) on growth as function of sum of temperatures, per functional group. Solid, black line for functional group A, dashed, black line for functional group B, dotted, grey line for functional group C, and dash-dot, grey line for functional group D. On the original model (for northern hemisphere, season (sum of temperature 0) starts on 1 Aug. SEA starts decreasing when the reproductive (REP) period begins, and is at minimum at the end of REP.

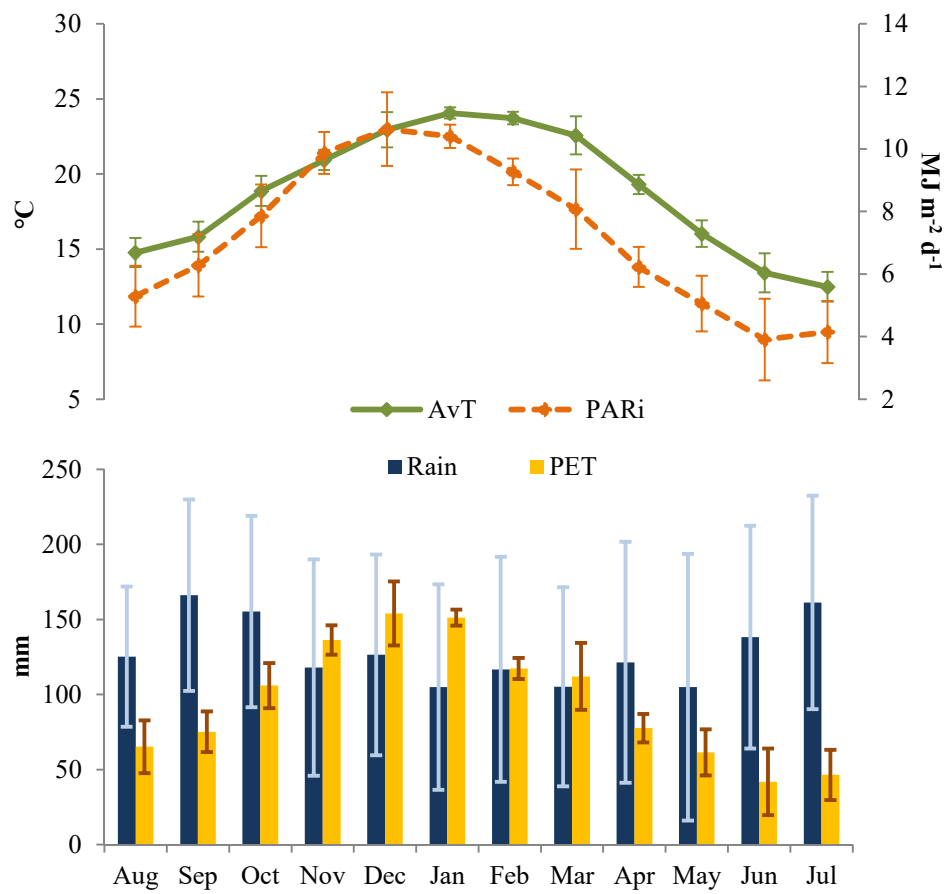


Figure 3. Average daily temperature (AvT) and photosynthetic active radiation incident (PARi; a) and cumulative monthly precipitation (Rain) and potential evapotranspiration (PET; b), and respective standard deviations, from Aug 1988 to Jul 2013 in Eldorado do Sul, Brazil

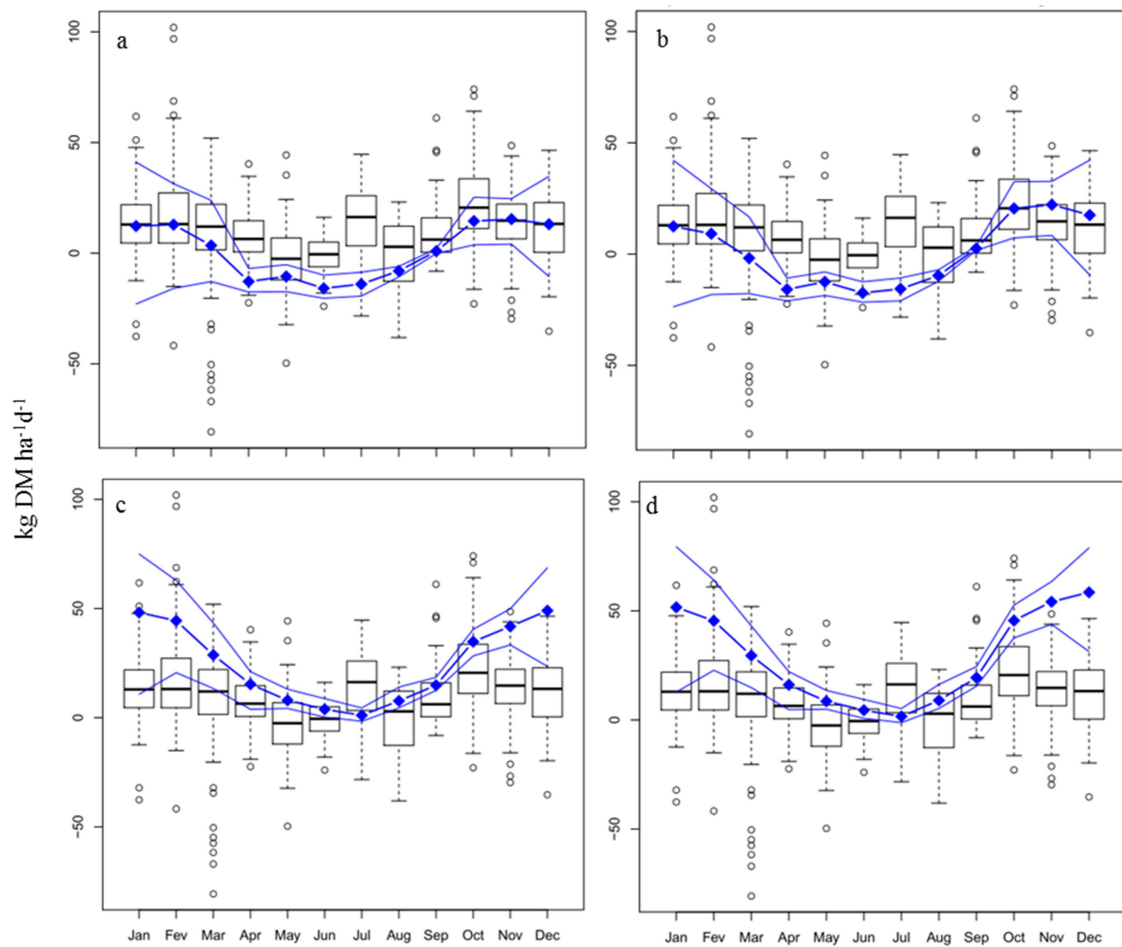


Figure 4. Observed (boxplot) and simulated (lines, upper and lower lines represent 95% confidence interval) for FG A (a-b) and B (c-d). Simulation lines in upper charts (a, c) represent no cutting management, and in bottom charts (b, d) cutting was applied monthly, to a 5-cm stubble height.

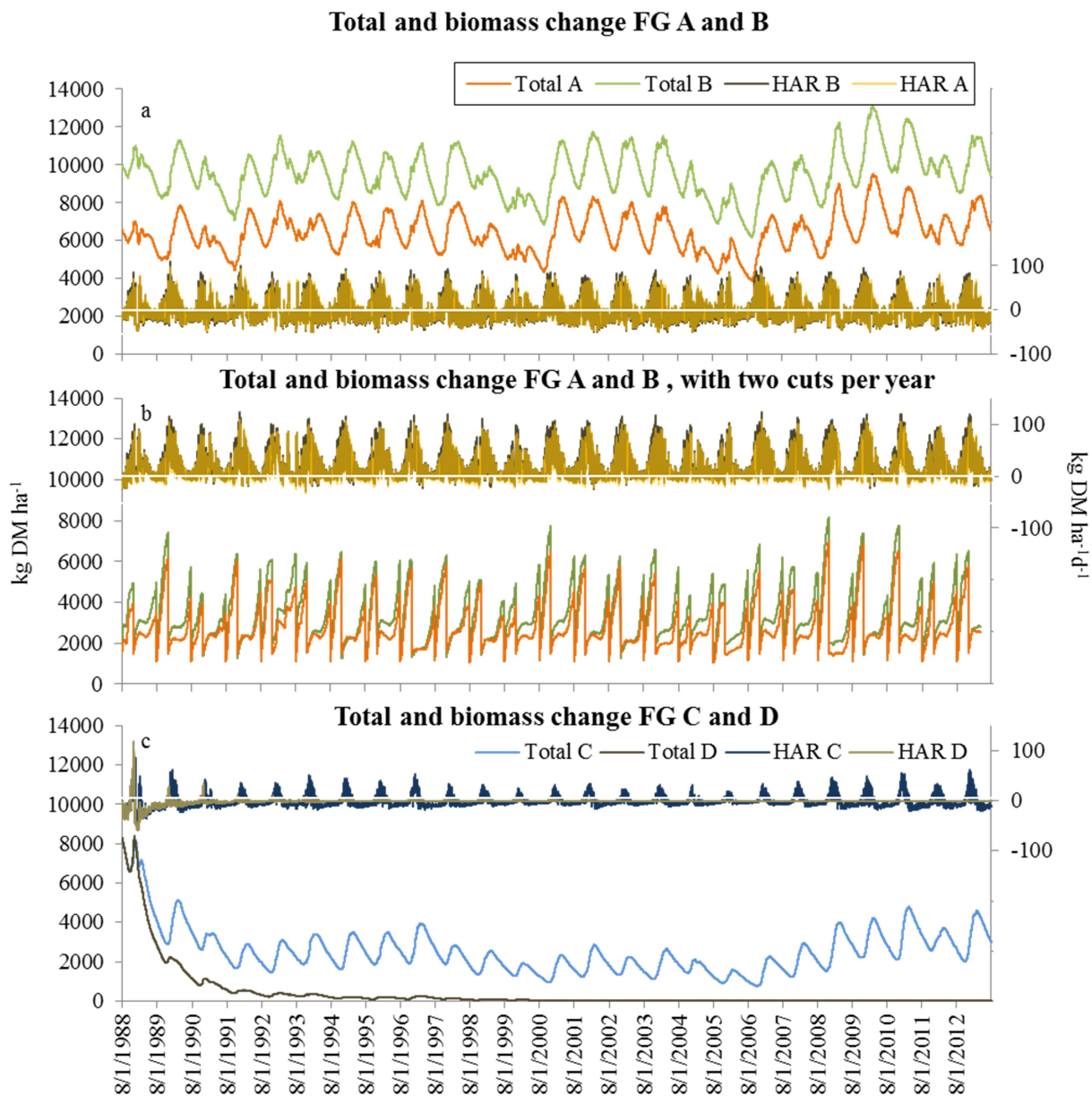


Figure 5. Total biomass and herbage accumulation rate simulated for 25 years (Aug – 1988 to Jul – 2013) for functional groups (FG) A and B, without (a) and with (b) two cuts per year (Oct-31 and Mar -30), and FG C and D (c). Upper lines in chart (a) and bottom lines in charts (b) and (c) represent total biomass at the specific date, while the other set of lines represents herbage accumulation rate. Top, boxed legend is referent to both (a) and (b) charts.

