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Shade induces contrasting light photosynthetic performance between Signal and Guinea Grasses

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ABSTRACT. Signal grass (*Urochloa decumbens*) and guinea grass (*Megathyrsus maximus*) are African grasses that are well established in the Brazilian Savannah and we tested their adaptation to different light intensity. Plants were grown for 45 days under 0% shade (full sun) and 25, 40, and 80% induced shade to evaluate their photosynthetic performance. Light curves showed higher values of electron transport rate, photochemical quenching, and effective quantum yield in plants subjected to 0 and 25% shade for signal grass and in 25 and 40% shade for guinea grass. The potential quantum yield evaluations revealed that signal grass felt the effects of excessive light around 11:30 am on plants subjected to 0 and 25% shade. Conversely, guinea grass showed these photoinhibition effects at the same shade level but in a longer time range (9:30 am to 1:30 pm). As shade increased, there was a reduction tendency of the pigment content in signal grass and the opposite was observed for guinea grass. Stomatal conductance showed different values during the day and among different shade levels and there were no differences in relative water content between treatments and species. Results indicated better photosynthetic performance for signal grass under high intensity and better photosynthetic performance for guinea grass subjected to intermediate and higher levels of shade. Altogether, the results indicate that guinea grass seems to be a more appropriate choice for silvopasture systems.

Keywords: C4 grasses; pastures systems; photoinhibition; shade.

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Introduction

During development, plants are subjected to many environmental adversities, such as high and low temperatures, water and nutrient availability, predation, and light quality and intensity fluctuations (Zhu, 2016). Variations in light intensity and quality lead to morphological and physiological acclimation responses (Walters, 2005; Laanisto & Niinemets, 2015; Valladares, Laanisto, Niinemets, & Zavala, 2016). In relation to the photosynthetic apparatus, the most common acclimation responses to light availability are alterations on PSII/PSI ratio, cytochrome b/f complex, ATP synthase, and Calvin-Benson cycle components (Takahashi & Badger, 2011).

Variations in light intensity can result in predictable morphophysiological responses but these responses are only predictable if the range of variation does not exceed the species acclimation capacity (Walters, 2005). When pushed beyond their limit of acclimation capacity, plants tend to reduce their growth capacity. The restriction of light intensity and quality imposed by shade on understory plants in silvopasture systems, for example, can result in acclimation or reductions in photosynthetic capacity, depending on the acclimation capacity of the species subjected to this condition (Yang, Webster, Adam, Lindahl, & Andersson, 1998; Walters, 2005). Despite the fact that shade is not the only variable in environments, such as silvopasture systems (Bernardino & Garcia, 2009), light intensity variation should be considered because it is a primary environmental factor for plant development in the photosynthetic process (Sæbø, Krekling, & Appelgren, 1995).

When exposed to higher irradiance and temperature, C4 plants present the highest photosynthetic rates, when compared to C3 and CAM plants, since their strategy of accumulating CO_2 does not make it a limiting factor in these conditions (Kluge, Tezotto-Uliana, & Silva, 2015). In contrast, under shade situations, grasses can undergo morphological and physiological changes, such as etiolation, making them weak and susceptible to disease (Jiang, Duncan, & Carrow, 2004). Much has been studied about the influence of shade levels on grass production (East & Felker, 1993; Deinum, Sulastri, Zeinab, & Maassen, 1996; Castro, Garcia, Carvalho, & Couto, 1999; Horton, Fortner, & Goklany, 2010) because its use is basically for forage. However, it is important to have information about changes in photosynthetic rates under shade conditions. A good approach to access the differences in photosynthetic processes is thorough chlorophyll ʻa' fluorescence, a method in which one of the three pathways that light can go through when absorbed, i.e., photochemistry, heat, and chlorophyll fluorescence are used to evaluate the status of PSII of plants acclimated to different light conditions (Kalaji et al., 2016; Hanelt, 2018). To compare the capacity of these acclimated plants to different levels of light, rapid light curves can be performed and give clear and reliable results (White & Critchley, 1999; Ralph & Gademann, 2005). In addition to the accuracy of potential quantum yield (Fv/Fm) measurements, such parameters can give information about the occurrence of photodamage and consequently, the photoinhibition process (Lemos-Filho, 2000; Krause et al., 2012; Vass, 2012).

