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Nitrogen Fertilization Contributes to the Flexible Use of Defoliation Severity in the Management of Aruana Guinea Grass

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Authors' contributions

This work was carried out in collaboration between all authors. All authors read and approved the final manuscript.

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ABSTRACT

Defoliation severity and nitrogen fertilization trigger physiological and morphological responses in individual plants. The objective of this study was to evaluate the capacity of Aruana guinea grass to respond to severe defoliation and to determine whether nitrogen fertilization interferes with the biomass partitioning and nitrogen concentration of this plant. Cylinders containing plant + soil material were collected on Aruana guinea grass pasture and the experiment was conducted in a greenhouse between November 2012 and March 2013. The treatments consisted of four nitrogen rates (50, 100, 150 and 200 mg dm⁻³) and two defoliation severities (10 and 15 cm heights) in a randomized complete block design, with four replications in a 4 x 2 factorial arrangement. More severe defoliation (10 cm) compared to lenient defoliation (15 cm) seems to induce compensatory growth, since greater biomass accumulation in leaves, a larger leaf area and a higher leaf/stem ratio were observed at the highest nitrogen rate evaluated (200 mg dm⁻³). Aruana guinea grass can be managed using more severe defoliation (10 cm) as long as sufficient nitrogen is supplied to compensate for the greater removal of tissues through morphological and physiological alterations.

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Keywords: Cutting height; *Panicum maximum*; morphological composition; nitrogen concentration; root biomass.

1. INTRODUCTION

Aruana guinea grass (*Panicum maximum* Jacq. cv. Aruana) is widely used in tropical environments as pastures for grazing sheep. According to [1] the pre-grazing sward height recommended for Aruana guinea grass swards is 30 cm, and a post-grazing height of 15 cm compared to 10 cm contributed to greater total and leaf biomass and to reduce presence of weeds, demonstrating limited ability for competition of Aruana guinea grass with increasing grazing severity under nitrogen fertilization of 150 kg N ha⁻¹ as urea.

However, sheep are extremely susceptible to infestation with the larvae of gastrointestinal parasites when kept on tropical pastures. The use of a post-grazing height less than 15 cm is a good alternative since it reduces gastrointestinal larvae in tropical pastures by increasing the penetration of solar radiation to the base of canopy, killing the larvae and controlling their development [2]. This approach can be an alternative to mitigate the incidence of this problem. Within this context, basic studies on the management of Aruana guinea grass focusing on defoliation severity and nitrogen fertilization are important to identify their potential use and management flexibility in order to increase the productivity of sheep grazing tropical grass pastures.

Defoliation has numerous consequences for plant growth and biomass allocation [3,4]. Reduced growth of defoliated grasses due to loss of photosynthetic tissue has been observed in many experiments. However, in some situations defoliation can promote growth through the stimulation of photosynthesis, removing old and dead tissues and altering biomass allocation [5-8]. In some cases, defoliated plants produce more biomass than non-defoliated plants. This phenomenon is called compensatory growth, which varies as a function of the defoliation severity and resource availability for forage grass species [9], particularly plant nutrition. Nitrogen (N) is the most important nutrient that determines the growth dynamics and biomass partitioning of forage grasses [10]. This can be explained by the fact that the main physiological adaptation of plants after cutting or defoliation is the preferential allocation of carbon to the meristems in an attempt to maximize the expansion of the

new leaf area, and these processes depend on adequate nitrogen nutrition [11]. According to [12], the addition of nitrogen can lead to increases in biomass accumulation as a result of the modifications promoted by this nutrient in morphogenic characteristics (leaf appearance rate, leaf elongation rate, and leaf lifetime). Consequently, structural characteristics (tiller population density, number of green leaves per tiller, leaf size, and leaf/stem ratio) that determine the leaf area, are often highly correlated with plant and animal responses on pastures [13].

