

The superior re-sprouting performance of exotic grass species under different environmental conditions: the study case of *Paspalum atratum* (Swallen) and *Urochloa brizantha* (Hochst. ex A. Rich. - Stapf.)

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Abstract The invasive success of exotic grass species has been linked to a better physiological performance under a variety of environmental conditions. Several studies showed that disturbances such as fire and herbivory might favor invasions by exotic grasses in detriment of native species. However, studies comparing how native and exotic grasses respond to variation in environmental resources under natural conditions after a disturbance are scarce. A clear understanding on how disturbances and environmental resources influence plant populations' resistance and resilience is important, and might contribute for management actions to control invasive processes in natural ecosystems. The aim of this study was to investigate how variations in light, nutrient and

water availability influence the regrowth of native and exotic grasses after a simulated disturbance (defoliation). Two C₄ grass species with similar morphological and physiological characteristics were selected: the native *Paspalum atratum* and the African exotic *Urochloa brizantha*. The study was set up in a Cerrado sensu stricto area that was cleared for the experiment. Biomass production was monitored at regular intervals, and absolute growth rates for both grasses were calculated. Although irrigation did not promote further growth for both grasses, *U. brizantha* benefited more from fertilization and shade than *P. atratum*, sustaining higher growth rates until the end of the rainy season. We show that under natural conditions the exotic grass presented a higher regrowth ability than the native grass species, suggesting a stronger resilience to the variation in resource availability. Thus, natural disturbances might further stimulate the invasion and dominance of this exotic grass.

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1 Introduction

Biological invasions affect all ecosystems on earth (Richardson 2011). It is estimated that more than one million square kilometers of the humid and sub-humid tropics have been converted to grasslands dominated

by African C₄ grasses (Williams and Baruch 2000). This conversion is still increasing due to persistent forest clearing and pasture creation and subsequent spread of these grasses into natural areas. Exotic grasses frequently escape from planted, pasture areas, becoming invaders of native vegetation, aided in part by the opening of native communities by fire and deforestation (Williams and Baruch 2000). Invasive plants may affect floristic composition and ecosystem functioning (Hejda et al. 2009) by promoting modifications of biotic and abiotic factors, changing ecological relations, such as seed dispersal and pollination interactions (Pyšek et al. 2012), leading to direct impacts in the native flora (Vilà et al. 2011; Pyšek et al. 2012). Furthermore, biological invasions are recognized as one of the main causes of biodiversity declination, which translates into reduced ecosystem services worldwide (Pyšek and Richardson 2010).

The relative performance between native and exotic species and the consequent environment susceptibility to invasions may be related to resource availability. Communities subjected to pronounced fluctuation in their resources, either due to changes on the influx from external sources or changes in the activity of the resident organisms, will have a higher susceptibility to invasion (Grime 2001). In areas with high availability of resources, some exotic plants may present a better growth performance than the native species (Daehler 2003). Moreover, studies have also shown that some exotic plants are more efficient in areas with limited resource availability (Funk and Vitousek 2007). Exotic species usually present important functional traits for their successful establishment, such as low biomass production costs, high seed production, high growth rate, fast reproductive cycles, high tolerance to disturbance (e.g. fast resprout after fires) and high phenotypic plasticity (Daehler 2003; Foxcroft et al. 2010; Aires et al. 2014; Tooth and Leishman 2014). These traits might give to exotic grasses adaptive benefits in the gain and use of resources compared to native species, contributing to the invasion success (Rejmánek 1996; Vilà and Weiner 2004; Davidson et al. 2011; Funk 2013).

The frequency of disturbances may also contribute to exotic species invasions (Davis et al. 2000, Foxcroft et al. 2010; Masocha et al. 2011). Disturbance alter the supply of several resources, either increasing it, as for nutrients and light, or reducing it, in the case of superficial soil organic matter.

Tropical savannas are characterized by a mosaic distribution of trees and grasses, being strongly influenced by resource availability (e.g. water, nutrients, light), and by the frequency and intensity of disturbances (e.g. fire and herbivory) (Scholes and Archer 1997; Higgins et al. 2000, Sankaran et al. 2004). For instance, the Brazilian savanna (Cerrado) is an ecosystem with a high frequency of fires, every 2 or 3 years (Hoffmann et al. 2002). The Cerrado savanna is dominated by C₄ grass species, and is under heavy invasion pressure from African grass species, mostly by *Melinis minutiflora*, *Hyparrhenia rufa*, *Megathyrus maximus*, *Urochloa* spp. (brachiaria grass species) and *Andropogon gayanus* (Klink and Joly 1989; Pivello et al. 1999a, b; Hoffmann et al. 2004; Matos and Pivello 2009; Horowitz et al. 2013).

