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Canopy structural variations affect the relationship between height and light interception in Guinea Grass

Vitor Hugo Maués Macedo [a], Antônio Marcos Quadros Cunha [a], Ebson Pereira Cândido [b], Felipe Nogueira Domingues [a], Wilton Ladeira da Silva [b,1], Márcio André Stefanelli Lara [c], Aníbal Coutinho do Rêgo [b,*]

[a] Federal University of Pará, Av. dos Universitários, 68746-360, Castanhal, PA, Brazil
[b] Federal Rural University of the Amazon, Av. Tancredo Neves, 2501, 66077-830, Belém, PA, Brazil
[c] Federal University of Lavras, P. O. Box 3037, 37200-900, Lavras, MG, Brazil

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ABSTRACT

The study of canopy structures is essential for the precise management of local forage. Although the relationship between the canopy height (CH) and light interception (LI) allows the best use of forage, there are other characteristics of the canopy that, if not observed, can lead to errors in grazing management. This study analyzes the effect of the defoliation frequencies (DF) and season on the productive and structural characteristics of Guinea grass and defines whether tiller population density (TPD) should be considered in the mathematical models that relate CH to LI. The experimental design used includes randomized blocks with six defoliation frequencies (DF) of 14, 21, 28, 35, 42, and 49 days, over three seasons: rainy season 2015 (RS2015), dry season (DS), and rainy season 2016 (RS2016), in the Amazon biome. Yield characteristics and forage structure were evaluated. The interaction between the DFs and seasons in all evaluated variables included forage accumulation, proportions of stem, leaves and dead material, tiller population density (TPD), CH, LI, and leaf area index. The curve steepness constant (CSC) of the nonlinear models between CH and LI was different from that of the DFs. A DF of 14–28 days averaged a TPD of 616 tillers m^{-2} and CSC of 0.0407, and a DF of 35–49 days averaged a TPD of 496 tillers m^{-2} and CSC of 0.0368. An agreement index (d) of 0.87, a bias of 1.5 %, and a determination coefficient (R^2) of 0.6187 were obtained for the model that estimated a CH with the inclusion of LI and TPD when validated with data from studies published in the literature. TPD associated with CH and LI allowed for more precise management of the ideal defoliation moment.

1. Introduction

The adoption of more precise criteria for the entry and exit of animals in the pasture is the next step to improve utilization the forage produced on commercial farms (Araujo and de, 2018). In the last few decades, the management techniques applied to pastures managed under intermittent stocking have evolved, especially in pastures cultivated with tropical forage species. Light interception (LI) is a very important tool for managing cultivated pastures in monocultures or mixed pastures (Alviarez et al., 2020; Husse et al., 2016). LI has been correlated with many important variables in studies on cultivated forage, such as harvest yield and leaf area index (Husse et al., 2016; Pezzopane et al., 2018). LI as a target for the entry of animals in pastures has been applied in several studies; however, to facilitate the use of the LI technique in farms, defoliation goals have been established based on the canopy height (CH). Thus, it is possible to use CH as a management goal by finding the ideal physiological and structural moment for the grazing event through its association with the LI of the canopy when it reaches 95 % of the

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Abbreviations: CH, canopy height; CSC, curve slope constant; *d*, Willmott's agreement index; DF, defoliation frequencies; DM%, dead material; DS, dry season; FA, forage accumulation; FRP, fixed rest periods; LAI, leaf area index; LB%, leaf blade; LI, light interception; R^2, determination coefficient; RS2015, rainy season 2015; RS2016, rainy season 2016; S%, stem; TFA, total forage accumulation; TPD, tiller population density; %BIAS, percentage of bias; %RMSE, root-mean-square error in percentage.

[*] Corresponding author.
E-mail address: anibal.cr@ufra.edu.br (A.C. Rêgo).

[1] Present address: Federal University of Goiás, Av. Esperança, 74690-900, Goiânia, GO, Brazil.

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incident light; the proposal was initially published by Brougham (1958), and later applied in several studies with tropical forages in Brazil (Alvarenga et al., 2020; Barbosa et al., 2007; Carnevalli et al., 2006; Da Silva et al., 2015; Silva et al., 2019; among others).

Although the relationship between CH and LI has already been established in the literature, for more accurate management, it is important to consider other variables that make up the canopy structure, which may impact the forage accumulation (FA), how the plant intercepts the light incident on the canopy and, consequently, the ideal defoliation height. One of these variables is the tiller population density (TPD), representing the number of tillers per unit area. In addition to other structural characteristics of the canopy, TPD varies between seasons and depends on the grazing management adopted (Lara and Pedreira, 2011a; Santana et al., 2017), directly affecting the LI of the forage canopy. Although many studies have simultaneously evaluated TPD, CH, and LI, the researchers only relate CH to LI and do not consider the nonlinear relationship between these variables. Additionally, they do not include TPD as a covariate (Baldissera et al., 2016; Pedreira et al., 2017), generating estimates that may differ depending on the TDP variation.

Pasture management based only on CH, although widespread and practical, can be a limited goal for precise adjustments and should be viewed with caution, especially in tussock grasses, such as cultivars of the species *Megathyrsus maximus*. Plants with this growth habit need to be well managed to avoid stem elongation, especially in intensive production systems in tropical regions (Hare et al., 2015; Paciullo et al., 2016). Thus, to avoid greater losses of forage production and reduced animal performance, it is important to understand how the accumulation process of plant biomass and the modification of the structural characteristics of plants with an erect growth habit occurs due to variations in management and environmental conditions. Additionally, to understand whether the structural characteristics of the canopy, such as TPD, can affect the relationship between CH and LI in the search for a more careful adjustment in pasture management.

We hypothesized that management actions, such as different defoliation frequencies (DFs) and their interactions with the season, cause changes in the structural characteristics of the canopy and FA. Therefore, we characterize the effect of the combination of DFs and season on the productive and structural characteristics of Guinea grass (*Megathyrsus maximus* (syn, *Panicum maximum*) (Jacq.) B.K.Simon & S.W.L. Jacobs, cv. Tanzânia) and to define whether TPD should be considered in the mathematical models that relate CH to LI.

2. Methodology

2.1. Experimental site and climatic conditions

The experiment was carried out at the research farm of Igarapé-Açu (01°07′21″ S, 47°36′27″ W, 47 m above mean sea level). The climate of the place is tropical rainy type, Am (Alvares et al., 2013), according to the Köeppen-Geiger classification. The photoperiod throughout the year was constant, ranging from 11:55 to 12:05 h a day. During the experimental period, from March 2015 to July 2016, the minimum temperature ranged from 20 to 24 °C and the maximum from 31 to 35 °C, solar radiation ranged from 374–521 W m^{-2}, precipitation varied from 467 mm average for March (2015 and 2016), and 6 mm in October 2015 (Fig. 1). The local soil is classified as yellow latosol or ferralsol (IUSS Working Group W.R.B, 2015) with a sandy loam texture. The chemical analysis in the 0–20 cm layer showed a $pH_{(KCl)}$ of 4.16, organic matter in the proportion of 30.59 g kg^{-1}, phosphorus content of 1.44 mg dm^{-3}, and potassium, calcium, magnesium, and aluminum content of 0.03, 0.74, 0.28 and 0.72 cmolc dm^{-3}, respectively. At the time of the experiment, the soil was corrected by applying 2900 kg ha^{-1} of dolomitic limestone. The limestone was incorporated into the soil on December 15, 2013, with the aid of disc harrows coupled with an agricultural tractor. The amount of lime was calculated to raise the base saturation to 60 % and was spread over the total soil surface in a single dose.