Therefore, fertility and management are the main factors that influence the composition of species and productivity of the forage canopy [14-16]. However, the characteristics that determine the adaptation of Aruana guinea grass plants and their tolerance to severe defoliation are still uncertain, specifically on a possible relationship between defoliation severity and nitrogen fertilization, provided sufficient nitrogen is supplied to compensate for greater tissues removal through morphological and physiological adjustments, interfering with the growth and biomass partitioning of this plant. Within this context, the objective of the present study was to evaluate the plasticity and adaptation capacity of Aruana guinea grass to severe defoliation, and to determine whether nitrogen fertilization interferes with the growth and biomass partitioning of this plant.

2. MATERIALS AND METHODS

The experiment was conducted in a greenhouse of Instituto de Zootecnia/APTA/SAA, Nova Odessa, São Paulo, Brazil (22°42' S, 47°18' W and 528 m a.s.l.). This study was carried out under controlled conditions to avoid interferences of other nutrients (e.g., transfers of nutrients via animal manure) and ensure an adequate water supply to optimize plant growth. The mean maximum, minimum and average air temperatures during the experiment were 35°C, 22°C and 28,5°C, respectively. The mean air relative humidity was 60%. Soil moisture was maintained at 80% of field capacity. The samples were collected from an Aruana guinea grass pasture established in 2001 and used for sheep grazing in a rotational stocking management. The soil is an Yellow Argisol [17]. The chemical soil analysis (0-20 cm) showed the following results: pH (CaCl₂) = 4.7; organic matter = 20 g

dm⁻³; P (ion-exchange resin extraction method) = 8 mg dm⁻³; K, Ca, Mg, Al = 2.5, 19, 9 and 1 mmolc dm⁻³, respectively; H+Al (potential acidity), sum of bases and cation exchange capacity = 38, 30.8 and 68.8 mmolc dm⁻³, respectively; V (base saturation) = 45%, and m (aluminum saturation) = 4%.

The experiment was conducted between November 2012 and March 2013. Each soil + plant sample were collected with a cylinder (15 cm diameter and 20 cm deep) [18] and transferred to 32 ceramic pots with this same size inside. The pots were randomly assigned to experimental blocks using plant uniformity as a criterion. The treatments consisted of four nitrogen rates (50, 100, 150 and 200 mg dm⁻³) combined with two defoliation severities (cutting heights of 10 and 15 cm) in a randomized complete block design, with four replications in a 4 x 2 factorial arrangement.

Plants had 20 days to acclimatize in the glasshouse before the first cut (performed at 10 and 15 cm heights). Next, a solution containing essential nutrients, except N, was applied (boron: 0.25 mg kg⁻¹ = 5.0 mg H₃BO₃ pot⁻¹; copper: 1 mg kg⁻¹ = 9.4 mg CuCl₂·2H₂O pot⁻¹; zinc: 1.0 mg kg⁻¹ = 7.3 mg ZnCl₂ pot⁻¹; molybdenum: 0.1 mg kg⁻¹ = 0.88 mg Na₂MoO₄·2H₂O pot⁻¹; potassium and phosphorus: 98 mg K pot⁻¹ and 78 mg P pot⁻¹ = 342.4 mg KH₂PO₄ pot⁻¹; sulfur: 70.6 mg pot⁻¹ = 313.3 mg Na₂SO₄ pot⁻¹). The N rates were then supplied in the form of ammonium nitrate (NH₄NO₃) according to the treatments. The subsequent cuts were always performed when the plants had reached 30 cm height. After each cut, the collected material was separated into leaf blades (leaves), stems (stems + sheaths), and dead material. The leaf blade fraction was used to determine the leaf area per pot using an LI-3100 Area Meter (LI-COR, Lincoln, NE, USA). Samples were dried in a forced air oven at 65°C until a constant weight was achieved and then weighed. The results were used to calculate the accumulated biomass of each component after each cut, and these values were summed to obtain the total accumulated biomass per morphological component during the period studied. On the occasion of the last cut, the same procedure as described for the evaluation of accumulated biomass was used to determine the residual biomass (below cutting heights). Shoot biomass represents the sum of the accumulated biomass and residual biomass.