Defined as the reversible reduction of photosynthesis in response to light excess, photoinhibition can be intensified by environmental and edaphic conditions, such as cold, freeze, heat, and nutrient deficiencies (Long, Humphries, & Falkowski, 1994). The persistence of these conditions for long periods can greatly reduce net CO_2 fixation (Long et al., 1994). To avoid such impairments caused by photoinhibition, plants have developed mechanisms of photoprotection. The primary function of those mechanisms is to avoid the formation and accumulation of reactive oxygen species (ROS) through non-photochemical dissipation (qN). With great ecological importance, the type of mechanism used for photoprotection seems to be related to the plants habit. For instance, short-lived plants tend to rely on flexible dissipation mechanisms (qE), a rapidly reversible, ΔpH, and PsbS-dependent mechanism. Contrastingly, long-lived, slow-growing, tropical evergreen plants, due to prolonged exposure to stress, are more likely to present a sustained form of thermal dissipation (qI) that is ΔpH-independent and ΔpH-dependent only at low temperatures, which is mostly correlated with the rearrangement of the PSII core (D1 protein phosphorylation; Demmig-Adams & Adams, 2006). Both mechanisms can also rely on the xanthophyll cycle and are important in growing conditions where light intensity fluctuation is common, such as in silvopasture systems.

Silvopasture systems are composed of three fundamental parts: livestock, forage, and perennial woody vegetation. Such systems can provide long and short-term economic output to farms as a result of cattle raising for meat and milk, timber products, forage, fruits, and/or nuts (Bruck, Bishaw, Cushing, & Cubbage, 2019). Presenting not only economic advantages, silvopasture systems can provide ecological benefits, such as maintenance of native tree vegetation, besides mitigating anthropogenic climate change through carbon sequestration from perennial cultures (Bernardino & Garcia, 2009). Silvopasture systems not only lead to an economic advantage but implicate severe alterations in the local microclimate by slowing wind speed and reducing temperature and light intensity. Since forage is a main component of this system, it is important to choose, based on well-established physiological parameters, species that show a better acclimation response.

Urochloa decumbens (signal grass) and *Megathyrsus maximus* (guinea grass) are African grasses that are well-established in the Brazilian Savannah, with high nutritional value (Jank, Barrios, Valle, Simeão, & Alves, 2014), and these traits indicate their potential for use in silvopasture systems. Besides the nutritional status, it is expected that plants of this system are able to grow well under elevated and frequent incidence of shade. This study evaluated, through chlorophyll ʻa' fluorescence, the acclimation capacity of these two C4 grasses to different shade levels to assess which one is more appropriate to improve silvopasture systems in the Brazilian Savannah.

Material and methods

Plant material and growth condition

The experiment was carried out in greenhouse conditions in the Federal University of Minas Gerais (UFMG), state of Minas Gerais, Brazil. Seeds of *Urochloa decumbens* and *Megathyrsus maximus* were germinated in sand. After germination, plants were transferred to 0.75 L pots containing a mix of sand and vermiculite 1:1 ($v\ v^{-1}$) and irrigated with half strength Hoagland's solution daily. These plants were subjected to 4 different levels of shade: 0 (full sun), 25, 40, and 80% for 45 days.

Photosynthetic light curve evaluation

In this assay, rapid light curves were performed using a Mini-PAM modulated pulse fluorometer (Heinz Walz, Effeltrich, Germany) to determine the photosynthetic capacity of the plants cultivated under contrasting light regimens in response to saturating light intensities. The light curves were then performed by increasing the actinic light intensity (0-1800 μmol m^{-2} s^{-1}) divided in 8 steps of 30 s each, to obtain values of minimal (F) and maximum (F’m) fluorescence in the light adapted state for each light intensity. Based on these values we calculated: effective quantum yield of photosystem II (ΔF/F'm = [F’m - F]/F’m; Genty, Briantais, & Baker, 1989); electron transport rate (ETR = 0.5 * ΔF/F’m * PAR * 0.84; White & Critchley, 1999), and photochemical quenching (qP = [F’m - F]/[F’m - F0]; van Kooten & Snel, 1990).

The photoinhibition experiment was performed using a Mini-PAM fluorometer on the first fully expanded leaf on a clear day and the measurements were made every 2 hours. For this evaluation, at every interval, the leaves were dark adapted for 30 min to obtain the values of minimum (F_0) and maximum (Fm) fluorescence. From these parameters we calculated: maximum (Fv/Fm = [Fm – F0]/Fm) and effective (ΔF/F'm) quantum yield of photosystem II (Genty et al., 1989) and relative excessive photon flux (REPF = [Fv/Fm - F/Fm]/[Fv/Fm]; Bilger, Schreiber, & Bock, 1995). During the photoinhibition experiment, photosynthetically active radiation (PAR) was evaluated every 60 min for all shade treatments starting at 7:30 am (Table 1). The PAR values were measured using a Li-COR quantum sensor Li-190.

Table 1. Photosynthetic active radiation (PAR, μmoL m^{-2} s^{-1}) under all shade levels (%) during the day.

