An Acad Bras Cienc (2025) 97(3): e20240252 DOI 10.1590/0001-3765202520240252
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

ECOSYSTEMS

Allelopathic hypotheses revisited: the interactions between native and exotic species in the Brazilian savanna

CRISTIELE DOS SANTOS SOUZA, GABRIEL MARINS, ISABELA FERNANDA L.G. CAMARGO, LARISSA BOAZ DE LIMA, ANABELE STEFÂNIA GOMES & FABIAN BORGHETTI

Abstract: We investigated allelopathic interactions between native and exotic species of the Cerrado biome. We studied the effects of the exotic *Andropogon gayanus* and the native *A. bicornis* on the initial growth of two native (*A. fastigiatus* and *Lepidaploa aurea*) and two exotic species (*Melinis minutiflora* and *Stapfochloa elata*). Leaves or roots of the donors were each mixed at ratios of 0.75, 1.5 and 3% (litter/soil) with soil samples collected in the same areas where they spontaneously co-occur with their target species. We found that *A. gayanus* inhibited the growth of all target species, what agrees with the novel weapon hypothesis. The native *A. bicornis* stimulated the growth of the two native species and of *S. elata* but inhibited the growth of the exotic *M. minutiflora*, in line with the homeland security hypothesis. Our studies suggest that allelopathy may have a part in the invasiveness of *A. gayanus* and that the inhibitory effect of *A. bicornis* on the growth of *M. minutiflora* might help to control the spread of this exotic grass. We conclude that allelopathy may be involved in the interactions between species and be used in controlling the spread of exotic species over many areas of the Cerrado.

Key words: Allelopathy, initial growth, invasive grass, plant interaction, plant litter, savanna.

INTRODUCTION

Invasions by exotic species have disrupted native vegetation and compromised global biodiversity (Vilà et al. 2011, Linders et al. 2019). In particular, neotropical savannas have been largely invaded by African grasses (Pivello et al. 1999a, Pivello et al. 1999b, Barbosa et al. 2008, Lannes et al. 2012). Currently, more than 44% of native areas of the Cerrado biome (the Brazilian savanna) have been replaced by African grass species (Mapbiomas 2022). The effects of invasive species on plant recruitment and growth can reduce native species' distribution (Velazco et al. 2019) and even eradicate them from their original areas (Martins et al. 2017, Thomas et al. 2018), resulting in ecological imbalances due to changes in the structure and composition of the community (Pivello et al. 1999a, Hoffmann & Haridasan 2008, D'Antonio et al. 2011, Lorenzo et al. 2012, Horowitz et al. 2013, Sharma et al. 2017).

Studies suggest that allelopathy might play a part in successful invasion by exotic species (Callaway & Aschehoug 2000, Callaway & Ridenour 2004, Del Fabbro et al. 2014). Allelopathy is a phenomenon that involves the release of chemical compounds (allelochemicals) by donor plants, which can positively or negatively influence the growth and development of neighbors, also referred as target species (Rice 1984, Pires & Oliveira 2011). Allelochemicals can

be released into the environment via leaching from shoot, root exudation, and decomposing plant material (Rice 1984, Djurdjević et al. 2011, Hassan et al. 2014).

The susceptibility of the target species to allelochemicals might be linked to their shared evolutionary history (Callaway & Ridenour 2004, Cummings et al. 2012, Thiébaut et al. 2019). Species which share the same evolutionary history tend to be less susceptible to allelochemicals produced by each other (Callaway & Ridenour 2004) than species that evolved in different geographical regions but that eventually come into contact due to an invasion process (Reigosa et al. 1999).

Due to the lack of mechanisms of defense against unknown chemical compounds, the allelochemicals of invading species tend to have a greater, usually negative effect on species occurring in the invaded region than on species with which they coexist in their region of origin (Hierro & Callaway 2021). This relationship led to the concept of the *novel weapon hypothesis* (Callaway & Ridenour 2004). According to the hypothesis, species that coexist or have previously coexisted develop greater tolerance to allelochemicals produced by each other than species that have no historic of coexistence (Hierro & Callaway 2021).

On the other hand, native species also produce allelochemicals that might help to protect themselves against the invaders (Callaway et al. 2005, Goergen et al. 2011, Inderjit et al. 2011, Cummings et al. 2012). Moreover, native species might increase the production of allelochemicals in response to invasive species and it might increase the resistance of native to exotic species as a function of the time since invasion (Inderjit et al. 2011). These observations have contributed to the formulation of the *homeland security hypothesis*. According to this hypothesis, exotic species would be sensitive to allelochemicals produced by native species, what would reduce their growth and impacts on natural communities (Cummings et al. 2012). Consequently, allelopathic effects are expected to be milder between plant species that have a long period of co-occurrence than between species which co-occurrence resulted from invasion (Callaway & Aschehoug 2000, Callaway & Ridenour 2004, Cummings et al. 2012, Del Fabbro et al. 2014, Ning et al. 2016).

The present study investigated the allelopathic potential of leaves and roots of two congenerics, the exotic *Andropogon gayanus* and the native *A. bicornis* on the initial growth of two native (*Andropogon fastigiatus* Sw. and *Lepidaploa aurea* (Mart. Ex DC.) H. Rob.) and two exotic species (*Melinis minutiflora* P. Beauv. and *Stapfochloa elata* (Desv.) P.M. Peterson) of wide distribution in the Cerrado. We investigated: (1) Whether the two exotic target species are more sensitive to phytotoxic compounds produced by the native *A. bicornis* than to those produced by the exotic *A. gayanus*; (2) Whether the two native target species are less sensitive to phytotoxic compound produced by the native *A. bicornis* than to those produced by the exotic *A. gayanus*.

MATERIALS AND METHODS

Donor species

Andropogon gayanus Kunth. (locally known as gamba grass) is one of the most common African species in the Cerrado (Sampaio & Schmidt 2013). It was introduced into the region as forage in the 1980s (Zanin & Longhi-Wagner 2011), fruits year-round (Thomas & Andrade 1984) with around 604 ± 81 seeds per inflorescence and presents a high dispersal capacity (Musso et al. 2019), which may have contributed to its broad distribution across different environments. Due to its adaptation to drought and acidic soil (Thomas & Andrade 1984), this species also invades areas under

ecological restoration and usually compromises restoration processes (Sampaio et al. 2015, Liaffa, unpublished data).

Individuals of *A. gayanus* were shown to produce a considerably high biomass (Thomas & Andrade 1984), reduce native species richness (Flores et al. 2005), affect soil seed bank dynamics and increase fire intensity (Marinho & Miranda 2013). The impacts of this alien grass on ecosystem dynamics and its rapid spread over conservation units (Sampaio & Schmidt 2013) suggest that this species might benefit from some species- specific attribute that contributes with its invasion process. In the light of the novel weapon hypothesis (Callaway & Ridenour 2004), allelopathy could be behind its impacts on the dynamics of native vegetation.

On the other hand, allelochemicals produced by native species might in some way control the spread of exotic invaders, thus allowing native communities to resist invasions (Cummings et al. 2012). This possibility finds strong evidence in studies with native species (Cummings et al. 2012, Hou et al. 2012, Ning et al. 2016), including those from the Cerrado (Allem et al. 2014, Lopes et al. 2018, Grossi et al. 2021). As such, and in the light of the homeland security hypothesis (Cummings et al. 2012), it might be relevant to check whether native donor species exhibit greater allelopathic potential against exotic than against natives.

Andropogon bicornis L. (commonly known as donkey's tail grass) is a ruderal species native to the Cerrado (Pastore et al. 2012) that typically occurs at sites under early stages of succession and can rapidly cover degraded areas (Zanin & Longhi-Wagner 2011). It produces a large quantity of empty caryopses (approximately 60%) (Dairel & Fidelis 2020) which consequently reduces its germination potential (Carmona et al. 1998). The rapid growth and ability to colonize disturbed areas point *A. bicornis* as suitable for using in restoration programs conducted in Cerrado physiognomies (Filgueiras & Fagg 2008, Jacobi et al. 2008, Rodrigues et al. 2009, Neri et al. 2011, Sampaio et al. 2015). Besides, being congeneric of *A. gayanus*, we avoid phylogenetic bias in our study.

Native target species

Andropogon fastigiatus (Poaceae) is a native species of considerable distribution over the Cerrado (Zanin & Longhi-Wagner 2011). Its rapid growth and high survival rate promote ~30% soil coverage within one year after planting, what contributes with the establishment of other native species, such as *Aristida riparia* Trin, *Lepidaploa aurea* and *Schizachyrium sanguineum* (Retz.) Alston (Pellizzaro et al. 2017). *Andropogon fastigiatus* also colonizes disturbed areas, typically along roadsides, where it can form dense populations (Zanin & Longhi-Wagner 2011). Seeds of *A. fastigiatus* were collected in the municipality of Alto Paraíso de Goiás (14° 10' 11.4" S 47° 51' 34.7" W), in January 2020, and kept under dry storage in paper bags for one year at a temperature of 18/28 °C in a dark room at the *Rede de Sementes do Cerrado*, Brasilia (DF), Brazil.

Lepidaploa aurea is a native, ruderal subshrub of the Asteraceae family (Lorenzi 2008), which presents rapid growth and ability to colonize degraded areas (Farias et al. 2002). Seeds of *L. aurea* were collected in native Cerrado fragments at the Darcy Ribeiro Campus of the University of Brasília (15° 16' 48.15" S, 49° 47' 50.81" W), in July 2021 and were used in the experiments as soon as possible.

Exotic target species

Stapfochloa elata (synonyms: *Chloris elata* Desv., *C. dandyana* C.D. Adams and *C. polydactyla* (L.) Sw.) (Pereira & Barreto 1985) is a native grass from an indigenous reserve in Colombia (Brazilian Biodiversity Information System 2021).

First cited in 1788 by Swartz (Pereira & Barreto 1985), this species is frequently found along roadsides and open areas, and is well adapted to nutrient-poor soils, such as those of the Cerrado (Carvalho et al. 2005). Generally associated with secondary vegetation (Pereira & Barreto 1985), this species flowers almost all year-round (Kissmann & Groth 1997) and produces more than 90,000 seeds per plant, which are easily carried by the wind (Brighenti et al. 2007). Due to its efficient reproductive capacity, *S. elata* has been recognized as a weed in sugarcane (Carvalho et al. 2005) and citrus fruit crops (Villela et al. 2021). Seeds were collected from anthropized areas in the municipality of Rubiataba (15° 10' 18.77" S, 49° 48' 14.31" W), in February 2021, and immediately used in the experiments.

Melinis minutiflora was introduced accidentally in Brazil in the 19th century via the slave trade (Filgueiras 1990) and is currently one of the most common African grasses in the Cerrado (Hoffmann et al. 2004, Durigan et al. 2007). Its fast spread over the Cerrado has caused a sharp decline in its biodiversity (Durigan et al. 2007) and changed the fire dynamics of this biome (Hoffmann et al. 2004). This species can disperse over 81,000 seeds per square meter of soil (Durigan et al. 2007), and the seeds present a considerably high viability and germination rate (Martins et al. 2009, Aires et al. 2014). Seeds were also collected from anthropized areas in the municipality of Rubiataba, in February 2021. Important to mention that all the target species selected for this study can be found spontaneously occurring at the same sites as *A. gayanus* and *A. bicornis*, so they would be appropriate species for prospective studies of potential allelopathic effects of the donor species in their areas of occurrence.

