RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

RESEARCH ARTICLE

The influence of herbaceous vegetation on the colonization of native and invasive trees: consequences for semiarid forest restoration

Jeanne R. A. Franco[1], Gustavo B. Paterno[1,3], Gislene Ganade[1,2]

We evaluated the influence of herbaceous vegetation on the colonization of an invasive and two native tree species in a degraded area located at the Caatinga semiarid forest in Northeastern Brazil. Seedlings of the native trees *Anadenanthera colubrina* and *Astronium urundeuva* were planted in nine paired blocks with intact and removed herbaceous vegetation. In addition, seeds of the invasive tree species *Leucaena leucocephala* were sown in the same paired plots. Growth, germination, establishment, and survival of the tree species were monitored for 8 months. The results showed that herbaceous vegetation hampered native seedling growth in respect to leaf number, leaf size, height, and stem diameter. Conversely, herbaceous vegetation had a neutral effect on the germination, establishment, and growth of the invasive species *L. leucocephala*. Dominant ruderal herbaceous species strongly prevent the natural succession of native trees in this semiarid forest, while not affecting the establishment of an invasive tree. Management of herbaceous vegetation cover in degraded areas might be a key step for successful restoration in this dryland.

Key words: Caatinga, competition, degraded areas, drylands, invasive species, succession

Implications for Practice

- Ruderal herbaceous vegetation established in degraded Caatinga areas should be managed during restoration programs to avoid its negative influence on the growth of native transplanted trees.
- Selecting tree species that are more resistant to competition by herbaceous vegetation and transplanting larger tree seedlings could result in a higher restoration success.
- Herbaceous vegetation does not function as a biotic barrier against the establishment of *Leucaena leucocephala* trees. Therefore, this invasive species must be removed from restored areas and their surroundings.

Introduction

The restoration of native vegetation after degradation is a challenge that requires a deep understanding of the processes controlling native and invasive tree species colonization (Holmgren & Scheffer 2001; Vandenberghe et al. 2006; Bullock 2009). Facilitation and competition among plants are important ecological processes influencing the regeneration of degraded areas, especially in semiarid ecosystems (Callaway 1995; Flores & Jurado 2003; Gilliam 2007; Brooker & Callaway 2009; Gomez-Aparicio 2009). Degraded semiarid areas are firstly colonized by ruderal grass and herbaceous species, which are adapted to establish in open and sunny areas even under strong abiotic stress (e.g. high soil temperature, low water availability) (Scholes & Archer 1997; Holmgren & Scheffer 2001; Wiegand et al. 2005; Araújo et al. 2007; Verdoodt et al. 2010; Thrippleton et al. 2016). By covering the soil surface, the herbaceous vegetation layer can protect other seedlings against high temperatures, and reduce water and nutrient loss (Verdoodt et al. 2010; Yu et al. 2010; Santos et al. 2013). This vegetation can also increase soil organic matter due to leaf litter fall (Gilliam 2007; Elliott et al. 2014). However, the competitive or facilitative influence of herbaceous vegetation on the establishment of native and invasive trees remains controversial (Holzapfel & Mahall 1999; Maestre et al. 2003; Vandenberghe et al. 2006; Thrippleton et al. 2016; Tomiolo & Ward 2018). In the Brazilian semiarid region, the herbaceous layer contributes to a high proportion (56.3%) of the flora biodiversity (Queiroz et al. 2015; Fernandes et al. 2019). Similarly, the herbaceous layer is important for forest structure, biodiversity, and function in temperate ecosystems (Gilliam 2007). However, few studies have addressed the importance of the herbaceous

Author contributions: GBP, GG, JRAF created the research idea and performed statistical analysis; JRAF led the writing; all authors performed the experiments, collected data and commented on the manuscript.

[1]Departamento de Ecologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Natal, RN, Brazil
[2]Address correspondence to G. Ganade, email gganade@gmail.com
[3]Biodiversity, Macroecology & Biogeography, University of Göttingen, Göttingen, Germany

doi: 10.1111/rec.13595
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13595/suppinfo

layer in arid ecosystems and its role in community dynamics during restoration (Costa et al. 2006; Araújo et al. 2007).

Facilitation is a positive interaction process that occurs when established plants improve seedling growth and survival during their colonization in stressful environments (Callaway 1995; Callaway & Walker 1997). For example, native trees can maintain water availability, and reduce soil temperature through shading underneath their crown. This mechanism can further drive changes in community structure, increasing species diversity (Flores & Jurado 2003; Cavieres & Badano 2009; Paterno et al. 2016). Conversely, herbaceous vegetation can inhibit tree establishment and seedling growth due to strong competition for water, light, space, and nutrients (Callaway & Walker 1997; Davis et al. 1998; Maestre et al. 2003; Vandenberghe et al. 2006; Gomez-Aparicio 2009; Maestre et al. 2009). Herbaceous vegetation can also inhibit tree colonization through direct interference by producing allelopathic compounds, or when climbers strangle the plants they use as a support for growth (Scholes & Archer 1997; Gurevitch et al. 2009; Cummings et al. 2012; Camarero 2019). The herbaceous vegetation layer serves as a filter where regeneration of forests can only occur when plant species can germinate, survive, and grow underneath this vegetation layer (Gilliam 2014).

In dryland regions, soil temperature can be an important feature influencing plant survival and facilitation outcomes (Maraghni et al. 2010; Lewandrowski et al. 2021). Herbaceous leguminous species in the semi-arid Caatinga can contribute to a reduction in soil temperature and consequently to an increase in moisture (da Silva et al. 2016). Thus, herbaceous vegetation could act to reduce soil temperature and facilitate the establishment of tree seedlings. However, recent studies have shown that light exposure or grazing may be more important factors than soil temperature for tree seedling regeneration under herbaceous vegetation (Yu et al. 2010; Akhalkatsi et al. 2018). In addition, recent studies indicate that endemic species of the Caatinga may be affected by future climate changes due to increased temperature (Pinheiro et al. 2016). Therefore, the understanding of the relationship between soil temperature and facilitation might be important to foresee how plant–plant interactions can be modulated by global warming.

The control of exotic species invasion is also a major challenge for the restoration of degraded areas (Keane & Crawley 2002; Battaglia et al. 2009; Foster et al. 2015; Schuster et al. 2018). The success of invasive tree species colonization on degraded areas relies on biotic interactions with resident plants (Jones et al. 2013; Li et al. 2015; Feng & van Kleunen 2016). For example, strong competition for water and nutrients with the native herbaceous community can reduce the emergence, growth, and establishment of invasive trees depending on the age and structure of herbaceous vegetation (Scholes & Archer 1997; Bullock 2009). However, in open or degraded areas with low vegetation density, invasive plants can have a higher emergence probability (Bullock 2009). They can also grow faster than native species due to their higher competitive strategy, high fecundity (Keane & Crawley 2002; Wolfe & Bloem 2012), broad physiological niche (Wan & Wang 2018), and lack of natural enemies (Gurevitch et al. 2009). The exotic species *Leucaena leucocephala*, for example, was considered by the International Union for the Conservation of Nature's (IUCN) as one of the 100 most aggressive invasive species in the world (Lowe et al. 2000). This species shows high seed production, drought tolerance (Shelton & Brewbaker 1994; Chiou et al. 2013), and adaptation to degraded environments that contribute to the invasive potential of this species in semiarid regions.

