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ORIGINAL ARTICLE

Contribution of basal and aerial tillers to sward growth in intermittently stocked elephant grass

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Abstract

Elephant grass (*Pennisetum purpureum* Schumach. cv. Napier) is characterized by high dry matter production and a high contribution of aerial tillers to the tiller population. However, grazing management strategies that favor an increase in aerial tillers, such as long regrowth periods, particularly when associated with severe grazing, can result in a decrease in sward growth, as they are subject to a high level of intraclonal competition. We evaluated the contribution of basal and aerial tillers to sward growth in Napier elephant grass to comprehend how strategies of intermittent stocking management interfere with the relative contribution of each tiller class. Treatments corresponded to combinations of two post-grazing heights (35 and 45 cm) and two pre-grazing conditions (95% and maximum canopy light interception during regrowth—$LI_{95\%}$ and LI_{Max}, respectively) and were allocated to experimental units (850 m^2 paddocks) according to a 2 × 2 factorial arrangement in a randomized complete block design with four replicates from January 2011 to April 2012. Basal tillers were the main contributors to sward growth in elephant grass. In this way, although the production of aerial tillers is an important adaptive response of this forage grass species, grazing management strategies that maximize aerial tillering do not result in greater leaf growth or minimize stem growth rates. The frequency of defoliation was the main modulator of plant responses related to light competition, and the higher leaf growth associated with lower stem growth rates were obtained with the $LI_{95\%}$ pre-grazing target. Severe grazing (35 cm) associated with $LI_{95\%}$ is the grazing management strategy recommended to maximize leaf and sward growth rates in Napier elephant grass subjected to rotational stocking.

Introduction

In pastures maintained under intermittent stocking, the light availability is an important modulator of vegetal community responses. The progressive decrease in the quantity and quality of light as leaf area increases over the regrowth process affects leaf and stems growth and tiller survival, with impacts on the sward growth potential and its structure (Pereira *et al.* 2015a,b). Light availability can be regulated through adjustments in the frequency of defoliation. The definition of the frequency of defoliation based on the moment when swards reach 95% of the light interception ($LI_{95\%}$) maximizes the leaf growth in individual tillers and minimizes the senescence rates (Montagner *et al.* 2012) in several tropical grasses. When this sward target is adopted, it is possible to increase the leaf accumulation rates, minimize grazing losses (Carnevalli *et al.* 2006; Silveira *et al.* 2013) and maintain a sward structure that is more favorable to herbage intake (Trindade *et al.* 2007). As a result, higher animal performance (Gimenes *et al.* 2011) and utilization efficiency of the forage produced (Carnevalli *et al.* 2006; Da Silva *et al.* 2009; Difante *et al.* 2009) have been registered relative to the use of a predetermined and fixed number of days for regrowth (Pedreira *et al.* 2007).

The post-grazing conditions are also important and should be defined based on the plant's resistance and adaptation to grazing, since they interfere with how quickly sward leaf area is restored (Da Silva *et al.* 2015). Nascimento Júnior *et al.* (2010) reported that swards of Mombaça guinea grass (*Panicum maximum* Jacq. cv. Mombaça), Andropogon grass (*Andropogon gayanus* Kunth cv. Planaltina) and Xaraés palisade grass (*Brachiaria brizantha* (Hochst. ex A. Rich.) Stapf cv. Xaraés) are able to maintain high herbage accumulation rates within a range of post-grazing heights equivalent to a removal of 40–60% of the pre-grazing height when the pre-grazing target was based on $LI_{95\%}$. In this way, these post-grazing targets are within the limits of grazing resistance and use of plants (Da Silva *et al.* 2015) and ensure favorable conditions for high rates of herbage intake and animal performance (Carvalho *et al.* 2009; Fonseca *et al.* 2012).

Elephant grass (*Pennisetum purpureum* Schumach cv. Napier) is a bunchgrass widely known for its high potential for herbage production (Pereira *et al.* 2014). Despite, the current use of elephant grass under grazing has been avoided due to a significant stem elongation (Hillesheim and Corsi 1990), even during the vegetative growth phase. It has been assumed that aerial tillers have lower potential for stem elongation, which could maximize the sward leaf accumulation and the herbage production (Hillesheim and Corsi 1990). Thus, as a way to control stem elongation under intermittent stocking, Corsi *et al.* (1996) recommended the adoption of grazing strategies that favor aerial tillering, such as long regrowth periods associated to severe grazing.

In fact, this tropical perennial grass has abundant tillering (Pereira *et al.* 2014) and significant participation of aerial tillers (Corsi *et al.* 1996), which can compose up to 85% of the total tiller population in swards maintained under intermittent stocking (Pereira *et al.* 2015b). However, Pereira *et al.* (2015a) noted that aerial tillers are more susceptible to competition for light, particularly when swards are maintained under long regrowth periods. In this condition, a great part of the leaf growth is lost through senescence, and it has been observed that this process is more pronounced in aerial relative to basal tillers (Pereira *et al.* 2014). Besides, in temperate grasses such as *Lolium perenne* L., aerial tillering has a minor participation as a component for the sward herbage accumulation, regardless of the grazing strategies adopted (Korte *et al.* 1987). These results have suggested that an increase in aerial tillering does not necessarily result in higher herbage production.