2.2. Implementation of the experiment and experimental design

On March 6, 2014, the grass was sown by hand, with a sowing rate equivalent to 40 pure seeds m^{-2} after tillage. The experimental treatments included six DFs, based on fixed rest periods (FRP), with harvests performed every 14, 21, 28, 35, 42, and 49 days. The area was divided into 30 plots of 12 m^2 (3 m × 4 m) with corridors spaced 1 m apart. The experimental design was a randomized block design with five replicates per treatment. During 2014, the plots were harvested periodically considering the rest period stipulated for each treatment. From May to September 2014, while aiming to stimulate tillering in the initial growth phase, we adopted intense defoliation of the Guinea grass by cutting at 20 cm from the ground (Sbrissia et al., 2010; Silva et al., 2020). The plots were fertilized periodically with 200 kg of N ha^{-1} $year^{-1}$ and 75 kg of K_2O ha^{-1} $year^{-1}$.

The experimental evaluations began in March 2015 and were conducted until July 2016, completing 16 experimental months. The experimental period was separated into three seasons based on rainfall using the pentad climatology methodology (Franchito et al., 2008). The method included determining the beginning and end of the rainy and

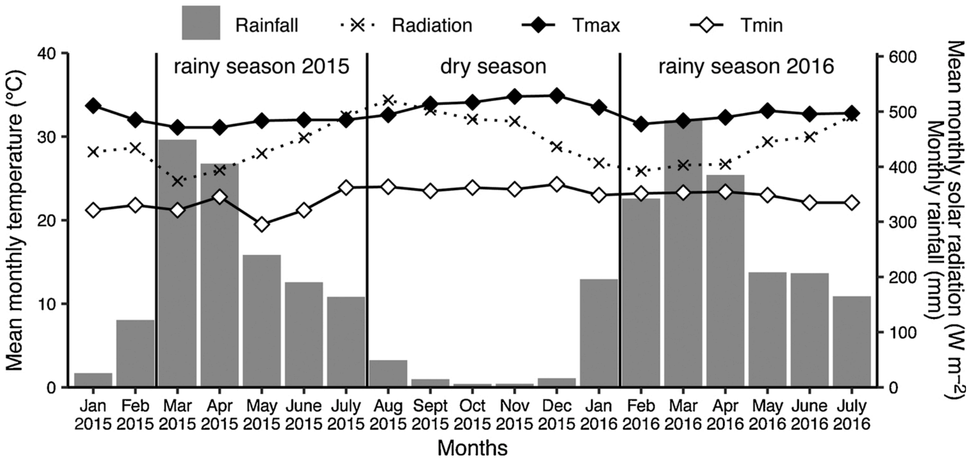

Fig. 1. Rainfall, radiation, and monthly maximum (Tmax) and minimum (Tmin) temperatures from January 2015 to July 2016. Rainfall and temperatures data obtained from the Embrapa Amazônia Oriental weather station in the municipality of Igarapé-Açu, Pará, Brazil. Radiation data obtained from Solcast (2019).

dry periods using formulae that use the relationship between the annual accumulated rain and accumulated rain every five days (pentads). The three seasons were then called the rainy season 2015 (RS2015), from February 20, 2015, to August 9, 2015 (170 days); dry season (DS), from August 10, 2015, to January 26, 2016 (169 days); and rainy season 2016 (RS2016), January 27, 2016, to July 29, 2016 (183 days) (Fig. 1).

The evaluations at the beginning of the experiment were conducted on March 28, 2015, in the RS2015, and on February 13, 2016, based on the period of replacement of the water in the soil because the first rains after the dry season cannot promote the growth of plants immediately. Growth will only occur after soil moisture presents favorable conditions for plant growth. The height of the residue was 35 cm above the ground. At the beginning of each rainy season (RS2015 and RS2016), phosphate fertilization was performed with a dose equivalent to 80 kg of P_2O_5 ha^{-1}, applying simple superphosphate to each plot. During the rainy season, nitrogen fertilizers were applied at the rate of 200 kg of N ha^{-1} $year^{-1}$ in the form of urea (45 % N) and potassium at the rate of 75 kg of K_2O ha^{-1} $year^{-1}$ in the form of potassium chloride (58 % K_2O), distributed in the same proportion among the treatments according to each DF. The plots with 14, 21, 28, 35, 42, and 49 days of FRP received doses equivalent to 17, 25, 34, 42, 51, and 59 kg of N ha^{-1} $cycle^{-1}$, and 7, 10, 14, 17, 20, and 24 kg of K_2O ha^{-1} $cycle^{-1}$, respectively.

2.3. Experimental measurements

The forage contained within a 0.5 m^2 quadrat frame (0.5 × 1.0 m, height of 35 cm) per plot was harvested using a hedge trimmer to quantify the FA. The samples were collected in the average visual condition of the height and mass of the forage canopy, taken from the plot center only to reduce edge effects. The samples were divided into two subsamples. The first subsample was packed in a paper bag and placed in a forced ventilation oven at 55 °C for 72 h for drying to determine the dry matter content and estimate the FA. The second subsample was intended for morphological separation and fractionated in the leaf blade, stem (true stem and leaf sheath), and dead material. After separation, the fractions were packed in paper bags and placed in a forced ventilation oven at 55 °C for 72 h for drying. The weights of these components were used to determine the proportions of the leaf blade (LB %), stem (S%), and dead material (DM%).

The TPD was measured at the end of the regrowth period for each treatment. The total number of live tillers within two 0.5 m^2 quadrats (area of 0.5 × 1.0 m) per plot was counted. The counting site was selected based on the average visual condition of the height and mass of the forage canopy, taken from the plot center to reduce edge effects. The average number of tillers in each sampling rectangle was considered as the average TPD of the plot.

The CH was obtained through an average of five measurements made in each plot, using a rod graduated in centimeters (Barthram, 1986). Likewise, the LI and leaf area index (LAI) of the canopy were obtained through the average of five measurements in each plot immediately before each defoliation, using the canopy analyzer model AccuPAR Linear PAR / LAI (LP-80, Decagon Devices, Pullman, WA, USA). Measurements with the canopy analyzer were carried out between 09:00 and 11:00 in the morning. Through simultaneous measurements with the use of two sensors, one above the canopy and one at ground level, the leaf distribution parameter adopted for a culture was equal to 1.00. During the rainy seasons of 2015 and 2016, both CH and LI were measured every week until the defoliation date of each treatment for the generation of nonlinear models between CH as an independent variable and LI as the dependent variable.

