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Original article

Does the presence of exotic species decrease the initial development of native species in Brazilian seasonally dry tropical forests?

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ABSTRACT

We assessed the impacts of the biological invasion of *Azadirachta indica* on the quality of plant species native to a Seasonally Dry Tropical Forest. We planted *Amburana cearensis*, *Libidibia ferrea*, *Mimosa caesalpiniifolia*, and *Cenostigma pyramidale* individuals alone and interacting with the exotic species. We measured their diameters at ground level and heights for four months, calculating their monthly and general average. After this period, seedlings were destroyed to obtain their number of leaves, leaf area, specific leaf area, length and primary root area, wood density, wood dry matter, leaf dry matter, shoot dry matter, primary root dry matter, secondary root dry matter, root system dry matter, and total dry matter. The presence of the exotic species affected the functional characteristics of native species in different ways. We observed negative effects in *M. caesalpiniifolia* and *A. cearensis*, positive effects in *C. pyramidale*, and mixed effects in *L. ferrea*. In addition, we identified conflicting demands between pairs of characteristics of the interacting species *A. cearensis* and *M. caesalpiniifolia*. Based on the results, it is possible to conclude that *A. indica* decreases the quality of individuals of most native species studied, which may have consequences for their establishment and the local biodiversity.

Keywords: *Azadirachta indica,* biodiversity reduction, biological invasion, caatinga, establishment in the field.

Introduction

The introduction of exotic species is one of the leading causes of biodiversity loss in natural communities (Kalusová *et al.* 2017; Leclerc *et al.* 2020), as they can become invasive and affect the establishment of native species (Wardle & Peltzer 2017; Giejsztowt *et al.* 2020). This biological invasion alters native species coexistence leading to significant changes in local communities (Hillerislambers *et al.* 2012). Although many studies depict community changes caused by biological invasion (Iles *et al.* 2016; Langeland & Hutchinson 2016; Kedzie-Webb & Sheley 2017; Uddin & Robinson 2017; Mahla & Mlambo 2019; Marin *et al.* 2019; Ren *et al.* 2019;), little is known about the mechanisms behind those changes. Studying changes in functional characteristics

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experimentally, through growing native with exotic species that affect native species performance, can point to possible mechanisms (Kraft *et al.* 2015). It is also noteworthy to understand that these mechanisms are poorly known, especially in seasonal environments such as the semi-arid region in northeastern Brazil.

A biological invasion event occurs when a species multiplies uncontrollably in a community to the point of changing its structure, composition, and functioning (Costa & Freire 2018). However, the possibility of a species becoming invasive depends on its characteristics and the environment where it is inserted (Bourg *et al.* 2017; Lyseng *et al.* 2018; Martinez & Manzano-Garcia 2019; Leclerc *et al.* 2020). Once established, the exotic species increases the interspecific competition for space, light, and nutrients (Bourg *et al.* 2017; Bialic-Murphy *et al.* 2020), which, in turn, can inhibit or hinder the development of native plants (Case *et al.* 2016; Dovrat *et al.* 2019; Ren *et al.* 2019), promoting a decrease in germination, growth, and biomass, and an increase in mortality rate (Wardle & Peltzer 2017; Giejsztowt *et al.* 2020). Besides, in response to the interaction, plants may show plasticity in their characteristics when exposed to biotic stress (Pierik *et al.* 2013), which favors the appearance of conflicting demands between important characteristics for the maintenance of species (Fernandez *et al.* 2016). However, such demands can hinder coexistence, as species are less able to persist under environmental pressure (Petry *et al.* 2018)