Thus, the objective of the present experiment was to evaluate the contribution of basal and aerial tillers to sward growth in elephant grass pastures subjected to strategies of intermittent stocking management, defined by combinations between two post-grazing heights (35 and 45 cm) and two pre-grazing conditions. The fraction of the incoming photosynthetically active radiation (PAR) intercepted by the sward canopy was the criterion to define the pre-grazing conditions: $LI_{95\%}$, grazing was performed when swards were intercepting 95% of the incoming PAR (short-grazing intervals); or LI_{Max}, grazing was performed when swards were intercepting the maximum proportion of the incoming PAR (long-grazing intervals).

Materials and methods

The experiment was carried out at College of Agriculture "Luiz de Queiroz" (ESALQ), University of São Paulo, Piracicaba, Brazil (22°430S, 47°250W and 554 m asl), in an elephant grass pasture (*P. purpureum* Schum. cv. Napier) established in 1970 on an Eutric Nitisol. Since its establishment, the area has been intermittently grazed by dairy cows.

The average soil chemical characteristics of the 0–20 cm layer were pH $CaCl_2$ = 5.9, organic matter = 54.9 g dm^{-3}, P (ion-exchange resin extraction method) = 29.43 mg dm^{-3}, Ca = 117.5 mmolc dm^{-3}, Mg = 35.62 mmolc dm^{-3}, K = 3.4 mmolc dm^{-3}, H + Al = 53.93 mmolc dm^{-3}, sum of bases = 148.91 mmolc dm^{-3}, cation exchange capacity = 190.63 mmolc dm^{-3}, and soil base saturation = 82%. The climate is subtropical with dry winters, Cwa according to the Köppen classification. The average annual rainfall is 1328 mm. The average mean air temperatures during the experimental period (January 2011 to April 2012) followed the historical pattern of variation (1917–2012), with lower mean temperatures recorded in June 2011 (16.3°C) and higher mean temperatures recorded in February 2012 (25.7°C). Summer I (i.e., the period from January–March 2011) was characterized by greater rainfall than summer II (January–March 2012). The rainfall began earlier (early spring) relative to the historical average (late spring), with lower precipitation during February and March 2012 (summer II). There were three periods of soil water deficit: in February 2011 (summer I), from July to the beginning of October 2011 (early spring) and from March to mid-April 2012 (late summer II) (Figure 1).

The treatments corresponded to combinations of two post-grazing (post-grazing heights of 35 and 45 cm) and two pre-grazing conditions ($LI_{95\%}$ and maximum canopy light interception during regrowth [LI_{Max}], respectively) and were allocated to experimental units (850 m^2 paddocks) according to a 2 × 2 factorial arrangement and in a complete randomized block design, with four replicates.

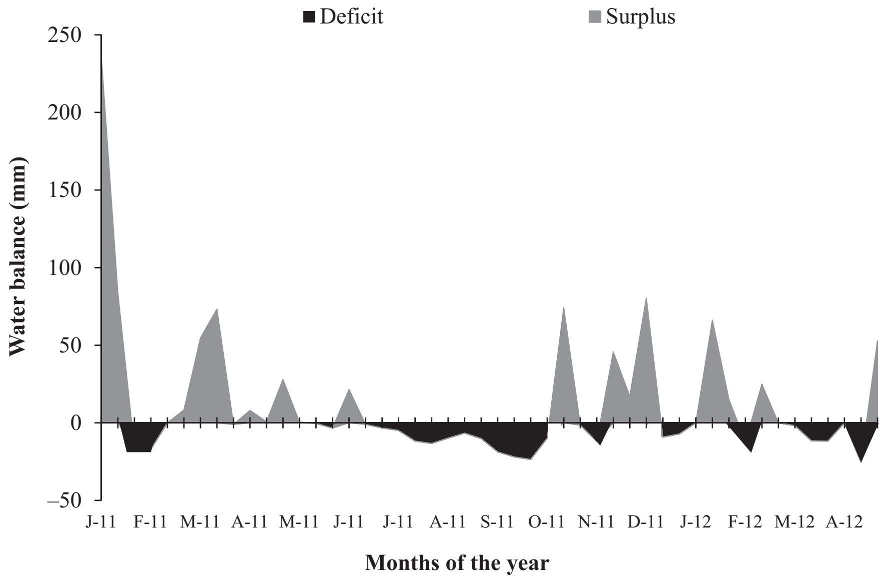

Figure 1 Monthly water balance (mm) from January 2011 to April 2012 in Piracicaba, Brazil. The available water capacity of the soil was assumed to be 50 mm. Black and gray bars represent, respectively, water deficit and surplus.