For each experimental unit, the height and LI data were adjusted for the following nonlinear model (Eq. 1):

$$LI = 100 \times [1 - \exp(-\mathrm{CSC} \times CH)] \tag{1}$$

where LI is expressed as a percentage and CH in centimeters, the intercept of the equation is equal to zero because the curve is considered to have begun at the origin (CH =0 cm and LI = 0 %). Parameter 100 is the maximum percentage expected for the LI or asymptote. The CSC parameter is the curve steepness constant of the exponential model that gives rise to the maximum LI value (Archontoulis and Miguez, 2015).

From Eq. 1, isolating the CH variable, we obtain the following mathematical model to estimate the pre-defoliation CH (Eq. 2):

$$CH = \frac{\ln[1 - (LI/100)]}{a \times TPD + b} \tag{2}$$

where LI is the light interception used as a management goal for defoliation, and TPD is the population density of the canopy tillers. *a* and *b* are the angular and intercept coefficients, respectively. They result from the regression analysis between the CSC values as a dependent variable and the TPD of treatments as an independent variable (CSC = a × TPD + b). As we hypothesize that the relationship between CH and LI depends on TPD, canopies with different TPD may have different nonlinear models that relate CH to LI. Showing the difference between the models is achieved by modifying their unique variable parameter, which is CSC. So, we replace the CSC value in the denominator with the expression a × TPD + b (Eq. 2).

2.4. Statistical analysis

As the DFs resulted in varied numbers of harvest cycles per treatment, TPD, CH, LI, and LAI values in each season were calculated by the average of the cycles in each season. The total forage accumulation (TFA) of the experiment was obtained from the sum of the FAs per cycle of each treatment in each season. For the morphological composition, only the cycles where FA occurred during the dry season were used. At the beginning of the RS2016, a uniform cut of the plots was made on February 13, 2016, to restart the plots for the second year of evaluation.

The TFA, LB%, S%, DM%, TPD, CH, LI, and LAI variables were analyzed using the mixed model procedure using the following statistical model (Eq. 3):

$$\mathrm{Y}_{ijk} = \mu + \mathrm{b}_i + \alpha_j + (\mathrm{b}\alpha)_{ij} + \beta_k + (\alpha\beta)_{jk} + \varepsilon_{ijk} \tag{3}$$

where Y is the response variable, μ is the fixed effect of the general mean, b is the random effect of the block; α is the fixed effect of the DFs, (bα) is the random effect associated with the plots that received the α treatment in blocks b, β and (αβ) are the fixed effects of the season and the interaction between the DF and the season, respectively, and ε is the random effect of the error. The seasonal effect was considered a repeated measure, and the Akaike information criterion was used to choose the covariance matrix. The probability of fixed effect factors was tested using the F-statistic. The DFs was adjusted for linear and quadratic effects using orthogonal polynomial contrasts. The comparison of means between the stations was performed using Tukey’s test at the 0.05 probability level.

For each experimental unit, a nonlinear model was generated between CH and LI (Eq. 1). The CSC of each model and its coefficient of determination (R^2) were used as response variables and analyzed by the following statistical model (Eq. 4):

$$Y_{ij} = \mu + b_i + \alpha_j + \varepsilon_{ij} \tag{4}$$

where Y is the response variable, μ is the fixed effect of the general mean, b is the random block effect, α is the fixed effect of the DF, and ε is the random effect of the error. The means were compared using the Scott Knott test at the 0.05 probability level to avoid ambiguities and similar group treatments. The relationship between the CSC values and the DF was also modeled using simple linear regression analysis to obtain the predicted CSC values for each treatment.

Then, a linear regression model was adjusted by the least-squares method with TPD as an independent variable, and the CSC predicted

Table 1
Experimental conditions of the studies that evaluated Guinea grass and were used in the validation process.

Studies evaluating Guinea grass	Experimental conditions of studies						Evaluated treatments
	Latitude	Longitude	Elevation (m)	Köppen climate classification	Soil [a]	Experimental period	
Barbosa et al. (2007)	20°26′42″ S	54°43′22″ W	530	Aw (tropical humid with rainy summers and dry winters)	Ferralsol	May 2003 to May 2004	Combinations of grazing intervals and defoliation intensities
Barbosa et al. (2011)	20°26′42″ S	54°43′22″ W	530	Aw (tropical humid with rainy summers and dry winters)	Ferralsol	May 2003 to May 2004	Combinations of grazing intervals and defoliation intensities
Cutrim Junior et al., (2011)	3°49′17″ S	39°20′07″ W	47	BSh (hot semi-arid)	Fluvisol	October 2005 to March 2006	Combinations of defoliation frequencies and post-grazing residue
Lemos et al. (2014)	21°14′02″ S	48°17′39″ W	601	Aw (tropical humid with rainy summers and dry winters)	Ferralsol	February 2008 to August 2008	Post-grazing residues based on leaf area index
Veras et al. (2020)	5°53′35″ S	35°21′47″ W	11	BSh (hot semi-arid)	Arenosol	September 2016 to April 2017	Performance of *Megathyrsus maximus* cultivars

[a] Soil classification according to IUSS Working Group W.R.B (2015).

for each treatment as a dependent variable. The slope (*a*) and intercept (*b*) of this model were used to form the mathematical model (Eq. 2) and then estimate the pre-grazing CH from the TPD and LI values. The performance of the model (Eq. 2) was verified by comparing the predicted CH data with the data observed in studies published corresponding to Guinea grass, measuring LI, CH, and TPD. We used the work of Barbosa et al. (2007), 2011; Cutrim Junior et al. (2011); Lemos et al. (2014), and Veras et al. (2020). These authors tested different management techniques applied to Guinea grass under different edaphoclimatic conditions (Table 1). However, the same methodologies for measuring CH, LI, and TPD were used in our experiment. We used pre-grazing TPD and CH measurements at LI levels ranging from 85 % to 97 % for Guinea grass from these studies.

Regression analysis was performed between the values observed in the literature and those predicted by the model (Eq. 2). This was done to evaluate the model's precision by calculating the determination coefficient (R^2) and the accuracy using the confidence interval of the model, slope, and the intercept of the equation (Tedeschi, 2006). The performance of the model (Eq. 2) was also verified using Willmott's agreement index (*d*) (Willmott, 1981) by the root-mean-square error in percentage (%RMSE) and by the percentage of bias (%BIAS).

The index *d* ranges from zero to one, where a value of 1 indicates perfect accuracy and 0 indicates no accuracy. The %BIAS has an optimum value equal to zero with low magnitude values indicating good accuracy, positive values indicating overestimation bias, and negative values indicating underestimation bias of the model, obtained from the following formulae:

$$d = 1 - \frac{\sum_{i=1}^{N} (O_i - S_i)^2}{\sum_{i=1}^{N} \left(\left| S_i - \overline{O} \right| + \left| O_i - \overline{O} \right| \right)^2} \tag{5}$$

$$\%\mathrm{RMSE} = \left[\sum_{i=1}^{N} \frac{(S_i - O_i)^2}{\mathrm{N}} \right]^{0.5} \times \frac{100}{\overline{O}} \tag{6}$$

$$\%\mathrm{BIAS} = 100 \times \frac{\sum_{i=1}^{N} (O_i - S_i)}{\sum_{i=1}^{N} O_i} \tag{7}$$

where *Si* is the value simulated by the model (Eq. 2), *Oi* is the observed value, $\overline{O}$ is the average of the observed values, and N is the number of observations.

