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Original Paper

Do native plant species functionally similar to invasive species suffer more impacts from the invasion in seasonally dry tropical forests?

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Abstract

We tested the hypothesis that of the species studied in the Brazilian Semiarid, the ones most functionally similar to tree *Azadirachta indica* would be more affected by this exotic species during germination and early development. At first, we produced a crude extract of A. indica fresh leaves in six different dilutions. We placed 25 seeds of four native species (*Cenostigma pyramidale*, *Libidibia ferrea*, *Mimosa caesalpiniifolia*, and *Amburana cearensis*) to germinate in Petri dishes for each dilution, with four replicates for each species. We assessed: radicle length, emergence percentage, emergence speed index, and mean emergence time. We conducted an experiment in a greenhouse to assess how the exotic plant affected the development of individual plants of the studied species. We planted five seeds of each native species alone and five in interaction with the exotic species using ten 20-l buckets. The experiment lasted four months, and the functional attributes of the individuals were collected. Among the native species analyzed, according to the cluster analysis using the functional attributes of the species planted alone, *M. caesalpiniifolia, C. pyramidale* and *L. ferrea* were functionally more similar to the exotic species. In the germination experiment, the extract affected only root length, regardless of the functional similarity. We noticed that only *M. caesalpiniifolia* had its early development strongly inhibited when planted in interaction with the exotic species. Although the functional similarity between the exotic and the native species did not influence germination, it negatively affected the development.

Key words: allelopathy, Caatinga, exotic species, functional characteristics.

Resumo

Testamos a hipótese que das espécies estudadas do Semiárido brasileiro, as funcionalmente mais semelhantes com a arbórea exótica *Azadirachta indica* seriam mais afetadas na germinação e no desenvolvimento inicial. Inicialmente foi produzido extrato bruto das folhas frescas da exótica em seis diluições. Para cada diluição foram colocadas para germinar 25 sementes, de quatro espécies nativas (*Cenostigma pyramidale, Libidibia ferrea, Mimosa caesalpiniifolia* e *Amburana cearensis*), em placas de Petri com quatro repetições para cada espécie, onde foram avaliados: comprimento da radícula, porcentagem de emergência, índice de velocidade de emergência e tempo médio de emergência. Para avaliar a influência da exótica sobre o desenvolvimento dos indivíduos das espécies estudadas foi realizado um experimento em casa de vegetação. As sementes foram plantadas em 10 baldes de 20 l., sendo cinco baldes para cada espécie nativa isolada e cinco para ela em interação com a espécie exótica. O experimento durou quatro meses, e os atributos funcionais dos indivíduos foram coletados. Das nativas analisadas, de acordo com a análise de agrupamento usando os atributos funcionais das

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espécies plantadas isoladamente, *M. caesalpiniifolia, C. pyramidale* e *L. ferrea* foram funcionalmente mais próximas da exótica. No experimento de germinação notou-se que o extrato afetou apenas o comprimento da raiz, independente da proximidade funcional. Notamos que apenas *M. caesalpiniifolia*, plantada em interação, teve seu desenvolvimento inicial fortemente inibido. A semelhança funcional entre a exótica e as nativas não influenciou na germinação, mas afetou negativamente o desenvolvimento.

Palavras-chave: alelopatia, Caatinga, espécies exóticas, características funcionais.

Introduction

The introduction of invasive exotic species can occur naturally or due to anthropic action, which has been intensified over the past few years, mainly because of economic purposes (Zanuncio *et al.* 2016). The increase in the number of introduced invasive exotic species and their consequences has raised concerns among researchers since the 1980s. This issue is complex, as the invasion process can generate different responses in native species present in communities and different effects on the functioning of ecosystems where this process occurs (Rouget *et al*. 2015; Godoy 2019). The consequences of the invasion depend on the environment and the species involved, and the functional similarity between native and exotic species can drive the direction of the invasion (Case *et al.* 2016). However, studies have focused mainly on declining species richness in communities (Powell *et al.* 2013; Case *et al.* 2016).