Caatinga is one of the largest seasonally tropical dry forests (STDF) in the world and is home to a great diversity of plants, with many endemic species (Silva et al. 2017). This forest can act as a carbon sink, which increases its importance for restoration (Mendes et al. 2020), but it has been seriously degraded by extensive land use and chronic anthropogenic disturbance (Antongiovanni et al. 2018, 2020; Tomasella et al. 2018), which have led to an increase in desertification rates (Bezerra et al. 2020). Beyond degradation and desertification, this dry forest is commonly invaded by the invasive tree species *L. leucocephala*, which usually establishes and spreads along with degraded areas, threatening native plant diversity (Hata et al. 2010; Wolfe & Bloem 2012; Wan & Wang 2018). *Leucaena leucocephala* has a high invasion potential across different biomes, from temperate conifer forests to tropical and subtropical grasslands, savannas, and deserts (Wan & Wang 2018). To advance ecological restoration efficiency, there is a great need to investigate the processes that could restrain this invasive species and, at the same time, improve native tree colonization in semi-arid ecosystems (Holzapfel & Mahall 1999; Brooker 2006; Battaglia et al. 2009; Gomez-Aparicio 2009; Hata et al. 2010; Fernández 2013; Santos et al. 2013).

This study evaluated the influence of herbaceous vegetation on the colonization of two native tree species, *Anadenanthera colubrina* and *Astronium urundeuva*, and an invasive tree species, *L. leucocephala*, in degraded areas of a tropical dry forest. We predict that: (1) the herbaceous vegetation reduces soil temperature; (2) the competition by the herbaceous layer prevails despite the relative importance of micro-climatic and soil temperature alleviation (facilitation); and (3) the establishment of the invasive species is hampered by herbaceous layer competition.

Methods

Study Site

This study was conducted at the Nacional Forest of Açu (FLONA Açu—ICMBio), Rio Grande do Norte state, Brazil (5°34′20″S, 36°54′33″W). This protected area encompasses 413 ha of Caatinga seasonally dry tropical forest (SDTF), hereafter called Caatinga, the richest SDTF flora of the world with a high number of endemic species (Banda et al. 2016). The vegetation is characterized as xerophyte with physiognomic types that vary from woody forests to shrubby vegetation with scattered open areas, where herbaceous vegetation is dominant (Araújo et al. 2007; Silva et al. 2017). The Caatinga is characterized by high temperatures and evaporation rates (Araújo et al. 2007). In our site, the average annual temperature is around 28°C (Souza et al. 2014). The maximum temperature reaches 36.6°C and the minimum temperature is 18.6°C (data available at https://portal.inmet.gov.br). The average annual precipitation is around 500–800 mm, the rainfall reaches up to 300 mm from March and April (wet season) and decreases substantially in September, October, and November during the dry season (Souza et al. 2014).

The study site is a 5 ha degraded Caatinga area dominated by native herbaceous vegetation. In this study, we defined herbaceous vegetation as the non-tree vegetation covering the soil layer, which includes herbs, grasses, vines, and small shrubs. The dominant herbaceous species in the area are *Froelichia humboldtiana*, *Waltheria indica*, *Tephrosia purpurea*, and *Indigofera suffruticosa*. The site was degraded by farming and logging in the past decades and abandoned for more than 15 years, without any significant tree regeneration.

Herbaceous Vegetation Features

The study area presents 30 herbaceous species from 12 families, mostly herbs (10), grasses (2), small shrubs (10), and vines (8) (see Table S1 for the species list). The families with the highest number of species were Convolvulaceae and Malvaceae. According to Flora do Brasil 2020 (http://floradobrasil.jbrj.gov.br) and Tropicos (https://tropicos.org/home), 25 species found in the area are native and six species are exotic species in Brazil. The exotic species are: *Indigofera suffruticosa*, *Hyptis suaveolens*, *Lantana camara*, *Tarenaya spinosa*, and the two climbers *Merremia aegyptia* and *M. tuberosa*. The dominant species during the dry season were *T. purpurea*, *H. suaveolens*, and *W. indica*. During the rainy season, there was an increase in species numbers and a change in species composition at the study site. In May, the most frequent species were *W. indica*, *F. humboldtiana*, *L. camara*, *Macroptilium martii*, *T. purpurea*, and *Centrosema brasilianum*. The species *W. indica* and *F. humboldtiana* were very abundant at the experimental blocks.

Study Species

We studied one invasive tree species and two native tree species to the Caatinga. The invasive species was *Leucaena leucocephala* (Lam.) de Wit, a tree species native to Mexico, and the native species were *Anadenanthera colubrina* (Vell.) Brenan and *Astronium urundeuva* (M. Allemão) Engl. Regionally, they are named leucena, angico, and aroeira, respectively. We choose to use seeds of the exotic species because that is the way the invasion process naturally occurs in disturbed environments, while we used seedlings for the native species because restoration is normally performed by transplanting seedlings in degraded areas of the Caatinga biome.

Anadenanthera colubrina (Fabaceae) is a native species occurring in Argentina, Bolivia, Brazil, Paraguay, and Peru, with a wide distribution in the Caatinga. It is well adapted to dry climates and the deep soils from Caatinga and Cerrado biomes (Barrandeguy et al. 2014). *Anadenanthera colubrina* has a high genetic diversity and can reach 35 m in height (Barrandeguy et al. 2014) presenting a high potential to be used in restoration projects due to its rapid germination and survival under both light and shade conditions (Lorenzi 1992). This species is well adapted to establish and grow on sandy substrates, which enables its colonization in arid environments (Nery et al. 2018).

Astronium urundeuva (Anacardiaceae), a Brazilian tree that can reach up to 25 m in height is mainly found in the semi-arid region, has great importance in traditional medicine with anti-inflammatory, anti-microbial, and larvicidal properties, and is used as a source of wood and fuel (Soares et al. 2018; Pádua et al. 2019). *Astronium urundeuva* is a species threatened to extinction according to the list of the Brazilian Ministry of the Environment (MMA 2008).

The invasive tree *L. leucocephala* (Fabaceae) is a small- to medium-sized tree, ranging from 3 to 15 m and with a maximum height of 20 m. It is a perennial species, quite branched and with deep roots, its flowering and fruiting usually in early Spring, and most seeds are self-pollinated flowers (Orwa et al. 2009). This is a very aggressive invasive tree, which has already spread throughout tropical and subtropical regions of the world (Wan & Wang 2018).

Experimental Design

A factorial split-plot experiment was implemented in March 2014. Nine blocks were spread randomly in the study site to account for environmental heterogeneity. Each block (2.5×3 m) was at least 5 m apart from each other. To analyze the effect of herbaceous vegetation on tree species performance, two treatments were randomly applied in the blocks: intact and removed herbaceous vegetation (split factor), in 2.5 m $\times$ 50–cm plots, 2 m apart within each block. In the treatment with removed herbaceous vegetation, the herbaceous layer was fully removed with the use of a hoe. Roots were also superficially removed to prevent intense resprouting. Soil removal was performed in a way to avoid extreme disturbance. The manual removal of herbaceous sprouts was continually performed during the experiment. Plots with herbaceous vegetation received no manipulation. All plots were divided into three 50×50–cm subplots, 50 cm apart. In the center of each subplot, one plant of each of the two native species was transplanted, and 15 seeds of *L. leucocephala* were sown and marked with wooden sticks. The seeds of the invasive tree *L. leucocephala* were covered by a thin layer of soil (0.5 cm) to avoid seeds being carried by rain and wind. Subplots were fully randomized within plots (see Fig. S1 for details on the experimental design).