Time (hour)	Shade level (%)			
	0	25	40	80
7:30 am	54	37	38	78
8:30 am	212	239	186	169
9:30 am	1273	922	778	212
10:30 am	1425	1088	677	255
11:30 am	1323	939	619	233
12:30 pm	1513	989	753	344
1:30 pm	1040	793	604	207
2:30 pm	1189	776	580	208
3:30 pm	534	306	330	78
4:30 pm	521	179	178	81
5:30 pm	44	18	17	9

Stomatal conductance and relative water content

The stomatal conductance (g_s) evaluation was made using a diffusion porometer AP4 (Delta T) on the first fully expanded leaf in all treatments every 2 hours. For relative water content (RWC) determination, leaf discs of 1 cm^2 from all treatments were collected at 3 different periods of the day: predawn (5:30 am), higher evapotranspiration demand hour (12:30 pm), and 1 h after sunset (7:30 pm). Right after being collected, the discs were weighed for fresh weight (FW) determination and the same discs were placed in petri plates filled with water for 24 hours at 4°C and weighed again for turgid weight (TW). The discs were then taken to the forced air circulation oven and dried under 70°C until a constant dry weight (DW) was obtained. The RWC was then calculated by the formula: RWC = [(FW-DW)/(TW-DW)]*100.

Chloroplastic pigments

For chloroplastic pigment analyses, 5 leaf discs of 0.5 cm^2 were weighed and placed on amber glass containing 5 mL of 80% acetone. This material was then held for 72 hours. After the solution with the leaf discs was macerated and the resulting solution was filtered, the volume was constituted to 10 mL with the same extraction solution. This 10 mL solution was centrifuged for 3 min. at 10,000 rpm and the supernatant was analyzed with a spectrophotometer reading under 3 wavelengths: 470, 646, and 663 nm. The concentration of chlorophyll a (C_a), b (C_b), and carotenoids (C_{x+c}) were calculated according to Lichtenthaler and Wellburn (1983).

Statistical analyses

All curves were calculated using GraphPad Prism, version 5.00 (GraphPad Software, San Diego, CA; www.graphpad.com). The pigment data were subjected to ANOVA analyses and the means were compared by a Tukey 5% probability test using JMP statistical software from the SAS (Statistical Analysis System, U.S; www.sas.com).

Results and discussion

Photosynthetic performance

The photosynthetic performance of *U. decumbens* and *M. maximus* showed a differential behavior in all variables (Figure 1). Higher values of effective quantum yield of photosystem II (ΔF/F'm) were observed in plants of *U. decumbens* growing under a lower shade regimen (0 and 25% shade) (Figure 1A). For *M. maximus,* higher values were obtained for 25 and 40% intermediate shade (Figure 1B). In the same way, higher ETR values were observed for plants of *U. decumbens* grown under lower shade intensities and for *M. maximus* grown under an intermediate shade regimen (Figure 1C and D) and likewise for photochemical quenching (qP) values (Figure 1E and F). The highest values of ETR measured were 102 μmoL m^{-2} s^{-1} for *U. decumbens* subjected to 0% shade and 105 μmoL m^{-2} s^{-1} for *M. maximus* under 25% shade. The higher light saturation point for *U. decumbens* was approximately 900 of photosynthetically active radiation (PAR) subjected to 0% shade and 550 PAR for other treatments. For *M. maximus,* these values reached 1,200 for 25% shade and 700 for 80% shade.