The competitive advantages of exotic species are specially important during the early stages of the invasive process, in particular during the seed germination and seedling establishment (Corbin and D'Antonio 2004; Mangla et al. 2011, Skálová et al. 2012). However, once new individuals successfully establish in the field, the competition for space and resources between exotic and native plants will be crucial for the maintenance of native populations, or the advance of exotic species (Corbin and D'Antonio 2004). In particular, the resilience of a given population will depend greatly on its ability to tolerate and regrow after disturbance, and on the use of resources under a variety of environmental conditions. In this context, studies on the regrowth capability of native and exotic grasses after disturbance are scarce, particularly in Neotropical savannas (Baruch and Jackson 2005). Due to the strong effect of exotic grasses invasions in reducing biodiversity in savannas (Pyšek and Richardson 2010), this study seek to contribute to a better understanding about the resilience capability of native and exotic grass populations in the Cerrado vegetation. Thus, the aim of this study was to test how variations in water, nutrients, and light availability influence the biomass production and regrowth of a native (*Paspalum atratum* Swallen) and an exotic grass (*U. brizantha*) species after a simulated disturbance.

2 Materials and methods

2.1 Experimental area

The experiment was set in the University of Brasilia campus (15°46'12"S; 47°52'07"W), Brasilia, Federal

District, Brazil. The field site was at an elevation of approximately 1040 m. In the region the climate is classified as Aw in Köppen-Geiger (Peel et al. 2007), with a pronounced dry season from May to September, which the mean minimum and maximum temperatures are 14 and 26 °C, respectively. During the rainy season, the mean minimum and maximum temperatures are 18 and 30 °C, respectively (Lenza and Klink 2006), with a mean annual precipitation (MAP) of about 1500 mm (Geiger et al. 2011). The soil of the experimental site is classified as Red Latosol, which is typically nutrient-poor acid soils with high levels of aluminum (Al) and iron (Fe), and poor in phosphorus (P) and calcium (Ca). Soil analysis of the field site revealed a clay content around 60 % and a sand content around 16 % (see Sect. 3).

The selected field site was a fenced area of approximately 1530 m², covered by a vegetation typical of a Cerrado sensu stricto. Fifteen months before the beginning of the experiment, the vegetation was removed and the area ploughed to homogenize the soil with the objective of giving to the treatments similar start conditions. Due the proximity of the experimental blocks (all blocks were set up within this area) and due to the overall homogenization of the soil in the experimental area prior to the start of the experiment, we assumed a similarity on the soil characteristics in all blocks and plots.

2.2 Grass species and planting procedures

To compare the performance between an exotic and a native grass, we selected the perennial C₄ African grass *U. brizantha* (Hochst. ex A. Rich.) Stapf., a species which occurs from Central-West to South territories in the African continent. *U. brizantha* have high biomass productivity when growing under full sun and under moderate levels of shade (Andrade et al. 2004). Due to its high productivity, this grass was introduced in Brazil for pasture, but rapidly became an invader species in native ecosystems and in degraded areas (Klink 1996; Pivello et al. 1999a). Currently, *U. brizantha* can be found distributed over large parts of the Brazilian territory, spread over virtually every fragment of the Cerrado biome (Pivello et al. 1999a, b). The native species selected is also a perennial C₄ grass, *P. atratum* Swallen, a species of large distribution, occurring naturally in the Brazilian biomes Cerrado, Amazônia and Caatinga (Maciel et al.

2009). Similar to the exotic *U. brizantha*, this native grass has a tussock-shape growth, fast growth rate, high productivity and good tolerance to low-fertility soils, such characteristics that has positioned this species as a viable alternative for planted pastures in Brazil, Argentina, Thailand and Filipinas (Valentim et al. 2000; Oliveira 2004). *U. brizantha* individuals was surveyed in areas with different types of soils (clay, sandy or rocky soils), under wet or drier environmental conditions and also in river banks.

In order to establish a uniform grass cover, 50 g of seeds of *P. atratum* and *U. brizantha* were sowed separately in 4 m² plots and cultivated under daily irrigation during 15 months (November 2009–February 2011) to assure grass establishment. Whenever needed new sowing was done during this period to develop a homogeneous grass cover in all plots. After 15 months of growth (February 2011), the grasses were cut about 2 cm aboveground to simulate a biomass lost due to a disturbance. In the following months the plots received freely the water provided by rainfall events. The plots did not received extra water supply during the following dry season (March–September 2011).

2.3 Experimental and treatments design

The experimental area was divided in five replicate blocks, each block being divided in three parcels of 54 m² each. One parcel was covered with a shading net and a transparent plastic which reduced the natural light by around 80 % and intercepted natural rainfall. The second parcel was covered only with a transparent plastic, thus intercepting only natural rainfall. The third parcel was not covered, thus subjected to both natural sunlight and rainfall. Each parcel was further divided in six plots of 4 m² each, separated from each other by a gap of 2 m, a total of 90 plots. In these plots the grasses were sowed as already described.

The native (G1) and exotic (G2) grasses were independently subjected to incomplete crossed treatment, resulting in six treatments combinations: (1) fertilized (N1) not fertilized (N0); (2) shaded (L1) not shaded (L0); (3) irrigated (W1) not irrigated (W0). The treatments were replicated five times (five blocks).