In the past few years, some authors studied changes in the community and characteristics of native species subjected to interactions with exotic species (Iles *et al.* 2016; Marin *et al.* 2019; Ren *et al.* 2019). Mahla & Mlambo (2019), for example, reported the impacts of *Lantana camara* and *Dichrostachys cinerea*. on the community structure of native woody species in the Chipinge Safari area in Zimbabwe. In Australia, Uddin & Robinson (2017) reported that in areas with the presence of the invasive *Phragmites australis*there was a decrease in the native plant community richness, making the sampling plots monospecific. Langeland & Hutchinson (2016) and Kedzie-Webb & Sheley (2017) obtained similar results when studying the invasion potential of the species *Lygodium microphyllum* and *Cynoglossum officinale*, respectively, in the United States. In Brazil, Pegado *et al.* (2006) recorded a decrease in native species richness, resulting from the process of biological invasion by *Prosopis juliflora*. In China, Ren *et al.* (2019) presented results that can help explain the diversity reduction in the invaded communities by discussing the impacts caused by the species *Solidago canadensis* to the native species *Artemesia argyi*. They reported an increase in the root biomass fraction in the invasive plant, making it more successful, leading to a potential exclusion of competitors.

Thus, the success of a biological invasion depends on how native species behave in the presence of the exotic species (Iles *et al.* 2016; Marin *et al.* 2019; Ren *et al.* 2019). However, it is crucial to assess several interactions and species characteristics to predict invasion success. Given the above, we raised the hypothesis that exotic species considered imminently invasive may compromise the development of individuals of species native to the Seasonally Dry Tropical Forest, located in the semi-arid region of northeastern Brazil. From an experimental point of view, our study aims to demonstrate how an invasive species can affect the performance of native species in the early stages of development. We sought to answer the following questions: (1) In the presence of an exotic species, do individuals of native plant species have a reduced maximum height and diameter, as well as lower growth speed? (2) Do individuals of exotic species compromise the initial development of native plant individuals? (3) When interacting, do native species individuals present conflicting demands between pairs of functional characteristics that reflect the development above and below ground?

Material and methods

Experiment setup

The present study was carried out in a 6x6 m experimental plant nursery, with 50 % shading, and in the Laboratory of Wastes, Effluents, and Bioenergy, both located at the Federal Institute of Education, Science, and Technology of Ceará (IFCE), Campus Quixadá (4º 58’ 40” S, 39º 03’ 27” O), state of Ceará, northeastern Brazil. The region has a Tropical Hot Semi-arid climate, with an average temperature from 26 to 28 °C and an annual rainfall of 838.1 mm (Ceará 2017). The vegetation is the Caatinga, a type of Seasonally Dry Tropical Forest in South America (Ceará 2017; Silva *et al.* 2017; Brazil 2020).

We chose *Azadirachta indica* A. Juss, popularly known as Neem, as the potentially invasive exotic species used in our study. The species was introduced in Brazil in the 1980s (Carpanezzi 2010), for commercial and ornamental purposes (Moro *et al.* 2013), and has been broadly distributed in northeastern Brazil (Azevedo *et al.* 2015) to the point of being considered naturalized (Moro *et al.* 2013). Its cultivation has raised concerns because the species has a germination potential of up to 60 %, occurs in different soil classes, tolerates temperature variation, and has allelopathic potential, possibly hindering the germination and development of other plants (Fabricante 2014).

We created a field experiment to answer our questions on how invasive species can hinder the development of native species. According to information found in the literature and virtual databases, we selected native species characteristics, such as germination time, occurrence, and availability in the region (Northeast Plant Database 1996; Flora do Brasil 2020 2021; Maia 2004; Tropicos 2018). We selected the following species due to their availability in the study area: *Amburana* *cearensis* (Allemão) A.C.Sm., *Cenostigma pyramidale* (Tul.) E. Gagnon & G.P. Lewis, *Libidibia ferrea* (Mart. ex Tul.) L.P.Queiroz, and *Mimosa caesalpiniifolia* Benth., all members of the family Fabaceae.

For the experiment setup, we planted seeds of native and exotic species in 20-l buckets (perforated at the base and sides for water drain) through direct sowing and placed the buckets in the plant nursery. Seed dormancy of *L. ferrea* and *M. caesalpiniifolia* was broken through chemical scarification in H_2SO_4 for 15 minutes (Araújo *et al.* 2017). The substrate used followed a 2:2:1:1 ratio, producing a mixture of two parts of rough soil, and sand for a part of *Copernicia prunifera* (Mill.) HE Moore straw (carnauba straw) and bovine manure. Irrigation took place in the early morning and late afternoon, with 100 % field capacity, distributed across three days of the week.