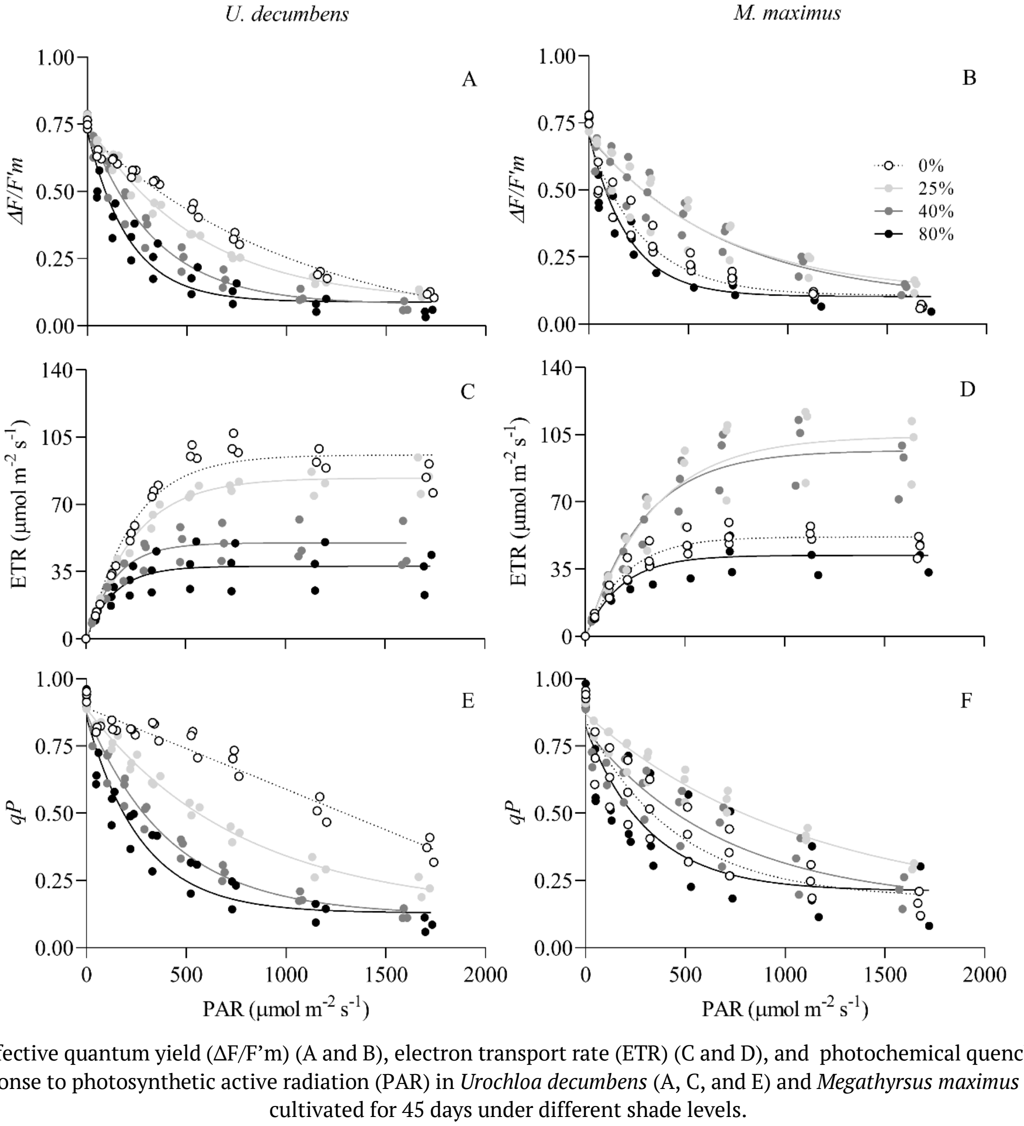

Figure 1. Effective quantum yield (ΔF/F'm) (A and B), electron transport rate (ETR) (C and D), and photochemical quenching (qP) (E and F) in response to photosynthetic active radiation (PAR) in *Urochloa decumbens* (A, C, and E) and *Megathyrsus maximus* (B, D, and F), cultivated for 45 days under different shade levels.

Photoinhibition evaluation

Different levels of photosynthetic active radiation (PAR, μmoL m^{-2} s^{-1}) are expressed under the different shade levels applied to plants during growth on a typical clear day (Table 1) with the same light intensities used to perform the photoinhibition experiment (Figure 2).

In the photoinhibition evaluation, *U. decumbens* showed no signs of photoinhibition (values of Fv/Fm below 0.8) in the highest levels of shade treatment (Figure 2A). Reductions of Fv/Fm were detected for this species only around 11:30 am when exposed to 0 and 25% shade, with full recovery after 1:30 pm (Figure 2A). For *M. maximus* (Figure 2B), there was no sign of photoinhibition in plants grown in 80 and 40% shade and the same was observed for *U. decumbens*. However, for *M. maximus,* the photoinhibition process in 0 and 25% shade was detected at 9:30 am and recovery was only observed after 3:30 pm (Figure 2B).

