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Effects of native and exotic grasses on the survival and growth of tree seedlings in a neotropical savanna

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Abstract

Invasive grasses have spread over large areas of ancient savannas worldwide and have extensively impacted native landscapes in the neotropics. However, our understanding on how the displacement of native by exotic grasses may affect tree-grass coexistence in neotropical savannas is still poor. The present study tested the imposed effects of an exotic grass (*Urochloa brizantha*) and a native grass (*Paspalum atratum*) on survival rates, stem growth and biomass of seedlings of native tree species representative of savanna physiognomies of the Cerrado biome. We conducted multiple tree species experiments under natural field conditions subjected to experimental manipulations of light, water supply and fertilization. We found that both the native and exotic grass species reduced tree seedling survival, and these effects were not alleviated by shade or fertilization. Seedling stem length was reduced by the presence of either native or exotic grasses, irrespective of fertilization. Seedling biomass was reduced by both native and exotic grasses, irrespective of light conditions, irrigation, or fertilization. The negative impacts of the exotic grass on seedling survival and growth were larger than those imposed by the native grass, indicating that the displacement of native by exotic grasses can strongly impact recruitment potential of tree species. Due to the magnitude of exotic grass invasiveness in neotropical savannas, and its potential impacts on recruitment patterns of native trees, adequate policies and management plans are needed to control exotic grass spread to conserve native biodiversity and ecosystem services.

Keywords: competition; grasses; recruitment; savanna; seedling

Introduction

Biological invasions are recognized as one of the main causes of declines of biodiversity, which translates into reduced ecosystem services worldwide (Foxcroft et al. 2010; Pyšek et al. 2012; Dostál et al. 2013; Linders et al. 2019). Biological invasions by exotic grasses are usually related to the conversion of native vegetation to pastures for livestock, leading to extensive and significant land cover change in tropical and subtropical regions (D'Antonio and Vitousek 1992; Masocha et al. 2011; Damasceno et al. 2018). African C₄ grasses have been widely used as forage for livestock, and frequently escape from pasture areas and invade native vegetation usually promoted by frequent fires and deforestation (Baruch and Jackson 2005; Foxcroft et al. 2010; Bao et al. 2015; Ratnam et al. 2016).

In neotropical savannas, such as those occurring over the Brazilian highlands, many African grasses selected for high quality forage and seed production were introduced in the 1970s (Pivello et al. 1999b, a; Williams and Baruch 2000; Zenni and Ziller 2011; Damasceno et al. 2018). Recent assessment of the distribution of exotic grasses over the country revealed that exotic species are present in virtually every fragment of Brazilian savanna (Pivello et al. 1999a, b; Beuchle et al. 2015). Whether promoted by human-induced environmental change or not, the spread of invasive grasses over native savannas in the Neotropics has modified species composition and vegetation structure so intensely that these may be viewed as novel ecosystems; in comparison to the ancient savanna vegetation, these derived savannas are poorer in species composition, dominated by exotic species, and have reduced ecosystem services (Veldman 2016).

Exotic grasses usually perform better than native grasses when sharing the same area. In an Australian savanna, African grasses were shown to exhibit higher germination, growth rates and biomass production than native species (Han et al. 2012). In the neotropics, African grasses were shown to allocate more biomass to assimilating surfaces (Williams and Black 1994) and respond better to fertilization in comparison to native grasses (Bustamante et al. 2012). A comparative study conducted in a Brazilian savanna revealed that the African grass *Urochloa brizantha* benefited more from fertilization and shade, and sustained a higher regrowth ability after clipping than the native *Paspalum atratum* (Caramaschi et al. 2016). Indeed, the success of introduced African C₄ grasses in the neotropics might be also attributed to their water-stress evasion strategy and high nitrogen use efficiency (Foxcroft et al. 2010).

The direct impacts of exotic grasses on tree seedling recruitment and vegetation cover are diverse. In general, exotic grass species tend to suppress the initial growth stages of native tree species (Davis et al. 2004; Martins et al. 2005; Manea and Leishman 2015), which might lead to an overall reduction of recruitment rates of native trees in invaded savannas (Hoffmann and Haridasan 2008; Setterfield et al. 2018). Several studies suggest that competition for soil resources (water and nutrients) represent a major way by which grasses suppress tree seedlings

(Van Der Waal et al. 2009; Cramer et al. 2012; Barbosa et al. 2014a; Tomlinson et al. 2019). Therefore, a more complete assessment of the impacts of exotic grasses on tree recruitment requires that such effects be compared with that produced by native grass for a better understanding of the long-term impact of exotic grasses on savanna vegetation dynamics and structure.

