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Influence of a Silvopastoral System on Anatomical Aspects and Dry Matter Quality of Mombasa and Marandu Grasses

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Authors' contributions

This work was carried out in collaboration between all authors. Author LBTO designed the study, performed the statistical analysis, wrote the protocol, and wrote the first draft of the manuscript. Author ACS managed the analyses of the study. Authors TBA, JGDS and HMRO managed the literature searches. All authors read and approved the final manuscript.

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ABSTRACT

The goal of this paper was to evaluate the influence of the shading levels in a silvopastoral system on the association of anatomical structures with nutritional parameters and gas production of Poaceae species. Plants of two forage species (*Panicum maximum* cv. Mombasa and *Brachiaria brizantha* cv. Marandu) were exposed to three shading levels (full sun, 25 and 50%). The shading was arranged in contiguous bands, and treatments were allocated in a completely randomized design with four replications. Leaf blades were measured for parenchyma thickness (mesophyll), vascular bundle components (metaxylem and metaphloem), vascular bundle sheath, sclerenchymatic sheath, sclerenchymatic cap, sclerenchymatic extension, and epidermis secondary growth. In addition, measures of NDF and ADF contents, gas production, and dry matter

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degradability at 96 h incubation were also obtained. The results were subjected to t-test at 5% and correlation analysis for each genotype and shading level. The proportion of lignifying tissues such as secondary wall thickening and sclerenchyma was reduced under shading on an average of 66% and 60%, respectively. The proportions of metaphloem in Mombasa and Marandu grasses under the full sun were 5.5% and 3.7%, respectively. However, this response was reversed with shading, reducing the proportion of metaphloem in Mombasa. Gas production in shaded Marandu grasses was higher than was in Mombasa grasses because of the higher proportion of metaphloem. Considering the anatomical traits and gas production for shaded plants, Marandu grass showed the highest dry matter degradability if compared to Mombasa.

Keywords: Brachiaria brizantha; degradability; Panicum maximum; parenchyma.

1. INTRODUCTION

Most plant tissues contain cellulose fibrils in the cell wall [1], ergastic substances and minerals in the cellular content, thus these tissues are considered highly digestible, as well as are phloem cells [2,3].

Other structural elements of the inner leaf anatomy also have essential roles in the plant functioning. Sclerenchyma fibers are responsible for mechanical support functions and structural conformation, so the leaves and stems can stay upright [4]. Due to the structural function, the fibers are composed of rigid compounds with a pronounced thickness in the cell walls. Therefore, the cells of these tissues are largely susceptible to secondary growth and cell death. Cell lignification in sclerenchyma and xylem tissues is a result of pairing between compounds derived from the secondary metabolism and its deposition in these tissues, affecting animal intake variables [5].

Lignin is the major chemical entity responsible for fiber digestibility reductions. Inasmuch as a plant grows, subsidized by optimal production thresholds, some compounds derived from the secondary metabolism begin to interfere with the plant structural aspects. [3] correlated lignin and sclerenchyma cell wall thickening with dry matter digestibility and found a significant negative correlation in the majority of the evaluated tissues [6].

The use of both wall components and cell contents varies with their constitution and degradation potential, which is defined by low degradability constituents [7,8].

At first, cell wall constituents such as cellulose, hemicellulose, and lignin are defined as insoluble compounds; however, a group of compounds from the secondary metabolism of plants such as hydroxynamic acids may also be associated with lignin [8,9] at a varying concentration.

These compounds have an association profile dependent on the genetic ability of each species to express modulating genes involved in the synthesis of secondary metabolism compounds. Thus, insoluble compound degradation may vary as a function of the concentration of phosphocoumarins and ferulic acids associated with lignin [8,9,10].

Gas production has a strong correlation with fiber digestibility and carbohydrate concentration in leaves, being mitigated by changing the concentration of lignified components in fiber [11]. Therefore, fluctuations in environmental variables can result in major changes in plant physiological mechanisms, particularly in secondary metabolism and activation of enzymes responsible for photosynthesis, resulting in increased synthesis of phenolic compounds [12].

Taking into account climatic variations, shaded plants tend to synthesize and incorporate a lesser amount of lignin [12], which encrusts the cellulose of the cell wall and may impregnate sclerenchymatic tissues and metaxylem fibers. On the other hand, higher luminosity is directly proportional to the synthesis of lignin and lactones. In addition, a higher proportion of sclerenchymatic tissue and metaxylem can reduce dry matter degradability and gas production, increasing the retention time in the rumen and thus affecting animal consumption [7,13].