In the irrigation treatment (W1) a drip irrigation system was installed and set to irrigate the grasses twice a day. The volume of water used in this treatment was 37.5 L m⁻² (37.5 mm) per week,

totalizing an equivalent of 1050 mm of rain uniformly distributed from October to April. In the treatment with no irrigation (W0) the plots received only the water provided by rainfall events during the experimental period (Fig. 1). In the fertilization treatment (N1), Osmocote® inorganic fertilizer (15:9:12) was applied every month from April to July 2011 (26.7 g/m² per application). This quantity was determined based on the addition of 4 g of nitrogen per square meter (Tilman 1987; Kraaij and Ward 2006; Tomlinson et al. 2012; Barbosa et al. 2014).

After the defoliation done in February of 2011, the regrowth of the grasses was followed during the wet season by periodically harvesting the aboveground biomass to assess growth performance. The harvesting was done four times during the wet season; (1) begin of the rainy season (October 2011), (2) early middle (December 2011), (3) late middle (February 2012) and (4) at the end of rainy season (April 2012). The aboveground biomass of the grasses was collected by using pruning shears at around 2 cm above the ground. To avoid interference of one harvest in the next, the plots were divided into 32 sub-plots of 0.125 m², and the harvesting was done randomly in different sub-plots, avoiding sub-plots previously selected. For dry biomass estimates the samples were oven-dried at 70 °C for 48 h.

After the last harvesting (April 2012), soil samples of the plots W0L0N0 (natural rainfall, full sun and no

nutrient addition) without grass cover (bare soil), and with grass cover (from both grass species) were collected, mixed and sent for physical and chemical analysis. Leaf samples of both grasses were also sent for macro and micro-nutrients analysis.

2.4 Data analysis

Based on the total shoot biomass measured at each interval the absolute growth rate (AGR) was calculated. The AGR was calculated according to the formula below (Tomlinson et al. 2012; adapted from Hoffmann and Poorter 2002):

$$\text{AGR} = \frac{\text{BM2} - \text{BM1}}{60}, \quad (1)$$

where AGR defines absolute growth rate, BM2 defines aboveground dry biomass in time 2 (T2) and BM1 = aboveground dry biomass in time 1 (T1).

To calculate the AGR during the rainy season (October 2011–April 2012), the growth measurements of the grasses were divided in three intervals of 2 months: Start, represented by the absolute growth rate during the months from October 2011 up to December 2011; Middle, represented by the absolute growth rate during the months from December 2011 up to February 2012; and Late, represented by the absolute growth rate between February 2012 up to April 2012.

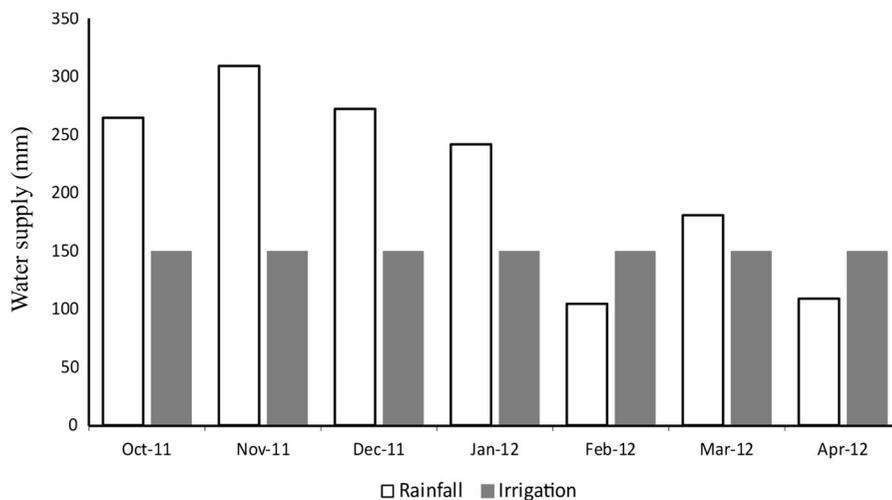


Fig. 1 The monthly water supply on the plots during the experimental period. In the irrigation treatment (W1) a drip irrigation system was installed, set to irrigate the grasses twice a day. The volume of water used in this treatment was 37.5 mm

per week, totalizing an equivalent of 1050 mm of rain uniformly distributed from October to April. In the no irrigation treatment (W0) the plots were received only the water prevented from the rainfall events during the experimental period

The data were analyzed using linear mixed models (GLMMs). The dependent variable was the AGR, and the independent variables were: species (G1 and G2), irrigation (W0 and W1), light (L0 and L1), nutrients (N0 and N1) and time (T1, T2, and T3). To account for the nested sampling design, plots within block were included as random variables. The statistical package used in the analysis was the IBM SPSS Statistics, 21.0 (IBM Corp. IBM SPSS Statistics for Windows, Version 22.0 Armonk, NY). Due to logistic constraints, it was not possible to have a full factorial design. Since there was not the L1W0 (shade and natural rainfall) treatment, the variables were analyzed independently, i.e. treatments with and without shading or treatments with and without irrigation.