Plant material of the donor species and preparation of the substrates

Leaves and roots of the native *A. bicornis* were collected from at least ten individuals selected by chance and at least 2m apart from each other in the municipality of Rubiataba (15° 10' 18.77" S, 49° 48' 14.31" W), in an area formerly used for livestock.

Leaves and roots of the exotic *A. gayanus* were collected from at least ten individuals each randomly selected from five different populations occurring in an anthropized area of Cerrado in the University of Brasília campus (15°16' 48.15" S, 49° 47' 50.81" W). Leaves and roots of both donor species were collected during the rainy season between November 2020 and January 2021. The leaves and roots of each species were dried in an oven at 60°C for 72 h (Lopes, unpublished data). After, the plant material was separately chopped into 3 to 5cm fragments to ease their incorporation into the soil samples taken from the same areas where the donor and target species spontaneously occur (see Table I). Before mixing, the soil of each site (see below) was sieved and dried at 18/28°C for 72 hours before use, reaching around 56% of moisture. These procedures followed the methodology as described in Allem et al. (2014).

Fifteen soil samples were collected from each of the two sites under study. The soil samples were collected at random but covering much of each site from a depth between 0-10 cm with the aid of a hoe. These samples were separately homogenized per site and stored for up to five days at dark in a thermic container at 8°C. Five samples of 250g from each site were sent for soil analysis (*Centro de Tecnologia Agrícola e Ambiental, Campo Análises*) following standard procedures for soil analysis (Manaus: Embrapa Amazônia Ocidental 2005).

We decided to collect soil samples from the same sites where donor and target species spontaneously co-occur due to the importance of considering the interaction of the donor

Table I. Analysis of soil samples collected in the experimental areas. Results of the analysis of soils sampled in the collection area of the native donor *Andropogon bicornis* L. (municipality of Rubiataba, Goiás - 15° 10' 18.77" S, 49° 48' 14.31" W) and of the exotic donor *Andropogon gayanus* Kunth. (Darcy Ribeiro Campus of the University of Brasília - 15° 46' 29.5" S, 47° 52' 6.9" W). Soil analysis were performed at the *Centro de Tecnologia Agrícola e Ambiental, Campo Análises*, Paracatu city (MG), Brazil.

Variable	Soil sampling site	
	Native	Exotic
pH	5.3	6.3
Organic matter	1.7 dag/Kg	1.4 dag/Kg
C	1 dag/Kg	0.8 dag/Kg
P	1.9 mg/dm^3	0.5 mg/dm^3
K	36.5 mg/dm^3	42.9 mg/dm^3
S	1 mg/dm^3	2.3 mg/dm^3
Ca	1.6 c/dm^3	3.1 c/dm^3
Mg	0.5 c/dm^3	0.2 c/dm^3
Al	0.4 c/dm^3	<0.1 c/dm^3
N	0.1 %	0.05 %
B	0.13 mg/dm^3	0.17 mg/dm^3
Cu	1.3 mg/dm^3	0.6 mg/dm^3
Fe	394 mg/dm^3	54 mg/dm^3
Mn	29.3 mg/dm^3	6.8 mg/dm^3
Zn	1.57 mg/dm^3	2.45 mg/dm^3
Sand	49.8 %	55.2 %
Silt	30.2 %	11.4 %
Clay	20 %	33.4 %

plant, in particular its rhizosphere, with the soil microbiota (Lorenzo et al. 2013).

The leaves and roots of the donor species were separately incorporated into the soil at ratios of 0.75, 1.5 and of 3%. These ratios were calculated according to the amount of litter produced by each donor species per month per square meter of soil. For the exotic donor (*A. gayanus*) the amount of plant litter produced is between 81.7 and 229 grams per square meter (Thomas & Asakawa 1993). For the native donor (*A. bicornis*) the absence of this information in literature prompted us to check for it under field conditions. For that, between August-September 2020 ten adult individuals were randomly selected in the same experimental area and any plant material fallen around them was gently removed; as well, the soil surrounding each individual was cleaned from debris. One month later, the litter produced in 1 square meter surrounding each individual were taken and dried in an oven at 60°C for 72 h. Based on the amounts recorded, we estimated a production of litter between 82 and 164 grams per square meter.

So, assuming a soil depth of 1 cm, where most of seedling roots are located during their initial establishment, a soil volume of 0.01m^3 (1m^2 × 0.01m, or 10 L) would be directly influenced by the plant litter. Considering that 1 L of red latosol (the most typical soil type of the Cerrado) weighs approximately 1.090 Kg (Allem et al. 2014), the percentage of plant material per unit of soil volume would be between 0.75 and 1.5 %. The treatment of 3% was also included in order to assess the eventual effect of accumulated litter on seedling growth. The experiments were all conducted at the *Laboratório de Termobiologia L.G. Labouriau* of the University of Brasilia, Federal District, Brazil.

Bioassays

The mixtures of plant material and soil at different proportions (0.75, 1.5 and 3%) were separately conditioned in 200 mL plastic flasks. The controls consisted of seedlings planted in plastic flasks containing only soil as substrate (0%). The seeds employed for the bioassays

were collected from at least ten adult individuals per target species. Seeds of the target species were previously germinated in Petri dishes lined with filter paper and moistened with distilled water in incubators (Eletrolab EL202/3LED) set to provide a temperature regime of 17/27°C (night/day) under a 12-hour photoperiod (white light). After a few days, seedlings of each target species were visually selected by uniformity of size (around 1cm) and randomly distributed among the flasks (filled with the mixtures, or only with soil) in order to homogenize seedling sizes for the growth experiment. Three seedlings of each target species (pseudo-replicates) were separately planted in each of ten plastic flasks (replicates) per each combination of donor species (*A. bicornis*, *A. gayanus*) x target species (*A. fastigiatus*, *L. aurea*, *M. minutiflora*, *S. elata*) x treatment (0, 0.75, 1.5, 3.0%). The seedling growth experiment was conducted in the same incubator and under the same parameters of germination experiment as described above. The flasks were irrigated daily with 10 mL of distilled water to keep the substrates wet during the experimental period. This experiment was carried out for 13 days, except for *L. aurea*, whose slower growth required 18 days to reach comparable sizes (see below). At the end of the experiments, the shoot and root length of the target plants were measured using a digital pachymeter (Mitutoyo). Additionally, the number of leaves and lateral roots were counted for each seedling, and 15 seedlings from each experiment were selected by chance to determine total dry biomass.

Considering that the experiments were conducted with different species and carried out on different substrates, and to make the results comparable to each other, the growth parameters of the seedlings in each treatment were relativized in relation to their respective controls according to Ribeiro & Borghetti (2013).

Thus, the percentage of inhibition or promotion of seedling growth in each of the treatments in respect to their respective controls was calculated according to the equation:

$$\% \text{ inhibition/promotion} = (XT * 100 / XC) - 100$$

Where, XT is the average growth in the treatment and XC is the average growth in the control.

Statistical Analyses

Generalized linear mixed models (GLMMs) were used to compare the growth parameters among the concentration levels for each species and response variable separately. The appropriate distributions and link functions used in the models were chosen according to the nature of the variable. More information can be found in the supplementary material, along with the corresponding model diagnostics. The diagnostics were performed using Randomized Quantile Residuals, as proposed by Gelman (2007), using the DHARMa package (Hartig 2024). Some models were accepted even with bad diagnostics due to underdispersion of the data, meaning that these models overestimated the true variance of the measured variables. We caution readers about interpreting the results from these models but we prioritized more conservative models, in which overestimating variance makes the model less sensitive to detecting effects, reducing the likelihood of falsely detecting significant effects. The following variables were used as predictors: donor species (exotic or native), treatments (roots or leaves) and ratios (0, 0.75, 1.5, 3%); and the response variables: shoot and root growth, total dry biomass, number of leaves and lateral roots. For the analysis the results of the pseudo-replicates were averaged within each replicate, and replicates were included as random effect in the models. Analyses were performed in R

software, version 4.1.3 (R Core Team 2022) using the following packages: glue (Hester & Bryan 2024), tidyverse (Wickham et al. 2019), readxl (Wickham & Bryan 2023), carData (Fox et al. 2022), car (Fox & Weisberg 2019), MASS (Venables & Ripley 2002), lsmeans (Lenth 2016), LMERConvenienceFunctions (Tremblay et al. 2020), lme4 (Bates et al. 2015), multcomp (Hothorn et al. 2008), outliers (Komsta 2022), MuMIn (Bartoń 2024), lmerTest (Kuznetsova et al. 2017), TMB (Kristensen et al. 2016), glmmTMB (Brooks et al. 2017), performance (Lüdecke et al. 2021b), patchwork (Pedersen 2024) and see (Lüdecke et al. 2021a).

RESULTS

Effects of the donor species on the growth of native target species

Treatments prepared with roots of the native donor (*A. bicornis*) promoted shoot growth in *A. fastigiatus* between 20 and 31% (P<0.001, Table II, Fig. 1a), but those prepared with leaves inhibited root growth between 22 and 29% (Fig. 1a). These same treatments had no significant effect on the growth of *L. aurea* seedlings (Table II, Fig. 1b).

Treatments prepared with leaves of the exotic donor (*A. gayanus*) reduced the shoot and root growth of *A. fastigiatus* seedlings between 8 and 25%, and 19 and 26%, respectively (Fig. 1c). These same treatments reduced shoot and root growth of *L. aurea* seedlings between 7 and 17%, and 25 and 34%, respectively (Fig. 1d). Treatments prepared with roots of the exotic donor also inhibited shoot and root growth of *A. fastigiatus* between 14 and 18%, and between 26 and 35%, respectively (Fig. 1c); These same treatments reduced shoot and root growth of *L. aurea* seedlings between 19 and 26%, and between 32 and 48%, respectively (P<0.001, Table II, Fig. 1d). In general, treatments prepared with roots of the exotic donor were more harmful to seedling growth of native species than those prepared with roots of the native donor (Fig. 1).

Treatments prepared with leaves of the native donor decreased total biomass of *A. fastigiatus* seedlings between 15 and 21% (P<0.01, Table II, Fig. 2a), but had no effect on total biomass of *L. aurea* (Fig. 2b); leaves and roots of the exotic donor reduced biomass of *A. fastigiatus* seedlings between 10 and 20%, and between 6 and 16%, respectively (P<0.05, Table II, Fig. 2c) and of *L. aurea* seedlings between 27 and 31%, and between 15 and 40% respectively (P<0.001, Table II, Fig. 2d). For the exotic donor, treatments prepared with roots were slightly more harmful to seedling growth than those prepared with shoots (P<0.01, Table II, Fig. 2).