Invasive exotic species change the structure and composition of plant communities, resulting in biodiversity loss (Pimentel 2011; Rouget *et al.* 2015; Fragoso-Moura *et al.* 2016). Pegado *et al.* (2006), Mantovani *et al.* (2013), and Silva *et al.* (2014) reported that invasive exotic species had a negative influence on the richness, abundance, and growth of native species in natural communities. Such community changes may occur due to competition, as invasive species tend to be better competitors than native ones (Pegado *et al.* 2006; Mantovani *et al.* 2013; Silva *et al.* 2014; Galon *et al.* 2017). However, no studies were found on the influence of functional similarity on the germination response or the influence of functional characteristics on the competitive ability of native species when interacting with invasive exotic species with allelopathic activity.

A species ability to be a better competitor, regardless of its origin, results from its ability to avoid or resist suppression. This ability is positively associated with some characteristics, such as root development and the ability to suppress a neighbor, related to characteristics, such as plant size, growth rate, and the production of allelopathic compounds, which together shape the competitive performance of the species in interaction (Wang *et al.* 2010; Aschehoug *et al.* 2016). In the case of biological invasion of exotic species, the production and release of allelochemicals in the environment can affect seed germination of native species and, therefore, their growth and development (Wardle & Peltzer 2017; Lenda *et al.* 2019).

It is known that the interaction strength varies between the pairs of species involved (Case *et al.* 2016; Farias *et al.* 2020), and these interactions can affect the fitness of organisms. The more similarities between species, the more they compete for the same resources, making it difficult for them to coexist on the same site (Powell *et al.* 2013; Kraft *et al.* 2015; Agostinetto *et al.* 2017). However, even though the similarity can be assessed through functional characteristics, and thus influence the coexistence and help to predict the invasion impacts at the species level (Case *et al.* 2016), these characteristics have been rarely considered in studies that assess changes in the community after the biological invasion (Molinari & D'Antonio 2014).

Some studies evaluated changes in natural communities in Brazil after biological invasion (Andrade *et al*. 2009; Fabricante *et al*. 2012), but there are many exotic species with an invasion history in country (I3N 2020) that need to be studied. One of them, *Azadirachta indica* A. Juss (Meliaceae), is native to the Asian region and introduced in Brazil in 1984, initially in the state of Paraná and later was disseminated to several states in different regions of the country (Neves & Carpanezzi 2008, 2009), has been widely used in afforestation (Edson-Chaves *et al.* 2019; Silva *et al.* 2019) due to its rapid growth and shady canopy (Neves *et al.* 2013; Lima *et al.* 2018; Almeida *et al.* 2019), causing concern among scientists. This plant has characteristics that favor invasion, such as early reproduction under several environmental conditions and large seed production, which can be dispersed by birds, bats and land mammals over large distances (Neves & Carpanezzi 2009; Moro *et al.* 2013). It also produces an allelopathic substance, known as azadirachtin, which negatively influences seed germination and the early development of some plant species (Albuquerque *et al.* 2015).

The competitive ability of invasive exotic species can affect the germination and growth of native species and, consequently, community diversity (Abd-Helgawad *et al.* 2020; Hassan & Mohamed 2020). Besides, approaching functional characteristics can help predict changes in environments under anthropogenic pressures (Molinari & D'Antonio 2014). Hence, we aimed to assess the competitive ability through the allelopathic activity of *Azadirachta indica* in interaction with native plant species from a seasonally dry tropical forest. We raised the hypothesis that the interaction strength depends on the functional similarity of the species involved. We expect that native species functionally similar to *A. indica* are more negatively affected, showing lower seed germination and lower investment in leaves, stems, and roots, reducing the possibility of their coexistence with the exotic species.