The data were subjected to analysis in the presence of outliers and normality of residues using the Shapiro-Wilk test. Analysis of the statistical models (Eqs. 3 and 4) and the nonlinear models of the experimental units (Eq. 1) was performed using the MIXED and NLIN procedures of the SAS software (SAS Institute Inc, 2015), respectively. The Scott Knott test, simple linear regression analysis, and calculation of the performance indices (Eqs. 5,6, and 7) of the model (Eq. 2) were performed using R software (R Core Team, 2019).

3. Results

3.1. How does the action of management and water availability affect the structure of the canopy?

Variations in local rainfall allowed the experimental period to be divided into three periods. Two periods encompassed the summer and one of them the winter, represented by rainy and dry seasons (Fig. 1). Most of the cycles occurred in DS. In this season, the number of cycles in which there was no forage accumulation was equal to 9; 6; 4; 3; 2 and 1 cycles, in the DFs of 14; 21; 28; 35; 42, and 49 days, respectively (Fig. 2).

There was an interaction between the DFs and seasons for all variables (TFA ($p < 0.0001$), LB% ($p = 0.0016$), S% ($p < 0.0001$), DM% ($p = 0.0010$), TPD ($p = 0.0045$), CH ($p < 0.0001$), LAI ($p < 0.0001$), and LI ($p < 0.0001$)).

Among the DFs, the TFA of Guinea grass showed linear ($p < 0.007$) and quadratic ($p < 0.0003$) response patterns. There was greater TFA during the RS2015 than RS2016; on average, the TFA was 15,343 kg ha^{-1} in the RS2015 and 11,329 kg ha^{-1} in the RS2016, both larger than in the DS with an average TFA of 2513 kg ha^{-1} (Fig. 3a). The LB% decreased with the reduction of the DF, with linear adjustment in the DS and RS2016 ($p < 0.0001$), and linear ($p < 0.0001$) and quadratic ($p = 0.0006$) adjustments in the RS2015, from approximately 96.3 % for a 14–days DF to 70.3 % for a 49–day DF. The LB% was similar between RS2015 and RS2016, on average 17.7 % higher than in the DS (Fig. 3 b). The S% increased with the lowest DF, with linear ($p < 0.0001$) and quadratic ($p = 0.0001$) adjustments in the RS2015 and linear ($p < 0.0001$) during RS2016. However, there was no linear ($p = 0.2126$) or quadratic ($p = 0.5343$) adjustments during the DS. There was an increase in the difference of the average S% between the RS2015 and RS2016 than the DS after 35 days of regrowth, from 1.8 % for a 14-day DF to 14.7 % for 49 days of regrowth (Fig. 3 c). The DM% increased with reduction in the DF, with linear ($p < 0.0001$) and quadratic ($p = 0.0120$) adjustments in the RS2015 and only linear adjustment in the DS ($p < 0.0001$) and RS2016 ($p < 0.0001$), increasing on average from 7.4 % for a 14-day DF to 19.8 % for a 49-day DF. The DM% was similar between the RS2015 and RS2016, on average 76.0 % lower than in the DS, increasing from 6.5 % to 27.0 % on average (Fig. 3 d).

The TPD of Guinea grass showed a linear response pattern for the RS2015 ($p < 0.0001$) and DS ($p < 0.0001$), with an average of 562.5 tillers m^{-2} for the 14-day DF, decreasing to 393.5 tillers m^{-2} for the 49-day DF. The linear ($p < 0.0001$) and quadratic ($p = 0.0199$) response pattern for the RS2016, decreased from 891 tillers m^{-2} for the 14-day DF

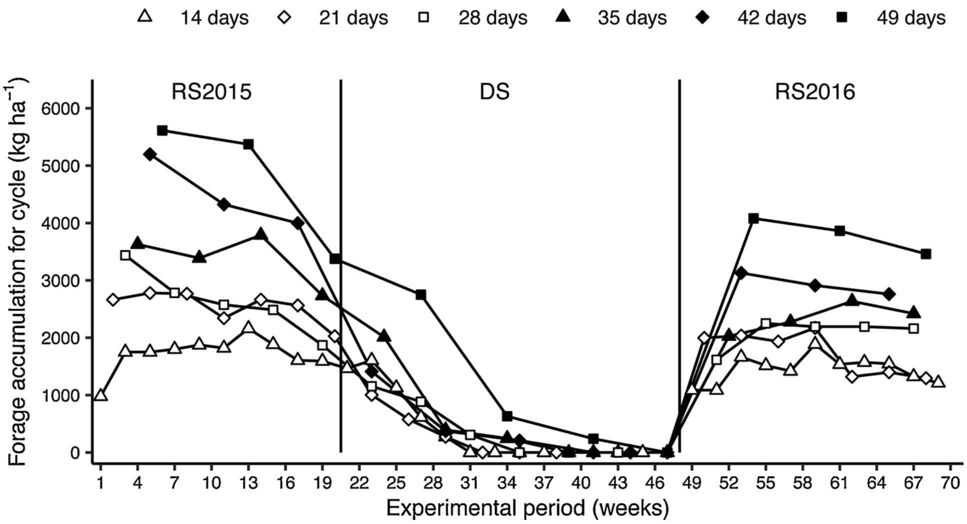

Fig. 2. Forage accumulation (kg ha^{-1}) in each regrowth cycle for each defoliation frequency (days) over the three seasons: Rainy Season 2015 (RS2015), Dry Season (DS), and Rainy Season 2016 (RS2016).