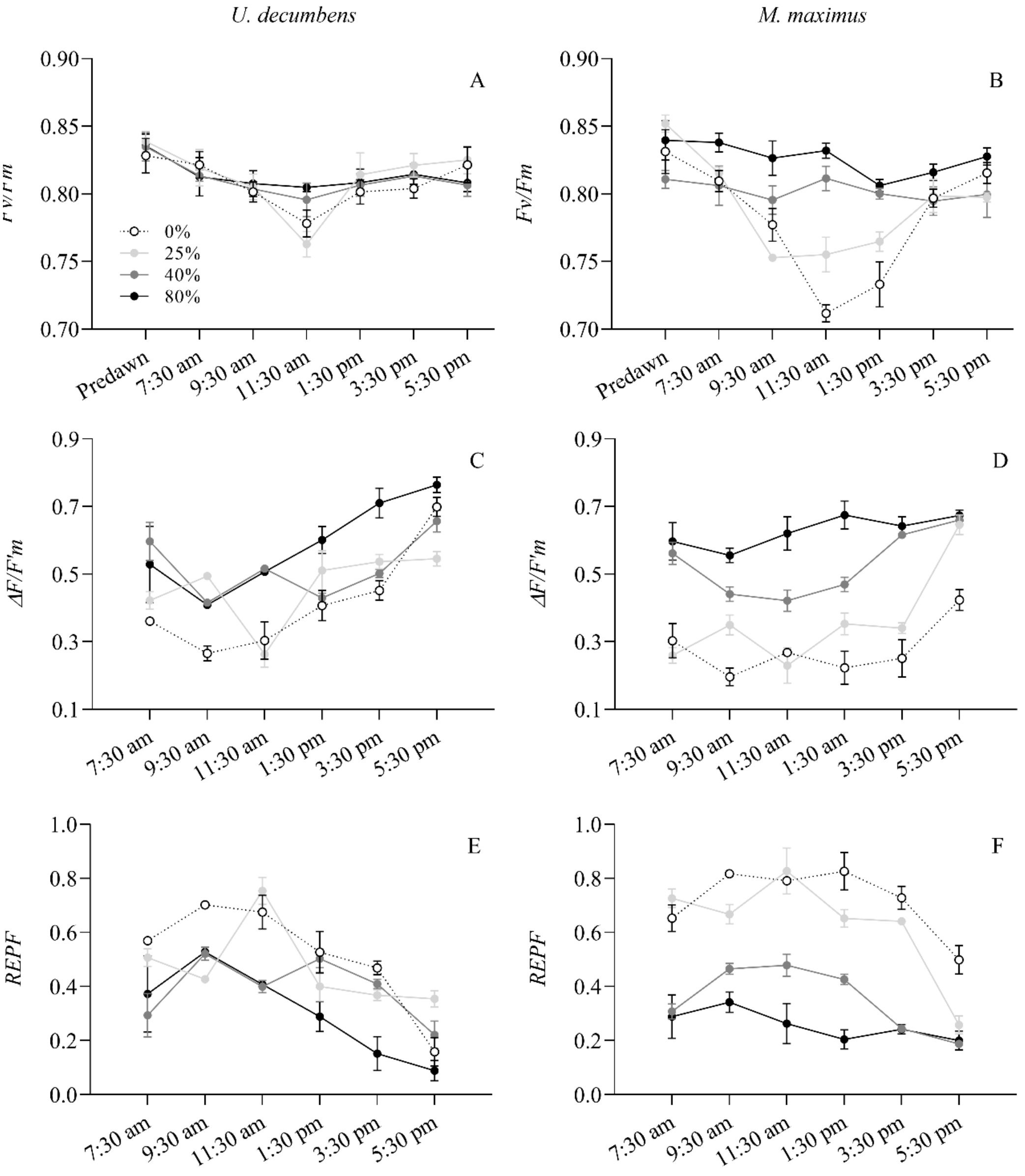

Figure 2. Potential quantum yield (Fv/Fm) (A and B), effective quantum yield of photosystem II (ΔF/F'm) (C and D), and relative excessive photon flux (REPF) (E and F), obtained during different times of the day in *Urochloa decumbens* (A, C, and E) and *Megathyrsus maximus* (B, D, and F), cultivated for 45 days under different shade levels.

For both species, the highest values of ΔF/F'm were observed in 80% shade (Figure 2C and D), as expected, but this behavior seemed to be more pronounced for *M. maximus*. Additionally, for *M. maximus,* higher values of ΔF/F'm were observed under 40% shade, while for *U. decumbens,* the highest values with the same level of shade were observed only at 7:30 and 11:30 am. The lowest values of ΔF/F'm were 0.26 for *U. decumbens* at 9:30 am subjected to 0% shade and 0.20 for *M. maximus* also at 9:30 am in the same level of shade. The highest values, 0.76 and 0.68, were obtained at 5:00 and 1:30 and 5:30 pm, respectively, for *U. decumbens* and *M. maximus* respectively, in 80% shade. For *U. decumbens,* the highest value of REPF was obtained at 11:30 am in 25% shade (0.76) and the lowest value at 5:30 pm in 80% shade (Figure 2E). *M. maximus* presented the lowest value at 5:30 pm (0.19) in 40% shade and the highest value in 25% shade (0.83) at 11:30 am (Figure 2F).

Stomatal conductance and relative water content

In general, values of g_s observed for *U. decumbens* were slightly lower than those observed for *M. maximus* (Figure 3A and B). For both species, the lowest values of g_s were observed at 5 pm, the time of day when the natural light in all plants subjected to shade was reduced. *U. decumbens* showed a range of stomatal conductance varying from 12.3 mmoL m^{-2} s^{-1} in 25% shade treatment at 5 pm to 210.9 mmoL m^{-2} s^{-1} in 80% shade treatment at 9:00 am. For *M. maximus,* the lowest value was 25.5 mmoL m^{-2} s^{-1} for 80% shade at 1 pm and the highest value was 211.3 mmoL m^{-2} s^{-1} at 7:00 am for 40% shade treatment. There was no significant pattern verified for any of the species and times observed. Although there were differences in g_s based on the measurement time, there was no significant difference in relative water content (Figure 4) for any daytime for both species, with values close to 85%.