Material and Methods

Study area

The present study was carried out in a 6 × 6 m experimental plant nursery, with 50% shading, and the germination experiments were carried out in the Laboratory of Microbiology and Limnology - LAMILI and the Laboratory of Wastes, Effluents, and Bioenergy - LAREB, located at the Federal Institute of Education, Science, and Technology of Ceará (IFCE), in the municipality of Quixadá. Where the tropical hot semi-arid climate prevails, with an annual rainfall of 838.1 mm, distributed mainly between February and April, and an average temperature ranging from 26 to 28 ºC (Ipece 2020). The vegetation in the area is the seasonally dry tropical forest, known as Caatinga.

Species selection

We used the following species in the experiments: *Cenostigma pyramidale* (Tul.) E. Gagnon & G.P. Lewis (locally known as "Catingueira"), *Libidibia ferrea* (Mart. *ex* Tul.) L.P.Queiroz (Brazilian ironwood), *Mimosa caesalpiniifolia* Benth. ("Sabiá"), and *Amburana cearensis* (Fr. All) A.C Smith (locally known as "Cumaru"), all members of the family Fabaceae. Species selection was based on frequent occurrences in seasonally dry tropical forest areas (Costa *et al.* 2007), located in Quixadá. We chose these plants because invasive species have stronger negative impacts on regionally common species than rare species (Powell *et al.* 2013). The high demand for these native species and their disordered exploitation also contributed to our choice (Maia 2004; Rebouças *et al.* 2018). Some of those native plants are endangered (Ibama 2008; Martinelli & Morais 2013).

Data collect

We conducted experiments that assessed germination and the investment in the root, stem, and leaf to test the hypothesis that native species functionally similar to *A. indica* are more negatively affected by the invasion.

Influence of competitive ability on seed germination

An aqueous extract was produced with fresh leaves of *Azadirachta indica* collected from 30 different individuals, 10 per population, and each population is about 200 meters away from each other, found at the IFCE *campus*. Two hundred grams of leaves for each liter of distilled water were processed in a blender, then passed through a filtration process to produce a crude extract (100%). The extract was dissolved in six different concentrations: 0 (T1), 20 (T2), 40 (T3), 60 (T4), 80 (T5), and 100% (T6) of crude extract (Rickli-Horst *et al.* 2011). T1 was the control treatment and consisted only of distilled water.

Next, we performed the pH test and the dilution to the desired concentrations and stored the extracts in closed containers at room temperature (Rosa *et al.* 2011; Souza & Zampar 2016). The pH values found in the treatments were between 6.33 in T6 and 6.54 in T2, with an average value of 6.47 ± 0.06, being close to neutrality and within the limits of 6 to 7.5, ideal for germination (Baskin & Baskin 2014), therefore this parameter probably did not affected the tests performed (Rosa *et al.* 2011).

The seeds of the native species *L. ferrea* and *M. caesalpiniifolia* underwent chemical scarification in H_2SO_4 (Bruno *et al.* 2001; Oliveira *et al.* 2017) at the Laboratory of Wastes, Effluents, and Bioenergy - LAREB. *C. pyramidale* and *A. cearensis* has no tegument dormancy (Guedes *et al.* 2010; Ferreira *et al.* 2014; Souza & Souza 2020).

We used as substrate double layers of germitest paper, suitable for 15-cm diameter Petri dishes, moistened with the extract of *A. indica* leaves, and re-moistened whenever necessary.

We used an autoclave at 121 ºC for 20 minutes to sterilize Petri dishes (Brasil 2009). After the preparation, we placed Petri dishes in a BOD type chamber (manufactured by SOLAB Científica Equipamentos para Laboratórios, model SL - 200/300) with the adjusted temperature and photoperiod for each species. As *L. ferrea* seeds are neutral photoblastic, they remained in the absence of light and at a temperature of 30 ± 3 °C (Biruel *et al.* 2007; Fonseca & Jacobi 2011). *C. pyramidale* and *M. caesalpiniifolia* remained at 25 ± 3 °C (Guedes *et al.* 2010; Holanda *et al.* 2015; Mendonça *et al.* 2016), and 12 h photoperiod (Holanda *et al.* 2015; Vasconcelos *et al.* 2019). The chamber was washed with soap and water and then disinfected with 70% ethanol (Brasil 2009). The experimental design was completely randomized, with six treatments and four replications of 25 seeds, totaling 100 seeds per treatment. It was not possible to carry out the germination experiment with *A. cearensis* for technical limitation.