Before starting the experiment, seedlings of each native tree species were paired up by similar height, stem diameter at the ground level and the number of leaves, and each similar pair were randomly assigned within each block to homogenize the blocks. At the start of the experiment, *A. colubrina* and *A. urundeuva* seedlings measured on average approximately 30 and 40 cm in height, respectively. There were no initial differences in seedling height, stem diameter, or the number of leaves for seedlings planted at different herbaceous treatments (Table S2; Fig. S2). During the first week, all seedlings were watered to withstand the initial transplantation stress. The experiment was carried out using 72 seedlings of native tree species (36 of each species).

Native seedling performance was monitored between March (initial size) and September (7 months), a period that included the rainy season (from March to June) and the dry season (from July to October). Measurements of performance were: seedling height, stem diameter at soil level, and the number of leaves. For stem diameter, the central stem was measured at the soil surface, in the rare cases where the central stem was branched from the soil surface we measured only the stem with the largest diameter. Just before the end of the experiment, we also recorded the size of the three largest leaves from each native seedling. Leaf length and width were used to calculate the leaf area of every species assuming an ellipsoid shape.

Leucaena leucocephala seeds were collected from 10 different adult plants growing at the vicinities of the Federal University of Rio Grande do Norte campus. Dormancy treatments were applied for *L. leucocephala* seeds due to their waterproof tegument. We used thermal scarification with 80°C for 3 minutes defined by Fernández (2013) as the best method for seed scarification of this species. Seeds from different individual trees of *L. leucocephala* were fully mixed before sowing in the field. The experiment was carried out using 270 seeds marked with wooden sticks, 5 cm apart. The number of germinated seeds (root emergence), established seedlings (leaf emergence), and the number of leaflets per seedling of the invasive tree *L. leucocephala* was monitored between March and August. The number of germinated seeds was monitored by active searching marked seeds on the soil. The number of leaflets was counted for each established seedling.

Soil temperature was measured once in May between 11:00 and 14:00 o'clock to evaluate the effect of herbaceous vegetation on microclimatic conditions. The thermometer (Hitachi Maxell LR44) was placed 10 cm deep in the soil at the center of each three subplots (three measures per plot).

Statistical Analyses

The effect of herbaceous vegetation on native seedling growth was tested with a linear mixed model (LMM) (Bolker et al. 2009). Seedling height (cm), number of leaves, and stem diameter at the soil level (mm) were used as response variables. The treatments: herbaceous vegetation, species, and time (number of days since transplanting), and all possible treatment interactions were used as fixed effects in the model. To account for the experimental spatial structure, where repeated measures were taken for each seedling, plant identity was set as a random effect nested within blocks (Crawley 2012). For the number of leaves (counts), we fitted a zero-inflated Poisson mixed model (ZIP) after testing and detecting an excess of zeros in the data. To test for the effect of the herbaceous vegetation on leaf area (mm^2) of native tree seedlings, we have performed linear mixed models with herbaceous vegetation, species, and their interaction as fixed effects while block was set as a random effect. To test the effect of the herbaceous vegetation on seed germination and seedling establishment of *L. leucocephala*, we used generalized linear mixed models with Poisson error structure. The number of germinated seeds and established seedlings were used as response variables while herbaceous vegetation, time, and their interaction were used as fixed effects. Block was set as a random effect in the model. For the number of leaflets, we have fitted a zero-inflated Poisson mixed model (ZIP) after testing and detecting excess of zeros in the data. Plant identity nested in blocks was set as a random effect.

We used generalized linear mixed models because they provide a flexible approach to model non-normally distributed data (i.e. counts), while random effects can be used to control for the non-independence between data points (i.e. repeated measurements) (Bolker et al. 2009; Harrison et al. 2018). In cases where the excess of zeros is statistically detected in the data, a zero-inflated modeling approach is recommended to avoid bias in parameter estimates (Blasco-Moreno et al. 2019). To test for zero inflation in data, we used a simulation approach and compared the proportion of zeros in the data to the simulated ones expected based on a Poisson model (Hartig 2019).

The influence of herbaceous vegetation on soil temperature was analyzed with a paired *t*-test using soil temperature as a response variable and vegetation treatment (removed or intact) as an explanatory variable. The software R (version 3.6.3) was used for all statistical analysis and graphics (R Core Team 2020). Generalized and linear mixed models were fitted using the R package *glmmTMB* (Magnusson et al. 2017) and model diagnostics and zero-inflation tests were performed with the R package *DHARMa* (Hartig 2019). Inference for fixed effects was performed through likelihood ratio tests (LRT) (Bolker et al. 2009; Crawley 2012) using an alpha level of 0.05. The graphs were built using the R *ggplot2* package (Wickham 2016).

Results

Effect of Herbaceous Vegetation on Native Tree Growth

The presence of herbaceous vegetation inhibited seedling growth of native species for all variables evaluated (height, number of leaves, and stem diameter). The intensity of this effect varied over time, within species, and within the response, variable considered (Fig. 1). Mortality was low during the study period. The only two individuals that died were seedlings of *Astronium urundeuva* located in plots with herbaceous vegetation.

For seedling height, there was a significant interaction between the herbaceous vegetation treatment and time ($\chi^2 = 8.60$, $df = 1$, $p = 0.00336$, Table S3), with seedlings of both species increasing in height faster in removed vegetation plots than in plots with intact vegetation (Fig. 1A & 1B). For the number of leaves, there was a significant interaction between herbaceous vegetation and time ($\chi^2 = 55.98$, $df = 1$, $p < 0.00001$, Table S3). The number of leaves increased over time, with a higher value in plots where herbaceous vegetation has been removed. The number of leaves increased until the end of the wet season, in mid-June, when plants begin to lose their leaves due to the beginning of the dry season (Fig. S3). Seedlings of *Anadenanthera colubrina* growing in plots where herbaceous vegetation has been removed, produced twice as many leaves than seedlings in plots with herbaceous vegetation. In addition, this effect was up to four-fold stronger for *A. urundeuva* (Fig. 1C & 1D). Stem diameter, for both species,

