



Effects of native and invasive 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 invasive grasses may affect tree-grass coexistence in neotropical savannas is still poor. The present study tested the imposed effects of an invasive grass (*Urochloa brizantha*) and a native grass (*Paspalum atratum*) on survival rates, stem growth and biomass of seedlings of six native tree species representative of savanna physiognomies of the Cerrado biome. We conducted experiments under field conditions subjected to experimental manipulations of light, water supply and fertilization. Considering that grass performance might be reduced by shade,

and that irrigation and fertilization might relax competition between grasses and tree seedlings for water and nutrients, respectively, we postulated that these treatments would modulate the effects of the grasses on tree seedling survival and growth. We found that both grass species reduced tree seedling survival, and the effects were not alleviated by shade, irrigation, or fertilization. The presence of either native or invasive grasses reduced seedling stem length, irrespective of fertilization and shade. Irrigation alleviated the negative effects of both grasses on stem length. Both grass species reduced seedling biomass, irrespective of light conditions, irrigation, or fertilization. The impacts imposed by the invasive grass on the tree seedlings were larger than those imposed by the native grass, indicating that the displacement of native by invasive grasses can strongly affect recruitment potential of tree species. Due to the extent of

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grass invasion in neotropical savannas, and its potential impacts on recruitment patterns of native trees, adequate policies and management plans are needed to control invasive 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 alien 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. 1999a, b; Williams and Baruch 2000; Zenni and Ziller 2011; Damasceno et al. 2018). Recent assessment of the distribution of invasive grasses over the country revealed that they are present in virtually every fragment of Brazilian savanna (Pivello et al. 1999a, b; Beuchle et al. 2015). Additionally, the risk posed by invasive grasses in still not-invaded protected areas is high (Guimarães Silva et al. 2020). Whether promoted by human-induced environmental change or not, the spread of invasive grasses over ancient savannas in the neotropics has modified species composition and vegetation structure so intensely that they may be viewed as novel ecosystems; in comparison to the ancient savanna vegetation, the derived savannas are poorer in species composition, dominated by alien

species, and have reduced ecosystem services (Veldman 2016).

Invasive 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. 2012b). Greenhouse studies showed that invasive grass presented an early growth advantage over native grasses under nutrient manipulation (Reichmann et al. 2016). A comparative study conducted under field conditions 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).

Studies conducted in a neotropical savanna showed that the growth of native C₃ grasses was affected by the presence of invasive C₄ grasses when fertilizers were added to the soil (Bustamante et al. 2012b). Moreover, exotic species were more common in areas with low canopy closure and less common in areas with high canopy closure, whereas the occurrence of native species was not affected by the canopy closure; In particular, the African grass *Urochloa decumbens* was less common at high canopy closure than at more open physiognomies (Xavier et al. 2017), suggesting that this species has low tolerance to shade. 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). However, a field study showed that regular irrigation did not influence the absolute growth rate of *U. brizantha* and *P. atratum* when compared to their growth rate under natural rainfall (Caramaschi et al. 2016), suggesting that both grasses keep high growth rates even under the irregular rainfall distribution during the wet season.

The direct impacts of invasive grasses on tree seedling recruitment and vegetation cover are diverse. In general, they tend to suppress the initial growth 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). A study conducted in a semi-arid vegetation in Australia showed a decline in herbaceous species abundance and richness in the presence of an exotic grass, a long-term effect apparently linked to competition for resources (Clarke et al. 2005). The high growth rates and large biomass produced by exotic grasses may deplete soil moisture, causing water deficit and mortality of young trees (Hoffmann and Haridasan 2008; Foxcroft et al. 2010). On the other hand, a study in an African savanna showed that native grasses outcompeted 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). Taking together, these studies suggest that competition for soil resources, including water and nutrients, represent a major way by which grasses, irrespective whether they are invasive or native, 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 invasive grasses on tree recruitment requires that such effects be compared with that produced by native grasses for a better understanding of the long-term impact of invasive grasses on savanna vegetation dynamics and structure.