3 Results

3.1 The growth of the grasses during the dry and rainy seasons

The present work followed the aboveground regrowth after defoliation of native and exotic grasses over 14 months under field conditions. During the dry season (May–October 2011), the aboveground biomass and growth rate was low and similar for both grasses (data not shown). However, during the rainy season both grasses showed a pronounced and similar increase in their biomass. Although no statistical differences were detected, the exotic grass always presented a higher biomass production than the native one (Fig. 2). The statistical analysis showed a high variation on the growth of grasses during the rainy season ($p < 0.0001$, $F_{162.959} = 8.580$, Table 1). In the beginning of the rainy season (October–December), native and exotic grasses showed a similar increase in biomass allocation, followed by a peak of biomass production between December and February. However, only the exotic *U. brizantha* sustained high growth rates in the end of the rainy season (February–April) (Fig. 2).

3.2 Irrigation and fertilization effects on the growth rates of the grasses

Our results show that irrigation and fertilization, alone, have no influence in the AGR of both grasses

($p = 0.230$ and $p = 0.866$, respectively, Table 1). However, a trend to a significant difference between exotic and native AGR was observed ($p = 0.086$). Moreover, the interaction between the factors water and time ($p = 0.058$), species and time ($p = 0.082$) and between water, nutrient and time ($p = 0.095$) also showed values close to the borderline of statistical significance (Table 1).

In plots without fertilization (N0), the absolute growth rates of native and exotic grasses were similar (Fig. 3). In the first months of the rainy season the native grass showed higher AGR, however, in late rainy season, only the exotic grass maintained a high AGR, while the native grass species showed a decreased in the absolute growth rate (Fig. 3). Under fertilization treatment this trend was observed in the first months. However, under fertilization, the AGR presented by the exotic grass was always higher than that of the native grass. Moreover, both species showed a decline in the AGR at the end of the rainy season (Fig. 3). In contrast, the native grass did not show a positive response to fertilization; on the contrary, negatives values of AGR were detected at the end of the rainy season (Fig. 3).

3.3 Effect of fertilization on the growth rates of the grasses under shade

Due to logistic constraints (impossibility to set up a shaded environment under natural rainfall), it was not possible to analyze the influence of irrigation and the interaction between irrigation and shade. However, it was possible to evaluate how shade influences the response of the grasses species to fertilization. Shade ($p = 0.125$) and fertilization ($p = 0.592$) alone did not influence the AGR values of both grasses (Table 2). Moreover, no significant differences were found for the growth rates of native and exotic grasses growing under shade ($p = 0.147$) (Table 2). However, shade affected the AGR over time ($p < 0.0001$, $F_{162.898} = 15.166$), leading to significant variations in the AGR during the growing season (Table 2). Furthermore, significant results were detected in the interactions among fertilization and time ($p = 0.014$, $F_{162.898} = 4.398$), species and time ($p = 0.011$, $F_{162.898} = 4.685$) and in the interaction between shade, species and time ($p = 0.018$, $F_{162.898} = 4.124$) (Table 2). Our analyses suggest that the effects

Fig. 2 The average aboveground biomass produced during the rainy season (October 2011–April 2012) of the grass species *P. atratum* and *U. brizantha*. Time 1 (October 2011–December 2011), time 2 (December 2011–February 2012) and Time 3 (February 2012–April 2012). Error Bars represents 95 % confident intervals. *ns* no significant; * $p > 0.05$; *** $p > 0.0001$

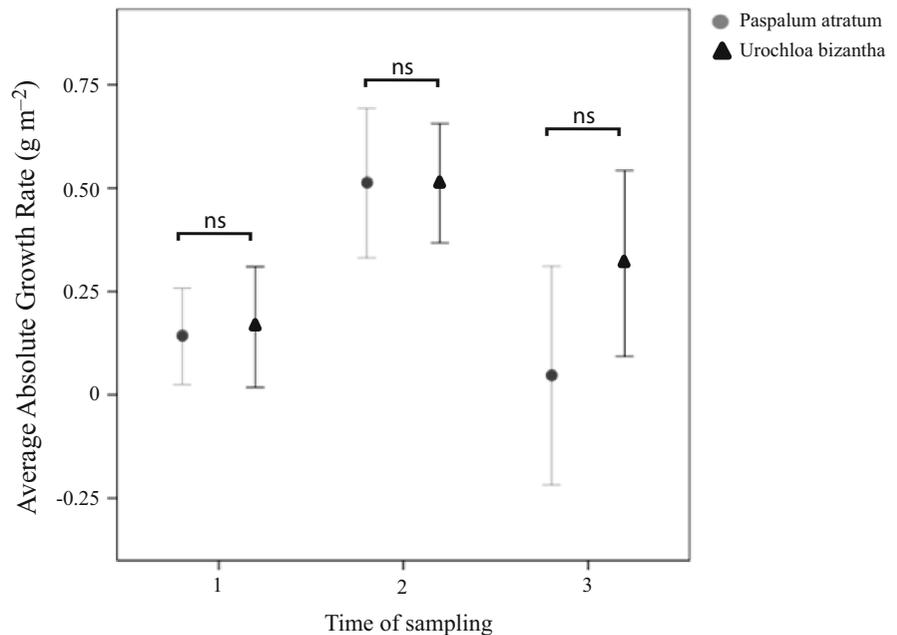


Table 1 Results from the general linear mix models analysis testing the effects of irrigation, fertilization, time and species on the absolute growth rate (AGR) of grass species *P. atratum* and *U. brizantha*