We used ten buckets per species, five containing only one individual plant of a native species and five with two individual plants, exotic + native, to assess the interaction. The experimental design used was completely randomized, composed of two treatments and five replications.

Collection of functional characteristics

Once a month, for four months, after planting the seeds, we measured the stem diameters at ground level in the bucket and heights of all individual plants, with a digital caliper and measuring tape, respectively. After gathering the data for the whole period, we calculated the general average of height and diameter, hereinafter average height (AH) and average diameter (AD). With monthly averages, we could test for differences in growth time. After completing the four months of the experiment, we divided the seedling parts (leaves, roots, and wood) in the laboratory to obtain investment data in functional characteristics.

At the termination of the experiment, we measured the following characteristics in each plant: number of leaves (NuL), leaf area (LA), specific leaf area (SLA), leaf dry matter (LDM), primary root dry matter (PRDM), secondary root dry matter (SRDM), primary root length (PRL), primary root area (PRA), wood density (WD), wood dry matter (WDM), shoot dry matter (SDM), root system dry matter (RSDM), and total dry matter (TDM). Collections and analysis of functional data followed the protocol proposed by Pérez-Harguindeguy *et al.* (2016).

Regarding leaf data, we counted all leaves of each plant to obtain the number of leaves. Then, we separated ten healthy leaves and placed them on a four-digit analytical scale to measure the water-saturated fresh weight of each one. Next, leaves were scanned, and we used each image to calculate the leaf area (cm^2) in the Image-Pro Plus 7 software for Windows operating system. After being scanned, we stored the leaves in paper envelopes and placed them in the oven for three days at 60 °C. After that period, we obtained the dry weights on the scale to calculate the specific leaf area ($mm^2.mg^{-1}$), *i.e.*, the ratio of leaf area to leaf dry matter. At last, we calculated the leaf dry matter dividing the dry weight (mg) of a leaf by its water-saturated fresh weight (g) (Ali *et al.* 2015).

After leaf removal, plants had their roots separated from the stem. Next, secondary roots were separated from the primary root, and both were washed and weighed on the scale to obtain the water-saturated fresh weight (mg). Please note that, once collected, the samples were wrapped in moist paper and placed in sealed plastic bags, so that they remained water-saturated while the measurements were made. Only the primary root was scanned and measured with a measuring tape to obtain the primary root area (cm^2) and primary root length (cm), respectively; secondary roots were only weighed. Next, primary and secondary roots remained in the oven at 60 °C for three days. After that period, we collected the dry weight (g) and calculated primary and secondary root dry matter ($mg.g^{-1}$). We collected from the cut base of the stem a 3-cm sample, used as a proxy for wood density. First, we obtained the wet weight of this part using an analytical scale. Next, the sample was immersed in water for five days to reach the saturation point necessary for measurement. At the end of this period, each sample was left to rest for five minutes to remove water excess. Then, the sample was immersed in another container with water to determine the volume (ml) based on the water displacement inside the container caused by the immersion of the piece. After that, the sample was placed in the oven at 60 °C for another five days to obtain the dry weight (mg). At last, we calculated wood density, which is the ratio between dry weight and the water volume ($mg.mm^{-3}$), and the wood dry matter, which corresponds to the stem dry weight divided by the water-saturated weight (expressed in $mg.g^{-1}$).

We calculated the shoot dry matter ($mg.g^{-1}$) using the sum of the leaf dry matter and stem dry matter. For calculating the root system dry matter ($mg.g^{-1}$), we used the sum of the primary and secondary root dry matter. At last, we obtained the total dry matter ($mg.g^{-1}$) summing the shoot dry matter and root system dry matter.

Data analysis

We carried out statistical tests with functional characteristics data to assess the influence of the interaction between species, *i.e.*, to test whether the means of the characteristics obtained for plants of native species planted alone differ from those of the same species planted together with the exotic species.

First, we performed a Student's t-test at 5 % probability for average height (AH) and average diameter (AD) and other functional characteristics of native species planted alone and together with the exotic species. As a measure of the effect size, we calculated Cohen's coefficient (or Cohen's d) to test whether the values of those variables, whose Student's t-test showed significant differences ($p < 0.05$), have a small (< 0.2), medium (0.5) or large effect (> 0.8), *i.e.*, whether they are close to or distant from significance (Cohen 1988; Mcgrath & Meyer 2006; Lakens 2013).

