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# PATRÓN DE DEFOLIACIÓN DE COMUNIDADES DE CAMPO NATURAL BAJO DOS OFERTAS DE FORRAJE

**por**

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**RESUMEN**

En pasturas naturales la combinación a diferentes escalas de factores bióticos-abióticos e internos del animal determinan el patrón defoliación. El objetivo fue evaluar el efecto de factores bióticos-abióticos y la condición corporal (CC) de vacas de cría sobre el patrón de defoliación en un campo natural en otoño, invierno y primavera, y dos ofertas de forraje (OF). Se evaluó la probabilidad (P) e intensidad de defoliación (ID), y atributos foliares de las 14 especies dominantes. Los tratamientos fueron alta y baja OF, 8 y 5 kg materia seca (MS) kg peso vivo-1. Los factores bióticos fueron los atributos foliares (área foliar especifica (AFE), contenido de MS foliar (CMSF), resistencia al corte (LTS) y ancho de lámina), MS total en la parcela, MS en cuadros de 20 x 20 cm (MSc), MS de cada especie dentro de los cuadros (MSsp), tasa de crecimiento (TC), carga, dotación y OF. Los factores abióticos fueron la distancia al agua (dA) y sombra (dS) de cada cuadro, y la CC de las vacas. En base a los atributos foliares se definieron 4 grupos funcionales (GFs: A, B, C y D). La P en otoño fue afectada por: MSc, CC y LTS de las especies. Los GFs A, B, C fueron más pastoreados (0,417) en relación al GF D (0,075). En invierno la P fue afectada por: TC, MSsp y dS, pero las vacas no mostraron selectividad entre GFs (0,175). En primavera la P fue afectada por dA y dS, y LTS. La selectividad entre GFs incrementó nuevamente, siendo el GF B el más defoliado (0,289). En promedio la ID fue similar entre GFs y estación (66% de remoción de lámina). Los factores que la afectaron en otoño fueron MSc, CC y CMSF, en invierno MSc y en primavera CMSF, ancho de lámina y LTS. Las vacas modificaron la defoliación entre estaciones y OF, modificando principalmente la P. Variaciones en la OF determinaron cambios en la defoliación a través de la selección de GFs. Las vacas mostraron diferentes estrategias de pastoreo, integrando factores bióticos, abióticos e internos al animal, independientemente de la escala espacial.

**Palabras clave**: probabilidad de defoliación, intensidad de defoliación, grupos funcionales, selectividad.

**Grazing Defoliation Pattern Under Variable Herbage Allowance in Campos Grassland**

**SUMMARY**

In native pastures, animals are confronted with different species at spatial-temporal dimensions, affecting the defoliation pattern. The objective was to evaluate the relationship between herbage allowance (HA) and leaf traits, and the effect of biotic-abiotic and cows body condition score (BCS) on defoliation pattern of cows in Campos grassland in autumn, winter and spring. We evaluated the grazing probability (GP), intensity of defoliation (ID), and leaf traits (leaf dry matter content (LDMC), specific leaf area (SLA), leaf tensile strength (LTS) and width leaf) on 14 dominants species. Treatments were High HA and Low HA (8 and 5 kg dry matter kg live weight-1). Models included biotic factors (paddock herbage mass (HM), HM in quadrants (20 * 20 cm, HMq), HM of each species within the quadrant (HMsp), herbage accumulation rate (HAR), stocking density and rate, real HA and leaf traits), abiotic factors were distance to water (dW) and shade (dS) of each quadrant, and cows BCS. Factors affecting GP in autumn were HMq, BCS and LTS. Grazing was concentrated on FGs A, B and C (GP = 0.417), while the GP for FG D was 0.075. Factors affecting GP in winter were HAR, dS and HMsp. The average GP was 0.175, and FGs C and D were more defoliated than autumn. The GP shifted in spring to FG B (0.289). Factors affecting GP were dW, dS and LTS. The ID was similar to all FGs and seasons (66 % leaf removed), but factors affecting ID were different. In autumn were HMq, BCS, and LDMC, for winter was only HMq and for spring were LDMC, LTS and leaf width. Cows behaved differently in the defoliation pattern, modifying mainly the GP on FGs rather than the ID, integrating biotic, abiotic and internal factors at different scales. Variation in HA across season determined changes in defoliation pattern, allowing to express selectivity in autumn and spring, but not in winter.

**Keywords**: grazing probability, intensity of defoliation, functional groups, selectivity.

# 1. INTRODUCCIÓN

Las pasturas naturales en el Uruguay ocupan el 64% de la superficie terrestre lo que representa unas 10.500.000 hectáreas (DIEA, 2018). Estas pasturas se denominan Campos, donde dominan gramíneas, en menor medida otras familias de plantas herbáceas, pequeños arbustos y ocasionalmente árboles (Allen et al., 2011). Tienen como característica una concentración en la producción de forraje en primavera y verano, un contenido de proteína variable (6-15%) y una baja digestibilidad (58%, Berretta et al., 2000). La productividad primaria presenta una variabilidad muy alta entre y dentro de años en respuesta a la temperatura y principalmente a las precipitaciones (Berretta et al., 2000). Los tipos de vegetación son determinados por el material geológico, tipo de suelo, topografía, oscilaciones climáticas y manejo del pastoreo (Berretta, 2001), determinando un complejo mosaico, constituido por un número muy grande de especies, diferentes en sus hábitos fisiológicos y ecológicos (Millot et al., 1987).

El sistema de producción predominante sobre las pasturas naturales es la ganadería de carne y dentro de ella la cría vacuna. Dicho sistema ocupa el 51% de la superficie ganadera del país y representan el 53% de las explotaciones ganaderas (DIEA, 2018). La cría vacuna es un proceso biológico de larga duración e ineficiente en el uso del forraje con respecto a la recría e invernada (Soca et al., 2013). El resultado físico de las empresas ganaderas uruguayas en el año 2017 fue de 74 kg carne ha-1 (Aguirre, 2018), muy inferior a la producción potencialmente alcanzable a través del manejo del pastoreo (Soca, 2013).

La gran variabilidad de estas pasturas determina que tanto la producción primaria como secundaria se incrementen con el empleo de cargas variables entre y dentro de años, y dentro de predios (Briske y Heitschmidt, 1991; Soares et al., 2005; Do Carmo et al., 2016). Esto se asocia con orientar el pastoreo en base a niveles de cantidad de forraje que optimicen la captura, utilización y transformación de la energía (Briske y Heitschmidt, 1991; Do Carmo et al., 2018). La oferta de forraje (OF) es la variable que mejor relaciona la disponibilidad de forraje (kg materia seca) y la carga animal (kg peso vivo) (Sollenberger et al., 2005), resultando en la principal herramienta para controlar la intensidad de pastoreo en los sistemas de producción (Maraschin et al., 1997).

Se observó que OF contrastantes generan disponibilidades de forraje contrastantes y cambios en la estructura de la pastura (Neves et al., 2009). En estos casos es modificada la selectividad animal, definida a través de la frecuencia e intensidad que visitan los sitios de alimentación (Gonçalves et al., 2009) y la composición química del forraje cosechado por los animales (Piaggio, 1994). A su vez, el consumo es afectado por variaciones en la tasa y peso de bocados (Piaggio, 1994), tiempo de pastoreo y tiempo de rumia (Scarlato 2011, Da Trindade et al., 2012). En relación a la pastura se detectaron cambios en la composición botánica (Olmos et al., 2013), y cambios en la contribución de grupos funcionales de plantas y en los atributos foliares de algunas especies como resultado de intensidades de pastoreo contrastantes (Cruz et al., 2010).

El control de la intensidad de pastoreo a través de la OF también genera cambios a nivel interno de los animales, mejorando la respuesta reproductiva y productiva asociado a una mejor condición corporal (CC, Claramunt et al., 2018), metabolismo y expresión de genes (Casal et al., 2014; Laporta et al., 2014). Por lo tanto, el conocimiento generado en el país y la región sobre los procesos que ocurren a diferentes escalas espacio temporales como resultado del manejo de la OF ha sido muy importante. A nivel planta-animal se ha generado información que permitió comprender mejor los procesos que ocurren a este nivel. Sin embargo, no hay estudios que hayan cuantificado el efecto de la OF y la estación del año en el patrón de defoliación a través de la cuantificación de la probabilidad e intensidad de defoliación a nivel de las especies y su estudio a diferentes escalas. Entender el efecto de los atributos funcionales de las especies dominantes de la pastura sobre la selectividad, las características de la pastura a diferentes escalas espacio-temporales, el efecto del ambiente y la CC de las vacas que determinan la defoliación o no de especies resulta esencial para entender la dinámica de la vegetación, las vías de aumentar la producción animal y predecir impactos bajo ofertas de forraje contrastantes.

## 1.1. OBJETIVO GENERAL

Entender cómo el patrón de defoliación de las especies dominantes es afectado por la OF, la estación del año, las características de la pastura a diferentes escalas espacio-temporales, los factores ambientales y la CC de las vacas.

### 1.1.1. Objetivos específicos

Determinar la probabilidad e intensidad de defoliación de las principales especies cuando se modifica la oferta de forraje.

Realizar medidas objetivas de los atributos foliares, definir grupos funcionales de plantas en función de esas características y relacionarlos con la probabilidad e intensidad de defoliación.

Determinar los principales factores abióticos, características de la pastura a diferentes escalas espaciales y factores internos al animal que afectan el patrón de defoliación de las especies.

## 1.2. HIPÓTESIS

La probabilidad e intensidad de defoliación será mayor en invierno asociado a la menor OF. Mayores OF determinan una menor probabilidad e intensidad de defoliación sobre las especies dominantes de la pastura en otoño y primavera.

Los atributos foliares de una misma especie serán dependientes de la OF y la estación del año, determinando que pertenezcan a más de un grupo funcional y condicionando la probabilidad e intensidad de defoliación.

Los factores que determinen el patrón de defoliación de las especies dominantes serán relacionados a la calidad de la pastura en otoño y primavera como resultado de una mayor OF, mientras que en invierno asociado a la menor OF serán relacionados a la cantidad de forraje. A su vez, los factores abióticos afectarán al patrón de defoliación en otoño y primavera, mientras que vacas con mayor CC seleccionarán un forraje de mayor calidad.

### 1.3. MODELO CONCEPTUAL

La selectividad de los animales ocurre a distintos niveles jerárquicos (Senft et al., 1987), definidos por escalas espacio temporales (Bailey et al., 1996). Los factores abióticos intervienen a diferentes niveles jerárquicos determinando la distribución del pastoreo (Stuth 1991), el cual, a su vez, es afectado por las características de la pastura y por los factores internos al animal, determinando una utilización diferencial sobre las especies (Bailey et al., 1996). La selectividad se encuentra relacionada a la probabilidad y la intensidad a la que una especie sea defoliada (Nabinger et al., 2011). La probabilidad de defoliación puede ser definida como el número de veces en que la planta es defoliada en un tiempo dado, mientras que la intensidad de defoliación se define como la cantidad de material removido de la planta en cada evento de pastoreo (Gillen et al., 1990; Lemaire et al., 2009).

En dicho trabajo se propone un modelo conceptual que intenta relacionar la probabilidad e intensidad de defoliación a nivel de las especies y como es afectada por factores bióticos, abióticos e internos al animal a distintas escalas (Figura 1). El modelo considera diferentes escalas espacio-temporales considerando las variables a nivel de la parcela (masa de forraje, tasa de crecimiento y carga animal) modificadas por la OF y la estación del año. A su vez considera las características a nivel de cuadrantes dentro de la parcela, los cuales también son modificados por la OF y la estación del año. A nivel de cada cuadrante, las variables que lo definen son la masa de forraje, el conjunto de especies presentes en dicho cuadrante, sus atributos foliares y su contribución a la masa de forraje. La menor escala considerada, es a nivel de cada especie. A este nivel se consideran los atributos foliares y el estado fenológico de la especie, los cuales son modificados por la OF y la estación del año. El ambiente considera las características del suelo a nivel de la parcela, determinando la composición de cada cuadrante, y la distancia al agua y a la sombra a la que se encuentra cada cuadrante. Además, se considera la CC de las vacas, que son determinadas por la OF, estación del año y las características a nivel de parcela.

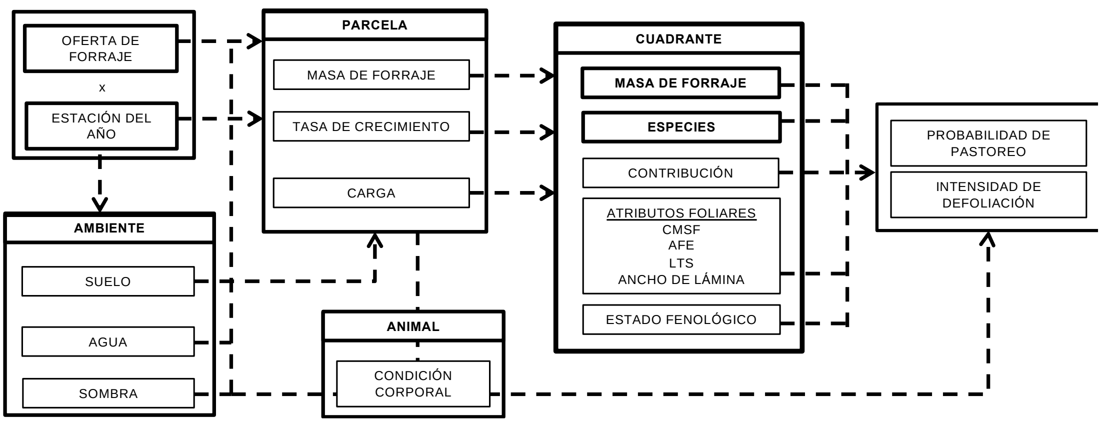


Figura 1 Modelo conceptual del patrón de defoliación bajo diferentes ofertas de forraje y estación del año, bajo el efecto de factores bióticos, abióticos a diferentes escalas espaciales y condición corporal de las vacas

Los factores abióticos considerados en el modelo son la distancia al agua y a la sombra que determinan cambios en la probabilidad de defoliación de las especies (Senft et al., 1987). Putfarken et al. (2008) mostraron que la probabilidad de defoliación es mayor en sitios cercanos al agua. A medida que son defoliados los sitios cercanos al agua, los animales se concentran en sitios lejanos, hasta volver a comer el rebrote de las especies próximas al agua, utilizando la memoria espacial y las consecuencias postingestivas en cada caso (Bailey y Provenza, 2008). En relación a la sombra, se ha visto que juega un rol importante en algunas estaciones del año en la selección de los sitios de alimentación por parte de los vacunos (Díaz Falú et al., 2014). A su vez, las características del suelo tienen un efecto indirecto sobre la probabilidad e intensidad de defoliación de las especies. Esto se debe a que la capacidad de almacenaje de agua, textura y posición topográfica determinan la biomasa disponible a nivel de potrero, la composición botánica predominante y su disposición espacial (Millot et al., 1987; Berretta, 2001).

Los factores bióticos como la disponibilidad de forraje y la tasa de crecimiento de la pastura son afectados por la estación del año y la OF (Maraschin et al., 1997). La relación entre la disponibilidad de forraje y la OF objetivo (kg materia seca kg peso vivo-1), determina la capacidad de carga estacional de la pastura (Sollenberger et al., 2005). Esta variable de respuesta afecta la probabilidad de defoliación de las diferentes especies (Lemaire et al., 2009) y modifica la composición botánica de la pastura a largo plazo.

A su vez, variaciones en la disponibilidad de forraje a lo largo del año como resultado de OF variables, determinan diferentes estrategias de pastoreo estacionales (Stuth et al., 1987). Como resultado, ocurre una defoliación diferencial sobre las diferentes especies (Andrew, 1986; Ash y McIvor, 1998), y se generan áreas sobrepastoreadas y otras no utilizadas (Owens et al., 1991). Cuando el forraje de mayor calidad se vuelve limitante, los animales pastorean zonas de mayor cantidad de biomasa, independientemente del material verde (Coleman et al., 1989; Stuth, 1991). En estos casos, incrementa la probabilidad de defoliación y la selectividad es prácticamente cero, por lo que las especies no deseadas son pastoreadas (Nabinger et al., 2011). Cuando la altura de la pastura y el contenido de hojas disminuye, la probabilidad e intensidad de defoliación aumentan (Gillen et al., 1990; Grant y Marriott, 1994). En este caso, la cantidad cosechada por bocado disminuye, lo que aumenta el tiempo de pastoreo para mantener el consumo resultando en defoliaciones más frecuentes (Curll y Wilkins, 1982).