	Degrees of freedom	F-value	p value
Intercept	5.321	30.423	0.002
Irrigation (W)	163.374	1.451	0.230
Fertilization (N)	163.252	0.028	0.866
Species (S)	163.374	2.980	0.086
Time (T)	162.959	8.580	0.000
W × N	163.252	0.898	0.345
W × S	163.374	1.081	0.300
W × T	162.959	2.895	0.058
N × S	163.252	1.073	0.302
N × T	162.959	2.059	0.131
S × T	162.959	2.545	0.082
W × N × S	163.252	0.227	0.634
W × N × T	162.959	2.385	0.095
W × S × T	162.959	0.941	0.392
N × S × T	162.959	0.189	0.828
W × N × S × T	162.959	0.351	0.705

The block and plot was used as random variables in the model of the treatments on the AGR of the grasses become more evident throughout the growing period (Fig. 4).

3.4 Soil physical and chemical analysis of the experimental area

The soil analysis of the experimental area revealed the presence of an acid sandy-loam soil, pH between 4.5 and 4.8 and a relatively high concentration of potassium, sulfur, iron and manganese (Table 3). The soil of the area is classified as Red Latossoil, the most common type of soil in the Cerrado biome (Reatto et al. 2008). Soil samples from plots covered by *P. atratum* and *U. Brizantha* showed similarities in the quantities of most mineral elements, however, there were differences in the amounts of sulfur and manganese, which were lower in plots covered by *P. atratum* (Table 3). In contrast, plots with native grass presented a higher amount of organic matter. The base saturation (V) and cation exchange capacity (CEC) was low for both grasses, and similar to bare soil (Table 3). The most evident differences between bare soil and soils covered with grasses were the lower quantities of potassium and iron elements in the first case (Table 3). Furthermore, the grasses did not interfere in other relevant parameters such as soil pH and fertility, and had a minor effect on the soil organic matter.

Fig. 3 Average absolute growth rate (AGR) of the grass species *P. atratum* and *U. brizantha* during the rainy season (from October 2011 up to April 2012). Time 1 (October 2011–December 2011), time 2 (December 2011–February 2012) and Time 3 (February 2012–April 2012). Error bars represent 95 % confident intervals. The figure represents the results showed in Table 1. ns no significant; * $p > 0.05$; *** $p > 0.0001$

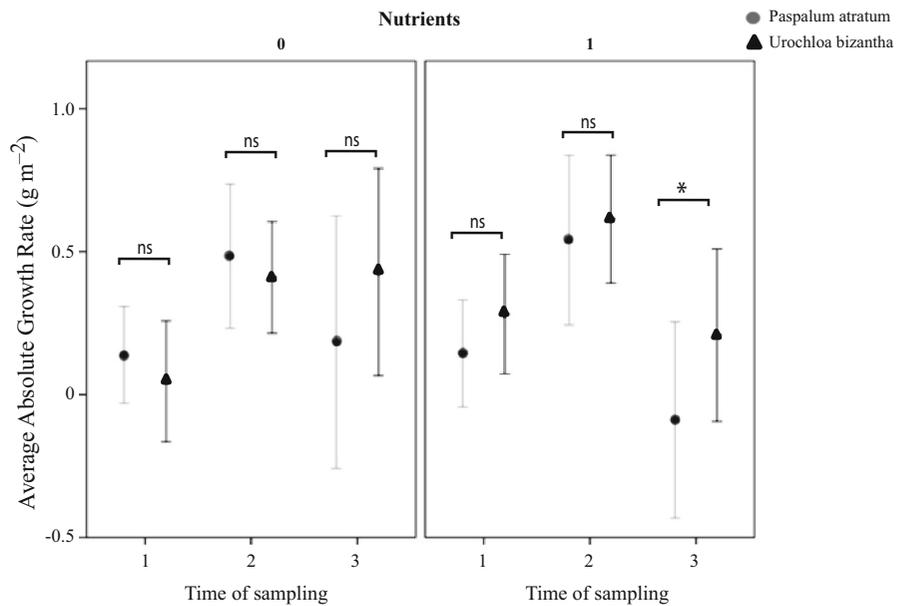


Table 2 Results from the general linear mix models analysis testing the effects of shade, fertilization, time and species on the absolute growth rate (AGR) of grass species *P. atratum* and *U. brizantha*