During the first pasture growing season (January–April 2011), a total of 250 kg N ha^{-1} was applied, with 80 kg ha^{-1} after mowing and 170 kg ha^{-1} in installments during the remainder of the season. During the second pasture growing season (November 2011–March 2012), a total of 300 kg N ha^{-1} was applied in installments throughout the season. Fertilizer applications were performed following grazing using a commercial N:P:K formula (20:0:10). Because the grazing interval was variable (a consequence of the way the experimental treatments were defined), the amount of N applied to each paddock was divided across the grazing cycle and was proportional to the rest period for each paddock, ensuring that all of the paddocks had received the same amount of fertilizer by the end of the experiment.

Canopy light interception was monitored with a LAI 2000 canopy analyzer (LI-COR, Lincoln, USA); measurements were taken on a weekly basis during regrowth until interception reached 90%, when the measurements began to be taken every 2 days to ensure that the $LI_{95\%}$ and LI_{Max} targets were reached precisely. Maximum canopy light interception was attained when the recorded value did not change over two consecutive evaluations and corresponded to an average of 98%. Readings were taken from six random sampling areas per paddock that were representative of the sward condition at the time of sampling (visual assessment of sward herbage mass and height). In each sampling area, one reading was taken above the canopy, and five were acquired at ground level, with a total of six readings above the canopy and 30 at ground level per experimental unit.

Sward height was monitored throughout each regrowth cycle using a meter stick graduated in cm through 80 systematic readings along four transect lines (20 readings per line) in each paddock. Readings of sward height were taken from the ground level using the "leaf horizon" at the top of the sward as a reference, even when the plants were reproductive and produced taller, flowering stems. The post-grazing heights were as planned on the paddocks managed with the target $LI_{95\%}$ but remained above the target for the LI_{Max} condition as a consequence of excessive stem elongation under those conditions. However, the grazing severity was similar for all treatments and corresponded to a removal of 50% of the pre-grazing sward height (detailed information in Pereira *et al.* 2014).

Grazing was performed by dairy cows, both lactating and non-lactating, or dairy heifers, and the number of animals required to finish grazing in 10–12 h (day grazing only) was calculated using the mob stocking method (Gildersleeve *et al.* 1987). The average number of grazing cycles and grazing intervals (days) during the experiment were, respectively, 12.7 ± 1.5 and 23.6 for $LI_{95\%}$/35, 13.5 ± 1.3 and 21.3 for $LI_{95\%}$/45, 8.7 ± 0.5 and 32.4 for LI_{Max}/35 and 9.5 ± 0.6 and 29.4 for LI_{Max}/45.

The tiller population density (TPD) was determined by counting the number of tillers within three 0.75 × 1.25 m metallic frames positioned at points representative of the average sward condition at the time of sampling (visual assessment of herbage mass and height). This procedure was performed at three stages during regrowth: post-grazing, mid regrowth and pre-grazing. During each measurement event, all tillers within the frames were counted, and the data were used to calculate the average TPD values for each regrowth cycle. The counting considered three tiller categories: basal tillers, aerial tillers and decapitated tillers with aerial tillers attached (referred to subsequently as vascular connections; Pereira *et al.* 2014).

Herbage accumulation was calculated based on the results from the evaluations of the morphogenetic and structural characteristics of individual tillers. The measurements were obtained from tillers specifically marked for that purpose. Monitoring was performed throughout the entire regrowth period during all grazing cycles. Six tussocks were chosen per paddock in representative areas of the average sward condition (visual assessment of height and basal area of the tussocks) at the time of the tagging procedure. In each tussock, five tillers were selected (minimum of two basal tillers) and identified using plastic rings (Bircham and Hodgson 1983). Tillers in both the central and peripheral areas of each tussock were selected to represent the average condition of the tussocks (Wan and Sosebee 2000). A total of 30 tillers were marked per paddock, i.e., 120 tillers per treatment. Measurements were taken every 5 days during the seasons with fast plant growth (summers I and II and late spring) and every 7 days during seasons with slow plant growth (autumn, winter and early spring). At the end of each measurement period (i.e., the regrowth cycle), the marked tillers were harvested, and the lengths of the leaf laminae stems were measured separately for the basal and aerial tillers. Leaves were classified as expanding, expanded (mature) or senescing, where “expanding” meant that the ligule was not exposed, in which case lamina length was measured from the ligule of the last expanded leaf, “expanded” meant that the ligule was visible and/or there was no variation in lamina length between two consecutive measurements, and “senescing” meant that part of the lamina showed signs of senescence. Stem length was measured as the distance between ground level for basal tillers, or from the insertion point for aerial tillers, up to the ligule of the last expanded leaf. The morphological components were hand separated and dried in a forced-draught oven at 65°C until they reached a constant mass. After weighing, a conversion factor (CF) between length and weight (g cm^{-1}) was calculated by dividing the total mass of each morphological component (g) by the corresponding total length (cm). Herbage accumulation from each tiller class was calculated based on the variation in length of the leaf laminae and stems throughout the measurement periods. Positive variation in both laminae and stems was used to calculate the rates of leaf and stem elongation, respectively, while negative variation in lamina length was used to calculate the rates of leaf senescence. For each tiller category (basal and aerial), the resulting rates of leaf elongation and senescence per tiller (cm $tiller^{-1}$ day^{-1}) were used to calculate leaf and stem growth rates and the senescence rates (kg ha^{-1} day^{-1}) using the CF generated for each morphological component for basal and aerial tillers (CF of expanding leaves for the calculation of leaf growth, CF of mature leaves for the calculation of senescence, and CF of stems for the calculation of stem growth) and the corresponding average values of TPD (Bircham and Hodgson 1983).