Altas OF determinan alta disponibilidad de forraje, generalmente excedente a la demanda animal, por lo que la selectividad incrementa (Clark y Harris, 1985; Nabinger et al., 2011). Los animales tienden a concentrar su actividad de pastoreo en áreas particulares e ignorar otras, y la probabilidad de defoliación sobre el total de las especies de la parcela disminuye (Neves et al., 2009). Cuando el forraje es excedente, la probabilidad de que un área previamente defoliada sea nuevamente visitadas será mayor respecto a una no defoliada. En esta situación, los animales seleccionan forraje joven en relación a maduro (Ring et al., 1985), con mayor contenido de nitrógeno (Cid y Brizuela, 1998). Así es que se desarrolla un mosaico dinámico de parches defoliados y no defoliados (Hodgson, 1990). El forraje disponible se vuelve más heterogéneo espacialmente y los animales concentran su atención en las comunidades que permiten maximizar la tasa de cosecha de forraje verde, independientemente de las especies que la componen (Coleman et al., 1989), incrementando la probabilidad de defoliación del total de las especies (Gillen et al., 1990). En algunas áreas la vegetación se vuelve sobreutilizada, mientras el forraje remanente se vuelve duro con la acumulación de material muerto (Ring et al., 1985). Un modelo de OF variable a lo largo del año (Soares et al., 2005; Do Carmo et al., 2016) modifica la utilización de la pastura en las diferentes estaciones del año, favoreciendo la selectividad en algunas estaciones y restringiendo en otras, evitando la sobreutilización de algunos parches y la subutilización de otros.

A nivel interno del animal hay pocos trabajos que relacionen la CC de los animales con la selectividad. La CC refleja el estado nutricional de los animales en base al grado de gordura en relación al tamaño del animal (Vizcarra et al., 1986). Murden y Risenhoover (1993) encontraron en ambientes áridos que ciervos y cabras con mejor estado nutricional son más selectivos y eligen una dieta diferente en relación a los animales con bajo estado nutricional. A su vez Mellado et al. (2004) observaron en el mismo ambiente, que cabras con mejor CC rechazaban especies de menor calidad, mientras que animales con baja CC y por lo tanto con bajo estado nutricional, consumían especies que eran rechazadas por animales de mayor CC. Es posible plantear la hipótesis que cambios en el balance de energía de las vacas de cría modifiquen el patrón de defoliación, modificando la dieta y la selección de las diferentes especies.

A nivel de especies, la probabilidad e intensidad de defoliación es el resultado de su contribución especifica al total de materia seca y su morfología (Heitschmidt et al., 1990) y de los efectos postingestivos de cada especie (Provenza, 1995). Las variables morfológicas características de cada especie resultan del largo de hojas y resistencia al corte y masticación, textura, relación verde seco-1, altura de vainas y presencia de inflorescencias (Senft et al., 1985; Boggiano, 1995). Estas características afectan la facilidad de cosecha y el consumo instantáneo por bocado, lo que sugiere que especies que permiten altas tasas de cosecha de forraje sean más frecuentadas por los animales (Stuth, 1991; Utsumi et al., 2009). Los efectos postingestivos, determinan que los animales rechacen algunas especies por experiencias pasadas y por aprendizaje social (Provenza, 1995), determinando que la probabilidad de defoliación sea muy baja o nula.

Dichos antecedentes justifican el estudio de la probabilidad e intensidad de pastoreo de vacas de cría ante cambios en la OF de campo natural a diversas escalas (desde las características de la parcela, a nivel de cuadrante y a nivel de especie). Esto permitirá evaluar los cambios en la relación planta animal que se generan cuando se trabaja con niveles de OF que “optimicen” la producción y uso del forraje.

### 1.4. ESQUEMA GENERAL DE LA TESIS

La tesis consta de cinco capítulos: Capítulo 1: introducción a la temática, justificación del problema, objetivos e hipótesis de la investigación y presentación del modelo conceptual en el que se desarrolla la tesis. Capítulo

2: corresponde al primer artículo científico, el cual se titula *Changes in defoliation patterns of Plant Functional Groups under variable herbage allowance in Campos grasslands,* siguiendo el formato de la revista Rangeland Ecology and Management. Capítulo 3: corresponde al segundo articulo científico titulado *Factors affecting defoliation pattern by cattle in heterogeneous grassland,* siguiendo el formato de la revista Applied Animal Behaviour Science. Capítulo 4: discusión general de los artículos científicos en base a la justificación del problema y al modelo conceptual propuesto en el Capítulo 1. Capítulo 5: conclusiones de la tesis.

# 2. CHANGES IN DEFOLIATION PATTERNS OF PLANT FUNCTIONAL GROUPS UNDER VARIABLE HERBAGE ALLOWANCE IN CAMPOS GRASSLANDS

## 2.1. ABSTRACT

Several studies have evaluated separately forage production, botanical composition, leaf traits and animal performance. However, none of them have focused on defoliation patterns at the level of functional groups (FGs) under different and variable herbage allowance (HA), especially in natural, diverse grasslands. The objective was to evaluate the relationship between HA and leaf traits on defoliation patterns of pregnant beef cows in the autumn, winter and spring. We evaluated the grazing probability (GP), intensity of defoliation (ID), and leaf traits on 14 species that represent more than 80% of total dry matter of the pasture. The experiment at which we evaluated those traits and responses has been managed under High HA (HHA) and Low HA (LHA) (8 and 5 kg dry matter kg live weight-1, respectively). Four plant FGs (A, B, C and D) were defined according to leaf traits, and a selectivity index (SI) was developed for each group (considering the proportion of grazed and ungrazed species). Grazing patterns shifted across seasons. In the autumn, grazing was concentrated on FGs A, B and C groups (GP = 0.417). While for FG D, represented by high-biomass tussocks, the GP was lower (0.075). During winter, when herbage accumulation rate is limited, the average GP was 0.175. FGs C and D were more defoliated in relation to autumn, and during spring the GP shifted to FG B (0.289). The ID was similar to all FGs and seasons (66 % of leaf removed). In autumn and spring, the SI was affected by FGs and HA while in winter were similar between FGs but higher in HHA. Cows behaved differently in the defoliation pattern, modifying mainly the GP on FGs rather than the ID. Variation in HA across season determined changes in defoliation pattern (i.e.: selectivity), allowing to express selectivity in autumn and spring.

**Keywords:** grazing probability, intensity of defoliation, Campos grasslands, functional groups.

## 2.2. INTRODUCTION

Campos grasslands is a biome composed by heterogeneous environments dominated by herbaceous flora, mainly C4 grasses, herbs, small shrubs and trees appears occasionally (Allen et al., 2011). The degree of heterogeneity is the result of soil types, edaphic fertility, botanical composition, topography and grazing management (Berretta, 2001). Spatially heterogeneous grasslands affect animal intake (Laca, 2008); determining that herbivores utilize these systems unevenly (Bailey et al., 1998). The interaction between pasture and animal affect daily intake, but also the diet composition and the impact of grazing on vegetation (Piaggio et al., 1996; Prache et al., 1998).

The link between the pasture and grazing animals is the defoliation pattern, defined as the frequency and intensity of defoliation (Nabinger and Carvalho, 2009). The animal distribution during grazing and in fact the defoliation pattern occurs at different temporal and spatial scales (Bailey et al., 1996). At spatial scales the defoliation pattern respond to herbage allowance (HA) and herbage mass (HM) (Gonçalves et al., 2009; Nabinger et al., 2011), botanical composition (Brown and Stuth, 1993), abiotic factors like distance to water and shade (Bailey and Provenza, 2008; Putfarken et al., 2008), and plant functional traits, ultimately determining the animal performance (Cruz et al., 2010; Jaurena et al., 2012). Consequently, changes in some of these factors affects grazing strategies, determining the results of grazing systems.

One approach to predict plant strategies, grazing response and defoliation pattern is the use of plant functional traits (Wilson et al., 1999; Díaz et al., 2001). Plant and leaf functional traits allow to group a big number of species in a small number of functional groups (FGs) through the quantification of different functional traits, and the clustering of the species by its functional traits values (Duru et al., 2005). It result advantageous in comparison to the taxonomic methods (Cruz et al., 2010). Moreover, consist of a simple and very useful method of grouping species that respond similar to biotic and abiotic factors (Duru et al., 2019), and allows to evaluate the forage services and species richness (Duru et al., 2013).

The more common functional traits are specific leaf area (SLA), leaf dry matter content (LDMC), leaf width, leaf tensile strength (LTS) and leaf nitrogen content (Garnier et al., 2015). These leaf traits can be associated with nutritive value of each FG (Duru et al., 2005; Cruz et al., 2010). The HA that promote a higher proportion of species with low LDMC and high SLA determine the higher daily gain, and *vice versa*, a higher proportion of high LDMC species determine the lower daily gain (Cruz et al., 2010). Species with higher SLA and lower LTS has higher quality and herbage accumulation rate (HAR), and are more tolerant to herbivory (Cingolani et al., 2005; Garnier et al., 2015), and species with higher LDMC, lower digestibility and high LTS are less selective by animals (Boggiano, 1995; Cingolani et al., 2005). Jaurena et al. (2012) showed that the grazing pattern is related to LDMC and SLA and species are decreasers, neutral and increasers according to stocking rate (Dyksterhuis, 1949). Also, functional traits responds to HA, determining the relative biomass of each FG (Cruz et al., 2010), associated with the animal performance (Nabinger et al., 2011). Grazing tends to favor species with a high SLA and low LDMC (Garnier et al., 2015). An increase in the frequency of defoliation determine an increase in SLA, and a reduction in leaf size, LDMC, and LTS due to reduction in supporting tissues in the grass leaf (Garnier et al., 2015).

There are few evaluations in Campos grasslands on plant functional traits considering HA or grazing pressure variables (Cingolani et al., 2005; Cruz et al., 2010; Jaurena et al., 2012). Moreover, there's no studies that relates the specific contribution of different FGs and the defoliation pattern of cows over these groups in the heterogeneous grasslands under variable HA. The objective of the study was to evaluate the relationship between HA variations and plant FGs on the defoliation patterns and selectivity of beef cows in three different seasons. We addressed the following questions: (1) can HA, variable through seasons, modify leaf traits of frequent grasses and the specific contribution of each species? (2) if so, is the specific contribution of FGs variable within treatments and seasons? (3) how will be the defoliation pattern of cows according to specific contribution of FGs, HM and HA?

## 2.3. MATERIALS AND METHODS

### 2.3.1. Experimental site

The experiment was carried out in the Experimental Station "Bernardo Rosengurtt" of Faculty of Agronomy, Universidad de la República in northeastern Uruguay, where the main land area is covered by Campos grasslands. Evaluations were done during three periods: 1st Mar – 15th Apr (autumn), 30th Jul – 26th Aug (winter) and 1st Oct – 15th Nov (spring), 2017. The historical average temperature and rainfall (1980-2009) was 18 ºC and 1411 mm (Castaño et al., 2011). Average daily temperature for autumn, winter and spring, were 23, 16 and 20 ºC, 2 ºC more than the historical monthly average. The historical monthly rainfall was 113, 105 and 123 mm, while the evaluation periods were 87, 213 and 135 mm for autumn, winter and spring, respectively. Soils of the experimental area are Hapluderts, Argiudolls, Hapludalfs and Natruaqolls (Durán et al., 2005).

### 2.3.2. Treatments and experimental design

The experiment where the measurements were carried out is a long-term experiment that evaluates the effect of two levels of HA on grassland and beef cows primary and secondary productivity (Do Carmo et al., 2016). The layout of the experiment is a complete random design with two treatments: High HA (HHA) and Low HA (LHA) with two replications each, totaling four paddocks. Treatments HHA and LHA are represented in kg dry matter (DM)/kg live weight (LW) (Sollenberger et al., 2005). Target annual average HA is 8 and 5 kg DM/kg LW, HHA and LHA respectively, variable in each season. During spring the target level is 12 and 8 kg DM/kg LW, during summer and autumn is 8 and

4 kg DM/kg LW, and during winter 4 and 4 kg DM/kg LW for HHA and LHA, respectively (Do Carmo et al., 2018). The LHA paddocks have an area of 10 ha per repetition, and HHA 14 ha per repetition, totaling 48 ha (Do Carmo et al., 2018).

The experimental area was continuously stocked throughout the year, with variable stocking rate adjusted monthly using the “put and take” method (Mott and Lucas, 1952) to encompass natural variations in herbage accumulation with induced variations in stocking rate. Animals used were multiparous pregnant beef cows (Hereford, Angus and reciprocal Hereford and Angus cross), of 446 ±63 kg of LW (Table 1). The real HA for HHA and LHA were 7.6 and 3.7 kg DM/kg LW for autumn, 2.2 and 3.7 kg DM/kg LW for winter and 6.3 and 4.0 kg DM/kg LW for spring. The stocking rate, average live weight, stocking density and average body condition score are shown in Table 1.

#### 2.3.3. Sampling procedures, measured and estimated variables

Samples were collected and response variables pooled at four different scales: paddock, transects, quadrats and quadrants. In each paddock, fixed 50-m transects (7 in HHA and 5 in LHA per paddock) were delimited according to soil type and topography, totaling 24 transects. Natruaqolls represented the 19.2 % of total area, Hapludalfs represented the 23.4 % of total area and Hapluderts and Argiudolls represented the 57.4 % of total area. Four transects were delimited in Natruaqolls, which represents 16.6 % of total transects, five transects were delimited in Hapludalfs (20.8 %) and 15 transects in Hapluderts and Argiudolls (62.5 %). The proportion of transects in each soil type lets assume that transects represents the variability of soil types and topography of the paddock. In each transect ten 40 x 40-cm quadrats were fixed every 5 m and divided in 4 quadrants of 20 x 20-cm. A total of 960 quadrats were assessed per sampling date (560 in HHA and 400 in LHA).

The HM for the whole paddock was measured at the beginning and at the end of each period by the comparative yield method (Haydock and Shaw, 1975). The herbage accumulation rate (HAR) was estimated through double sampling method using grazing exclusion cages (Klingman et al., 1943).

**Table 1** Stocking rate (SR, n: animal paddock-1), average live weight (LW kg a-1) ± s.d., stocking density (SD, kg LW ha-1); average body condition score (BCS) ± s.d., for autumn, winter and spring, in Low (LHA) and High herbage allowance (HHA). s.d.: standard deviation

| | | LHA | | HHA | |
|---|---|---|---|---|---|
| | Paddock | 1 | 2 | 3 | 4 |
| Autumn | SR (n) | 20 | 14 | 14 | 16 |
| | LW (kg a-1) | 410 ±54 | 399 ±63 | 438 ±82 | 436 ±65 |
| | SD (kg ha-1) | 745 | 559 | 472 | 499 |
| | BCS | 3.8 ±0.7 | 3.6 ±0.3 | 5.0 ±0.9 | 3.6 ±0.3 |
| Winter | SR (n) | 8 | 9 | 20 | 21 |
| | LW (kg a-1) | 422 ±24 | 452 ±46 | 485 ±49 | 475 ±75 |
| | SD (kg ha-1) | 307 | 407 | 746 | 712 |
| | BCS | 3.4 ±0.3 | 3.5 ±0.2 | 4.6 ±0.9 | 3.9 ±0.8 |
| Spring | SR (n) | 6 | 6 | 6 | 5 |
| | LW (kg a-1) | 465 ±34 | 467 ±37 | 460 ±22 | 468 ±38 |
| | SD (kg ha-1) | 254 | 280 | 212 | 167 |
| | BCS | 4.3 ±0.6 | 4.5 ±0.4 | 4.3 ±0.6 | 3.9 ±0.5 |

During each evaluation period, all quadrants were assessed 4 or 5 times, in 5-7 days intervals, in order to avoid re-grazing at this scale between sampling moments. In each quadrant, botanical composition was estimated visually, determining species that represented about 95% of total dry matter

(Brown, 1954). Grasses were identified up to species level while most forbs and graminoids were identified at genus level.

In each quadrant a grazing event was recorded by marking the tip of the leaf using a water-marker pen (Davies, 1993). The grazing probability (GP) of each species in the whole paddock per period was estimated by:

$$GP = \frac{\text{sum of grazing events of each species}}{\text{total number of records of each species}}$$

The intensity of defoliation (ID) was visually estimated as the percentage of leaf removed per grazing event: 25 % when a quarter of leaf was removed, 50 % half of the leaf removed, 75 % three quarter of leaf removed and 100 % when the whole leaf was removed (Lemaire et al., 2009). The ID in each plant species in the whole paddock for each period was calculated averaging the percentage of leaf removed by a grazing event for each period, recorded in all the measurement points.

Leaf functional traits measured were: leaf dry matter content (LDMC), specific leaf area (SLA), leaf width (width) and leaf tensile strength (LTS). Measurements were done in 10 leaves per plant species per paddock at the end of each period. Selected leaves were ungrazed, newly expanded, without disease and water saturated over 8 hours according to protocol developed by Cornelissen et al. (2003). To estimate the SLA ($m^2$ kg-1) leaves were scanned and then measured the leaf area, while leaf width was measured in the widest section of the used leaves using the software ImageJ (Schneider et al., 2012). LDMC (g kg-1) was calculated as the mass of the same leaves, oven dried during 72 hours at 60 ºC (g), divided by its water saturated fresh mass (kg). LTS was measured in the central section of the leaf using the apparatus descripted by Hendry and Grime (1993) to determine the force required to tear leaf in two pieces.

The selectivity index (SI), adapted from Cingolani et al. (2005) considered the number of grazed records of each species (nGR) and number of ungrazed records of each species (nUGR).

$$SI = \frac{nGR - nUGR}{nGR + nUGR}$$

The index varies between -1 and 1. Values near -1 indicates avoidance, values near 1 indicates maximum selectivity, and 0 indicates indifference.