Treatments prepared with leaves and roots of the native donor did not affect the number of leaves but increased the number of lateral roots of *A. fastigiatus* (P<0.01, Table II, Fig. 3a) and *L. aurea* seedlings (P<0.05, Table II, Fig. 3b). Treatments prepared with leaves and roots of the exotic species did not affect the number of leaves and lateral roots of *A. fastigiatus* (Table II, Fig. 3c), however, they reduced the number of leaves and increased the number of lateral roots of *L. aurea* (P<0.001, Table II, Fig. 3d).

Effects of the donor species on the growth of exotic target species

Treatments prepared with leaves of the native donor inhibited the shoot growth of *M. minutiflora* between 5 and 17% (P<0.05), and root growth between 20 and 26% (P<0.01, Table III, Fig. 4a), while treatments prepared with roots of the native donor had minimal impact on shoot growth but reduced root growth of *M. minutiflora* (Fig. 4a). Treatments prepared with leaves and roots of the native donor varied from promotion to inhibition of shoot (P<0.05, Table

Table II. Statistical analysis of growth parameters. Generalized linear mixed models (GLMMs) testing the influence of leaves and roots of *Andropogon bicornis* L. (native donor) and *Andropogon gayanus* Kunth. (exotic donor) incorporated into the soil on the shoot and root growth, total biomass and number of leaves and roots of the native target species *Andropogon fastigiatus* Sw. and *Lepidaploa aurea* (Mart. Ex DC.) H. Rob.

		NATIVE			EXOTIC	
Target species	**Variable**	**Treatment**	**Estimative ± SEM**	**p-value**	**Estimative ± SEM**	**p-value**
Andropogon fastigiatus Sw.	**Shoots**	0.75%	0.6 ± 0.05	0.2	-0.1 ± 0.05	<0.01
		1.5%	0.12 ± 0.05	<0.05	-0.2 ± 0.05	<0.001
		3%	-0.07 ± 0.05	0.1	-0.1 ± 0.05	<0.05
		Plant part	0.2 ± 0.3	<0.001	-0.007 ± 0.04	0.8
	Roots	0.75%	-0.1 ± 0.05	<0.01	-0.2 ± 0.06	<0.001
		1.5%	-0.1 ± 0.05	<0.05	-0.2 ± 0.06	<0.001
		3%	-0.2 ± 0.05	<0.001	-0.2 ± 0.06	<0.001
		Plant part	-0.1 ± 0.04	<0.01	-0.05 ± 0.04	0.1
	Total biomass	0.75%	-0.1 ± 0.04	<0.01	-0.06 ± 0.04	0.1
		1.5%	-0.7 ± 0.04	0.08	-0.1 ± 0.04	<0.05
		3%	-0.11 ± 0.04	<0.01	0.01 ± 0.04	0.8
		Plant part	0.06 ± 0.03	0.052	0.01 ± 0.03	0.7
	Leaves	0.75%	0.06 ± 0.1	0.5	-0.09 ± 0.76	1
		1.5%	0.07 ± 0.1	0.5	-0.25 ± 0.75	0.8
		3%	-0.01 ± 0.1	0.8	-0.001 ± 0.76	0.9
		Plant part	0.09 ± 0.1	0.2	0.08 ± 0.11	0.7
	Lateral roots	0.75%	0.3 ± 0.2	0.1	-0.04 ± 0.4	1
		1.5%	0.5 ± 0.2	<0.01	-0.7 ± 0.4	0.5
		3%	0.2 ± 0.2	0.2	0.6 ± 0.4	0.4
		Plant part	0.8 ± 0.1	<0.001	-0.3 ± 0.6	0.08
Lepidaploa aurea (Mart. Ex DC.) H. Rob.	**Shoots**	0.75%	0.9 ± 0.02	0.2	-0.1 ± 0.02	<0.001
		1.5%	-0.03 ± 0.03	0.2	-0.1 ± 0.02	<0.001
		3%	0.03 ± 0.03	0.8	-0.2 ± 0.02	<0.001
		Plant part	0.01 ± 0.02	0.4	-0.08 ± 0.02	<0.001
	Roots	0.75%	0.9 ± 0.05	0.5	-0.2 ± 0.04	<0.001
		1.5%	0.04 ± 0.06	0.8	-0.3 ± 0.04	<0.001
		3%	-0.01 ± 0.06	0.4	-0.4 ± 0.04	<0.001
		Plant part	0.07 ± 0.04	0.1	-0.08 ± 0.03	<0.01
	Total biomass	0.75%	0.05 ± 0.07	0.4	-0.05 ± 0.03	0.1
		1.5%	0.06 ± 0.07	0.4	-0.2 ± 0.03	<0.001
		3%	0.03 ± 0.07	0.6	-0.3 ± 0.03	<0.001
		Plant part	0.05 ± 0.05	0.2	-0.08 ± 0.02	<0.01
	Leaves	0.75%	-0.08 ± 0.1	0.4	-0.1 ± 0.1	0.2
		1.5%	0.09 ± 0.1	0.3	-0.1 ± 0.1	0.8
		3%	0.05 ± 0.1	0.6	-0.1 ± 0.1	0.9
		Plant part	-0.04 ± 0.07	0.5	-0.2 ± 0.07	<0.01
	Lateral roots	0.75%	0.2 ± 0.3	0.4	1.6 ± 0.4	<0.001
		1.5%	0.6 ± 0.2	<0.05	1.9 ± 0.4	<0.001
		3%	0.2 ± 0.3	0.4	1.7 ± 0.4	<0.001
		Plant part	0.2 ± 0.2	0.2	-0.7 ± 0.2	<0.001

***Note*: Confidence level: 0.95.**

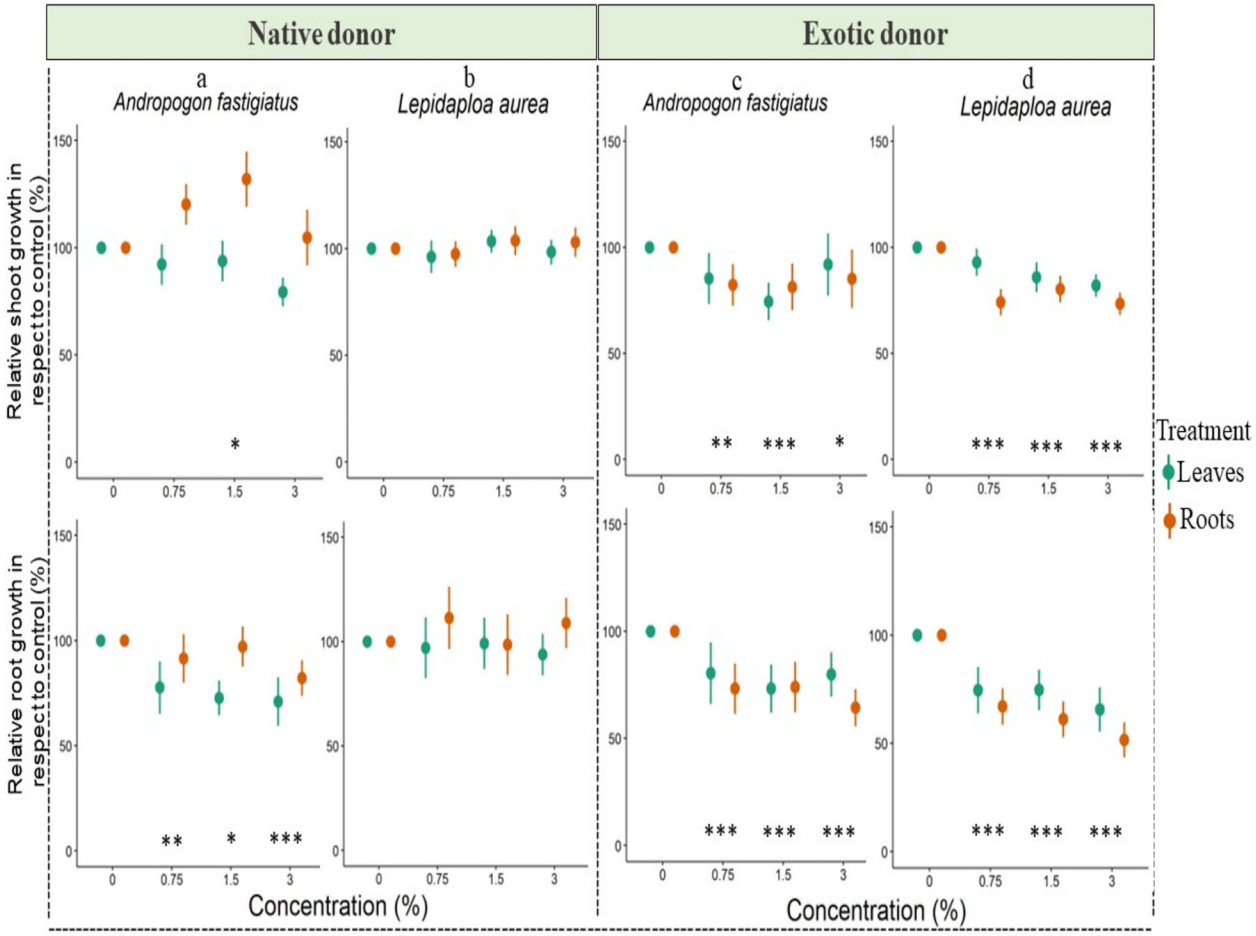

Figure 1. Relative growth of native species. Influence of leaves and roots of *Andropogon bicornis* L. (native donor - a, b) and *Andropogon gayanus* Kunth. (exotic donor - c, d) incorporated into the soil on the shoot and root growth of the native target species *Andropogon fastigiatus* Sw. and *Lepidaploa aurea* (Mart. ex DC.) H. Rob. Seedlings were grown for 13 days (except *L. aurea* which was grown for 18 days) at a temperature regime of 17/27°C (night/day) under a 12-hour photoperiod (white light). Level of significance of the effects of treatments in respect to control: * significant at 5%; ** significant at 1%; * significant at 0.1%. Data not marked with asterisks are not significant. GLMMs (Confidence level: 0.95).**

III, Fig. 4b) to a minor promotion of root growth (P<0.01, Table III, Fig. 4b) of *S. elata* seedlings.

Treatments prepared with leaves and roots of the exotic donor reduced the shoot growth of *M. minutiflora* seedlings between 22 and 29%, and between 21 and 32%, respectively (P<0.001, Table III, Fig. 4c), and inhibited root growth between 16 and 17%, and between 18 and 24%, respectively (P<0.05, Table III, Fig. 4c). These same treatments inhibited the shoot growth of *S. elata* seedlings between 7 and 11%, and between 8 e 14%, respectively; and root growth between 3 and 18%, and between 23 and 26%, respectively (P<0.05, Table III, Fig. 4d). In general, treatments prepared with roots of the exotic donor were slightly more harmful to growth of the target species than those prepared with leaves (P<0.001, Table III, Fig. 4).