Immediately after the final cut of the shoot, the roots were separated from the soil and washed

under running water and then with deionized water by using sieves with 0.25 mm meshes. For evaluation of root length (cm pot⁻¹), volume (cm³ pot⁻¹), total area (cm² pot⁻¹) and mean diameter (mm), a subsample of the root system (about 20%) was collected after washing. These subsamples were stained with gentian violet and the images were digitized and analyzed with the SAFIRA software (Analysis System for Fibers and Roots). After digitalization, samples were dried in a forced air oven at 65°C until a constant weight was achieved and then weighed. The subsamples mass was used to correct root system length and surface as a function of total root dry mass as described by [19].

After the initial cut, four tillers per pot were chosen randomly to evaluate the number of green leaves per tiller and leaf size. Tillers were monitored twice a week and a new group of tillers was selected after each cutting event. In each tiller selected, the leaves were numbered and classified regarding defoliation as intact or defoliated, and regarding leaf type as growing leaves (no visible ligule), expanded leaves (visible ligule), or senescing leaves (when some portion of the leaf blade had started the process of senescence). The number of green leaves per tiller was obtained from the mean number of growing and expanded leaves per tiller.

Nitrogen concentration was determined (micro-Kjeldahl method [20]) in accumulated leaf and stem biomass and residual leaf biomass from the last cut, and root and stem biomass.

Before being submitted to analysis of variance, the datasets were tested to ensure that the basic assumptions (model activity, independence of errors, normality of the data, and homogeneity of variances) were met. The analyses were performed using the SAS 9.3 statistical package (Statistical Analysis System). The PROC GLM procedure was used for analysis of variance. When no defoliation severity and N rate interaction was observed, the mean defoliation severities were compared by the F test. Polynomial equations were applied to evaluate the effects of N rates using the PROC REG procedure. When the interaction of defoliation severity and N rate was significant, the factors were broken down. Polynomial equations were used to compare the effect of N rate according to defoliation severity, and the F test was used to compare the effect of defoliation severity according to N rate. A 5% level of significance was adopted for analysis of variance. The

correlations between variables were obtained and tested using the PROC CORR procedure.

3. RESULTS AND DISCUSSION

There was a significant interaction between defoliation severity and N rate for accumulated leaf, stem and dead biomass, and residual leaf biomass per pot. Differences in accumulated leaf biomass between defoliation severities were only observed at an N rate of 200 mg dm⁻³, with leaf biomass accumulation being greater for the 10 cm cutting height (Fig. 1a). It was observed greater stem biomass accumulation for the 10 cm cutting height compared to 15 cm at N rates of 100 and 150 mg dm⁻³ (Fig. 1b). Accumulated leaf biomass values increased as a function of N rates ($Y = -0.925 + 0.08695x - R^2 = 0.99$) as well as accumulated stem biomass ($Y = -0.78125 + 0.0198x - R^2 = 0.90$). Differences in accumulated dead biomass between defoliation severities were observed at N rates of 50, 100 and 150 mg dm⁻³, with greater accumulation of dead biomass for the 10 cm cutting height (Fig. 1c). Residual leaf biomass was similar for the two severities only at an N rate of 200 mg/dm³ and higher for the 15 cm cutting height compared to 10 cm at the other N rates studied (Fig. 1d). These responses indicate that plants respond and adapt to defoliation through compensatory photosynthesis or changes in biomass allocation patterns between and within organs [21-23].

There was no significant interaction between defoliation severity and N rate for residual biomass of stems and dead material. However, a significant separate effect of N rates on these components was observed, which increased with increasing N rates ($Y = 4.21875 + 0.01945x - R^2 = 0.93$ and $Y = 7.73125 + 0.03347x - R^2 = 0.99$, for biomass of stems and dead material, respectively). Moreover, defoliation severity exerted a separate effect, with the observation of higher values for both components at the 10 cm cutting height compared to 15 cm (Fig. 1e, Fig. 1f).

