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Original Paper

Drought responses and phenotypic plasticity of *Maprounea guianensis* populations in humid and dry tropical forests

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Abstract

The wide distribution of *Maprounea guianensis* populations in contrasting environments (dry and humid forests) in the Chapada Diamantina, northeastern Brazil, can indicate the phenotypic plasticity of this species in relation to seasonal rainfall, drought regimes, and soil characteristics at different sites. Functional traits were measured in five individuals in each vegetation types. Water potential, succulence, thickness and density leaf, were evaluated during the dry and rainy periods; wood density and the saturated water content of the wood were evaluated in rainy period. Rainfall was monitored monthly for two years. The functional traits and the phenotypic plasticity indices (PPI) were submitted to analysis of variance. Our results demonstrated seasonal and spatial variations in plant functional traits. We found a low capacity for storing water in leaves and woody tissues, associated with soil properties and the seasonal rainfall/drought regimes, conditioning water potential variations that were greatest during the rainy season. Local environmental parameters influenced variations in the functional traits of *M. guianensis* populations, reflecting phenotypic plasticity. We highlight the connections between drought regimes and plant responses, demonstrating the importance of functional traits associated with water availability (especially water potential). Our study evidences the factors associated with the wide distribution of *M. guianensis*.

Key words: functional traits, soil properties, water availability.

Resumo

A ampla distribuição das populações de *Maprounea guianensis* em ambientes contrastantes (florestas secas e úmidas) na Chapada Diamantina, Brasil, pode indicar a plasticidade fenotípica dessa espécie associada aos regimes sazonais de chuva/seca e características do solo. Características funcionais foram medidas em cinco indivíduos/sítio. Potencial hídrico, suculência, espessura e densidade foliar foram avaliados nos períodos seco e chuvoso; densidade da madeira e teor de água saturada da madeira foram avaliados no período chuvoso. As chuvas foram monitoradas mensalmente por dois anos. Características funcionais e os índices fenotípicos de plasticidade (IPP) foram submetidos à análise de variância. Nossos resultados demonstraram variações sazonais e espaciais nas características funcionais das plantas. Encontramos baixa capacidade de armazenamento de água em folhas e tecidos de madeira, associada às propriedades do solo e aos regimes sazonais de chuva/seca, condicionando as variações de potencial hídrico que foram maiores durante a estação chuvosa. Parâmetros ambientais influenciaram variações nas características funcionais das populações de *M. guianensis*, refletindo a plasticidade fenotípica. Destacamos as conexões entre regimes de seca e respostas das plantas, demonstrando a importância das características funcionais associadas à disponibilidade de água (principalmente potencial hídrico). Nosso estudo evidencia causas associadas a ampla distribuição de *M. guianensis*.

Palavras-chave: características funcionais, propriedades do solo, disponibilidade de água.

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Introduction

Species occupying heterogeneous environments are subject to selective pressures that very either temporally or spatially (Simons 2011; Botero *et al*. 2015), and must develop generalist phenotypes or show phenotypic plasticity to adapt to disparate environmental conditions (Ganie *et al*. 2014; Sultan 1987). As such, phenotypic plasticity can be considered adaptive if it promotes a direct and positive impact on the plant's fitness (Nicrota *et al*. 2010). Such variations can allow a species to grow and reproduce in contrasting sites, as there are improvements in the plants' performances that can increase and facilitate their distributions in heterogeneous environments (Nicotra *et al*. 2010). As such, quantifying phenotypic plasticity can provide essential information about the mechanisms affecting the current and future distributions of plant species (Choi *et al.* 2018). This is especially the case for plant functional aspects, such as those related to water stress resistance (hydraulic properties of the stem, leaf characteristics, and water use patterns) (Rosado & Mattos 2007; Toledo *et al*. 2012; Worbes *et al*. 2013).

Studies of the physiological, morphological or phenological characteristics that indirectly affect plant fitness, *i.e.* functional traits (Violle *et al*. 2007), are fundamental to understanding plant phenotypic plasticity. Although it is often more practical to describe plant strategies by describing their morphological traits, knowledge of their integration with physiological aspects is fundamental to capturing the functioning of individuals and species (Rosado & Mattos 2017). Among functional traits, wood density, leaf succulence, thickness and density, and leaf water potential have been examined in studies dealing with plant persistence under water availability gradients (Garnier *et al*. 2001; Wright *et al*. 2002; Roche *et al*. 2004; Ibanez *et al*. 2017; Neves *et al*. 2017). Many of them reported that plants are able to maintain their water balances through changes in specific root and leaf traits (Dolman 1993; Rosado 2006).