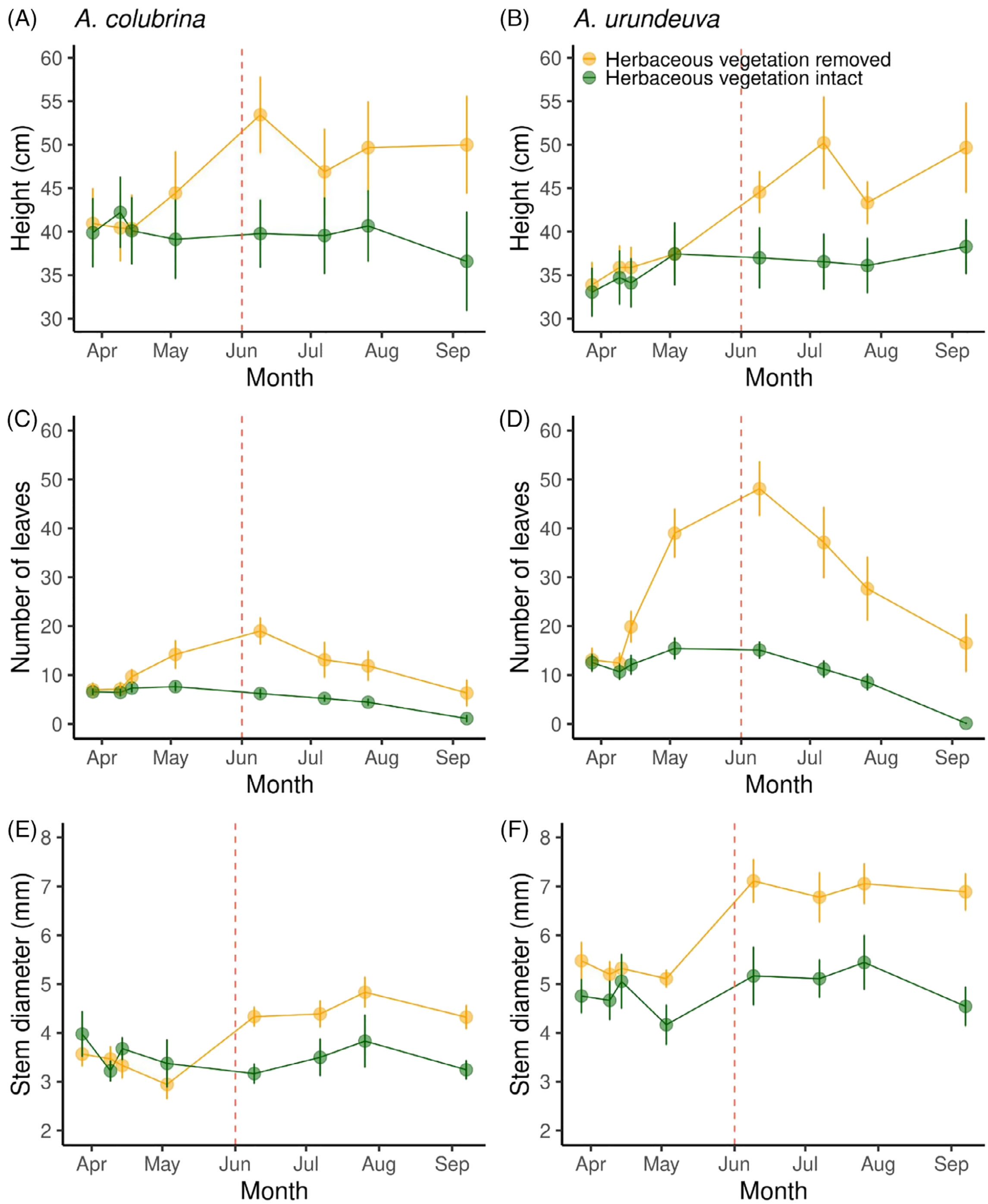

Figure 1. Seedling height (A, B), number of leaves (C, D), diameter at the soil level (E, F) across time for the native species *Anadenanthera colubrina* (A, C, E), and *Astronium urundeuva* (B, D, F). Error bars represent ± SE. The vertical red line indicates the beginning of the dry season in the experimental year (2014).

increased when herbaceous vegetation was removed (Fig. 1E & 1F). However, there was a significant interaction between herbaceous vegetation and time ($\chi^2 = 19.17$, $df = 1$, $p < 0.00001$, Table S3), showing that stem diameter was similar between vegetation treatments at the beginning of the experiment, but had a higher increase over time when herbaceous vegetation was removed (Fig. 1E & 1F). There was also a significant interaction between herbaceous vegetation and species ($\chi^2 = 10.46$, $df = 1$, $p = 0.00122$, Table S3) only for stem diameter, where *A. urundeuva* showed a higher decrease in stem diameter when in competition with the herbaceous vegetation than *A. colubrina* (Fig. 1E & 1F).

The presence of herbaceous vegetation also had a clear negative effect on the leaf area of both native tree species by the end

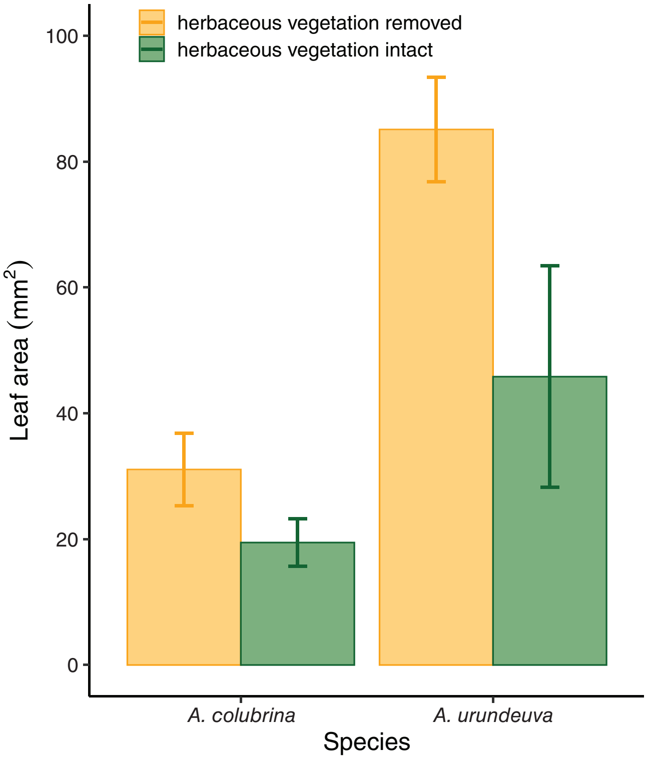

Figure 2. Leaf area for native species *Anadenanthera colubrina* and *Astronium urundeuva* growing in plots with removed and intact herbaceous vegetation. Bars represent average and error bars represent ± SE. Averages were calculated from the three largest leaves from each native seedling before the end of the experiment.

of the experiment (χ^2 = 6.13, *df* = 1, *p* = 0.013, Table S4; Fig. 2). The average leaf area of both species was reduced in plots with herbaceous vegetation in comparison to plots without the herbaceous layer. This negative effect was stronger for *A. urundeuva*, although the interaction between vegetation and species treatments was not statistically significant (Table S4; Fig. 2). On average, the herbaceous layer has caused a reduction of 37% and 47% on the leaf area of *A. colubrina* and *A. urundeuva*, respectively.

Effect of Herbaceous Vegetation on the Invasive Tree Species

The germination of *Leucaena leucocephala* seeds was affected by the interaction between herbaceous vegetation and time (χ^2 = 4.38, *df* = 1, *p* = 0.03639, Table S5). The number of established seedlings of *L. leucocephala* was affected only by time (χ^2 = 21.39, *df* = 1, $p < 0.0001$, Table S5). Seed germination and seedling establishment were higher in plots where herbaceous vegetation was removed at the beginning of the rainy season but this difference disappeared in the dry season (Fig. 3A & 3B). The number of leaflets of *L. leucocephala* seedlings was also affected by the interaction between herbaceous vegetation and time (χ^2 = 4.67, *df* = 1, *p* = 0.03062, Table S6). The number of leaflets did not differ between removed and intact herbaceous vegetation treatments during the wet season, but seedlings lost their leaves more quickly under intact vegetation than when the vegetation was removed (Fig. S4). In summary, the early establishment of *L. leucocephala* in the study area was minimally affected by the presence of herbaceous vegetation.