Substrates prepared with leaves and roots of the native donor reduced the biomass of *M. minutiflora* between 31 and 54%, and between 25 and 48%, respectively; by contrast, they increased biomass of *S. elata* seedlings (P<0.001, Table III, Figs. 5a and 5b). Treatments prepared

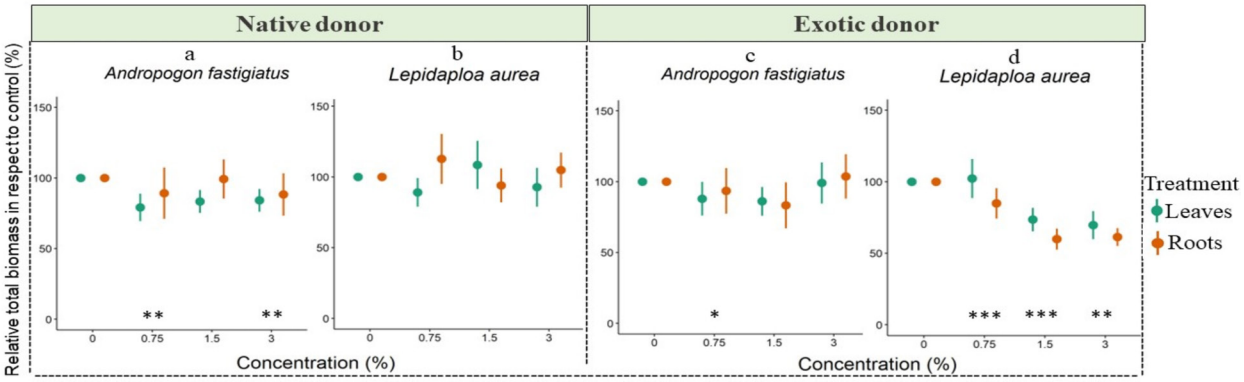

Figure 2. Biomass incorporation of native seedlings. Influence of leaves and roots of *Andropogon bicornis* L. (native donor - a, b) and *Andropogon gayanus* Kunth. (exotic donor - c, d) incorporated into the soil on the total biomass of the target native species *Andropogon fastigiatus* Sw. and *Lepidaploa aurea* (Mart. Ex DC.) H. Rob. Seedlings were grown for 13 days (except *L. aurea* which was grown for 18 days) at a temperature regime of 17/27°C (night/day) under a 12-hour photoperiod (white light). Level of significance of the effects of treatments in respect to control: * significant at 5%; ** significant at 1%; * significant at 0.1%. Data not marked with asterisks are not significant. GLMMs (Confidence level: 0.95).**

with leaves and roots of the exotic grass did not affect biomass of both *M. minutiflora* and *S. elata* seedlings (Table III, Figs. 5c and 5d).

Treatments prepared with plant material of the native donor did not affect the number of leaves but decreased lateral roots of *M. minutiflora* seedlings (P<0.001, Table III, Fig. 6a); these treatments did not significantly affect the number of leaves and lateral roots of *S. elata* seedlings (Table III, Fig. 6b). Treatments prepared with leaves and roots of the exotic donor did not influence the number of leaves of *M. minutiflora* and *S. elata* seedlings, but significantly reduced the number of lateral roots for *M. minutiflora* seedlings (P<0.01, Table III, Figs. 6c and 6d).

DISCUSSION

Effects of the donor species on the growth of native target species

Treatments prepared with roots of the native grass (*A. bicornis*) promoted shoot growth of the native *A. fastigiatus* and increased lateral root profusion for both *A. fastigiatus* and *L. aurea* seedlings. Although the treatments prepared with leaves of the native donor inhibited root growth and reduced total biomass for *A. fastigiatus*, however, these negative effects might be counteracted by the positive effects on shoot growth and lateral root profusion. Taking together, the overall effect of the native grass on the initial growth of the native species approaches varied in general between -16 and 19 % for *A. fastigiatus* and between -2 and 6% for *L. aurea*. Previous studies reported that allelochemicals may promote plant growth of congeneric species (Loayza et al. 2017, Thiébaut et al. 2019) what might explain the growth stimulus of *A. fastigiatus* by *A. bicornis* reported in the present study.

Indeed, our results suggest that the plant litter (containing both senescent leaves and roots) of *A. bicornis* might not inhibit seedling growth of the two target species under field conditions; instead, it might stimulate the initial growth of *L. aurea* and the number of leaves and lateral roots for both native species, indicating that the potential allelopathic properties of *A. bicornis* might not arrest the initial establishment of both native species in the field.

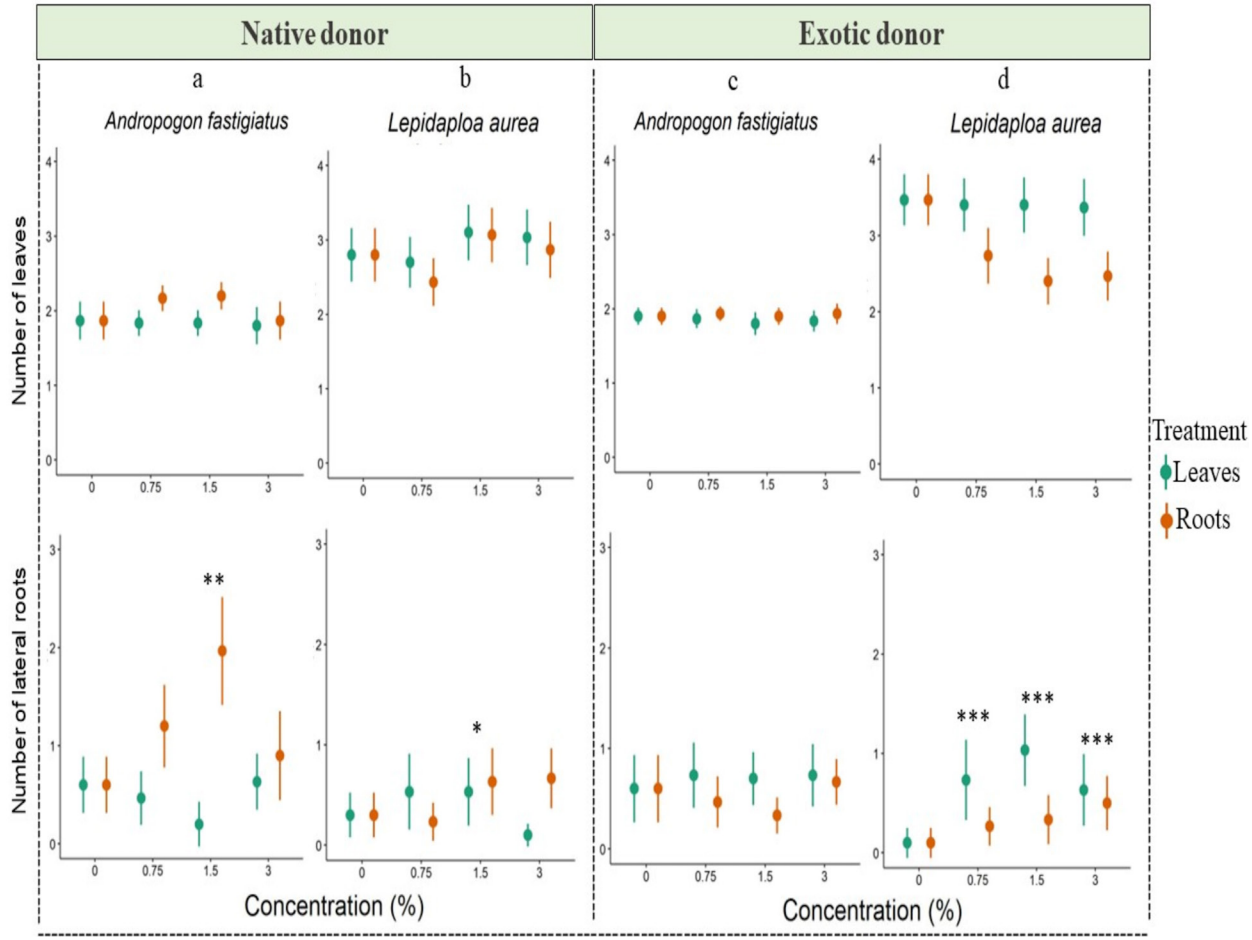

Figure 3. Number of leaves and lateral roots of the target species under the influence of donor species. Influence of leaves and roots of *Andropogon bicornis* L. (native donor - a, b) and *Andropogon gayanus* Kunth. (exotic donor - c, d) incorporated into the soil on the number of leaves and lateral roots of target native species *Andropogon fastigiatus* Sw. and *Lepidaploa aurea* (Mart. Ex DC.) H. Rob. Seedlings were grown for 13 days at a temperature regime of 17/27°C (night/day) under a 12-hour photoperiod (white light). Level of significance of the effects of treatments in respect to control: * significant at 5%; ** significant at 1%; * significant at 0.1%. Data not marked with asterisks are not significant. GLMMs (Confidence level: 0.95).**

A larger number of lateral roots might optimize nutrient uptake from the soil by increasing the absorption area of the root system (Pélissier et al. 2021). Such potential allelopathic effects of the native grass on other native species might also contribute with restoration approaches, for example, because the fast development of native species, in particular *L. aurea* (Lopes et al. 2018) would be desirable in order to overcome the potential negative impacts of exotic species that usually stablish faster and impair soil coverage by native ones (Sampaio et al. 2015, Liaffa, unpublished data). If so, allelopathic studies with an ecological approach might contribute with the management and conservation of natural areas (Bensusan 2006). However, since potentially allelopathic interactions are mediated by several factors, including competition (Del Fabbro et al. 2014), field studies are extremely important to unravel how allelopathy could effectively interfere with plant growth and community dynamics under natural conditions (Silva et al. 2017, Uesugi et al. 2019).

Table III. Statistical analysis of growth parameters. Generalized linear mixed models (GLMMs) testing the influence of leaves and roots of *Andropogon bicornis* L. (native donor) and *Andropogon gayanus* Kunth. (exotic donor) incorporated into the soil on the shoot and root growth, total biomass and number of leaves and roots of the exotic species *Melinis minutiflora* P. Beauv. and *Stapfochloa elata* P.M. Peterson.