Analysis of variance of the data was performed using the Mixed Procedure of SAS, version 8.2 for Windows. The choice of the covariance matrix was made using the Bayesian information criterion, and the analysis was performed separately for each tiller class considering pre-grazing light interception, post-grazing height, season of the year and their interactions and blocks as fixed effects (Littell *et al.* 1996). Season of the year was treated as a repeated measure. When appropriate, means were calculated using the “LSMEANS” statement, and comparisons were made using “PDIFF”. Significant differences were declared when $P < 0.05$.

Results

Basal tillers

The leaf growth rate in basal tillers (LGR_{basal}) varied with the frequency of defoliation ($P < 0.0001$), post-grazing heights ($P = 0.0144$) and season of the year ($P < 0.0001$). Adoption of $LI_{95\%}$ maximized the leaf growth rates in basal tillers, and the values were 42% higher compared to LI_{Max}. Leaf growth rates were higher in swards subjected to post-grazing heights of 35 cm, and the values were 16% higher than swards grazed down to 45 cm. Seasonal patterns of LGR_{basal} were characterized by higher values during early and late spring, intermediate values in summer I and II, and lower during autumn and winter (Table 1).

Stem growth rates in basal tillers (SGR_{basal}) varied with the frequency of defoliation ($P = 0.0017$) and season of the year ($P < 0.0001$). The sward target of $LI_{95\%}$ resulted in values 34% lower compared with LI_{Max}. The highest values for SGR_{basal} were observed during summer I, early and late spring and summer II, intermediate values were registered during autumn, and the lowest values were recorded during winter (Table 1).

Leaf senescence rates in basal tillers (LSR_{basal}) varied with the season of the year ($P < 0.0001$) and with the interactions between the frequency of defoliation × season of the year ($P = 0.0014$), frequency of defoliation × post-grazing height ($P = 0.0093$) and frequency of defoliation × season of the year × post-grazing height ($P = 0.0339$). During summer I and autumn, the highest values of LSR_{basal} were observed for the post-grazing

Table 1 Leaf and stem growth rates and leaf senescence rates (kg DM ha^{-1} day^{-1}) for basal and aerial tillers (means ± standard error) in Napier elephant grass subjected to strategies of intermittent stocking characterized by the pre-grazing targets of 95% ($LI_{95\%}$) and maximum canopy light interception (LI_{Max}) and the post-grazing heights of 35 and 45 cm from January 2011 to April 2012

	Leaf growth rates		Stem growth rates		Leaf senescence rates	
	Basal	Aerial	Basal	Aerial	Basal	Aerial
Pre-grazing LI targets						
$LI_{95\%}$	112.9 ± 3.47^{A}	63.7 ± 2.44^{A}	44.6 ± 4.42^{B}	20.5 ± 2.05^{B}	37.6 ± 1.37^{A}	47.7 ± 4.67^{B}
LI_{Max}	79.5 ± 3.47^{B}	59.9 ± 2.44^{A}	67.9 ± 4.42^{A}	32.2 ± 1.94^{A}	33.9 ± 1.39^{A}	64.9 ± 4.67^{A}
Post-grazing heights						
35 cm	103.5 ± 3.47^{A}	64.1 ± 2.44^{A}	63.2 ± 4.42^{A}	28.3 ± 2.02^{A}	35.4 ± 1.39^{A}	58.2 ± 4.67^{A}
45 cm	88.9 ± 3.47^{B}	58.8 ± 2.44^{A}	48.9 ± 4.42^{A}	24.4 ± 1.97^{B}	36.2 ± 1.37^{A}	54.4 ± 4.67^{A}
Season of the year						
Summer I	115.9 ± 6.02^{C}	60.9 ± 3.85^{C}	72.8 ± 6.36^{A}	15.2 ± 3.51^{C}	24.8 ± 1.35^{C}	24.7 ± 2.00^{C}
Autumn	12.5 ± 6.02^{F}	30.6 ± 3.14^{D}	30.3 ± 6.36^{B}	48.0 ± 3.37^{A}	79.6 ± 3.73^{A}	209.5 ± 16.79^{A}
Winter	34.4 ± 6.02^{E}	30.7 ± 2.28^{D}	14.5 ± 6.36^{C}	4.4 ± 3.51^{D}	16.3 ± 0.71^{D}	21.9 ± 1.81^{C}
Early Spring	178.8 ± 6.02^{A}	50.5 ± 4.49^{C}	76.0 ± 6.36^{A}	12.8 ± 3.65^{C}	38.7 ± 3.09^{B}	21.7 ± 2.93^{C}
Late Spring	145.9 ± 6.02^{B}	84.0 ± 4.32^{B}	67.7 ± 6.36^{A}	23.2 ± 3.37^{B}	33.5 ± 2.70^{B}	27.0 ± 2.33^{BC}
Summer II	89.8 ± 6.02^{D}	114.0 ± 3.52^{A}	76.4 ± 6.36^{A}	54.5 ± 3.37^{A}	21.9 ± 1.43^{C}	32.8 ± 3.15^{B}