A few studies have checked the impacts of resource manipulation on the survival and/or growth of neotropical savanna tree seedlings. A study on seedling recruitment and mortality of *Bowdichia virgilioides* under two physiognomies differing in shade level and seasonal drought, found that water stress did not represent a determinant mortality factor but that shade was a major constraint for seedling growth (Kanegae et al. 2000). Experiments with *Kielmeyera coriacea* seedlings (Nardoto et al. 1998) and *Dimorphandra mollis* seedlings (Borghetti et al. 2019b) suggest that the dry season was not a major influence on survival, though it did suppress growth. By contrast, an irrigation experiment with *Roupala montana* and *Miconia albicans* demonstrated that rain-free periods within the wet season had negative effects on seedling establishment (Hoffmann 1996), but a moderate level of shade benefited the establishment of several tree seedlings. This, in addition to the influence of shade on invasive grasses, might mean that shade could suppress their negative effects on tree seedlings. In absence of grasses, nutrient addition was found to stimulate the growth rate of *Dalbergia miscolobium*

seedlings, in particular the shoot growth (Sasaki and Felipe 1998). However, a field study conducted in an African savanna showed that nitrogen enrichment increased the competitive ability of fast-growing grasses more than that of the N-fixing tree recruits (Kraaij and Ward 2006). Taken together, these studies showed that: water restriction during the growing season can limit tree seedling establishment; some levels of shade favour seedling survival but constrain seedling growth; fertilization seems to promote tree seedling growth in the absence of grasses.

Studying the effects of experimental resource manipulation on the interaction between grasses and tree seedlings represents a powerful approach for understanding how land use and climate changes can impact the dynamics of savanna worldwide. Climate change models predict a reduction in rain amount and an increase in rainfall irregularity for most of central South America (Castellanos et al. 2022). So, one could expect that increasing water deficit predicted for the future would intensify water competition between grasses and tree seedlings. If so, irrigation might relax the competitive interaction between these functional groups. Due to rising industrial nitrogen emissions and changes in land use (Adams et al. 2004), nitrogen deposition is expected to increase over the world during the next decades (Miyazaki et al. 2012). Soil nitrogen enrichment might impact the interactions between grasses and tree seedling in savannas by relaxing their competition for nutrients. Given this scenario in combination with the higher competitive ability of invasive C_4 grasses, one could expect that increasing availability of nutrients as nitrogen (Baruch and Jackson 2005) would benefit invasive grasses more than native grasses and tree species in the neotropics. Moreover, considering the abovementioned studies regarding shade effects on grasses and seedlings, one could expect that shade might favour tree seedling survival by reducing growth performance of grasses.

In this study, we investigated the impacts of a native and an invasive 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. 2019a). 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 African grasses, so the Cerrado is a relevant area to study the impacts of an invasive grass on the recruitment of native tree species.

We sought to compare the impacts of invasive and native grasses on tree seedling recruitment under resource manipulation. To do this we grew seedlings of native tree species in grass plots composed of either the native or exotic grass species, combined with experimental manipulations of water, nutrients, and light. 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 would relax the negative impacts of grasses on tree seedling survival and growth (hypothesis 1). As the growth of grasses is usually reduced by shade (Siemann and Rogers 2003; Barbosa et al. 2014b), and shade seems to promote tree seedling survival, we expected that shade would favour tree seedling survival and growth by reducing the competitive ability of the grasses (hypothesis 2). Considering that invasive grasses are usually stronger competitor and perform better than native grasses over several experimental conditions (Williams and Black 1994; Bustamante et al. 2012a, b; Han et al. 2012; Reichmann et al. 2016), we expected a stronger suppression of tree seedling growth by the invasive than by the native grass (hypothesis 3).

Material and methods

Grass species

The 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 in Brazil for pasture back in the 1970s, but rapidly became an invasive species (Blackburn et al. 2011) 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 abundant, semideciduous to deciduous, tree species representative of savanna physiognomies of the Cerrado (Ratter et al. 2003; Sano et al. 2008) (Table S1). The seeds used to produce seedlings were collected between September 2010 and August 2011 from at least five adult individuals of each species in natural areas of savanna located in the Brasilia National Park (15° 38' 28" S; 48° 1' 15" W), Federal District, Brazil. The seeds were stored in paper bags at room temperature (around 23 °C) for up to one year before use (depending on the time difference between the species' period of dispersal and the beginning of germination experiments). The seeds were germinated in climate chambers set at constant temperature of 30 °C and photoperiod of 12 h (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) and grown from August to November 2011. To avoid seedling mortality due to desiccation, the seedlings were irrigated daily until they were transplanted into the experimental area. Seed germination and seedling initial growth experiments were conducted at the experimental area of the *Laboratório de Termobiologia L.G. Labouriau* located at the University of Brasilia, Federal District, Brazil.