		NATIVE			EXOTIC	
Target species	**Variable**	**Treatment**	**Estimative ± SEM**	**p-value**	**Estimative ± SEM**	**p-value**
Melinis minutiflora P. Beauv.	**Shoots**	0.75%	-0.01 ± 0.04	0.1	-0.2 ± 0.04	<0.001
		1.5%	-0.002 ± 0.04	0.9	-0.2 ± 0.04	<0.001
		3%	-0.009 ± 0.04	<0.05	-0.2 ± 0.04	<0.001
		Plant part	0.004 ± 0.03	0.8	-0.02 ± 0.03	0.4
	Roots	0.75%	-0.1 ± 0.05	<0.01	-0.07 ± 0.08	0.3
		1.5%	-0.2 ± 0.05	<0.001	-0.03 ± 0.08	0.6
		3%	-0.1 ± 0.05	<0.01	-0.2 ± 0.08	<0.05
		Plant part	0.07 ± 0.04	0.07	-0.03 ± 0.06	0.5
	Total biomass	0.75%	-0.4 ± 0.08	<0.001	0.006 ± 0.05	0.8
		1.5%	-0.3 ± 0.08	<0.001	0.04 ± 0.05	0.4
		3%	-0.4 ± 0.08	<0.001	0.05 ± 0.05	0.3
		Plant part	-0.03 ± 0.05	0.5	0.01 ± 0.03	0.6
	Leaves	0.75%	0.01 ± 0.1	0.8	0.0002 ± 0.8	1
		1.5%	0.04 ± 0.1	0.7	0.3 ± 0.8	0.8
		3%	0.05 ± 0.1	0.6	-0.06 ± 0.7	0.7
		Plant part	-0.03 ± 0.08	0.6	0.2 ± 0.01	0.8
	Lateral roots	0.75%	-0.1 ± 0.1	0.3	-0.5 ± 0.1	<0.001
		1.5%	-0.1 ± 0.1	0.3	-0.4 ± 0.1	<0.01
		3%	-0.4 ± 0.1	0.001	-0.6 ± 0.1	<0.001
		Plant part	-0.1 ± 0.09	<0.05	-0.1 ± 0.1	<0.01
Stapfochloa elata P.M. Peterson	**Shoots**	0.75%	0.1 ± 0.07	<0.05	-0.08 ± 0.03	<0.05
		1.5%	0.07 ± 0.07	0.3	-0.06 ± 0.03	0.09
		3%	-0.03 ± 0.07	0.5	-0.1 ± 0.03	<0.01
		Plant part	-0.09 ± 0.05	0.07	-0.02 ± 0.02	0.4
	Roots	0.75%	0.2 ± 0.07	<0.01	-0.1 ± 0.05	<0.05
		1.5%	0.1 ± 0.07	0.1	-0.1 ± 0.05	<0.05
		3%	0.09 ± 0.07	0.2	-0.2 ± 0.05	<0.001
		Plant part	-0.04 ± 0.05	0.4	-0.1 ± 0.03	<0.001
	Total biomass	0.75%	0.1 ± 0.05	0.051	-0.02 ± 0.06	0.7
		1.5%	0.1 ± 0.05	<0.05	0.02 ± 0.06	0.7
		3%	0.2 ± 0.05	<0.001	-0.08 ± 0.06	0.2
		Plant part	0.09 ± 0.03	<0.01	-0.02 ± 0.04	0.6
	Leaves	0.75%	0.08 ± 0.1	0.5	-0.04 ± 0.1	0.7
		1.5%	0.1 ± 0.1	0.2	-0.03 ± 0.1	0.7
		3%	0.2 ± 0.1	0.1	-0.09 ± 0.1	0.4
		Plant part	-0.03 ± 0.1	0.7	0.008 ± 0.09	0.9
	Lateral roots	0.75%	0.02 ± 0.2	0.9	0.3 ± 0.2	0.1
		1.5%	-0.3 ± 0.2	0.1	0.2 ± 0.2	0.3
		3%	-0.4 ± 0.2	0.06	0.009 ± 0.2	0.9
		Plant part	-0.6 ± 0.1	<0.001	-0.4 ± 0.1	<0.01

***Note*: Confidence level: 0.95.**

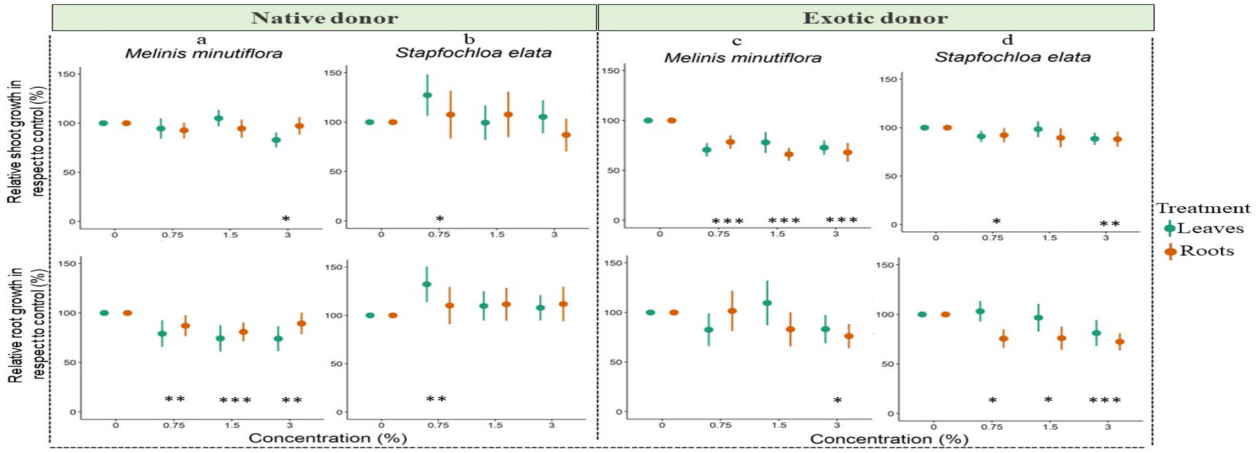

Figure 4. Relative growth of exotic species. Influence of leaves and roots of *Andropogon bicornis* L. (native donor - a, b) and *Andropogon gayanus* Kunth. (exotic donor - c, d) incorporated into the soil on the shoot and root growth of target exotic species *Melinis minutiflora* P. Beauv. and *Stapfochloa elata* P.M. Peterson. Seedlings were grown for 13 days at a temperature regime of 17/27°C (night/day) under a 12-hour photoperiod (white light). Level of significance of the effects of treatments in respect to control: *significant at 5%; ** significant at 1%; * significant at 0.1%. Data not marked with asterisks are not significant. GLMMs (Confidence level: 0.95).**

In contrast with the effects produced by the native donor, we found that treatments prepared with leaves and roots of the exotic donor *A. gayanus* reduced shoot and root growth and total biomass of both native species, suggesting that plant litter of the exotic grass might inhibit the initial growth of these native species under field conditions. Although the number of lateral roots of *L. aurea* were slightly increased by the exotic donor, the number of leaves were sharply reduced, so the overall effect of *A. gayanus* on seedling differentiation varied from positive to negative.

Previous studies showed that delayed root growth compromises seedling survival, and such allelopathic interferences might ultimately affect the composition of communities (Facelli & Picket 1991, Catalán et al. 2013, Arroyo et al. 2015). As the root system is generally the first plant tissue to come into contact with substances in the soil (Chung et al. 2001, Maraschin-Silva & Aquila 2006), allelochemicals tend to have a greater effect on root than shoot growth parameters (Tawaha & Turk 2003, Wakjira et al. 2005), and we have found evidence for this in the present study.

Soil by itself may have also contributed for the growth stimulus we observed among native species (Table I); As native species are in theory better adapted to Cerrado soils than exotic ones (Furley & Ratter 1988, Lopes & Guilherme 2016), the higher aluminum content and more acidic soil of the area where the donor and target natives coexist might benefit the growth of native in comparison to exotic species. So, native species might benefit when growing in more acidic soils (as the donor native's area) in comparison to less acidic soils (donor exotic's area).

The fact that the treatments prepared with exotic plant material reduced the initial growth and seedling biomass of native species might be related to the fact that the potentially allelochemicals compounds produced by the exotic grass are not recognized or are more harmful to native species than allelochemicals eventually produced by native donors (Hierro & Callaway 2021). This suggests that allelochemicals produced by *A. gayanus*

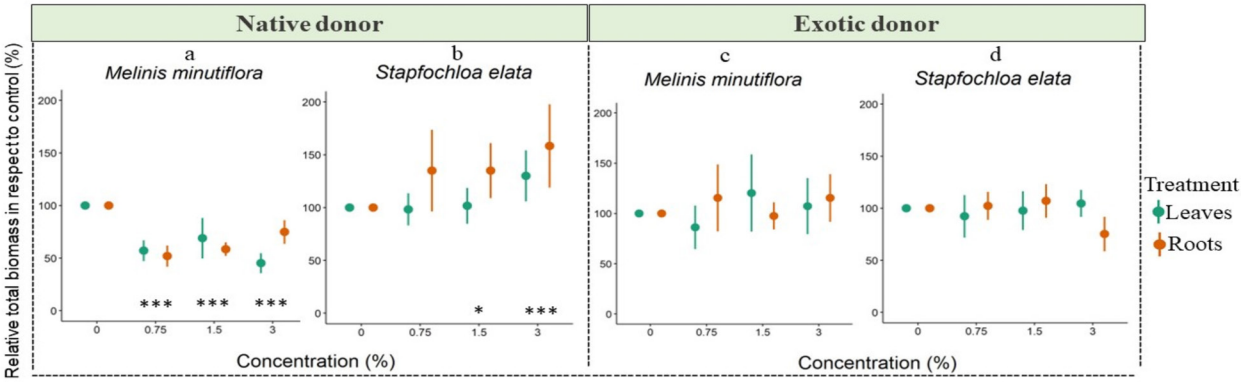

Figure 5. Biomass incorporation of exotic seedlings. Influence of leaves and roots of *Andropogon bicornis* L. (native donor - a, b) and *Andropogon gayanus* Kunth. (exotic donor - c, d) incorporated into the soil on the total biomass of target exotic species *Melinis minutiflora* P. Beauv. and *Stapfochloa elata* P.M. Peterson. Seedlings were grown for 13 days at a temperature regime of 17/27° C (night/day) under a 12-hour photoperiod (white light). Level of significance of the effects of treatments in respect to control: * significant at 5%; ** significant at 1%; * significant at 0.1%. Data not marked with asterisks are not significant. GLMMs (Confidence level: 0.95).**

might somewhat facilitate its invasion of areas previously covered by native species, such a finding that agrees with the novel weapons hypothesis (Callaway & Ridenour 2004). The studies of Yuan et al. (2021) showed a similar pattern of allelopathic response as ours. They showed that exotic species promoted greater effects on the growth of natives, and native donor species promoted greater effects on exotic target species. Their results supported both the novel weapons hypothesis and the homeland-security hypothesis. However, they did not find a response associated with coevolution (Yuan et al. 2021).

Effects of the donor species on the growth of exotic target species

Substrates containing leaves and roots of the donor native reduced root growth, total biomass, and the number of lateral roots of *M. minutiflora* seedlings, indicating a potentially negative allelopathic effect of *A. bicornis* on the growth of this African grass. In contrast to their positive effects on the growth of native seedlings, the negative impacts of the native donor on the growth of *M. minutiflora* substantiate the homeland security hypothesis, which suggests that the lack of shared evolutionary history (Callaway & Ridenour 2004) and biochemical recognition (Hierro & Callaway 2021) might make exotic invaders more susceptible to chemical compounds produced by native species (Cummings et al. 2012). Similar response patterns were reported in other studies (Cummings et al. 2012, Hou et al. 2012, Lopes et al. 2018, Ning et al. 2016) and indicate the potential use of *A. bicornis* in hampering the growth and spread of this exotic grass over both native and degraded areas of the Cerrado.