Species growing in humid sites, despite showing small variations in their water statuses, are in more favorable conditions to maintain their leaf water potentials (Miranda *et al*. 2011; Moraes *et al*. 2017) than plants growing in drier environments and therefore subject to greater water availability fluctuations (Neves *et al*. 2017). Each species will demonstrate specific tolerance limits to environmental variables, which are linked with distinct morphofunctional variations that allow the efficient use of available resources (Sing & Kushwaha 2005; Kooyers 2015; Souza *et al*. 2015). In many tropical environments characterized by marked rainfall seasonality, plants exhibit morphofunctional traits designed to deal with periods of low water availability, such as: deciduousness or discontinuous canopy cover; early closure of their stomata; deep roots (Rojas-Jimenez *et al*. 2007; Markesteijn & Poorter 2009; Miranda *et al*. 2011; Neves *et al*. 2017) and leaf and trunk water storage (Rosado & Mattos 2007; Lima *et al*. 2012). Another important strategy to deal with water deficits in plants that do not store water in their trunks, is to produce dense woods that provide protection against cavitation (Marks & Lechowicz 2006; McDowell *et al*. 2008; Chave *et al*. 2009; Lima *et al*. 2012).

Within the context of water use in seasonal systems, individuals and species may demonstrate specific phenological and physiological strategies, such as an evergreen habit and the ability to store water in their less dense wood (which can be later used to supply water to the leaf) (Meinzer 2003; Toledo *et al*. 2012; Moraes *et al*. 2017). Others may assume a deciduous or semi-deciduous canopy linked with high wood densities and leaf production associated with rainfall (Goulart *et al.* 2005; Toledo *et al*. 2012; Worbes *et al.* 2013). In addition to those strategies, some leaf aspects may also reflect the ecophysiological performances of plants in relation to maintaining positive water balances are, ensuring resistance when under water stress (Rosado & Mattos 2007; Ogburn & Edwards 2012). In species presenting high values of leaf thickness and succulence, associated with higher water storage capacities, those leaves will serve as alternative sources of water (Lamont & Lamont 2000; Rosado & Mattos 2007). High leaf densities are linked to high fiber and sclereid contents that favor water retention through capillarity, and those leaves demonstrate greater cellular resistance to wilting (Oertli *et al*. 1990; Salleo *et al*. 1997). In environments with higher for soil water deficits, the plants tend to have denser, thicker, and more succulent leaves (especially when exposed to high light intensities) (Witkowski & Lamont 1991; Niinemets 2001; Rosado & Mattos 2007). As such, plants growing in dry forests generally show greater variations in terms of those attributes, having leaves that are more succulent, denser, and more coriaceous, to deal with periods of low water availability (Witkowski & Lamont 1991; Lohbeck *et al*. 2015). In contrast, species growing in environments with greater water availability and shorter drought periods generally show fewer temporal variation in the attributes of the leaves (Niinemets 2001).

Plant water statuses generally reflect groundwater availability, with water deficits becoming established when the water supply is insufficient to meet evaporative demands (Welcker *et al*. 2011). Thus, the physio-chemical characteristics of soils are highly relevant in understanding ecological processes (Cardoso *et al*. 2012; Neves *et al*. 2016), especially soil texture (which influences water infiltration and the capacity to retain nutrients needed for plant growth). Sandy soils contain less organic matter and fewer nutrients than clayey soils - with the latter retaining more water and more nutrients, although they have slow drainage and poor gas circulation (Perkins *et al.* 2013).

The Chapada Diamantina mountains hold vegetation mosaics of *campo rupestre*, savanna, humid forests, and dry seasonal forest that are defined by elevation, topography, soils, and contrasting microclimatic conditions (especially in terms of water availability) (Funch *et al*. 2009). *Maprounea guianensis* Aubl. (Euphorbiaceae) is widely distributed in Brazil and represents possibly the only tree species that occurs on both clayey and sandy soils in dry and humid forests in the Chapada Diamantina mountains (Miranda *et al*. 2011; Couto-Santos *et al*. 2015; Neves *et al*. 2017). In previous studies, *M. guianensis* was shown to have a deciduous habit in seasonally dry tropical forests (Neves *et al*. 2017) and a brevideciduous habit in humid forests (Miranda *et al*. 2011). Santos *et al*. (2020) recently showed that, although macroclimatic conditions were similar throughout the range of its occurrence, phenological behavior and leaf longevity differed according to micro-site differences, which suggests a high degree of functional trait plasticity.

The present study therefore investigated the phenotypic plasticity of *M. guianensis* in terms of its functional traits (leaf succulence, thickness and density, water potential, wood density, and wood saturated water content) and their relationships with rainfall regimes. We hypothesized that the functional traits associated with water availability are the primary drivers of its adaptive strategy. We expected that *M. guianensis* individuals growing in seasonally dry tropical forests (SDTF) would show greater phenotypic plasticity (with greater variation in water potential and morphological characteristics) that would enhance their ability to survive under the most severe drought periods in this environment, including: denser woods that are more resistant to cavitation, and leaves with high succulence, density, and thickness. Individuals growing in humid forest sites, on the other hand, would be expected to show less phenotypic plasticity, with less variations in their functional traits: less dense woods with greater water storage capacities that would facilitate more positive values of water potential throughout the year , and leaves with less succulence, density, and thickness.