Experimental area

The seedling growth experiments were also conducted at the University of Brasilia campus (15° 46'

12° S; 47° 52' 07" W). 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 experimental area is at an elevation of approximately 1040 m. The soil of the experimental area is classified as red latosol, 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 experimental area 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. 2019a). However, because this area was within the limits of the campus, it was regularly cleaned of large trees and shrubs by the university staff, and only grasses and annual herbs were allowed to resprout. This area was eventually subjected to accidental fires. Two years before the beginning of the experiment, the grass cover was removed, and the area was ploughed to homogenize the soil to give all treatments similar start conditions. During these two years, resprouting individuals were hand-picked from the ground to keep the area as clean of vegetation as possible. This experimental area was fenced and divided in five blocks; each block being further divided in three plots of 54 m² each. Each plot was then divided in six sub-plots of 4 m² each, separated from each other by a gap of 2 m (Fig. S1).

Grass planting

To test the impacts of the native and invasive grasses on survival and growth of tree seedlings, seeds of both grass species were first sown in the sub-plots. Two sub-plots of each plot were planted with the native *P. atratum* (referred to as treatment G1), two sub-plots were planted with the invasive *U. brizantha* (G2), and in two sub-plots no grass was sown (G0). The grasses were seeded during the rainy season (December) of 2009 (~50 g of seeds per sub-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 sub-plot. As stated above, during the experimental period the ground of the experimental area was kept clean of other species by the regular hand-picking of emerging seedlings and resprouts of undesirable individuals.

Experimental design

In each block (Fig. S1) 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 (Fig. S1). Light and water treatments were applied at the 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 plot subjected to full sunlight and natural rainfall (L0); a plot covered by a 2 m-high transparent plastic blocking no solar radiation (L0); a 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 plots a drip irrigation system was installed to irrigate the seedlings twice a day (W1). Light and irrigation treatments were not fully crossed because we had no plot covered by transparent plastic but subjected to natural rainfall at the same time (Fig. S1). Therefore, we analysed the effects of irrigation (W0, W1) only on the uncovered plots (L0), and the effects of light (L0, L1) only on the irrigated treatment (W1). As the treatments of grass competition (G0, G1, G2) and fertilization (N0, N1) were managed at the sub-plot level within each plot, they were fully crossed (see below).

The amount of water supplied to the seedlings by irrigation was equivalent to a rainfall of 37.5 mm per week. The uncovered (L0) plot was subjected to natural rainfall (W0). According to the National Meteorology Institute (INMET), the precipitation in the region during the experimental period (December 2011–June 2012) was 1071 mm, which is equivalent

to rainfall of 41.2 mm per week. Important to mention that the plastic cover and, when present, the shade cloth were large enough to avoid rain and solar radiation over the sub-plots, but high enough to permit ventilation through the plots, so avoiding temperature increase and permitting total gas exchange.

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 sub-plots within each plot were fertilized with a slow-release fertilizer (Osmocote® NPK 15:9:12, 106 g per sub-plot) (Kraaij and Ward 2006). Four applications were made during the experimental period (N1), and the respective controls consisted of sub-plots with no addition of fertilizer (N0).

Tree seedling planting

The seedlings were around 120 days-old at the time of transplanting from the plastic bags into the experimental area. Before transplanting the seedlings, 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/24 h before weighing them (Table 1). By the end of November 2011,

two seedlings of each tree species were planted per sub-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 h 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

Table 1 Growth parameters of seedlings of savanna tree species of the Cerrado prior to seedling transplanting into the experimental area

Species	Shoot length (mm)	Root length (mm)	Shoot dry weight (mg)	Root dry weight (mg)	Root/shoot length ratio	Number of leaves ^a	Seedlings with cotyledons ^b
<i>Copaifera langsdorffii</i>	50.3 ± 8.6	73.6 ± 22.0	0.53 ± 0.26	0.18 ± 0.05	1.46	2	0
<i>Dalbergia miscobium</i>	52.9 ± 8.0	42.2 ± 18.8	0.11 ± 0.01	0.02 ± 0.01	0.79	3.5 ± 0.7	9
<i>Dimorphandra mollis</i>	45.2 ± 7.4	72.9 ± 21.1	0.21 ± 0.02	0.03 ± 0.01	1.61	2	1
<i>Dipteryx alata</i>	44.1 ± 5.7	105.8 ± 12.1	0.70 ± 0.07	0.17 ± 0.03	2.40	2	10
<i>Kielmeyera coriacea</i>	18.2 ± 3.1	87.0 ± 13.6	0.20 ± 0.01	0.13 ± 0.05	4.77	2.1 ± 0.5	10
<i>Qualea grandiflora</i>	30.4 ± 5.4	73.5 ± 24.8	0.11 ± 0.01	0.01 ± 0.01	2.42	2	10