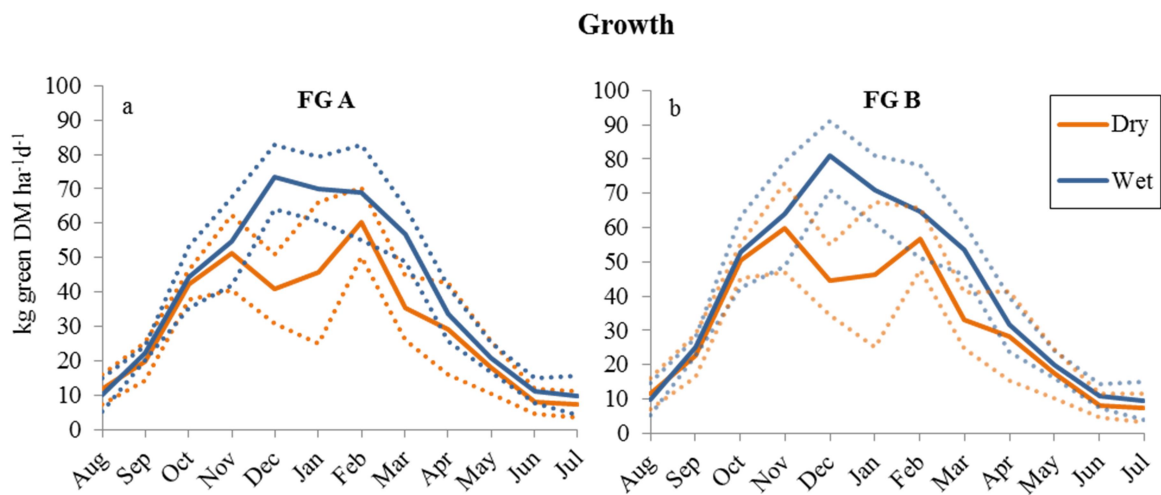


Figure 6. Herbage growth (kg green DM ha⁻¹ d⁻¹) for functional groups (FG) A (a) and B (b), on Dry (orange) and Wet (blue) conditions, without cutting regimes. Solid lines are average for 5 years, and dashed lines are one standard deviation above and below average.

Total and harvested biomass for FG B

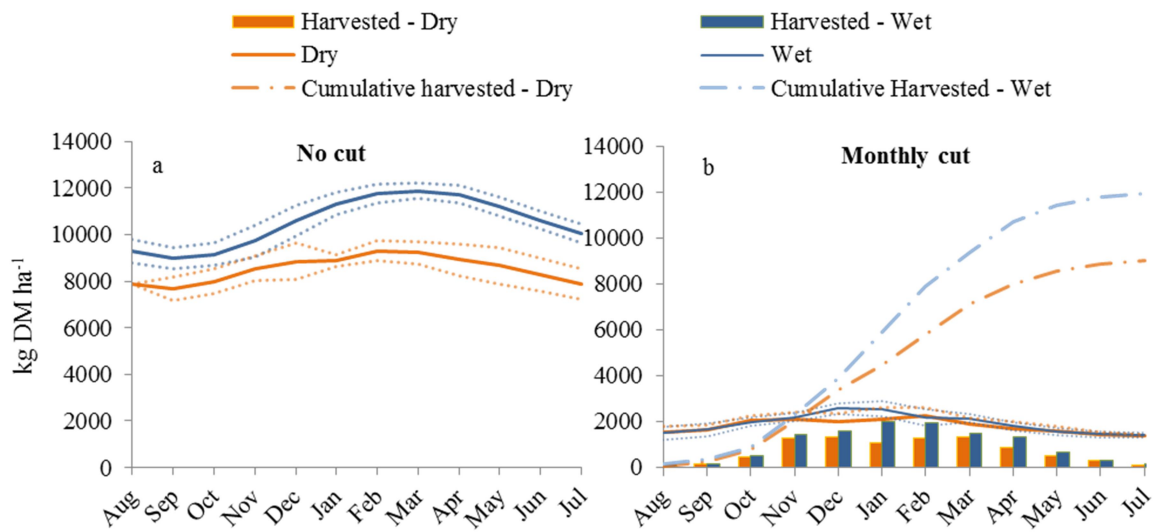


Figure 7. Total and harvested biomass for functional group B, with 0 (a) or 12 (b) cuts per year, for dry (orange) or wet (blue) conditions. Solid lines are average monthly total biomass, dashed lines represent one standard deviation above and below average, and point-dash lines (b) represent cumulative harvest. Bars on chart (b) represent monthly harvested biomass.

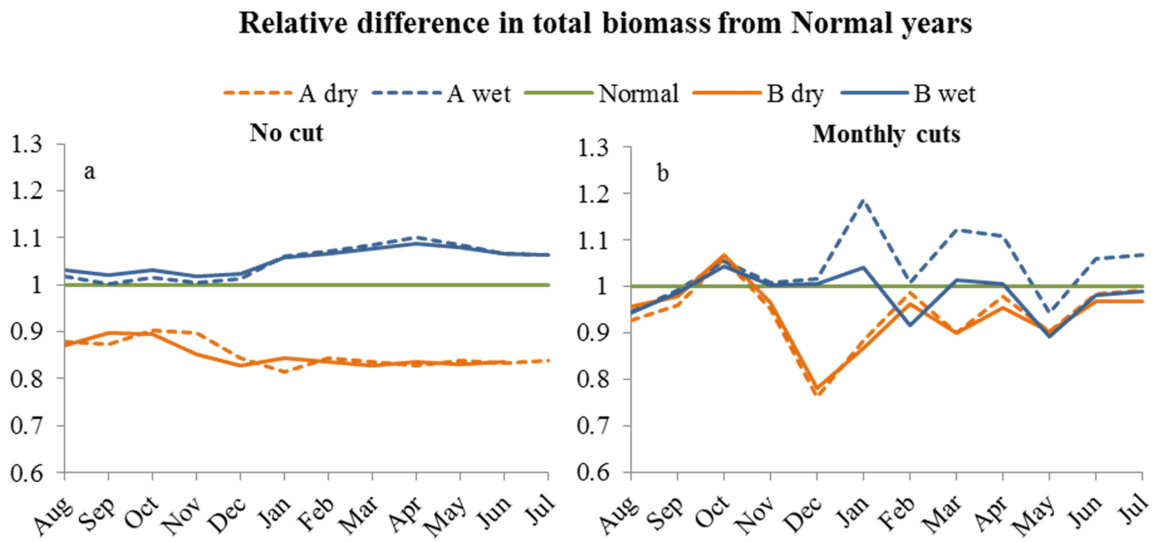


Figure 8. Relative difference in total biomass of Dry (orange) and Wet (blue) years from Normal, for functional groups A (dashed lines) and B (solid lines), for 0 (a) or 12 (b) cuts per year.

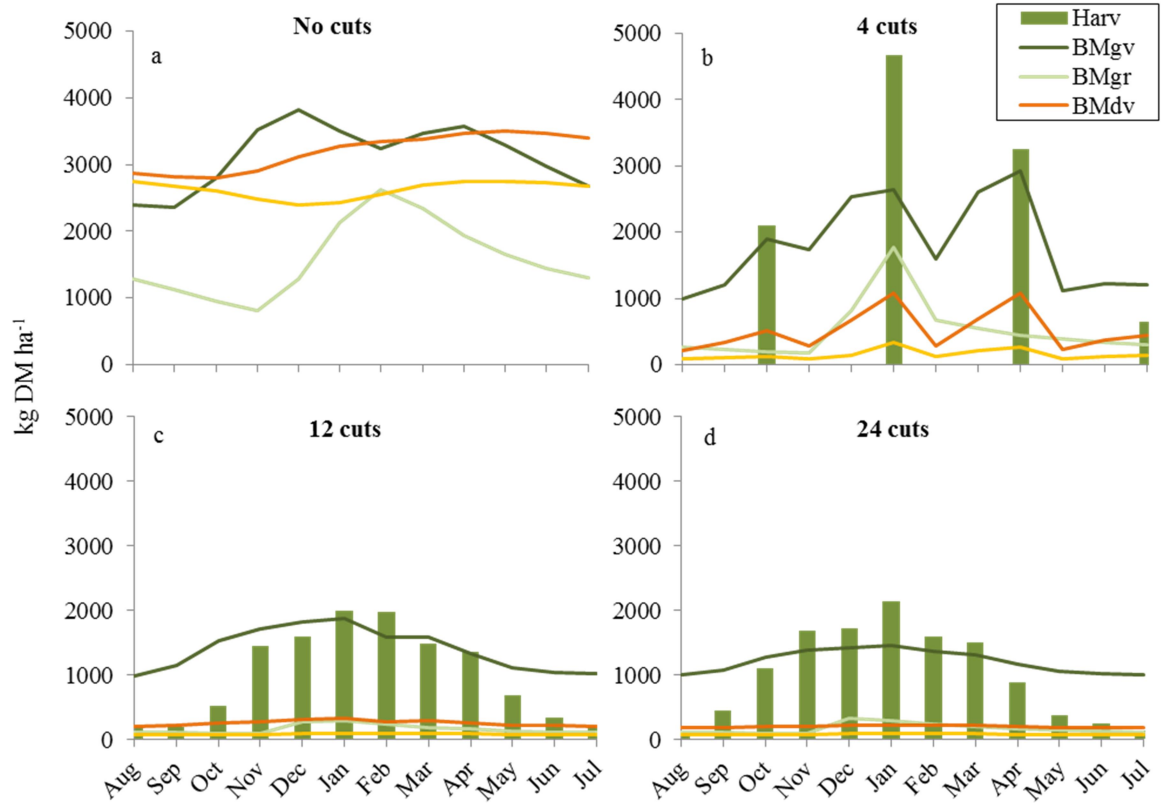


Figure 9. Total biomass for each compartment (green vegetative, BM_{GV} , green reproductive, BM_{GR} , dead vegetative, BM_{DV} , dead reproductive, BM_{DR}) and total harvested (bars) for functional group B in wet years, with 0 (a), 4 (b), 12 (c) or 24 (d) cuts per year. Lines are means over 5-year simulations.