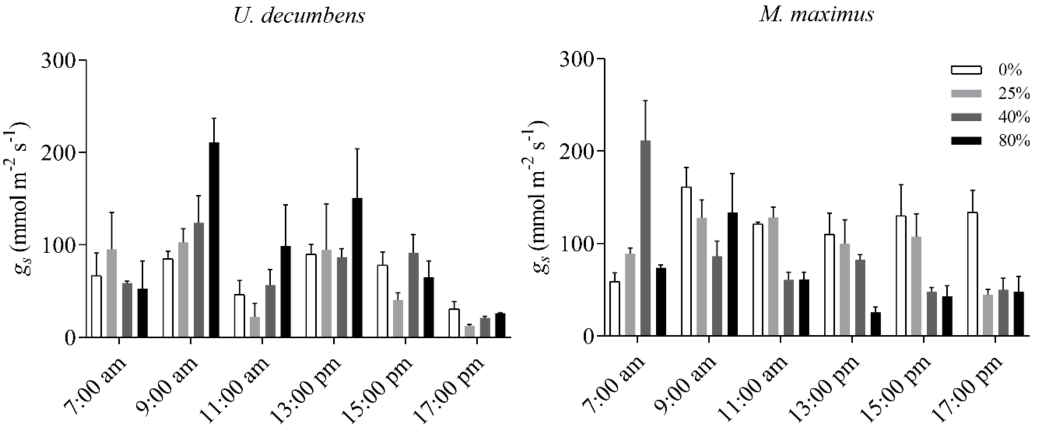

Figure 3. Stomatal conductance (g_s) obtained during different times of the day in *Urochloa decumbens* (A) and *Megathyrsus maximus* (B) cultivated for 45 days under different shade levels.

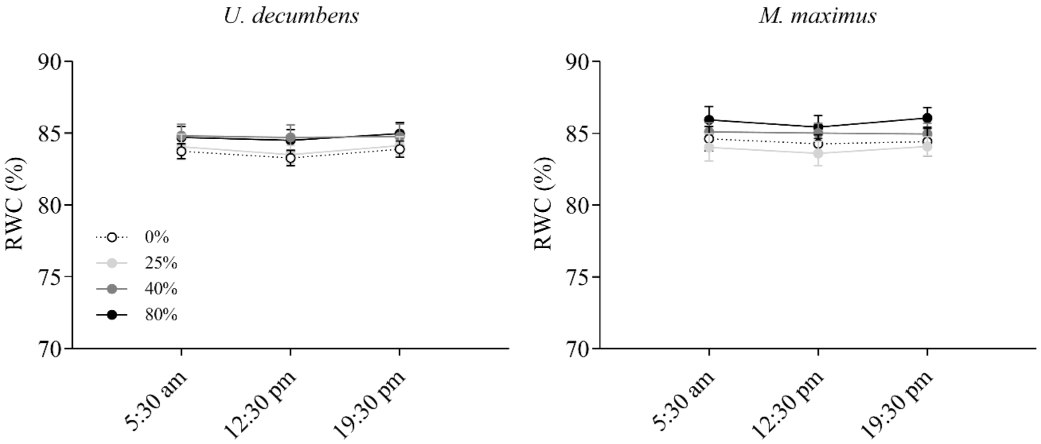

Figure 4. Relative water content (RWC) obtained during different times of the day in *Urochloa decumbens* (A) and *Megathyrsus maximus* (B) cultivated for 45 days under different shade levels.

Photosynthetic pigments

U. decumbens plants cultivated under 0 and 80% shade presented the highest values of chlorophyll 'a' (1.43 and 1.39 μg mg^{-1} FW, respectively; Table 2). The lowest values of chlorophyll 'a' for *U. decumbens* were obtained in plants in the 40% shade treatment (0.81 μg mg^{-1} FW). For *M. maximus,* the highest value was obtained from 40% shade treatment (1.13 μg mg^{-1} FW) and the lowest value (0.65 μg mg^{-1} FW) obtained from 0% shade. For chlorophyll 'b' results, *U. decumbens* showed a higher value of 0.43 μg mg^{-1} from 80% shade plants and lowest value of 0.22 μg mg^{-1} FW for plants in the 40% shade treatment. For *M. maximus,* 25, 40, and 80% shade presented the highest values (0.27, 0.28, and 0.26 μg mg^{-1} FW, respectively). A result of 0.41 μg mg^{-1} FW of carotenoids was found in plants of *U. decumbens* from the 0% shade condition. This value was higher than those obtained from all other shade levels. For *M. maximus,* the highest value of carotenoid were obtained from 80% shade (0.26 μg mg^{-1} FW) and the lowest from 40% shade (0.19 μg mg^{-1} FW).