Means followed by the same uppercase letters in columns are not different ($P > 0.05$). DM, dry matter. Summer I corresponds to the period from January–March 2011 and the summer II from January–March 2012.

height of 45 cm when the frequency of defoliation of $LI_{95\%}$ was adopted (Figure 2). There were no differences between post-grazing heights in those seasons of the year for the LI_{Max}. When the pre-grazing targets were compared, differences were observed during autumn for both post-grazing heights, where the LI_{Max} resulted in higher LSR_{basal} when associated with a post-grazing height of 35 cm and $LI_{95\%}$ when the post-grazing height of 45 cm was utilized. There were no differences between the treatments during winter and early spring. For late spring and summer II, higher values were obtained in $LI_{95\%}$ compared with LI_{Max} for both post-grazing heights (Figure 2).

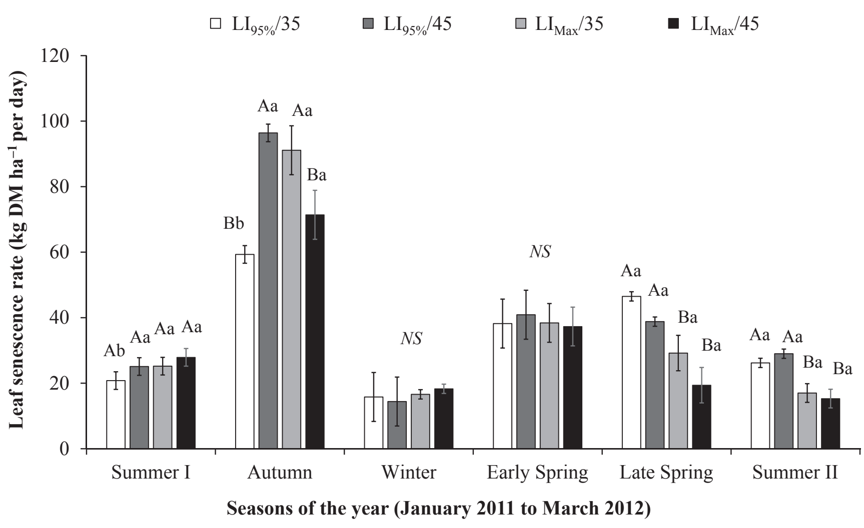

Figure 2 Leaf senescence rates (kg DM ha^{-1} day^{-1}) of basal tillers in Napier elephant grass subjected to strategies of intermittent stocking according to the interaction between pre-grazing targets ($LI_{95\%}$ and LI_{Max}), post-grazing heights (35 and 45 cm) and seasons of the year. $LI_{95\%}$ and LI_{Max} represent, respectively, 95% and maximum canopy light interception. Summer I corresponds to the period from January–March 2011 and the summer II from January–March 2012. For each season of the year, lowercase letters compare post-grazing heights within pre-grazing targets and uppercase letters compare pre-grazing targets within post-grazing heights. *NS* represent non-significant differences. Bars represent the standard error of the mean. DM, dry matter.

Aerial tillers

Leaf growth rates in aerial tillers (LGR_{aerial}) varied with the season of the year ($P < 0.0001$) and with the interactions between the frequency of defoliation × season of the year ($P < 0.0001$) and season of the year × post-grazing height ($P = 0.0253$). Differences between the frequencies of defoliation were observed only during summer I, with higher values for $LI_{95\%}$. The post-grazing height of 35 cm resulted in higher LGR_{aerial} during early spring, and similar values between post-grazing targets were observed for the other seasons of the year (Table 2). The seasonal pattern revealed higher values of LGR_{aerial} during summer II followed by late spring and summer I, and lower values were observed in autumn and winter.

Stem growth rates in aerial tillers (SGR_{aerial}) varied with the frequency of defoliation ($P = 0.0001$), post-grazing height ($P = 0.0282$) and season of the year ($P < 0.0001$) and with the interaction between the frequency of defoliation × season of the year ($P = 0.0012$). The post-grazing height of 35 cm resulted in SGR_{aerial} that were approximately 16% higher than those at 45 cm. Differences between the frequency of defoliation treatments were observed only during summer II and early spring, and higher values were obtained with the LI_{Max} compared to $LI_{95\%}$ (Table 2).

Leaf senescence rates in aerial tillers (LSR_{aerial}) varied with the frequency of defoliation ($P = 0.0014$) and season of the year ($P < 0.0001$). The frequency of defoliation of $LI_{95\%}$ resulted in values approximately 27% lower than for the LI_{Max}. Comparing seasons of the year, the LSR_{aerial} were higher during autumn and summer II and lower during summer I, winter and early spring (Table 1).