CHAPTER IV – THE GRAZING MODEL

4. MODELING HERBAGE INTAKE FROM HETEROGENEOUS, COMPLEX GRASSLANDS

Abstract

Mechanisms of grazing in heterogeneous and diverse environment are influenced by a myriad of complex interaction of the plant-animal interface, involving many underlying factors rather subjective and not completely understood. Simulating foraging behavior in those environments is quite challenging, and model can be wrapped in many assumptions that soon become cumbersome with increasing vegetation complexity. On the other hand, simulation models can help unveiling those multifaceted relationships, leading to a better understanding of herbivores herbage intake response to, and effect on vegetation characteristics. In a step towards that direction, we propose adapting the *prey model* to a compartmentalized, spatially explicit vegetation model, to simulate grazing dynamics in diverse, heterogeneous grasslands. As base for implementation we utilize a spatialized version of PampaGraze (Chapter 3), a mechanistic vegetation model based on functional groups of plants, adapted to subtropical perennial pastures. The grazing model incorporates the classical mathematical solution with empirical observations on foraging behavior, to simulate herbivore grazing on rangelands and test the patterns of intake and diet selection over different vegetation types. The optimality approach for diet selection offers a solid theoretical basis with clear assumptions to evaluate the grazing process in pastures with varied characteristics. The proposed model was successful on simulating daily intake, bite mass, bite rate, and short-term intake rate, according to literature available on intake mechanism for native grasslands. Analyzing the component's relationships given the determined constraints, we identified a possible strong limitation by digestibility (physical capacity) from one side, and behavioral (limited time grazing), impeding the animal to achieve desirable intake. The higher heterogeneity with increased stocking rates offered higher opportunity for selection, but with a tradeoff between nutritive value and total herbage intake. We consider the model successful in simulating intake, although more broader simulation (in terms of pasture composition and stocking rates) should be performed to verify the flexibility of the model with increased heterogeneity and different grazing managements.

4.1. Introduction

Diet selection and intake have been subject of study in many areas of ecological (e.g. Wilmshurst et al., 2000; Prins and van Langevelde, 2008) and agronomical (e.g. Stobbs, 1973; Dumont et al., 2002) research, from theoretical (e.g. Westoby, 1974; van Langevelde et al., 2008) to applied (e.g. Grant et al., 1996; Bremm et al., 2012) perspectives. However, when it comes down to actually assembling diets on heterogeneous, complex environments and its influence on intake and performance, very little is known, especially in subtropical grasslands (but see Murray and Illus, 1996; Prins and van Langevelde, 2008). Most of the behavioral studies are very particular to the specific scenario, even within tested environment or experimental arrangement (Bonnet et al., 2015). On the other hand, most simulation models have very generalized approaches that end up losing the fine relationship of the herbivore with the food environment (Newman et al., 1995; Hengeveld et al., 2009). Finding a model that can incorporate both mechanistic and empirical approaches seems to be the most reasonable alternative to study the relationship between food environment and forager (Westoby, 1974; Laca and Demment, 1996), especially if it is possible to simulate very distinct herbage and grazing pressure scenarios that would be difficult to achieve with field experiments. Thus, understanding those mechanisms of intake and selection could help comprehending the effects of management on ecosystem dynamics, and improving the *status quo* of range management.

There are many underlying aspects of foraging behavior poorly understood and highly dependable on the food environment characteristics (i.e. difficult to evaluate in field experiments and to transpose to different scenarios). Grazing responds to variation in the vegetation, as vegetation pattern is a response to grazing in a feedback loop (Parsons and Dumont, 2003; Laca, 2008). This heterogeneity affects herbage intake through various mechanisms, such as searching time, bite dimensions and selectivity, which are fundamental parameters to build realistic and general mathematical model for grazing behavior (Laca and Demment, 1990). Those questions can be very difficult to both answer and to model, depending on the level of details we add to our conceptual model, and on the temporal and spatial scales we are analyzing (Laca, 2008). Integrating all those aspects in a grazing model which would then be incorporated to a vegetation model has proven to be quite challenging, both in terms of feasibility and computation. At certain point, assumptions start to be cumbersome and difficult to be held, and generalizations can do more harm than improving predictions. The lack of experimental data and understanding on the temporal scales on the

variability of resources and foraging decisions makes difficult to parametrize more realistic models (Owen-Smith, 2008).

Early grassland models simulated intake (e.g. Johnsons and Parsons, 1985, Parsons et al 1988) using simple approaches based on leaf area index. Vegetation growth was divided in leaf compartments, evenly distributed across the pasture (not spatialized), and grazing was considered a homogeneous, deterministic process, taking even shares from each compartment. In an evolution of this line of modeling, Swinning and Parsons (1999) addressed the discrete and stochastic nature of the defoliation process, and modelled grazing at bite scale, but still considering vegetation as only one compartment. Those models did not consider forage nutritive value, which was later proved to be an important parameter affecting the intake functional response (e.g. van Langevelde et al., 2008). Models accounting for multiple species are rare and often very complex (e.g. Richardson et al., 2010), including many parameters that are poorly understood, especially for range species (Duru et al., 2009). Analytical approaches, such as those based on post-ingestive feedback, dietary experiences and sensory stimuli are interesting alternatives (Prache et al., 1998). However, although being largely accepted grazing theories (Provenza and Cincotta, 1993), those are based on many variables and empirical assumptions (e.g. palatability, taste) which makes modeling mathematically more difficult and challenging (Gregorini et al., 2015).

The foraging models based on the optimality principles (“optimal foraging theory”; Pike, 1984; Stephens and Krebs, 1986) offer a relatively simple, consistent mathematical approach, with a solid theoretical base, clear assumptions and well defined objectives for simulating foraging strategy (Laca and Demment, 1996). The goal is to maximize an objective function, considering that the evolutionary fitness and environmental adaptation of an animal led to that specification (Stephens and Krebs, 1986; Newman, 2007). Diet choice is a response to the changes in the food environment, as the environment will also respond to diet choices and grazing pressure. This plasticity in selection (Belovsky and Schmitz, 1991) as food conditions changes is well accommodated by such models. As environment changes (i.e species composition in the pasture or increase in dead or reproductive herbage) the optimality approach still holds since the decision will always be made based on the overall state of the pasture at the specific point which decision is being made.

Here, we present a hybrid approach between classical behavioral strategies to determine food selection, along with empirical observations of food acquisition to represent grazing and intake in an heterogeneous, complex grassland. Our objective is to implement a grazing model to study intake as a function of vegetation heterogeneity

in complex grassland environments. For representing diversity, species were grouped into functional groups, and with variable canopy characteristics (proportion of canopy structures and nutritive value). The base vegetation model is a spatialized and adapted version the model proposed by Jouven et al. (2006) and adapted by Wallau et al. (Chap 3) for subtropical, C4-dominated grasslands of southern Brazil. We explore the idea that digestive constraint is the major limitation in forage abundant native grasslands, while grazing time (i.e. behavioral limit) is the major constraint when low-availability but highly-digestible forage is available. Those two mechanisms acting together, limit, most of the time, the intake capacity of the animal, further impeding it from achieving desirable performance.

4.2. Materials and methods

4.2.1. Concepts and assumptions

4.2.1.1. General description

There are many factors influencing foraging behavior and diet selection in herbivores, from vegetation characteristics and animal physiology all the way to social interactions. Accounting for all or most of those is virtually impossible and, to some extent, pointless, since few factors influence majorly. Here, we attempt to simulate diet selection and intake by beef cattle in a heterogeneous pasture, composed by two functional groups of plants with distinct acceptance, nutritive value and productivity. For simplify, we assume that mechanisms of diet selection are function abundance and digestibility of available vegetation, which interact with the processes of food intake and digestion relative to animal size and digestive physiology (Ilius and Gordon, 1987, 1991, 1993; Laca and Demment, 1996). As a common denominator, we use intake of digestible organic matter as function of time grazing and time digesting per bite. Our model has two levels of heterogeneity: the functional composition, which represents diversity, and the vegetation compartments, which represents canopy structure.

The conceptual framework for the diet selection of grazing model is based on the prey model, where animals decide which food items should be taken based on the rate of “currency” uptake of the selected patch in relation to the whole environment (Owen-Smith and Novellie, 1982; Stephen and Krebs, 1986; Laca and Demment, 1990). In a heterogeneous environment with abundant food items varying in (bite) size and nutritive value (digestibility), the optimization procedures identify items that, if added to the diet, will bring the best benefit in terms of intake rate given the digestive capacity of the animal. As surrogate for currency, we use digestive dry matter intake as

function of the most limiting factor between handling and digesting time (Vanderlin and Wiley, 1989; Hirakawa, 1997).

The model is structured around *the bite*: each cell has a specific set of bite characteristics (bite mass, digestible dry matter per bite, bite rate, number of bites) which, compared to all available food items, will determine how much to eat from the encountered cell. Assuming the forager has complete knowledge of the food environment and energy is the most limiting nutrient, the decision about the number of bites taken per cell (from a total number of bites set by bite area relative to total cell area) is given by comparing “profitability” per bite in the specific cell visited to all other available bites in the pasture. The model is spatially explicit, being patches (cells of size 0.1 m²) considered as discrete, internally homogenous structures (Kotliar and Weins 1990), which allow a uniform distribution of homogenous bites (Hirakawa, 1997) only from the readily-available (first) layer of vegetation. The digestive kinetics of each food item is independent, having no carryover effect of previously chosen items (Hirakawa, 1997). Rumen is a “storage” compartment which can hold only as much dry matter in a day as it can be digested, based on the animal’s maximum intake capacity given the digestibility of each bite (Verlinden and Wiley, 1989; Laca and Demment, 1990, 1991; Hirakawa, 1995, 1997).

For representing bite characteristics, we chose to use empirical data collected from field observations on grazing behavior (Bonnet et al. 2015, and unpublished data). The great botanical diversity and large difference in canopy structure creates a very particular feed environment, where choices many times swing from short, high nutritive value but low bite mass grazing lawns, to selected one-leaf, deep bites in tall tussocks (Parsons and Dumont, 2003; Bonnet et al., 2015). Considering that most of the studies on bite components have been done in homogenous monocultures or simple mixtures (e.g. Stobbs, 1973), or using hand-made microswards (e.g. Laca et al., 1994) and sods (WallisDeVries et al., 1999), the choices for the classical approaches (i.e. Stobbs, 1973; Burns and Sollenberger, 2002) for representing bite and intake relationships would be less transferable to our reality. In one hand, our approach may limit application across other scenarios, but on the other, it gives a more realistic description for studying the relationship between cattle and the foraging environment for this type of grasslands.

The choice for a hybrid approach between the diet breadth model and empirical equations is for attempting a more realistic description of foraging behavior and the interaction of the grazer and the feed environment for our native grasslands (Laca and Demment, 1990; 1996). This can allow us to better explore the functional

response of intake to heterogeneity in quantity and quality of forage, and how it affects intake and, lately, animal performance. To implement the grazing model, first we had to spatialize and adapt PampaGraze (Jouven et al., 2006; Chapter 3.) to produce the needed inputs for the grazing functions, then employing diet selection and intake.

4.2.1.2. Defining constraints

A clear definition of constraints is key for the correct functioning of the model and interpretation of results (Vanderlin and Wiley, 1989; Fryxel, 2008). Constraints are the factors limiting the acquisition of the currency, and are define the animal's relationship with the changing environment (i.e. the relationship between decision variables and the currency), which will then be determinant for performance (Laca and Demment, 1996). Herbivores, generally, face a situation where food items are abundant (although specific, and generally more preferable food items might be scarce) but limited by the intake capacity, driven wither by digestibility of the selected material (i.e. digestive capacity; Owen-Smith and Novellie, 1982; Belovsky, 1984) or selection of preferred material (i.e. behavioral compensation; Ungar, 1996; Bonnet et al., 2015). Thus, in many cases, digestion is more limiting than pre-ingestive handling time as dominant constraint in diet choice (Dade et al., 1989; Hirakawa, 1997), if herbage allowance is not limiting (Sollenberger and Vanzant, 2011).