Materials and Methods

Study sites and species

The present study was conducted in a humidity gradient extending from rain forest remnants (cloud, gallery, and tableland forests) to seasonally dry tropical forest (SDTF) vegetation (12º27’06”–12º33’39”S and 41º23’14”–41º35’52”W), from 500–1,000 m a.s.l., on the eastern border of the Chapada Diamantina mountains (Fig. 1a-f), where it was possible to encounter individuals of *Maprounea guianensis* Aubl. (Euphorbiaceae), a tree 5–15 m tall (Fig. 1g), widely distributed in Brazil. *M. guianesis* is found in different vegetation types in the Chapada Diamantina mountains, where it is locally known as “folha miuda” (little-leaf) (Funch *et al*. 2005; Couto-Santos *et al*. 2015; Neves *et al*. 2016).

Rain forest sites have a continuous evergreen canopy. The cloud forest site (12°27’49”S, 41°28’34”W, at 940–1,000 m a.s.l., Fig. 1a-b), on the slopes of Serra da Bacia, experiences consistent mistiness throughout the year, even during dry months; the gallery forest site (12º33’38.6”S, 41º24’40”W, at 500 m a.s.l., Fig. 1c) is situated along the Lençóis River and experiences sporadic and rapid flooding pulses during the rainy season (Funch *et al*. 2002); the tableland forest (12º28’31”S, 41º23’14”W, at 500–600 m a.s.l., Fig. 1d) occurs on clayey yellow-red soils (Couto *et al*. 2011); the SDTF site (12º27’6.46”S, 41º35’51.81”W, at 657 m a.s.l., Fig. 1e-f) has a discontinuous deciduous canopy, with *M. guianensis* individuals reaching 1–12 m in height (Neves *et al*. 2016).

The regional climate in the study area is type Aw by the Köppen climate classification system (Alvares *et al*. 2013), with maximum rainfall in the austral summer (between November and April) and

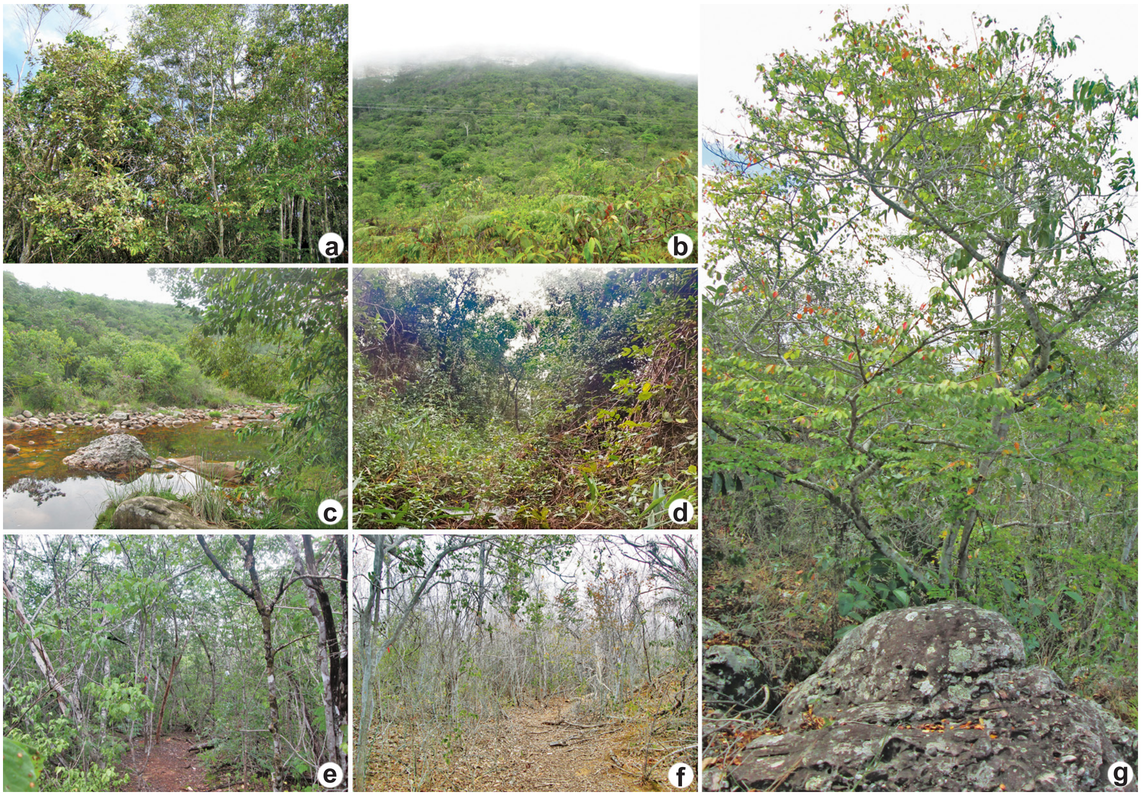

Figure 1 – a-g. Photographs of the study areas and focal species – a. cloud forest; b. cloud forest with mist; c. gallery forest; d. tableland forest; e. Seasonally dry tropical forest during the rainy period; f. Seasonally dry tropical forest during the dry period; g. *Maprounea guianensis*.

dry winters (between June and October). Historical climatic data were obtained from the National Institute of Meteorology (INMET), based on the Lençóis Meteorological Station (Fig. 2).