After the third day of the experiment, we started counting the germinated seeds daily until there were no new germinations. We considered germinated seeds those with a root length longer than 2 mm (Ferreira 2011; Rosa *et al.* 2011; Diógenes *et al.* 2014).

With the number of germinated seeds, it was possible to analyze the following variables: Emergence Percentage (EP) (formula 1), which considers the total number of seedlings that emerged (N) and the total number of plants sown (A) (Ferreira 2011);

$$EP = N/A \times 100 \qquad (1)$$

The Emergence Speed Index (ESI) (formula 2) considers the daily emergence and lists the number of normal seedlings emerged (E_1, E_2 ... E_n) and the number of days of sowing (N_1, N_2 ... N_n). The result is represented in number of emergences per day (N/d) (Maguire 1962).

$$ESI = (E_1+E_2+...+E_n) / (N_1+N_2+...+N_n) \qquad (2)$$

The Mean Emergence Time (MET) (formula 3) is equivalent to the days required to reach the maximum emergence (number of seedlings), considering the number of seedlings that emerged during the counting interval (n_i) and the average time between the beginning of emergence and the last count (t_i) (Baskin & Baskin 2014).

$$MET = (\Sigma\, n_i t_i) / (\Sigma t_i) \qquad (3)$$

In addition, at the last count of germinated seeds, we measured the radicle length with a high-precision digital caliper (Rosa *et al.* 2011).

Influence of the competitive ability on the investment in leaf, stem, and roots

To assess the investment in functional characteristics, we distributed the individual plants of each species in ten 20-liter buckets, with 50% shading in the experimental plant nursery of the Federal Institute of Education, Science, and Technology of Ceará (IFCE) - Campus Quixadá (04°58'41.40"S, 39°3'25.67"W).

All buckets were perforated on the sides and at the base, filled with sand, rough soil, and substrate (50% manure and 50% carnauba straw) in a 2:2:1 ratio. We divided buckets into two treatments (native species planted alone and native species planted in interaction with the exotic species) with five replications each and a completely randomized design. In the buckets of the native species alone, five seeds were placed to germinate, while in the buckets exposed to the interaction, 10 seeds were placed, five of the native and five of the exotic. After seed emergence, thinning was done and only one seedling remained in the sample. Thus, each bucket represents a repeat treatment.

Native species seeds used in both treatments were purchased from the Associação Caatinga, whereas exotic species seeds were collected at the IFCE - Campus Quixadá. In the Association, the seeds of the species are collected between 12 to 30 healthy trees per population, spaced between 100 and 200 m from each other, within three to five populations. Planting was carried out through direct sowing, but, before that, some species had to undergo a pre-germination treatment following the same procedures used in the germination experiment. After sowing, seedlings were irrigated manually, on alternate days, throughout the experiment.

At the termination of the experiment, realized in the second half of 2019, after four months (short period due to the size reached by individuals of some species, which made it impossible to continue the experiment), we measured the maximum height (MH, in cm) with a measuring tape and the maximum diameter (MD, in mm) with a digital caliper. Then, we recorded all species' functional characteristics, following the protocols of Cornelissen *et al.* (2003) and Pérez-

Harguindeguy *et al.* (2013). The characteristics analyzed related to roots, leaves, and stem were as follows:

Roots - After being removed from the bucket, the plant had its roots separated from the stem at ground level. Next, secondary roots, which are ramifications arising from the primary root, were separated from the main root, and both were weighed on an analytical scale to obtain the water-saturated weight (g). The primary root was scanned and had its length (PRL) and area (PRA) measured. Then, both roots were placed in the oven for 72 hours at 60 °C. After that period, roots were removed to obtain their dry weight, and we calculated the primary (PRDM) and secondary root dry matter (SRDM), which is the ratio between dry weight (mg) of roots (primary or secondary) divided by the water-saturated weight (g), expressed in mg.g^{-1}. The sum of both root dry matters comprises the root system dry matter (RSDM).