After germination, the seedlings were grown in 11 plastic bags filled with a mixture of red latosol soil and washed sand (3:1), fertilized with NPK (10:10:10) under natural conditions of temperature and moisture, 50% sunlight and daily irrigation. n = 10 seedlings per species

^aAverage number of leaves per seedling

^bNumber of seedlings with cotyledons still attached

on different models. We analysed the effects of irrigation (W0, W1) only on the uncovered 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 (six) and blocks (five) 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 ($\Delta\text{AIC} < 2$). Posthoc multiple comparison tests were conducted using the sidak 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 grass treatment x nutrient supply under natural light conditions (Type III Wald chi-square tests, $\chi^2 = 16.23$, $p = 0.0003$; supplementary material, Tables S2 and S3), and between grass treatment 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 S4 and S5).

Under full sun, tree seedlings growing in the absence of grasses had higher survival than those grown amidst either native or invasive grass in fertilized plots (Fig. 1A), but seedling survival did not differ among grass treatments in unfertilized plots (Fig. 1A). Under irrigated conditions, seedling survival did not differ among grass treatments in unfertilized plots (Fig. 1B and C); however, seedling survival was lower with either invasive or native grass in fertilized plots, but only when exposed to full sun (Fig. 1B). Finally, seedling survival was increased by irrigation under full sun conditions, irrespective of the presence of grasses and fertilization (Fig. S2).

Effects of treatments on seedling stem growth

The seedling stem length was influenced by grass treatment (under natural light; Type III Wald chi-square tests, $\chi^2 = 6.58$, $p = 0.037$; supplementary material, Tables S6 and S7) and by the interaction between grass treatment x light conditions (under irrigation; Type III Wald chi-square tests, $\chi^2 = 13.82$, $p = 0.001$; supplementary material, Tables S8 and S9). Although present amongst the most parsimonious models ($\Delta\text{AIC} < 2$; 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 grass treatment x nutrient supply (Type III Wald chi-square tests, $\chi^2 = 2.98$, $p = 0.23$) did not affect seedling stem length.

Seedling stem length was not affected by the presence of either native or invasive grasses under irrigation and full sun (Fig. 2A), but the stem length increased under shade conditions, except when the seedlings were grown in the presence of the exotic grass (Fig. 2A). Although not statistically significant, stem elongation of the tree seedlings was marginally stimulated by fertilization under irrigation and in absence of grasses (Fig. 2B).

Effects of treatments on seedling biomass

Seedling biomass was influenced by the presence of grasses (Table 2). Seedling biomass was strongly affected by the presence of grasses under irrigated

Table 2 Model selection outcomes for generalized linear mixed models of seedling survival, seedling stem length (square-root transformed), and seedling biomass (natural log-transformed) in relation to the presence of grasses, light conditions, irrigation, and nutrient supply

Parameter	Condition	Model	K	AICc	Δ AICc	Weight
Survival	Natural light	Irrigation + Grass \times Nutrient	10	848.01	0	0.71
		Null	4	880.29	32.28	0
	Irrigation	Light \times Grass \times Nutrient	14	893.91	0	0.87
		Null	3	914.04	20.13	0
Stem length	Natural light	Grass + Nutrient	6	1438.22	0	0.21
		Grass	5	1438.26	0.04	0.21
		Grass \times Nutrient	8	1439.45	1.23	0.11
		Irrigation + Grass + Nutrient	7	1439.94	1.72	0.09
		Irrigation + Grass	6	1439.96	1.74	0.09
		Null	3	1441.1	2.88	0.05
	Irrigation	Light \times Grass + Nutrient	9	1716.42	0	0.54
		Light \times Grass	8	1716.95	0.52	0.42
		Null	3	1781.68	65.26	0
		Grass	5	879.33	0	0.38
Biomass	Natural light	Irrigation + Grass	6	880.76	1.43	0.19
		Grass + Nutrient	6	881.17	1.84	0.15
		Null	3	939.08	59.75	0
		Grass	5	1019.32	0	0.33
	Irrigation	Grass + Nutrient	6	1020.47	1.15	0.19
		Light + Grass	6	1020.63	1.31	0.17
		Null	3	1102.5	83.19	0