2.3.4. Statistical analysis

A mixed model analysis of variance (ANOVA) ($P< 0.05$) was performed for HM and HAR considering HA and period as fixed effects and paddocks as random effect (1). The relative specific contribution of each species or group of species to total paddock dry matter were analyzed using mixed model with *lmerTest* package (Kuznetsova et al., 2017) in R 3.5.1 (R Development Core Team, 2018). The model considered included species and groups (graminoids and forbs), treatment (HHA and LHA) and period as fixed effects and paddocks as random effects (2).

*1:* *a: HM ~ HA + period + HA*period + (1 | paddock)*

*b: HAR ~ HA + period + HA*period + (1 | paddock)*

*2:* *Specific contribution ~ species + HA + period + species*period + species*HA + HA*period + (1 | paddock)*

The FGs were defined considering functional traits of each species measured over periods and treatments. The FGs were grouped by cluster analysis using *vegan* package (Oksanen et al., 2017) in R 3.5.1 (R Development Core Team, 2018). The matrixes for identifying each FG were designed including all species in rows and all leaf traits (LDMC, SLA, LTS and width) in columns. The leaf traits data considered for the matrixes was the average trait of ten leaves for each paddock in each period, resulting in 12 means per trait per species. The matrixes output was standardized and FGs were defined using 'Ward' method and Euclidean distance. Four FGs were defined based on the optimal number of FGs determined by the observed difference in the within groups sum of squares, which after four groups a stabilization of the decrease in the sum of squares within the groups begins.

After defining FGs, was calculated the specific contribution, GP, ID and SI for each FG, in each period and treatment. The specific contribution of FG was the sum of the specific contribution of each species corresponding to their corresponding group. The GP for FG (FG*) was defined as:

$$\text{GP (FG*)} = \frac{\text{sum of grazing events on species corresponding to FG*}}{\text{total records of species corresponding to FG*}}$$

The ID for each FG* was calculated averaging the percentage of leaf removed by grazing, considering the whole grazed species corresponding to each FG*. Thus, the prorated average considered different number of records and also grazing events of each species. Finally, the SI for each FG was calculated considering the number of grazed records of each specie corresponding to FG* and number of ungrazed records of each species corresponding to FG* as:

$$\text{SI (FG*)} = \frac{\text{nGR FG* - nUGR FG*}}{\text{nGR FG* + nUGR FG*}}$$

The specific contribution, GP and ID of each FG were analyzed by ANOVA (P< 0.05) for each period. Once defined the FGs (after the cluster analysis), they were added to the model as fixed effects for the analysis of plant-animal interaction. Also, HA was used as fixed effect, while paddock was used as random effect (3). Furthermore, the SI was analyzed by ANOVA (P< 0.05) using two models (4). First model considered HA and FGs as fixed effect and paddock as random effect, while second model considered FG and period as fixed effect and paddock as random effect. Data were analyzed using mixed model in R 3.5.1 (R Development Core Team, 2018), with *lmerTest* package (Kuznetsova et al., 2017).

*3:* *a: Specific contribution ~ HA + FG + HA*FG + (1 | paddock)*

*b: GP ~ HA + FG + HA*FG + (1 | paddock)*

*c: ID ~ HA + FG + HA*FG + (1 | paddock)*

*4:* *a: SI ~ HA + FG + HA*FG + (1 | paddock)*

*b: SI ~ FG + period + FG*period + (1 | paddock)*

## 2.4. RESULTS

### 2.4.1. Herbage mass and herbage accumulation rate

The HM varied among periods and also HA (P = 0.001) (Table 2). Higher values of HM occurred in autumn, while the lowest values occurred in spring. In autumn, in HHA the HM was higher than LHA. In winter and spring there were no differences between treatments. In relation to HAR, there were also differences among period and HA (P = 0.003). The higher HAR occurred in autumn in HHA and in spring in both treatments, while winter in LHA had the lowest HAR.

**Table 2** Herbage mass (kg DM ha-1) and herbage accumulation rate (HAR, kg DM ha-1 day-1) in autumn, winter and spring in High (HHA) and Low (LHA) herbage allowance

| | Autumn | | Winter | | Spring | |
|---|---|---|---|---|---|---|
| | HHA | LHA | HHA | LHA | HHA | LHA |
| HM | 3681 ± 206 [a] | 2379 ± 298 [b] | 1564 ± 34 [c] | 1259 ± 76 [cd] | 1164 ± 104 [d] | 1045 ± 93 [d] |
| HAR | 17.5 ± 2.6 [a] | 12.1 ± 0.8 [ab] | 7.0 ± 1.9 [bc] | 4.2 ± 0.1 [c] | 14.6 ± 5.0 [a] | 15.5 ± 1.9 [a] |

Different letters following means in rows indicate statistical significance at P < 0.05.

#### 2.4.2. Species specific contribution

In all cases the species selected (Appendix I) represented more than 82% of total dry matter (Table 3). *A. affinis,* Forbs, Graminoids, *M. selloana* and *P. notatum* had the highest contribution. In autumn, more than 50% of the contribution was explained by *A. affinis,* Graminoids*, M. selloana* and *P. notatum*. In winter, Forbs and Graminoids became important rather than *M. selloana* and *P. notatum*. In spring occurred the same as in winter, where *A. affinis* was the species that most contributed to the total dry matter. The interaction species*HA was only explained in *C. dactylon* (P = 0.018). In all periods, the contribution of *C. dactylon* was higher in HHA in relation to LHA. The others species didn´t modified the contribution according to HA.

#### 2.4.3. Leaf functional traits

The leaf traits of each species in both HA and period are presented in Appendix II. From A to D groups it can be observed an increase in LTS and a decrease in SLA and leaf width. The increase in LDMC just occurred from C to D. FGs were maintained fixed over periods and HA, determining that if species changed its leaf traits values, they belong to a different FG.

**Table 3** Relative species and groups contribution to total dry matter of the pasture (%) in autumn, winter and spring, in High (HHA) and Low (LHA) herbage allowance

| | Autumn | | Winter | | Spring | |
|---|---|---|---|---|---|---|
| Species | HHA | LHA | HHA | LHA | HHA | LHA |
| ***Axonopus affinis*** | **12.8** | **10.6** | **17.7** | **15.6** | **15.4** | **15.0** |
| *Andropogon ternatus* | 3.9 | 4.0 | 4.6 | 2.1 | 2.3 | 1.6 |
| *Bothriochloa laguroides* | 4.0 | 4.7 | 1.1 | 1.6 | 2.8 | 3.5 |
| *Cynodon dactylon* | 9.1 | 3.8 | 4.8 | 1.8 | 4.1 | 1.5 |
| **Forbs*** | 1.2 | 1.2 | **10.2** | **11.1** | **5.5** | **7.0** |
| **Graminoids**** | **7.7** | **7.9** | **18.7** | **19.2** | **13.5** | **13.4** |
| ***Mnesithea selloana*** | **12.3** | **12.1** | **8.8** | **6.2** | **8.4** | **7.7** |
| *Nassella charruana* | 5.4 | 5.8 | 4.1 | 3.1 | 3.3 | 3.3 |
| *Nassella mucronata* | 1.6 | 2.4 | 3.1 | 4.8 | 2.7 | 3.3 |
| *Paspalum dilatatum* | 5.5 | 5.0 | 2.2 | 3.3 | 3.9 | 4.3 |
| ***Paspalum notatum*** | **20.5** | **19.8** | **8.9** | **11.3** | **11.9** | **10.7** |
| *Paspalum plicatulum* | 1.9 | 4.9 | 2.1 | 1.5 | 4.2 | 2.8 |
| *Piptochaetium stipoides* | 1.1 | 2.0 | 1.0 | 0.9 | 1.4 | 1.2 |
| *Steinchisma hians* | 1.5 | 3.3 | 1.6 | 3.1 | 3.1 | 5.0 |
| *Sporobolus indicus* | 0.4 | 1.9 | 0.8 | 2.8 | 0.5 | 1.3 |
| *Schizachyrium microstachyum* | 3.6 | 3.9 | 3.4 | 2.7 | 3.0 | 2.5 |
| Total | 92.1 | 91.2 | 92.3 | 88.4 | 85.4 | 82.7 |

* Forbs:, *Dichondra microcalyx* (Hallier f.) Fabris; *Gamochaeta spicata* Cabrera; *Oxalis* sp. L.; *Richardia humistrata* (Cham. & Schtdl.) Steud.

** Graminoids: *Carex bonariensis* Desf. ex Poir.

LDMC, SLA, width and LTS for each species varied over periods and HA. As a result, the number of species in each group was variable between HA and period (Table 5). *N. charruana* was the unique species that presented the leaf traits combination of FG D in all periods and HA. *A. affinis, N. mucronata, P. dilatatum, P. notatum, P. stipoides and S. indicus* had the combination of traits belonging to two FGs, and *A. ternatus, B. laguroides, C. dactylon, P. plicatulum* and *S. microstachyum* were very variable, and had the combination of traits to belonging to three different FGs.

**Table 4** Mean ±s.d. of leaf dry matter content (LDMC), specific leaf area (SLA), leaf width (Width) and leaf tensile strength (LTS) for each functional group

| | A | B | C | D |
|---|---|---|---|---|
| LDMC (g kg-1) | 319 ±44 | 306 ±40 | 385 ±43 | 427 ±66 |
| SLA ($m^2$ kg-1) | 23.7 ±3.8 | 17.1 ±2.8 | 12.9 ±3.3 | 7.3 ±2.0 |
| Width (mm) | 4.9 ±1.4 | 3.5 ±0.7 | 2.0 ±0.6 | 1.3 ±0.7 |
| LTS (N mm-1) | 0.20 ±0.12 | 0.37 ±0.12 | 0.54 ±0.22 | 1.93 ±1.14 |

#### 2.4.4. Specific contribution

The specific contribution was variable according to HA and FG for all periods. In autumn the HA affected the specific contribution of FGs ($P < 0.001$, Table 6). Within treatments, in HHA group A presented the higher contribution, while in LHA group A, B and C presented the same contribution. Within FG, the specific contribution of FG A was higher in HHA (55.4 %) than LHA (28.1 %), while the groups B, C and D presented the same contribution in both treatments.

The specific contribution in winter differed between FGs*HA ($P< 0.001$, Table 6). The contribution of FG A was higher in HHA (19.3 %) than LHA (3.3 %), while the contribution of group B was higher in LHA (31.2 %) than HHA (8.9 %). Groups C and D presented the same contribution in both treatments. Within treatments, in HHA 45.7 % of total DM was explained by groups A and C, and in LHA 51.5 % of total DM was explained by groups B and C.

**Table 5** Functional groups (A, B, C or D) that each species belongs to, according to leaf traits values in autumn, winter and spring in High (HHA) and Low (LHA) herbage allowance

| | Autumn | | Winter | | Spring | |
|---|---|---|---|---|---|---|
| **Species** | HHA | LHA | HHA | LHA | HHA | LHA |
| *Axonopus affinis* | A | A | A | B | B | B |
| *Andropogon ternatus* | B | A | C | C | C | C |
| *Bothriochloa laguroides* | A | A | C | B | B | B |
| *Cynodon dactylon* | A | A | C | C | C | C |
| *Mnesithea selloana* | B | C | C | C | B | B |
| *Nassella charruana* | D | D | D | D | D | D |
| *Nassella mucronata* | C | C | C | C | D | D |
| *Paspalum dilatatum* | A | A | A | A | B | A |
| *Paspalum notatum* | A | B | B | B | B | B |
| *Paspalum plicatulum* | B | B | D | C | B | C |
| *Piptochaetium stipoides* | C | C | D | D | D | D |
| *Steinchisma hians* | - | - | - | - | C | B |
| *Sporobolus indicus* | C | C | D | C | D | D |
| *Schizachyrium microstachyum* | A | B | C | B | A | A |

During spring, the specific contribution of each FGs differed for different HA (P = 0.035, Table 6). In both treatments, the contribution of group B (44.3 %) was higher than group A (4.8 %), C (7.6 %) and D (8.5 %), and no differences between treatments in each FG specific contribution were detected.

#### 2.4.5. Grazing probability and intensity of defoliation

In autumn the grazing probability was different only between FGs (P = 0.011), resulting higher in groups A, B and C (0.417) than group D (0.075, Table 6). Conversely, in winter the grazing probability was only affected by HA (P = 0.003), resulting higher in HHA (0.230) than LHA (0.121). During spring, the grazing probability was affected by the interaction FGs*HA (P = 0.045). The higher grazing probability occurred in group B in LHA (0.357), while the lower values occurred in HHA groups A (0.035) and D (0.106), and in LHA group D (0.119).

The interaction between FGs and HA affected the intensity of defoliation during autumn (P = 0.048, Table 6). Higher values of leaf removed occurred in LHA group B (73.7 %) while the lower values occurred in HHA group C (57.6 %) and LHA group D (52.1 %). The average leaf removed in the others groups and HA combinations was 62.9 %. Conversely, no difference was observed in winter intensity of defoliation between HA (P = 0.612), FGs (P = 0.168) and interaction (P = 0.142). The average leaf removed value in this period was 69 %. During spring, the intensity of defoliation was constant among HA and FGs (P = 0.802), averaging 66%.

#### 2.4.6. Selectivity index

In autumn SI was affected by FGs (Figure 1 and Table 7). In this period the higher SI was observed in FGs A and B, while the lower SI occurred in FG D. During winter the SI was only different between HA, where the high SI occurred in HHA (- 0.54), while the low SI occurred in LHA (- 0.76). In spring, SI was different among HA and FG. The higher SI was observed in FG B in LHA (- 0.29), which differed in HHA with FG A (- 0.93) and D (- 0.79), and in LHA with FG D (- 0.76).

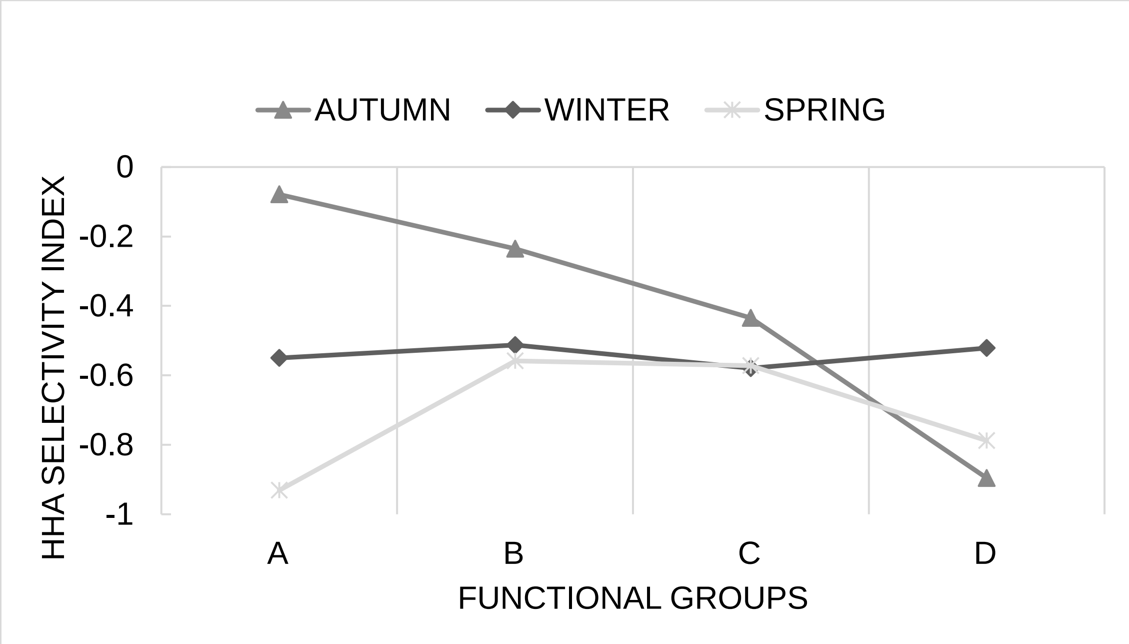
Comparing the SI within FG across periods we observed that for FGs A, B and C the SI was different between period. For FG A the higher SI was in autumn (- 0.09), while the lower values were in winter (- 0.63) and spring (- 0.69). For FG B, the higher value was observed in autumn (- 0.13), intermediate in spring (- 0.43), and lower in winter (- 0.65). As in FG A, the higher SI for FG C was observed in autumn (- 0.29), and the lower in winter (- 0.67) and spring (- 0.61). Finally, the SI of FG D was similar in both treatments and period.