Leaves - At first, we counted the number of leaves of the plant individual (NL) and separated ten healthy leaves with intermediate size to obtain the water-saturated weight on an analytical scale. Next, leaves were scanned, and we calculated their leaf area (LA) in the computer program Image-Pro Plus. Then, we let leaves in the oven for three days at 60 °C and obtained their dry weights. We calculated the leaf dry matter (LDM) by dividing the dry weight (mg) of a leaf by its water-saturated weight (g), expressed in mg.g^{-1}, and obtained the specific leaf area (SLA) by calculating the ratio between leaf area and its dry weight, expressed in mm^{2}mg^{-1} (O'Neal *et al.* 2002).

Stem - We removed from the stem a 3-cm sample and obtained its wet weight on an analytical scale. Next, the sample was immersed in water for five days to rehydrate and reach the saturation point necessary for measurement (Chave 2005). After this period, each sample was left to rest for 5–10 minutes to drain water excess. Then, each sample was immersed in a Becker filled with water to determine the volume, based on the displacement of the liquid caused by the immersion. Weight was obtained on an analytical scale. After that, the sample was placed in the oven at 60 °C for five days, and we measured its dry weight on an analytical scale at the end of the process. We obtained the stem density (SD) through the ratio between dry weight and water volume (expressed in mg.mm^{-3}) and calculated the stem dry matter (SDM) by dividing the dry weight (mg) by the water-saturated weight (g), expressed in mg.g^{-1}. The sum of the stem and leaf dry matters composes the shoot dry matter (ShDM), and the ShDM together with the root system dry matter (RSDM) corresponds to the total dry mass (TDM)

Data analysis

We performed a cluster analysis to analyze the functional similarity between species, including all data collected from individual native and exotic species planted alone, using the Euclidean distance and Ward's hierarchical clustering method. The analyses were performed in PC-Ord 6.0. After the analysis, we verified that *Mimosa caesalpiniifolia*, *Cenostigma pyramidale* and *Libidibia ferrea* were the species most functionally similar to the exotic species (Fig. 1).

To assess the influence of the competitive ability of *A. indica* on the germination and early development of native species plants interacting with the exotic species, the germination data, maximum height, maximum diameter, and functional characteristics of each species were subjected to the Shapiro-Wilk normality test and the Levine test (homogeneity of variances), at 5% confidence. The data that did not meet these premises were transformed using log10, ln and square root transformations.

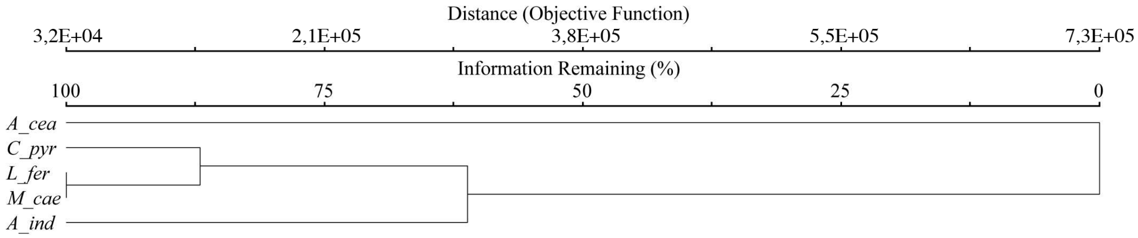

Figure 1 – Cluster analysis for *Azadirachta indica* and *Caatinga* native species. A_ind = *Azadirachta indica*; P_pyr = *Cenostigma pyramidale*; A_cea = *Amburana cearensis*; M_cae = *Mimosa caesalpiniifolia*; C_fer = *Libidibia ferrea*.