In this study, we investigated the impacts of a native and an exotic grass species on seedling survival and growth of savanna tree species native to the Brazilian Cerrado during their first growing season. The Cerrado is the second largest biome in Brazil, covering around 25% of the territory and spreading mostly over the highlands of central Brazil (Ribeiro and Walter 2008; Borghetti et al. 2019). Most of this biome occurs on deep well-drained, nutrient-poor, acid soils with high levels of aluminium and iron (Haridasan 2008; Franco et al. 2014). This biome is composed of forest, savanna, and grassland physiognomies, with around 70% of the biome covered by savanna (Ribeiro and Walter 2008). Fire frequency, edaphic factors and water availability are among the major determinants of variation in vegetation cover (Hoffmann et al. 2012; Franco et al. 2014). Large areas of this biome, in particular savanna and grassland physiognomies, have been invaded by several exotic grasses, so the Cerrado is a relevant area to study the impacts of exotic grass invasion on the recruitment of native tree species.

We sought to compare the impacts of exotic and native grasses on potential tree seedling recruitment under different resource constraints. To do this we grew seedlings of multiple native tree species in grass plots composed of either the native or exotic grass species, combined with experimental manipulations of light, water, and fertilizer. Considering that grasses and tree seedlings compete for resources (van Langevelde et al. 2010; Donzelli et al. 2013), we expected that the experimental addition of water and nutrients will reduce the negative impacts of grasses on tree seedling survival and growth (hypothesis 1). Although the growth of grasses is usually suppressed by shade (Siemann and Rogers 2003; Barbosa et al. 2014b), we expected that shade would favour tree seedling survival and growth by reducing the competitive ability of the grasses (hypothesis 2). Considering that exotic grasses strongly reduce survival and growth of native tree seedlings (Davies et al. 2005; Hoffmann and Haridasan 2008; Zenni et al. 2019), we expected a stronger suppression of tree seedling growth by the exotic than by the native grass (hypothesis 3).

Material and Methods

Grass species

The alien species *Urochloa brizantha* (Hochst. ex A. Rich.) Stapf. is a perennial C₄ grass which occurs from the Central to Southern Africa (Pivello et al. 1999b). This species shows high biomass productivity when growing under full sun and under moderate levels of shade (Andrade et al. 2004). Due to its high rates of productivity, this grass was introduced into Brazil for pasture

back in the 1970s, but rapidly became an invasive species of native ecosystems over large parts of Brazil (Pivello et al. 1999a, b).

The native grass *Paspalum atratum* Swallen. is a perennial C₄ grass which occurs naturally in the Cerrado, Amazon and Caatinga biomes of Brazil (Maciel et al. 2009). This native grass has a tussock-shape growth, fast growth rate, high productivity and tolerates low-fertility soils. Due to these characteristics, this grass species is also a viable alternative for pastures (Valentim et al. 2000).

Tree species

We selected six locally abundant, semideciduous to deciduous, tree species representative of the vegetation cover in savanna physiognomies of the Cerrado (Ratter et al. 2003; Sano et al. 2008) (Table S1). The tree seeds used to produce seedlings were collected from at least five adult individuals of each species in natural areas of savanna located in the Federal District of Brazil. The seeds were stored in paper bags at room temperature (around 23°C) until use. The seeds were germinated in climate chambers set at constant temperature of 30°C and photoperiod of 12h (white light). After radicle protrusion, the seedlings were transferred to 1L plastic bags filled with a mixture of red latosol soil and washed sand (3:1) fertilized with NPK (10:10:10). To avoid seedling mortality due to desiccation, the seedlings were irrigated daily until they were transplanted into the experimental area.