The goal of this paper was to evaluate the responses of two *Poaceae* species to different shading levels on the association of anatomical structures with nutritional parameters and gas production.

2. MATERIALS AND METHODS

The experiment was conducted at the School of Veterinary Medicine and Animal Science (SVMAS), Federal University of Tocantins, in a silvopastoral system set in a native thinned forest on a flat terrain (2% slope). According to Köppen system, the climate is classified as Aw (hot and humid), with rains from October to May and annual averages of 1800 mm rainfall and 28℃ temperature. The soil was classified as Quartzipsamment soil (Entisols), in which was performed a chemical characterization using samples taken at 0-20 cm depth (Table 1).

The experiment was implanted under natural shading of plant rows in Cerrado-Amazon transition zone enriched with two forage species. The experimental design was completely randomized with four replications. Treatments were arranged in a 2x3 factorial scheme - two forage species [*Urochloa brizantha* cv. Marandu (syn. *Brachiaria brizantha*) and *Panicum maximum* cv. Mombasa] and three shading levels (0, 25, and 50%), totaling 24 experimental units.

The forest was thinned in October 2009, aiming to achieve the shading levels of 0, 25, and 50% light transmission to the environment, being rechecked once more in June 2012, with the aid of a luximeter.

Afterwards, in October 2013, 800 kg lime, 45 kg P_2O_5, and 50 kg K_2O were applied per hectare. Then, the forage species were sown and, when pasture was established, they were uniformly mowed to 20 cm with a shoulder type lawn mower. After that, the time for the appearance of 3 and 4.5 leaves per tiller was waited for Mombasa and Marandu grasses respectively. Later, animals were released into the paddocks (2,250 m²). Three days after the removal of animals from paddocks, nitrogen fertilization was again performed at a rate of 40 kg N ha^{-1}.

2.1 Anatomical Analysis

Prior to grazing, forage material at the seventh vegetative cycle was harvested, and the last fully expanded leaves were selected for histological sections. During the harvesting, the leaves intended for anatomical analyses were placed immediately into a thermal box at 12º C, as a way to conserve the main components of vegetative organs.

Once collected, the material was sent to the laboratory of Biochemical and Morphology Analyses of SVMAS. Portions of about 1 cm² were removed from the middle third of leaves, being then dehydrated in absolute alcohol I and II at 70, 75, 80, 85, and 90%, and then in absolute alcohol-xylene mixture for clarification (each run lasted 30 minutes). Subsequently, the fractions were further clarified with xylene I and II (dimethylbenzene) and fixed with 5:5:90 solution [14] (40% formaldehyde, 50% ethanol, and pure glacial acetic acid). The fragments were embedded in paraffin, and 5-µm cross sections were generated using a microtome. Hereafter, these sections were attached to glass slides and stained with toluidine blue.

These sections were measured for the thicknesses of parenchyma tissue (mesophyll), vascular bundle components (metaxylem and metaphloem), vascular bundle sheath, sclerenchymatic sheath, sclerenchymatous cap, sclerenchymatous extension, and secondary growth of the epidermis (Fig. 1). Tissue thickness was determined using light microscopy and Motic Plus 2.0 software.

Table 1. Chemical soil characterization at the beginning of the experiment, preceding the first cycle

	pH	Ca^{2+}	Mg^{2+}	Al^{3+}	H+Al	K^{+}	P	MO	CTC	V
	CaCl2	$cmol_c dm^{-3}$					$mg dm^{-3}$		$cmol_c dm^{-3}$	%
BSP	4.78	0.67	0.59	0.66	2.26	0.012	2.92	5.62	3.54	36.18
B25	3.76	0.76	0.54	0.58	4.57	0.016	3.15	13.68	5.90	22.50
B50	3.84	0.61	0.59	1.17	5.61	0.016	2.79	14.05	6.83	17.83
MSP	4.57	0.86	0.57	0.42	4.64	0.009	2.80	8.04	6.08	23.70
M25	4.17	1.13	0.90	0.74	5.22	0.017	2.79	11.73	7.27	28.17
M50	3.97	0.78	0.78	1.10	4.76	0.013	3.13	12.51	6.35	24.95

Soil analysis at 0-20 cm depth in Quartzipsamment soil. BFS: Marandu Full Sun; B25: Marandu 25% shade; B50: Marandu 50% shade; MFS: Mombasa Full Sun; M25: Mombasa 25% shade; M50: Mombasa 50% shade.