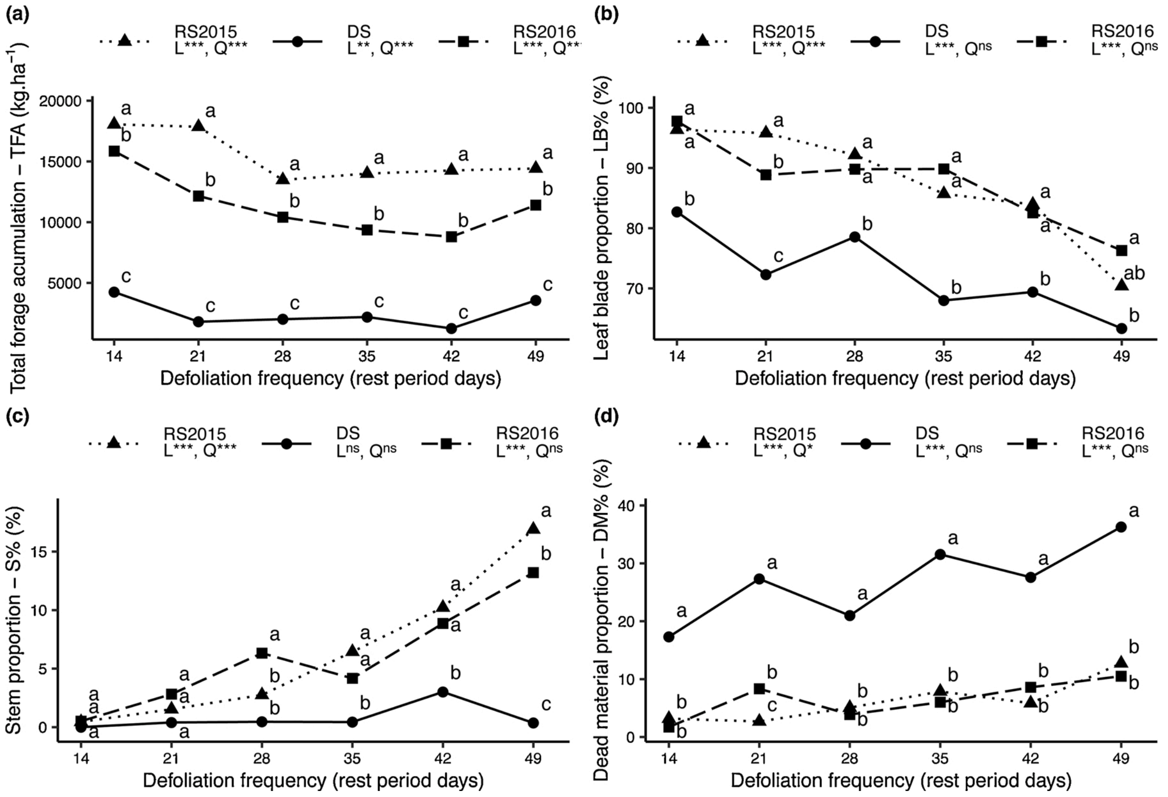

Fig. 3. Total forage accumulation (a), leaf blade proportion (b), stem proportion (c), and dead material proportion (d) of Guinea grass in response to defoliation frequencies (DF) in three seasons: Rainy Season 2015 (RS2015), Dry Season (DS) and Rainy Season 2016 (RS2016). L = linear adjustment of the DF in each station. Q = quadratic adjustment of the DF in each station. *** = $p < 0.001$. ** = $p < 0.01$. * = $p < 0.05$. ns = $p > 0.05$. Points followed by the same letter for stations, do not differ significantly by the Tukey test ($p < 0.05$).

to 560 tillers m^{-2} for the 49day DF. There was no difference in TPD between the DS and the RS2016; both had an average of 227 tillers m^{-2}, less than in the RS2015 (Fig. 4 a). The CH increased with the reduction of the DF, with linear adjustments in the RS2015 ($p < 0.0001$) the DS ($p < 0.0001$), and linear ($p < 0.0001$) and quadratic ($p = 0.0018$) adjustments in the RS2016. The difference in CH between RS2015 and RS2016 was 7.7 cm in the 28-day DF and 17.5 cm in the 49-day DF. The average CH in the RS2015 and RS2016 was 84 cm, and 46 cm in the DS (Fig. 4 b). The LAI in RS2015 increased in a linearly ($p < 0.0001$) and quadratically ($p = 0.0004$), and linearly in the DS ($p = 0.0059$) and RS2016 ($p < 0.0001$), with a reduction in DF (Fig. 4 c).The mean LAI during RS2015 and RS2016 increased at an average of 3.5, in the 14-day FD to 5.6, in the 49-day FD, while in the DS, it only increased from 2.2 to 2.6. LI increased linearly and quadratically in the RS2015 (both $p < 0.0001$) and RS2016 ($p < 0.0001$ and $p = 0.0109$), and presented a quadratic adjustment in the DS ($p = 0.0175$) (Fig. 4 d). In the RS2015, the LI increased from 90.8 % in the 14-day DF to 98.3 % in the 49-day DF, while in the RS2016, it increased from 83.6 % to 97.7 %. In the DS, the LI

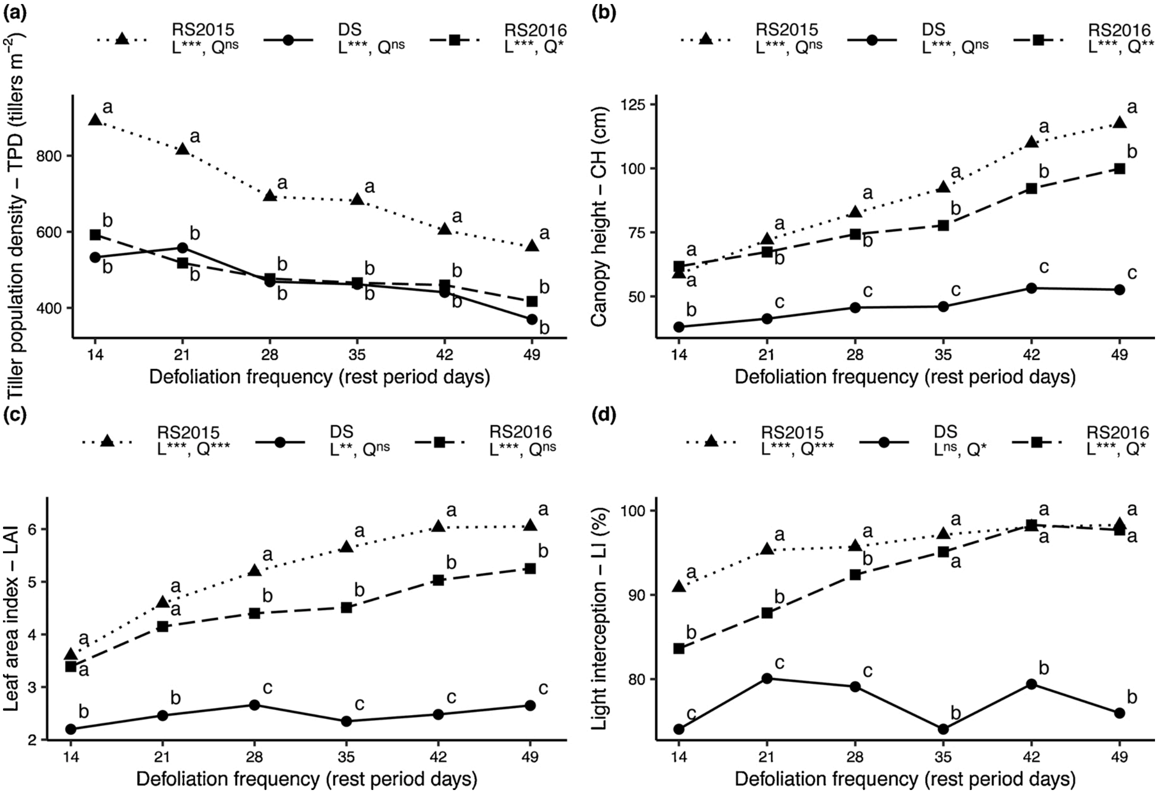

Fig. 4. Tiller population density (a), canopy height (b), leaf area index (c), and light interception (d) of Guinea grass in response to defoliation frequencies (DF) in three seasons: Rainy Season 2015 (RS2015), Dry Season (DS) and Rainy Season 2016 (RS2016). L = linear adjustment of the DF in each station. Q = quadratic adjustment of the DF in each station. *** = $p < 0.001$. ** = $p < 0.01$. * = $p < 0.05$. ns = $p > 0.05$. Points followed by the same letter for stations, do not differ significantly by the Tukey test ($p < 0.05$).

reached a maximum value of 80.1 %, with an average among the DFs of 77.1 % (Fig. 4 d).