Thus, there are two constraints at the instantaneous currency uptake rate level, and four limitations for total daily intake based on physical aspects of digestion, and behavioral characteristics. For the currency level, constraints are the processing (i.e. time for actually cropping and chewing the bite) and digesting time for each bite, in relation to bite mass and dry matter digestibility of the selected material. Intake is limited by the a digestive constraint (digestion time for the amount of harvested material cannot exceed 24 h); a fill constraint [total intake should be lower than 2.8% of animal live weight (LW)]; and two behavioral constraints (time actually grazing cannot exceed 12 h and area explored in one day has be at most 0.2 ha). This should address the range in nutritive value and in herbage allowance to be explored.

4.2.2. Adapting PampaGraze to grazing submodel

PampaGraze is a mechanistic, dynamic model, developed to study “the effects of management (type and intensity) on biomass, structure and quality dynamics” of multi-specific perennial pastures (Jouven et al., 2006). The model was developed using JAVA (Java SE 8). We changed the structure of PampaGraze to a cellular automata model (Deutsch and Dormann, 2005), composed by a grid of 450 by 450 hexagonal cell, where each cell corresponds to one functional group and is independent of

neighbors. The whole assembly of the model is based on the processes within each of the four structural compartments of the canopy: green vegetative ($_{GV}$), green reproductive ($_{GR}$), dead vegetative ($_{DV}$) and dead reproductive ($_{DR}$) (Carrère et al., 2002). Each compartment works separately, and is described by a set of state variables for standing biomass [BM_c , kg dry matter (DM) ha^{-1} , where “ c ” designates each of the four compartments] and nutritive value. A set of differential equations control biomass accumulation and disappearance, and aging dynamics within each compartment, in a daily time step. The model was originally developed for temperate mixed grasslands, and further adapted to sub-tropical, C4-dominated grasslands (Chapter 3.), which will serve as base for the implementation of the grazing model. For implementing grazing, the model was spatialized in a 450 by 450 grid of hexagonal 0.1 m^2 cells, representing approximately a 2 ha pasture.

In the vegetation model (Jouven et al., 2006; Chapter 3.), each cell, at a specific time, is characterized by the biomass available in each of the four vegetation compartment (BM_c , in $kg\ ha^{-1}$) and organic matter digestibility for each compartment (OMD_c , as %). For implementing the grazing functions, a new set of variables were calculated based on mechanistic (e.g. canopy height) or empirical equations (e.g. bite mass). Variables added are canopy height based on green vegetative (H_i , in m), proportion of each compartment (p_c , fraction), bite mass and possible number of bites ($BiMa_i$, in g, and $P_{bites,i}$ respectively), to finally calculate short-term intake rate of digestible dry matter (or profitability; e_i/t_i , in g of digestible dry matter s^{-1}).

Canopy height (H_i , in m) was calculated by dividing BM_{GV} by the respective bulk density ($kg\ DM\ m^{-3}$) of the specific functional group, assuming a constant density through the whole canopy, and that animals will seek for green vegetation for placing bites. Bulk density plays an important role on bite formation (e.g. Stobbs, 1973; Laca et al., 1994) and has a large variation with height and grazing management (e.g. 3.4 to 1.75 $kg\ m^{-3}$ from 4- to 16-cm grazed canopies; Gonçalves et al., 2009), but this effect could not be captured since it is a fixed parameter of the model. The proportion of each compartment (p_c , fraction) composing each cell is given by dividing the BM_c by the total cell's biomass ($\sum BM_c$).

The number of possible bites per cell is variable and dependent on the bite area (BA , cm^2), which was calculated based on an equation adapted from Baumont et al (2004):

⁶ Underwritten “ c ” refers to compartment within cell, and underwritten “ i ” refers to cell characteristics

$$BA = 2 \times DA^2 \times \left(1 + \frac{5}{H \times 1000}\right)^{-1} \times \exp[-0.3 \times (BkD_{GV} - 1)] , \quad \text{eq. (1)}$$

where DA is the dental arcade of the grazing animal, in cm, after Illus and Gordon (1987; $DA = 0.86 \times LW^{0.36}$, in cm); and BkD_{GV} is the bulk density of the green vegetative compartment in kg m^{-3} . The number of possible bites possible per cell ($P_{bites,i}$) is equivalent to the cell area divided by BA . Within a cell, at given time, all bites are homogenous and only on the upper layer of the canopy (readily available) can be grazed, without overlap of bites. This also impedes the cell from being depleted of biomass.

Both bite mass ($BiMa_i$, in g) and time per bite (t_g , s), considered as the actual time the animal takes to harvest the bite, were calculated based on direct observations and measurements on native grasslands (Bonnet et al., 2015; and unpublished data). Bites type, and therefore mass, changed according to functional group and canopy structure, which is also related to season, and given by a set of rules [Eq. (2)]. This approach was used to better characterize the grazing process on heterogeneous environments where there is a vast range of bite type choices for the animal.

$$BiMa_i = \begin{cases} 3.5 \times H - 0.04, & \text{if } FG = A, \text{ for spring} \\ 2.3 \times H - 0.02, & \text{if } FG = A, \text{ for all other seasons} \\ 2.7 \times H, & \text{if } FG = B, \text{ for spring} \\ 3.8 \times H - 0.02, & \text{if } FG = B, \text{ for all other seasons} \\ 4.5 \times BiDep, & \text{if } FG = C \text{ or } D, \text{ and } H \leq 0.25 \text{ m} \\ 4.8 \times BiDep - 0.04, & \text{if } FG = C \text{ or } D, \text{ and } H > 0.25 \text{ m} \end{cases} , \quad \text{eq. (2)}$$

As bite mass was measured for approximately 250-kg beef heifers, we used an allometric approach calculated from data presented by Shipley et al. (1994) to adjust bite mass ($BiMa_{a,i}$, in g) by live weight (LW , in kg).

$$\ln(BiMa_{a,i}) = \ln 0.026 + \frac{[\ln(BiMa_i/0.026) \times \ln(LW)]}{\ln(250)} \quad \text{eq. (3)}$$

Bite depth ($BiDep$, in m), was used to characterize bites on tussocks (FG C and D). It was calculated as being the minimum between 60% of H and a random value generated by an inverse normal distribution with mean and standard deviation specific for each functional group and H category (Table 1). This approach accounts for deep bites on single or few leaves, sometimes observed in tussocks (O. Bonnet, unpublished data). Time per bite (t_g) was calculated based on bite rate (BR_i , bites min^{-1}), which was also divided by functional group and canopy characteristic to better fit the observed data. No adjustments were made for correcting t_g for LW , as in $BiMa_a$, since we believe that changes in time per bite due to body size would be minimal (Shipley et al., 1994).

$$BR_i = \begin{cases} -112 \times H + 63.48 & \text{if } FG = A \\ -180 \times H + 63, & \text{if } FG = B, \text{ and } 0.03 \leq H < 0.10 \text{ m} \\ -180 \times H + 53, & \text{if } FG = B, \text{ and } H < 0.03 \text{ or } H \geq 0.10 \text{ m} \\ -115 \times BiDep, & \text{if } FG = C \text{ and } H < 0.30 \text{ m} \\ EXP(-0.46 \times BiDep + 3.7), & \text{if } FG = C \text{ and } H \geq 0.30 \text{ m} \\ -34 \times BiDe - 23.5, & \text{if } FG = D \end{cases}$$

eq.(4)

Then,

$$t_g = \frac{60}{BR_i},$$

eq. (5)

where 60 represents $s \text{ min}^{-1}$.

Digestive constraint can be one of the most limiting intake restrictions in grazing, because of the high availability but low nutritive value material available (Stephen and Krebs, 1986; Spallinger and Hobbs, 1992; Laca and Demment, 1996). To determine the amount of forage of specific digestibility a ruminant could eat in one day (24 h) for filling the rumen (physical limitation), maximum intake (I_d , % of LW, in DM) was calculated from data presented by Lalman (no year) as a function of relative OMD (fraction), as a simplification for dry matter digestive kinetics (Van Soest, 1994).

$$I_d = 0.0025 \times \exp[3.8129 \times \sum(OMD_c \times Q_c)],$$

eq. (6)

where Q_c is the relative proportion of each compartment that composes a bite. Assuming a maximum dry matter intake of I_d , and that digestion is a continuous, constant process along the day, and independent from previous meals, the clearance time per unit of dry matter (t_d , in $s \text{ bite}^{-1}$) is given by

$$t_d = \frac{BiMa_a}{(I_d \times LW) / 86.4},$$

eq. (7)

where the denominator represents the passage rate in $g \text{ DM s}^{-1}$, where $86.4 \text{ s kg d}^{-1} \text{ g}^{-1}$ is a factor for transforming the units from kg d^{-1} to g s^{-1} .

Q_c was calculated based on the proportion of each compartment in the canopy (p_c) multiplied by an acceptance coefficient (a_c) based on Parsons et al (1994), which determines the “selectivity” of the animal within the canopy compartments. Empirical “acceptability” values were assigned for each biomass compartment for each functional group (Table 4). The proportion of each compartment that will compose the bite mass, therefore the proportion of each compartment harvested, is given by the equation:

$$Q_c = \frac{a_c \times p_c}{\sum a_c \times p_c},$$

eq. (8)

Finally, the profitability of each bite (e_i/t_i , in g of OMD s^{-1}), or the relative rate which the currency to be maximized is uptake, is given by the sum of the amount of digestible organic matter harvested from each compartment ($\sum BiMa_c \times Q_c \times OMD_c$), divided by the maximum constraint between time grazing per bite (t_g) and time digesting the harvested material (t_d). Since those two processes are simultaneous, the more constraining will be the limiting factor for diet selection (Verlinden and Willey 1989; Hirakawa 1997). This, however, is a virtual parameter, and does not indicate the intake rate per se, since the divisor can be either of two scales: one relative to the maximum time the animal grazing, and the other one to a day, since digestion is a 24-h process. For actual intake calculation, each time constraint is accounted for independently, and limited accordingly (see section 4.2.3.3 Grazing limitation).

4.2.3. Implementing the grazing process

The implementation of the grazing process has two main parts: first, cell choice and diet selection; then the actual computing of daily intake restrained by the grazing limitations. Since pasture size simulated is relatively small (~2 ha) and for simplification, cell selection was implemented as random. However, the model can be updated to a more sophisticated selection process, such as a correlated random walk model (e.g. Codling et al., 2008). At each visited cell, the diet breadth model determines selection and gives parameters for intake accounting, which takes place separately.

4.2.3.1. The mathematical framework of diet selection

Diet selection is based on one simple decision: how many bites to take from each encountered cell. This decision can range from zero to the maximum number of bites possible to be taken from each cell, depending on the profitability of the cell (e_i/t_i) in relation to the maximum marginal value (E/T , Charnov, 1976). Assuming that the animal is familiar with the whole feed environment, and the profitability values for all food items is known, cells are ranked in decreasing order of e_i/t_i . The marginal profitability considering the encounter rate (λ_i , in bites s^{-1}) is calculated as $[(\sum \lambda_i e_i) / (1 + \sum \lambda_i t_i)]$ at each step of the rank, as if food items were to be added to the optimal diet in that specific order. This, however, does not mean that all food items will be taken in rank order, but that those of higher rank order (i.e. $e_i/t_i > E/T$) should be taken upon encounter.