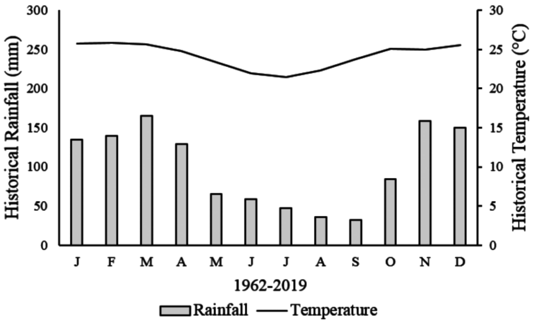

Figure 2 – Historical climate data of the study sites in the municipalities of Lençóis and Palmeiras, in the Chapada Diamantina mountains, Bahia state, Brazil: rainfall and temperature (source: Instituto Nacional de Meteorologia).

Environment variables

Environmental data used in the analysis of morphofunctional traits were collected near the study populations. Rainfall data were obtained using pluviometers installed at each site. For the gallery forest site, rainfall data were obtained from the National Institute of Meteorology (INMET), based on the Lençóis Meteorological Station, due to its proximity to the station (1.41 km). The physical properties of the soils were determined at each site by collecting soil samples at depths between 0 and 20 cm; each final sample was formed by pooling three 330-g subsamples collected every 50 m in each site; the analyses of the granulometric compositions of the soils were performed by the Soil, Water and Plant Analysis Laboratory, Embrapa Semiarid - PE.

Functional traits

At each site, five adult individuals (approximately 10 meters tall and distant 4 meters from each other) were marked for data collection.

Two measurements were taken in the rainy season (March/2018 and 2019) and two in the dry season (September/2017 and 2018), always using the same individuals during each evaluation. All functional traits data were collected on the same day at all sites. For the measurement of leaf traits, 10 fully expanded leaves were collected from each marked individual, at each site in each season (with a leaf longevity of 7.8 to 11.8 months). Using a cork borer, a 0.23 cm² disk was removed from a leaf of each plant between the center vein and the leaf edge to determine leaf succulence (SUC), leaf thickness (LTH), and leaf density (LDE). The disks were soaked in distilled water for at least 24 h to determine their thicknesses (in mm, using a digital caliper, KINGTOOLS: 0.01mm) and their saturated masses were measured (using a MARTE - AY220 precision electronic balance: 0.0001g); the disks were then placed in a drying oven at 55 ºC for 72 h to obtain their dry masses. Those values were used to calculate SUC (the difference between the saturated and dry masses divided by the disk area, in $g.cm^{-2}$, and the leaf mass per unit area (LMA - calculated by dividing the dry mass by the disk area, in $g.cm^{-2}$). LDE ($mg.mm^{-3}$) values were calculated using the formula: LDE = LMA/LTH (Witkowski & Lamont 1991). Water potential measures were made (Ψ) on the same individuals and on the same dates as the collection of the leaf physiological data (using a Scholander pressure chamber [PMS Instrument Co - Model 1000 - USA]). Three branches (from the middle third of the crown) were collected (each approximately 20 cm long) from each individual at each site. The branches were immediately placed in plastic sacks after cutting and stored in a cooler to minimize water losses. Two Ψ_W measurements were taken of each individual tree during each day of monitoring: predawn (Ψ_{PD}) (between 04:30 h and 05:30 h), to determine the maximum value at the start of the day; a second measurement was made after midday (Ψ_{MD}) (between 12:30 and 13:30 hour), to determine the lowest daily potential. The amplitudes of the daily variations in water potential ($\Delta\Psi$) were calculated using the formula $\Delta\Psi = \Psi_{PD} - \Psi_{MD}$. Wood density (WD) sampling was performed in March/2018. As wood density is a conservative trait and relatively little plastic, it was expected that there would be very little variation between periods of drought and rainfall, being considered only a measure for this study. Therefore, four stem samples (approximately 5 cm long and 3 cm in diameter) were removed from five individuals in each site (bark + heartwood + alburnum) and treated with an aqueous solution of copper sulfate (2%) and calcium oxide (2%) to prevent the action of pathological microorganisms. The samples were then immersed in distilled water for 72 h and subsequently weighed to determine their saturated masses (Msat) (using a MARTE - AY220 precision electronic balance: 0.0001g); to determine their volumes (V), each stem section was completely submerged in a beaker of water placed on precision electronic balance. The weight of the dislocated water corresponded to the sample volume. The samples were then dried under forced ventilation (55 °C for five days) to a constant dry mass (Dm). The resulting values were used to calculate wood density (WD = Dm/V) (Ilic *et al*. 2000) and the saturated water content in the wood (SWC) = (Msat - Dm) / Dm (Trugilho *et al*. 1990). The density classification followed the parameters adopted by Borchert (1994).