2.2 Gas Production and Dry Matter Degradability

In the seventh cycle, samples simulating grazing were taken, considering a 50% efficiency (sampled from 3 expanded leaves for Mombasa and 4.5 for Marandu). They were then led to a forced ventilation oven at 55℃, where dried for 72 hours. After, they were ground in a Willey mill and 2-mm sieve.

About 0.2 grams of ground samples were added into sealed Ankom bags, which were sent to fermentation tubes and received rumen fluid from a cannulated animal kept grazing Marandu grass for 15 days. Around 1 L of inoculum was placed in a preheated vacuum bottle at 39ºC. Immediately after collection, the inoculum was sent to the laboratory where it was filtered. Of this liquid fraction, 10 mL was added to the sample + bag and then added to 20 mL culture medium in a tube sealed with vaseline.

As soon as incubation started, gas production was measured at 0, 3, 6, 9, 12, 24, 48, 72, and 96 hours, with the aid of graduated scale. The model by [15] was fitted to the data, as expressed below:

$$Y = A \{1 - \exp^{[-b(t-L) - c \times (\sqrt{t} - \sqrt{L})]}\}$$

The parameters regarding gas production kinetics are cumulative gas production (mL), incubation time "t" (hours), total gas "A" (mL), lag time "T" (hours), and fractional degradation rate "μ" (h^{-1}). The equations generated were compared using parallelism and curve identity tests according to [16].

At 96-hour incubation, effective degradability was obtained using the method of [15], as follows:

$$EF = S_0 e^{-kT} (1 - kI)/ (S_0 + U_0)$$

In which:

EF = Effective degradability
k = passage rate; calculated for k=0.02; 0.03; 0.04 e 0.05.
S_0 e U_0= initially fermentable fractions and non-fermentable fractions, respectively, as follows:

$$I = \int_{\infty} \exp -[(b + k)(t - T) + c(t - T)]dt.$$

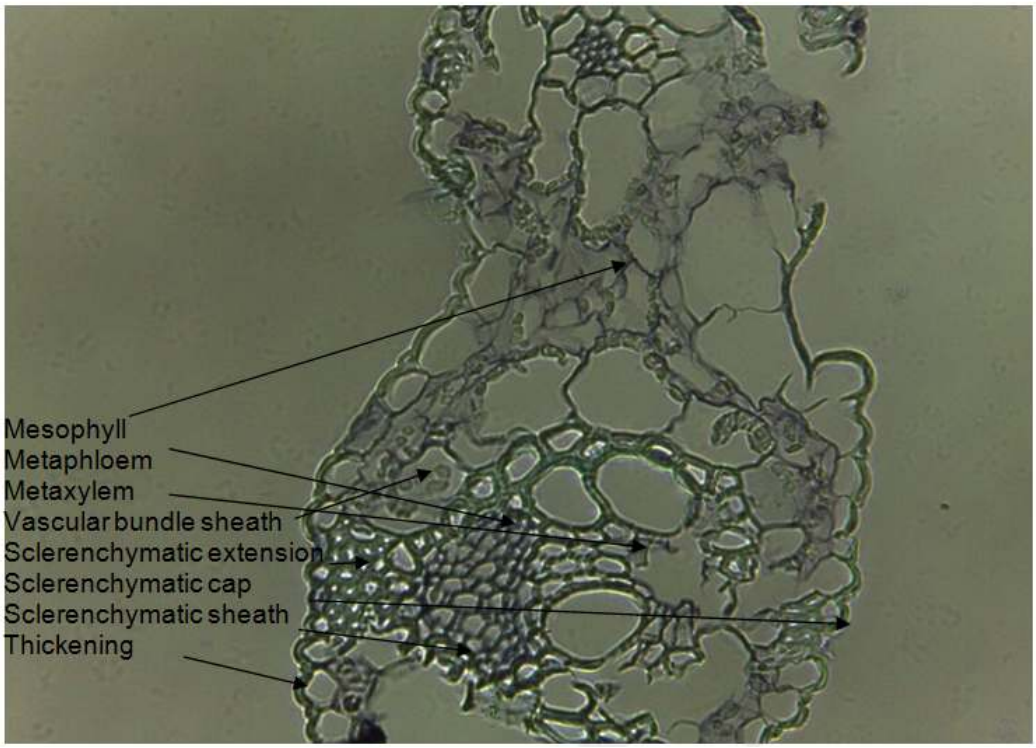

Fig. 1. Anatomical structure of the leaf blade of *Urochloa brizantha* cv. Marandu (syn. *Brachiaria brizantha* cv. Marandu) grown in full sun