3.2. *The precise management of canopy height based on the light interception and tiller population density: the evaluation of an empirical model*

The DFs showed no change with respect to the R^2 value for the adjusted nonlinear models (Eq. 1), and the average of the R^2 value for the nonlinear models between CH and LI of the six DFs was 0.99. There was a difference in the CSC values of the nonlinear models between the DFs ($p = 0.0124$). From the Scott-Knott post hoc test, two groups were defined: the first with rest periods from 14–28 days, with CSC values of -0.0413, -0.0397, and -0.0440 for the DFs of 14, 21, and 28 days, respectively. The second included rest periods of 35–49 days, with CSC values of -0.0374, -0.0376, and -0.0355 for the DFs of 35, 42, and 49 days, respectively (Fig. 5 b). Thus, two CH × LI relationship curves can be generated. The first considers FDs from 14–28 days, with an average CSC value of -0.0407 (Fig. 5 a), and average R^2 value of 0.9990. The second considers FDs from 35–49 days, with an average CSC value of -0.0368 (Fig. 5 a), and average R^2 value of 0.9991.

The CSC values were also adjusted to a linear regression model with

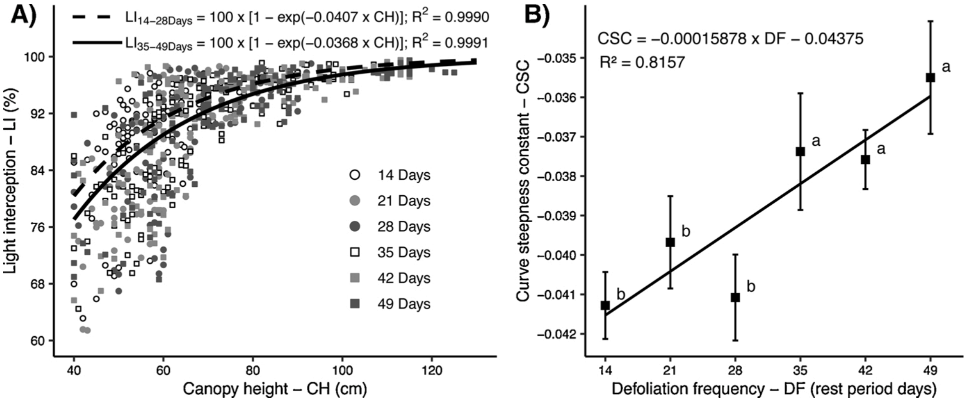

Fig. 5. Nonlinear models between canopy height (CH) and light interception (LI) for defoliation frequencies of 14 to 28 days and 35 to 49 days (a). A linear relationship between the defoliation frequencies (DF) in the rest period and the curve steepness constant (CSC), according to the Scott-Knott test ($p < 0.05$) DFs with the same letter have the same CSC (b).

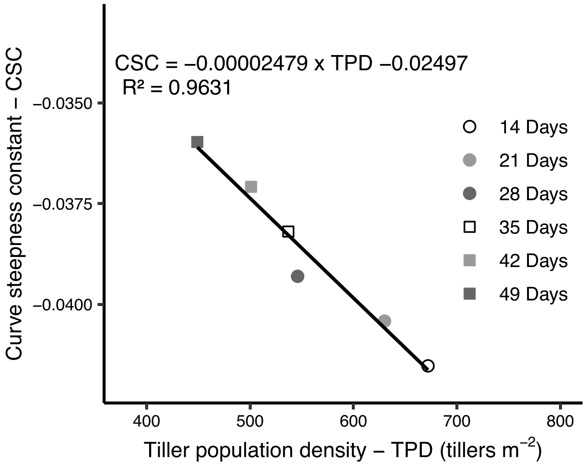

Fig. 6. The relation between the curve steepness constant (CSC) and tiller population density (TPD) for defoliation frequencies.

the DFs (Fig. 5 b). We used the predicted CSC values to relate them to the TPD of each DF (Fig. 6). This relationship was adjusted for a second simple linear regression analysis, such that we obtained an R^2 of 0.925, slope (*a*) of -0.00002479, and an intercept (*b*) equal to -0.02497 (Eq. 2). These parameters were used in conjunction with TPD as the denominator in the model (Eq. 8) to estimate the CH based on the LI and TPD as independent variables:

$$CH = \frac{\ln[1-(LI/100)]}{-0,00002479 \times TPD - 0,02497} \tag{8}$$

In the relationship between the values of CH simulated from the model (Eq. 8) and those observed in the literature (Fig. 7), the angular coefficient of the regression model between the observed and simulated values is within the 95 % confidence interval, between 0.70805 and 1.34434, that is, equal to 1.00 ($p < 0.05$). The intercept value was -0.79095 is statistically equal to zero ($p = 0.9417$). The value of Willmott's agreement index (*d*) (0.87), %RMSE (16 %), and %BIAS (1.5 %) characterize the accuracy of the model. The pre-harvest CHs closest to the CH simulated by the model were those measured by Barbosa et al. (2007) and Barbosa et al. (2011) at 90 % LI during the winter and 95 % LI during the summer and those measured by Cutrim Junior et al. (2011) at 95 % LI.

4. Discussion

The experiment was conducted in the Brazilian Amazon biome, which has important climatic characteristics concerning the generation and use of mathematical prediction models. Beginning with the premise that plant growth occurs based on five variables: photoperiod, solar radiation, temperature, plant nutrition, and water availability, the experimental environment provided homogeneity for almost all variables, except precipitation. As it is close to the equator, the photoperiod is constant, reflecting temperatures that are also constant throughout the year, including dry winters (Pezzopane et al., 2018).

On average, the maximum temperature approached 32 °C with a minimum temperature of 22 °C, satisfying the growth needs of most tropical forage species, far from the lower basal temperature (Tb), approximately 11.7 °C for Guinea grass (Lara and Pedreira, 2011a). The variables controllable by the actions of people, such as making nutrients and water available to plants, were also controlled through fertilization and the differentiation of growth cycles divided by the water availability in the soil. Thus, the location allows plants to express production patterns and changes in the morphological composition of the canopy depending on their management, making the region an excellent option for modeling and grazing management studies.