**Table 6** Effect of functional groups (A, B, C and D) and herbage allowance (HHA and LHA) on specific contribution (%), grazing probability and leaf intensity defoliation in autumn, winter and spring

| Period | | | Functional Groups | | | | Probability values | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | A | B | C | D | FGs | HA | FGs*HA |
| Autumn | Contribution | HHA | 55.4$^{a}$ | 18.1$^{bc}$ | 3.2$^{c}$ | 5.4$^{c}$ | **<0.001** | 0.989 | **0.001** |
| | | LHA | 28.1$^{b}$ | 28.6$^{b}$ | 18.3$^{bc}$ | 5.8$^{c}$ | | | |
| | GP | HHA | 0.461 | 0.382 | 0.283 | 0.052 | **0.011** | 0.278 | 0.897 |
| | | LHA | 0.454 | 0.489 | 0.431 | 0.098 | | | |
| | ID % | HHA | 59.9$^{ab}$ | 63.0$^{ab}$ | 57.6$^{b}$ | 61.3$^{ab}$ | **0.035** | 0.128 | **0.048** |
| | | LHA | 64.3$^{ab}$ | 73.7$^{a}$ | 66.4$^{ab}$ | 52.1$^{b}$ | | | |
| Winter | Contribution | HHA | 19.9$^{b}$ | 8.9$^{cd}$ | 25.8$^{ab}$ | 8.1$^{cd}$ | **<0.001** | 0.443 | **<0.001** |
| | | LHA | 3.3$^{d}$ | 31.2$^{a}$ | 19.3$^{bc}$ | 4.0$^{cd}$ | | | |
| | GP | HHA | 0.225 | 0.244 | 0.210 | 0.239 | 0.935 | **0.003** | 0.769 |
| | | LHA | 0.147 | 0.104 | 0.126 | 0.105 | | | |
| | ID % | HHA | 73.0 | 66.7 | 62.8 | 76.7 | 0.168 | 0.612 | 0.142 |
| | | LHA | 62.7 | 66.1 | 76.8 | 67.2 | | | |
| Spring | Contribution | HHA | 3.0$^{b}$ | 46.6$^{a}$ | 9.4$^{b}$ | 7.8$^{b}$ | **<0.001** | 0.377 | **0.035** |
| | | LHA | 6.7$^{b}$ | 41.9$^{a}$ | 5.8$^{b}$ | 9.1$^{b}$ | | | |
| | GP | HHA | 0.035$^{b}$ | 0.221$^{ab}$ | 0.214$^{ab}$ | 0.106$^{b}$ | **0.017** | **0.023** | **0.045** |
| | | LHA | 0.272$^{ab}$ | 0.357$^{a}$ | 0.173$^{ab}$ | 0.119$^{b}$ | | | |
| | ID % | HHA | 62.5 | 67.2 | 60.1 | 66.1 | 0.795 | 0.198 | 0.802 |
| | | LHA | 65.6 | 68.2 | 71.8 | 73.7 | | | |

Different letters following means in rows indicate statistical significance at $P < 0.05$.

**Figure 1** Selectivity index of functional groups in autumn (A), winter (W) and spring (S) for high (HHA) and low herbage allowance (LHA)



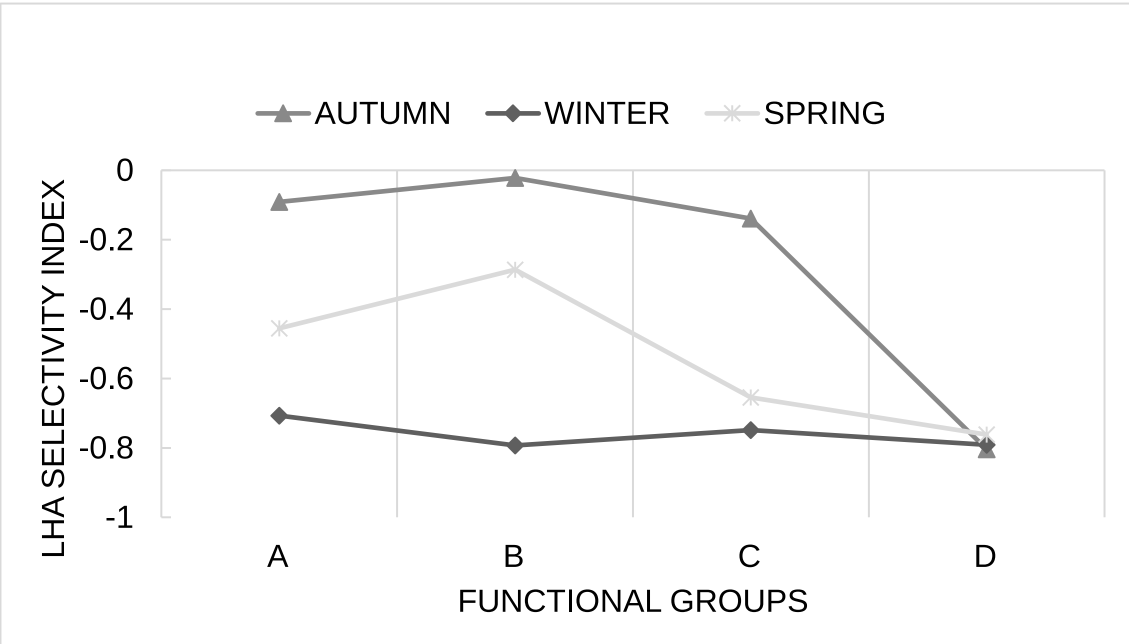



**Table 7** Selectivity index for each functional group, period and treatment, and probability values for herbage allowance (HA), functional group (FG), period, and simple interaction (HA*FG, HA*period)

| | | Functional Groups | | | | Probability values | | |
|---|---|---|---|---|---|---|---|---|
| Period | Treatment | A | B | C | D | FGs | HA | FGs*HA |
| Autumn | HHA | -0,08 | -0,24 | -0,43 | -0,90 | **0.011** | 0.277 | 0.897 |
| | LHA | -0,09 | -0,02 | -0,14 | -0,80 | | | |
| Winter | HHA | -0,55 | -0,51 | -0,58 | -0,52 | 0.934 | **0.002** | 0.767 |
| | LHA | -0,71 | -0,79 | -0,75 | -0,79 | | | |
| Spring | HHA | -0,93 $^{b}$ | -0,56 $^{ab}$ | -0,57 $^{ab}$ | -0,79 $^{b}$ | **0.017** | **0.022** | **0.045** |
| | LHA | -0,46 $^{ab}$ | -0,29 $^{a}$ | -0,65 $^{ab}$ | -0,76 $^{b}$ | | | |
| Probability values | HA | 0.446 | 0.632 | 0.838 | 0.365 | | | |
| | period | **0.036** | **0.033** | **0.013** | **0.082** | | | |
| | HA*period | 0.273 | 0.216 | 0.095 | 0.084 | | | |

Different letters following means in rows indicate statistical significance at $P < 0.05$.

## 2.5. DISCUSSION

### 2.5.1. Herbage mass, herbage accumulation rate and specific contribution

As expected, HM and HAR was associated to HA: paddocks with higher HA had higher HM and HAR (Table 1), coincidentally with the results obtained by Moojen and Maraschin (2002). The HM was higher in autumn, as a result of the accumulation of HM produced and higher HA in last spring and summer, according to the objective of experimental management. In winter the HM decreased accordingly with the lower HA, raised in the experimental design (Do Carmo et al., 2016). In spring, the HM was lower since measurements were taken early in the season and right after a stocking rate adjustment (i.e. there was no time to recover from the heavier grazing pressure in both treatments during the winter). The HAR in winter was also lower for both HA compared to autumn and spring (except for LHA in fall). The dominance of perennial C4 (summer) grasses is characteristic of the region (App I, Berretta, 2001), contributes to explained the lower HAR in winter.

### 2.5.2. Leaf traits

The leaf traits values are coincident with those reported by Cruz et al. (2010) and Jaurena et al. (2012). According to Garnier et al. (2001) LDMC has a negative correlation with SLA and leaf width, and a positive correlation with LTS. This means that species with high LDCM (group D) also represents long leaf lifespan (Garnier et al., 2015) and higher LTS, because of the greater accumulation of leaf structure (i.e. cell wall), resulting in lower digestibility (Al Haj Khaled et al., 2006).

Species varied their leaf traits in relation to period and HA, determining that over period and HA belong to different FG. Garnier et al. (2001) and Al Haj Khaled et al. (2005) found that species varied LDCM and SLA over season In our case, some species varied leaf traits and others maintained stables, as a result of different phenotypic plasticity degrees (Garnier et al., 2001). From autumn to winter the number of species of FG A and B decreased, and therefore, the number of species of FG C and D increased. During winter, the leaf appearance rate and leaf elongation rate decrease, increasing leaf lifespan (Gastal and Lemaire, 2015). The increase in leaf age and low leaf production determine an increase in LDMC, LTS and decrease SLA (Garnier et al., 2001; Garnier et al., 2015), explaining that the number of species of FG C and D increased. Cruz et al. (2010) considering variable HA, reported that only *Andropogon lateralis* Nees modifies leaf traits in response to grazing pressure and found that variation in trait values between treatments was more likely due to changes in floristic composition rather than plasticity of leaf traits. Our results allow to confirm that period affected leaf traits more than HA. In both treatments, winter grasses (*N. charruana*, *N. mucronata and P. stipoides)* increased LCDM and LTS from autumn to spring, related to advance in phenological state. Conversely, mainly summer grasses (*B. laguroides, M. selloana, P. plicatulum* and *S. microstachyum*) increased LDMC and LTS from autumn to winter (increasing the number of FG C and D), but from winter to spring, increased the number of FG A and B, possibly associated with regrowth of these species.

#### 2.5.3. Functional groups contribution

In autumn the higher specific contribution in HHA was explained by group A, associated with higher nutritive value (Al Haj Khaled et al., 2006; Cruz et al., 2010). This group is represented by summer grasses (Rosengurtt, 1979), which are in the last vegetative stage and adapted to grazing (Rosengurtt, 1943). These species adapted to grazing showed an increase SLA, while LDMC decreases (Garnier et al., 2015). Furthermore, FG A is represented by species classified as resource capture strategy with high photosynthetic rate (Wilson et al., 1999). In LHA the specific contribution of FGs A, B and C were similar, explained by *M. selloana* which belong to FG C. Anyway, the specific contribution of resource capture strategy groups (A and B) explained the 57 %

of total dry matter (Table 6) which could be assumed that is a high value of specific contribution.

During winter, predominate species of higher nutritive value in HHA (FGs A and B) and FG C explained mainly by *M. selloana*. Species of FGs A and B were *A. affinis, P. dilatatum* and *P. notatum*, species associated with short lifespan (Eggers et al., 2004; Lemaire et al., 2009; Machado et al., 2013), while *M. selloana* (C), have a long lifespan, determining an increase in LDMC (see Appendix II b). The short lifespan of species in FG A and B, and presence of stolon and rhizome in *A. affinis* and *P. notatum* provides an adaptation to grazing (Rosengurtt, 1943) determining the higher SLA and lower LDMC (Garnier et al., 2015). The same occurred in LHA, which the higher specific contribution was due to FG B, explained by *A. affinis* and *P. notatum*.

In spring, *A. affinis*, *M. selloana* and *P. notatum* were the species that explained the higher contribution of group B in both treatments. These species are fast growing (resource capture) summer grasses which are re-growing in this period (Rosengurtt, 1979), explaining the higher HAR (Table 2). At the same time, the HM was lower (Table 2), that could be determined by short leaf length (Gastal and Lemaire, 2015), mainly in *M. selloana*, associated with low LDMC than winter (see Appendix II c).

#### 2.5.4. Functional groups defoliation pattern

The GP of each FG in autumn was associated to their leaf traits (increasing from D to A) rather than their specific contribution to HM. Cows defoliated the same proportion of groups A, B and C regardless the specific contribution, and avoided group D, which correspond to higher LTS and LDCM. However, the higher GP of FG C (high nutritive value than FG D but lower than A and B) showed that cows selected forage quality but also forage quantity, mainly in LHA. The difference in SI between treatments in FG C could be explained by the higher HM and HAR in HHA, which allowed to express more selectivity between FGs. In this condition, cows could select species of FG A and B in HHA, while in LHA, cows grazed FG A, B and C.

The winter GP was only different between HA. Even though HM and HA were not different, pasture structure (Casalás, 2019) and mainly the body condition of cows (Table 1) could explain a better exploration and selectivity in HHA (Figure 1). This could be a carry effect of HM, HAR and mainly HA, from autumn to winter. The GP in this period was smaller than autumn, explained by a lower HM, HAR and HA. Gonçalves et al. (2009) found that the probability of defoliation increases with lower height and HM. Conversely, Lemaire et al. (2009) showed that the probability of leaf defoliation decreases with lower HAR, as found in this work, determining the lower GP and lower selectivity. FGs were grazed similarly regardless the nutritive value and the specific contribution. It could be assumed that cows oriented the foraging strategy to energy intake, rather than forage quality (Sollenberger and Vanzant, 2011). Furthermore, the SI was not different between FGs, contrary to autumn. The GP was higher in HHA than LHA, possibly associated to the number of animals in each treatment, determining an increase kg LW/ha, as showed Lemaire et al. (2009), but also, by an increase in animals/ha to reach the target HA (1.43 cows/ha vs 0.85 cows/ha).

In spring the group D was the least grazed due to the lower quality of the component species rather than the lower specific contribution (Table 6). Cows avoided these groups, determining the lower SI (Figure 1). The higher GP observed in FG A in LHA than HHA was due to the presence of *P. dilatatum* in LHA, a desirable specie, while in HHA, FG A was only conformed by *S. microstachyum*, a less desirable species (Rosengurtt, 1979). Comparing to winter, was observed difference in GP and SI between FGs. In terms of HM was lower but HAR was higher than winter. Also, the number of cows was lower. Therefore, the higher selective capacity showed by cows was explained by high HAR and lower number of animals.

In all periods, the average of ID was 60 - 70%, barely higher value than expressed by Lemaire et al. (2009). This could be by a higher capacity of cows to grazed intense, regardless the nutritive value and leaf traits. In this condition, cows modified the GP of each FG rather than the ID. The fact that the ID was similar in FGs could be by a little variation in traits in this section of the lamina.

## 2.6. CONCLUSIONS

We concluded that leaf functional traits are modified by seasons, associated to variations in HA determining that the specific contribution of FGs was the result of these factors. The defoliation pattern on FGs was differently explained by the GP. In this heterogeneous pasture, cows adjust the defoliation pattern by adjusting the proportion of grazed species, regardless the specific contribution of each FG. The ID remained constant in many different situations.

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## 2.8. APPENDIX

**Appendix I** List of species selected and growth season

| Species name | Growth season |
|---|---|
| *Andropogon ternatus* (Spreng.) Nees | warm-season |
| *Axonopus affinis* Chase | warm-season |
| *Bothriochloa laguroides* (DC.) Herter | warm-season |
| *Cynodon dactylon* (L.) Pers. | warm-season |
| *Mnesithea selloana* (Hack.) de Koning & Sosef | warm-season |
| *Nassella charruana* (Arechav.) Barkworth | cool-season |
| *Nassella mucronata* (Kunth) R.W. Pohl | cool-season |
| *Paspalum dilatatum* Poir. | warm-season |
| *Paspalum notatum* Flüggé | warm-season |
| *Paspalum plicatulum* Michx. | warm-season |
| *Piptochaetium stipoides* (Trin. & Rupr.) Hack. ex Arechav. | cool-season |
| *Schizachyrium microstachyum* (Desv. ex Ham.) Roseng., B.R. Arrill. & Izag. | warm-season |
| *Sporobolus indicus* (L.) R. Br. | warm-season |
| *Steinchisma hians* (Elliott) Nash | warm-season |