The germination data showed a normal distribution ($p > 0.05$) and were assessed using the Analysis of Variance (one-way ANOVA). Means were compared with the Tukey test at 5% probability. We used the T-test for independent samples to compare maximum height, maximum diameter, and functional characteristics of native species planted alone and in interaction with the exotic species. Statistical analyses were carried out in the SPSS V25.0 software.

We used data on native species' root length and maximum height to calculate the Allelopathic Index (AI) using the following formula: AI (%) = (RL_{int} or MH_{int} / RL_{alo} or MH_{alo} - 1) × 100. Where RL means root length and MH, maximum height, "int" is the treatment in which the native plant is in interaction with the exotic species, and "alo" is the treatment in which the native plant is planted alone (adapted from Williamson & Richardson 1988). Next, we calculated the Synthetic Allelopathic Index (AI_S), which indicates whether the species is being stimulated or inhibited by the interaction. The AI_S was calculated as $AI_S = (AI_{rl} + AI_{mh}) / 2$, where $AI_S > 0$ indicates stimulus, and $AI_S < 0$ indicates inhibition (Liao *et al.* 2007).

Results

Seed germination of native species

The extract affected only the radicle length of the species analyzed, including those with high functional similarity (Tab. 1). The extract positively affected the root growth of *Libidibia ferrea* and *Cenostigma pyramidale*, classified as having high functional similarity. There was an increase in radicle length at intermediaries concentrations of the extract in *L. ferrea*. *C. pyramidale* showed the lowest value in the control treatment (29.19 mm) and the highest in T4 (65.47 mm).

The extract did not significantly affect the germination of *Mimosa caesalpiniifolia*, which does not corroborate our expectations either, as it is one of the most similar species to *A. indica* (Tab. 1).

It is worth noting that, although the prediction related to the influence of functional similarity has not been corroborated in the germination experiment when the extract was more concentrated, some native species tested were negatively affected, regardless of their functional similarity to the exotic species. Such a result indicates that the exotic species presence can affect the germination of some native species and, consequently, change the community structure.

Investment in leaf, stem, and roots

When assessing investment data during the early development, measured through functional characteristics, we observed that the hypothesis of higher competitive ability for the species with less functional similarity was partially corroborated, as the development of species with high functional similarity (*M. caesalpiniifolia* and *L. ferrea*) was negatively affected. When planted in interaction with the exotic species, *M. caesalpiniifolia* showed a decrease in ten (SD, SDM, ShDM, MH, MD, PRA, PRL, PRDM, RSDM, and TDM) out of fifteen characteristics analyzed, whereas *L. ferrea* showed a decrease in maximum height (MH) and primary root length (PRL) and an increase in specific leaf area (SLA) (Tabs. S1; S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.21513834.v1>).

Regarding species with less functional similarity to *A. indica* (*A. cearensis* and *C. pyramidale*), we observed that A. cearensis showed a decrease in maximum height (MH), maximum diameter (MD) (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.21513834.v1>), and primary root area (PRA) (Tab. S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.21513834.v1>) when planted in interaction with the exotic species. On the other hand, the interaction with the exotic species positively affected *C. pyramidale* in PRA and root system dry matter (RSDM) (Tab. S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.21513834.v1>).

The Synthetic Allelopathic Index (AI_S) corroborated those results (Tab. S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.21513834.v1>). The AI_S showed that the presence of the exotic species with allelopathic potential inhibited the species *M. caesalpiniifolia* and *L. ferrea*, as they showed $AI_S < 0$, (-49.62 and -17.63, respectively). In contrast, according to the index, the exotic species presence stimulated *C. pyramidale* ($AI_S > 0$).

Discussion

Our results showed that the allelopathic activity of the *A. indica* extract was poorly effective in hindering seed germination in native species, regardless of the functional similarity between them. It should also be noted that the extract at low concentrations positively affected root growth

Table 1 – Mean values and standard deviation of the emergence percentage (EP, in %), emergence speed index (ESI, in number of emergences per day), mean emergence time (MET, in days), and root length (RL, in mm) of three native species of the seasonally dry tropical forest submitted to different concentrations of the aqueous extract of Azadirachta indica leaves. TR = Treatment; T1 = 0%; T2 = 20%; T3 = 40%; T4 = 60%; T5 = 80%; T6 = 100% of crude extract.