We applied the analysis of variance (ANOVA) using height and diameter data collected throughout the study period to assess the growth of plants of each species over time, planted alone and together with the exotic species. We also applied a post-hoc Tukey test at 5 % to identify disparities. In addition, we used Pearson's correlation coefficient at 5 % and 1 % to analyze correlations of final height (FH; height collected in the last month of treatment), primary root length (PRL), shoot dry matter (SDM), and root system dry matter (RSDM) data of each species analyzed in both treatments, enabling to identify the existing relationships between variables and conflicting demands between pairs of characteristics above and below ground.

Basic assumptions for Student's t-tests, ANOVA, and Pearson's correlation coefficient, such as normal error distribution and homogeneity of variances, were examined by the Shapiro-Wilk test and the Levene test at 5 % confidence, respectively. Data that did not meet these premises were transformed using log10, ln, and square root transformations. Statistical analyses were performed using the SPSS Statistical software V25.0 IBM Corp., CA, USA, available for all computing platforms.

Results

Our results confirmed that the invasive exotic plant, *Azadirachta indica*, hindered the development of plant species native to the Seasonally Dry Tropical Forest. However, the affected characteristics, which hindered their development, varied among species.

The Student's t-test indicated that individual plants of native species showed a reduced Average Height (AH) and Average Diameter (AD) in the presence of *A. indica* (Figs. 1, 2). The AD of *Amburana cearensis* specimens, planted alone (3.632 mm) and together with the exotic species (3.001 mm), differed statistically, whereas their AH were similar in both treatments (17.100 cm and 14.304 cm, respectively). However, both parameters showed lower values in the treatment of individual plants interacting with *A. indica* (Figs. 1, 2). The Cohen's coefficient corroborated this result, showing values greater than 0.8, which indicates a strong influence of the exotic species in the treatment with interaction.

We noticed that although *Cenostigma pyramidale* specimens were similar when planted alone and together with the exotic species, both variables showed lower averages when planted in interspecific interaction (AH: 22.506 cm and AD: 3.834 mm). *Libidibia ferrea* specimens showed a lower AH (101.240 cm), and *Mimosa caesalpiniifolia* showed lower AH (7.775 cm) and AD (1.887 mm) when planted in interspecific interaction (Figs. 1, 2).

According to ANOVA, *A. indica* significantly influenced the growth time over the months of the experiment, assessed through the comparison of the Maximum Height (cm) averages of native species over time. Among the four native species studied, *M. caesalpiniifolia* was the only species that showed a negative growth due to the presence of *A. indica* (Tab. 1).

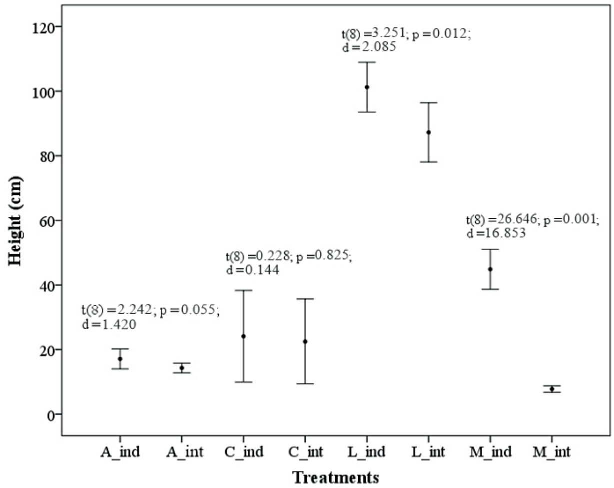

Figure 1. Comparison of the species Average Height per treatment. Legend: A_ind = *Amburana cearensis* planted alone and A_int = *Amburana cearensis* planted in interspecific interaction, C_ind = *Cenostigma pyramidale* planted alone and C_int = *Cenostigma pyramidale* planted in interspecific interaction, L_ind = *Libidibia ferrea* planted alone and L_int = *Libidibia ferrea* planted in interspecific interaction, M_ind = M*imosa caesalpiniifolia* planted alone and M_int = M*imosa caesalpiniifolia* planted in interspecific interaction.