Experimental area

The experiment was conducted at the University of Brasilia campus area (15° 46'12" S; 47° 52'07" W), Brasília, Federal District, Brazil. The climate in the region is classified as Aw in the Köppen-Geiger system (Peel et al. 2007), with a pronounced dry season from May to September, and a rainy season from October to April. During the rainy season, the mean minimum and maximum temperatures are 18 and 30°C, respectively, with an annual precipitation (MAP) of about 1500 mm (Silva et al. 2008). The field site is at an elevation of approximately 1040 m. The soil of the experimental site is classified as red latosol soil, which is typically nutrient-poor and acidic with high levels of aluminium (Al) and iron (Fe), and poor in phosphorus (P) and calcium (Ca). Soil analysis revealed a clay content around 60% and a sand content lower than 8%.

The field site selected for this study was originally covered by a savanna vegetation regionally named as *cerrado sensu stricto*, which is the most representative vegetation type of the Cerrado biome (Borghetti et al. 2019). Two years before the beginning of the experiment, the vegetation was removed, and the area was ploughed to homogenize the soil to give all treatments similar start conditions. This experimental area was fenced and divided in five blocks; each block being further divided into three parcels of 54 m² each. Each parcel was then divided in six plots of 4 m² each, separated from each other by a gap of 2 m (Figure S1).

Grass planting

To test the impacts of the native and exotic grasses on survival and growth of tree seedlings, seeds of both grass species were first sown in the experimental plots. Two plots of each parcel were planted with the native *P. atratum* (referred to as treatment G1), two plots were planted with the exotic *U. brizantha* (G2), and in two plots no grass was sown, and the soil was kept bare by regular hand-picking of emerging seedlings (G0). The grasses were seeded during the rainy season (December) of 2009 (~50 g of seeds per plot) and irrigated regularly to avoid desiccation and grass mortality. By November of 2011, almost two years after grass planting, a dense and uniform grass cover was visibly established in each respective plot.

Experimental design

In each block different treatment combinations involving variation in grass competition (G0, G1, G2), water (W0, W1), light (L0, L1) and nutrients (N0, N1) were set using a nested split plot design (Figure S1). Light and water treatments were applied at the whole-plot level, and nutrient and grass competition treatments were applied at the sub-plot level. To test whether tree species differed in their ability to tolerate shade and whether shade affected the competitive effects of grasses on the seedlings, we included a low light treatment representing the level of shading (around 20% natural light) recorded under closed canopies of savanna tree species (Kanegae et al. 2000; Bauhus et al. 2004). The light treatment was divided in two levels: an uncovered whole plot subjected to full sunlight and natural rainfall (L0); a whole plot covered by a 2 m-high transparent plastic blocking no solar radiation (L0); a whole plot covered by a 2 m-high transparent plastic plus a shade net consisting of one layer of polyurethane shade cloth blocking 80% of incident solar radiation (L1). As the transparent plastic cover and shade cloth intercept natural rainfall, in these parcels a drip irrigation system was installed to irrigate the seedlings twice a day (W1). The amount of water supplied to the seedlings by irrigation was equivalent to a rainfall of 37.5 mm per week. The uncovered (L0) whole plots were subjected to natural rainfall (W0). According to the National Meteorology Institute (INMET), the precipitation in the region during the experimental period (Dec 2011 - Jun 2012) was 1071 mm, which is equivalent to rainfall of 41.2 mm per week.

To test whether the tree species differed in their response to fertilization, and whether fertilization affected the competitive effects between grasses and seedlings, three out of six subplots of each whole plot were fertilized with a slow-release fertilizer (Osmocote ® NPK 15:9:12, 106 grams per plot) (Kraaij and Ward 2006). Four applications were made during the experimental period (N1), and the respective controls consisted of subplots with no addition of fertilizer (N0).

Tree seedling planting

Before transplanting the seedlings from the plastic bags into the experimental area, we randomly selected 10 seedlings of each species for initial measurements: root and stem length and dry biomass, number of leaves and presence/absence of cotyledons. For dry biomass estimates, the seedlings were dried in an oven at 70°C / 24h before weighing them (Table 1). By the end of November 2011, two seedlings of each tree species were planted per plot, which resulted in 10 seedlings per treatment combination. The seedlings were carefully selected from the pool and randomly planted in holes previously prepared in the ground. During the first days after planting, the seedlings were abundantly irrigated to assure a high rate of seedling establishment in the experimental area.

Seedling mortality and growth were monitored from December 2011 to April 2012. At the end of the experiment, the number of surviving seedlings per species per treatment combination was recorded. The longest stem length (from ground level to shoot tip) was measured for each seedling. After that, the shoots were harvested and dried at 70°C for 24 hours for shoot biomass estimates.