Effect of the Herbaceous Vegetation on Soil Temperature

Soil temperature was on average 4.4°C lower in plots with herbaceous vegetation in comparison to plots where herbaceous vegetation has been removed (*t* = −10.82, *df* = 8, $p < 0.0001$). Average soil temperature with herbaceous vegetation was 32.4°C ± 0.25 SE, while soil average temperature without herbaceous vegetation was 36.8°C ± 0.46 SE (see Fig. S5).

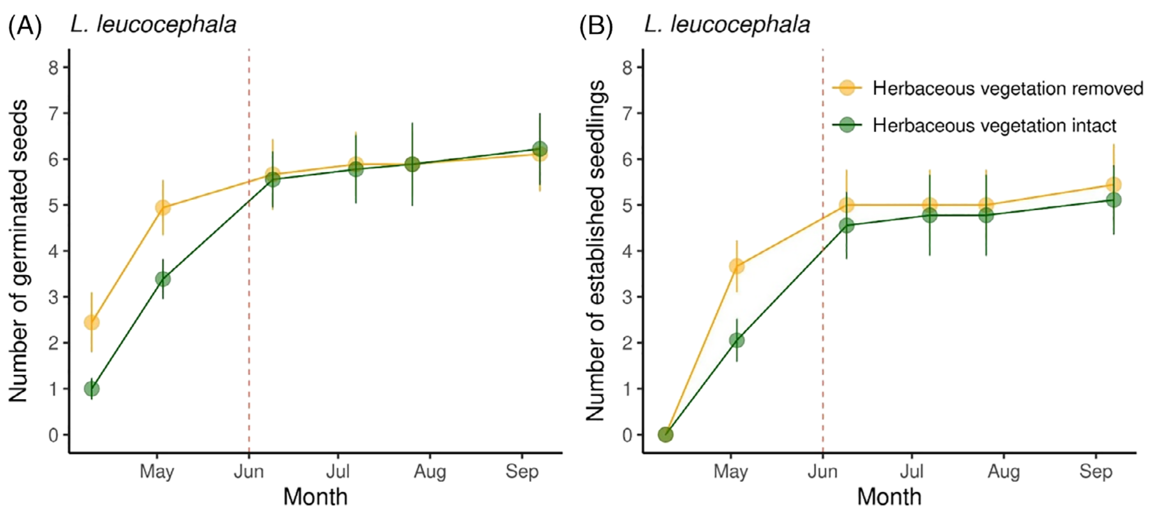

Figure 3. Number of germinated seeds (A) and number of established seedlings (B) of the invasive tree species *Leucaena Leucocephala* in treatments with removed and intact herbaceous vegetation. Error bars represent ± SE. The vertical line indicates the beginning of the dry season in the experimental year (2014).

Discussion

According to our hypothesis, facilitation was not an important mechanism that has shaped the relationship between herbaceous vegetation and tree transplant performance, although herbaceous vegetation has attenuated soil temperature (Kitzberger et al. 2000; Flores & Jurado 2003; Zhang et al. 2015). Instead, the presence of herbaceous vegetation has greatly inhibited all aspects (number of leaves, height, and stem diameter) of native tree performance, showing that ruderal herbaceous vegetation must be constantly managed to improve the performance of transplanted seedlings. It is important to note that the herbaceous vegetation differently affected the study tree species, inhibiting growth and survival of *Astronium urundeuva* (a threatened species) more intensely than *Anadenanthera Colubrina* (a widespread species). In addition, according to our hypothesis, the invasive tree species *L. leucocephala* was weakly affected by the herbaceous layer and its establishment was widespread.

We did not find any studies reporting the influence of herbaceous plants on tree seedling survival in the semiarid Caatinga, but many studies in other ecosystems showed negative effects on the growth of tree seedlings in the presence of herbaceous vegetation. Similarly to our results, the negative effect of herbaceous plants on height, diameter, and survival has been verified for tree seedlings in a temperate forest (George & Bazzaz 1999; Quinteros et al. 2016). Seedlings of the tree species *Fagus sylvatica* showed lower growth in diameter and height when in the presence of grasses in meadow habitats (Coll et al. 2004). In an experiment with and without the presence of herbaceous plants in northeastern Ohio, North America, *Juniperus virginiana* showed a lower growth rate when in interspecific competition with herbaceous species, and this growth was lower in the low rainfall season. This indicates that abiotic factors influence the interaction between species (Tomiolo & Ward 2018). These examples come from ecosystems that are not similar to Caatinga in terms of climate or species identity, which demonstrates the wide scope of our results and the importance of our findings.

There are various ways in which herbaceous vegetation can suppress tree growth. In general, competition occurs when similar zones for resource acquisition are overlapped (Scholes & Archer 1997; Vanette & Fukami 2014). Considering ecosystems with similar climatic conditions to the one in our study, as in savanna-grassland, it was found that dense grasses reduce the establishment of tree seedlings, and gaps of roots allow recruitment (Wakeling et al. 2014). In the Mojave Desert, for example, herbaceous vegetation can reduce soil water content during moister periods reducing the growth of their shrub neighbors (Holzapfel & Mahall 1999). Roots of the herbaceous layer may be more homogeneously spread in the soil, which increase the absorption of water and nutrients (Wiegand et al. 2005; Zhang et al. 2015; Quinteros et al. 2016). In addition, roots of herbaceous vegetation are located in the soil surface where tree species transplants have to obtain water and nutrients for growth and survival. In Savanna-grassland, Wakeling et al. (2014) found that more than half of the grass biomass occurred up to 10 cm below the soil surface. This high root density of herbaceous species at the soil surface can induce an overlap in root zone triggering a strong competition between tree seedlings in the early stages of growth (Scholes & Archer 1997; Holzapfel & Mahall 1999; Tomiolo & Ward 2018). The 0–20 cm soil layer in semiarid Caatinga is important for plant root profiles, and temperature directly influences soil moisture especially during dry periods (Pinheiro et al. 2016). Tree seedling growth depends on the amount of light on the forest floor; therefore, light competition should not be overlooked, given that seedlings were completely covered by the herbaceous layer in our experiment. Indeed, herbaceous vegetation can reduce light availability by 30% in forest landscapes (Gilliam 2014; Thrippleton et al. 2016).

Several species from the herbaceous community are native annual plants that grow quickly in the rainy season and highly contribute for plant diversity in Caatinga (Queiroz et al. 2015; Fernandes et al. 2019). Within them, ruderal species are more aggressive and may become abundant as they are more competitive than other species. In our study site, eight ruderal climber species occurred in the herbaceous layer, the most abundant ones were *Macroptilium martii* and *Centrosema brasilianum*. These climber species can wrap themselves around the whole seedling covering most of its leaves; thus, reducing seedling photosynthetic capacity. Indeed, vine species use native plants as support and may hinder their growth (Chen et al. 2008; Paul & Yavitt 2011). In subtropical forests, the relative growth rate and stem height of tree species are reduced in the presence of lianas with climbing mechanisms due to above- and belowground competition (Schnitzer et al. 2005; Campanello et al. 2007; Chen et al. 2008). Moreover, vine species also negatively affect the sapling recruitment of native species (Horvitz & Koop 2001). High diversity and abundance of herbaceous climbers can be found in dry forests and grasslands (den Dubbelden & Oosterbeek 1995; Ferrero et al. 2017). These species quickly colonize habitats with high light availability, such as gaps in tropical forests, secondary forests, and open degraded areas (Dillenburg et al. 1992; César et al. 2016; Lai et al. 2016). In a tropical dry forest, the removal of climbing plants and soil plowing can increase tree aboveground biomass, canopy cover, and recruitment rates (Méndez-Toribio et al. 2019). Future works should investigate how certain species and life forms that constitute the herbaceous community could influence the performance of transplanted seedlings during restoration.