**Appendix II** Range of leaf traits for each species in autumn (a), winter (b) and spring (c) for high (HHA) and low (LHA) HA. LDMC: leaf dry matter content; SLA: specific leaf area; Width: leaf width; LTS: leaf tensile strength

| **(a) Autumn** | HHA | | | | LHA | | | |
|---|---|---|---|---|---|---|---|---|
| Species | LDMC | SLA | Width | LTS | LDMC | SLA | Width | LTS |
| *A. affinis* | 261-262 | 16.8-25.6 | 5.4-6.3 | 0.13-0.15 | 277-299 | 21.4-25.6 | 4.2-4.3 | 0.14-0.17 |
| *A. ternatus* | 316-382 | 18.9-20.7 | 3.2-4.2 | 0.13-0.21 | 381-407 | 20.1-37.4 | 2.8-3.3 | 0.15-0.24 |
| *B. laguroides* | 308-340 | 27.1-33.8 | 3.8-3.9 | 0.09-0.11 | 330-337 | 22.5-23.8 | 4.3-4.9 | 0.07-0.09 |
| *C. dactylon* | 394-399 | 25.0-36.7 | 2.1-2.2 | 0.05-0.08 | 393-399 | 22.7-32.8 | 2.1-2.2 | 0.05-0.07 |
| *M. selloana* | 377-387 | 17.7-25.5 | 2.3-3.8 | 0.13-0.33 | 381-434 | 16.5-25.8 | 2.2-2.4 | 0.19-0.24 |
| *N. charruana* | 456-481 | 8.2-8.3 | 1.3-1.5 | 1.69-1.78 | 482-494 | 6.7-7.9 | 1.2-1.4 | 1.47-1.92 |
| *N. mucronata* | 417-442 | 11.4-13.0 | 1.2-1.9 | 0.15-0.29 | 400-462 | 17.6-19.3 | 2.3-2.5 | 0.18-0.21 |
| *P. dilatatum* | 262-347 | 23.9-24.0 | 4.8-7.2 | 0.11-0.15 | 259-272 | 22.0-22.2 | 6.0-6.6 | 0.14-0.15 |
| *P. notatum* | 293-300 | 21.8-24.1 | 4.2-5.2 | 0.14-0.18 | 305-340 | 16.4-23.0 | 3.2-4.8 | 0.14-0.27 |
| *P. plicatulum* | 248-323 | 12.7-16.7 | 2.6-3.2 | 0.23-0.38 | 252-280 | 13.0 | 2.7 | 0.41 |
| *P. stipoides* | 392-421 | 15.8-22.4 | 1.3-1.6 | 0.12-0.18 | 440-445 | 12.4-19.9 | 1.3-1.4 | 0.30-0.34 |
| *S. indicus* | 323-384 | 12.3-13.17 | 2.2-3.0 | 0.74-0.89 | 341-406 | 8.4-13.0 | 2.2-3.3 | 0.52-0.75 |
| *S. microstachyum* | 299-329 | 21.9-28.9 | 3.8-5.9 | 0.17-0.20 | 320-396 | 17.7-19.6 | 4.7-4.9 | 0.26-0.29 |

| **(b) Winter** | HHA | | | | LHA | | | |
|---|---|---|---|---|---|---|---|---|
| Species | LDMC | SLA | Width | LTS | LDMC | SLA | Width | LTS |
| *A. affinis* | 295-364 | 8.4-33.9 | 4.9-5.2 | 0.32-0.35 | 323-340 | 13.1-16.5 | 4.5-4.7 | 0.20-0.33 |
| *A. ternatus* | 374-377 | 11.3-12.7 | 1.7-2.2 | 0.58-0.75 | 334-401 | 7.8-13.7 | 2.2-2.4 | 0.58-0.58 |
| *B. laguroides* | 403-424 | 13.3-14.0 | 2.9-3.1 | 0.33-0.36 | 306-327 | 20.4-23.1 | 3.5-3.7 | 0.24-0.31 |
| *C. dactylon* | 391-417 | 10.9-15.4 | 0.9-1.0 | 0.67-0.78 | 391-393 | 14.2-20.4 | 1.0-1.1 | 0.60-0.64 |
| *M. selloana* | 405-414 | 12.6-13.5 | 2.0-2.3 | 0.34-0.39 | 372-466 | 11.7-12.1 | 1.8-2.2 | 0.28-0.57 |
| *N. charruana* | 448-492 | 4.6-6.1 | 1.0-1.0 | 4.20-4.27 | 411-440 | 4.6-7.6 | 0.9-1.1 | 1.08-1.74 |
| *N. mucronata* | 399-425 | 7.9-8.4 | 2.3-3.7 | 0.58-0.61 | 409-424 | 5.2-10.7 | 1.2-2.3 | 0.49-0.94 |
| *P. dilatatum* | 301-304 | 23.1-25.3 | 6.6-6.9 | 0.22-0.27 | 290-300 | 17.2-19.4 | 5.7-6.5 | 0.21-0.22 |
| *P. notatum* | 319-344 | 13.1-15.8 | 3.0-4.0 | 0.28-0.31 | 306-336 | 11.6-11.9 | 3.1-3.2 | 0.22-0.33 |
| *P. plicatulum* | 595 | 4.3-5.8 | 2.9-3.7 | 0.33-0.37 | 253-368 | 8.5-9.7 | 1.7-2.6 | 0.53-0.59 |
| *P. stipoides* | 446-491 | 6.1-6.1 | 0.6-1.0 | 0.78-1.00 | 423-483 | 4.2-7.0 | 0.6-0.7 | 0.20-0.57 |
| *S. indicus* | 422-467 | 6.4-7.3 | 1.7-2.2 | 1.17-1.58 | 412 | 6.5-10.5 | 2.0-3.4 | 0.39-0.73 |
| *S. microstachyum* | 361-411 | 12.1-15.1 | 2.6-3.6 | 0.29-0.36 | 344-368 | 13.1-16.5 | 3.3-3.9 | 0.35-0.44 |

| **(c) Spring** | HHA | | | | LHA | | | |
|---|---|---|---|---|---|---|---|---|
| Species | LDMC | SLA | Width | LTS | LDMC | SLA | Width | LTS |
| *A. affinis* | 244-264 | 15.7-16.4 | 4.9-5.0 | 0.39-0.40 | 252-271 | 15.7-17.2 | 4.1-5.7 | 0.42-0.43 |
| *A. ternatus* | 304-326 | 11.9-12.7 | 1.3-2.0 | 0.74-0.93 | 357 | 12.3 | 2.01 | 0.68 |
| *B. laguroides* | 282-287 | 15.0-20.4 | 2.8-3.7 | 0.37-0.42 | 283-285 | 17.5-19.1 | 3.1-3.4 | 0.37-0.41 |
| *C. dactylon* | 393-416 | 10.4-17.2 | 1.1-1.4 | 0.79-0.98 | 350-400 | 10.9-17.1 | 1.2-1.5 | 0.62-0.66 |
| *M. selloana* | 281-344 | 18.3-23.1 | 2.1-2.9 | 0.54-0.65 | 328-333 | 15.9-17.5 | 2.1-2.2 | 0.64-0.68 |
| *N. charruana* | 250-398 | 5.6-9.9 | 0.8-1.1 | 3.55-4.59 | 433-435 | 5.5-7.8 | 1.1-1.1 | 3.68-3.74 |
| *N. mucronata* | 348-380 | 11.9-14.4 | 1.1-1.2 | 1.15-1.37 | 333-365 | 7.7-9.3 | 0.8-1.1 | 1.29-1.81 |
| *P. dilatatum* | 252-267 | 15.7-16.0 | 4.7-5.1 | 0.41-0.42 | 237-274 | 17.6-18.7 | 6.0-6.1 | 0.33-0.37 |
| *P. notatum* | 267-279 | 16.6-17.5 | 3.2-3.7 | 0.45-0.47 | 277-282 | 12.2-16.7 | 2.8-3.4 | 0.45-0.55 |
| *P. plicatulum* | 250-270 | 15.7-16.2 | 2.1-3.9 | 0.41-0.64 | 252-276 | 8.9-11.0 | 1.2-2.3 | 0.66-1.23 |
| *P. stipoides* | 382-391 | 9.0-10.3 | 0.3-0.7 | 1.38-2.66 | 385-411 | 6.4-7.7 | 0.7-0.7 | 1.77-2.05 |
| *S. hians* | 332-354 | 12.3-13.1 | 2.3-2.9 | 0.48-0.63 | 305 | 21.1 | 3.75 | 0.42 |
| *S. indicus* | 374-389 | 6.9-7.8 | 1.8-2.0 | 1.42-1.56 | 375 | 5.5 | 1.82 | 1.65 |
| *S. microstachyum* | 317-327 | 20.5-22.9 | 5.5-5.8 | 0.45-0.46 | 329-358 | 19.8-21.1 | 5.9-6.1 | 0.43-0.46 |

# 3. FACTORS AFFECTING DEFOLIATION PATTERN BY CATTLE IN HETEROGENEOUS GRASSLAND

## 3.1. ABSTRACT

The objective of the study was to evaluate the effect of biotic and abiotic factors on defoliation pattern of cows in the Campos grassland across seasons, under two herbage allowance (HA) levels. Treatments were High (HHA) and Low (LHA) HA, variable between seasons (8 and 5 kg dry matter/kg live weight, annual average for HHA and LHA, respectively). To identify factors that affected the defoliation pattern in those seasons we proposed a conceptual model of grazing probability (GP) and intensity of defoliation (ID) of each species. Models included biotic, abiotic and cows body condition score (BCS) at different scales. Biotic factors were: total herbage mass (HM) in a paddock (HMp), HM in quadrants (20*20 cm, HMq), HM of each species within the quadrant (HMsp), herbage accumulation rate, stocking density, real HA and leaf traits of 14 dominated species: leaf dry matter content (LDMC), specific leaf area (SLA), leaf tensile strength (LTS) and width leaf. Abiotic factors were distance to water and shade of each quadrant, and cows BCS, as an indicator of nutritional status. A multivariate analysis using conditional inference tree was performed to analyze each factor. Factors affecting GP in autumn were mainly HMq, BCS and LTS. For winter were HMq, distance to shade and HMsp, while for spring were distance to water and shade, and LTS. Factor which affected ID in autumn were HMq, BCS, and LDMC, for winter was only HMq and for spring were only leaf traits: LDMC, LTS and leaf width. Cows integrated information of different spatial scales, not following hierarchical decisions. Cows had different foraging strategies, modifying the grazing distribution and selected diet. Cows adjusted grazing intensity according to leaf traits mainly in autumn and spring.

**Keywords:** grazing probability, intensity of defoliation, decision tree, Campos grasslands

## 3.2. INTRODUCTION

In the early 2000s, Wade and Carvalho (2000) concluded that the knowledge of defoliation dynamics had large gaps. After almost 20 years some gaps are still existing, mainly regarding heterogeneous grasslands. Due to the importance of this grasslands and grazing systems, it is necessary to improve the knowledge on defoliation pattern and the interaction of biotic and abiotic factors. Defoliation pattern was defined by frequency or the probability for each plant unit to be defoliated, and the intensity or severity of defoliation, expressed as the ratio between leaf length removed by grazing in a single defoliation event and the length of the leaf before defoliation (Lemaire et al., 2009). The defoliation pattern is the last decision taken by animals, after integrating information at different scales. Senft et al. (1987), Stuth (1991) and Bailey et al. (1996) proposed a hierarchical foraging model of grazing distribution pattern, which integrates different spatial and temporal scales, and considered biotics and abiotic factors.

Grazing distribution is affected by topography and water availability, selecting species in sites near water (Bailey and Provenza, 2008; Putfarken et al., 2008), increasing the probability of defoliation. Furthermore, grazing distribution is also affected by HM and quality (Bailey and Provenza, 2008). The average HM and the herbage accumulation rate (HAR) are the result of herbage allowance (HA) (Moojen and Maraschin, 2002). The HM is positively related with HA (Do Carmo et al., 2018), while stocking density (SD) is negatively related to HA (Sollenberger et al., 2005). High HM and low SD allow more selectivity, with the number of visited sites lower than the potential sites (Nabinger et al., 2011) and therefore reducing the probability for each plant to be defoliated (Gonçalves et al., 2009a; Lemaire et al., 2009). Spatial heterogeneity increases with grazed and ungrazed sites (Laca, 2000). Animals tend to select grazed sites, rather than ungrazed, searching for fresh, newly regrown forage (Ring et al., 1985), with higher nitrogen content (Cid and Brizuela, 1998), regardless botanical composition (Coleman et al., 1989), increasing frequency of defoliation in those sites (Jensen et al., 1990). Conversely, with low average HM, despite the high forage nutritive value (Sollenberger and Vanzant, 2011), animal selected species in patches with high HM to increase intake (Da Trindade et al., 2016). The number of grazing sites is similar to the number of available sites, and selectivity become null (Nabinger et al., 2011). This results in higher frequency and ID (Jensen et al., 1990), increasing animal spatial distribution.

At species level, the specific contribution and inherent characteristics of each species affect the probability and ID. The probability of each species to be defoliated is the result of the specific contribution, green and dead standing biomass, height sheath, presence of inflorescence and defoliation pattern of neighbor plants (Senft et al., 1985; Lemaire, 2001). Moreover, plant traits such as leaf dry matter content (LDMC), specific leaf area (SLA), leaf width, leaf tensile strength (LTS) and texture also affect the probability of defoliation (Boggiano, 1995; Cingolani et al., 2005; Jaurena et al., 2012; Garnier et al., 2015). Those variables determine the grazing distribution, where animals concentrate in areas that allow higher intake rate (Stuth, 1991; Utsumi et al., 2009).

The effect of animal nutritional status on grazing distribution and defoliation patterns is also unknown. Few studies related the nutritional status (i.e.: body condition score, BCS) of each animal and the defoliation pattern. In arid environments, Murden and Risenhoover (1993) and Mellado et al. (2004) found that deer and goats with higher nutritional status were more selective, and reject low quality species, than deer and goats with lower nutritional status, which were less selective and grazed lower quality species. It possible to assume that cows with different BCS modify defoliation pattern and diet selection in heterogeneous grasslands.

Although the effect of pasture attributes and environment on defoliation pattern is already know, the combination of paddock forage mass at different scales, species contribution and leaf traits, distance to attractive points and BCS, and the degree of influence of each one on frequency and ID is still unknow, especially for heterogenous and diverse environments. The objective of the study was to evaluate the effect of pasture attributes at different spatial scales, environmental factors and cows BCS on defoliation pattern of multiparous pregnant beef cows in a heterogeneous Campos grassland in different seasons under two HA levels. We hypothesized that factors which affect GP of species and ID are different according to HA, HM at different scales, distance to attraction points and season.

## 3.3. MATERIALS AND METHODS

### 3.3.1. Site, experimental design and treatments

The study was carried out on 48 ha of native grassland in the Experimental Station Bernardo Rosengurtt, Cerro Largo, Uruguay, during three periods: 1st March – 15th April (autumn), 30th July – 26th August (winter) and 1st October -15th November (spring), 2017. Dominant soils in the experimental area were Hapluderts, Argiudolls, Hapludalfs and Natruaqolls (Durán et al., 2005). The average monthly rain (1980-2009, Castaño et al., 2011) was 113 mm, 105 mm and 123 mm for Mar-Apr, Aug and Oct-Nov. During 2017 rainfall were 87, 213 and 135 for these periods, representing a decrease in 23%, and an increase in 102% and 11%, respectively. The historical average daily temperature for these months were 22 ºC, 13 ºC and 19 ºC (Castaño et al., 2011). During the evaluation months the average temperature were 23 ºC, 16 ºC and 20 ºC, in average 2 ºC more than the historical average temperature. The native grassland was dominated by *Axonopus affinis* Chase, *Carex bonariensis* Desf. ex Poir., *Mnesithea selloana* (Hack.) de Koning & Sosef, *Nassella charruana* (Arechav.) Barkworth, *Nassella mucronata* (Kunth) R. W. Pohl, *Paspalum dilatatum* Poir., *Paspalum notatum* Flüggé and *Schizachyrium microstachyum* (Desv. ex Ham.) Roseng., B. R. Arrill. & Izag.

Two treatments were defined considering HA (HHA: high HA, LHA: low HA), as the relation between HM and live weight (kg dry matter (DM)/kg live weight (LW)) (Sollenberger et al., 2005). The target annual average HA was 8 kg DM/kg LW for HHA and 5 kg DM/kg LW for LHA, variable among seasons (summer and autumn: 8 and 4 kg DM/kg LW, winter: 4 and 4 kg DM/kg LW, and spring: 12 and 8 kg DM/kg LW, for HHA and LHA, respectively) (Do Carmo et al., 2016). The experiment was a randomized complete design with two replications, totaling four paddocks. The area of HHA paddocks were 14 ha while the area of LHA paddocks were 10 ha.

### 3.3.2. Animals

The experiment was continuously stocked with pregnant multiparous Hereford, Aberdeen Angus and F1 reciprocal Hereford and Aberdeen Angus crosses cows of 446 kg ± 63 average weight. Animals were weighted every month for adjusting stocking by the "put and take" method (Mott and Lucas, 1952), according to HA treatment. During autumn were used 1.7 and 1.1 animals/ha, during winter 0.9 and 1.5 animals/ha and during spring were used 0.6 and 0.5 animals/ha for LHA and HHA, respectively (Table 1). The minimum number of "tester" animals for both treatments were 5 cows/paddock. HM, HAR, stocking rate, SD, body condition score and HA were different between treatments and periods (Table 1).

### 3.3.3. Measurements

The HM of each paddock was measured using the comparative yield method (Haydock and Shaw, 1975) at the beginning and the end of each period of evaluation. Between 120 and 150 measurements were made in each paddock per evaluation period. HAR were estimated through the double-cage method (Klingman et al., 1943), using nine cages per paddock at HHA and eight cages per paddock at LHA.

To measured pasture attributes, fixed 50-m transects were defined in each paddock considering topography and soil type. In HHA paddocks were delimited seven transects/paddock and in LHA were delimited five transects/paddock, totaling 14 transects in HHA and 10 in LHA. Every five meters within each transect were located ten fixed quadrats (40*40 cm), divided in 4 quadrants (20*20 cm), totaling 140 quadrats in HHA and 100 in LHA, and 560 and 400 quadrants in HHA and LHA, respectively.

Botanical composition, HM, presence of defoliation and the ID were measured in each quadrant (20*20 cm) every 5-7 days ("week") to avoid re-grazed at this scale. Botanical composition was estimated determining the specific contribution of species that represented close to 95% of total dry matter of each quadrant (Brown, 1954). The HM of each quadrant was estimated visually every week. Visually estimation was adjusted every week, cutting forage samples of different quadrants that not belong to transects. Samples were dried in stove over 72 hours at 60 ºC until constant weight to obtain the dry matter content. Considering the total dry matter of each quadrant and the specific contribution of species, was estimated the contribution of species in kg DM/ha in each quadrant every week.

At the same time of measured of HM and botanical composition of each quadrant, was measured the presence or absence of defoliation, using a water-marker pen in the top of the leaf grazed, totaling 4-5 times per period per quadrant (every 5-7 days). The grazing probability (GP) of each species per period was estimated as the ratio between the sum of grazing events of each species and the total number of records of each species. When presence of defoliation was detected, the ID of each leaf was estimated as the ratio between the leaf length removed and the length of the leaf before defoliation (Lemaire et al., 2009). Four scores were defined subjectively considering the percentage of removed leaf blade as 25% (a quarter leaf removed), 50% (a half leaf removed), 75% (three quarter leaf removed) and 100% (whole leaf removed).

