Cryptostegia Madagascariensis Alters the Litterfall and Nutrient Cycling of Litter Inputs in An Invaded Tropical Cambisol From North-Eastern Brazil

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Abstract

The invasive *Cryptostegia madagascariensis* occupies riparian areas covered by tropical Cambisols throughout the North-eastern Brazil however litter is known regarding its ability to impact litter inputs, and ecosystem processes. This study aimed to characterize the effects of the invader on the litter deposition, soil physical-chemical properties, litter nutrient content, and the litter decay rate in a Tropical Cambisol. Comparisons of native and invaded environments showed that *C. madagascariensis* alters the quantity of litter deposition during both dry and rainy seasons. In contrast to native species, *C. madagascariensis* litterfall displayed litter seasonal variation (rainy vs. dry season), however invaded sites had higher litter biomass compared to native sites. *C. madagascariensis* litter was enriched in soil organic matter, N, P, and K contents as compared to the native litter. Compared to native environments, invaded ones had significantly decreased soil temperature and soil water content. Results suggest that *C. madagascariensis* enhances litter and N, P, and K availability in ways that have potential to impact soil ecosystem in the Tropical Cambisols from Caatinga ecoregion, Brazil.

Introduction

Invaded environments in tropical zones are mainly characterized by changes in plant community diversity, soil properties, litter decomposition, litter decay rate, and biochemical processes, as a strategy of invasive plant species spread, growth, development, and reproduction (Souza et al. 2016; Rodríguez-Caballero et al. 2020; Jo et al. 2020; Tesfaye et al. 2020). The biological invasion process is influenced by the continuous invader litter input, and its quality (e.g., nutrient-rich tissues) which promotes drastic changes into soil ecosystem (See the “island of fertility” hypothesis described by Souza et al. 2016). The biological invasion process is specifically linked with invasive species traits (e.g., light availability, biodiversity reduction, phenological patterns, and litter deposition). The effects of invasion by *Pinus* spp., and *Acacia* spp., and their mechanisms underlying invasion success have been well described around the world (Laurindo et al. 2021; Keet et al. 2021).

Cryptostegia madagascariensis Bojer ex Decne is an invasive plant species that occurs into the North-eastern Brazil (e.g., Caatinga ecoregion) promoting negative changes into the plant-soil feedback of tropical Cambisols (Souza et al. 2018). This invasive plant species has a strategy to improve their spread into new ranges. It is an invasive liana that grows up the native tree species. Thus, totally covering them and preventing light passage. Overtime it causes the death of the native plant species by excessive and continuous shading. As the invader kills the native plant species, it is common to find below the drip line high litter deposition (e.g., invasive litter plus native litter on soil surface. In advanced levels of *C. madagascariensis* invasion, the invader progressively increased its biomass production and litter deposition (Souza et al. 2016).

High litter deposition on soil surface is positively correlated with improved physical-chemical soil properties (Tefaye et al., 2020). In tropical soils, the seasonal variation is one of the main limiting factors that affects both plant biomass production, and litter deposition (Queiroz et al. 2019, Cunha et al. 2020).

On the other hand, litter decomposition rate is positively correlated with litter quality. Plant tissues with high lignin content, and low C:N ratio, usually present low decomposition rate (Wang et al. 2020). Some studies showed that the litter decomposition and nutrient release into invaded soil occurs faster when compared to the non-invaded soils (Wang et al. 2018, Chen et al. 2019). However, the biomass production, litter decomposition, and litter quality of tropical invaded soils are rare and poorly described. Also, it remains unclear as *C. madagascariensis* changes the soil ecosystem, litter deposition, and nutrient cycling. Thus, as far so we know this is the first report showing changes on litter deposition, litter quality, soil chemical properties, nutrient cycling, and soil plant-feedback of tropical Cambisols invaded by *C. madagascariensis*.

Studies considering the biological invasion process by *Cryptostegia madagascariensis* in tropical Cambisols are rare (Döbert et al. 2018; Lucena et al. 2019). In general, tropical Cambisols present high acid levels, high plant diversity (e.g., most of the plant species are endemic and some of them classified as endangered plant species), and low soil fertility (Souza et al. 2018, Joshi et al. 2019, Waddell et al. 2020). On the other hand, there are studies that shown the tropical ecosystems suffering any degree of biological invasion by exotic plant species (Wang et al. 2019). The seasonal variation (e.g., rainy vs. dry seasons) into these ecosystems are described increasing both habitat and niche changes, which can contribute to the biological invasion process. This phenomenon can be explained by the “seasonal priority effects” hypothesis as described by Hess et al. (2019). The early-active phenology of many invasive plant species may act as a positive trait that confers competitiveness, quickly germination, fast growth with the onset of the rainy season, and reach out a higher abundance than the native plant species (Souza et al. 2016; Ren et al. 2021). Thus, we hypothesized that the *C. madagascariensis* can promote change both habitat and niche provision by altering litter deposition and nutrient cycling when compared to the native plant species.