Data analysis

General linear mixed models (GLMM) were performed to test the effects of irrigation (W0, W1), light condition (L0, L1), grass (G0, G1, G2) and fertilization (N0, N1) on the stem length and shoot biomass of seedlings of six savanna species, whereas generalized linear mixed models with binomial error distribution and logit link type were used for survival. Because light and irrigation treatments were not fully crossed, we analysed the effects of light and irrigation on different models. We analysed the effects of irrigation (W0, W1) only on the uncovered whole plots (L0), and the effects of light (L0, L1) only on the irrigated treatment (W1). For modelling the seedling stem length, only the surviving seedlings at the end of the experiment were considered. In all models, three-level interactions among the above-mentioned treatments (irrigation, grass and nutrients; or light, grass and nutrients) were included. We included tree species and blocks as random effects in the models. The interaction variable combining light and irrigation treatments nested within blocks were also included as random effects in models of seedling survival under natural light.

We first tested whether all random effect terms were necessary in the full model using bootstrapped confidence intervals. Where 95% confidence intervals for variances of random terms included 0, those terms were removed as they were assumed not to be significantly different from 0. We compared all possible subset models for each response variable (“survival”, “stem length” and “biomass”), including the null model, using the AIC (Akaike Information Criterion) (Christ 2009). Log natural and square-root transformations of the raw data of biomass and stem length, respectively, were necessary to normalize the residuals. We performed Type III Wald chi-

square tests to evaluate the significance of predictors in the most parsimonious models ($\Delta AIC < 2$). Posthoc multiple comparison tests were conducted using the Tukey method (command lsmeans (Lenth 2016). All analyses were run in R (R Core Team 2017).

Results

Effects of treatments on seedling survival

The probability of seedling survival was influenced by irrigation (Type III Wald chi-square tests, $\chi^2 = 5.71$, $p = 0.017$) and the interactions between the presence and type of grass x nutrient supply under natural light conditions (Type III Wald chi-square tests, $\chi^2 = 16.23$, $p = 0.0003$), and between the presence and type of grass x nutrient supply x light condition under the irrigated conditions (Type III Wald chi-square tests, $\chi^2 = 11.75$, $p = 0.003$; Table 2; supplementary material, Tables S2 and S3).

Our results indicate that under full sun and with soil fertilization tree seedlings growing in the absence of grasses had higher survival probability than those cultivated either with native or exotic grass (Figure 1A), but without fertilization seedling survival did not differ among grass treatments (Figure 1A). Under irrigated conditions without soil fertilization, seedling survival did not differ among grass treatments (Figure 1B). However, under irrigated condition with soil fertilization, seedling survival was lower when cultivated either with exotic or native grass but only when exposed to natural light condition (Figure 1B). Finally, irrigation increased seedling survival under full sun conditions irrespective of the presence of grasses and fertilization (Figure S2).

Effects of treatments on seedling stem growth

The seedling stem length was influenced by the presence of grasses (under natural light; Type III Wald chi-square tests, $\chi^2 = 6.58$, $p = 0.037$; supplementary material, Table S4) and by the interaction between the presence and type of grasses x light conditions (under irrigation; Type III Wald chi-square tests, $\chi^2 = 13.82$, $p = 0.001$; supplementary material, Table S5). Although present amongst the most parsimonious models ($\Delta AIC < 2$; Table 2), irrigation (Type III Wald chi-square tests, $\chi^2 = 0.37$, $p = 0.54$), nutrient supply (Type III Wald chi-square tests, natural light conditions: $\chi^2 = 2.12$, $p = 0.15$; irrigated conditions: $\chi^2 = 2.64$, $p = 0.10$), and the interaction between the presence and type of grass x nutrient supply (Type III Wald chi-square tests, $\chi^2 = 2.98$, $p = 0.23$) did not affect seedling stem length.

Under irrigated and full sun, seedling stem length was not affected by the presence of either native or exotic grasses (Figure 2A) Under shade conditions, the stem length increased, except when the seedlings were grown in the presence of the exotic grass (Figure 2A). Although

not statistically significant, fertilization marginally promoted stem elongation of the tree seedlings under irrigation and in absence of grasses (Figure 2B).