Melinis minutiflora represents a very undesirable species in areas under ecological restoration, since its rapid growth patterns and fast spread hinders the establishment of native species and compromises restoration efforts (Sampaio et al. 2015, Liaffa, unpublished data). Native species, such as *Caryocar brasiliense* Cambess., *Qualea parviflora* Mart. and *Eugenia dysenterica* DC. were shown to reduce the germination and initial growth of *M. minutiflora* through the release of chemical compounds by their leaves (Aires, unpublished data). Considering the positive effects of *A. bicornis* on seedling growth of some native species

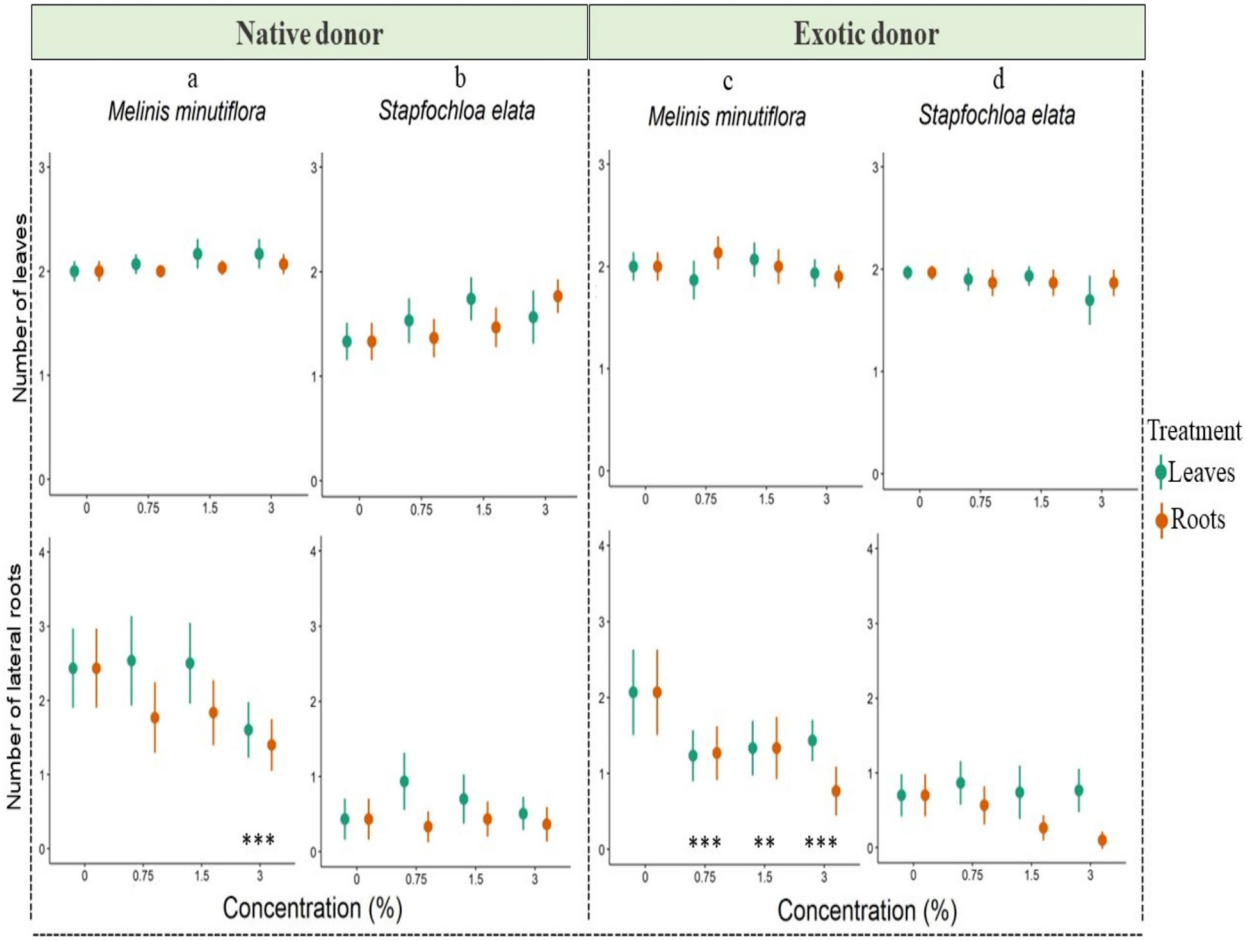

Figure 6. Number of leaves and lateral roots of the target species under the influence of donor species. Influence of leaves and roots *Andropogon bicornis* L. (native donor - a, b) and *Andropogon gayanus* Kunth. (exotic donor - c, d) incorporated into the soil on the number of leaves and lateral roots of the exotic species *Melinis minutiflora* P. Beauv. and *Stapfochloa elata* P.M. Peterson. Level of significance of the effects of treatments in respect to control: * significant at 5%; ** significant at 1%; * significant at 0.1%. Data not marked with asterisks are not significant. GLMMs (Confidence level: 0.95).**

and the negative impacts on seedling growth of this exotic grass, the use of *C. brasiliense*, *Q. parviflora*, *E. dysenterica* and *A. bicornis* in areas under restoration represent a promising approach to control the spread of exotic species, in particular *M. minutiflora*. However, it is important to mention that, except the present study, all the inhibitory effects described above were obtained under laboratory condition and using filter paper as substrate. Therefore, to overcome such constraints (Silva et al. 2017), studies should be also conducted under natural conditions (and using soil as substrate) to check whether such inhibitory effects of native species on *M. minutiflora* growth would also take place in the field.

In contrast to the negative effects of *A. bicornis* on the growth parameters of *M. minutiflora*, this donor native had a positive effect on the growth of *S. elata*. Considering that the biogeographical origin of the South American *S. elata* is closer than that of the African *M. minutiflora*, our findings indicate that this native donor might have a milder allelopathic impact on species with a closer biogeographic origin and/or that have coexisted for longer than on

species from more distant regions (Callaway & Aschehoug 2000, Callaway & Ridenour 2004, Cummings et al. 2012, Del Fabbro et al. 2014, Ning et al. 2016). A longer period of co-occurrence between species might contribute for a better biochemical recognition of allelochemicals produced by each other (Hierro & Callaway 2021) and, consequently, for the potential development of chemical defenses (Callaway & Ridenour 2004).

The exotic *A. gayanus* reduced seedling growth of the exotics *M. minutiflora* and *S. elata*. The negative effects between exotic species were previously reported by Barbosa et al. (2008); they showed that the African grass *Brachiaria decumbens* (Ness) Stapf. reduced the germination of caryopses of *M. minutiflora* through the release of allelochemicals. This might help to explain the displacement of *M. minutiflora* by *B. decumbens* in Cerrado areas (Pivello et al. 1999a, b). Since all three exotic grasses have similar physiological characteristics, such as rapid growth and efficient photosynthesis and reproduction (Brighenti et al. 2007, Durigan et al. 2007, Martins et al. 2009, Aires et al. 2014, Musso et al. 2019), our studies suggest that the potential allelopathic effects of *A. gayanus* on the initial growth of *M. minutiflora* and *S. elata* might provide this exotic grass a competitive advantage over the other two and consequent predominance in areas under invasion. Our results contrast with the novel weapon hypothesis, since the African donor significantly reduced the initial growth of the other two exotics, in particular the African *M. minutiflora*, what would not be expected to occur between species which share a close biogeographical origin (Callaway & Ridenour 2004). It is important to mention, however, that the exotic donor did not affect consistently the seedling biomass of both exotic species, so further studies are required to disentangle the effects of the exotic donor on seedling differentiation from seedling biomass incorporation of exotic species.

It was shown that root exudates of *A. gayanus* inhibit biological nitrification (Subbarão et al. 2007), which might compromise N availability in soil and consequently arrest plant growth (Tothill et al. 1985). This might help to explain why roots of *A. gayanus* had a stronger influence than leaves on the initial growth of all target species, including the exotic *M. minutiflora*. Also, it is important to mention that our studies were conducted using Cerrado's soil as substrate, which chemical and physical properties are distinct from the African soils where these species come from (Scholes 1997). Consequently, the potential allelopathic interactions between exotic donor and exotic targets reported here might not represent what might be observed among exotic species in their natural regions of occurrence. In this sense, in situ studies might provide new insights about the dominance of *A. gayanus* in respect to *M. minutiflora* and *S. elata* in their areas of occurrence and the involvement of allelopathy in their interactions.

We conclude that the negative effects of *Andropogon gayanus* on the initial growth of the native species might be contributing with its successful and fast spread over tropical South America. It is important to mention that our studies compared the effects of two congeneric donor species, hence the exotic-native comparison is not phylogenetically biased. Our findings reinforce the need to consider allelopathic interactions in management efforts of native and exotic species in both natural ecosystems and disturbed areas, particularly those under restoration, where the control of invasive species is essential for the restoration success and conservation of the native vegetation. Furthermore, we recognize that studies that investigate the allelopathic effects

in the donor species themselves are important to strengthen the interpretation of the results obtained and are therefore a proposal for future complementary research.

Acknowledgments

The authors are grateful to Professor Sarah Caldas for providing laboratory facilities and relevant comments on this study. The authors are grateful to the Rede de Sementes do Cerrado for providing the seeds used in this study.

REFERENCES

AIRES SS, SATO MN & MIRANDA HS. 2014. Seed characterization and direct sowing of native grass species as a management tool. Grass Forage Sci 69: 470-478.

ALLEM LN, GOMES AS & BORGHETTI F. 2014. Pequi Leaves Incorporated into the Soil Reduce the Initial Growth of Cultivated, Invasive and Native Species. An Acad Bras Cienc 86: 1761-1768. https://doi.org/10.1590/0001-3765201420130420.

ARROYO AI, PUEYO Y, SAIZ H & ALADOS CL. 2015. Plant-plant interactions as a mechanism structuring plant diversity in a Mediterranean semi-arid ecosystem. Ecol Evol 5: 5305-5317.

BARBOSA EG, PIVELLO VR & MEIRELLES ST. 2008. Allelopathic evidence in *Brachiaria decumbens* and its potential to invade the brazilian cerrados. Braz Arch Biol Technol 51: 825-831.

BARTOŃ K. 2024. MuMIn: Multi-Model Inference. R package version. 48.4, <https://CRAN.R-project.org/package=MuMIn>.

BATES D, MAECHLER M, BOLKER B & WALKER S. 2015. Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67: 1-48. doi:10.18637/jss.v067.i01.

BENSUSAN N. 2006. Conservação da biodiversidade em áreas protegidas. FGV, n. 1. Rio de Janeiro: Editora FGV, 176 p.

BRAZILIAN BIODIVERSITY INFORMATION SYSTEM. 2021. https://sibbr.gov.br/?lang=pt_BR (accessed 15 November 2021).

BRIGHENTI AM, VOLL E & GAZZIERO DL. 2007. *Chloris polydactyla* (L.) Sw., a perennial Poaceae weed: Emergency, seed production and its management. Weed Biol Manag 7: 84-88.

BROOKS ME, KRISTENSEN K, VAN BENTHEM KJ, MAGNUSSON A, BERG CW, NIELSEN A, SKAUG HJ, MAECHLER M & BOLKER BM. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9: 378-400. doi: 10.32614/RJ-2017-066.

CALLAWAY RM & ASCHEHOUG ET. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Sci 290: 521-523.

CALLAWAY RM & RIDENOUR WM. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Front Ecol Environ 2: 436-43.

CALLAWAY RM, RIDENOUR WM, LABOSKI T, WEIR T & VIVANCO JM. 2005. Natural Selection for resistance to the allelopathic effects of invasive plants. J Ecol 93: 576-583.