After the first floristic composition assessment (1st – 8th March), species that explained 80% or more of the total DM were identified for paddock. Those were 14 perennial grasses: *Andropogon ternatus* (Spreng.) Nees*, A. affinis, Bothriochloa laguroides* (DC.) Herter*, Cynodon dactylon* (L.) Pers., *M. selloana, N. charruana, N. mucronata, P. dilatatum, P. notatum, Paspalum plicatulum* Michx.*, Piptochaetium stipoides* (Trin. & Rupr.) Hack. ex Arechav.*, S. microstachyum, Sporobolus indicus* (L.) R. Br. and *Steinchisma hians* (Elliott) Nash*.*

For each of those species it was measured leaf functional traits at the end of each evaluation period. Leaf traits, defined according to the effect on defoliation pattern, were: specific leaf area (SLA, $m^2$/kg), leaf dry matter content (LDMC, mm/g), leaf width (mm) and leaf tensile strength (LTS, N/mm), measured after water saturation over 8 hours. A total of 40 ungrazed, newly expanded, free of disease leaves were selected per species per month at each paddock, following the protocol developed by Cornelissen et al. (2003). SLA ($m^2$/kg) was estimated scanning leaves and then measured the leaf area with ImageJ software (Schneider et al., 2012). Leaf width was measured using a leaf scanner, considering the widest section of each one. The LDMC (g/kg) was calculated in the same leaves, oven dried during 72 hours at 60 ºC (g), divided by its water saturated fresh mass (kg). LTS (N/mm) was measured in the central section of leaves using the Hendry and Grime (1993) apparatus to determine the force required to tear leaf in two.

To determine the effect of abiotic factors on defoliation pattern was estimated at the middle of each transect the distance to water and shade, using satellite images of Google Earth Pro 7.3 (2019) (Table 2). In LHA, the maximum distance to shade was 281 m and the maximum distance to water was 278 m, while the minimum distance to shade was 70 m and to water was 67 m. In HHA, the maximum distance to shade was 314 m and to water was 234 m, while the minimum distance was 53 m and 70 m, respectively.

### 3.3.4. Conceptual model of defoliation pattern

To identify which are the mainly variables that defined the defoliation pattern in different seasons we proposed a conceptual model of GP and ID of each species (Figure 1). The model suggest that defoliation pattern is affected by abiotic factors (environment: soil, distance to water and shade), HA variable between seasons, attributes at paddock level as HM, HAR and SD, attributes at quadrants level as HM, specific contribution of each species, leaf traits of each species and phenological state as vegetative or reproductive state and consider the cows body condition score.

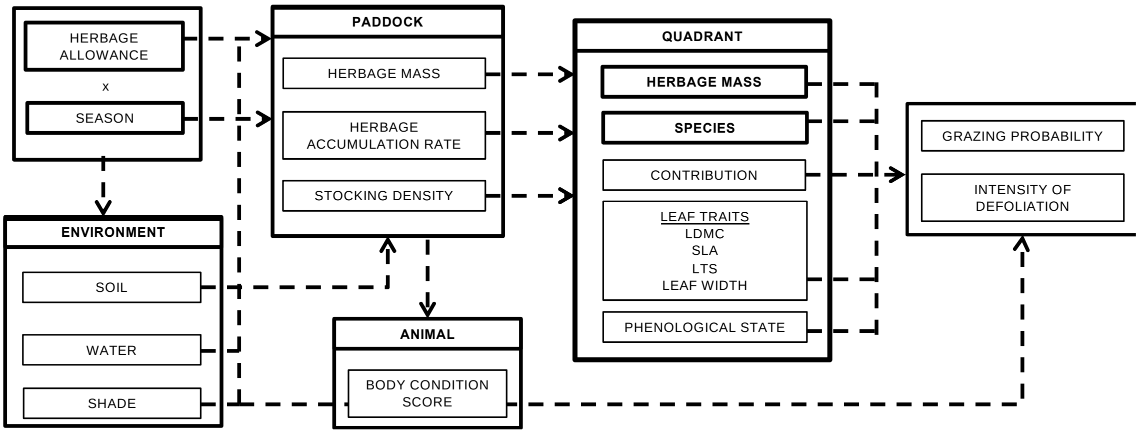



**Figure 1** Conceptual model of defoliation pattern (grazing probability and intensity of defoliation) affected by environmental factors, herbage allowance, paddock, quadrant attributes and body condition score

### 3.3.5. Statistical analysis

#### 3.3.5.1. Grazing probability and intensity of defoliation

A multivariate analysis of conditional inference tree was performed to analyze the GP and the ID, using *party* package and `party::ctree` function (Hothorn et al., 2006) in R 3.5.1 (R Development Core Team 2018). Trees were developed for each period (season), considering both treatments, based on conceptual model of defoliation pattern (Figure 1).

The model developed to predict grazing probability was:

GP ~ HMp + HMq + HMsp + HAR + SD + SR + aHA + BCS + Water + Shade + SLA + LDMC + LTS + Width + PS

while the model developed for ID was:

ID ~ HMp + HMq + HMsp + HAR + SD + SR + aHA + BCS + Water + Shade + SLA + LDMC + LTS + Width + PS

where: HMp: average herbage mass for each paddock and period (kg DM/ha); HMq: herbage mass of each quadrant at each week (kg DM/ha); HMsp: herbage mass of each species at each week within each quadrant (kg DM/ha); HAR: herbage accumulation rate for each paddock and period (kg DM/ha/day); SD: average stocking density for each paddock and period (kg LW/ha); SR: stocking rate for each paddock and period (animals/ha); aHA: actual herbage allowance for each paddock and period (kg DM/kg LW); BCS: average body condition score of cows for each paddock and period; Water: distance to water of each transect (m); Shade: distance to shade of each transect (m); SLA: specific leaf area of species for each paddock and period ($m^2$/kg); LDMC: leaf dry matter content of species for each paddock and period (g/kg); LTS: leaf tensile strength of species for each paddock and period (N/mm); Width: leaf width of species for each paddock and period (mm); PS: phenological state of species at each record. Soil types were not considered in the models for their indirect effect on botanical composition, herbage mass at each quadrant and herbage accumulation rate, which are included in the models.

The whole dataset was considered to evaluate GP, expressing the probability of species defoliated every week (5-7 days) for each period. The dataset used for evaluated the ID considered only when occurred grazing event, expressing the species defoliated at 25, 50, 75 and 100 % of leaf length removed every month.

#### 3.3.5.2. Model prediction

To evaluate model predictions the whole dataset used for both variables were randomly partitioned in training (70 % of whole dataset) and test data (30% of whole dataset). Trees were built using training data, and model was validated using test data. The evaluation of model predictions considered the observations from the test data (for GP and ID) against the tree model predictions, using the observations/predictions regression method based on Piñeiro et al. (2008). The coefficient of determination ($r^2$) is used to measure the variance of observed values in test data is explained for the model developed with training data (Piñeiro et al., 2008). These authors also strongly recommend to calculate the root mean square deviation (RMSD) which represent the mean deviation of predicted values respect the observed values.

**Table 1** Mean (± SD) herbage mass (HM, DM kg/ha), herbage accumulation rate (HAR, DM kg/ha/day), stocking rate (SR, animals/ha), stocking density (SD, LW kg/ha), body condition score (BCS, ± SD) for each treatment (LHA: low herbage allowance; HHA: high herbage allowance) and period (autumn, winter and spring)

| Period | Autumn | | Winter | | Spring | | | |
|---|---|---|---|---|---|---|---|---|
| Treatments | LHA | HHA | LHA | HHA | LHA | HHA | P-value | SE |
| HM (DM kg/ha) | 2379 (298) $^{b}$ | 3682 (206) $^{a}$ | 1259 (76) $^{cd}$ | 1564 (34) $^{c}$ | 1045 (93) $^{d}$ | 1165 (104) $^{d}$ | 0.004 | 162 |
| HAR (DM kg/ha/day) | 12.1 (0.8) $^{ab}$ | 17.5 (2.6) $^{a}$ | 4.2 (0.1) $^{c}$ | 7.0 (1.9) $^{bc}$ | 15.5 (1.9) $^{a}$ | 14.6 (5.0) $^{a}$ | 0.003 | 2.6 |
| SR (animals/ha) | 1.7 (0.4) $^{a}$ | 1.1 (0.1) $^{ab}$ | 0.9 (0.1) $^{b}$ | 1.5 (0.1) $^{a}$ | 0.6 (0.0) $^{b}$ | 0.5 (0.1) $^{b}$ | 0.008 | 0.2 |
| SD (LW kg/ha) | 657 (82) $^{a}$ | 482 (35) $^{ab}$ | 338 (54) $^{bc}$ | 661 (8) $^{a}$ | 264 (9) $^{c}$ | 219 (23) $^{c}$ | 0.001 | 44 |
| BCS | 3.66 (0.61) $^{b}$ | 4.26 (0.99) $^{a}$ | 3.50 (0.26) $^{b}$ | 4.23 (0.87) $^{a}$ | 4.39 (0.49) $^{a}$ | 4.05 (0.56) $^{a}$ | 0.008 | 0.24 |
| Real HA | 3.7 (0.0) $^{bc}$ | 7.6 (0.1) $^{a}$ | 3.7 (0.8) $^{bc}$ | 2.2 (0.1) $^{c}$ | 4.0 (0.5) $^{bc}$ | 6.3 (1.1) $^{ab}$ | 0.002 | 0.6 |

Different letters following means in rows indicate statistical significance at $P < 0.05$.

**Table 2** Distance to shade (DS; m) and distance to water (DW; m) for each transect within paddocks (1, 2, 3 and 4) and treatments (LHA: low herbage allowance; HHA: high herbage allowance)

| | LHA | | | | HHA | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | |
| Transect | DS (m) | DW (m) | DS (m) | DW (m) | DS (m) | DW (m) | DS (m) | DW (m) |
| 1 | 192 | 126 | 281 | 208 | 70 | 234 | 106 | 126 |
| 2 | 170 | 95 | 181 | 67 | 137 | 193 | 71 | 120 |
| 3 | 93 | 127 | 70 | 121 | 53 | 94 | 242 | 137 |
| 4 | 196 | 232 | 95 | 212 | 96 | 82 | 308 | 176 |
| 5 | 184 | 256 | 80 | 278 | 110 | 91 | 314 | 119 |
| 6 | | | | | 185 | 93 | 290 | 70 |
| 7 | | | | | 131 | 90 | 227 | 116 |

## 3.4. RESULTS

### 3.4.1. Pastures attributes

The HM was variable between treatments and periods (Table 1). The higher value was in autumn in HHA while the lower value was in spring in LHA and from the autumn to the spring a decrease in HM was observed. The maximum HAR occurred in autumn in HHA and spring in both treatments. As expected, the lower HAR was in winter. The SD in LHA was maximum in autumn, medium in winter and lower in spring, while in HHA was maximum in winter, medium in autumn and lower in spring. This factor was the result of HM and target HA.

### 3.4.2. Regression trees

Explaining variables for GP and ID were different according to the period. The GP in autumn (Figure 2) was explained in first order by the HMq in which species were grazed by cows. At second order variables were the mean BCS of cows in each paddock and the LTS of each species. At third order, significant variables were the average HM in each paddock and the leaf width. Finally, at quarter order, HM of each species influenced the GP. Abiotic variables (distance to water and shade), SD, HA, HAR, LDMC, SLA and PS did not affect the GP. The higher GP (0.528) was found with HMq ≤ 1600 kg DM/ha, BCS > 3.8, in paddock with HM ≤ 2590 kg DM/ha and with high HM of each species (> 715 kg DM/ha). The lower GP (0.017) occurred in quadrants with HM > 1600 kg DM/ha and in species with LTS > 0.41 N/mm. Furthermore, at terminal node, species with higher grazing intensity were those with LTS ≤ 0.41 N/mm (0.123 vs 0.017 for species with LTS > 0.41 N/mm), leaf width > 3.88 mm than species with leaf with ≤ 3.88 (0.351 vs. 0.184), and with higher specific contribution within the quadrant (> 715 kg DM/ha) than species with lower contribution (0.528 vs. 0.175).

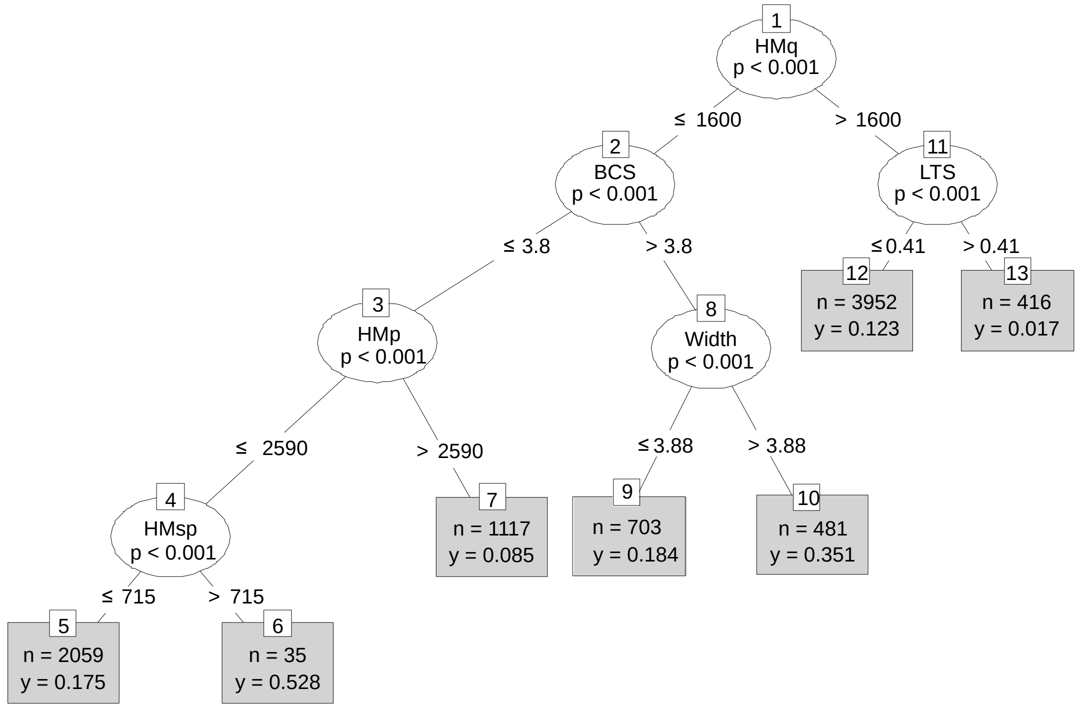



**Figure 2** Autumn regression tree for grazing probability (y) in both treatments. HMq: herbage mass in each quadrant (kg DM/ha); BCS: paddock mean body condition score; LTS: leaf tensile strength of each species (N/mm); HMp: herbage mass in each paddock (kg DM/ha); width (mm): leaf width of each species; HMsp: herbage mass of each species (kg DM/ha)

The GP during the winter was explained in first order by the HAR in each paddock and at second order by distance to shade and the HM of each species (Figure 3). The higher GP (0.138) was observed with HAR > 5.6 kg DM/ha/day and HMsp > 440 kg DM/ha. The lower GP (0.027) was observed with HAR ≤ 5.6 kg DM/ha/day and sites near to shade (≤ 290 m). At lower HAR, animals grazed more species in quadrants further from shade (> 290 m) than quadrants near shade (0.068 vs. 0.027). As in autumn, higher specific contribution of each species determined higher GP (0.137 vs. 0.066). Only comparing GP as a result of HAR, cows grazed more in paddocks with high HAR (> 5.6 kg DM/ha/day) than in paddocks with low HAR (0.075 vs. 0.033).