Studies have shown that herbaceous vegetation can facilitate invasive species during early establishment (Zarnetske et al. 2013). However, in general, there was no expressive effect of the herbaceous vegetation on the establishment of invasive tree *Leucaena leucocephala*, apart from a small delay of germination and a slightly faster leaf loss at the beginning of the dry season. This slightly higher germination rate of *L. leucocephala* in soils where herbaceous plants have been removed can be explained by an initial sensitivity of this invasive species to shading and competition with the herbaceous community (Hata et al. 2010; Fernández 2013). Germination of *L. leucocephala* might also be delayed by herbaceous vegetation litterfall (Bullock 2009; Hata et al. 2010). The faster leaflet loss under herbaceous vegetation at the beginning of the dry season could be due to competition or higher herbivory under the herbaceous community (Wolfe & Bloem 2012; Fernández 2013). A high level of herbivory under vegetation reduces seedling survival (Gilliam 2014). However, these processes had no consequences on the final number of germinated seeds or established seedlings. In the Caatinga, the germination of *L. leucocephala* can be widespread below and far from nurse tree canopies (Fernández 2013). *Leucaena leucocephala* can be established in degraded areas with little shade and poor soils, being able to resist these adverse conditions due to its ability to fix nitrogen, lose leaves during the dry season, germinate, and grow rapidly (Lamarque et al. 2011; Wolfe & Bloem 2012).

In conclusion, the herbaceous species hindered the growth of native arboreal species, but did not affect the early performance of the invasive tree species *L. leucocephala*. These results support previous findings of a study performed in a subtropical dry forest, where survival of native species under herbaceous vegetation reached 40%, while for invasive species, such as *L. leucocephala*, survival reached 80% (Wolfe & Bloem 2012). Our results show that degraded areas in the Caatinga can offer a possibility for invasion of *L. leucocephala* during years where rare climatic events could cause the spread of this exotic species. This study also reveals the need for periodic management of herbaceous vegetation to improve the performance of transplanted native tree species as a strategy to promote successful restoration.

Acknowledgments

We thank the members of the Restoration Ecology Laboratory of the Federal University of Rio Grande do Norte (UFRN), who have helped in the field collections and offered suggestions for the improvement of the manuscript. We would like to also thank the UFRN Herbarium for its support identifying plant species. This study was funded in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)—Finance Code 001 which provided grants to JRAF and GG and by Conselho Nacional de Pesquisa e Tecnologia (CNPQ) processo 400672/2013-8.

LITERATURE CITED

Akhalkatsi M, Abdaladze O, Nakhutsrishvili G, Smith WK (2018) Facilitation of seedling microsites by *Rhododendron caucasicum* extends the *Betula litwinowii* alpine treeline, Caucasus Mountains, Republic of Georgia. Arctic, Antarctic, and Alpine Research 38:481–488

Antongiovanni M, Venticinque EM, Fonseca CR (2018) Fragmentation patterns of the Caatinga drylands. Landscape Ecology 33:1353–1367

Antongiovanni M, Venticinque EM, Matsumoto M, Fonseca CR (2020) Chronic anthropogenic disturbance on Caatinga dry forest fragments. Journal of Applied Ecology 57:1–11

Araújo EL, Castro CC, Albuquerque UP (2007) Dynamics of Brazilian Caatinga—a review concerning the plants. Environment and people. Functional Ecosystems and Communities 1:15–28

Banda KR, Delgado-Salinas A, Dexter KG, Linares-Palomino R, Oliveira-Filho A, Prado D, et al. (2016) Plant diversity patterns in neotropical dry forests and their conservation implications. Science 353:1383–1388

Barrandeguy ME, Garcia MV, Prinz K, Pomar RR, Finkeldey R (2014) Genetic structure of disjunct Argentinean populations of the subtropical tree *Anadenanthera colubrina* var. cebil (Fabaceae). Plant Systematics and Evolution 300:1693–1705

Battaglia LL, Denslow JS, Inczauskis JR, Baer SG (2009) Effects of native vegetation on invasion success of Chinese tallow in a floating marsh ecosystem. Journal of Ecology 97:239–246

Bezerra FGS, Aguiar APD, Alvalá RCS, Giarolla A, Bezerra KRA, Lima PVPS, Nascimento FR, Arai E (2020) Analysis of areas undergoing desertification, using EVI2 multi-temporal data based on MODIS imagery as indicator. Ecological Indicators 117:1–15

Blasco-Moreno A, Pérez-Casany M, Puig Morante M, Castells E (2019) What does a zero mean? Understanding false, random and structural zeros in ecology. Methods in Ecology and Evolution 10:949–959

Bolker BM, Brooks ME, Clarck CJ, Geange SW, Poulsen JR, Stevens MHH, White JS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135

Brooker RW (2006) Plant–plant interactions and environmental change. New Phytologist 171:271–284

Brooker RW, Callaway RM (2009) Facilitation in the conceptual melting pot. Journal of Ecology 97:1117–1120

Bullock JM (2009) A long-term study of the roles of competition and facilitation in the establishment of an invasive pine following heath land fires. Journal of Ecology 97:646–656

Callaway RM (1995) Positive interactions among plants. The Botanical Review 61:306–349

Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78:1958–1965

Camarero P (2019) Exotic vine invasions following cyclone disturbance in Australian wet tropics rainforests: a review. Austral Ecology 44: 1359–1372

Campanello PI, Garibaldi JF, Gatti MG, Goldstein G (2007) Lianas in a subtropical Atlantic Forest: host preference and tree growth. Forest Ecology and Management 242:250–259

Cavieres LA, Badano EI (2009) Do facilitative interactions increase species richness at the entire community level? Journal of Ecology 97:1181–1191

César RG, Holl KD, Girão VJ, Mello FNA, Vidal E, Alves MC, Brancalion PHS (2016) Evaluating climber cutting as a strategy to restore degraded tropical forests. Biological Conservation 201:309–313

Chen YJ, Bongers F, Cao KF, Cai ZQ (2008) Above- and below-ground competition in high and low irradiance: tree seedling responses to a competing liana *Byttneria grandifolia*. Journal of Tropical Ecology 24:517–524

Chiou C-R, Wang H-H, Chen Y-J, Grant WE, Lu M-L (2013) Modeling potential range expansion of the invasive shrub *Leucaena leucocephala* in the Hengchun peninsula, Taiwan. Invasive Plant Science and Management 6:492–501

Coll L, Balandier P, Picon-Cochard C (2004) Morphological and physiological responses of beech (*Fagus sylvatica*) seedlings to grass-induced belowground competition. Tree Physiology 24:45–54