	Degrees of freedom	F-value	p value
Intercept	6.052	21.692	0.003
Shade (L)	165.233	2.380	0.125
Fertilization (N)	164.600	0.289	0.592
Species (S)	165.233	2.125	0.147
Time (T)	162.898	15.166	0.000
L × N	164.600	1.397	0.239
L × S	165.233	0.003	0.959
L × T	162.898	2.430	0.091
N × S	164.600	0.928	0.337
N × T	162.898	4.398	0.014
S × T	162.898	4.685	0.011
L × N × S	164.600	0.207	0.650
L × N × T	162.898	1.542	0.217
L × S × T	162.898	4.124	0.018
N × S × T	162.898	0.006	0.994
L × N × S × T	162.898	0.368	0.693

The block and plot was used as random variables in the model

3.5 Leaf nutrient analysis of the grasses

Nutrients analysis of leaves of *U. brizantha* and *P. atratum* showed similar contents of phosphorus,

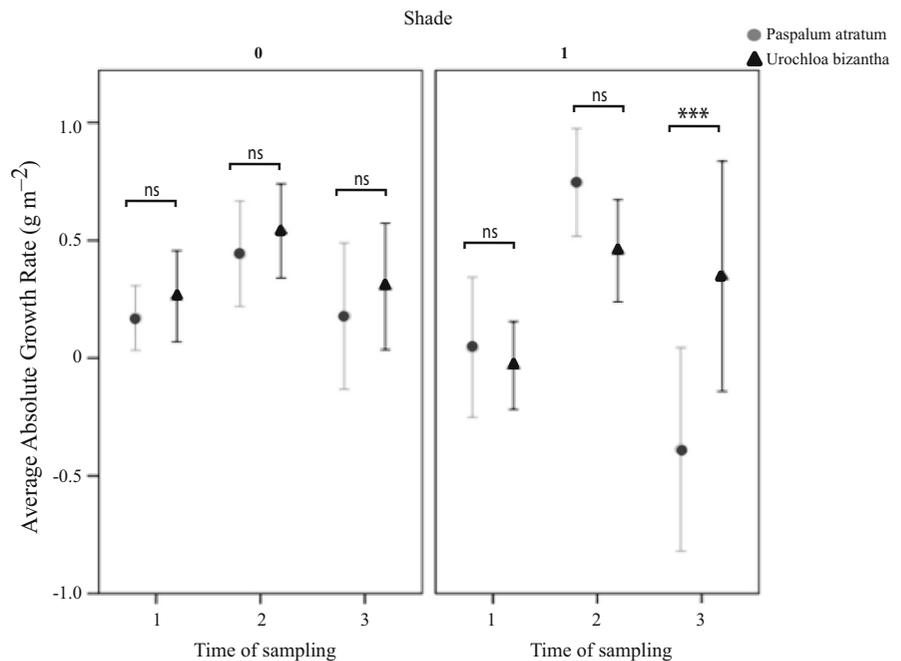
sulfur, boron, zinc and manganese (Table 4). A higher concentration of potassium, magnesium and iron was found in the leaves of *P. atratum*, and a higher concentration of nitrogen and calcium was found in the leaves of *U. brizantha* (Table 4).

4 Discussion

4.1 The growth of the grasses during the dry and rainy seasons

Studies comparing the growth of grasses under diverse experimental conditions have showed that exotic grasses usually have higher rates of growth when compared to native species (D'Antonio and Vitousek 1992; Pivello et al. 1999a; Rossiter et al. 2003; Han et al. 2012). Moreover, previous studies suggested that the high growth rates are possibly related to the fact that invasive species tend to have higher photosynthetic efficiency and better performance in the acquisition of resources as water and nutrients, when compared to native grasses (D'Antonio and Vitousek 1992; Foxcroft et al. 2010; Firn et al. 2012). The statistical analysis showed a high variation on the growth of grasses during the rainy season ($p < 0.0001$, $F_{162.959} = 8.580$, Table 1). When dividing the growing season in periods of 2 months, the results show that

Fig. 4 Average absolute growth rate (AGR) of the grass species *P. atratum* and *U. brizantha* growing under different nutrient levels (*NO* no nutrient addition and *NI* nutrient additions) during the rainy season (from October 2011 up to April 2012). Time 1 (October 2011–December 2011), time 2 (December 2011–February 2012) and Time 3 (February 2012–April 2012). Error bars represents 95 % confident intervals. The figures represent the results showed in Table 2. *ns* no significant; * $p > 0.05$; *** $p > 0.0001$



native and exotic grasses had the peak of biomass production between December 2011 and February 2012. However, only the exotic *U. brizantha* sustained high growth rates in the end of the rainy season

(February–April) (Fig. 2). The higher performance of the exotic grass after defoliation denotes its great ability to recover rapidly after disturbance, increasing their potential to spread over disturbed sites.