In this study, our aim was to evaluate the effects of the biological invasion promoted by *C. madagascariensis* in a native environment of tropical seasonal dry forest under: i) the litter deposition; ii) soil physical-chemical properties (e.g., soil temperature, soil water content, and soil organic matter); iii) litter nutrient content (e.g., N, P, K); and iv) litter decay rate in a tropical Cambisol. To accomplish this aim, we combined: a) soil samplings to characterize the soil ecosystem as described by Nascimento et al. (2021); b) the quantification of litter biomass to estimate litter inputs as described by Castro et al. (2019); and c) litter chemical composition to understand nutrient inputs and cycling into invaded and non-invaded environments as described by Jo et al. (2020). All these tasks were done during two seasons (rainy and dry) in both native and invaded environments.

Material And Methods

Experimental area

The phenological patterns of litter deposition were examined in two environments of the Brazilian seasonal dry forest, Pombal, Paraíba, Brazil. Both environments occurred into riparian areas (178 m.a.s.l.)

in a sandy loam Cambisol. For each environment, we established 4 transects of 30 m in length (Fig. 1). We selected into the native environment *Mimosa tenuiflora* (Wild) Poir as a model plant, and for the invaded environment *C. madagascariensis* was our model plant. The plant community in the invaded environment was dominated by *C. madagascariensis* (80% of dominance and fully covering the native plant species). In the native environment, *M. tenuiflora*, was chosen by presenting 67% of importance value. In each transect, we have placed a litter collector, and twenty litter bags. We collected four soils samples below the canopy of each model plant (native and invaded environment). The litter collectors were distributed below drip line of each the model plant, the litter bags were distributed around the collectors, and the soil samples were collected along the whole transect.

Litter deposition

Litter deposition was sampled during two seasons (e.g., rainy, and dry seasons) to evaluate if there were significative differences among the studied model plants on litter deposition. To evaluate the litter production, we used a litter collector (1 x 1 m) with a nylon mesh of 2 x 2 mm. The litter collector was distributed in the region below the drip line of each model plant. To minimize nutrient loss due to leaching after rain events, the litter was collected every 60 days, from May, 2017 to August, 2018. Litter samples were air-dried at 65°C for 48 hours and weighed to estimate litter dry biomass ($\text{kg ha}^{-1} \text{ year}^{-1}$) as described by Forstall-Sosa et al. (2020).

Litter quality and soil properties

To characterize litter quality, we analysed the litter N, P, and K content, and the soil organic matter content in both exotic and native litter tissues. All analysis were determined using four samples from each litter collector. The N content was determined by digestion using sulfuric acid. Next, the P content was determined by atomic absorption spectrophotometry. For the K content was determined by spectrophotometry of flame. Finally, to characterize the soil organic matter content, we collected four soil samples (0.0-0.1 m soil depth), in each period and studied environment. All analysis were done following the protocol described by Tedesco et al. (1995) and Teixeira et al. (2007).

Litter decomposition (litter decay rate)

To determine the litter decay rate (k), we used 20 litter bags (20 × 20 cm, with 2 mm mesh) in each studied environment following a 60-days schedule of litter sampling for 10 months (Thomas and Asakawa 1993). Each litter bag received 50 g of dry leaf litter tissue. To evaluate de mass loss, we sampled five litter bags every 60 days. The samples were oven-dried at 60°C to determine the remain litter dry biomass. The changes in litter biomass were used to determine the leaf litter decomposition rate (k) as described by Olson (1963) using the following equation: $x/x_0 = e^{-kt}$. Where, $x(g)$ is the remaining biomass after t years (e.g., 60 days), x_0 (g) is the initial litter biomass (e.g., 50 g). Also, we have determined the half decay time (hd), total decay time (td), and the remaining biomass. First, for the half decay time, we used a nonlinear regression model, $hd = \ln(1-0.5)/\ln(e)^*(1/-k)$, as described by Costa e Atapattu. Next, for the total decay time (td), we used the following equation: $td = \ln(1-0.95)/\ln(e)^*(1/-k)$.