Even with the delay of the rainy season in 2015 due to El Niño (Jiménez-Muñoz et al., 2016), the rainy period remained constant compared to 2016. The number of regrowth cycles between the two rainy seasons was the same, considering the pentad climatology methodology (Franchito et al., 2008). Our study confirms the hypothesis that the interaction between DF and the season modifies the structure of Guinea grass. In this case, the isolated factor was the lack of water between the seasons (Fig. 1).

The lowest DF allows the highest FA per cycle (Silva et al., 2015). However, the FA per cycle is lower in intervals of shorter defoliation, and the TFA may be similar or even higher in this condition because of the greater number of cycles (Fig. 2). The TFA in the smallest DF is possible due to the naturally occurring elongation of the stem and the accumulation of dead material, which are greater (Figs. 3 c and d, respectively). The high TFA results from greater tillering and tissue renewal at higher frequencies (Lara and Pedreira, 2011b) (Fig. 4 a). This characterizes the quadratic TFA responses observed during each season (Fig. 3 a).

Between seasons, the lack of water was an important factor that resulted in the lower vegetative growth of tillers in the DS, bringing the TFA closer to all the DFs (Fig. 2 and Fig. 3 a). Additionally, the lack of water contributed to reducing the number of tillers per m^2 in all DFs in

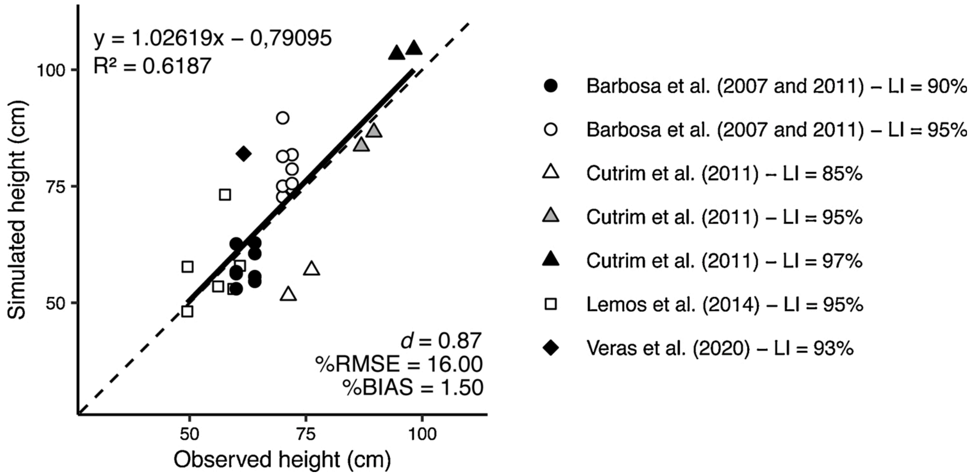

Fig. 7. The relationship between pre-harvest canopy height values observed in the literature and those simulated based on the mathematical model (Eq. 8) that considers light interception (IL) and tiller population density for Guinea grass. R^2 = coefficient of determination, *d* = Willmott's agreement index, %RMSE = root-mean-square error in percentage, %BIAS = percentage of bias.

the DS, remaining stable in the RS2016 (Fig. 4 a). Therefore, there was less TFA in RS2016 than in RS2015 (Fig. 3 a). During the rainy periods, water availability was responsible for the greatest expression of the productive potential of Guinea grass, resulting in the highest FA in RS2015 and RS2016 (Fig. 2).

Changes in DFs resulted in variations in the morphological composition of tillers. With lower DFs, there were fewer LB%, while there was an increase in S% and DM% (Fig. 3 b, c, and d). Although there is an increase in DM% between 14 and 49 days of rest in the rainy seasons, this morphological component increases from 4 % to 9 %. In these same seasons, there was an inversion in the behavior of the leaf and stem fractions. The intraspecific dispute between the tillers for light stimulates the elongation of stems and takes the leaves to the top of the canopy, where light is abundant (Zanine and de, 2018). Furthermore, the phenology related to low defoliation frequency also impacts the increase in the stem fraction. Longer periods between defoliations can allow time for the beginning of the reproductive stage. In that stage, the tillers elongate the true stem, which can impact the increase in the stem fraction (Beecher, 2015) Consequently, a higher S% is observed in the lowest DFs to the detriment of the lowest proportion of LB% (Fig. 3 b and c). An important detail of this change in the morphological components is that even with lower TPD and lower TFA in RS2016, the morphological composition of tillers between rainy seasons has not changed; that is, in RS2016, individual tillers accumulate less biomass but preserve their morphology.

When water is available, the FA includes important botanical components to perform photosynthesis in plants, such as the highest LB% (Fig. 3 b). The DM% represented a large part of the morphological composition of tillers during the DS, with less participation of LB% and S %, because the stress due to the low supply of water decreases the growth process of new tissues, leaving older tissues in the tillers, whose senescence is enhanced by the lack of water (Chapman et al., 2014) (Fig. 3 d). In such situations, there is an inversion of the LB% and DM% fractions (Fig. 3 b and d) because the S% remains stable during the DS due to the slower growth of plants and the stabilization of the LAI (Fig. 4 c).

The elongation of the stem (true stem and leaf sheath) in tussock grasses is one of the main factors for the increase in CH. The favorable conditions and the time for vegetative growth and stem elongation make CH higher in seasons with greater water availability and lower DF (Fig. 4 b). Higher canopies have a higher S% (Fig. 3 c). The greater CH limits the passage of light to the canopy base, preventing the basal tillers from developing and negatively affecting tillering (Santana et al., 2017). Therefore, regardless of the season, the lower the DF, the greater the height of the canopy, and the lower the TPD (Fig. 4 a and b). The decrease in the rate of appearance of new tillers and TPD due to the increase in defoliation height was also observed in other studies on tropical forages, including Guinea grass (Zanine and de, 2013), *Brachiaria decumbens* (Portela et al., 2011), and *Digitaria eriantha* (Sousa and de, 2019).

Another important factor that can increase tillering is the increase in defoliation intensity (Tuñon et al., 2014). Therefore, it was expected that at the beginning of the experimental evaluations, in the RS2015, the TPD would be higher for the RS2016. This is because in the previous year (2014), we used a more severe defoliation intensity for Guinea grass (20 cm residue height), and from the beginning of the current experiment in 2015, we used a 35 cm residue height. The increase in the residue height from 2015 and the mortality of tillers during the DS resulted in a lower TPD during the RS2016, characterizing the TPD stabilization from the second rainy season (Fig. 4 a). The highest TPD and CH were also related to the increase in forage production by area (Duchini et al., 2014; Veras et al., 2020), justifying the higher biomass production in the RS2015 than in the RS2016 in almost all treatments (Fig. 3 a).

As previously mentioned, the amount of leaf blades decreases with an increase in the share of stem and dead material. However, the number and size of leaf blades increased with the rest period, which may have contributed to increased LAI in treatments with lower DF (Giacomini et al., 2009). The increase in LAI in canopies with longer rest periods was accompanied by a decrease in TPD (Fig. 4 c and a) and an increase in the size of individual tillers, characterizing the compensation mechanism of the density and size of tillers (Calsina et al., 2012; Duchini et al., 2014).