There was no significant interaction between defoliation severity and N rate as well as defoliation severity alone for total aerial, root and crown biomass or root/shoot ratio. Significant responses to N rates were observed for total

aerial biomass and root/shoot ratio. Total aerial biomass increased with increasing N rates ($Y = 3.5375 + 0.12817x - R^2 = 0.98$), while the opposite was observed for root/shoot ratio ($Y = 1.16875 - 0.00232x - R^2 = 0.76$). Studying the responses of Aruana guinea grass to different N rates, [24] reported a root/shoot ratio of 1:1 for the lowest N rate, similar to the present results, and that this ratio decreased with increasing N rates as shown in this experiment. The authors therefore suggested preferential allocation of carbon for shoot rather than root formation with increasing N rates, characterizing plasticity in biomass allocation as a function of nitrogen availability. This mechanism has been widely described in the literature as an adaptation used for the survival of N-deficient plants based on the optimal partitioning theory which assumes that plants will try to maximize their growth by allocating biomass to the organ that is responsible for acquiring the most limited resource [25-27]. Thus, plants preferentially allocated biomass to the root due to the possible limitation of N for growth of the aerial part. Similar results have been reported by [28-30] for different plant species.

The interaction of defoliation severity and N rate as well as N rates alone had no effects on root length, volume, area or mean diameter per pot. Significant responses to defoliation severity were only observed for root volume (Fig. 2a) and area (Fig. 2b) per pot. The lower root volume and area per pot at the 10 cm cutting height indicate that the assimilated carbon was mainly allocated to the accumulated leaf biomass of the aerial part, which did not differ between defoliation severities at N rates of 50, 100 and 150 mg dm⁻³ (Fig. 1a). In addition to this fact, lower residual leaf biomass below cutting heights was observed for the 10 cm defoliation height (Fig. 1d). This lower residual leaf biomass probably contributed to the need to use root biomass reserves for the production of aerial biomass, decreasing the root volume and area at the 10 cm cutting height compared to 15 cm. One observation that supports this behavior is the fact that N concentration in crown and root biomass did not vary significantly between the treatments studied, indicating the allocation of carbon for growth of the aerial part, especially at N rates of 50, 100 and 150 mg dm⁻³.