Data analysis

Before analysis, all the variables were tested for normality (e.g., by Shapiro-Wilk test) and homoscedasticity (e.g., by the Bartlett test), and log transformations were applied to meet both required criteria. To find possible spatial autocorrelation, we used the Moran.I function (Gittleman and Kot 1990). We did not detect any relationship between the variables and the sampling points, indicating spatial independent samples. Litter deposition, litter quality, soil properties, and litter decay rate were analysed with a two-way ANOVA. The dissimilarities between the transect sections (e.g., by Bray-Curtis distance measure) were analysed using a principal component analysis (Zuur et al. 2007). It also enables us to reduce the number of the variables used to determine which variable have explained most of the variation in the transect section across invaded and non-invaded environments (Oksanen et al. 2013). All analyses were run using R 3.4.0 statistical software (R Core team 2018).

Results

Litter deposition

The two-way ANOVA results showed significant differences for litter deposition between the studied environments into the dry and rainy season ($F = 48.34$, $p < 0.001$). The highest value of litter biomass (kg ha^{-1}) was observed in the invaded environment during the dry period ($4.287.90 \pm 520.1 \text{ kg ha}^{-1}$), and it correspond to 431.38% more litter biomass deposited on soil surface into the invaded environment by *C. madagascariensis* when compared to the native one (Fig. 2).

Litter quality and soil properties

For both litter quality and soil properties, we found significant differences between studied environments into the dry and rainy season (Table 1). We found the highest values of litter N, P, and content in the invaded environment. Considering the rainy and dry seasons, we did not find significant differences for litter quality in the invaded environment. On the other hand, we found the highest values of soil temperature and soil water content into the native environment. For these both soil properties, we did not find significant differences among the rainy and dry season on soil temperature in the native environment, while for soil temperature, we found the highest values during the rainy season in the native environment. Finally, we found the highest value of soil organic matter in the invaded environment during the dry season (Table 1).

Table 1

Litter quality (N, P, and K contents, g kg^{-1}), and soil properties (Mean $\pm$ SD) in both invaded and native environments during the rainy and dry seasons in a Tropical Cambisol, Caatinga ecoregion, Paraiba, Brazil.

Studied variables	Invaded		Native	
	Rainy	Dry	Rainy	Dry
Litter N content (g kg^{-1})	20.05 (0.47) Aa	20.25 (0.11) Aa	19.75 (0.63) Ab	19.65 (0.21) Ab
Litter P content (g kg^{-1})	3.01 (0.03) Aa	2.9 (0.02) Aa	2.27 (0.04) Ab	2.30 (0.05) Ab
Litter K content (g kg^{-1})	7.60 (0.04) Aa	7.64 (0.14) Aa	6.26 (0.26) Ab	6.34 (0.10) Ab
Soil temperature ($^{\circ}\text{C}$)	26.2 (0.85) Ab	26.5 (0.42) Ab	31.8 (0.42) Aa	32.7 (0.91) Aa
Soil water content (g g^{-1})	12.44 (3.44) Ab	5.51 (1.73) Ba	17.66 (4.70) Aa	5.56 (4.70) Ba
Soil organic matter (g kg^{-1})	8.45 (1.73) Ba	9.83 (1.74) Aa	4.91 (1.74) Ab	4.78 (1.41) Ab

The standard deviation in parentheses. Within the invaded and native environments same small letters represent no significant differences, whereas within the rainy and dry season same capital letters represent no significant differences by Bonferroni's test ($p < 0.05$).

Litter decomposition

There were significant differences in litter decay rate, half decay time, and total decay time between the invaded and native environments ($p < 0.05$). For the litter decay rate, we found the highest value in the invaded environment, while for the half and total decay the highest values were found in the native environment (Table 2).

Table 2

Litter decay rate (k), half decay time (hd), and total decay time (td) in both invaded and native environments in a Tropical Cambisol, Caatinga ecoregion, Paraiba, Brazil.

Studied environments	k	hd (days)	td (days)
Invaded environment	1.10 (0.48) a	0.75 (0.39) b	3.45 (2.00) b
Native environment	0.94 (0.71) b	1.00 (0.64) a	4.37 (2.78) a

The standard deviation in parentheses. Within the invaded and native environments same small letters represent no significant differences by Bonferroni's test ($p < 0.05$).