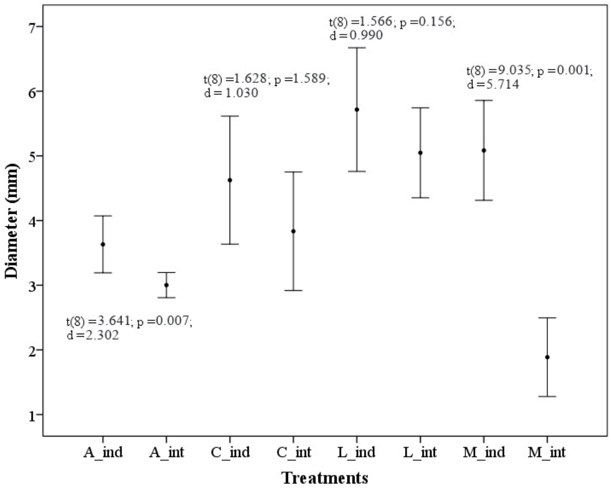

Figure 2. Comparison of the species Average Diameter per treatment. Legend: A_ind = *Amburana cearensis* planted alone and A_int = *Amburana cearensis* planted in interspecific interaction, C_ind = *Cenostigma pyramidale* planted alone and C_int = *Cenostigma pyramidale* planted in interspecific interaction, L_ind = *Libidibia ferrea* planted alone and L_int = *Libidibia ferrea* planted in interspecific interaction, M_ind = M*imosa caesalpiniifolia* planted alone and M_int = M*imosa caesalpiniifolia* planted in interspecific interaction.

The growth in diameter of *A. cearensis* plants, assessed through the comparison of the Maximum Diameter (mm) averages of native species over time, differed over the months of the experiment when they were planted alone and in interaction with the exotic species. According to our expectations, the growth in height showed only differences when the species were interacting with the exotic plant (Tab. 1). Likewise, regarding the growth in diameter of *C. pyramidale,* individuals differed over the months when they were isolated and in interaction with the exotic species. However, the growth in height showed differences only when the individuals were planted together with *A. indica*. The post-hoc analysis showed that differences in height were only visible at the end of the experiment, when *A. cearensis* and *C. pyramidale* were in interaction with the exotic plant, but for diameter, the changes occurred gradually, visible every month in both treatments. At last, for *L. ferrea*, time caused significant differences in both height and diameter growth when they were planted alone and in interaction (Tab. 1).

The values of functional characteristics obtained for most native species analyzed decreased when the plant interacted with the exotic species (Tab. 2). The Student's t-test showed that *M. caesalpiniifolia* was the species that showed the most significant reduction in the values of functional characteristics when in interspecific interaction. The functional characteristics total dry matter (TDM), shoot dry matter (SDM), primary root dry matter (PRDM), wood dry matter (WDM), wood density (WD), primary root area (PRA), and primary root length (PRL) showed differences in the means of individuals between treatments, which showed a better development and values for functional characteristics in the treatment without the presence of the exotic species. Individuals of the species *A. cearensis* showed differences in PRA values between treatments, with a lower development in interspecific interaction.

Although most native species characteristics showed lower values when the plant interacted with the exotic species, some presented a distinct behavior. In *L. ferrea.*, for example, the specific leaf area (SLA) and the PRL showed differences in means between treatments; the SLA developed better when in interspecific interaction, and the PRL developed better when isolated from *A. indica*. Besides, we observed a positive influence of the interaction on the root system dry matter (RSDM) of *C. pyramidale* plants (Tab. 2).

Table 1. Comparison of the Maximum Height (cm) and Maximum Diameter (mm) averages of native species over time. Legend: TR = Treatments, IND = planted alone, INT = planted in interspecific interaction with *Azadirachta indica*. Note: Means followed by different letters show significant differences by the Tukey test at 5 % probability.