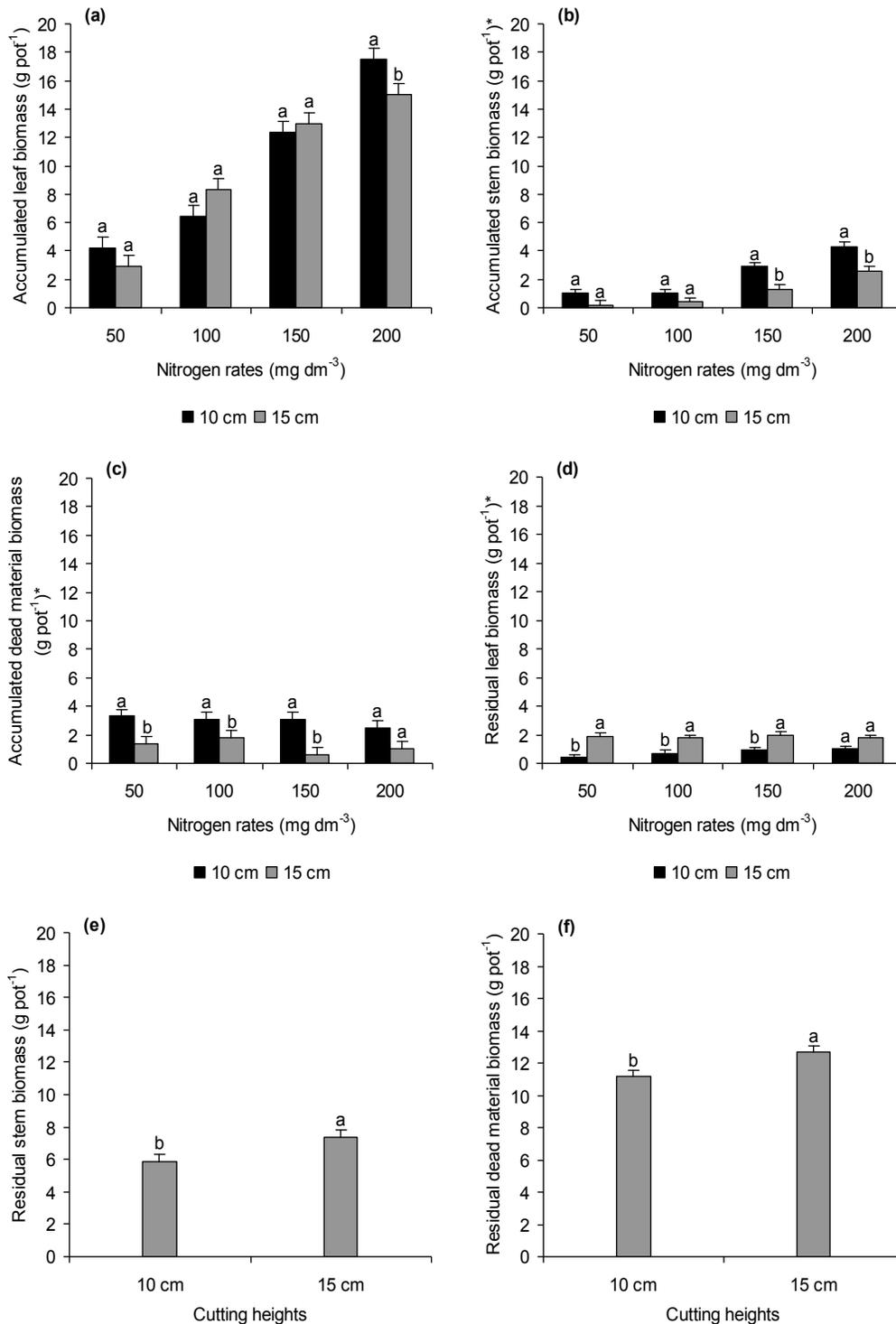


Fig. 1. Accumulated and residual biomass of morphological components in Aruana guinegrass submitted to cutting heights and nitrogen rates

Lower case letters compare cutting heights within nitrogen rates in (a) to (d), and mean of four nitrogen rates in (e) and (f); Vertical bars correspond to standard error of the mean; *Analysis of variance carried out on transformed data (square root)

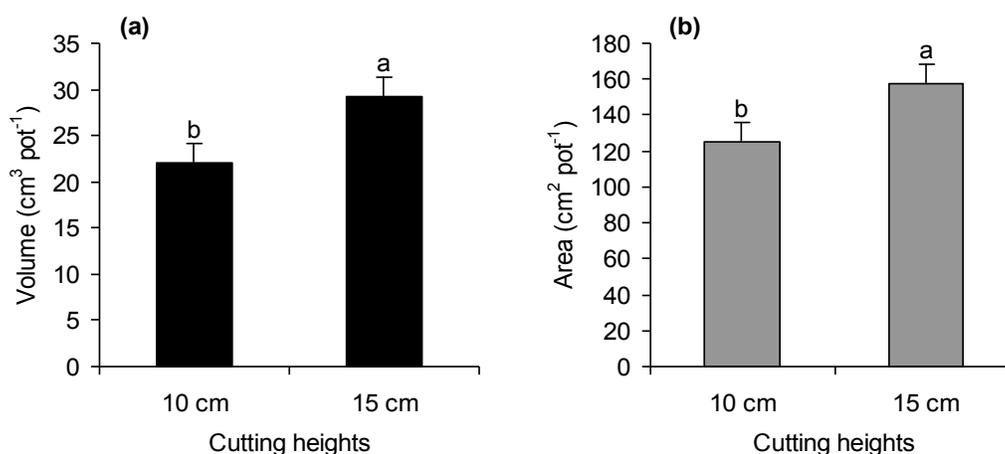


Fig. 2. Volume (a) and total area (b) of the root system per pot in Aruana guinegrass submitted to cutting heights and nitrogen rates

*Lower case letters compare mean of four nitrogen rates
Vertical bars correspond to standard error of the mean*