2.3 Statistics

Variance analysis and mean test were performed after residual normality test, data normality [17] and variance homogeneity. The Student's t test was used for mean comparisons at 5% significance. The relationships among anatomical components, shading levels, and dry matter degradability were tested by Person's correlation test, also at 5%.

3. RESULTS AND DISCUSSION

Similar proportions of sclerenchyma and parenchyma tissues were obtained to the same shading levels for both Marandu and Mombasa grasses (Table 2), with no difference in the interaction between the variables ($p<0.05$).

However, shading effect on sclerenchyma promoted higher proportions of sclerenchyma to Mombasa if compared to Marandu ($p <0.01$). As expected, altogether, the shading reduced the proportion of this tissue for both species. Plants under full sunlight had increased thicknesses of this tissue. On the other hand, for both Mombasa and Marandu species, there were no significant differences ($p <0.05$) neither under 25 nor 50% shading.

Means followed by different lowercase letters in the same column (f test) and uppercase in the same row (t-test) differ from each other at 5% significance ($p<0.05$). Degradability of dry matter at 96-hour incubation. FS: Full Sun; 25%: silvopastoral system under 25% shading; and 50%: silvopastoral system under 50% shading. DM: Dry Matter.

Changes in sclerenchyma proportions reflect oscillations in environmental conditions. Even though Mombasa grasses presented a smaller reduction of such tissue, this forage still shows a greater proportion of lignifying tissues, such as sclerenchyma, in addition to presenting a parenchyma decrease similar to that of Marandu grasses. Greater amounts of sclerenchyma in leaves indicate the low degradability of forage and hence less nutrient availability [8].

Table 2 also shows the ratio parenchyma: sclerenchyma. As far as shading level increases, the proportion of parenchyma tissue is increased, wherein Marandu grasses had higher proportions if compared to Mombasa ($p <0.05$), particularly under 50% shading. Mombasa grasses featured more subtle changes in this ratio. Yet Marandu grasses presented a higher proportion of parenchyma, which indicates a reduced synthesis of secondary metabolites and sclerenchymatic tissues, that is, undergoing drastic changes in nutritional aspects, as indicated by dry matter degradability (Table 2) and gas production (Fig. 1).

Dry matter degradability variations indicate the responses of the plants to diverse shading levels. Here, the responses to the shading treatments were similar in Mombaça grass and different in Marandu grass ($p <0.01$); in the latter, this variable presented an increasing growth as the shading increased.

The secondary thickening of the epidermis was significant ($p<0.01$) for the split, showing gradual reduction as the shading varied from Full Sun to 50%, in Marandu grasses. Conversely, Mombasa grasses responded differently, which remained unchanged under all shading levels but with a lower epidermal thickness for plants under FS (Table 2).

Significant results were obtained for a metaphloem increase in Marandu grass leaves and reduction in Mombaça grass leaves, where the highest proportions were registered in the first species (Table 2). By comparing Table 2 and Fig. 2 (A and B), it is noteworthy a smaller gas production (Fig. 2B) given the stability of lignifying tissues and parenchyma in Mombasa grasses. Besides that, we can note a sudden reduction in metaphloem, which is digested as a highly degradable tissue [18]. In addition, we can highlight a similarity among the shading degrees. By contrast, Marandu grasses showed an increased gas production (Fig. 2A). This might have been a reflection of a higher metaphloem content, increasing gas production due to an improved degradability [19,18]. Studying two *Axonopus* species, [2] reported higher degradability in phloem and parenchyma if compared to lignified tissues. The phloem has a cell wall composed mostly of cellulose, what brings with it a greater susceptibility to degradation in the rumen [20].

Cellulose, as well as hemicellulose, is part of the cell wall chemical entities, which have significant degradability, besides constituting the fractions in NDF.

Table 3 presents the contents of NDF and ADF. Interestingly, no significant interference was observed for the shading levels on NDF and ADF contents in both species.