CARMONA R, MARTINS CR & FÁVERO AP. 1998. Fatores que afetam a germinação de sementes de gramíneas nativas do Cerrado. Rev Bras Sementes 20: 16-22.

CARVALHO SJP, SILVA RFP, NICOLAI M & CHRISTOFFOLETI PJ. 2005. Crescimento, desenvolvimento e produção de sementes da planta daninha capim-branco (*Chloris polydactyla*). Planta daninha 23: 603-609.

CATALÁN P, VÁZQUEZ-DE-ALDANA BR, DE LAS HERAS P, FERNÁNDES-SERAL A & PÉREZ-CORONA ME. 2013. Comparing the allelopathic potential of exotic and native plant species on understory plants: are exotic plants better armed? Anales de Biología 35: 65-74.

CHUNG IM, AHN JK & YUN SJ. 2001. Assesment of allelopathic potential of barnyard grass (*Echinochloa crus-galli*) on rice (*Oriza sativa* L.) cultivars. Crop Prot 20: 921-928.

CUMMINGS JA, PARKER IA & GILBERT GS. 2012. Allelopathy: a tool for weed management in forest restoration. Plant Ecol 213: 1975-1989.

D'ANTONIO CM, HUGHES RF & TUNISON JT. 2011. Long-term impacts of invasive grasses and subsequent fire in seasonally dry hawaiian woodlands. Ecol Appl 21: 1617-1628.

DAIREL M & FIDELIS A. 2020. How does fire affect germination of grasses in the Cerrado? Seed Sci Res 30: 275-283.

DEL FABBRO C, GÜSEWELL S & PRATI D. 2014. Allelopathic effects of three plant invaders on germination of native species: a field study. Biol Invasions 16: 1035-1042.

DJURDJEVIĆ L, DINIC A, PAVLOVIC P, MITROVIC M, KARADZIC B & TESEVIC V. 2011. An allelopathic investigation of the domination of the introduced invasive *Conyza canadensis* L. Flora 206: 921-927.

DURIGAN G, SIQUEIRA MF & FRANCO GADC. 2007. Threats to the Cerrado remnants of the state of São Paulo, Brazil. Sci Agrar Paran 64: 355-363.

FACELLI JM & PICKETT STA. 1991. Plant litter: its dynamics and effects on plant community structure. Bot Rev 57: 1-32.

FARIAS R, ALVES ER, MARTINS RC, BARBOZA MA, ZANENGAGODOY R, REIS JB & RODRIGUES-DA-SILVA R. 2002. Caminhando pelo cerrado: plantas herbáceo arbustivas, caracteres vegetativos e organolépticos, 1st ed., Brasília: Editora UnB, 94 p.

FILGUEIRAS TS. 1990. Africanas no Brasil: gramíneas introduzidas da África. Cadernos de Geociências 5: 57-63.

FILGUEIRAS TS & FAGG CW, 2008. Gramíneas nativas para a recuperação de áreas degradadas no cerrado. In: Bases para a recuperação de áreas degradadas na Bacia do São Francisco. Brasília: Editora UnB, p. 89-108.

FLORES TA, SETTERFIELD SA & DOUGLAS MM. 2005. Seedling recruitment of the exotic grass *Andropogon gayanus* (Poaceae) in Northern Australia. Aust J Bot 53: 243-249.

FOX J & WEISBERG S. 2019. An R Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA. <https://www.john-fox.ca/Companion/>.

FOX J, WEISBERG S & PRICE B. 2022. carData: Companion to Applied Regression Data Sets. R package version 3.0-5, <https://CRAN.R-project.org/package=carData>.

FURLEY PA & RATTER JA. 1988. Soil Resources and Plant Communities of the Central Brazilian Cerrado and Their Development. J Biogeogr 15: 97-108.

GELMAN A & HILL J. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge university press.

GOERGEN EM, LEGER EA & ESPELAND EK. 2011. Native perennial grasses show evolutionary response to *Bromus tectorum* (Cheatgrass) invasion. PloS One 6: e18145.

GROSSI SM, MAGALHÃES NM, OLIVEIRA SCC, GOMES AS & BORGHETTI F. 2021. Avaliação do potencial alelopático e fitotoxicidade de *Hymenaea stigonocarpa* em espécies invasoras e cultivadas. Heringeriana 15: 30-39.

HARTIG F. 2024. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R Package version 0.4.7. https://github.com/florianhartig/dharma.

HASSAN MO, GOMAA NH, FAHMY GM, GONZÁLEZ L, HAMMOUDA O & ATTEYA AM. 2014. Influence of *Sonchus oleraceus* L. residue on soil properties and growth of some plants. Philipp. Agric Sci 97: 368-376.

HESTER J & BRYAN J. 2024. glue: Interpreted String Literals. R package version 1.8.0, <https://CRAN.R-project.org/package=glue>.

HIERRO JL & CALLAWAY RM. 2021. The Ecological Importance of Allelopathy. Annu Rev Ecol Evol Syst 52: 25-45.

HOFFMANN WA & HARIDANSAN M. 2008. The invasive grass, *Melinis Minutiflora*, inhibits tree regeneration in a neotropical savanna. Austral Ecol 33: 29-36.

HOFFMANN WA, LUCATELLI VMPC, SILVA FJ, AZEUEDO INC, MARINHO MDS, ALBUQUERQUE AMS, LOPES ADO & MOREIRA SP. 2004. Impact of the invasive alien grass *Melinis minutiflora* at the savanna-forest ecotone in the Brazilian Cerrado. Divers Distrib 10: 99-103.

HOROWITZ C, MARTINS CR & WALTER B. 2013. Flora exótica no parque nacional de Brasília: levantamento e classificação das Espécies. BioBrasil 3: 50-73.

HOTHORN T, BRETZ F & WESTFALL P. 2008. Simultaneous Inference in General Parametric Models. Biometrical Journal 50: 346-363.

HOU YP, PENG SL, GUANG-YAN N & CHEN L. 2012. Inhibition of invasive species *Mikania Micrantha* HBK by native dominant trees in China. Allelopathy J 29: 307-314.

INDERJIT DA, KARBAN WR & CALLAWAY RM. 2011. The ecosystem and evolutionary contexts of allelopathy. Trends Ecol Evol 26: 655-662.

JACOBI CM, CARMO FFD & VINCENT RDC. 2008. Estudo fitossociológico de uma comunidade vegetal sobre canga como subsídio para a reabilitação de áreas mineradas no Quadrilátero Ferrífero, MG. Rev Árvore 32: 345-353.

KISSMANN KG & GROTH D. 1997. Plantas infestantes e nocivas, 2nd ed., São Paulo: BASF, 825 p.

KOMSTA L. 2022. outliers: Tests for Outliers. R package version 0.15, <https://CRAN.R-project.org/package=outliers>.

KRISTENSEN K, NIELSEN A, BERG CW, SKAUG H & BELL BM. 2016. TMB: Automatic Differentiation and Laplace Approximation. J Stat Softw. 70: 1-21. doi:10.18637/jss.v070.i05.

KUZNETSOVA A, BROCKHOFF PB & CHRISTENSEN RHB. 2017. lmerTest Package: Tests in Linear Mixed Effects Models. J Stat Softw 82: 1-26. doi:10.18637/jss.v082.i13 <https://doi.org/10.18637/jss.v082.i13>.

LANNES LS, BUSTAMANTE MMC, EDWARDS PJ & VENTERINK HO. 2012. Alien and endangered plants in the brazilian cerrado exhibit contrasting relationships with vegetation biomass and N:P stoichiometry. New Phytol 196: 816-823.

LENTH RV. 2016. Least-Squares Means: The R Package lsmeans. Journal of Statistical Software 69: 1-33. doi:10.18637/jss.v069.i01.

LINDERS TEW, SCHAFFNER U, ESCHEN R, ABEBE A, CHOGE SK, NIGATUL, MBAABU PR, SHIFERAW H & ALLAN E. 2019. Direct and indirect effects of invasive species: biodiversity loss is a major mechanism by which an invasive tree affects ecosystem functioning. J Ecol 107: 2660-2672.

LOAYZA AP, HERRERA-MADARIAGA MA, CARVAJAL DE, GARCIA-GIZMÁN P & SQUEO FA. 2017. Conspecific plants are better 'nurses' than rocks consistent results revealing intraspecific facilitation as a process that promotes establishment in a hyper-arid environment. AoB Plants 9: plx056.

LOPES AS & GUILHERME LRG. 2016. A career perspective on soil management in the Cerrado region of Brazil. Adv Agron 137: 1-72.

LOPES PG, OLIVEIRA SCC, SALLES KA, SAMPAIO AB & SCHIMIDT IB. 2018. Allelopathy of a native shrub can help control invasive grasses at sites under ecological restoration in a neotropical savanna. Plant Ecol Divers 11: 527-538.

LORENZI H. 2008. Manual de identificação de plantas daninhas: plantio direto e convencional, 5th ed. Nova Odessa: Plantarum, 339 p.

LORENZO P, HUSSAIN MI & GOZÁLEZ L. 2013. Role of allelopathy during invasion process by alien invasive plants in terrestrial ecosystems. In: CHEEMA ZA, FAROOQ M & WAHID A (Eds), Allelopathy: current trends and future applications, Berlin: Springer-Verlag, Berlin, DEU, p. 3-21.

LORENZO P, PAZOS-MALVIDO E, RUBIDO-BARÁ M, REIGOSA MJ & GONZÁLEZ L. 2012. Invasion by the leguminous tree *Acacia dealbata* (Mimosaceae) reduces the native understorey plant species in different communities. Aust J Bot 60: 669-675.

LÜDECKE D, PATIL I, BEN-SCHACHAR MS, WIERNIK BM, WAGGONER P & MAKOWSKI D. 2021a. see: An R Package for Visualizing Statistical Models. Journal of Open Source Software 6: 3393. https://doi.org/10.21105/joss.03393

LÜDECKE D, BEN-SCHACHAR MS, PATIL I, WAGGONER P & MAKOWSKI D. 2021b. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. J Open Sour Softw 6: 31-39. https://doi.org/10.21105/joss.03139.

MANAUS: EMBRAPA AMAZÔNIA OCIDENTAL. 2005. Amostragem de solos.http://www.infoteca.cnptia.embrapa.br/infoteca/handle/doc/667898 (accessed 15 March 2022).

MAPBIOMAS. 2022. Coleção 6 da Série Anual de Mapas de Cobertura e Uso de Solo do Brasil. http://mapbiomas.org/stats (accessed 21 March 2022).

MARASCHIN-SILVA F & AQUILA MEA. 2006. Potencial alelopático de espécies nativas na germinação e crescimento inicial de *Lactuca sativa* L. (Asteraceae). Acta Bot Bras 20: 61-69.

MARINHO MS & MIRANDA HS. 2013. Efeito do fogo anual na mortalidade e no banco de sementes de *Andropogon gayanus* Kunth. no Parque Nacional de Brasília/DF. BioBrasil 3: 149-158.

MARTINS CR, HAY JDV & CARMONA R. 2009. Potencial Invasor de duas cultivares de *Melinis Minutiflora* no cerrado brasileiro – características de sementes e estabelecimento de plântulas. Rev Árvore 33: 713-722.