Table 3 Physical and chemical analysis of soil samples from the experimental area collected after the end of the experiments: bare soil—without vegetation, soil covered with *P. atratum* and soil covered with *U. brizantha*

	Bare soil	<i>P. atratum</i>	<i>U. brizantha</i>
Silt:clay:sand (%)	16:23:61	17:30:53	16:23:61
Soil classification	Clay loam–sandy	Clay loam–sandy	Clay loam–sandy
Water pH	4.7	4.5	4.8
Organic material (dag kg ⁻¹)	2.4	3.2	2.5
P (mg dm ⁻³)	0.5	0.5	0.6
K (mg dm ⁻³)	22	32.6	37.2
S (mg dm ⁻³)	7.5	2.6	6.8
Ca (cmolc dm ⁻³)	0.2	0.4	0.3
Mg (cmolc dm ⁻³)	0.1	0.1	0.1
Al (cmolc dm ⁻³)	0.2	0.3	0.2
CTC total (cmolc dm ⁻³)	4.0	5.7	3.8
V (%)	10	11	13
m (%)	33	33	29
B (mg dm ⁻³)	0.1	0.1	0.1
Zn (mg dm ⁻³)	1.5	0.9	1.6
Fe (mg dm ⁻³)	55.5	83	93.2
Mn (mg dm ⁻³)	41.7	16.9	65
Cu (mg dm ⁻³)	1.1	1.1	1.3

Table 4 Leaf nutrients analysis of *P. atratum* and *U. brizantha*

	<i>P. atratum</i>	<i>U. brizantha</i>
N (g kg ⁻¹)	0.7	0.9
P (g kg ⁻¹)	0.6	0.5
K (g kg ⁻¹)	7.1	4.7
Ca (g kg ⁻¹)	7.9	10
Mg (g kg ⁻¹)	4.7	1.8
S (g kg ⁻¹)	0.6	0.8
B (mg kg ⁻¹)	6	5
Zn (mg kg ⁻¹)	23	27
Fe (mg kg ⁻¹)	647	119
Mn (mg kg ⁻¹)	166	164
Cu (mg kg ⁻¹)	12	6

The experiments were conducted in an experimental area located at the University of Brasilia, between May 2011 and April 2012. Leaf certificate of analysis: field agricultural and environmental analysis

4.2 Irrigation and fertilization effects on the growth rates of the grasses

Due to the irregularity in the rainfall distribution during the rainy season in the Cerrado biome (Assad and Evangelista 1994; Baruch and Jackson 2005), the expectation was that the regular irrigation regime would increase the (re)growth of grasses compared to treatments subject to natural rainfall. However, no significant differences were detected in the growth rates for both species when compared to the individuals growing under regular (W1) or irregular (W0) water regimes (Fig. 1). These results suggest that the regrowth of grasses established at least 15 months is not affected by the dry spells observed during the rainy season, as both native and exotic grasses showed similar performance in their biomass allocation to aboveground in both water treatments (Table 1, W interaction \times S \times T, $p = 0.392$). Furthermore, although it is reported that irrigation significantly promoted the sprouting of exotic grasses (e.g. *M. minutiflora* and *H. rufa*, see Baruch and Jackson 2005) in comparison to native grass species, it is suggested that the water use efficiency of the plants is not among the factors that explain the differences in performance of exotic native species (Daehler 2003).

In plots without fertilization (N0), the absolute growth rates of native and exotic grasses were similar

(Fig. 3). Under fertilization treatment, the AGR presented by the exotic grass was always higher than that of the native grass. Moreover, both species showed a decline in the AGR at the end of the rainy season (Fig. 3). The ability of invasive species to rapidly resprout or even present a high seedling growth has been linked to their greater ability to mobilize resources, especially nitrogen, when compared to native species, which represents a strong competitive advantage for the exotic plants (Lambers and Poorter 1992). In particular, *Urochloa* species are characterized by their ability to survive in different soils conditions, including acidic and nutrient-poor soils (Andrade et al. 2004) as is the case of the soils of savanna formations in the Cerrado (Reatto et al. 2008). In contrast, the native grass did not show a positive response to fertilization; on the contrary, they showed negatives values of AGR at the end of the rainy season (Fig. 3). These results indicate that the AGR of the native grass may decrease during the growing season. Despite the low availability of several nutrients, the Cerrado soils are eventually subjected to temporary inputs of nutrients due to the mineralization of burned plant material during a fire (Nardoto et al. 2006). Studies show that these nutrient inputs are more beneficial to exotic than native plant species (Huenneke et al. 1990; Kolb et al. 2002; Vallano et al. 2012), supporting the hypothesis that high frequency of disturbance is a major determinant of exotic species success in disturbed areas (Davis et al. 2000; Masocha et al. 2011). Our results corroborate the idea that exotic grasses have a higher capacity to use nutrients more rapidly and efficiently when compared to native grass, increasing the chances of establishment after a disturbance. This helps to explain the expansion of alien species in several areas of the Cerrado biome.