Table 2. Sclerenchyma, parenchyma, metaphloem and epidermal thickening (µm) percentages (%) of cross-sections and degradability of Marandu and Mombasa grasses under different shade percentages

	SSP	25%	50%	Means	CV(%)
		Sclerenchyma a (%)			
Marandu	3.4	2.0	2.0	2.5 b	
Mombasa	6.5	3.1	3.1	4.3 a	23
Means	4.9 A	2.6 B	3.3 B		
		Parenchyma (%)			
Marandu	56.9	57.3	60.0	58.1	
Mombasa	56.1	62.9	59.9	59.6	8
Means	56.5	60.1	59.9		
		Epidermal thickening (µm)			
Marandu	3.6 aA	2.5 aB	2.1aB	2.7	
Mombasa	2.5 bA	2.5 aA	1.9 aA	2.3	18
Means	3.8	2.5	2.0		
		Metaphloem (%)			
Marandu	3.77 bB	5.04aA	4.4aAB	4.5	
Mombasa	5.5 aA	2.55bB	3.2bB	3.7	16
Means	4.6	3.98	3.8		
		Associating parenchymal and sclerenchyma			
Marandu	18 aB	21 aB	35.2aA	24.7	
Mombasa	16 aB	22.5 aA	20.2bAB	19.1	17
Means	16.5	21.6	27.7		
		Degradability of dry matter			
Marandu	48.5 aC	53.1 aB	57.8 aA	53.1	5
Mombasa	51.7 aA	51.5 aA	51.7 bA	51.6	
Means	50.1	52.3	54.8		

Means followed by different lowercase letters in the same column (f test) and distinct uppercase letters in the same row (t test) differ at 5% significance (P <0.05). Degradability of dry matter in 96 hours of incubation. FS: Full Sun, 25%: Silvopastoral 25% shade and 50%: 50% Silvopastoral 50% shade. DM: Dry Matter.

Table 3. NDF and ADF dry matter content of Marandu and Mombasa grasses under different shade percentages

	SP	25%	50%	Means	CV (%)
		Neutral detergent fibre (NDF), %			
Marandu	59.76	64.85	59.95	62.7 b	
Mombasa	62.68	66.48	63.73	63.9 a	9
Means	61.22A	65.68 A	61.84 A		
		Acid detergent fibre (FDA), %			
Marandu	23.18	26.72	24.38	25.36a	
Mombasa	24.96	27.88	25.65	25.57a	12
Means	24.07A	27.30A	25.01A		

Means followed by different lowercase letters in the same column (f test) and distinct uppercase letters in the same row (t test) differ at 5% significance (P <0.05). Neutral detergent fibre (NDF); Acid detergent fibre (FDA). FS: Full Sun, 25%: Silvopastoral 25% shade and 50%: 50% Silvopastoral 50% shade.

Neutral detergent fiber (NDF) is constituted by cellulose, hemicellulose, and lignin, whereas acid detergent fiber (ADF) is composed of cellulose and lignin; both of them have a relationship with the ingestive behavior of animals. It is known that the higher the dry matter content, the lower the digestibility and hence the lower the intake. Notwithstanding, the proportions of cellulose and hemicellulose may vary with climate changes and exceeds lignin increment in NDF, reflecting on different results for the degradability variables [21]. Lignin is a rigid compound present in vascular plants. This element has the purpose of preserving plant physical integrity, and its herbivory resistance depends on its association with hydroxamic compounds (p-ferulic acid, p-coumaric, and sinapic acid) [22].

Even if there were no significant differences among treatments, we could observe a greater phloem proportion in Marandu grasses. This element is basically composed of cellulose, what allowed the forage an improved dry matter degradability [19].

Under full sun, Mombasa grasses showed the highest increase in gas production, concomitantly to a greater proportion of metaphloem and lower secondary epidermal thickening. The largest proportion of sclerenchyma tissue in Mombasa suggests that cell wall components can be encrusted by lignin, reducing the time span of cell-wall degradation [23]. The profile of soluble and structural carbohydrates also influence grass fermentability [23]. The shading might have had an influence on the proportion of polymers, reducing the quantity of lignin in the cell wall of shaded Marandu grasses [24].

The high number of parenchymal tissue cells in Mombasa grass was insufficient to express differences within the same species for all shading levels ($p > 0.05$). This result was proportional to a variation in sclerenchyma and xylem cells [3]. Environmental fluctuations have an influence on plant anatomical changes, which might still be associated with the peculiarities inherent to the species. [25] reported that there might be anatomical differences within the same species or physiological group, which are further accentuated by climate changes.