The λ_i calculated as

$$\lambda_i = \frac{sw \times V_{max} \times sr_i \times P_{bites,i}}{CA \times NC}, \quad \text{eq. (9)}$$

where sw is the searching width of the animal (in m); V_{max} is the maximum speed of the animal, which is $0.5 \times LW^{0.13}$ (in $m\ s^{-1}$; Calder, 1983), and sr is a speed reducer factor to decrease maximum speed while searching and grazing; $P_{bites,i}$ is the number of possible bites on a cell of CA area (m^2), multiplied by the total number of cells (NC) in the model. Speed reduction (Spallinger and Hobbs, 1992; Hirakawa, 1997) is calculated as

$$sr_i = \frac{sw \times P_{bites,i} / CA}{BR_i} - \frac{1}{V_{max}}, \quad \text{eq. (10)}$$

A forager should only add to the diet encountered items of lower rank order when doing so increases overall return rate: the marginal value for including the j^{th+1} item is larger than the cumulative profitability of the already-included items. In other words, the highest j that satisfies this inequality [Eq.(11)] is the lowest ranked item that should be included in the diet (Stephens and Krebs, 1986).

$$\frac{\sum \lambda_i e_i}{1 + \sum \lambda_i t_i} > \frac{e_{j+1}}{t_{j+1}}, \quad \text{eq. (11)}$$

Based on the rule above, at each encountered cell, if

$$\begin{cases} \frac{e_i}{t_i} \geq \frac{E}{T}, & p_i = 1 \\ \frac{e_i}{t_i} < \frac{E}{T}, & p_i = 0 \end{cases}, \quad \text{eq. (12)}$$

where p_i represents the probability of cell being taken (1) or avoided (0). This bimodal decision is called the “zero-one rule” (Stephens and Krebs, 1986) which applies well to certain species (like carnivores and insectivores). The decision rule for herbivores, however, is not so clear as zero-one, since “preys” (patches) are constant and abundant, with other characteristics (e.g. digestibility) imposing limitations rather than encountered rates. Thus, herbivores experience “partial preference” (Stephens and Krebs, 1986; McNamara and Houston, 1987; Berec and Křivan, 2000), which means that they may take bites from below-threshold patches or skip patches of higher profitability. For representing this we used a normal cumulative probability density function, where $x = e_i/t_i$, $\mu = E/T$ and standard deviation (σ) to be set for adjusting the shape of the curve (the smallest the σ , the more like “zero-one rule” the distribution will behave; Figure 1).

Dung and urine spots were not considered influencing diet selection. The time step of the model is one day, but foraging was further broken down to cell selection for allowing simulation of multiple animals and cell revisit. After taking x many bites from visited cell i , new values for each biomass compartments are updates (see next

section), a new cell ($i + 1$) is selected, and all items ranked again for determining the new E/T . The process continues for all simulated animals until one of the grazing limitations is met (section 4.2.3.2).

4.2.3.2. Updating the vegetation model

The amount of forage harvested in each compartment, for each cell ($GRZ_{c,i}$, in kg ha^{-1}) is given by

$$GRZ_{c,i} = Q_c \times BiMa_{a,i} \times N_{bite} \quad \text{eq. (15)}$$

This value is aggregated to the differential equations for biomass change (1 – 4 in Jouven et al., 2006) in the vegetation model. Biomass values are updated each time the cell is visited, so cell can be visited multiple times within a day.

4.2.3.3. Grazing limitation

We considered three main factors for limiting daily intake: maximum total time grazing, maximum time digesting and maximum dry matter intake; assuming that, due to the generally low nutritive value of native grasslands, the chemical constraint would not be achievable. Maximum time grazing was limited to 12 h, which is the maximum time the animal is able to graze at low herbage allowances (da Trindade et al., 2012), while the digestive constraint is in a 24 h basis. Total DM intake was considered as being 2.8% of live weight and although being accounted for on the maximum time digesting, it is still included as a limiting factor because the equation [eq. (6)] used has no upper limit (i.e. to account for decreased intake at higher digestibility levels). At each cell visited, dry matter harvested ($BiMa_{a,i} \times N_{bite}$) adds to the cumulative intake; time grazing per cell ($t_g \times N_{bite}$) plus time between encounters (t_s ; Belovsky and Schmitz, 1990) adds to the cumulative time grazing; and time digesting the harvested material per cell ($BiMa_{a,i} \times N_{bite} \times t_d$) is added to the cumulative digesting time. Independent of how many bites are taken, t_s is fixed, calculated as

$$t_s = \frac{CA}{sw \times V_{max} \times sr}, \quad \text{eq. (13)}$$

Thus, limits to grazing are

$$L = \begin{cases} \text{Digestive constraint} & \sum BiMa_{a,i} \times N_{bite} \times t_d \leq 24 \text{ h} \\ \text{Behavioral constraint} & \sum t_s + t_g \times N_{bite} \leq 12 \text{ h} \\ \text{Fill constraint} & \sum BiMa_a \times N_{bite} \leq 2.8\% LW \end{cases} \quad \text{Eq. (14)}$$

Another behavioral limitation was added to limit the number of visited cells per day to be 20000, which represents and explored area per animal per day of 0.2 ha.

Hence, daily intake is then limited by whichever of the abovementioned constraints is reached first.

4.2.4. Model exploration and analysis

For exploring the model, we set vegetation to a grid of 450 x 450 cell, composing a pasture of aggregations with radius of 5 m of functional groups A and B (50 % in composition of each group), representing roughly 2 ha. Functional groups are divided by leaf life span, specific leaf area and leaf dry matter content. Those are parameters tightly related to physiological processes and morphological characteristics of those plants, being a reasonable characteristic for separating according to grazing choice and response to defoliation. Functional group A is composed mainly by species like *Axonopus affinis* and *Panicum sabulorum*, while functional group B is composed by *Coelorachis selloana*, *Paspalum paucifolium* and *Paspalum notatum* (Cruz et al., 2010; for more information on parameters, see Chapter 3). Organic matter digestibility was set to 0.8, 0.5, 0.65 and 0.5, for maximum and minimum digestibility of green vegetative and green reproductive compartments, for functional group A; 0.65, 0.5, 0.55 and 0.45, respectively, for functional group B. Those values were manipulated from those presented in Chapter 3 to increase separation between the two functional groups, adding to the heterogeneity of the pasture. Functional groups C and D were not used, since the model cannot predict herbage production for those.

For simulation runs, we used real measured weather data (years 2004 to 2009; Chapter 3), for 5-year runs. Management practices applied on the simulations were low and high stocking rates (SR; 1 and 5, 400-kg animals in the 2 ha pasture). This would be just below (low SR) recommended grazing pressures for the region, and around 3.5 times the recommended SR for high for the type of pasture we are simulating. It is important to note that the model, as it is (Chapter 3), is overestimating herbage production, so “recommended SR” could be increased for the sense of interpretation. Since results from statistical significant tests can be “manipulated” by increasing the number of runs, thus losing biological significance (White et al., 2014), we majorly performed graphical analysis, observing the relationships between intake parameters and total intake, and pasture characteristics with intake parameters and total intake. Values presented are mean and standard deviations (or mean of the standard deviations) of response variables per simulation day (i.e. each data point on Figures 2 to 4 represent mean over one day for represented variable).

4.3. Results and discussion

4.3.1. Intake mechanisms

To check the functioning of the specific parts of the model and behavior of the components of intake, we separated some of them available in the output of the model to take a closer look and compare to literature data. Values presented are average over one simulation day. Both bite mass (g bite^{-1}) and time per bite (s bite^{-1}) were modeled as function of canopy height, so a thigh relationship would be expected (Figure 2a). Figure 2a shows mean pasture canopy height, which is shorter and more heterogeneous at high stocking rate, increasing the variability in bite mass. Deviation in bite mass was apparently linearly related to deviation in canopy height, as it would be expected (data not shown). The upper group of points represents spring months, where bite mass increases with the flush of new growth. Mean bite mass ranged from around 0.1 g to almost 0.6 g (0.25 to $1.5 \text{ mg kg LW}^{-1}$; Table 3), while standard deviation for bite mass was also in the same range, and increased linearly when the variation in canopy height also increased. This indicates that, high canopy heights offer opportunity for a larger range of bite mass. This heterogeneity had an effect of apparently increasing the ODM concentration of intake. Similar effect was observed in the relationship between time per bite and bite mass, which decreased in a rather linear fashion as bite mass decreases, as it has been previously reported (Laca et al., 1994; Ungar, 1996; Gonçalves et al., 2009). At higher average canopy height, not only bite mass was higher but also standard deviation for bite mass, which means the range of bites was greater, due to a larger availability of bite choices. When bite size reduced, because of reduction in forage available, the range of possible bites was smaller, and so the range in time per bite.

As expected, short-term intake rate (g min^{-1} ; Figure 2) responded linearly to the increase in bite mass, independent of stocking rate. Five works which measured short-term intake rate and other bite characteristics in native pastures are summarized in Table 3 for easier comparison to simulated results (Gonçalves et al., 2009, Bremm et al., 2012, Bonnet et al., 2015; da Trindade et al., 2016; and Carvalho et al., in prep). The latest three were measured in natural conditions, under continuous stocking with variable herbage allowance regimes (1 to $4 \text{ kg DM kg LW}^{-1}$). The first two works were field measurements on manipulated swards composed by distinct proportion (in relation to tussocks; Bremm et al., 2012) or canopy heights (Gonçalves et al., 2009) of functional groups A and B. The equations used in this model for determining bite mass and bite rate come from the same data partially used by Bonnet et al. (2015), so naturally the values are very similar. It is important to note that the experimental

protocol in Gonçalves et al (2009) included fastening the animals for 5 h prior to the grazing evaluations, what increased bite mass and bite rate at the same time. In Bremm et al. (2012), lower-stratum canopy height was maintained at around 11 cm, and values presented include bites in tussocks. The upper range of simulated bite mass was similar to Gonçalves et al. (2009) and Bremm et al. (2012), while the lower range is well below, due to shorter canopy height (compared to Bremm et al., 2012) and fasted animals in Gonçalves et al. (2009). Similar results were also observed for bite rate. Still comparing the simulated results to those two experiments cited above, short-term intake rate reported was considerably larger, but for the same reasons mentioned before, regarding fasting and ranges of canopy height. Now, when comparing short-term intake rate to Bonnet et al. (2015), da Trindade et al. (2016), and Carvalho et al. (in prep), the values were very similar. Despite not being a true validation, it denotes the well-functioning of the intake predictions. The very low range of the simulated intake was due to high stocking rates in low-productivity season (fall and winter), reducing drastically the amount of forage available.