Costa RC, Araújo FS, Lima-Verde LW (2006) Flora and life-form spectrum in an area of deciduous thorn woodland (Caatinga) in northeastern, Brazil. Journal of Arid Environments 68:237–247

Crawley MJ (ed) (2012) The R book. 2nd ed. Wiley-Blackwell, Chichester, United Kingdom

Cummings JA, Parker IM, Gilbert GS (2012) Allelopathy: a tool for weed management in forest restoration. Plant Ecology 213:1975–1989

da Silva DMN, de Oliveira FL, Teodoro RB, Fávero C, Quaresma MAL (2016) Temperature and humidity of soil covered with perennial herbaceous legumes in the semiarid region of Minas Gerais state, Brazil. Bioscience Journal 32:11–19

Davis MA, Wrage KJ, Reich PB (1998) Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. Journal of Ecology 86:652–661

den Dubbelden KC, Oosterbeek B (1995) The availability of external support affects allocation patterns and morphology of herbaceous climbing plants. Functional Ecology 9:628–634

Dillenburg LR, Whigham DF, Teramura AH, Forseth IN (1992) Effects of below- and aboveground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar styraciflua*. Oecologia 93:48–54

Elliott KJ, Vose JM, Knoepp JD, Clinton BD, Kloeppel BD (2014) Functional role of the herbaceous layer in eastern deciduous forest. Ecosystems 18: 221–236

Feng Y, van Kleunen M (2016) Phylogenetic and functional mechanisms of direct and indirect interactions among alien and native plants. Journal of Ecology 104:1136–1148

Fernandes MF, Cardoso D, de Queiroz LP (2019) An updated plant checklist of the Brazilian Caatinga seasonally dry forests and woodlands reveals high species richness and endemism. Journal of Arid Environments 174:104079

Fernández LM (2013) Ajudando os inimigos: espécies nativas facilitam a invasão do semiárido brasileiro por árvores exóticas. PhD dissertation. University Federal of Rio Grande do Norte, Natal

Ferrero MC, Zeballos SR, Whitworth-Hulse JI, Giorgis MA, Gurvich DE (2017) Functional strategies and distribution of climbing plant communities in different vegetation patches in a subtropical dry forest, Central Argentina. Journal of Plant Ecology 12:23–33

Flores J, Jurado E (2003) Are nurse-protégé interactions more common among plants from arid environments? Journal of Vegetation Science 14:911–916

Foster BL, Houseman GR, Hall DR, Hinman SE (2015) Does tallgrass prairie restoration enhance the invasion resistance of post-agricultural lands? Biological Invasions 17:3579–3590

George LO, Bazzaz FA (1999) The fern understory as an ecological filter: Growth and survival of canopy tree seedlings. Pages 265–282 In: Gilliam FS (eds) The herbaceous layer in forests of eastern North America. Oxford University Press, New York.

Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate Forest. Ecosystems 57:845–858

Gilliam FS (2014) The herbaceous layer in forests of Eastern North America. Oxford University Press, New York

Gomez-Aparicio L (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. Journal of Ecology 97:1202–1214

Gurevitch J, Scheiner SM, Fox GA (2009) Ecologia Vegetal. 2nd ed. Artmed, Porto Alegre, Rio Grande do Sul

Harrison XA, Donaldson L, Correa-Cano MA, Evans J, Fisher DN, Goodwin CED, Robinson BS, Hodgson DJ, Inger R (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 2018:1–32

Hartig F (2019) *DHARMa*: residual diagnostics for hierarchical (multi-level/ mixed) regression models. R package version 03.0

Hata K, Suzuki JI, Kachi N (2010) Fine-scale spatial distribution of seedling establishment of the invasive plant, *Leucaena leucocephala*, on an oceanic Island after feral goat extermination. Weed Research 50:472–480

Holmgren M, Scheffer M (2001) El Niño as a window of opportunity for the restoration of degraded arid ecosystems. Ecosystems 4:151–159

Holzapfel C, Mahall BE (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. Ecology 80:1747–1761

Horvitz CC, Koop A (2001) Removal of non native vines and post-hurricane recruitment in tropical hardwood forests of Florida1. Biotropica 33: 268–281

Jones EI, Nuismer SL, Gomulkiewicz R (2013) Revisiting Darwin's conundrum reveals a twist on the relationship between phylogenetic distance and invasibility. Proceedings of the National Academy of Sciences 110: 20627–20632

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17:164–170

Kitzberger T, Steinaker DF, Veblen TT (2000) Effects of climatic variability on facilitation of tree establishment in northern Patagonia. Ecology 81: 1914–1924

Lai HR, Hall JS, Turner BL, van Breugel M (2016) Liana effects on biomass dynamics strengthen during secondary forest succession. Ecology 98: 1062–1070

Lamarque LJ, Delzon S, Lortie CJ (2011) Tree invasions: a comparative test of the dominant hypotheses and functional traits. Biological Invasions 13: 1969–1989

Lewandrowski W, Stevens JC, Webber BL, Dalziell EL, Trudgen MS, Bateman AM, Erickson TE (2021) Global change impacts on arid zone ecosystems: seedling establishment processes are threatened by temperature and water stress. Ecology and Evolution 11:8071–8084

Li S peng Cadotte M.W., Meiners S.J., Hua Z.S., Shu H.Y., Li J.T., Shu W.S. (2015) The effects of phylogenetic relatedness on invasion success and impact: deconstructing Darwin's naturalisation conundrum. Ecology Letters 18:1285–1292

Lorenzi H (1992) Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil. Plantarum, São Paulo

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the World's worst invasive alien species—a selection from the global invasive species database. The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), Auckland, New Zealand.

Maestre FT, Bautista S, Cortina J (2003) Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. Ecology 84:3186–3197

Maestre FT, Callaway RM, Valladares F, Lortie CJ (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. Journal of Ecology 97:199–205

Magnusson A, Skaug H, Nielsen A, Berg CW, Kristensen K, Mächler M, van Benthem K, Bolker B, Brooks M (2017) *glmmTMB*: Generalized Linear Mixed Models using Template Model Builder. R package version 1.0.2.1

Maraghni M, Gorai M, Neffati M (2010) Seed germination at different temperatures and water stress levels, and seedling emergence from different depths of *Ziziphus lotus*. South African Journal of Botany 76:453–459

Mendes KR, Suany C, Lindenberg L da S, Mutti PR, Ferreira RR, Medeiros SS, et al. (2020) Seasonal variation in net ecosystem CO2 exchange of a Brazilian seasonally dry tropical forest. Scientific Reports 10:1–16

Méndez-Toribio M, Benítez-Malvido J, Zermeño-Hernández IE, Castillo-Mandujano J (2019) Removal of climbing plants and soil plowing as a strategy to enhance forest recovery in tropical dry forests old fields. Ecological Restoration 37:113–122

Ministério do Meio Ambiente (2008) Lista Oficial das Espécies da Flora Brasileira Ameaçada de Extinção. https://www.mma.gov.br/estruturas/ascom_boletins/_arquivos/83_19092008034949.pdf .

Nery FC, Nery MC, Prudente PDO, Alvarenga AA, Paiva R (2018) Morphological and physiological germination aspects of *Anadenanthera colubrina* (Vell.) Brenan. Notulae Botanicae Horti Agrobotanici Cluj-Napoca 46: 593–600

Orwa C, Mutua A, Kindt R, Jamnadass R, Anthony S (2009) *Leucaena leucocephala* (Lam.) De Wit (Mimosaceae). Agroforestree Database: a tree reference and selection guide version 1–8.