Principal component analysis

The PCA analysis showed that litter N, P, and K contents, soil organic matter, soil temperature, and soil water content were the main factors contributing to the data variance (Fig. 2). Our results showed that the studied environments were dissimilar to each other. We also found 3 main aspects: i) a positive correlation between litter K content and soil organic matter into the invaded environment; ii) a positive correlation between soil temperature and soil water content into the native environment; iii) negative correlations between litter P content and soil temperature, and litter K content and soil water content. The two axes of the PCA analysis explained 89.17% of data variation.

Discussion

The biological invasion process by *C. madagascariensis* into the Tropical Cambisol impacts the litter deposition, litter quality, soil properties (e.g., soil temperature, soil water content, and soil organic matter), and litter decomposition. Our results indicate positive changes into litter deposition and litter quality, whereas there were negative changes into soil temperature, soil water content, and litter decomposition into the invade environment. This can be explained by the changes into the habitat and niche provision as we have hypothesized into the invaded environments. We found the highest values of litter deposition, litter N, P, and K contents in the invaded environments, which supports the “island of fertility” hypothesis as previously described by Souza et al. (2016). Invasive plant species can modify the new range, to facilitate its invasion, and future establishment (Anning et al. 2018, Eisenhaure et al. 2021, Kariyawasam et al. 2021). Recent studies have demonstrated that into invaded environments, there were high litter deposition by invasive plant species, which changes the natural nutrient cycling process (Wang et al. 2020, Ahmad et al. 2021). For this study, the litter deposition in the invaded environment were of 431.38% higher than in the native one. This high quantity of litter produced by *C. madagascariensis* in invaded environment is a positive trait that helps the invader to kills the soil seed bank by creating a physical barrier on soil surface (Souza et al. 2016, Pinto et al. 2020).

The “seasonal priority effects” hypothesis was also confirmed in our study. The invader negatively changed the soil temperature and soil water content into the invaded environment. We found into the invaded environment 6 °C less on soil surface when compared to the native one. This occurs because the invader creates a physical barrier (e.g., litter deposited on soil surface) which created a new habitat for a Tropical Cambisol. It also reduces the soil water content because the invader leaves have a hydrophobic trait that in turns increase the water runoff on soil surface. This high quantity of a hydrophobic litter deposited on the soil surface forms a physical barrier that prevents light passage to the soil surface. It in turns reduce litter decomposition and decomposers activity (Lucena et al. 2021). Similar results were found by Vieira et al. (2020) and Shiferaw et al. (2021) in invaded areas by *Brachiaria brizantha* and *Prosopis juliflora* in the Brazilian Cerrado ecoregion, and North-eastern Ethiopia, respectively.

The high litter quality (e.g., N, P, and K content) and soil organic matter content in the invaded environment are positively correlated with the high litter deposition promoted by the invasive plant species as described by Weand (2020). Higher contents of P in the litter of invasive species were also observed in studies carried out by Mallerman et al. (2018) and Anning et al. (2018) in tropical soils. In the

case of invasive plant species, we must consider different strategies that the invader uses to promote changes into soil chemical properties as previously described by Souza et al. (2016) in the “island of fertility” hypothesis. Also, we must consider that into invaded environment we can find changes on soil fertility (e.g., usually described as soil fertility increase) as described by Malleran et al. (2018). The invasive traits (e.g., life history, physiology, leaves morphology, behaviour, and nutritional needs) are very dissimilar from the native plant species. It is expected that the nutrient contents in the invasive litter could be different to the native litter (Weand et al. 2020). But, in our study we found evidence for high N, P, and K contents in the invasive litter. These alterations may account for the greater tolerance of the invader to soil conditions even when limited, as previously described by Souza et al. (2016). These authors described the effects of *C. madagascariensis* in areas with different stages of invasion. They found that the invader altered the soil properties as well as the microbial community, which generates a negative feedback for the native plant species.