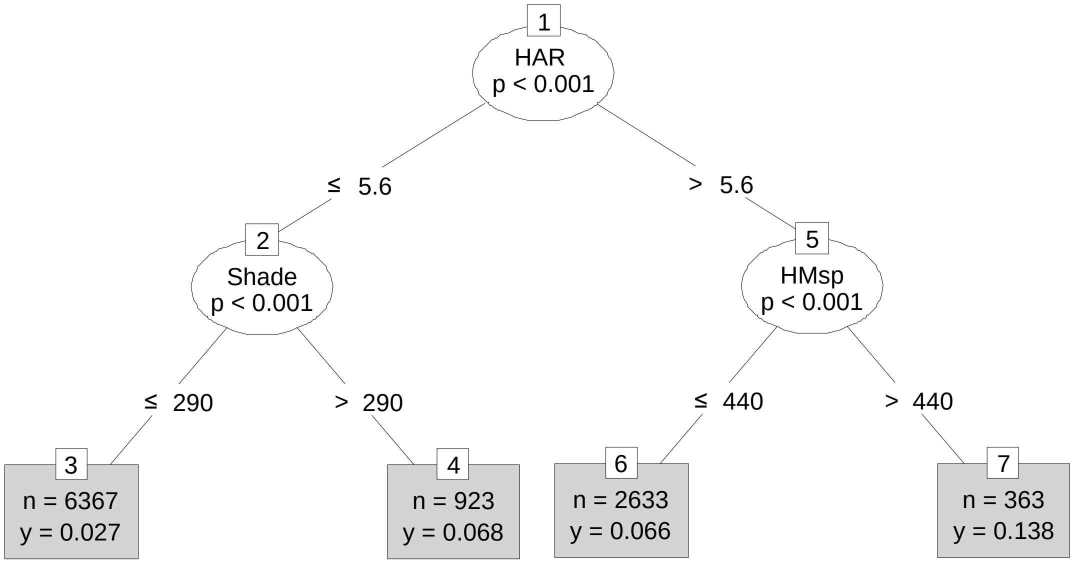



**Figure 3** Winter regression tree for grazing probability (y) in both treatments. HAR: paddock herbage accumulation rate (kg DM/ha/day); Shade: distance to shade (m); HMsp: herbage mass of each species (kg DM/ha)

The spring GP was explained at first order by distance to water (Figure 4). At second order by distance to shade and LTS, at third order by SD and HAR and at fourth order by HMsp. As in autumn, the number of factors explanatory were six, twice as in winter. The higher GP was observed in sites near to water (≤ 137 m), further from shade (> 110 m) and in paddock with HAR ≤ 11 kg DM/ha/day (0.102). The lower GP (0.015) occurred in sites near water (≤ 137 m) and shade (≤ 110 m) and low SD (≤ 212 kg LW/ha). Moreover, species were more grazed with higher SD (0.059 vs. 0.015), and lower LTS (0.100 vs 0.035). Contrary to winter, with low HAR, GP increased and as in autumn, higher grazing events were observed in species with higher specific contribution to quadrant HM (0.078 vs 0.036).

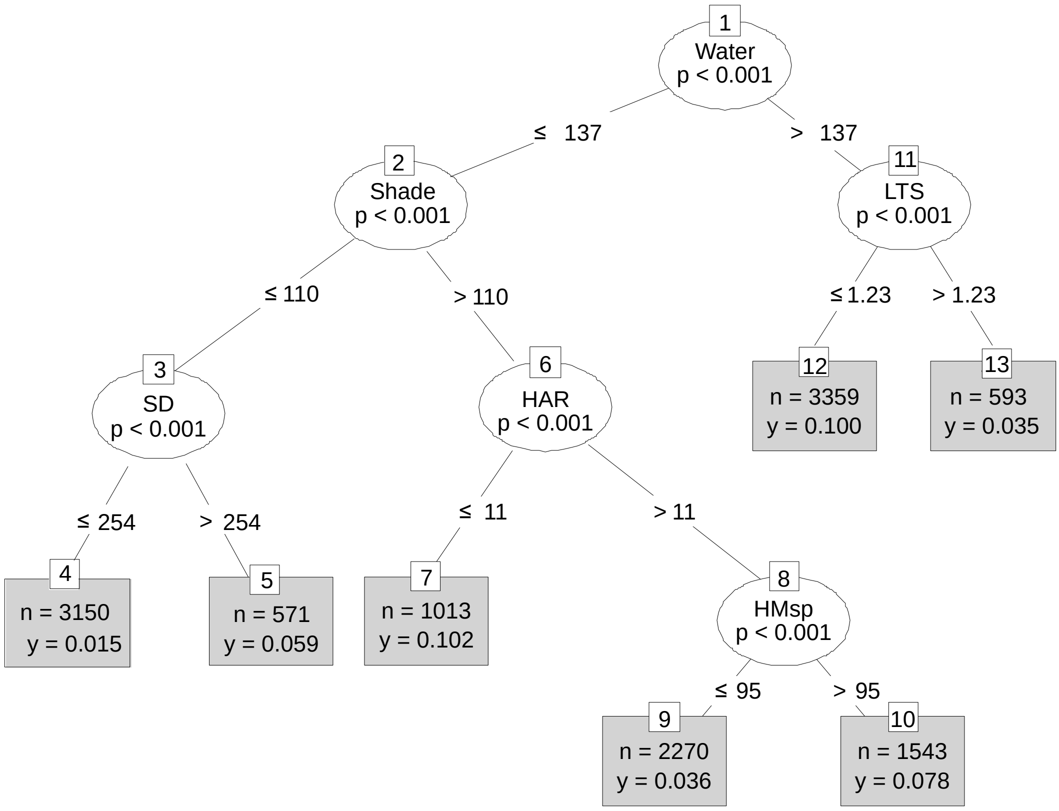



**Figure 4** Spring regression tree for grazing probability (y) in both treatments. Water: distance to water (m); Shade: distance to shade (m); LTS: leaf tensile strength of each species (N/mm); SD: stocking density (kg LW/ha); HAR: paddock herbage accumulation rate (kg DM/ha/day); HMsp: herbage mass of each species (kg DM/ha)

The ID in autumn was explained at first and second order by HMq (Figure 5). At third order was explained by average BCS, while at fourth order was explained by LDMC. The lightly ID was observed in quadrants with HMq > 3700 kg DM/ha, where cows grazed 97 % of species at 25-50 % of intensity, and in quadrants with HM between 2100-3700 kg DM/ha, cows grazed 74 % of species at 25-50 % of intensity. Also, in quadrants with HM ≤ 2100 kg DM/ha, cows lightly grazed species with LDMC > 0.43 mm/g. Conversely, the higher ID occurred in quadrants with HM ≤ 2100 kg DM/ha, cows in average BCS ≤ 3.8 and LDMC ≤ 0.43 mm/g. In this condition, 51 % of grazing events occurred at 75 and 100 % of leaf intensity.

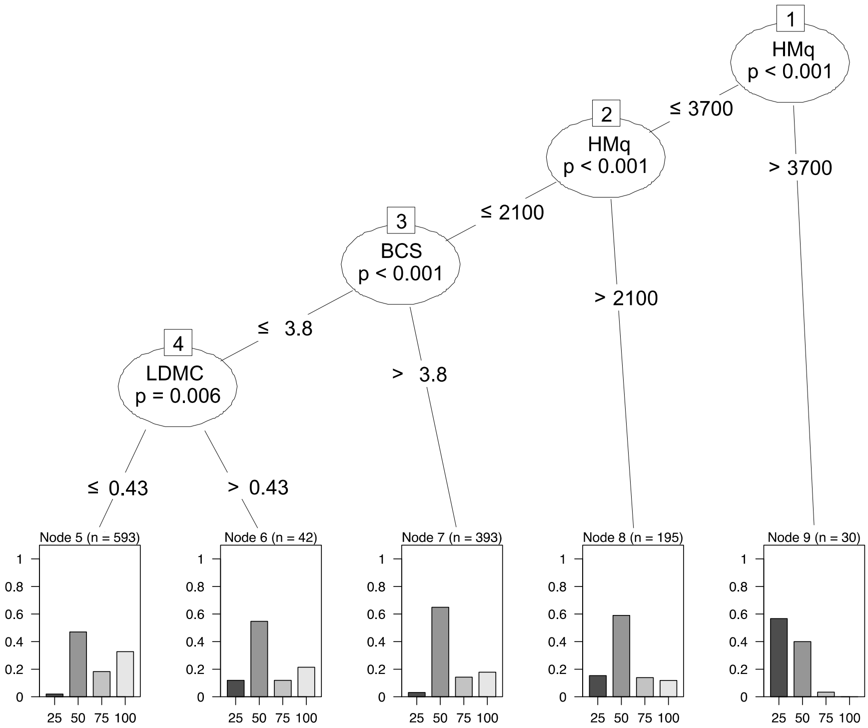



**Figure 5** Autumn regression tree for degrees of intensity of defoliation in both treatments (25, 50, 75 and 100 % of leaf removed). HMq: quadrant herbage mass (kg DM/ha); BCS: paddock mean body condition score; LDMC: leaf dry matter content (g/kg)

The winter ID (Figure 6) was only affected by the HMq. In quadrants with ≤ 1600 kg DM/ha, cows removed a quarter leaf at 6 % of grazed species, removed a half of leaf at 36 % of species, three quarter at 22 % of species and whole leaf was removed at 36 % of species. Conversely, in quadrants with HMq > 1600 kg DM/ha, cows removed the whole leaf at 13 % of grazed species, three quarter of the leaf at 34 % of species, a half leaf at 45 % of species and a quarter leaf at 8 % of species.

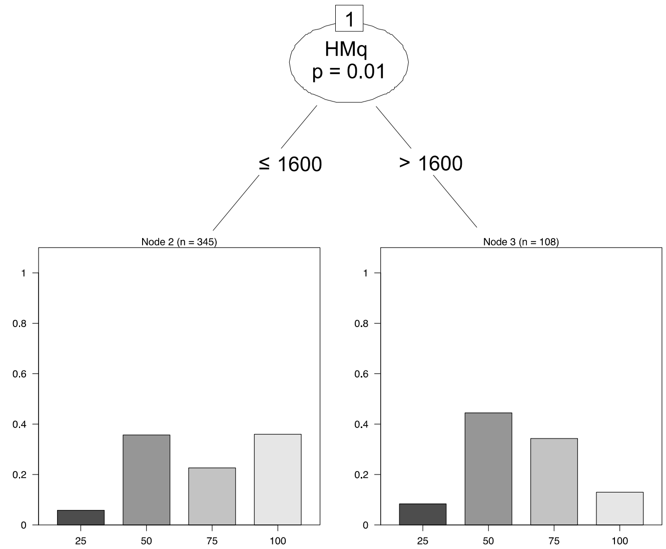



**Figure 6** Winter regression tree for degrees of intensity of defoliation in both treatments (25, 50, 75 and 100 % of leaf removed). HMq: quadrant herbage mass (kg DM/ha)

Factors affecting the ID in spring (Figure 7) were at first order LDMC (g/kg), at second order LTS (N/mm) and at third order leaf width (mm). Lightly leaf intensity was observed in species with LDMC > 0.38 mm/g (70 % of species were grazed at 50 % or lower intensity) and in species with LDCM ≤ 0.38 but LTS > 1.65 N/mm (74 % of species were grazed at 50 % or lower intensity). Higher ID was observed in species with low LDCM (≤ 0.38 g/kg), low LTS (≤ 1.65 N/mm) and wider leaves (> 1.51 mm). In this case, cows removed at least three quarter of leaf at 57 % of species.

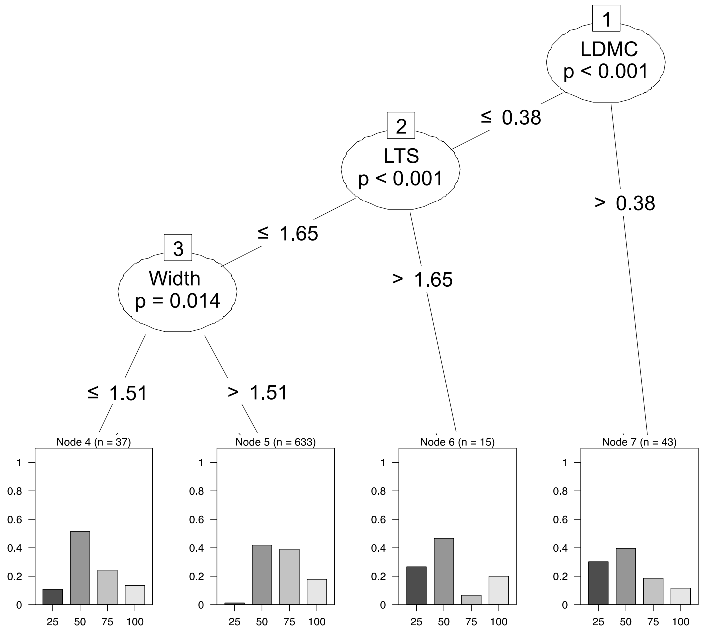
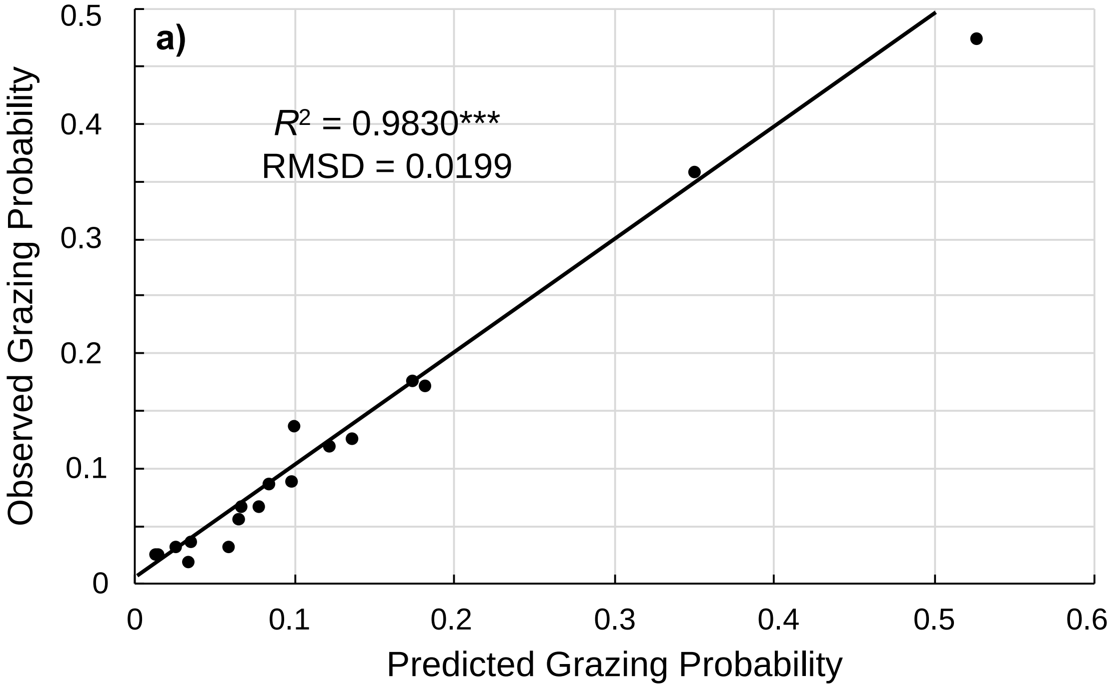



**Figure 7** Spring regression tree for degrees of intensity of defoliation in both treatments (25, 50, 75 and 100 % of leaf removed). LDMC: leaf dry matter content of each species (g/kg); LTS: leaf tensile strength of each species (N/mm); Width: leaf width of each species (mm)

#### 3.4.3. Model prediction

Model predictions were evaluated by regressing observed (y-axis) and predicted data (x-axis) and tested the significance of intercept = 0 and slope = 1 for the GP model (Figure 8a) and the ID model (Figure 8b), following the recommendations from Piñeiro et al. (2008). The proportion of the variance in observed values which was explained by predicted values for the GP model was 98.3 % ($R^2$ = 0.9830) and the RMSD = 1.997. The proportion of the variance explained by the ID model was 84.2% ($R^2$ = 0.8419), and the RMSD = 0.083.



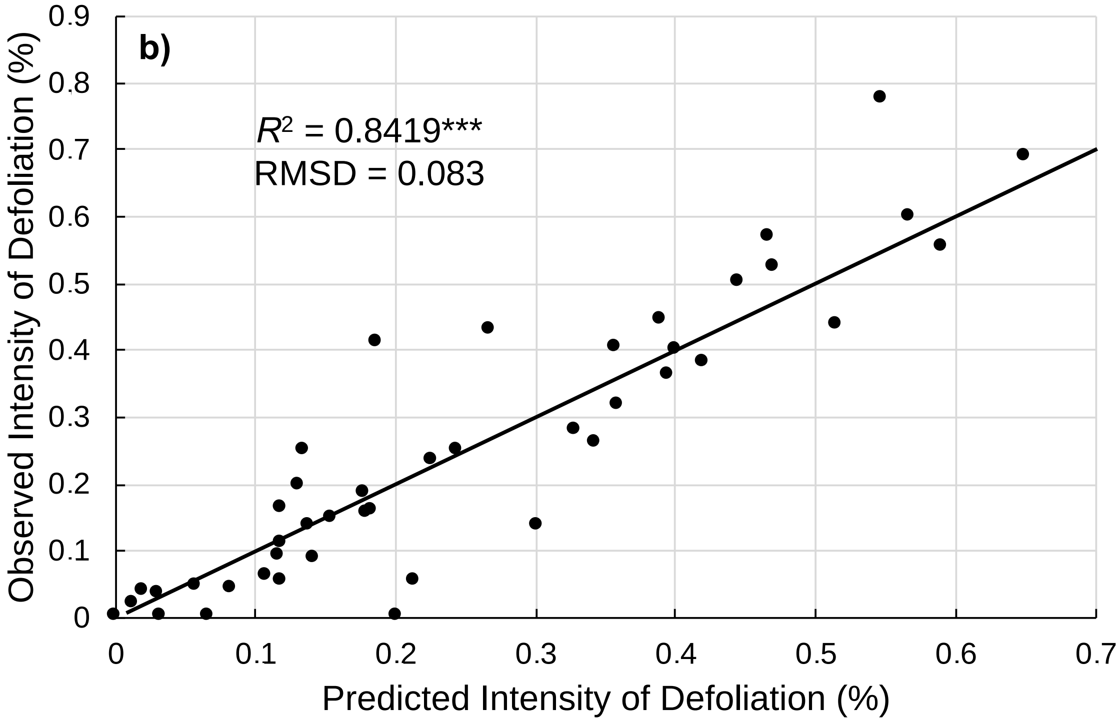




**Figure 8** Observed vs predicted value regression for grazing proportion model (a) and intensity of defoliation model (b). *** P < 0.0001

## 3.5. DISCUSSION

### 3.5.1. Grazing probability

The higher GP was observed with HMq ≤ 1600 kg DM/ha and HMp ≤ 2590 kg DM/ha. Different thresholds at different scales, implies that cows integrated herbage mass differently at paddock scale and quadrant scale. The HM in those quadrants not optimize the daily intake (Gonçalves et al., 2009b; Carvalho, 2013; Da Trindade et al., 2016). According to those authors, short term intake rate is optimized when HM = 2000 kg DM/ha and height = 12 cm. Therefore, we can assume that cows were not optimizing short term intake rate all the time. While the higher HMp (i.e. higher HA) could mean increase in dead material determining that animals search species in quadrants with higher green mass, regardless total HM (Ring et al., 1985). This means that cows must increase the number of grazed sites to maintain the forage intake (Nabinger et al., 2011). Conversely, higher HMp allows to increase selectivity while the GP decrease (Nabinger et al., 2011). The GP decrease in quadrants with > 1600 kg DM/ha and species with higher LTS (> 0.41). Similar results obtained by Gonçalves et al. (2009a) who found that increasing height, hence HM, the probability of defoliation decreases. Also, Boggiano (1995) found that high LTS reduced animal selectivity, which coincides with our work, where GP decreases. A negative relationship has been reported between bite size and high LTS (Laca et al., 2001), reducing animal intake (Wallau, 2017), which could explain that cows reduced selectivity in those quadrants.