Effects of treatments on seedling biomass

Seedling biomass was influenced by the presence of grasses (Table 2). Under irrigated conditions, seedling biomass was strongly affected by the presence of grasses, but exotic grasses exerted a stronger effect than native grasses on this parameter (Type III Wald chi-square tests, $\chi^2 = 100.22$, $p < 0.0001$; Table S7; Figure 3A). Under full sun, tree seedling biomass was strongly affected by the presence of both native and exotic grasses (Type III Wald chi-square tests, $\chi^2 = 72.23$, $p < 0.0001$; Table S6; Figure 3B). Although present amongst the most parsimonious models ($\Delta AIC < 2$, Table 2), irrigation (Type III Wald chi-square tests, $\chi^2 = 0.66$, $p = 0.42$), nutrient supply (natural light conditions: Type III Wald chi-square tests, $\chi^2 = 0.25$, $p = 0.62$; irrigated conditions: $\chi^2 = 0.92$, $p = 0.34$), and light conditions (Type III Wald chi-square tests, $\chi^2 = 0.76$, $p = 0.38$) did not affect seedling biomass.

Discussion

In a comparative approach, we studied the impacts of native (*Paspalum atratum*) and exotic (*Urochloa brizantha*) grasses on survival and growth of multiple native tree seedlings under field conditions subjected to experimental manipulations of light, water supply and fertilization. In general, we found that grasses reduced tree seedling survival, and these effects were not alleviated by shade or fertilization. Seedling growth performance (stem length and biomass) was significantly reduced by the presence of either native or exotic grasses, irrespective of light conditions, irrigation, or fertilization. However, the impacts of the exotic grass were more intense than those imposed by the native grass. Our study suggests that the displacement of native by exotic grass may hinder rates of recruitment under natural conditions by its direct effects on seedling performance.

We show that grasses effectively suppress seedling growth of tree species, what is in line with several other studies demonstrating that tree seedling growth and survival are impaired by competition with grasses (Kraaij and Ward 2006; Riginos and Young 2007; Van Der Waal et al. 2009; Cramer and Bond 2013; Setterfield et al. 2018; Tomlinson et al. 2019). Grasses were shown to outcompete tree seedlings likely due to water shortage and reduced nutrient availability, impacting the suitable growing conditions for tree seedlings (Sankaran et al. 2004; Riginos 2009). The high growth rates and large biomass produced by grasses may deplete soil moisture, causing water deficit to- and mortality of young trees (Hoffmann and Haridasan 2008; Foxcroft et al. 2010). These results imply that root competition between grasses and seedlings for soil resources represent a major determinant of seedling survival and growth under natural conditions (Manea and Leishman 2015; Wakeling et al. 2015; Tomlinson et al. 2019; Issifu et al. 2021).

In a neotropical savanna, grass species exhibited higher rates of photosynthesis by area and leaf biomass, greater specific leaf area and higher water use efficiency in comparison to other life forms as shrubs and trees (Rossatto and Franco 2017). Our study demonstrated that within a wide range of experimental condition, grass presence was a key factor limiting tree seedling growth, even under apparently favourable recruitment conditions. On the other hand, tree seedling establishment might be favoured if grass abundance was severely suppressed, for example, by herbivory and/or changes in fire frequency (Riginos and Young 2007; Riginos 2009).

In general, the results of our experimental manipulation in resource availability did not alleviate consistently the negative effects of both native and exotic grasses on seedling survival and growth, so hypothesis 1 was not supported. Indeed, fertilization was shown to reduce the survival of seedlings growing amidst grasses (Figure 1B), likely due the positive effect of nutrients on the growth rates of both native and exotic grasses (Van Der Waal et al. 2009; Barbosa et al. 2014b; Caramaschi et al. 2016). Our results reveal that resource supply promotes primarily grass growth, consequently leading to a negative impact of grasses on tree seedling survival and growth.