MARTINS CR, HAY JDV, SCALÉA M & MALAQUIAS JV. 2017. Management techniques for the control of *Melinis minutiflora* P. Beauv. (molasses grass): Ten years of research on an invasive grass species in the Brazilian Cerrado. Acta Bot Bras 31: 546-554.

MUSSO C, MACEDO MA, ALMEIDA NN, RODRIGUES DDM, CAMARGO MEMS, PÔRTO ACCQ & MIRANDA HS. 2019. *Andropogon gayanus* Kunth invasion in the Cerrado: from seed production to seedling establishment along roadsides. Biol Invasions 21: 1683-1695.

NERI AV, SOARES MP, MEIRA NETO JAA & DIAS LE. 2011. Cerrado species with potential for recovery of degraded areas for gold mining, Paracatu-MG. Rev Árvore 35: 907-918.

NING L, YU FH & VAN KLEUNEN M. 2016. Allelopathy of a native grassland community as a potential mechanism of resistance against invasion by introduced plants. Biol Invasions 18: 3481-3493.

PASTORE M, RODRIGUES RS, SIMÃO-BIANCHINI R & FILGUEIRAS TS. 2012. Plantas exóticas invasoras na Reserva Biológica do Alto da Serra de Paranapiacaba, Santo André-SP: guia de campo, 1st ed. São Paulo: Instituto de Botânica, 46 p.

PEDERSEN T. 2024. patchwork: The composer of plots. Pacote R versão 1.2.0.9000. https://github.com/thomasp85/patchwork, https://patchwork.data-imaginist.com

PÉLISSIER PM, MOTTE H & BEECKMAN T. 2021. Lateral root formation and nutrients: nitrogen in the spotlight. Plant Physiol 187: 1104-1116.

PELLIZZARO KF, CORDEIRO AOO, ALVES M, MOTTA CP, REZENDO GM, SILVA RRP, RIBEIRO JF, SAMPAIO AB, VIEIRA DLM & SCHMIDT IB. 2017. 'Cerrado' Restoration by Direct Seeding: Field Establishment and Initial Growth of 75 Trees, Shrubs and Grass Species. Rev Bras Bot 40: 681-693.

PEREIRA SC & BARRETO IL. 1985. O gênero *Chloris* Swartz (Gramineae) no Rio Grande do Sul. Rodriguésia 37: 9-20.

PIRES NM & OLIVEIRA VR. 2011. Alelopatia. In: OLIVEIRA JUNIOR RS, CONSTANTIN J & INOUE MH (Eds), Biologia e manejo de plantas daninhas, Curitiba: Omnipax, Curitiba, BRA, p. 95-124.

PIVELLO VR, CARVALHO VMC, LOPES PF, PECCININI AA & ROSSO S. 1999b. Abundance and Distribution of Native and Alien Grasses in a 'cerrado' (Brazilian Savanna) Biological Reserve. Biotropica 31: 71-82.

PIVELLO VR, SHIDA CN & MEIRELLES ST. 1999a. Alien grasses in brazilian savannas: a threat to the biodiversity. Biodivers Conserv 8: 1281-1294.

R CORE TEAM. 2022. The R Project for Statistical Computing (Version 4.1.3). https://www.r-project.org.

REIGOSA MJ, SÁNCHEZ-MOREIRAS AM & GONZÁLEZ L. 1999. Ecophysi- ological approach in allelopathy. Crit Rev Plant Sci 18: 577-608.

RIBEIRO LC & BORGHETTI F. 2013. Comparative effects of desiccation, heat shock and high temperatures on seed germination of savanna and forest tree species. Austral Ecol 39: 267-278.

RICE EL. 1984. Allelopathy, 2nd ed., New York: Academic Press, 422 p.

RODRIGUES RR, LIMA RAF, GANDOLFI S & NAVE AG. 2009. On the restoration of high diversity forests: 30 Years of Experience in the Brazilian Atlantic Forest. Biol Conserv 142: 1242-1251.

SAMPAIO AB & SCHMIDT IB. 2013. Espécies exóticas invasoras em unidades de conservação federais do Brasil. BioBrasil 3: 32-49.

SAMPAIO AB ET AL. 2015. Guia de restauração do Cerrado: volume 1: semeadura direta, 1st ed., Brasília: Embrapa Cerrados-Livro técnico (INFOTECA-E), 40 p.

SCHOLES RJ. 1997. Savanna. In: COWLING RM, RICHARDSON DM & PIERCE SM (Eds), Vegetation of Southern Africa, Cambridge: Cambridge University Press, Cambridge, UK, p. 258-277.

SHARMA S, BATISH DR, SINGH HP, JARYANA V & KOHLI RK. 2017. The impact of invasive *Hyptis suaveolens* on the floristic composition of the periurban ecosystems of Chandigarh, northwestern India. Flora 233: 156-162.

SILVA ER, OVERBECK GE & SOARES GLG. 2017. Something old, something new in allelopathy review: what grassland ecosystems tell us. Chemoecology 27: 217-231.

SUBBARÃO GV, RONDON M, ITO O, ISHIKAWA I, RAO IM, NAKAHARA K, LASCANO C & BERRY WL. 2007. Biological nitrification inhibition (BNI): is it a widespread phenomenon? Plant Soil 294: 5-18.

TAWAHA AM & TURK MA. 2003. Allelopathic effects of black mustard *Brassica nigra* on germination and growth of wild barley *Hordeum spontaneum*. J Agron Crop Sci 189: 298-303.

THIÉBAUT G, TARAYRE M & RODRÍGUEZ-PÉREZ H. 2019. Allelopathic Effects of Native Versus Invasive Plants on One Major Invader. Front Plant Sci 10: 854.

THOMAS D & ANDRADE RPDE. 1984. Desempenho agronômico de cinco gramíneas tropicais sob pastejo na região dos Cerrados. Pesqui Agropecu Bras 19: 1047-1051.

THOMAS PA, SCHÜLER J, BOAVISTA LR, TORCHELSEN FP, OVERBECKGE & MÜLLER SC. 2018. Controlling the invader *Urochloa decumbens*: Subsidies for ecological restoration in subtropical Campos grassland. Appl Veg Sci 22: 96-104.

THOMAS RJ & ASAKAWA NM. 1993. Decomposition of leaf litter from tropical forage grasses and legumes. Soil Biol Biochem 25: 1351-1361.

TOTHILL JC, NIX AH, STANTON JP & RUSSELL MJ. 1985. Land use and productive potential of Australian savanna lands. In: TOTHILL JC & MOTT JJ (Eds), Ecology and management of the world's savannas, Austrália: Australian Academy of Science, Canberra, AUS, p. 125-141.

TREMBLAY A, CANADA S, RANSIJN J & COPENHAGEN UO. 2020. LMERConvenienceFunctions: Model Selection and Post-Hoc Analysis for (G)LMER Models. R package version 3.0, <https://CRAN.R-project.org/package=LMERConvenienceFunctions>.

UESUGI A, JOHNSON R & KESSLER A. 2019. Context-depend Context-dependent induction of allelopathy in plants under competition. Oikos 128: 1492-1502.

VELAZCO SJE, VILLALOBOS F, GALVÃO F & MARCO JÚNIOR P. 2019. A dark scenario for Cerrado plant species: Effects of future climate, land use and protected areas ineffectiveness. Divers Distrib 25: 660-673.

VENABLES WN & RIPLEY BD. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.

VILÀ M, ESPINAR JL, HEJDA M, HULME PE, JAROŠIK V, MARON JL, PERGL J, SCHAFFNER U, SUN Y & PYŠEK P. 2011. Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. Ecol Lett 14: 702-708.

VILLELA ALG, MARTINELLI R, ZENATTI TF, RUFINO-JR L, MONQUERO PA, CONCEIÇÃO PM & AZEVEDO FA. 2021. Potential of two cover crops, signal grass and ruzi grass: suggested allelopathic effect on some important weeds. Aust J Crop Sci 15: 260-270.

WAKJIRA M, BERECHA G & BULTI B. 2005. Allelopathic effects of *Parthenium hysterophorus* extracts on seed germination and seedling growth of lettuce. Trop Sci 45: 159-162.

WICKHAM H ET AL. 2019. Welcome to the tidyverse. J Open Sour Softw 4: 16-86. doi:10.21105/joss.01686 <https://doi.org/10.21105/joss.01686>.

WICKHAM H & BRYAN J. 2023. readxl: Read Excel Files. R package version 1.4.3, <https://CRAN.R-project.org/package=readxl>.

YUAN L, LI JM, YU FH, ODUOR AM & VAN KLEUNEN M. 2021. Allelopathic and competitive interactions between native and alien plants. Biol Invasions 23: 3077-3090.

ZANIN A & LONGHI-WAGNER HM. 2011. Revision of Andropogon (Poaceae-Andropogoneae) from Brazil. Rodriguésia 62: 171-202.

How to cite

SOUZA CS, MARINS G, CAMARGO IFLG, LIMA LB, GOMES AS & BORGHETTI F. 2025. Allelopathic hypotheses revisited: the interactions between native and exotic species in the Brazilian savanna. An Acad Bras Cienc 97: e20240252. DOI 10.1590/0001-3765202520240252.

Manuscript received on March 12, 2024;
accepted for publication on March 9, 2025

CRISTIELE DOS SANTOS SOUZA[1]
https://orcid.org/0000-0002-6251-1733

GABRIEL MARINS[2]
https://orcid.org/0000-0003-3610-4832

ISABELA FERNANDA L.G. CAMARGO[3]
https://orcid.org/0000-0002-7690-9347

LARISSA BOAZ DE LIMA[1]
https://orcid.org/0000-0003-2051-6859

ANABELE STEFÂNIA GOMES[1]
https://orcid.org/0000-0003-4747-6375

FABIAN BORGHETTI[1]
https://orcid.org/0000-0001-7141-265X

[1]Universidade de Brasília, Departamento de Botânica, Laboratório de Termobiologia L.G. Labouriau, Campus Universitário Darcy Ribeiro, Asa Norte, s/n, 70919-970 Brasília, DF, Brazil

[2]Universidade de Brasília, Departamento de Ecologia, Laboratório de Ecologia de Insetos, Campus Universitário Darcy Ribeiro, Asa Norte, s/n, 70919-970 Brasília, DF, Brazil

[3]Universidade de Brasília, Departamento de Engenharia Florestal, Laboratório de Manejo de Bacias Hidrográficas, Campus Universitário Darcy Ribeiro, Asa Norte, s/n, 70919-970 Brasília, DF, Brazil

Correspondence to: **Fabian Borghetti**
E-mail: borghetti.fabian@gmail.com

Author Contributions

Cristiele dos Santos Souza: conceptualization, methodology, data curation, writing-original draft, validation, investigation, experimental design, formal analysis and software. Anabele Stefânia Gomes: conceptualization, methodology, experimental design, formal analysis and software. Fabian Borghetti: conceptualization, methodology, supervision, resources, writing-reviewing and editing, project administration and funding acquisition. Gabriel Marins, Isabela Fernanda L. G. Camargo and Larissa Boaz de Lima: validation and investigation.