Contribution of basal and aerial tillers to the herbage production

The herbage production (HP, ton dry matter [DM] ha^{-1}) varied with the post-grazing height ($P = 0.0033$) and season of the year ($P < 0.0001$). The post-grazing height of 35 cm (18.0 ± 0.52 ton DM ha^{-1}) resulted in higher average HP compared to 45 cm (15.7 ± 0.52 ton DM ha^{-1}). Throughout seasons of the year, the highest HP was registered during summer II (30.1 ± 0.90 ton DM ha^{-1}) followed by summer I (23.8 ± 0.90 ton DM ha^{-1}) and late spring (19.2 ± 0.90 ton DM ha^{-1}), with significant differences between these seasons ($P < 0.05$). The lowest HP was observed during winter (7.5 ± 0.90 ton DM ha^{-1}). The herbage production of basal and aerial tillers varied with an interaction between frequency of defoliation × season of the year ($P = 0.0279$ and $P < 0.0001$ for basal and aerial tillers, respectively). Differences between pre-grazing LI targets regarding the HP of aerial tillers were registered in summer I, when values were approximately 87% higher in $LI_{95\%}$, and during summer II, in which the inverse occurred and the HP of aerial tillers was 28% higher in LI_{Max} (Figure 3). There were non-significant differences between pre-grazing LI targets during autumn, winter, early spring and late spring

Table 2 Rates of leaf and stem growth (means ± standard error) for aerial tillers in Napier elephant grass subjected to strategies of intermittent stocking according to the interactions between pre-grazing light interception (LI) targets vs. season of the year and post-grazing heights (PGH) vs. season of the year

Season of the year (January 2011 to April 2012)	Pre-grazing LI targets		PGH	
	$LI_{95\%}$	LI_{Max}	35 cm	45 cm
Leaf growth rates (kg DM ha^{-1} day^{-1})				
Summer I	80.9 ± 5.44^{Ba}	40.9 ± 5.44^{Cb}	58.0 ± 5.44^{Ca}	63.9 ± 5.44^{Ca}
Autumn	30.0 ± 4.44^{CDa}	31.2 ± 4.44^{Da}	29.2 ± 4.44^{Da}	32.0 ± 4.44^{Da}
Winter	27.9 ± 3.22^{Da}	33.5 ± 3.22^{Da}	34.0 ± 3.22^{Da}	27.4 ± 3.22^{Da}
Early Spring	43.5 ± 6.35^{Ca}	57.5 ± 6.35^{Ca}	63.6 ± 6.35^{Ca}	37.4 ± 6.35^{Db}
Late Spring	86.2 ± 6.10^{Ba}	81.8 ± 6.10^{Ba}	84.2 ± 6.10^{Ba}	83.7 ± 6.10^{Ba}
Summer II	113.6 ± 4.98^{Aa}	114.5 ± 4.98^{Aa}	119.8 ± 4.98^{Aa}	108.2 ± 4.98^{Aa}
Stem growth rates (kg DM ha^{-1} day^{-1})				
Summer I	18.8 ± 5.16^{Ba}	11.7 ± 5.16^{DEa}	16.4 ± 5.16	14.1 ± 5.16
Autumn	41.6 ± 4.76^{Aa}	54.3 ± 4.76^{Ba}	45.1 ± 4.76	50.8 ± 4.76
Winter	3.6 ± 5.16^{Da}	5.2 ± 5.16^{Ea}	6.0 ± 5.16	2.8 ± 5.16
Early Spring	6.1 ± 5.52^{Cb}	19.5 ± 5.52^{Da}	19.7 ± 5.16	5.9 ± 5.16
Late Spring	18.5 ± 4.76^{Ba}	27.9 ± 4.76^{Ca}	22.7 ± 4.76	23.7 ± 4.76
Summer II	34.4 ± 4.76^{Ab}	74.4 ± 4.76^{Aa}	59.9 ± 4.76	48.9 ± 4.76

Means followed by the same uppercase letters in columns and lowercase letters in lines are not different ($P > 0.05$). DM, dry matter. $LI_{95\%}$ and LI_{Max} represent, respectively, 95% and maximum canopy light interception. Summer I corresponds to the period from January–March 2011 and the summer II from January–March 2012.