Daily intake limitations can be very clearly seen on Figure 4. Line C represents an intake of 2.8% of LW, which would be considered appropriate for beef cattle for sustaining reasonable production levels. At high bite mass, which is achieved in tall canopies, intake is limited by the digestibility (line A). The animal cannot increase intake because digesting capacity is already filled, therefore not reaching the intended intake (line C). This limit is governed by equation 6 and determined by forage organic matter digestibility, which, in this exercise, ranged from 0.49 to 0.62. The top portion of the data points (closer to line A) represent intake at higher digestibility levels, and reducing digestibility would shift line A down. On the other side intake is limited by a behavioral constraint, which is the point up to which the animal can compensate low bite masses by continuing grazing until reaching the set maximum grazing time. This is also associated to the increase in bite rate at low bite mass (Figure 2). Maximum grazing time was set to 43,200 s (12 h). Given that time per bite at the lower end of bite mass (0.1 g) ranges from 1 to 1.5, the animal can take about 40,000 bites per day (which is dependent on the number of cells visited because of the addition of t_s to cumulative time grazing). Reducing time grazing per day will shift line B downwards and pivot it clockwise, being a stronger limitation to intake at low bite mass (low canopy height). At the set conditions, the breakpoint between digestibility and behavioral constraints is at bite mass of around 0.23 g. Reducing time allowed for grazing to 30,000 s (8.3 h) would shift this breakpoint to around 0.36 g bite⁻¹; decreasing pasture's digestibility from 0.6 to 0.5, for example, would reduce possible intake (line A) down to

around 7 kg DM d⁻¹. This indicates that the forager is always limited, in one side by behavioral constraints, in the other side by digestive constraints, never reaching the intended herbage intake for sustaining high weight gains. It reinforces the idea that, especially in native grasslands, only higher herbage allowance does not translate in higher productivity (Carvalho et al., 2008; Sollenberger and Vanzant, 2011).

4.3.2. Partial preference

The “zero-one” rule is one of the three main results of the diet optimization solution, since partial preference for a prey is never mathematically optimal (Stephens and Krebs, 1986; McNamara and Houston 1987). But it also has been a frequently criticized and reviewed points of the foraging theories (Stephens, 1985; Pyke, 1984; Berec and Křivan, 2000), especially comparing to field experiment (e.g. Krebs et al., 1977). The decision whether a prey should be taken is not truly absolute, and items may be included in the diet or not depending on abundance of high-ranked choices (Pyke, 1977; McNamara and Houston, 1987) or how constraints are applied (Hirakawa, 1997). This means that at sufficient large encounter rates of more profitable items, less profitable items should always be ignored; but if abundance of those high ordered items is low, more lower-order items will be included in the optimal diet. When assuming the threshold value indeed has some variance (i.e. the animal does not know the true encounter rate of all prey types), this rule can be flexibilized by a cumulative normal distribution (Figure 1). If we consider the threshold encounter rate as mean, and add some variance by increasing the standard deviation previously set to zero, since we assume the animal has complete knowledge of the food environment, a partial selection behavior emerges (McNamara and Houston, 1987). The larger the uncertainty about the encounter rate, the more flexible the decision is, up to a point where diet choices are essentially random (very low line in Figure 1). Another solution for addressing partial preference was presented by Berec and Křivan (2000). They used the concept of local abundance (vs. global abundance; McNamara and Houston, 1987), where the predator takes a (deterministic) decision whether to attack or not a prey is given by an assessment of local prey density (vs. total prey density). This can be more realistic than considering complete knowledge, and facilitate computation in spatially-explicit models by decreasing the number of calculations at each movement of the animal (i.e. animal just looks in the immediate j^{th} order neighborhood; Beecham and Farnsworth, 1998).

In our approach, instead of considering variation in encounter rate, we simplified by adding variation to the E/T threshold, assuming that the forager does not have complete knowledge about the real maximum profitability possible to be obtained

in the pasture. The standard deviation is manually set for determining a high (low SD) or low (high SD) selectivity behavior (Figure 1), and the probability given by the normal cumulative distribution is the multiplier of the total number of bites possible to get the number of bites taken. In other words, high-rank bites will still be taken to (close to full) amount when encountered, while “average bites” may or may not be taken given the selectivity behavior selected. Results for changed selectivity are shown in Figure 5.

At very high selectivity levels, the forager only takes virtually all bites from encountered cells of higher rank order (higher profitability), while taking none from those which profitability is below threshold. This means that the rejection rate is high, reducing the mean amount of bites per cell. Those very selective bites tend to be smaller bites in high-nutritive value cells. As selectivity becomes more flexible, the probability of accepting more lower-rank bites increases, thus, increasing the number of bites taken per cell. This is beneficial for the animal because it dilutes the fixed time (t_s) per cell, potentially increasing intake capacity (which follows the same trend as short-term intake rate), especially in low biomass situations. Those lower-ranked bites tend to be larger bites in taller, generally older, canopies, with reduced digestibility. Larger bites result in reduced bite rate, but increase in short-term intake rate up to medium-low selectivity. At low and very low selectivity levels, the simulated animal, as expected, is not optimizing any aspect of the diet, and selection strategy is virtually the same as random. This caused a decline in bite mass and short-term intake rate, because bite mass taken is the same as average bite mass available, and organic matter digestibility of intake is the same as the weighted average of available digestibility in the pasture, given the acceptance coefficient (Table 2). In other words, the animal is virtually taking random samples of available choices in the whole pasture. The most interesting fact is that the strict-rule optimized diet (i.e. only take the best items) does not result in the highest intake. Obviously intake refers to dry matter, while the optimized currency was digestible organic matter. Still, when thinking the consequences of this result, at the end of the day, the increased dry matter intake should be more beneficial to the animal, since total intake is generally the most limiting factor for performance (Sollenberger and Vanzant, 2011). Thus, a more flexible diet selection would be a preferred approach. This, in fact, is probably influenced by the mathematical features of the model, and should the whole diet assembly be based on the prey model, including cell choice and costs of displacement and cell rejection, both strategies would be very similar. The short come of this alternative is the high computational cost for implementation, and more complex mathematical solution.

Linking those responses to Figure 4, we can place the high selective strategy close to line B, where total intake is limited by the behavior of the animal. Despite the higher digestibility of intake, the lower bite mass cannot be compensated by the increased bite frequency, and the animal reaches the maximum time grazing before harvesting an adequate amount of forage. At medium level selectivity strategy, there is a balance between nutritive value of harvested material and instantaneous intake rate, placing the strategy close to line A. Limit, then, will be set by the pasture's digestibility and acceptance coefficient. Random selection, however, has low bite mass and lower nutritive value, being limited by average bite mass and average digestibility of the pasture. This means that the best diet choice for our forager is not being extremely selective, because will spend too much time searching and taking low-mass, high nutritive value bites; nor just accepting all bites encountered, being potentially limited by digestive capacity; but a mid-term behavior where both quantity and nutritive value can be maximized (Belovsky, 1984). This behavior has been documented in field experiments, trying to explain (large) bites taken in low-nutritive value species, such as tussocks (Bonnet et al., 2015). Even though the "optimized diet" should accommodate for the balance between bite mass and nutritive value (i.e. no need for "adjusting selectivity"), the amount of forage harvested per day has a high significance for the herbivore, being normally a major limit of performance (Van Soest, 1994; Sollenberger and Vanzant, 2011)

4.4. Conclusions

Composing a model integrating mechanistic and empirical equations seems to be a reasonable alternative to study real scenarios. It can help dissembling phenomena into mechanical components, while keeping a global view of the system. However, it can also be a trap since large errors can be hidden in the data used, and are potentialized when simulating higher level hierarchies. While this is part of the modeling and studying process, it can be specially harmful for predictive simulations, where the intent of the model is to help on decision making. Thus, a good share of skepticism should be used on interpreting the results (Mateus, 2017). Our model seemed to be very successful in simulating bite characteristics and intake in response to variability in pasture composition and availability. The simulation outputs for bite mass, bite rate and intake rate had very reasonable results, and in agreement with available literature on intake components in native pastures. The relatively low daily intake support the idea that cattle grazing on native grasslands are frequently limited by digestive or behavioral constraints, even if forage allowance levels should sustain higher performance levels. This is an important insight for understanding the relationships of herbage allowance,

canopy structure and weight gain in our experiments. When coupling the two approaches (empirical and optimality), the best intake alternative was not a strict optimal diet, but a more flexible alternative, allowing for lower-ranked items to be taken when encountered.

The capabilities of the model are far from being fully explored. A more detailed analysis will require improvements on the vegetation model for increasing sensitivity of the vegetation to disturbances and limitations; for accommodating growth of tussock-forming species; and the implementation of a behavior-oriented cell selection process on the grazing model, for analyzing the creation and maintenance of vegetation patterns. Further exploration should include a larger spectrum of simulations especially including tussock forming functional groups, and responses of vegetation under grazing to variable weather constraints.

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Table 1. Average and standard deviation of observed bite depths (O. Bonnet, unpublished data).

FG	H	Average cm	Standard deviation cm
C & D	<30 cm	0.08	0.024
C	≥ 30 cm	0.15	0.062
D	≥ 30 cm	0.19	0.089

Table 2. Acceptability coefficients for each compartment for a given functional group.

Acceptability by biomass compartment	Functional group			
	A	B	C	D
a_{gv}	1	1	1	1
a_{gr}	0.8	0.7	0.5	0.4
a_{dv}	0.6	0.5	0.3	0.2
a_{dr}	0.4	0.3	0.2	0.1

Table 3. Comparison of mean bite mass (mg DM kg LW⁻¹) bite rate (bites min⁻¹) and short-term intake rate (mg DM kg LW⁻¹ min⁻¹) of published works with native grasslands in southern Brazil to simulated output

Source	Bite mass (mg DM kg LW ⁻¹)		Bite rate (bites min ⁻¹)	Short-term intake rate (mg DM kg LW ⁻¹ min ⁻¹)
	Mean range	SD range	Mean range	Mean Range
Simulated	0.25 – 1.50	0.13 – 1.43	40 – 59	12.5 – 62.5
Gonçalves et al., 2009	0.9 – 3.25		54 – 66	94 – 221
Bremm et al., 2012	1.5 – 2.03		42 – 53	63 – 127
Bonnet et al., 2015	0.25 – 3.25			40 – 60
da Trindade et al., 2016				29 – 52
Carvalho et al., in prep				30 – 85

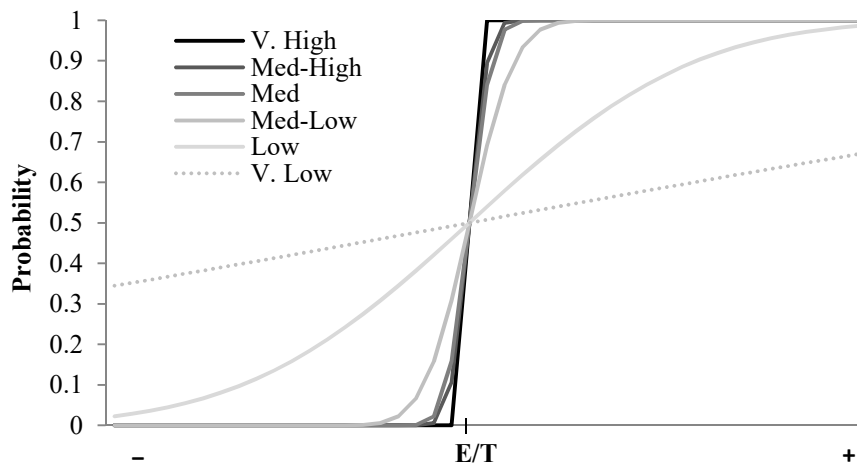


Figure 1. Partial preference for diet selection, given by a normal cumulative distribution, with average as E/T . Lines simulated are selectivity levels, represented by different standard deviations for altering the shape of the curve: Very High ($SD = 0.001$), Medium-High ($SD = 0.008$), Medium ($SD = 0.01$), Medium-Low ($SD = 0.02$), Low ($SD = 0.1$), and Very Low ($SD = 0.5$).