Only the most parsimonious models (Δ AICc < 2) and the null models are shown. See all model candidates in the Supplementary Material tables

Parameter: response variable (plant trait). Condition: Experimental condition, i.e. under natural light (full sun) or under irrigation. K=number of parameters, AIC=Akaike's Information Criterion, Δ AICc=model AIC minus the minimum AIC value, weight=model weight (Akaike's weight). Random term: tree species (all models); blocks (models of seedling survival); interaction variable combining light and irrigation treatments nested within blocks (models of seedling survival under natural light)

conditions, but the invasive grass exerted a stronger effect than the native grass on this parameter (Type III Wald chi-square tests, $\chi^2=100.22$, $p<0.0001$; Fig. 3A; supplementary material, Tables S10 and S11). Seedling biomass was strongly affected by the presence of both native and invasive grasses under full sun (Type III Wald chi-square tests, $\chi^2=72.23$, $p<0.0001$; Fig. 3B; supplementary material, Tables S12, S13 and S14). Although present amongst the most parsimonious models (Δ 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 a native grass (*Paspalum atratum*) and an invasive grass (*Urochloa brizantha*) 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 invasive grasses, irrespective of light conditions, irrigation, or fertilization. However, the impacts of the invasive grass were more intense than those imposed by the native grass. Our study suggests

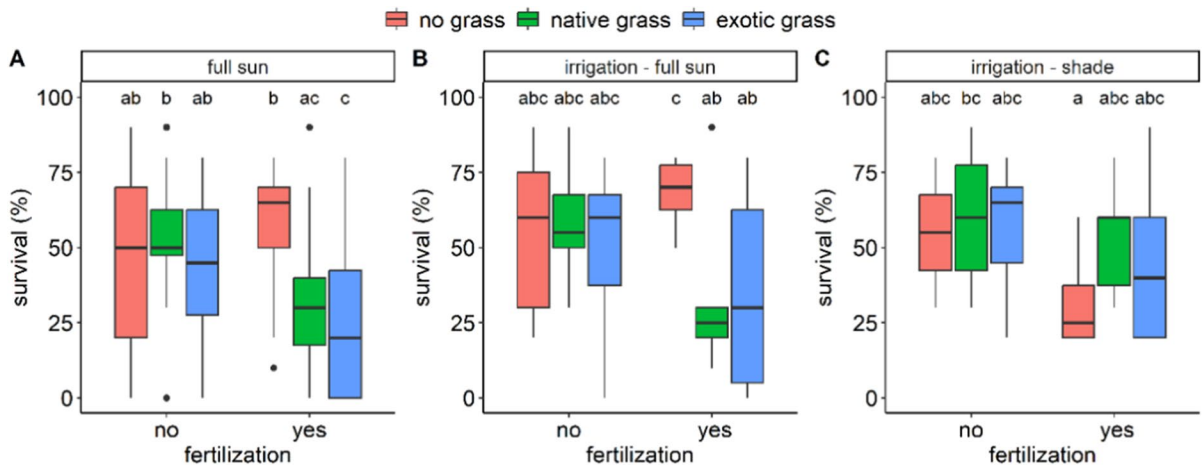
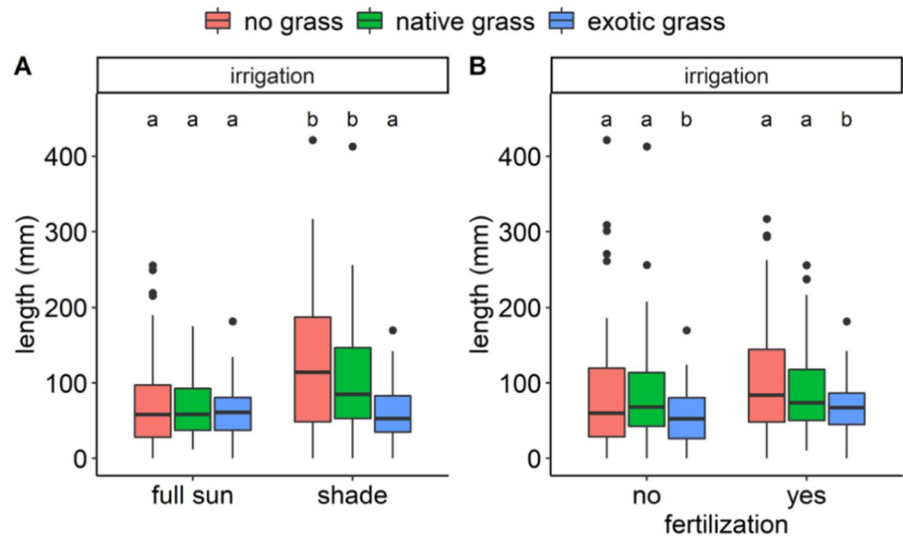