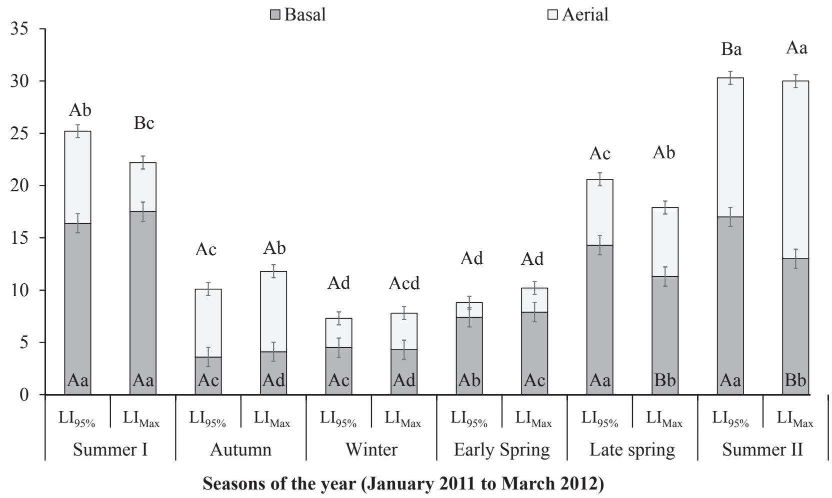

Figure 3 Herbage production (ton DM ha^{-1}) of basal and aerial tillers in Napier elephant grass subjected to strategies of intermittent stocking according to the interaction between pre-grazing light interception (LI) targets ($LI_{95\%}$ and LI_{Max}) *vs* season of the year. $LI_{95\%}$ and LI_{Max} represent, respectively, 95% and maximum canopy light interception. Summer I corresponds to the period from January–March 2011 and the summer II from January–March 2012. For each tiller class, lowercase letters compare seasons of the year within pre-grazing LI targets and uppercase letters compare pre-grazing LI targets within season of the year. Bars represent the standard error of the mean. DM, dry matter.

($P > 0.05$). The HP of basal tillers was higher in $LI_{95\%}$ than LI_{Max} during late spring and summer II, but non-significant differences were observed in the previous seasons. In $LI_{95\%}$, the contribution of basal tillers to the total herbage production corresponded to 65.1, 35.6, 61.6, 84.1, 69.4 and 56.1% during summer I, autumn, winter, early spring, late spring and summer II, respectively. In LI_{Max}, they corresponded to 78.8, 34.7, 55.1, 77.5, 63.1 and 43.3% of the total herbage production during summer I, autumn, winter, early spring, late spring and summer II, respectively.

Discussion

The results of this experiment highlighted the high potential for herbage production of Napier elephant grass under grazing, which produced approximately 75 ton DM ha^{-1} year^{-1}. The pre-grazing targets significantly affected the sward growth rates. Interruption of the regrowth process when 95% of the incoming PAR was intercepted by the sward canopy ($LI_{95\%}$) resulted in higher leaf growth rates in basal tillers associated with lower stem growth rates in both basal and aerial tillers (Table 1).

Despite being postulated by other authors that aerial tillers have lower potential for stem elongation (Hillesheim and Corsi 1990), it is clear that this process is also significant in aerial tillers when targets for grazing management favor situations of light competition within the sward canopy, such as those imposed by long regrowth periods. The stem growth rates increased 52% in basal tillers and 57% in aerial tillers when the LI_{Max} target was used relative to $LI_{95\%}$. Under rotational stocking, as the plant canopy develops, there is a reduction in the red (R):far red (FR) ratio in the available light because FR wavelengths are filtered through or reflected by the vegetation (Morelli and Ruberti 2000). A decrease in the R:FR ratio operates as an accurate indicator of neighbor proximity and triggers shade avoidance responses (Aphalo *et al.* 1999; Morelli and Ruberti 2000). These responses are characterized by morphological changes, including increasing the stem elongation in order to position leaf blades higher in the canopy (Aphalo *et al.* 1999).

In the traditional grazing management strategies adopted for elephant grass swards, the regrowth period has been defined as a fixed and pre-determined number of days, varying from 30 to 45 days (Deresz 2001; Paciullo *et al.* 2003). This practice could play a minor impact to the stem accumulation during periods of slowly sward growth, such as during autumn, winter and early spring. However, for the most part of the growth season (particularly late spring and summer) that duration of the regrowth period is longer than what is adequate for this grass species, since it varied from 21.3 to 23.6 days in swards subjected to $LI_{95\%}$. This explains why traditional management strategies have not been able to control stem elongation in elephant grass, and also indicates that the frequency of defoliation may be used as a modulator of the plant responses related to light competition in both tiller classes, as lower stem elongation rates were observed in $LI_{95\%}$ (Table 1).

In practical terms, light interception is a field criterion not easily measured, since it requires expensive equipment, which are normally not accessible at farm level. In this way, Barbosa *et al.* (2007), Pedreira *et al.* (2007) and Da Silva *et al.* (2009) reported that sward surface height is a reliable parameter for defining pre-grazing conditions, as it has a consistent and high positive association with the values of light interception measured at the field. In Napier elephant grass, the sward surface height that corresponds to $LI_{95\%}$ is approximately 85 cm (Pereira *et al.* 2015b), and it can be used as a field guide to define the ideal time for interrupting the regrowth.