With the increase in LAI, LI also increases, a key factor in managing tropical pastures. The LI is registered through readings from ceptometers (Johnson et al., 2010), often not accessible to farmers. Therefore, it is common to relate LI with CH in controlled experiments, making the use of light relationships a more practical and reliable parameter through the assessment of CH (Carnevalli et al., 2006; Pedreira et al., 2017).

Another important detail of this relationship is that in the RS2016, the CH was lower in the smallest DF than in RS2015, resulting in the lower TFA and TPD in the second rainy season. Interestingly, even with differences in the CH of up to 15 cm and the LAI of up to 0.9, in the 49-day DF between the rainy seasons (Fig. 4 b and c), the LI was the same (Fig. 4 d), allowing the angle of the leaves to be responsible for the maintenance of LI, as the morphological structure of the tillers was the same in these seasons (Fig. 3 b, c, and d). Leaf angle is a factor that influences LI in grasses: the more horizontal the leaf arrangement relative to the stem, the greater the leaf angle, and the greater the LI through the leaves (Alviarez et al., 2020; Mantilla-Perez and Fernandez, 2017). Although we have not evaluated the leaf angle in this work, we based our research on the fact that the leaf angle represents one of the characteristics of phenotypic plasticity that grasses present in response to defoliation. Xiliang, (2021) demonstrated that, when palatable grasses (*Leymus chinensis*) are subjected to higher grazing intensities, there is an increase in their leaf angle, which is negatively correlated to plant height. The increase in leaf angle and decrease in size represent a mechanism employed to protect against grazing, changing the orientation of their leaves to a more prostrate position. Therefore, it is important to consider TPD in models that relate CH to LI, as the penetration of light into the canopy depends on the height and other structural characteristics such as TPD, accessible for use on farms. In addition to models based on edaphoclimatic factors, mathematical models that use structural characteristics such as TPD or seedling density are increasingly important for managing forage plants and assisting in predicting forage productivity (Zarza et al., 2020).

The TPD does not need to be measured in all cycles, as the greatest variation occurs between seasons. Once the forage is established, the variations in the canopy TPD occur according to the rest periods. In this way, it is possible to measure the TPD in specific periods of the year, such as once every season of the year, and to estimate the CH that farmers can work. So, if farmers intend to make grazing management more flexible in Guinea grass, the measurement of TPD can help in the decision of the best forage management. This is another way of regulating the CH and LI relationship, which should no longer be fixed at a single height once this ratio depending on TPD and the angle of the leaves. Thus, in order to achieve the best punctual relations between CH and LI at 95 % LI, the management should consider TPD, since not only the number of tillers but also the angle of the leaves affects LI (Lara and Pedreira, 2011b), allowing canopies reach the same 95 % of LI in different CH.

The TPD is the center of the structural characteristics of the forage canopy. Here, the luminous relationships and the CH are linked to it, in addition to changes in the architecture of the plants. Although the structure is similar between seasons and even between the newly formed plots (RS2015) for an established plot (RS2016), the change in the TPD affects the leaf angle, causing the canopies to reach the same LI with different heights and biomasses (Alviarez et al., 2020).

Experiments with tropical grasses generally have production cycles that do not exceed 28 days (4 weeks) as a matter of tradition and due to the fertilization, usually tested for medium to high yields. Accordingly, LI always reaches 95 % before 28 days during the summer. Through less frequent management reaching almost 50 days of rest, the structure of the canopy changes affecting the light relationships in the forage canopy, resulting in the Guinea grass needing two management goals based on light, that is, two estimation curves of LI based on CH (Fig. 5 a).

The difference in the CSC values between treatments allowed us to obtain two models depending on the adopted DFs (Fig. 5 a). The model with a higher DF (from 14–28 days), with a higher TPD, presented a lower mean value of CSC (-0.0407) for the treatments with a lower TPD (-0.0368). The closer to 0 or 100 % of the LI, the smaller the difference between the CH values for the two models (Fig. 5 a). The decrease in CSC values with increasing TPD confirms the need to use nonlinear models with different CSC values depending on the TPD of the canopy. Thus, the model (Eq. 8) seeks to include TPD in deciding process of defoliation CH based on LI.

The model evaluation indices (Eq. 8) used in predicting CH in the pre-harvest condition showed the accuracy of the model for the data observed in the literature (Fig. 7). This reinforces the use of TPD for managing Guinea grass. As an example, at 95 % LI, considered as the ideal time to carry out forage defoliation (Barbosa et al., 2007; Brougham, 1958; Carnevalli et al., 2006; Silva et al., 2019), if the TPD is 600, 880 and 1230 tillers m^{-2}, the Guinea grass CH will be 80.7, 70.1 and 60.1 cm, respectively.

The R^2 value of 0.6187 (Fig. 7) characterizes an inherent variation in the validation process, using data observed from experiments conducted at different times and locations. This shows that although using TPD in the management of pastures is a adequate alternative, empirical models must be conducted with care. Despite their easy application, these models are limited to the conditions in which they are generated. Therefore, they are more prone to errors when used widely (Andrade et al., 2016; Pezzopane et al., 2018). In our case, the model was generated from a database in which the TPD ranged from 283 to 940 tillers m^{-2}.

Finally, according to the factors studied, mainly CH, LI, and TPD, the change in response variables provides sufficient evidence to consider that the CH × LI relationship depends on TPD for adequate management of Guinea grass. Flexibility in management based on the luminous relationships affected by the structural components of the canopies when working in different DFs is feasible for use in commercial farms. Even though it was being carried out under cutting, the results of our experiment served as the basis for the development of a grazing management adjustment technique. This was validated when compared with the results of experiments that used various forms of defoliation, such as cutting (Veras et al., 2020), grazing by cattle (Barbosa et al., 2007, 2011), grazing by sheep (Cutrim Junior et al., 2011), and grazing by goats (Lemos et al., 2014).

5. Conclusions

Variations in the frequency of defoliation and water availability between seasons promote structural and biomass production changes of Guinea grass.

Of the structural characteristics of forage canopies, tiller population density is largely responsible for variations in management goals based on light relationships.

It is possible to harvest the forage produced within precise physiological and structural criteria for intermittent production systems using tiller population density as a tool to regulate the canopy height and light interception relationships.

CRediT authorship contribution statement

Vitor Hugo Maués Macedo: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing - original draft, Writing - review & editing. **Antônio Marcos Quadros Cunha:** Data curation, Investigation, Methodology, Visualization, Writing - review & editing. **Ebson Pereira Cândido:** Funding acquisition, Resources, Supervision, Validation, Writing - original draft, Writing - review & editing. **Felipe Nogueira Domingues:** Supervision, Validation, Visualization, Writing - review & editing. **Wilton Ladeira da Silva:** Supervision, Validation, Visualization, Writing - review & editing. **Márcio André Stefanelli Lara:** Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing. **Aníbal Coutinho do Rêgo:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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