Fig. 1 Survival (average proportion) of savanna tree seedlings grown under field conditions in the absence (no grass) or presence of native (*Paspalum atratum*) and exotic (*Urochloa brizantha*) grasses **A** under full sun, subjected to fertilization or

not; **B** under irrigation and full sun or shade; **C** subjected to fertilization or not. Different letters indicate statistically significant differences according with posthoc tests. The experiment was conducted during the rainy season of 2012

Fig. 2 Median stem length 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 subjected to irrigation and **A** under full sun or shade **B** subjected to fertilization or not. Different letters indicate statistically significant differences according with posthoc tests. The experiment was conducted during the rainy season of 2012



that the displacement of native by invasive grass hinders rates of tree 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 and mortality of young trees (Hoffmann and Haridasan 2008; Foxcroft et al. 2010). Moreover, our results imply that root competition between grasses and seedlings for soil resources may represent a major determinant of seedling survival and growth under natural conditions (Manea and Leishman 2015;

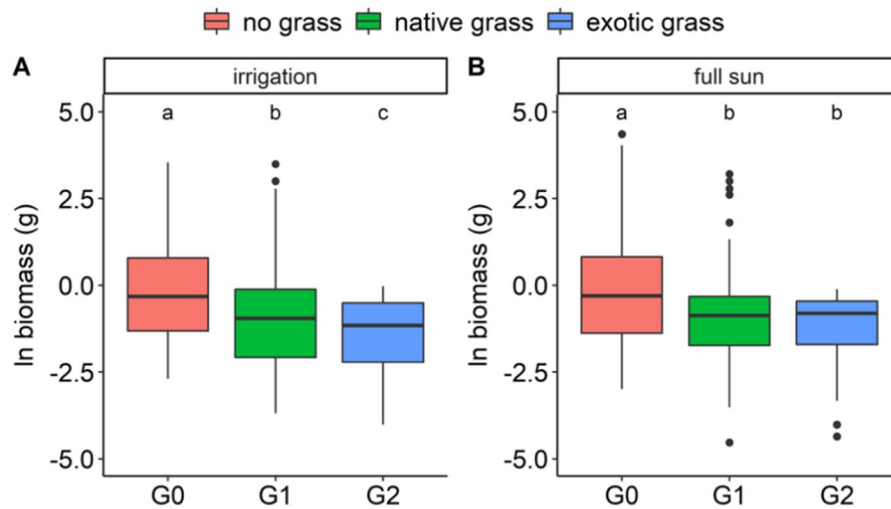


Fig. 3 Median total biomass (ln) of savanna tree seedlings grown under field conditions in the absence (no grass) or presence of native (*Paspalum atratum*) and exotic (*Urochloa brizantha*) grasses and; **A** subjected to irrigation and under different conditions of light and fertilization; **B** under full sun and

different conditions of irrigation and fertilization. Different letters indicate statistically significant differences according with posthoc tests. Raw data are shown in Table S14. The experiment was conducted during the rainy season of 2012

Wakeling et al. 2015; Tomlinson et al. 2019; Issifu et al. 2021). Grass species were shown to exhibit 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 in a neotropical savanna (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, our results imply that 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, our experimental manipulation of resource availability did not alleviate consistently the negative effects of both native and invasive grasses on seedling survival and growth, so hypothesis 1 was not supported. 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 (Tables S6 and S12). Although water supply promoted seedling survival (Fig. 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 (December 2011–June 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. For example, a long-term field study conducted with *Dimorphandra mollis* showed that fire was a more determinant constraint to seedling survival than the dry season itself, suggesting that water shortage did not increase seedling mortality during the dry season (Borghetti et al. 2019b). Field studies in a neotropical savanna showed that seedlings of *Kielmeyera coriacea* were able to survive soil water potential as low as -2.5 MPa generated during the dry season (Nardoto et al. 1998). Seedlings of *Dalbergia miscolobium* that recruited

during the wet season were shown to survive the following dry season; the authors reported that although the seedlings drop their leaves and had their shoot growth inhibited, the final number of surviving seedlings was not significantly impacted by the dry season (Franco et al. 1996). Our results shows that regular water supply promote tree seedling survival but has no effect on growth performance.