Table 2. Leaf pigments (µg mg^{-1} FW) of *Urochloa decumbens* and *Megathyrsum maximus* plants growing in different shade levels.

			U. decumbens		
Shade	Chlorophyll ‘a’	Chlorophyll ‘b’	Carotenoid	Ratio ‘a’:‘b’	Total
0%	1.43±0.059 a	0.33±0.079 ab	0.41±0.003 a	4.45±0.640 a	1.76±0.051 a
25%	1.01±0.010 b	0.29±0.079 ab	0.28±0.010 b	3.68±0.523 a	1.30±0.041 b
40%	0.81±0.091 c	0.22±0.026 b	0.24±0.057 b	3.73±0.172 a	1.02±0.065 c
80%	1.39±0.066 a	0.43±0.014 a	0.29±0.010 b	3.25±0.087 a	1.82±0.042 a
			M. maximus		
Treatment	Chlorophyll ‘a’	Chlorophyll ‘b’	Carotenoid	Ratio ‘a’:‘b’	Total
0%	0.65±0.019 c	0.18±0.005 b	0.25±0.005 ab	3.57±0.103 a	0.84±0.020 c
25%	0.97±0.033 b	0.27±0.034 a	0.20±0.014 bc	3.66±0.393 a	1.24±0.019 b
40%	1.13±0.012 a	0.28±0.013 a	0.19±0.013 c	4.08±0.234 a	1.41±0.009 a
80%	0.92±0.55 b	0.26±0.012 a	0.26±0.020 a	3.57±0.054 a	1.18±0.067 b

Values indicate means ± standard error. Different letters in the same column differ significantly by Tukey’s test at $p \leqslant 0.05$.

Photosynthetic response to shade

The light curves performed in both species, *U. decumbens* and *M. maximus,* demonstrated the influence of different levels of shade during the growth period in the subsequent photosynthetic performance. The parameters of qP, ETR, and ΔF/F’m calculated from the light curves are causally related to the photosynthetic efficiency of PSII. The ΔF/F’m values estimated the maximum quantum efficiency in a light-exposed state of PSII, the qP was related to the fraction of reaction centers of PSII that were in an oxidized or ‘open’ state in a specific light intensity, and ETR was the electron transport rate through the PSII (Kalaji, Goltsev, Zuk-Gołaszewska, Zivcak, & Brestic, 2017). *U. decumbens* showed higher values of qP, ETR, and ΔF/F’m in 0 and 25% shade, while for *M. maximus,* higher values were observed in 25 and 40% shade.

Working with the same species and other grasses, Castro et al. (1999) observed a decrease in total biomass accumulation for *U. decumbens* in response to 30 and 60% shade and an increase of biomass accumulation for *M. maximus* in intermediate light levels (30%), which corroborates our results, since the parameters evaluated are closely linked to biomass accumulation. By comparing both species under low light incidence, it was clearly observed that shaded *U. decumbens* plants had a photosynthetic disadvantage when related to *M. maximus* shaded plants.

Shade effect on photoinhibition

The reduction of Fv/Fm below 0.8 after exposure to relative high light intensity is currently being used as a photoinhibition indicator (Bjorkman & Demmig, 1987; Lemos-Filho, 2000; Lüttge, 2008). Reductions in Fv/Fm measurements can also indicate differences in the mechanism of primarily non-photochemical quenching (qN). The two main components of qN, the flexible (qE) and sustained (qI) forms of thermal dissipation, are very different in terms of relaxation time, ΔpH-dependency, and plant habit. The flexible form of thermal dissipation (qE) is usually associated with a ΔpH-dependence, fast relaxation in the dark, and is more pronounced in short-lived plants (Demmig-Adams & Adams, 2006). The other type of thermal dissipation (qI) is ΔpH-dependent only at low temperatures, usually associated with degradation of PSII (D1 protein), and consequently, presenting a slow relaxation time, which is more frequent in long-lived, slow growing evergreen tropical plants (Long et al., 1994). Fv/Fm decreases are considered photoinhibition when performed in the predawn or when leaves were dark acclimated long enough for complete relaxation of qI (Lichtenthaler, Buschmann, & Knapp, 2005). However, the interpretation of the decrease in Fv/Fm throughout the day is also valid and used to characterize photoinhibition (Werner, Correia, & Beyschlag, 2002; Prieto, Penuelas, LIusia, Asensio, & Estiarte, 2009). According to our results, *U. decumbens* showed no signs of photoinhibition, since the values obtained for these plants, even under high light intensity periods, were very close to 0.8. For *M. maximus* there were clear signs of photoinhibition between 9:30 am and 1:30 pm for 0 and 25% shade, a period in which plants faced light intensities higher than 1000 μmoL m^{-2} s^{-1}. The differential photoinhibitory response of these two species cultivated under different shade conditions could be a result of various factors. According to Takahashi and Badger (2011), the most common mechanisms to avoid photoinhibition of PSII are leaf and chloroplast movement, screening of photoradiation, ROS exclusion, thermal energy dissipation, PSI cyclic electron flow, and the photorespiratory pathway. The leaf arrangement of both species can be the most influential trait that differentiates their photosynthetic behavior. The horizontal inclination of *M. maximus* leaves can increase light capture under a low light environment, increasing photosynthesis under this condition, but the excess of energy intercepted by these leaves could increase photoinhibition potential under high light conditions. Conversely, the vertical inclination of *U. decumbens* leaves can increase resistance to photoinhibition, even under high light intensities, but reduces its potential under shaded environments (He, Chee, & Goh, 1996; Valladares & Pearcy, 1998; Werner, Ryel, Correia, & Beyschlag, 2001). It is also possible that *M. maximus* has higher levels of the sustained base thermal dissipation mechanism (qI) when exposed to high light intensities, considering the slow dark relaxation time (Demmig-Adams & Adams, 2006).