The post-grazing height defines the quantity of residual herbage mass and leaf area contributing to the new regrowth. In general, defoliation severities equivalent to 40–60% removal of the initial (pre-grazing) height are within the limits of grazing resistance and use of tropical perennial grasses and ensure favorable conditions for high rates of herbage accumulation when associated with the right pre-grazing targets (Da Silva *et al.* 2015). Within those ranges for post-grazing heights, severe grazing results in higher levels of herbage utilization efficiency, particularly when the $LI_{95\%}$ target is adopted (Carnevalli *et al.* 2006; Da Silva *et al.* 2009). The post-grazing height of 35 cm increased the rates of leaf growth in basal tillers by approximately 16% (Table 1) and, when associated with the $LI_{95\%}$ target, resulted in the lowest rates of leaf senescence for this tiller class relative to the other treatments during autumn (Figure 2). For aerial tillers, the 35 cm post-grazing height increased the leaf growth rates in early spring by approximately 70%, compared with 45 cm post-grazing height (Table 2), despite similar values being verified during the remaining seasons of the year.

Severe grazing during autumn-winter has also been reported to reduce the pools of dead and senescent material, favoring fast growth during the beginning of the next pasture growing season, in the spring (Montagner *et al.* 2012). Further, the adoption of severe grazing associated with frequent defoliation ($LI_{95\%}$) favors the renewal of the tiller population, since it increases the appearance of new tillers (Montagner *et al.* 2012), which results in a younger tiller profile of the sward population. Young tillers have higher leaf elongation and appearance rates compared with mature or older tillers (Paiva *et al.* 2015), and this likely contributed to the higher leaf growth rates found in this study (Table 1).

Similar to the results of this experiment, Barbosa *et al.* (2007) reported higher herbage accumulation for severe grazing (25 cm) relative to lenient grazing (50 cm) in Tanzania guinea grass (*Panicum maximum* cv. Tanzania). According to the authors, the greater number of grazing cycles observed in swards subjected to lenient grazing did not offset the lower herbage accumulation obtained in each grazing cycle. Thus, the adoption of severe grazing (35 cm) associated with $LI_{95\%}$ can be recommended as grazing management strategy to maximize leaf growth and minimize stem growth rates in Napier elephant grass subjected to rotational stocking.

There was a clear seasonal pattern in the growth rates, regardless of the grazing management strategies adopted. Higher growth rates occurred during late spring and summer, and lower growth potential was verified during autumn, winter and early spring (Table 1 and Figure 3). Besides, the highest senescence rates were registered during autumn, with a disproportional and higher contribution from aerial tillers. Pereira *et al.* (2015b) reported that aerial tillers composed more than 74% of the tiller population in Napier elephant grass during autumn and winter, regardless of the grazing management strategy. This tillering pattern is different to that commonly observed in other tropical grasses (Sbrissia and Da Silva 2008), since the contribution of aerial tillers to the population normally decreases during autumn and winter (Da Silva *et al.* 2009; Silveira *et al.* 2013). The increased participation of aerial tillers during those seasons appears to be linked to the perennation strategy expressed by Napier elephant grass. Matthew *et al.* (2000) described a similar response pattern for tillering in *Phleum pratense*, and indicated that it corresponded to a perennation strategy based on a "reproductive" pathway. This perennation strategy is characterized by an intense tiller population renewal in association with flowering, in which the majority of the new tillers are formed from the base of decapitated flowering tillers. As a result, *Phleum pratense* shows a high tiller mortality associated with flowering (Matthew *et al.* 2000). Elephant grass cv. Napier is considered a short-day plant, with a critical photoperiod between 12 to 15 h per day, a condition reached between April and May (autumn), when plants changed their growth pattern to the reproductive stage. Thus, the higher contribution of aerial tillers to the sward growth (Figure 3) and the higher senescence rates (Table 1) associated to this tiller class during autumn suggests that it exhibits a perennation strategy based on a "reproductive" pathway (Matthew *et al.* 2000), as described for *Phleum pratense*.

During summer II, the contribution of aerial tillers to the total herbage production was higher than basal tillers when the swards subjected to the LI_{Max} target (Figure 3). According to Pereira *et al.* (2014), long regrowth periods favor the decapitation of apical meristems by defoliation, which, in association with greater deposition of senescent and dead material in the central and basal area of the tussocks, seems to enhance the recruitment of tillers from the axillary buds (aerial tillers) instead of those originating from the basal buds (basal tillers). From this point of view, it is clear that aerial tillers are an important component of sward growth in Napier elephant grass. In spite of that, basal tillers were the main contributors to the herbage production in the remaining seasons of the year, particularly when $LI_{95\%}$ was adopted. Thus, the adoption of an adequate frequency of defoliation is crucial to avoid light competition, tiller death and dead material deposition, maximizing basal tillering and increasing leaf growth rates.

Therefore, higher leaf growth associated with lower stem growth rates are obtained when the $LI_{95\%}$ pre-grazing target is adopted. In this condition, basal tillers are the main contributors to sward growth in elephant grass. Although the production of aerial tillers is an important adaptive response of this forage grass species, grazing management strategies that maximize aerial tillering in Napier elephant grass do not result in greater leaf growth rates.

Conclusions

The adoption of severe grazing (35 cm) associated with $LI_{95\%}$ is the grazing management strategy recommended to maximize leaf growth and minimize stem growth rates in Napier elephant grass under rotational stocking.

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