Despite the importance of water for tree recruitment in neotropical savannas (Franco et al. 2014), our study showed that regular water supply did not promote seedling stem growth and biomass gain (Table S4 and S6). Although water supply promoted seedling survival (Figure S2), our data suggests that tree seedling growth was not under water limitation. Moreover, regular water supply did not relax the competitive effect of grasses on seedling performance. Our results agree with other field studies in savannas describing low or no effect of regular water supply on tree recruitment (Davies et al. 2005; Barbosa et al. 2014a). Two plausible explanations arise. Firstly, differences in water supply between irrigated and natural rainfall plots was not enough to cause a difference in the growth rate of the seedlings. During the experimental period (Dec 2011 to Jun 2012) the rainfall was relatively high and regular (1071 mm). This situation represents an average rainfall of 41.2 mm / week. This value was close to the amount of water experimentally provided by the irrigation system (37.5 mm / week). Secondly, the species selected for this study may have a strong ability to cope with soil water deficits frequently generated in these seasonal environments.

Fertilization of the plots did not increase seedling survival and only marginally promoted stem growth of seedlings growing in absence of grasses. When cultivated with grasses, however, fertilization reduced survival rates (Figure 1B) and had no effect on stem growth (Figure 2B) and biomass (Table S6) of the tree seedlings. Considering the positive effects of fertilization on the growth rate of grasses, irrespective of whether they are native or exotic (Kraaij and Ward 2006; Van Der Waal et al. 2009; Cramer et al. 2010; Barbosa et al. 2014a; Caramaschi et al. 2016) one picture emerges. Upon fertilization, grasses benefited more than seedlings due their higher competitive ability. Consequently, the higher growth rates and higher water and nutrient uptake

ability of grasses due to their shallow root system make the survival and initial growth of tree seedlings very difficult when growing amidst them (Cramer et al. 2012; Wakeling et al. 2015). Taking together, our results indicate that root competition among grasses and seedlings for resources might be a major factor hindering seedling establishment under natural conditions (Holdo and Brocato 2015; Vieira et al. 2019; Issifu et al. 2021).

In accordance with our expectations (hypothesis 2), shade increased tree seedling survival in presence of grasses (Figure 1A). Shade also promoted seedling stem growth in absence of grasses and in the presence of native grass but not in the presence of the exotic grass (Figure 2A). These results suggest that shade had a direct negative impact on grass growth performance, so indirectly favouring seedlings survival and growth. Although cultivation under low light intensity was found to negatively affect the performance of African grasses (Andrade et al. 2004; Martuscello et al. 2009; Barbosa et al. 2014b), our studies showed that shade did not reduce the suppressive effect of the exotic grass on seedling growth. Previous studies showed that, irrespective of the shade level, the exotic grass *Urochloa brizantha* produced three to five times more biomass than *Paspalum notatum*, a Brazilian grass recommended for pasture due to its high productivity and tolerance of shade (Andrade et al. 2004). In agreement with these studies, our results suggest a greater tolerance of the exotic grass to low light availability, corroborating the higher competitive advantage of the exotic over both native grass and tree seedlings (Corbin et al. 2004; Baruch and Jackson 2005; Ortega-Pieck et al. 2011; Fagúndez and Lema 2019; Tomlinson et al. 2019).

The impacts of the exotic grass on seedling survival and growth performance were more pronounced than that imposed by the native grass, thus corroborating our hypothesis 3. Previous studies showed that under field conditions the exotic *Urochloa brizantha* benefits more from fertilization and shade than the native *Paspalum atratum* (Caramaschi et al. 2016). Indeed, the exotic grass sustained a higher growth rate than the native grass over a variety of experimental conditions (Caramaschi et al. 2016; Vieira et al. 2019), corroborating the higher competitive ability exotic grasses have in comparison to native ones (Silva et al. 2013). Having a higher competitive ability, exotic grasses may impose a stronger negative pressure upon nearby tree seedlings in comparison to native grass species, as revealed by our study.

Studies conducted in African savannas revealed that native African grasses produced higher aboveground biomass upon fertilization and irrigation (Kraaij and Ward 2006; Van Der Waal et al. 2009; Bond 2010; Cramer et al. 2010), suggesting that wetter and more fertile soils stimulate the growth of these species. These different responses to nutrient supply might be linked with differences in the photosynthetic metabolic pathway for carbon fixation between these two life forms (C4 grasses and C3 trees). Although the C4 pathway is more energy-consuming than the C3 pathway, it suffers less photorespiration under hot and dry conditions than the C3 pathway thereby achieving higher water-use efficiency (Ehleringer et al. 1997).