Statistical analyses

We used the T-test for independent samples to compare the rainfall volumes in the dry (June to October) and rainy (November to April) seasons at each site ($p < 0.05$). 1-factor analysis of variance (ANOVA) was used to compare soil physical properties, wood density, and wood saturated water content, of the four sites, followed by the post-hoc Tukey test ($p < 0.05$), using the SigmaPlot 12.0 software.

Two-factor analysis of variance (ANOVA) was used to determine the temporal and spatial effects on traits of *M. guianensis* in the different habitats, with each evaluation month being considered a treatment. The ANOVA test was followed by a post-hoc Tukey test, using the SigmaPlot 12.0 software, at a 5% level of probability (Zar 2010). Some data were treated using Box-cox in order to normalize them. To better visualize the dispersion and asymmetry of the data, we present the results of leaf traits in the form of Box Plots, using R 4.0.1 software.

To evaluate the plasticity of the functional traits of the populations, we calculated the phenotypic plasticity indices (PPI) of the variables SUC, LTH, LDE, Ψ_{PD}, Ψ_{MD}, wood density, and saturated water content of the wood, following Valladares *et al*. (2000), where: PPI = (maximum-minimum) / maximum. A phenotypic plasticity index (PPI - ranging from zero to one) was calculated for each variable considering all seasons together - values close to 0 indicate low plasticity, and values close to 1, higher plasticity; plasticity indexes above 0.50 are considered high (Valladares *et al*. 2000). The PPIs were calculated in both the dry and rainy seasons in all populations to determine which population demonstrated greater plasticity. Differences in the PPI indices between populations for each trait were tested using 1-factor analysis of variance (ANOVA).

Results

Environment variables

The t-test showed variations between rainfall volumes in the dry and humid forests during the second rainy season period (dry forest × cloud forest) and for all the dry seasons (dry forest × humid forests) ($p < 0.05$) (Fig. 3; Tab. 1). The physical analyses of the soils showed that cloud and gallery forests have sandy loam soils, with tableland forest showing clayey soil, and SDTF having a sandy loam soil (Tab. 2).

Functional traits

Leaf traits varied between seasons (Leaf thickness: F = 36.87; Succulence: F = 6.34; Leaf density: F = 17.17, with $p < 0.05$ and df = 3), between populations (Leaf thickness: F = 18.95; Succulence: F = 31.55; Leaf density: F = 9.73, with $p < 0.05$ and df = 3), and between seasons and populations (Leaf thickness: F = 17.00, Succulence: F = 14.71; Leaf density: F = 7.58, with $p < 0.05$ and df = 9). (Fig. 4; Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.15202095.v1>). In the SDTF, *M. guianensis* showed greater temporal variations, with lower values of SUC and LTH in the dry season; in the cloud and tableland forests it showed less temporal variations of SUC, LTH, and LDE; in the gallery forest *M. guianensis* showed a more pronounced variation in LTH. Considering spatial variations, the LTH data indicated a greater difference between populations than the SUC or LDE data; the SUC and LDE values were similar in all of the humid forest populations (Fig. 4).

Water potentials varied between seasons (Ψ_{PD} : F = 24.30.87; Ψ_{MD} F = 156.24; Δ_{Ψ} : F = 1.95, with $p < 0.05$ and df = 3), between populations (Ψ_{PD}: F = 15.60; Ψ_{MD} F = 15.63; Δ_{Ψ} : F = 13.43, with $p < 0.05$ e df = 3), and between seasons and populations (Ψ_{PD} : F = 9.20; Ψ_{MD} F = 42.95; Δ_{Ψ} : F = 16.60, with $p < 0.05$ and df = 9) (Fig. 5; Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.15202095.v1>). The water potential data showed the highest Ψ_{PD} and Ψ_{MD} values in the rainy season. In terms of spatial variations, the $\Delta\Psi$ indicated significant differences between the dry and humid forest populations, with smaller values in humid forests during the rainy season. The lowest $\Delta\Psi$ (0.00 MPa) values in the SDTF population were recorded during the dry season, a period in which the Ψ_{PD} and Ψ_{MD} values were similar (Fig. 5).

Wood density was high in all populations, although there were differences between them, from 0.74 g/cm^{-3} in the cloud forest to 0.99 g/cm^{-3} in the SDTF. The Saturated water contents were low, and differed between populations, with the lowest percentage (42.57%) observed in SDTF and the highest (69, 24%) in the cloud forest (Tab. 3).