The PSII center reaction consists of a heterodimer of D1 and D2 proteins, which have the potential, together with other cofactors, to transport electrons through the chain (Vass, 2012). The photoinhibition process can be the result of abiotic environmental stresses. It is well established that environmental stress does not cause increases in D1 protein degradation but can cause reductions in the repair rate of photodamaged PSII by inhibiting the synthesis of the pre-D1 protein as an effect of H_2O_2 accumulation (Takahashi & Murata, 2008). Since there were no changes in RWC at any of the light intensities tested, it is believed that water stress was not an effective contributor to the *M. maximus* photoinhibition process and, in contrast, g_s might be contributing to this result. For *M. maximus* the lowest g_s was observed at the same light conditions (0 and 25% shade) in which the photoinhibition process was clearly observed. Once g_s is low and the light level is high, the energy excess could not flow to the carboxylation pathway because of carbon chloroplastic limitations that leads to an increase of reactive oxygen species (ROS). Therefore, the increased ROS levels might lead to a reduction in the PSII repair rate, leading to a higher level of photoinhibition in plants under such conditions.

Choroplastidic pigments in shade gradient

Pigments have a well-established function in capturing light energy and protecting PSI and II (Takahashi & Badger, 2011). In a controlled shade experiment with no other stressful variables, it is expected that increases in light intensity would result in reductions in chlorophyll ‘a’ and ‘b’ and increases in carotenoids (Baig, Anand, Mandal, & Bhatt, 2005; Bertamini, Muthuchelian, & Nedunchezhian, 2006; Krause et al., 2012). This behavior was observed for chl ‘a’ and ‘b’ in *M. maximus* since the lowest values were observed in 0% shade. For *U. decumbens,* the dynamics of pigment concentration were very different from what was expected for the higher and lower shade treatments. This variation may be a result of stressful conditions applied to 0% shade or indicative of how well-adapted this species is to such conditions. For *U. decumbens,* the carotenoid results were exactly the expected ones, being higher in stronger light intensity (Bertamini et al., 2006). These higher carotenoid concentrations in 0% shade treatments for *U. decumbens* were associated with effective photoprotection of PSII, as it can be seen by comparing the differences in Fv/Fm reductions at 11:30 am (Figure 2A) between the 0 and 25% shade treatments. However, for *M. maximus,* the highest values of carotenoids were observed in 0 and 80% shade, which differed from what was expected. The function of carotenoids is generally associated with photoprotection through thermal energy dissipation, via violaxanthin to zeaxanthin conversion (Takahashi & Badger, 2011). In a study with *Panicum* (*Megathyrsus*) species, Baig et al. (2005) did not find a direct relationship between light and carotenoid concentration, the same observation was made in our data. This lack of pattern in the concentration of pigments in relation to light makes us wonder if pigment concentration might be related to optimum and stressful conditions. Based on our observations, it is necessary to investigate the role of contrasting light conditions on determining the chlorophyll and carotenoid pattern and whether the response is an acclimation or a result of stressing conditions.

Conclusion

Our experiment revealed an interesting differential photosynthetic behavior between the *species U. decumbens* (signal grass) and *M. maximus* (guinea grass) in response to shade acclimation. The usual generalization that C4 grasses perform better under high light environments were only true for signal grass. For those plants, the higher levels of light (0 and 25% shade) resulted in higher values of ETR and qP and no signs of photoinhibition. Contrastingly, guinea grass evidenced, under intermediate shade levels (25 and 40%), a greater photosynthetic response (ETR and qP), similar to those obtained for signal grass acclimated to high light levels. Altogether, results indicated that guinea grass was the most suitable species for growth in environments subject to lower light intensity, and therefore, it would be more suitable for use in silvopasture systems.

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