The variation in leaf/stem ratio was significant for the interaction defoliation severity and N rate. No differences between defoliation severities were only observed at the N rate of 200 mg dm⁻³. At the other rates evaluated, the leaf/stem ratio was higher for the 15 cm cutting height compared to 10 cm (Fig. 3a). Leaf/stem ratio decreased as a function of N rate ($Y = 21.13125 - 0.07755x - R^2 = 0.88$). Tiller population density varied only with N rates, with values increasing as a function of N rate ($Y = 55.375 + 0.2105x - R^2 = 0.86$). This increase in tiller population density with increasing N rates agrees with the reserve meristem hypothesis proposed by [31] as an ecological explanation for the role of apical dominance in plants. According to this hypothesis, sufficient axillary meristems were probably available to promote the rapid growth and establishment of new tillers [32] with the addition of N. There was a significant interaction between defoliation severity and N rate on the number of green leaves per tiller. The number of green leaves for the 10 cm cutting height was higher at a rate of 50 mg dm⁻³ and lower at rates of 150 and 200 mg dm⁻³ (Fig. 3b). A quadratic effect of N rates on the number of green leaves was only detected for the 15 cm cutting height. The maximum number of leaves was observed when 169.6 mg N dm⁻³ was applied ($Y = -0.24375 + 0.004749x - 0.00014x^2 - R^2 = 0.98$). A significant effect of defoliation severity and N rate interaction was observed for accumulated and residual leaf area per pot. Accumulated leaf area per pot was higher for more drastic defoliation severity at 200 mg dm⁻³ N application rate (Fig. 3c), whereas lower values of residual

leaf area were always observed for the 10 cm cutting height at the other N rates (Fig. 3d). Accumulated leaf area per pot increased as a function of N rate for the 10 and 15 cm cutting heights ($Y = -150.54999 + 18.08115x - R^2 = 0.95$ and $Y = -389.44993 + 20.28659x - R^2 = 0.94$, respectively).

Nitrogen concentration in accumulated leaf and stem biomass varied with the interaction defoliation severity and N rate. Analysis of defoliation severity according to N rate showed an effect for the rates of 100 and 150 mg dm⁻³, with N concentration in accumulated leaf biomass being lower for the 10 cm cutting height (Fig. 4a). Nitrogen concentration in accumulated stem biomass was lower for more drastic defoliation at an N rate of 100 mg dm⁻³ and similar for the two severities at the other rates tested (Fig. 4b). Nitrogen concentration in accumulated leaf and stem biomass and in residual leaf biomass increased as a function of N rate ($Y = 0.5712 + 0.00542x - R^2 = 0.97$, $Y = 0.3575 + 0.00199x - R^2 = 0.97$, and $Y = 0.54062 + 0.00237x - R^2 = 0.85$, respectively). The treatments studied had no significant effects on N concentration in crown or root biomass, with values ranging from 0.64 to 0.74 and 0.55 to 0.62 g kg⁻¹, respectively. A significant correlation was observed between N concentration in accumulated leaf biomass ($r^2 = 0.97$), accumulated leaf area ($r^2 = 0.88$) and total aerial biomass ($r^2 = 0.81$), indicating that an increase in N concentration corresponds to an increase in aerial biomass of Aruana guinea grass plants. Other studies [33-35] demonstrated positive

effects of nitrogen fertilization in Aruana guinea grass, describing an increase in dry matter production of the shoot and tiller population density of Aruana guinea grass with increasing N supply.

The isolated effects of nitrogen fertilization shown in this experiment are already known and grounded in the literature. Within this context, the interaction of defoliation severity and N rate had an effect on 11 of the variables studied, demonstrating the importance of studies that address the combination of strategies for defoliation and fertilization management.

At the N rate of 50 mg dm⁻³, the similar accumulated leaf biomass obtained for the different defoliation severities (Fig. 1a) might have been influenced by the larger number of green leaves per tiller (Fig. 3b) and smaller

leaf:stem ratio (Fig. 3a), structural characteristics that probably contributed to the similar accumulated leaf area at the two cutting heights (Fig. 3c). Comparison of defoliation severity at 50 mg dm⁻³ N rate showed no difference for most of the variables studied. This finding agrees with the observation that in environments where the availability of essential resources (e.g., N) is low, plants often share some characteristics that permit efficient preservation of resources, including low growth rates and a high root/shoot ratio [36,37], both observed in the present study. This suggests that these characteristics contribute to increase resistance to stress, permitting plants to keep their shape even when resources are scarce [37,38]. Furthermore, the finding that the N concentration in accumulated leaf biomass was similar for the two cutting heights at an N rate of 50 mg dm⁻³ suggests a strategy of resource preservation.