In general, *M. guianensis* showed greater phenotypic plasticity in the SDTF, and lower plasticity in humid forests (Tab. 4). Even with the observed differences in the functional responses of the different populations, there was no variation in the mean PPI ($p > 0.05$), suggesting similar degrees of variation of functional traits (Tab. 4). Water

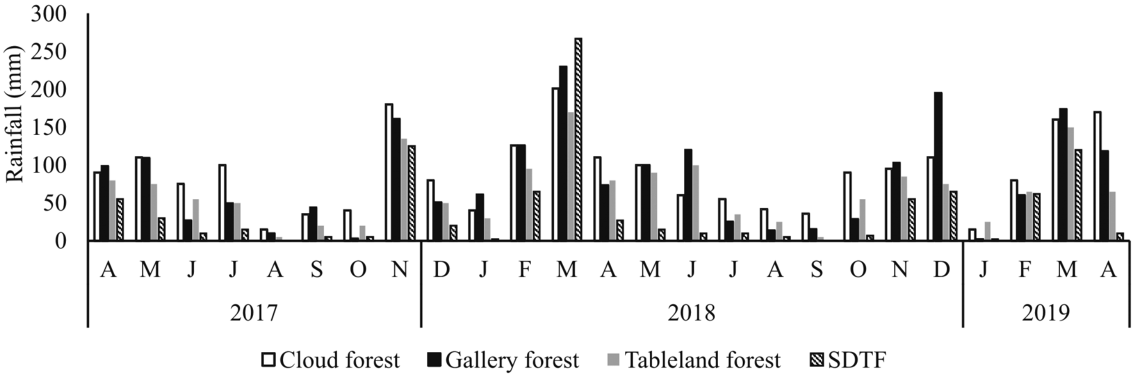

Figure 3 – Rainfall data for the study sites in the municipalities of Lençóis and Palmeiras, in the Chapada Diamantina mountains, Bahia state, Brazil: Cloud forest; Gallery forest; Tableland forest; Seasonally dry tropical forest (SDTF).

Table 1 – Independent t-test comparing rainfall volumes during the dry (Dry 1 = June/2017 to October/2017; Dry 2 = June/2018 to October/2018), and rainy (Rain 1 = November/2017 to April/2018; Rain 2 = November/2018 to April/2019) seasons in the gallery and tableland forests in the municipality of Lençóis and the cloud and SDTF forests in the municipality of Palmeiras, in the Chapada Diamantina mountains, Bahia state, Brazil.

		Rain 1			**Rain 2**		
		Gallery f.	Tableland f.	SDTF	Gallery f.	Tableland f.	SDTF
Cloud f.	p(t)	0.440 (0.154)	0.194 (0.904)	0.218 (0.810)	0.461 (0.099)	0.179 (0.962)	0.049 (1.815)
Gallery f.	p(t)		0.260 (0.667)	0.262 (0.660)		0.190 (0.928)	0.064 (1.657)
Tableland f.	p(t)			0.424 (0.197)			0.161 (1.040)
		Dry 1			**Dry 2**		
		Gallery f.	Tableland f.	SDTF	Gallery f.	Tableland f.	SDTF
Cloud f.	p(t)	0.687 (1.489)	0.119 (1.278)	0.020 (2.982)	0.245 (0.725)	0.260 (0.674)	0.003 (5.239)
Gallery f.	p(t)		0.401 (0.258)	0.054 (2.064)		0.448 (0.134)	0.083 (1.694)
Tableland f.	p(t)			0.041 (2.312)			0.041 (2.312)

$p < 0.05$ indicates significant difference

potential values (Ψ_{PD}, Ψ_{MD}, and $\Delta\Psi$) showed high PPI, highlighting the population of SDTF site, with the highest $\Delta\Psi$ (PPI) (Tab. 4).

Discussion

Maprounea guianensis exhibited different ecological strategies in dry and humid forests related to water availability traits. The phenotypic plasticity of *M. guianensis* was conditioned by variations of the physical soil properties and rainfall regimes (with seasonal droughts). On one hand, populations in humid forest sites demonstrated small water potential variations due to the availability of water in the soil associated with its physical properties. The wider variations in soil water availability observed in the dry forest led to greater fluctuations in plant water potentials in response to physical soil properties and rainfall regimes (with seasonal droughts) at each site, demonstrating greater phenotypic plasticity.

There were wide variations in rainfall distributions at the study sites, especially during the dry period, which was reflected in plant Ψ_{AM} and Ψ_{MD} values. According to Medrano *et al*. (2007), variations in water availability lead to the appearance of mechanisms that allow plants to accommodate situations of greater or lesser water stress. Studies carried out with other tree species from dry tropical forests have shown that in order to maintain or restore their water statuses,

Table 2 – Mean (± SE) for physical parameters of each soil type in the gallery and tableland forest sites in the municipality of Lençóis, and in the cloud and SDTF forests in the municipality of Palmeiras, in the Chapada Diamantina mountains, Bahia state, Brazil.

	Cloud forest	**Gallery forest**	**Tableland forest**	**SDTF**
Silt content (g/kg)	152.00 ± 14.18a	139.33 ± 38.43a	209.33a ± 17.85a	118.00 ± 11.59a
Sand content (g/kg)	749.67 ± 23.95a	783.00 ± 67.35a	333.33b ± 4.70b	673.33 ± 17.48a
Clay content (g/kg)	98.33 ± 38.12bc	77.660 ± 29.63c	457.33a ± 16.75a	208.66 ± 6.67b

Means followed by same letter indicate no statistically significant differences ($p < 0.05$).