It is also important to mention that the exotic grass presented a higher performance of growth compared to *P. atratum*, a native species which also presents a high productivity and performance under different conditions (Valentim et al. 2000; Oliveira 2004). This tiny difference in growth pattern can make a huge difference over time, and exotic grasses may become a major threat to native grass populations of the Cerrado, especially with the ongoing increase of human activities such as soil fertilization and increased fire frequency. These observations also contribute to understand why exotic grasses benefit more than native grasses from soil fertilization in

pasture areas and even in programs of reforestation with native grasses and tree seedlings (Martins et al. 2004).

4.3 Effect of fertilization on the growth rates of the grasses under shade

The native and exotic grasses growing under natural light conditions showed no significant differences in their absolute growth rates, although throughout this period the AGR values of the exotic grass was always higher than those calculated for the native grass (Fig. 4). Under shade, the native *P. atratum* showed higher growth rates in the first months, however, this species showed a sudden drop in the AGR in the end of the rainy season (Fig. 4). In contrast, *U. brizantha* sustained a high growth rates until the late rainy season, confirming its ability to maintain a high biomass production until the end of the growing period (Fig. 4). *Urochloa* species have a good capacity to adapt to different environmental conditions, including shaded environments. For instance, Dias-Filho (2000) observed that *U. brizantha* and *U. humidicola* reduced their growth rates under shade. However, our study also shows that even the individuals subjected to shade showed increase in their biomass production. Other exotic grasses, such as *M. minutiflora*, *M. maximus* and *Schizachyrium condensatum* also showed a great capacity to tolerate low light conditions (D'Antonio et al. 2001; Ammond et al. 2013).

Our results demonstrate that the exotic grass *U. brizantha* presented an overall better performance in the absolute growth rates than the native grass *P. atratum* under full light conditions, also keeping a higher AGR under shade in the late rainy season. These characteristics suggest that light conditions may not limit the spread of *U. brizantha* to shaded environments of the Cerrado.

4.4 Soil physical and chemical analysis of the experimental area

Soil samples from plots covered by *P. atratum* and *U. brizantha* showed similarities in the quantities of most mineral elements (Table 3). In contrast, plots with native grass presented a higher amount of organic matter. Furthermore, we found no evidence that different grass species have dissimilar interferences in other relevant soil parameters, such as, soil pH and

fertility, and had a minor effect on the soil organic matter.

In general, macro and micronutrients are more available during the rainy than during the dry season, due the fact that water is required for nutrient mobilization from the soil to the plants. Moreover, the microbial activity is also higher during the warm rainy season, increasing the nutrients availability in the soils (e.g. Pivello et al. 2010). Thus, in the beginning of the rainy season, the soils nutrients become more available and are rapidly overtaken by grasses to build their structural components (biomass), reducing its availability in the soils overtime. As invasive grass species showed efficiency in resource-limited habitats (Funk and Vitousek 2007), apparently these species demonstrate a lower nutritional requirement compared to native grasses species.

4.5 Leaf nutrient analysis of the grasses

The results obtained from the leaf nutrients analysis suggested that the native grass have higher absorption rates of potassium, magnesium, iron and copper in comparison to *U. brizantha*. In contrast, the exotic grass seems to have higher absorption rates of calcium, considering the reduced amount of this element in plots cultivated with *U. brizantha*. Despite the differences in the soil concentration of sulfur, the differences in the amounts of leaf elements between the two species were minor, suggesting similarities on the leaf nutrient-use strategies between these grasses (Table 4). Consequently, the better performance of exotic over the native grass observed here might be not related directly to differences in the mineral nutrient metabolism of them.

4.6 Final considerations

This study aimed to compare regrowth potential of two grasses, the native *P. atratum* and the exotic *Urochloa brizantha* after aboveground defoliation (simulating disturbances such as fire and herbivory) under different resource conditions. In general, the exotic showed higher growth rates, in particular at the end of the rainy season, and higher average biomass production compared with the native grass. Continuous water

availability did not enhance growth of both grass species. However, the exotic grass showed a better performance when grown in fertilized plots, and kept growing when subjected to shade.

The results of this study suggest that the exotic *U. brizantha* might increase its distribution under intensification in frequency of disturbances. In agreement with previous studies (Pivello et al. 1999a; Baruch and Jackson 2005; Masocha et al. 2011), our results suggest that exotic grasses performed better under a variety of conditions associated with the increased frequency of disturbance, and changes in land use might lead to modifications in the savanna grass composition, favoring the spread of exotic grasses and displacement of the native ones. Furthermore, considering also that exotic grasses reduce survival rates of savanna tree seedlings (Hoffmann and Haridasan 2008), the shifts in the grass cover of savanna areas may also lead to substantial effects on the dynamics of the tree community, with likely consequences for ecosystem structure and function. As species of the genus *Urochloa* are among the most common and aggressive exotic grass species introduced in the Cerrado biome (Pivello et al. 1999b; Almeida-Neto et al. 2010; Lannes et al. 2012), the ongoing increase of these and other exotic grasses in the Brazilian savanna ecosystems will likely lead to severe changes in the plant population composition and, consequently leading to losses in biodiversity and ecological services provided by the natural plant populations of the Cerrado Biome.

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