Fertilization of the sub-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 (Fig. 1B) and had no effect on stem growth (Fig. 2B) and biomass (Tables S10 and S12) of the tree seedlings. Considering the positive effects of fertilization on the growth rate of grasses, irrespective of whether they are native or not (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 to 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 study suggests 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 of fertilized plots (Fig. 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 invasive grass (Fig. 2A). Previous studies reported that under shade the native *P. atratum* had a drop in its absolute growth rates towards the end of the rainy season, while the invasive *U. brizantha* sustained its growth rate over the entire rainy season (Caramaschi et al. 2016), suggesting a higher tolerance of the exotic grass to shade in comparison to the native one. Other studies conducted under field conditions reported a considerable tolerance of *U. brizantha* to shade (Dias-Filho 2000). Our study found that seedlings were benefited by shade, which could be either a direct effect of low light intensity

on their performance, or an indirect effect of shade on the performance of the native grasses, thus relaxing its suppressive effect on seedling growth. On the other hand, although 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 invasive grass on seedling growth. Previous studies showed that, irrespective of the shade level, *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 invasive grass to low light availability, corroborating the higher competitive advantage of the invasive 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 invasive grass on seedling survival and growth performance were more pronounced than that imposed by the native grass, thus corroborating hypothesis 3. Previous studies showed that under field conditions *Urochloa brizantha* benefits more from fertilization and shade than *Paspalum atratum* (Caramaschi et al. 2016). Indeed, this invasive grass sustained a higher growth rate than the native one over a variety of experimental conditions (Caramaschi et al. 2016; Vieira et al. 2019), corroborating the higher competitive ability invasive grasses have in comparison to native ones (Silva et al. 2013). Having a higher competitive ability, invasive 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. Different responses to nutrient supply might be linked with differences in the photosynthetic metabolic pathway for carbon fixation between 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. 2012b). 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), what might affect the carbon flux from soils of natural ecosystems. Given this scenario in combination with the higher competitive ability of invasive C4 grasses, our results suggest that increasing availability of nitrogen and carbon dioxide (Baruch and Jackson 2005) might benefit invasive in detrimental of native grasses, leading to exotic grass expansion over neotropical savannas and 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). On the other hand, as CO₂ elevation was shown to be beneficial for seedling growth of a C3 neotropical tree (Melo et al. 2018), the impact of climate changes on tree seedling x grass dynamics over the neotropics deserves further studies.

In the future higher average temperatures and higher fire frequency are expected for central South America (Castellanos et al. 2022). The impacts of land use and climate changes on neotropical savanna vegetation may be diverse and depend largely on plant functional groups. Our study revealed that the invasive grass was more resilient to experimental manipulation of water than both the native grass and tree seedlings, suggesting that the ongoing rainfall shortage and increasing rainfall irregularity will further favour exotic grass spread to the detriment of native species.

Intensification of agricultural activities are expected to increase input of nutrients in natural ecosystems over the next decades (Bustamante et al. 2012a). The addition of phosphorus alone or in combination with nitrogen stimulated invasion by the African *Melinis minutiflora* (a C4 grass), whereas the native grass species *Echinolaena inflexa* (a C3 grass) benefited under nitrogen addition only when the invasive species was absent. The authors concluded that the invasion by the African species resulted in negative impacts on native grass species (Bustamante et al. 2012b). Considering

the wide distribution of exotic grasses in Brazilian landscapes, our study indicates that the displacement of native grasses by invasive grasses has the potential to strongly interfere with tree recruitment, and shift these ancient, species-rich native savannas to species-poor communities dominated by exotic species (Veldman et al. 2015; Veldman 2016). Thus, adequate policies and management plans to control the use and spread of alien grasses are essential for a long-term conservation of biodiversity and ecosystem services of native grasslands in the neotropics.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by BDSR, ERMB, DADS and PD. The first draft of the manuscript was written by BDSR and FB. FVL and KT commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability All data generated and analyzed during this study will be made available upon request.

Declarations

Conflict of interest The authors have no conflict of interest to declare.

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