	Species	**Variables**	**Treatments**					
			T1	**T2**	**T3**	**T4**	**T5**	**T6**
High functional similarity	*Mimosa caesalpiniifolia*	EP	26 ± 10.6^{a}	30 ± 8.3^{a}	33 ± 12.8^{a}	25 ± 8.9^{a}	18 ± 4^{a}	25 ± 3.8^{a}
		ESI	8.48 ± 2.4^{a}	10.49 ± 2.7^{a}	12.19 ± 4.6^{a}	8.40 ± 2^{a}	6.07 ± 0.9^{a}	7.26 ± 2.8^{a}
		MET	4.03 ± 0.8^{a}	3.85 ± 0.7^{a}	3.43 ± 0.2^{a}	3.95 ± 1.1^{a}	4.00 ± 0.8^{a}	5.60 ± 2^{a}
		RL	63.58 ± 25.2^{a}	75.65 ± 27.3^{a}	78.52 ± 22.1^{a}	82.70 ± 23.9^{a}	78.10 ± 24.3^{a}	75.80 ± 31.9^{a}
	Libidibia ferrea	EP	75 ± 17.4^{a}	80 ± 16.9^{a}	74 ± 11.5^{a}	84 ± 11.4^{a}	71 ± 11.5^{a}	67 ± 16.1^{a}
		ESI	20.11 ± 3.9^{a}	24.50 ± 7.1^{a}	22.82 ± 3.1^{a}	22.10 ± 1.2^{a}	17.45 ± 2.8^{a}	15.88 ± 6.6^{a}
		MET	4.55 ± 0.8^{a}	4.67 ± 1.5^{a}	3.93 ± 1.1^{a}	5.05 ± 0.3^{a}	5.50 ± 0.4^{a}	5.83 ± 1.4^{a}
		RL	62.12 ± 14.8^{ab}	70.91 ± 22.3^{a}	70.95 ± 18.1^{a}	70.81 ± 20.6^{a}	60.89 ± 14.2^{b}	65.48 ± 19.5^{ab}
	Cenostigma pyramidale	EP	55 ± 15.8^{a}	74 ± 11.5^{a}	75 ± 13.2^{a}	74 ± 5.2^{a}	67 ± 20.2^{a}	48 ± 18.5^{a}
		ESI	8.91 ± 2.9^{a}	16.01 ± 3.1^{a}	14.53 ± 2.9^{a}	12.62 ± 0.4^{a}	10.77 ± 4.2^{a}	8.76 ± 5.2^{a}
		MET	5.30 ± 0.4^{a}	6.54 ± 1.8^{a}	4.87 ± 0.3^{a}	7.17 ± 0.4^{a}	7.64 ± 0.8^{a}	9.78 ± 6^{a}
		RL	29.19 ± 11.7^{c}	55.49 ± 21.4^{ab}	56.85 ± 23^{ab}	65.47 ± 23^{a}	51.74 ± 22.1^{b}	45.72 ± 20.8^{b}

in *Libidibia ferrea* and *Cenostigma pyramidale*. However, at high extract concentrations, these species were negatively affected. Albuquerque *et al.* (2015) reported that the gradual increase in the concentration of the aqueous extract of *A. indica* led to a decrease in root length, germination speed rate, and germination percentage in the weed species analyzed. These authors observed that the response to the use of extracts might vary depending on the species and the extract concentration, which shows that the azadirachtin can be selectively toxic. Such results exemplify that negative impacts on the environment caused by the invasion do not necessarily affect all species or characteristics (Farias *et al.* 2020).