Cows with higher BCS (> 3.8) grazed more proportion of species (0.262) in relation to lower BCS (0.149). This showed that cows with higher BCS, and therefore, better nutritional status, selected a broader diet and explored better the paddock. Murden and Risenhoover (1993) and Mellado et al. (2004) found that the nutritional status affect diet selection. Our results confirm that selectivity depends on the metabolic state, which is well estimate by the BCS, and cows with higher BCS had the ability to obtain a different diet, performing a better spatial exploration.

The GP was higher in species with high HM (> 715 kg DM/ha). Similar values were obtained by Agnusdei and Mazzanti (2001), who found that species selectivity index increased with relative HM, at a decreasing rate at higher relative HM. Furthermore, species with wider leaf were more grazed than thinner leaves: the former have high SLA and low LDMC and LTS, which results in increased nutritive value (Al Haj Khaled et al., 2006). Those species generally have an scape strategy, with fast growth, resulting in species more adapted to grazing (Garnier et al., 2015). The HA did not affect the GP directly, but affect indirectly through structural variables as HMq and HMp, and the proportion of quadrants types were affected by HA (Neves et al., 2009). Species in paddocks with HM ≤ 2590 and quadrants ≤ 1600 were more grazed than species in quadrants with ≤ 1300 but HMp > 2590. That difference in heterogeneity showed that cows avoid poor quadrants in paddocks with high HM. But when HMp was not very different to HMq, the GP increased, showing a lower selectivity.

During winter, HAR played an important role determining at first order the GP (Figure 3). High HAR and high HM of each species determined the higher GP (0.137), since those plants are actively growing while others are dormant and with excess dead material or minimum biomass. As in autumn, cows selected species with high HM (Agnusdei and Mazzanti, 2001), which possibly allowed a greater bite mass. In conditions with low HAR, cows grazed more species in sites farther from shade than species near shade. Díaz Falú et al. (2014) found that distance to shade played a less important role in explaining daily variation in feeding site selection. We hypothesized that cows explored other areas, further from attractive sites, increasing the GP far shade. The low average GP value was observed with low HAR. This is explained by a season effect, which determined low growth rate, and the lower probability of defoliation of individual leaves during their lifespan (Lemaire et al., 2009).

Comparing winter and autumn trees, lower values of GP were observed in winter than autumn. One explanation could be the lower HAR at paddock level.

Abiotic factors affected GP during spring, which in first order were defined by distance to water and second order by distance to shade. In sites further from water (>137 m), LTS defined GP. As in autumn, species with low LTS were more grazed. The criterion of cows to graze or not in these sites was based only in a leaf trait variable which affect bite size and intake rate (Laca et al., 2001). It could be assumed that in those sites there was an increase in dead biomass, as a result of less exploration zone, and species were in late phenological state, thus of lower nutritive value. Conversely in sites near water, cows prioritized quadrants with high specific contribution of each species (Agnusdei and Mazzanti, 2001). But inversely to winter and the affirmation of Lemaire et al. (2009), cows grazed more in sites with low HAR. Possibly in the paddock with low HAR and low HM, cows had to increase GP to maintain the same intake. Although the SD is lower than those exposed by Lemaire et al. (2009), the relationship between SD and GP was the same as showed by these authors, which high SD determines an increase in the probability that one species be defoliated.

Comparing GP between periods, the average value was higher in autumn than winter and spring. Lemaire et al. (2009) showed the same relation for autumn, winter and late spring for other species. In our case, the explanation could be the higher HMp in autumn.

Variables which did not explained GP in autumn, winter and spring were HA, SLA, LDMC, width leaf and PS. Even though decision trees did not show direct effect of HA, this variable determines the specific contribution of quadrants (Neves et al., 2009), HMp (Moojen and Marashin, 2002), HAR (Table 1), BCS (Do Carmo et al., 2016), and leaf traits.

The ID in autumn was related to HMq. When HMq > 3700 kg DM/ha, cows defoliated lightly. These quadrants could be accumulated dead HM determining that cows blunted species, to obtain higher forage quality. Possibly in this case, species were in late phenological state, limiting bite are and bite mass (Laca et al., 2001), allowing to cows just to blunt leaves. In quadrants between 2100-3700 kg DM/ha, cows increased the ID, which mainly species were grazed at 50 % of intensity, similar to values obtained by Lemaire et al. (2009) in different species. Also, species with lower LDMC (≤ 0.43) were grazed more intensity than species with LDMC > 0.43. Even though LTS did not affect the ID in this period, was related to LDMC, explaining the more intensive defoliation in species with low LDMC (≤ 0.43).

The only variable that affected the ID in winter was HMq. Cows defoliated more intense in quadrants with low HM (≤ 1600 kg DM/ha), possibly an adjust their behavior to achieve the same intake rate. Quadrants witch low HM, affect bite depth and bite area, decreasing bite mass (Mezzalira et al., 2017). Considering the number of variables which affected GP and the ID, first ones were higher than ID. In fact, cows modified more the GP rather that the ID. Also, cows did not modify the ID according to leaf traits. In this period, HMp was between 1200-1600 kg DM/ha and occurred the lower HAR (4-8 kg DM/ha/day). A lower vertical and horizontal selectivity occurs, determining that cows prioritized forage quantity, rather forage quality.

During spring, the ID was defined by leaf “quality” traits as LDCM and LTS determines mainly the ID. Species with higher LDCM or lower LDCM but higher LTS were grazed more lightly than species with lower LDCM and LTS. These results were explaining by an inverse relationship between LDCM and leaf digestibility found by Al Haj Khaled et al. (2006), which determines a lightly grazing intensity by cows. Also, species with high LTS (> 1.65 N/mm) were less defoliated (Figure 4) and lightly grazed (Figure 7), showing a rejection by cows. Furthermore, in paddocks with low HAR (≤ 11 kg DM/ha/day) were more grazed (Figure 4) and more intensive (Figure 7). Considering the low HMp

(1091 kg DM/ha), and the lower HAR, cows must increase the GP over the species and the ID to achieved the daily intake.

Factors affecting GP were more than variables affecting ID. The GP were defined by abiotic factors and LTS until second order, while ID was defined by LDMC and LTS, variables related to forage quality (Al Haj Khaled et al., 2006) and facility of apprehensive (Laca et al., 2001). Contrasting to Díaz Falú et al. (2014), who found that vegetation type explained 21 % of feeding site selection, and abiotic factors explained only 13 %, in our study abiotic factors, and mainly distance to shade were the factors affecting GP at first and second order.

## 3.6. CONCLUSIONS

Our study allows to predict which factors will determine the defoliation pattern in heterogeneous grasslands. Cows integrated information of different spatial scales, from pasture characteristics to nutritional status, not following hierarchical decisions. The number and kind of factors affecting GP in each season were different, showing that cows had different foraging strategies, modifying the grazing distribution and selected diet. Cows adjusted grazing intensity according to leaf traits (i.e.: leaf quality) mainly in autumn and spring.

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# 4. DISCUSIÓN GENERAL

La hipótesis acerca de que la probabilidad e intensidad de defoliación sería variable en función de la estación del año y la OF fue confirmada y los factores que determinaron el patrón de defoliación en cada estación del año fueron diferentes. Las vacas integraron la información ambiental, el estado nutricional y las características de la pastura a diferentes escalas y en diferente combinación espacial al momento de la defoliación. A su vez mostraron diferentes estrategias de pastoreo y distribución en la parcela a lo largo de las estaciones, reflejado en una probabilidad de pastoreo variable entre estaciones y grupos funcionales.

La OF no presentó efecto sobre la probabilidad e intensidad de pastoreo, no obstante, indirectamente afectó ambas dimensiones a través de los cambios en la proporción de los distintos parches (Neves et al., 2009; Casalás, 2019), la cantidad de forraje en el potrero y tasa de crecimiento (Moojen y Maraschin, 2002; Do Carmo et al., 2018), CC de las vacas (Do Carmo et al., 2016), y atributos foliares. Estas variables si modificaron la probabilidad e intensidad de pastoreo en todas las estaciones del año.

La probabilidad de pastoreo en otoño de cada GF estuvo asociada a los atributos foliares (incrementos del GF D al A) más que por la contribución de cada GF a la materia seca presente. Las vacas defoliaron la misma proporción de las especies de los grupos A, B y C, independientemente de su contribución, y evitaron defoliar el grupo D, el cual podría estar asociado con inferior valor nutritivo, asociado a un alto CMSF y LTS (Al Haj Khaled et al., 2006). Esto supone una mayor selectividad por los grupos de mayor valor nutritivo y mejor calidad, relacionado a una mayor disponibilidad de forraje, mayor tasa de crecimiento y mayor oferta de forraje. La mayor disponibilidad de forraje estaría explicando una probabilidad de defoliación promedio mayor en otoño, similar a lo encontrado por Lemaire et al. (2009) para otras especies. Esta mayor disponibilidad de forraje en el otoño se explica por el modelo experimental en el cual se realizaron las mediciones (Do Carmo et al., 2016). Una mayor OF en primavera-verano anterior determina una acumulación de forraje hacia el otoño que es utilizado hasta fin de invierno (Do Carmo et al., 2018).

A su vez, las variables que determinaron la probabilidad de defoliación en otoño fueron superiores con respecto a invierno. Las variables estuvieron asociadas a las características de la pastura (masa de forraje y atributos foliares) y a la CC de las vacas. En esta estación las vacas modificaron mayormente la distribución y probabilidad de pastoreo sobre cada GF, pero no modificaron la intensidad de defoliación sobre dichos grupos.

La probabilidad de pastoreo de cada GF en invierno fue diferente solamente entre tratamientos. Si bien la masa de forraje y la oferta no fueron diferentes, posiblemente una diferencia en la estructura de la pastura (Casalás, 2019) y la CC de las vacas determinaron una mayor exploración y selectividad en AOF. Esto explicaría la mayor probabilidad de pastoreo en AOF en relación a BOF. En relación a los GFs fueron pastoreados de forma similar, independientemente del valor nutritivo (asociado a los atributos foliares), especie componente y su contribución especifica. Además, en esta estación las variables que determinaron la probabilidad de visitas estuvieron relacionadas a la cantidad de forraje más que a la calidad del mismo. Esto podría relacionarse con la menor disponibilidad, menor OF, y CC lo cual determina que modifiquen el patrón de defoliación, incrementando la defoliación sobre aquellas especies que le permitan maximizar el consumo, independientemente de la calidad (Coleman et al., 1989). En este caso, las vacas priorizaron el consumo de forraje más que la calidad de la pastura (Sollenberger y Vanzant, 2011). Esto se ve reflejado en el IS de los GFs, donde no se observaron diferencias entre GFs. En promedio, la probabilidad de pastoreo en ambos tratamientos fue menor en relación a otoño, explicado por una menor masa de forraje (Lemaire et al., 2009), tasa de crecimiento y CC de las vacas.

En primavera la masa de forraje fue menor pero la tasa de crecimiento mayor en relación al invierno, asociado a un incremento en la temperatura, lo cual favorece el rebrote de las especies estivales (Berretta, 2001). En este caso las vacas evitaron pastorear esas especies del GF D, posiblemente asociado a su menor calidad (Al Haj Khaled et al., 2006), independientemente de su contribución, determinando el menor IS en este GF. Las variables que determinaron la probabilidad de pastoreo fueron mayores a las que explicaron la intensidad de defoliación. La probabilidad de pastoreo fue definida por factores abióticos y resistencia al corte. En contraste a lo mostrado por Díaz Falú et al. (2014), quien encontró que el tipo de vegetación explica el 21 % de la elección del sitio de alimentación y los factores abióticos explican el 13 %, en nuestro trabajo lo factores abióticos resultaron los principales atributos en explicar la probabilidad de pastoreo. Esto podría reflejar una exploración espacio-temporal diferencial de las vacas, en función de la estación del año y características de la pastura (Bailey y Provenza, 2008). La intensidad de defoliación fue definida por el CMSF y resistencia al corte, variables relacionadas a la calidad de la pastura (Al Haj Khaled et al., 2006) y a la facilidad de aprehensión (Laca et al., 2001). Esto explica porque las vacas realizaron un pastoreo de despunte (poco intenso) en especies con mayor LDMC y LTS.

Dichos resultados, muestran que la probabilidad e intensidad de defoliación fueron variables entre estaciones del año y resultaron modificadas indirectamente por los cambios en la oferta de forraje. Esto confirma que la selectividad y por lo tanto la probabilidad de pastoreo estaría asociada con la prioridad en calidad o cantidad en función de la estación del año y las características de la pastura, nutricionales y ambientales. El hecho de que en invierno las variables explicativas fueran muy pocas se deben a que las vacas priorizarían el consumo de materia seca antes que la calidad de la pastura. Esto podría estar explicado por los cambios en el índice de selectividad de los grupos funcionales, el cual, durante invierno, no se modificó entre OF. Cuando se incrementó la cantidad de forraje y tasa de crecimiento, las vacas presentaron una selectividad superior. Esto les permitiría mejorar la calidad de la dieta y contribuye a explicar que las variables que explicaron la probabilidad de defoliación fueran muchas y a diversas escalas.

Esto contribuye a justificar el modelo conceptual empleado en el diseño del experimento donde la OF se ubicó en niveles de 2.2 y 7.6 kg de materia seca kg peso vivo-1, variable entre estaciones del año. La reducción en la OF de invierno determina un incremento en la utilización de las especies, la cual fue mayor en AOF. Dicha amplitud dietaria se asocia a que las vacas tuvieron una capacidad superior de seleccionar especies de menor valor forrajero. Contrariamente, en otoño, donde se observó la mayor disponibilidad de forraje debido a la acumulación primavero-estival, permite una mayor capacidad de selección, lo cual se acopla con la propuesta del desarrollo del experimento (Do Carmo et al., 2016), en que las vacas alcancen una condición corporal que le permita luego perder un punto y llegar al parto la condición óptima. Indudablemente, las variables más importantes resultaron la disponibilidad promedio y atado a esta variable, la biomasa a nivel de cuadrantes explicando el patrón de defoliación de las especies.

Considerando la probabilidad e intensidad promedio se encontró que los cambios en la OF en los niveles experimentales explicarían que las especies dominantes y de mejor valor forrajero no sean re pastoreadas. Por lo tanto, un aporte importante de este trabajo es plantear la hipótesis que el pastoreo continuo con niveles de OF óptimos para la producción primaria y secundaria, no provocaría sobrepastoreo en las especies más preferidas. Esto se refleja en una utilización variable de las especies a lo largo del año. En algunas estaciones las vacas seleccionan las especies preferidas, mientras que en otras estaciones el pastoreo incremente sobre las especies menos preferidas, logrando un balance entre especies preferidas y no preferidas. Esto determina que no dominen especies de menor valor forrajero por su mayor utilización en alguna estación del año.

# 5. CONCLUSIONES

La estrategia de pastoreo que mostraron las vacas fue variable en función de la OF y la estación del año. Se observó un efecto indirecto de la OF sobre las variables determinantes del patrón de defoliación que mostraron las vacas frente a las especies dominantes de la pastura.

Los factores considerados en el modelo explicaron gran parte de la variacion del patrón de defoliación. Las variables que determinaron la estrategia de pastoreo fueron diferentes en cada estacion del año e interactuaron a diferente escala. Esto demuestra lo complejo que resultan los sitemas pastoriles naturales y el entendimiento de la interacción entre la pastura y el animal debe ser profundamente estudiada, considerando los factores abióticos, las características de la pastura y el nivel interno del animal a diferentes escalas.

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