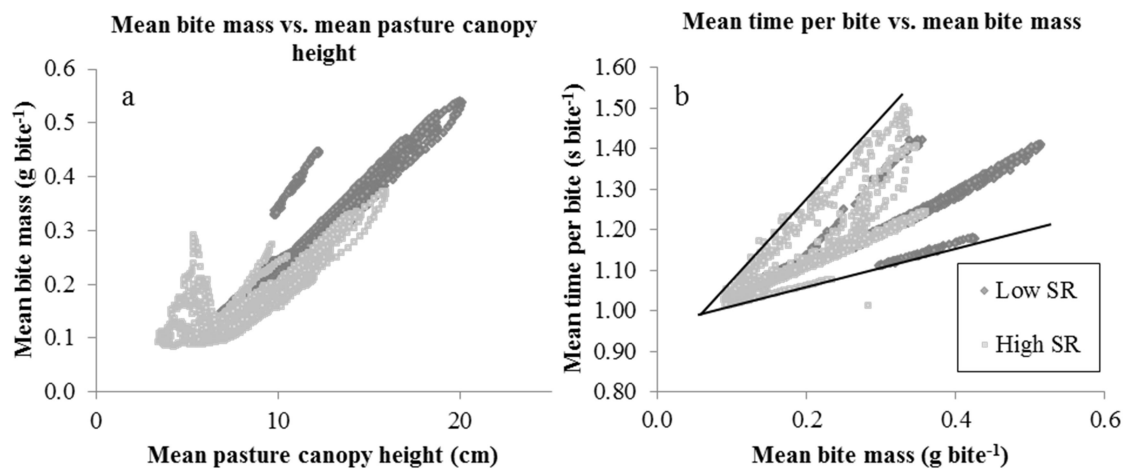


Figure 2. Mean bite mass (g bite^{-1}) as function of mean canopy height (cm; a), and mean time per bite (s bite^{-1}) as function of mean bite mass (g bite^{-1} ; b) for a 400-kg bovine. Simulations represent low (♦) and high (■) stocking rates (0.5 and 2.5 animals ha^{-1}), and data points are average of each parameter within one simulation day.

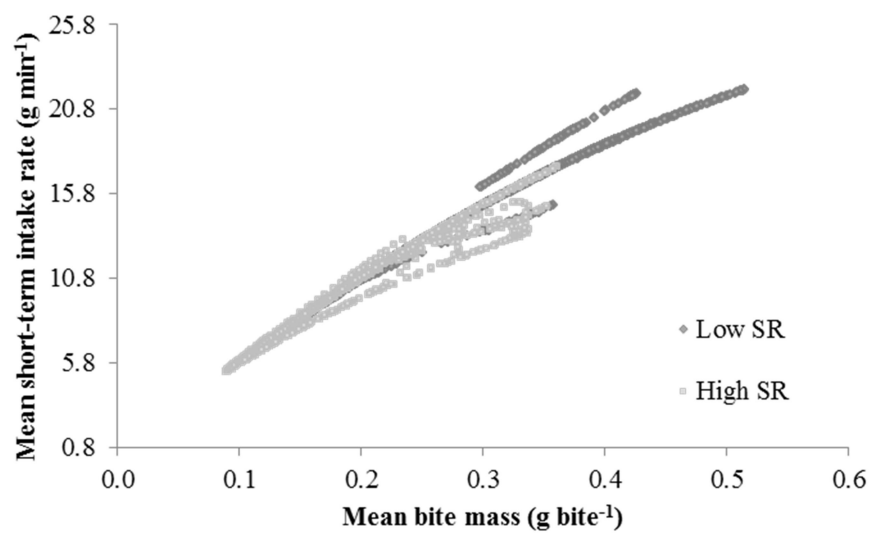


Figure 3. Mean short-term intake rate (g min^{-1}) as function of mean bite mass (g bite^{-1} ; b) for a 400-kg bovine, for simulations with low (\blacklozenge) and high (\blacksquare) stocking rates (0.5 and 2.5 animals ha^{-1}). Data points are average of each parameter within one simulation day.

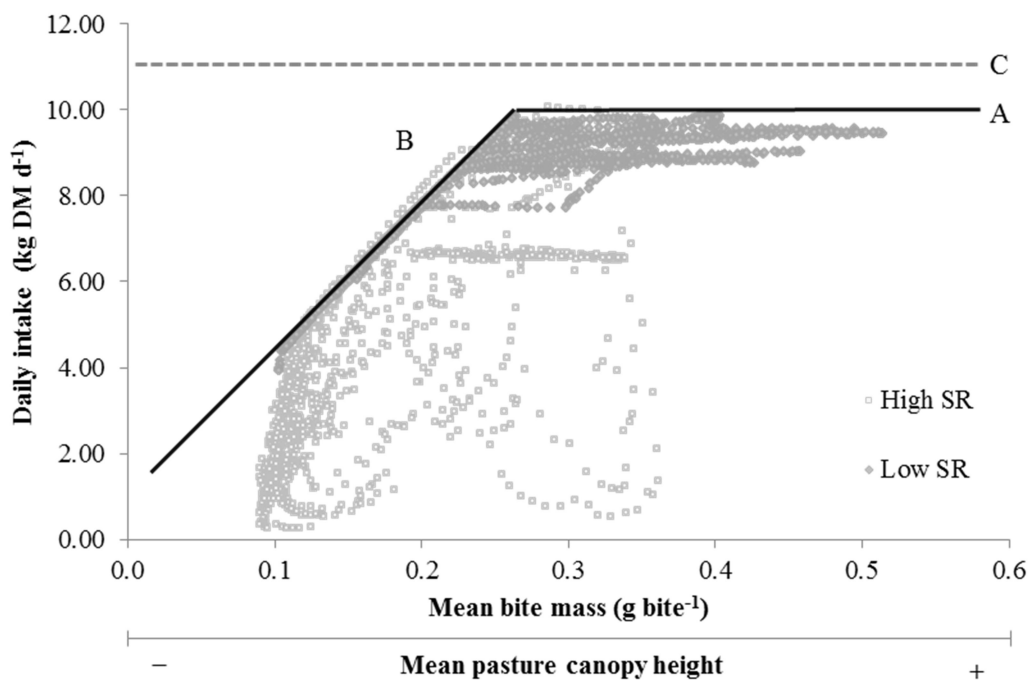


Figure 4. Daily intake (kg DMd⁻¹) of a 400-kg bovine, as function of bite mass (g bite⁻¹) for low (◆) and high (■) stocking rates (0.5 and 2.5 animals ha⁻¹). Horizontal, solid line (A) is the digestive constraint, which represents the physical limitation of intake, given forage's digestibility (eq. 6); perpendicular line (B) represents the behavioral constraint, where intake is limited by the amount of time allowed for grazing per day (set to 43,200 s); and horizontal, grey, dashed line (C) represents intended total daily intake, set to 2.8% live weight (11.2 kg DM d⁻¹).

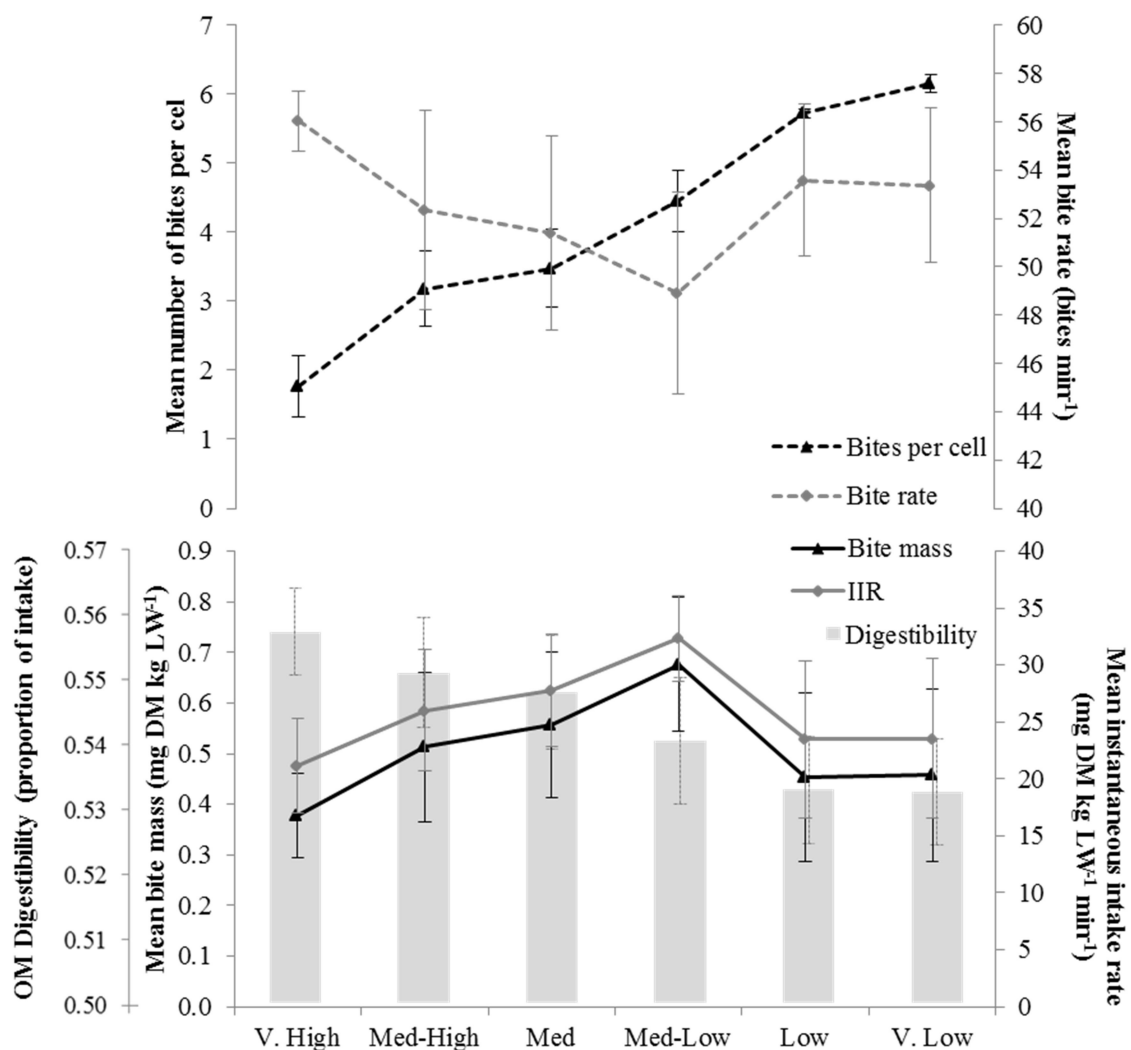


Figure 5. Effect of altered selectivity levels on components of intake and diet selection. Bottom chart represents mean bite mass (mg DM kg LW^{-1} ; solid, black line), mean instantaneous intake rate ($\text{mg DM kg LW}^{-1} \text{ min}^{-1}$; solid, gray line) and mean organic matter digestibility as a fraction of intake (bars); upper chart represents mean number of bites taken per cell (dashed, black line) out of a total of approximately 10 bites possible, and mean bite rate (bites min^{-1} ; dashed, grey line). Points are average for 100 observations of grazing simulation with 5, 400-kg bovines. Vertical lines represent one standard deviation below and above mean.