Studies conducted in a neotropical savanna showed that the growth of C3 grasses was also affected by the presence of C4 grasses when fertilizers were added to the soil (Bustamante et al. 2012). Due to rising industrial nitrogen emissions and changes in land use (Adams et al. 2004), it is expected an increase in nitrogen deposition over the world during the next decades (Miyazaki et al. 2012). Soil nitrogen enrichment might affect the carbon flux from soils of natural ecosystems (Allison et al. 2008). Given this scenario in combination with the higher competitive ability of exotic C4 grasses, our results suggest that increasing availability of nitrogen and carbon dioxide (Baruch and Jackson 2005) will benefit much more exotic grasses than native grasses and tree species, leading to exotic grass expansion over neotropical savannas, so affecting ecological functioning and services. The rapid loss of biodiversity observed in savanna areas of the Cerrado, for example, was linked to the introduction and spread of exotic species (Damasceno et al. 2018).

In conclusion, our study shows that the impacts of the exotic grass on tree seedling survival, stem growth and biomass production are more negative than those imposed by the native grass, regardless of experimental manipulation of resources. Due to the magnitude of exotic grasses invasiveness in Brazilian landscapes, our study indicates that the displacement of native by exotic grass have the potential to strongly interfere with tree recruitment, and potentially shift ancient, species-rich native savannas to another poorer in biodiversity (Veldman 2016). Thus, adequate policies and management plans to control the use and spread of exotic grasses are essential to preserve biodiversity and ecosystem services of native vegetation in the neotropics.

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Statements and Declarations

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Availability of data and material: All data generated and analyzed during this study will be made available upon request.

Figures

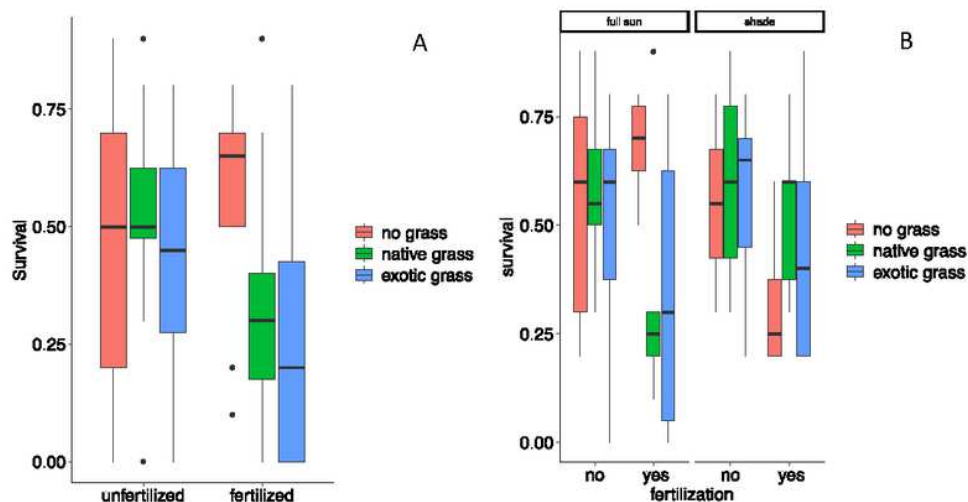


Figure 1

Survival (average proportion) of savanna tree seedlings grown under field conditions in the absence (no grass) or presence of native (*Paspalum atratum*) and exotic (*Urochloa brizantha*) grasses (A) under full sun, subjected to fertilization or not; (B) under irrigation and full sun or shade, subjected to fertilization or not. The experiment was conducted during the rainy season of 2012.

Figure 2

Mean stem length (square-root transformation) of savanna tree seedlings grown under field conditions in the absence (no grass) or presence of native (*Paspalum atratum*) and exotic (*Urochloa brizantha*) grasses and (A) subjected to irrigation and under full sun or shade; (B) under full sun but subjected to fertilization or not. The experiment was conducted during the rainy season of 2012.

Figure 3

Mean total biomass (ln) of savanna tree seedlings grown under field conditions in the absence (no grass) or presence of native (*Paspalum atratum*) and exotic (*Urochloa brizantha*) grasses and (A) subjected to irrigation and under different conditions of light and fertilization; (B) under full sun and different conditions of irrigation and fertilization. The experiment was conducted during the rainy season of 2012.

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