Species	TR	Maximum Height					Maximum Diameter				
		Nov	Dec	Jan	Feb	*p*	Nov	Dec	Jan	Feb	*p*
Amburana cearensis	**IND**	15.7^{a}	18.6^{a}	16.5^{a}	17.6^{a}	0.556	3.20^{ab}	2.94^{a}	4.18^{bc}	4.20^{c}	0.002
	INT	13.8^{a}	13.5^{a}	14.9^{a}	14.8^{b}	0.010	2.50^{a}	2.83^{ac}	3.18^{bc}	3.43^{b}	$7.31e^{-4}$
Cenostigma pyramidale	**IND**	10.3^{a}	17.8^{a}	25.2^{a}	43.1^{a}	0.114	2.58^{a}	4.00^{ab}	5.38^{bc}	6.54^{c}	$2.83e^{-4}$
	INT	8.7^{a}	16.6^{a}	28.9^{a}	34.7^{b}	0.007	2.28^{a}	3.10^{ab}	4.70^{bc}	4.70^{c}	$2.84e^{-4}$
Libidibia ferrea	**IND**	21.1^{a}	76.8^{b}	137.5^{c}	169.5^{d}	0.001	1.72^{a}	4.22^{b}	7.48^{c}	9.08^{d}	0.004
	INT	16.4^{a}	67.2^{b}	116.7^{c}	148.6^{d}	0.007	1.64^{a}	3.94^{b}	6.48^{c}	8.12^{dc}	0.002
Mimosa caesalpiniifolia	**IND**	8.8^{a}	31.4^{b}	55.0^{c}	84.2^{d}	$1.0e^{-4}$	1.52^{a}	3.02^{b}	6.08^{c}	9.72^{d}	$2.1e^{-4}$
	INT	6.6^{a}	6.6^{a}	5.9^{a}	5.6^{a}	0.267	0.98^{a}	1.66^{a}	1.52^{a}	1.88^{a}	0.100

Table 2. Results of the Student's t-test comparing functional characteristics between treatments. Legend: TR = Treatment, IND = planted alone, INT = planted in interspecific interaction with *Azadirachta indica,* TDM = total dry matter ($mg.g^{-1}$), RSDM = root system dry matter ($mg.g^{-1}$), SDM = shoot dry matter ($mg.g^{-1}$), LDM = leaf dry matter ($mg.g^{-1}$), PRDM = primary root dry matter ($mg.g^{-1}$), SRDM = secondary root dry matter ($mg.g^{-1}$), WDM = wood dry matter ($mg.g^{-1}$), WD = wood density ($mg.mm^{-3}$), LA = leaf area (cm^{2}), SLA = specific leaf area ($mm^{2}.mg^{-1}$), PRA = primary root area (cm^{2}), PRL = primary root length (cm), and NuL = number of leaves.

Species	TR	TDM	RSDM	SDM	LDM	PRDM	SRDM	WDM	WD	AF	SLA	PRA	PRL	NuL
Amburana cearensis	*p*	0.971	0.739	0.648	0.097	0.269	0.368	0.272	0.405	0.139	0.95	0.004	0.43	0.36
	IND	1356	731.6	625.1	361.51	594.17	137.45	263.62	0.342	15.60	79.23	11.38	17.00	5.60
	INT	1367	672.1	695.6	268.87	447.06	225.05	426.8	0.48	6.40	149.5	1.52	19.50	4.57
Cenostigma pyramidale	*p*	0.775	0.015	0.666	0.297	0.064	0.077	0.999	0.311	0.79	0.47	0.05	0.19	0.15
	IND	1808	992	816.6	453.4	516.8	475.2	363.1	0.493	74.69	137.5	7.30	19.84	17.60
	INT	1884	1176	708.2	344.8	594	582.3	363.3	0.548	62.86	161.6	12.60	24.17	10.02
Libidibia ferrea	*p*	0.336	0.387	0.62	0.885	0.75	0.202	0.586	0.358	0.12	0.04	0.88	0.01	0.13
	IND	1996	941.2	1055	398.9	596.6	344.6	656.4	0.661	143.2	113.2	27.22	28.58	63.40
	INT	2116	1043	1072	401.2	584.8	458.5	671.6	0.634	97.17	172.4	26.33	22.45	47.93
Mimosa caesalpiniifolia	*p*	0.001	0.056	2.00E-06	0.156	0.003	0.214	0.002	0.001	0.20	0.75	0.004	0.005	0.23
	IND	1863	910.7	953.1	361.7	549.3	361.4	591.3	0.558	143.5	248.9	12.14	24.24	19.80
	INT	823.8	514	309.7	293.9	347.4	166.6	15.82	0.209	91.46	216.8	0.61	11.35	13.31