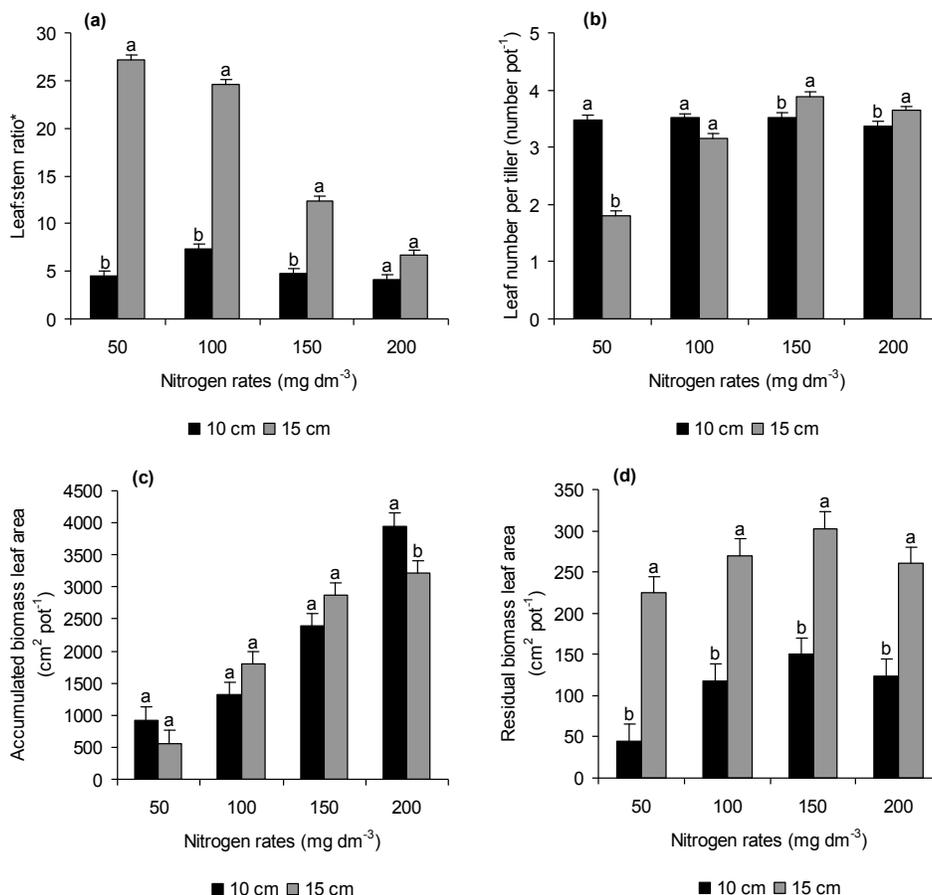


Fig. 3. Leaf:stem ratio (a), leaf number per tiller (b), accumulated biomass leaf area (c) and residual biomass leaf area (d) in Aruana guineagrass submitted to cutting heights and nitrogen rates

Lower case letters compare cutting heights within nitrogen rates; Vertical bars correspond to standard error of the mean; *Analysis of variance carried out on transformed data (log 10)