Granulometric composition: dispersion with NaOH Granulometric composition.

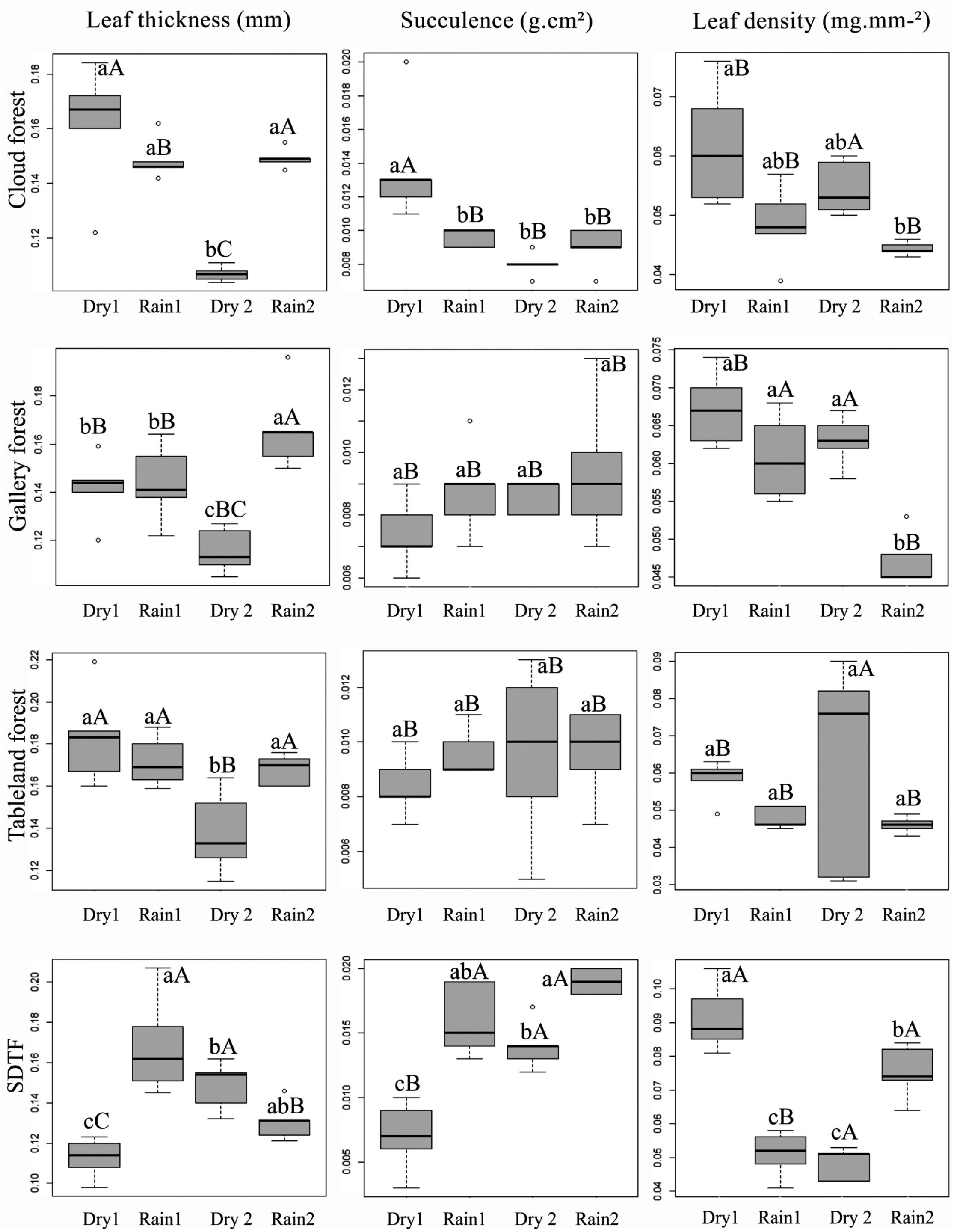

Figure 4 – Box plot data for leaf thickness (mm), succulence (g.cm²), and leaf density (mg.mm^{-2}) of *Maprounea guianensis* between seasons (dry and rain) and between sites (cloud forest, gallery forest, tableland forest, and seasonally dry tropical forest) in the Chapada Diamantina mountains, Bahia state, Brazil. Horizontal lines represent arithmetic means (middle line) ± standard deviation (upper and lower lines); outer horizontal lines represent minimum and maximum values; o = outliers. Lowercase letters compare the means of the sites during different seasons (dry and rainy). Uppercase letters compare the means of the sites during the same season. Means followed by the same letter do not differ ($p < 0.05$).

those plants have stem, leaf, or root tissues with specific traits that facilitate water storage (Rivera *et al.* 2002; Rojas-Jimenez *et al*. 2007; Lima *et al* 2012; Neves *et al.* 2017; Costa 2019). Wood density and leaf characteristics can be determinant to the ability of a given species to store sufficient quantities of water to allow the occupation of both arid and humid environments (Meinzer 2003; Lima *et al*. 2012). *M. guianensis* did not demonstrate wood morphological adaptations that could justify their distribution throughout the environmental gradient examined. According to the dichotomous classification of wood density, using 0.5 g cm^{-3} as a high or low density threshold (Borchert 1994), *M. guianensis* showed high wood density in all sites, with low water storage capacities. Wood density, however, is a numerical variable, and significant differences were seen between the populations of *M. guianensis* measured in this study.