Table 4 displays the correlation coefficients for the anatomical structures, shading, and dry matter degradability. When the responses of some variables are compared, the level of relationship between the studied variables evidences a mismatch between both species, e.g. metaphloem, sclerenchyma, dry matter degradability, and secondary thickening. The mean test revealed different results for each species to shading [5], reflecting on the relationship level between the variables.

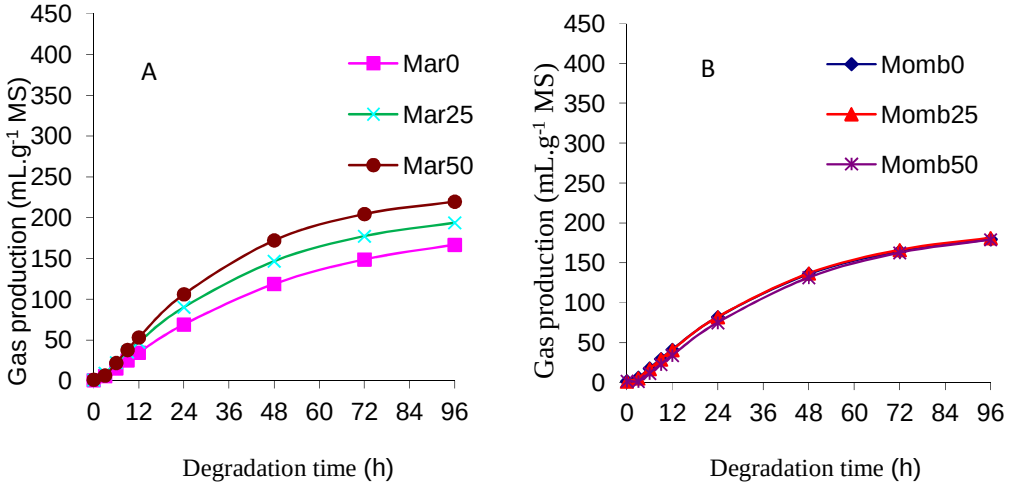

Fig. 2. Cumulative gas production within 96 hours of *Panicum maximum* cv. Mombasa and *Brachiaria brizantha* cv. Marandu leaves grown on Full Sun and 25 and 50% shading. Marandu Full Sun (Mar0) Marandu 25% shade (Mar25), Marandu 50% (Mar50), Mombasa Full Sun (Momb0), Mombasa 25% shade (Momb25), Mombasa 50% (Momb50)

Table 4. Linear correlations between leaf anatomical variables, shading and dry matter degradation

Marandu	Metafl	Escl	Parênq	Par: Es	DMS	Espess	Somb
Metafl	1						
Escl	-0.43	1					
Parênq	-0.39	-0.17	1				
Par:Esc	-0.17	-0.44	0.61*	1			
DMS	0.033	-0.63*	0.43	0.74*	1		
Espessam	-0.23	0.75*	-0.35	-0.58*	-0.66*	1	
Somb	0.28	-0.78*	0.46	0.68*	0.79*	-0.83*	1
Mombasa	**Metafl**	**Escl**	**Par**	**Par:Es**	**DE 96**	**Espess**	**Somb**
Metafl	1						
Escl	0.69*	1					
Parênq	-0.50	-0.60*	1				
Par:Esc	-0.68*	-0.75*	0.50	1			
DMS	-0.01	0.08	-0.28	-0.51	1		
Espess	0.19	0.12	-0.25	-0.03	0.06	1	
Somb	-0.67*	-0.45	0.2323	0.36	-0.009	-0.45	1

Metaph: metaphloem, Scl: sclerenchyma, Paren: parenchyma, Par:Scl: parenchymal: sclerenchyma relationship, DMD: dry matter degradation within 96 hours, Thick: Epidermal thickening, Shad: shading.
** Significant at 5% (P <0.05).*

Table 4 expresses the correlation coefficients between variables and the shading percentages. Metaphloem contents had no significant association with the shading levels in both Marandu (0.28) and Mombasa (-0.67) since its structure remained stable to changes in the light spectrum.