Pádua APSL, Freire KTLA, Oliveira TGL, Silva LF, Araújo-Magalhães GR, Agamez-Montalvo GS, Silva IR, Bezerra JDP, Souza-Motta CM (2019) Fungal endophyte diversity in the leaves of the medicinal plant *Astronium urundeuva* in a Brazilian dry tropical forest and their capacity to produce L-asparaginase. Acta Botanica Brasilica 33:39–49

Paterno GB, Siqueira Filho JAS, Ganade G (2016) Species-specific, ontogenetic shifts and consequences for plant community succession. Journal of Vegetation Science 27:606–615

Paul GS, Yavitt JB (2011) Tropical vine growth and the effects on Forest succession: a review of the ecology and Management of Tropical Climbing Plants. Botanical Review 77:11–30

Pinheiro EAR, Metselaar K, van Lier QJ, de Araújo JC (2016) Importance of soil-water to the Caatinga biome, Brazil. Ecohydrology 9:1313–1327

Queiroz RT, Moro MF, Loiola MIB (2015) Evaluating the relative importance of woody versus non-woody plants for alpha-diversity in a semiarid ecosystem in Brazil. Plant Ecology and Evolution 148:361–376

Quinteros CP, Bava JO, López Bernal PM, Gobbi ME, Defossé GE (2016) Competition effects of grazing-modified herbaceous vegetation on growth, survival and water relations of lenga (*Nothofagus pumilio*) seedlings in a temperate forest of Patagonia, Argentina. Agroforestry Systems 91: 597–611

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria URL https://www.R-project.org/ (accessed 10 Aug 2020)

Santos JMFF, Santos DM, Lopes CGR, Silva KA, Sampaio EVSB, Araújo EL (2013) Natural regeneration of the herbaceous community in a semiarid region in northeastern Brazil. Environmental Monitoring and Assessment 185:8287–8302

Schnitzer SA, Kuzee ME, Bongers F (2005) Disentangling above-and below-ground competition between lianas and trees in a tropical forest. Journal of Ecology 93:1115–1125

Scholes RJ, Archer SR (1997) Tree grass interactions in savannas. Annual Review of Ecology and Systematics 28:517–544

Schuster MJ, Wragg PD, Reich PB (2018) Using revegetation to suppress invasive plants in grasslands and forests. Journal of Applied Ecology 55:2362–2373

Shelton HM, Brewbaker JL (1994) *Leucaena leucocephala*—the Most widely used forage tree legume. Pages 15–29. In: Gutteridge RC, Shelton HM (eds) Forage tree legumes in tropical agriculture. CAB International Wallingford, UK

Silva JMC, Leal IR, Tabarelli M (2017) Caatinga: the largest tropical dry Forest region in South America. Springer, Recife, Pernambuco

Soares AMS, Rocha CQ, Oliveira JTA, Silva CR, Costa-Junior LM, Vilegas W, Ferreira ATS, Zanatta AC, Perales J (2018) *Astronium urundeuva* seed exudates proteome and anthelmintic activity against *Haemonchus contortus*. PLoS One 13:e0200848

Souza DNN, Camacho RGV, Melo JIM, da Rocha LNG, da Silva NF (2014) Estudo fenológico de espécies arbóreas nativas em uma unidade de conservação de caatinga no Estado do Rio Grande do Norte, Brasil. Biotemas 27:31–42

Thrippleton T, Bugmann H, Kramer-Priewasser K, Snell RS (2016) Herbaceous Understorey: an overlooked player in Forest landscape dynamics? Ecosystems 19:1240–1254

Tomasella J, Silva Pinto Vieira RM, Barbosa AA, Rodriguez DA, Oliveira Santana M, Sestini MF (2018) Desertification trends in the northeast of Brazil over the period 2000–2016. International Journal of Applied Earth Observation and Geoinformation 73:197–206

Tomiolo S, Ward D (2018) Soil properties and climate mediate the effects of biotic interactions on the performance of a woody range expander. Ecosphere 9:1–14

Vandenberghe C, Freléchoux F, Gadallah F, Butler A (2006) Competitive effects of herbaceous vegetation on tree seedling emergence, growth and survival: does gap size matter? Journal of Vegetation Science 17:481–488

Vanette RL, Fukami T (2014) Historical contingency in species interactions: towards niche-based predictions. Ecology Letters 17:115–124

Verdoodt A, Mureithi SM, Van Ranst E (2010) Impacts of management and enclosure age on recovery of the herbaceous rangeland vegetation in semi-arid Kenya. Journal of Arid Environments 74:1066–1073

Wakeling JL, Bond WJ, Ghaui M, February EC (2014) Grass competition and the savanna-grassland “treeline”: a question of root gaps? South African Journal of Botany 101:91–97

Wan JZ, Wang CJ (2018) Expansion risk of invasive plants in regions of high plant diversity: a global assessment using 36 species. Ecological Informatics 46:8–18

Wickham H (2016) *ggplot2*: create elegant data Visualisations using the grammar of graphics. R package version 32

Wiegand K, Saltz D, Ward D (2005) A patch-dynamics approach to savanna dynamics and woody plant encroachment—insights from an arid savanna. Perspectives in Plant Ecology, Evolution and Systematics 7: 229–242

Wolfe TB, Bloem SJV (2012) Subtropical dry forest regeneration in grass-invaded areas of Puerto Rico: understanding why *Leucaena leucocephala* dominates and native species fail. Forest Ecology and Management 267: 253–261

Yu F, Li P, Li S, He W (2010) *Kobresia tibetica* tussocks facilitate plant species inside them and increase diversity and reproduction. Basic and Applied Ecology 11:743–751

Zarnetske PL, Gouhier TC, Hacker SD, Seabloom EW, Bokil VA (2013) Indirect effects and facilitation among native and non-native species promote invasion success along an environmental stress gradient. Journal of Ecology 101:905–915

Zhang G, Yang Q, Wang X, Zhao W (2015) Size-related change in *Nitraria sphaerocarpa* patches shifts the shrub-annual interaction in an arid desert, northwestern China. Acta Oecologica 69:121–128

Supporting Information

The following information may be found in the online version of this article:

Figure S1. Scheme of an experimental block. Nine replicated blocks were used in the experiment.
Figure S2. Initial conditions of height, number of leaves, and diameter of native seedlings transplanted.
Figure S3. Precipitation data (mm) in the city closest to the experiment.
Figure S4. Number of leaflets produced over time by the exotic species.
Figure S5. Soil temperature in experimental treatments.
Table S1. Families, scientific and common names, life forms, and origin of herbaceous species.
Table S2. Results from linear mixed models comparing native tree species initial size within restoration treatments.
Table S3. Results from generalized mixed models for native tree species growth.
Table S4. Results from linear mixed models for native tree species leaf area modeled.
Table S5. Results from linear mixed models for seed germination and seedling establishment.
Table S6. Results from linear mixed models for number of leaflets of *Leucena leucocephala* in relation to herbaceous vegetation (herb) and time.

Coordinating Editor: Stephen Murphy

Received: 20 January, 2021; First decision: 3 March, 2021; Revised: 25 October, 2021; Accepted: 27 October, 2021