Our multivariate analysis showed interesting results and highlighted the dissimilarities among the invaded and the native environments. The exotic plant species once spreading into a new range that is characterized by low fertility and resources availability creates some strategies, such as: i) enhancing soil fertility by high quality litter deposition (e.g., N, P, and K contents); and ii) Promoting soil organic matter content, thus modifying the rhizosphere (e.g., island of fertility hypotheses) (Patil et al. 2020, Shiferaw et al. 2021). In tropical ecosystems with long dry season (e.g., more than 4 months) the native plant species usually present high water use efficiency (e.g., lower water loss by evapotranspiration), and reduces its metabolism during the dry season by: i) reducing the aboveground biomass allocation (e.g., producing thinner leaves and lower growth rates); ii) high wood and vessel density; iii) little seasonal variation in litter deposition (Kupers 2019, de Oliveira et al. 2020). So, our results showed a clear dissimilarity among both ecosystems (invaded vs. native). In the native ecosystem the plant species are extremely adapted at climate conditions (e.g., higher water use efficiency and little seasonal variation in litter deposition), thus creating a positive plant-soil feedback for the native plant species (Singh et al. 2018). In the invaded environment the exotic plant species create strategies (e.g., higher litter deposition, higher litter nutrients contents and change soil chemical properties) for their spread success (Gentili et al. 2019). Thus, the exotic species creates a negative plant-soil feedback in the ecosystem by altering the entire soil ecosystem. It may influence: i) the nutrient cycling due to litter decomposition as described by Souza et al. (2018), and Weand (2020); ii) the soil food web due to the physical barrier, which was created by the high litter deposition on soil surface. These both pathways can negatively affect the soil seed bank and the natural regeneration of native plant species in the invaded environment (Stanek et al. 2020).

This study found that invaded environment alters the litter decomposition in a tropical Cambisol. The invaded environment showed the highest value of decomposition coefficient and lowest total and half decay time. The hypothesis of Souza et al. (2016) suggested that *C. madagascariensis* invasion alters soil properties (e.g., soil pH, and total organic carbon), which can be caused by the accumulation of litter from the invasive plant species. Long-term impact of litter can modify nutrient cycling differently from native species (Veeraragavan et al. 2018). Besides that, the soil moisture is lowest in invaded environment (Afreen and Singh 2019), and this can be explained by litter hydrophobic trait (Zhang et al.

2019). The litter decomposition plays an important role in soil fertility maintenance, and the litter decomposition rate is closely related to changes in nutrient dynamic (Sun et al. 2020). Therefore, the slow litter decomposition changes the nutrient cycling process into the invaded environment. The litter of invasive plant species showed high nutrient content compared to the native environment, however, the higher concentration of recalcitrant compounds, and the high latex content likely contributed to their decreased decomposition (e.g., by reducing the activity of litter transformers and decomposers) (Pereira and Ferreira 2021). These processes disrupt the soil processes related to soil food web, preventing the natural regeneration of plants, soil quality, and seed dispersal (Laurindo et al. 2021, Nascimento et al. 2021).

Conclusion

Invaded environments by *Cryptostegia madagascariensis* promotes the increase of litter deposition, and N, P, and K content by litter input which provide changes into the soil habitat and niche provision into a Tropical Cambisol. The invader changed soil properties (e.g., soil temperature, soil water content, and soil organic matter) which changes the entire soil functioning, which in turns create a negative plant-soil feedback in the invaded Tropical Cambisols. Invaded environment is accompanied by high litter decay rate, and low half decay time, and total decay time in the litter material that can indicate a disturbance level into the nutrient cycling process. Future studies could be carried out to assess which biotic factors (e.g., soil organisms) are more important to recover invaded environments and could improve soil seed bank and native plant species growth into invaded environments. The results of this study contribute to a deeper view of litter deposition, litter quality, and nutrient influencing invaded environments that, in turn, may improve the interest in recover the biodiversity of the Caatinga ecoregion.

Declarations

Author's contributions

We declare that all the authors made substantial contributions to the conception, design, acquisition, analysis, and interpretation of the data. All the authors participate in drafting the article, revising it critically for important intellectual content, and finally, the authors gave final approval of the version to be submitted to Biological Invasion.

Compliance with Ethical Standards

Conflict of Interest: The authors declare that they have no conflict of interest.

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Figures

Figure 1

Location and experimental design of each studied transect into the experimental area, Pombal, Paraíba, Brazil. Native and invasive plant communities were examined within each environment. Inset shows the studied transects.

Figure 2

Litter deposition (kg ha⁻¹, Mean $\pm$ SD) in both invaded and native (non-invaded) environments during the rainy and dry season in a Tropical Cambisol, Caatinga ecoregion, Paraiba, North-eastern Brazil. Within the invaded and native environments same capital letters represent no significant differences, whereas within the rainy and dry season same small letters represent no significant differences by Bonferroni's test ($p < 0.05$).

Figure 3

PCA score plot of litter quality, and soil properties in the invaded and native environments during rainy and dry season. Triangles and points represent the invaded and native environment, respectively.