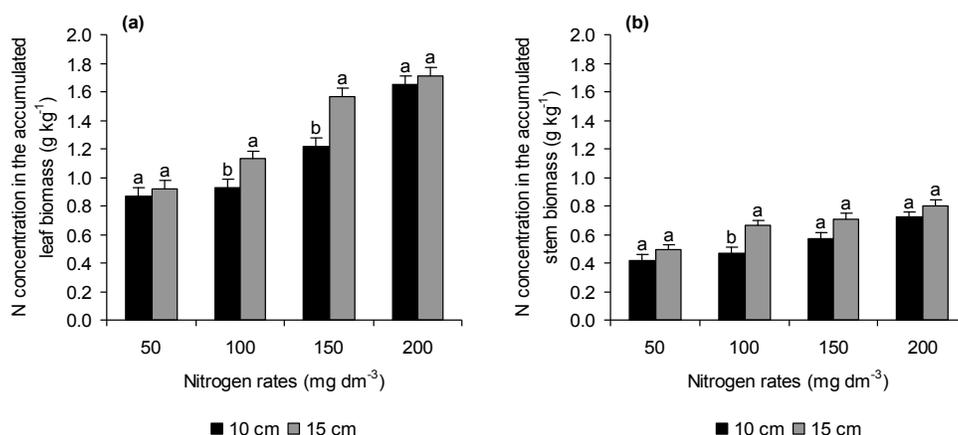


Fig. 4. Nitrogen concentration in the accumulated leaf (a) and stem (b) biomass in Aruana guinegrass submitted to cutting heights and nitrogen rates

Lower case letters compare cutting heights within nitrogen rates

Vertical bars correspond to standard error of the mean

Aruana guinea grass plants allocated 14% more biomass to the leaves (Fig. 1a), with a 19% greater leaf area (Fig. 3c) with more drastic defoliation (10 cm) in relation to lenient defoliation (15 cm) at the higher N rate (200 mg dm⁻³), despite the lower residual leaf area (Fig. 3d). This finding that corroborates the reports of [39,40] that drastic defoliation can lead to considerable loss of leaf area, but this fact does not always result in a proportional reduction in growth since some plant species are able to recover from defoliation due to characteristics that permit them to continue or even to increase their growth after defoliation. Many studies have shown that the productivity of forage grasses is stimulated by grazing/cutting through an increase in the rate of photosynthesis [8,39,41]. Since at the leaf level a strong correlation exists between photosynthesis and N concentration per unit area [42-44], plants managed by severe defoliation, but in the presence of adequate N supply, had N concentrations in accumulated leaf biomass that were similar to those of plants managed by lenient defoliation, but greater biomass accumulation in leaves associated with a greater leaf area. Other experiments also showed that plants can compensate for leaf removal, but only when nitrogen was above the critical level [45]. We can therefore infer that the same occurred with Aruana guinea grass managed by severe defoliation in conjunction with the highest N rate, since a greater leaf area and higher accumulated leaf biomass were observed, supported by the significant correlation ($r^2 = 0.97$) between accumulated leaf biomass and accumulated leaf

area. Within this context, the results indicate that Aruana guinea grass seems to be able to respond with compensatory growth to severe defoliation compared to lenient defoliation as along as adequate N is supplied, since the plants altered their allocation of accumulated and residual biomass in the presence of severe defoliation in conjunction with the highest N rate. Several studies also indicated that plants exhibit compensatory growth when nitrogen is abundant [46,47].

The N rates used in our experiment, in mg N dm⁻³, were calculated to be equivalent to the following N rates applied per hectare: 50, 100, 150 and 200 kg N ha⁻¹. Therefore, the present results agree with those reported by [1] since defoliation at 10 cm height was drastic for Aruana guinea grass when 150 mg N dm⁻³ were used (corresponding to 150 kg N ha⁻¹), with the observation of a lower leaf:stem ratio (Fig. 3a) and lower N concentration in accumulated leaf biomass (Fig. 4a). However, severe defoliation (10 cm) had a positive effect on the growth of Aruana guinea grass since it induced compensatory growth when N supply was high. Therefore, in agreement with the statement of [48], grasses of the genus *Panicum maximum* do not tolerate severe defoliation when soil fertility is low. We may therefore infer that Aruana guinea grass is also tolerant to defoliation due to its phenotypic plasticity and compensatory growth under severe defoliation compared to lenient defoliation as long as N supply is adequate.

4. CONCLUSION

Aruana guinea grass do not tolerate severe defoliation when soil fertility is low. The decrease in N supply reduced the management flexibility of Aruana guinea grass. Severe defoliation (10 cm height) had a positive effect on the growth of Aruana guinea grass when nitrogen nutrition is adequate.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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