However, we observed different results when assessing the early development of individuals of native species exposed to the interaction with the exotic plant. The reduction in investment in functional characteristics in the species *Mimosa caesalpiniifolia* and *Libidibia ferrea* is in line with our expectations, as according to Powell *et al.* (2013), invasive plants have the most significant impacts on native species functionally similar to them. Case *et al.* (2016) found similar results, showing that the invasion by *Aegilops triuncialis* had the strongest impacts on grass species within the same functional group as the invasive plant.

The many negative impacts observed in individual plants of *Mimosa caesalpiniifolia* exposed to the interaction with the exotic species (*e.g.*, reduction in investment in diameter, stem density, and dry matter content) demonstrated its vulnerability in the face of the invasion. According to Harclerode *et al.* (2016), Chen & Brockway (2017), and Yue *et al.* (2019), these reductions in investment can affect water and nutrient storage and biomass production, which can define the survival of individual plants in the wild and lead to a decrease in the number of species and their abundance, changing the functional structure of the community. Cadotte *et al.* (2011), and Sodhi *et al.* (2019) stated that the result of minimal changes in the richness and abundance of invaded communities make them more and more spatially homogeneous in their characteristics and less functionally diverse, with a consequent loss of balance in the ecosystem.

We observed that all native species studied showed at least one root system characteristic positively or negatively affected when exposed to the exotic species. The main root functions are to sustain the plant and absorb water and nutrients from the soil (Kramer & Boyer 1995). Therefore, under competitive situations (competition for resources), the root system may be reduced in size, as individuals are close to each other, interfering in the capture of resources below the ground, allowing the exotic plant to develop more effectively than the native one (Kramer & Boyer 1995; Lafolie *et al.* 1999). For example, deep rooting is a characteristic frequently correlated with species fitness, indicating competitive dominance (Wang *et al.* 2010; Kraft *et al.* 2015; Aschehoug *et al.* 2016). It is worth mentioning that the species studied are native to a water-restricted environment; therefore, the negative influence of the exotic plant on root system characteristics can compromise the establishment of these native species in their natural environment.

Height was also significantly affected in the studied plants, as three out of four species had their heights reduced due to the interaction with the exotic plant. According to Cornelissen *et al.* (2003), as the exotic species negatively affects height, it is a better competitor than the native species. Consequently, the authors suggest that native species may face difficulties protecting themselves and regenerating during disturbances and may have their fertility affected. The only species whose height was not affected was *C. pyramidale*, classified as the species most functionally similar from *A. indica*.

Our results showed differences among species in the impacts suffered and among the functional characteristics affected. According to Godoy (2019), these results are possible and expected because communities have specific responses to exotic species introduction. Therefore, negative effects may not reach all community members, and some species may even benefit from the interactions established (as observed in the AI_S values found in our study). Thus, certain species and their characteristics can persist with apparently little negative impact, whereas other species can be excluded from communities (Sodhi *et al*. 2019).

The specific responses to the introduction of exotic species are related to niche differences (assessed here through functional characteristics). Such differences work as control mechanisms for different competitive capacities, enabling species coexistence (Godoy 2019). However, analyses based on niche differences are rarely used in the ecology of the invasion, even though they provide relevant information about the mechanisms involved and the impacts suffered (Sodhi *et al.* 2019).

In the present study, we considered only the direct effects of one species on another, but in the wild, the interactions are multiple, so that when one species affects another, others may also be affected. In addition, Godoy (2019) reported that the effects of one species on another depend on the population density in the community. Thus, it is possible that in real situations, in native vegetation, other impacts, which were not identified in the present study, can be observed.

The extract of *A. indica* leaves did not cause the expected negative effects on the seed germination of species functionally similar to the exotic species. However, its negative effect on some germinative parameters of native species is evident, especially due to the extract concentration. As we expected, during the analysis of the early development of individual plants, we noticed that the most species with the highest functional similarity to *A. indica* were those that most suffered damage when planted in interaction with the invasive species.

Thus, we call attention to the danger of the naturalization of *A. indica* in the Brazilian semi-arid, as even though it does not affect all the characteristics of all native species, the interaction with this species can lead to a reduction in the community richness and, consequently, compromise ecosystem services.

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