In Marandu grasses, sclerenchyma and secondary epidermal thickening had a reverse and significant relation with the shading levels. Therefore, an increase in the shading level resulted in a decrease of those tissues. However, such correlation was positive with dry matter degradation ($p<0.05$), which has increased with shading (Fig. 2). Unlike, Mombasa grasses did not respond the same way since their tissues, except the metaphloem, are stable to environmental oscillations, which hindered an associative response. [3] correlated the anatomical components to chemical blades and stems of Marandu and Molasses grasses and found similar results to this study, in which the same variables showed no significant correlation in these two species.

Table 4 unravels that the significant negative correlation between parenchyma and sclerenchyma in Mombasa grasses can be explained by a reduction in sclerenchyma tissue. Differently, the same result was not found for Marandu grasses since the reduction in mesophyll related to sclerenchyma was non-significant.

The number of significant correlations in Mombasa grass was lower, most of them being mismatched from Marandu grass results (Table 4 and Fig. 2A). For example, through Fig. 2 we may state that the changes in tissue proportions must be intrinsic to a genetic factor of resilience, without affecting the dry matter degradability in Mombasa grass.

After 96-hour incubation, dry matter degradation showed different results for each forage species (Fig. 3). Due to the higher proportion of metaphloem and reduction of tissues that are able to lignify under shading, Marandu grass showed an increase in degradation compared to Mombasa grass, which in turn remained unchanged between the shading levels. The lignifying tissues, xylem, epidermis, and sclerenchyma, limit grass degradation, increasing the length of digestive processes [2,26]. Cell wall lignification in xylem and sclerenchymatic tissues increase their resistance to degradation by bacteria and fungi [11].

The silvopastoral systems create a milder microclimate under the canopy of trees, which leads to a change in the profile of wavelengths

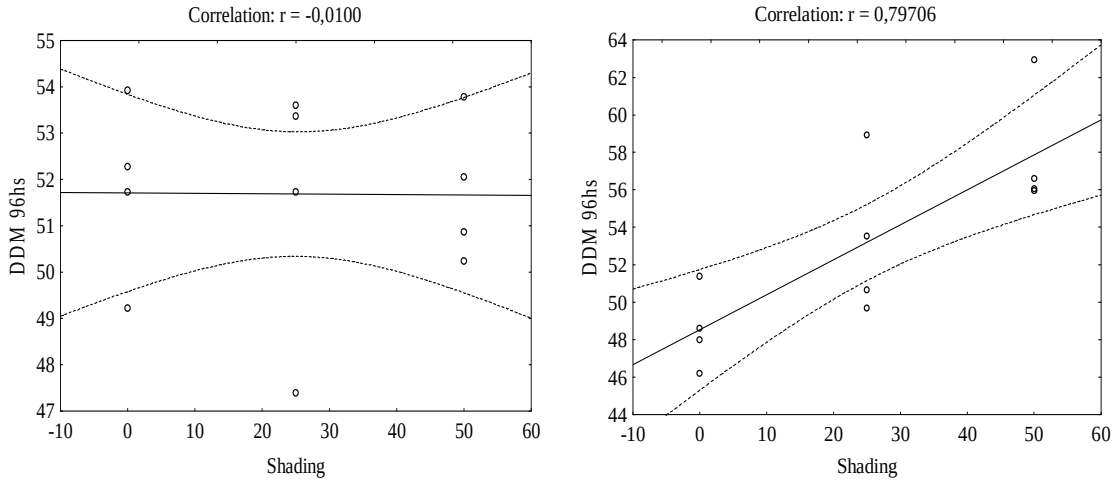

Fig. 3. Quantitative association between shading and dry matter degradability in 96 hours of incubation for Mombasa (A) and Marandu (B). DDS: degradation of dry matter

reaching the understory, reducing the net rate of photosynthesis. This effect denotes direct reductions of forage, sclerenchyma tissues, and chlorophyllic parenchyma [27]. Although many studies have shown this type of response [27,28] mainly in species of the genus Brachiaria, little research has been conducted on other specimens, which leaves a great gap in use of forage species in silvopastoral systems. The present study proves that Mombaça grass, of genus Panicum, has different qualitative responses compared to brachiaria, resulting in an adaptive responsiveness, in which changes in the light length pattern influenced less on plant anatomical variables.

4. CONCLUSIONS

Regarding plant anatomical traits and gas production, Marandu grass showed the best performance in nutritional terms when shaded in a silvopastoral system.

Mombasa grass is less sensitive to environmental variations, which improved the preservation of its low degradability tissues.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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