CHAPTER V – CONCLUSIONS AND FINAL REMARKS

5. CONCLUSIONS AND FINAL REMARKS

Transferring a mechanistic model across environments proved to be less straight-forward than just altering parameters. Many of the suitable approaches used for one environment, are not necessarily appropriate for another, while significant processes in this other scenario may not be accounted for in the original development of the model. This proved to be the case for several equations on ModVege for converting to PampaGraze, especially related to slow-growing bunchgrasses functional groups (C and D). This, however, is not detrimental, and serves as basis for new research and new modeling developments. I believe there was a large expansion in knowledge on the functioning of our ecosystem in pursuit for answers on mathematical simulations, and in putting the pieces of the system together for the assembly of this project.

The vegetation model was partially successful in simulating herbage production dynamics, working well for functional groups A and B, despite tending to overestimate accumulation. Nevertheless, season and annual trends were similar to observed and literature reported data. The model is less sensitive than desired to environmental constraints, and delays in physiological processes are not being accounted for. Those aspects are intensively discussed in Chapter 3, and can serve as guidance for further improvements of the model structure and parameters. In the grazing model, I believe we advanced greatly; especially considering this is the first attempt to model our environment with a mechanistic tool at this level of complexity. The simplicity of the approach but the solid framework made it easier to implement and enhanced our analysis capacity, despite the fact of possible errors embedded on empirical equations, magnified at higher hierarchical levels, as mentioned on the conclusions of chapter 4. The outputs obtained were in accordance with reported experimental results and there are only minor adjustments to be made on the general mechanics of the model. Further advances are noted below, and relate especially to the improvement in the vegetation model and on the implementation of a behavior-based cell-choosing mechanism, such as the correlated random walk approach.

The art of grassland and rangeland management is still beyond mathematical equations know to us. Slowly, we generate data, build information and create knowledge, filling the gaps for a better general understanding of our prairies. We definitely can simulate many aspects of the ecosystem, to various degrees of detail, with variable levels success. But accounting the human dimension, the perception and wisdom of an experienced manager is, if even possible, very difficult. However, for

improving rangeland management, we can give those operators better prediction tools, especially in terms of weather forecast and decision support systems. Here, we set up the stage towards that direction: a mechanistic model that can help us understanding the functioning of the system from an ecological perspective, at the same time it helps developing guidelines for better management and maintenance of ecosystem services. There is still a long way to go to reach those major goals we set in the aperture of this document, but with persistence and perception of the information we have in our hands, we can head towards that direction. If this first stage of the project did not result in very accurate outputs for predicting herbage dynamics in the Campos, it sure enhanced our understanding of the functioning of the system, and helped identifying the need for further developments. The tool has been cleaved, now it needs bruting and polishing. As a final contribution at the moment, here are some suggested further developments for this modeling project.

5.1. Further developments

Here a brief list of some improvements that can be done. First, on the vegetation model:

- In terms of field measurements, the major needs at this point are better measurements of herbage accumulation rate and biomass flows (senescence and decay) across seasons, especially for tussock-forming species, with and without grazing;
- Still about field measurements, we need information about and seasonal variations on physiological and morphological traits to help parametrizing the model;
- And, lastly, we need information on species dynamics under grazing management and water gradients, to implement species shift matrixes for simulating changes in botanical composition

For the grazing model:

- Implement a correlated random walk, considering food choices in general exploration area related to vegetation characteristics and attraction points (e.g. water sources), for accounting for spatial distribution of grazing and the effects on the structure and composition of plant community;
- Partial preference as proposed by Berec and Kriva (2000), with a similar structure of neighborhood order as proposed by Beecham and Farnsworth (1998) can better simulate partial preference, while improving computational performance by reducing amount of calculations per step;

- And, lately, add functions to predict animal performance.

In terms of the mechanics of the model:

- Possibly a different approach to simulate leaf area index and the effects of length of regrowth and cutting or grazing, along with a function for determining ceiling yield and reduce photosynthesis at old leaf age and/or high proportion of dead material;
- This leads also to a more detailed description of canopy structure, probably being simulated by layers, which then can also be beneficial for simulating the grazing process (variable bulk densities). It will allow for a better and more general representation of bite characteristics, and maybe allow for using mechanistic instead of empirical equation for bite-related variables;
- As suggested by Calanca et al. (2016), a simple soil sub-model could solve some of the issues inherent from the simplification of water reserves and storage, and could add to the P and N dynamics (already being developed by the INRA group; J. Bloor and R. Martin, personal communication).

Those points, however, do not necessarily add to the amount of data required, and most can be achieved with relatively simple changes in the mechanics of the model without making it over complex.

5.2. Personal remarks

Out of ordinal, I would like to register here some personal remarks, that I believe can motivate (and hopefully inspire) future students of our group on the path of science and modeling. From the conceptualization of the ideas to the analysis of the results, a vast literature was covered, as well as many productive and inspiring discussions with colleagues and researchers from around the world. In modern era, we are only one email apart from anyone, and information can be shared very easily. A large network has been created over the years by Paulo, and this project added to the network by reinforcing old partnerships and creating new ones. Those ought to be maintained. Even though briefly, many researchers around the world contributed; to mention a few, Drs. Kiniry, Hirakawa, Richardson, Benvenuti, Paruelo, Agnusdey, Louault, Pottier, Sainz, Jaurena, Nabinger, Overback, Tornquist, Bergamaschi, plus those mentioned in the acknowledgments, and many others that I apologize for forgetting to mention that were able to, in a few words in an email, or a brief talk, make my path

more clear, and encourage me to keep going. So, *networking is key of success in a globally-connected scientific and technical community.*

The perception of the range manager is key for the construction of the conceptual models and interpretation of the results obtained. Coming from a practical background into modeling facilitated the process of understanding the functioning of the equations and links between them, and evaluating the outputs. Fitting theoretical models to our experiments or to our experience, or further fitting numbers to our theoretical framework is an incredibly useful way to make sense of the whole system, to put pieces together in a global perspective. We then perceive aspects not accounted for when only looking at the factors separately, or only thinking about the “what ifs”. Mathematics is a straight forward way to understanding the way the systems works, and despite sometimes “scaring”, one can easily make sense of it and enjoy the clarifying power of the numbers. But, obviously, all this understanding comes only by reading, digging deep into the literature, searching from the newest outbreaks all the way back to the old masters. What is obvious but important to rephrase is that solid theoretical basis is essential for a good project. Many times, we “re-ask” many questions already, at least, partially answered (for this sense, see Yearbook of Agriculture 1948 - Grass, US. Department of Agriculture).

This project has been something completely new for me. But, I’ve always liked challenges, and this has been quite a large one. When I first started prospecting to work with Paulo, I told him beforehand that I could work in whichever project he would like me to, but for modeling and animal behavior. However, when I joined the Grazing Ecology Research Group, I realized the amount of data and information laying there, needing some general work to develop knowledge. I was not satisfied in conducting one more field experiment, to generate more data. Thus, I took the challenge for opening another line of research in his group, and decided to give a try on modeling. A while later, well into the third year of my PhD, he recalled this episode asking me how were my feelings about modeling and animal behavior at the time. Well, I mentioned I was enjoying a lot, but viewing modeling as a tool to reach my objectives, and the final goal that kept me going. We just need to find out how to work with the many tools we have available, and be persistent in pursuing our objectives. And this is the (first) result of that.

To wrap up, I leave here a quote from the astronomer Clifford Stoll “*Data is not information, information is not knowledge, knowledge is not understanding, understanding is not wisdom*”. There is, definitely, a long path towards wisdom.

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BIOGRAPHICAL SKETCH

Marcelo Osorio Wallau was born in May 11, 1988, in Porto Alegre, Rio Grande do Sul, Brazil, son of Carlos Augusto Wallau and Ana Maria Vasconcellos Osório. Soon thereafter, he “moved” to Santana do Livramento, in the border with Uruguay, where he grew up his family farm, raising sheep, horses, beef and dairy cattle, all in pasture-based systems. From early childhood, he learned the principles of cowboying, range management, and respect for the nature and for the elders. From his close contact with livestock and grazing, he developed a deep interest on pasture production. He moved out of his hometown in 2004, heading to Porto Alegre after period in Finland for high school. In 2006, Marcelo started his undergraduate degree in the Agronomy Department at the Universidade Federal do Rio Grande do Sul. As scientific initiation, Marcelo worked for three years at the Soil Microbiology Laboratory, under the supervision of Dr. Enilson Sá. During his undergraduate career, he took internships in south and central Brazil, and in Argentina. In 2009, he went to Texas Tech University in Lubbock, TX as an exchange student for one year, where he studied and worked in Dr. Vivien Allen’s forage lab. Marcelo graduated as an agronomy engineer in August 2011 and shortly after joined the Agronomy Department at the University of Florida, in Gainesville, FL for his Masters of Science degree. In Florida, under the coordination of Dr. Lynn Sollenberger, he worked as Graduate Research Assistant, developing a project on testing limpgrass hybrid lines under grazing. As fruit of that and previous work, two of the tested lines are now being planted by Florida’s Cattlemen, benefiting the livestock industry in the region. In 2014, back in Porto Alegre, Marcelo joined the Grazing Ecology Research Group, to work on his Ph.D. under the coordination of Dr. Paulo Cesar de Faccio Carvalho, working on the native grasslands line of research. During his Ph.D., he spent one year at the University of California – Davis, developing the modeling project which was part of his thesis with Dr. Emilio Laca, and spent one month at the *Institut National de la Recherche Agronomique* (INRA), in Clermont-Ferrand, France, working with Raphaël Martin and Dr. Juliette Bloor on the implementation of the model. Being back in Brazil during his PhD allowed him to work at the family ranch part time, an activity always loved and missed when abroad. Since 2014, Marcelo works as ambassador for Farmfair International, an event promoted by Northlands, in Edmonton, Canada, where he took groups of Southern American producers to visit one of the largest livestock shows in Canada, and local producers in Alberta. He also develop a volunteer extension project on feral hog management with the *Equipe Javali no Pampa*, resulting in the publication of a technical book on feral hog biology and control techniques, as well as many extension handouts and scientific publications. Marcelo was recently hired as Assistant Professor at the University of Florida, and will soon be returning to Gainesville to work as Forage Extension Specialist. His professional goals are to better understand forage-livestock systems around the world, and help developing sustainable practices to improve livestock production and agroecosystems, from a global, systemic view.