The correlations between pairs of functional characteristics (Tab. 3) demonstrated that when the native species studied interacted with *A. indica*, they showed conflicting demands between pairs of functional characteristics, reflecting different investment in the characteristics above and below ground. When planted alone, all correlations found for the species studied were positive. When subjected to interspecific interaction with the exotic species, two of the species studied showed conflicting demands. In *A. cearensis*, as plants showed higher heights, they reduced the root system dry matter (RSDM). In *M. caesalpiniifolia,* plants with higher heights showed a lower primary root length (PRL), and plants with higher PRL showed a reduction in RSDM and shoot dry matter (SDM).

Discussion

Our results demonstrate the negative influence of the interaction between exotic and native species in the seasonally dry tropical forest, as important characteristics for the establishment of the native ones, such as height, diameter, and biomass (assessed as dry matter contents), had their values reduced. This reduction points to a lower acquisition of resources for the investment in individual structural characteristics, as these resources are partitioned when the native species are exposed to interspecific interactions (Kalusová *et al.* 2017; Leclerc *et al.* 2020).

All native species studied showed a reduction in average height, average diameter, or both parameters in the presence of *Azadirachta indica*. *Mimosa caesalpiniifolia*, for example, showed a reduction in both parameters when interacted with the exotic species. Reduced stem diameters provide low water retention and biomass production, and limited heights do not provide a proper soil cover, facilitating degradation by exogenous agents, such as rain (Blanchard *et al.* 2016; Chen & Brockway 2017). Thus, we believe that these structural deficits, combined with other degradation sources, can provide a reduction in the number of individuals of native species in the field, mainly *M. caesalpiniifolia*.

The reduction in height and diameter found here was also observed in other studies. Costa & Freire (2018), for example, studied the development of *Mimosa tenuiflora*, putting it to germinate in tubes enriched with an extract made with parts of the exotic species *Prosopis juliflora*. The authors noticed that the extract caused a reduction in the diameter and height of native plants. Virginia & Jodie (2005) observed the same effect in their study, emphasizing the decrease in the height and diameter of plants of the native species *Nassella pulchra*, which competed in the wild with the invasive exotic species *Cynara cardunculus* showing a low survival rate.

The survival of individuals in the wild can also be defined by their dry matter contents, as higher investment in dry matter can provide the plant with higher resistance (Harclerode *et al.* 2016) against physical/geophysical damage (*e.g.*, landslides), meteorological (windstorms), hydrological (flooding) and, as part of the Brazilian reality, climate events (drought) and anthropic disturbances (Pérez-Harguindeguy *et al.* 2016; Oliveira *et al.* 2019). Thus, knowing that *M. caesalpiniifolia* and *Cenostigma pyramidale* were the species with the lowest investment in leaf dry matter, we assume that these species will face more difficulties in establishing themselves in the field, having their survival compromised in events of higher environmental stress.

Besides presenting the lowest dry matter contents, *M. caesalpiniifolia* showed a lower wood density due to the interaction with the exotic species. Stems with low wood density can cause huge problems for individuals, as this characteristic ensures a balance between positive continuous growth and investment in biomass; thus, it is essential for stability, structure, and the storage of nutrients and water (Pérez-Harguindeguy *et al.* 2016; Bin *et al.* 2019).

All native species showed structural losses in roots, whether in dry matter, length, or area when interacting

Table 3. Correlations made between pairs of functional characteristics using Pearson's correlation coefficient. The values below the diagonal refer to native species specimens planted alone and the values above the diagonal represent the individual plants in the treatment with *Azadirachta indica* (planted in interspecific interaction). Legend: FH= final height (cm), PRL = primary root length (cm), RSDM = root system dry matter (mg.g^{-1}), SDM = shoot dry matter (mg.g^{-1}). Note: *Significant correlation at 0.05; **Significant correlation at 0.01.

	Amburana cearensis				***Cenostigma pyramidale***				
	FH	**PRL**	**RSDM**	**SDM**	**SDM**	**RSDM**	**PRL**	**FH**	
FH	1	-0.523	**-0.92***	0.490	0.395	0.790	**0.967****	1	**FH**
PRL	-0.259	1	0.661	0.334	0.379	0.854	1	0.425	**PRL**
RSDM	-0.140	**0.897***	1	-0.211	0.460	1	0.142	-0.510	**RSDM**
SDM	0.585	0.380	0.433	1	1	-0.741	0.273	**0.935***	**SDM**

	Libidibia ferrea				***Mimosa caesalpiniifolia***				
	FH	**PRL**	**RSDM**	**SDM**	**SDM**	**RSDM**	**PRL**	**FH**	
FH	1	-0.345	0.201	0.420	**0.888***	**0.880***	**-0.92****	1	**FH**
PRL	-0.643	1	-0.627	-0.762	**-0.99***	**-0.93***	1	-0.079	**PRL**
RSDM	-0.003	-0.524	1	0.082	**0.939***	1	-0.556	0.056	**RSDM**
SDM	**0.963****	-0.581	-0.142	1	1	0.754	-0.437	0.695	**SDM**

with the exotic species. Virginia & Jodie (2005) described similar results; they observed that individuals of the native species *Nassella pulchra* showed smaller root sizes and lower dry matter when exposed to the exotic invasive *Cynara cardunculus*, Costa & Freire (2018) concluded that the root dry weight of *M. tenuiflora* seedlings decreased with the increase in the concentration of *P. juliflora* extracts in the tubes where they planted native plants.

Pérez-Harguindeguy *et al.* (2016) highlighted that the development of the primary root, whether in mass or extension, helps capture water and nutrients from the soil. For example, Ren *et al.* (2019) observed that the invasive species *Solidago canadensis* negatively affected the development and nutrient allocation of the roots of the native species *Artemisia argyi*. The problems in root development reported these studies could compromise the vertical growth and establishment of these native plants in the wild. In this perspective, Stinson *et al.* (2006) noted that in temperate forests of the United States and Canada, there was a reduction in the root length of some individuals of the species *Acer saccharum*and *Fraxinus americana*, which had difficulties in establishing themselves in the wild in the presence of the exotic species *Alliaria petiolata*.

Besides the lower investment in some characteristics, the conflicting demands found in *A cearensis* and *M. caesalpiniifolia* plants can express a functional strategy of the species in the face of the interaction with the exotic species. *A. cearensis* invested in higher heights at the expense of the root system dry matter (RSDM). *M. caesalpiniifolia* showed higher heights with lower primary root length (PRL) and RSDM, and a higher shoot dry matter (SDM) at the expense of the PRL. These conflicting demands are common strategies when there is a decrease in the available resources in the ecosystem, either due to natural events or, as in this case, the presence of exotic species, which can force native species to direct the resources extracted from the environment to specific organs at the expense of others (Kraft *et al.* 2015). However, these survival strategies can make individuals more fragile and vulnerable because they cannot invest in the development of all organs (Bialic-Murphy *et al.* 2020).

Once an exotic species affects the development of others, as we observed in several characteristics of the native species assessed, the environment has already undergone losses. These losses can include the imbalance of soil functions (due to the decrease in organic matter), impoverishment of the animal biota (as not all native animals use exotic plants as a food source), and, consequently, a decrease in the characteristic biodiversity of a region.

Final considerations

We can affirm that *A. indica* negatively affects the initial development of individuals of the native species studied in the Seasonally Dry Tropical Forest and may also affect the establishment of individuals and the local biodiversity. However, these effects vary in intensity. *M. caesalpiniifolia* was the most affected species. Some native species presented different functional strategies for survival, observed through conflicting demands between characteristics above and below ground.

This kind of information is vital to assist decision-making related to the control of *A. indica*, which has been broadly distributed for urban afforestation, and the monitoring of commercial plantations of this exotic species to prevent its spread to natural areas.

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