Maprounea guianensis was, nonetheless, able to maintain a positive water balance in the humid forest sites. Although seasonal, droughts in humid sites are moderate (low intensity and short duration), which favors the maintenance of a positive plant water balance. Even in humid forests it is possible to observe dynamic patterns of water use, which are coupled with high rates of transpiration (Rosado *et al*. 2012), which may explain small fluctuations in water potential, although it remained positive in humid forests. The high values of water potential observed here show the high capacity for water regulation among individuals in humid sites, suggesting no water restrictions. The clayey soils in the tableland forest, favor water retention, allowing *M. guianensis* individuals growing there to maintain positive water balances. There is a tendency in cloud and gallery forest for low availabilities of resources, mainly because of their sandy soils with low water retention capacities (Brady & Weil 2013; Perkins *et al*. 2013). Even with sandy soil, however, water availability in such humid forests tends to be higher than in SDTF, mainly because rainfalls are more evenly dispersed throughout the year, a characteristic reflected in individual traits such as wood density and leaf attributes. Plants with dense wood are strongly influenced by soil water availability, although they show rapid rehydration during when water is first available in the soil, even if they do not actually store water (Borchert 1994). As a result, the rainforest populations did not need to invest in succulent or high-density leaves to store water in their tissues, a characteristic that was more pronounced in the SDTF population.

Alternative sources of water can also favor species growing in cloud and gallery forests and help guarantee positive water potentials even during periods of low rainfall and high water demands. Direct contact of plant leaves and stems with the mist available in cloud forests allows condensed water to drain to the soil and maintain ground humidity throughout the year (Cavelier *et al*. 1996; Holder 2006; Bruijnzeel *et al*. 2011). This process occurs as a result of the advection of masses of hot and humid air over cold surfaces (Schemenauer & Cereceda 1992) and the adiabatic cooling of the air that results in condensation at certain elevations (Stadtmüller 1987; Holder 2006). It can occur in any environment where fog persists long enough, with a certain frequency, regularity, or periodicity, and in combination with the winds, so that the drops of the cloud merge on the surfaces

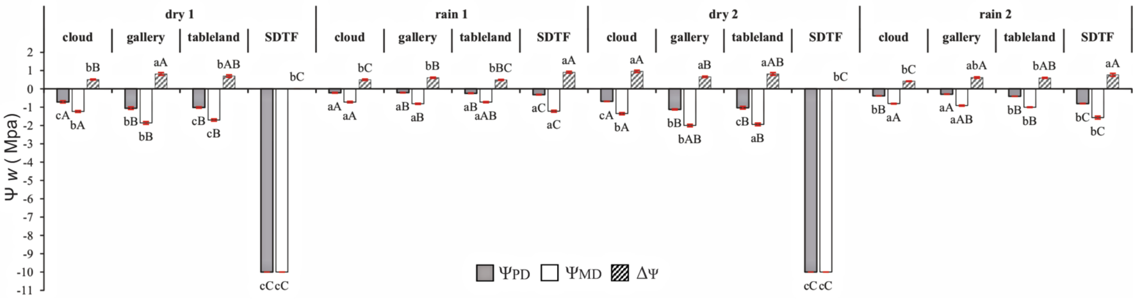

Figure 5 – Mean ± standard error for predawn (Ψ_{PD}) and midday (Ψ_{MD}) water potential values and water potential amplitudes (Δ_{Ψ}) for *Maprounea guianensis* in the gallery and tableland forest sites in the municipality of Lençóis and the cloud forest and SDTF in the municipality of Palmeiras, in the Chapada Diamantina mountains, Bahia state, Brazil. Lowercase letters compare the means of the sites during different seasons (dry and rainy). Uppercase letters compare the means of those sites during the same season. Means followed by the same letter do not differ ($p < 0.05$).

Table 3 – Mean (± SE) values of wood densities and saturated water content of the wood of *Maprounea guianensis* growing at the gallery and tableland forest sites in the municipality of Lençóis, and in the cloud and SDTF forests in the municipality of Palmeiras, in the Chapada Diamantina mountains, Bahia state, Brazil.

Sites	**Wood density (g.cm^{-3})**	**Saturated water content (%)**
Cloud forest	0.736 ± 0.024 d	69.244 ± 2.977 a
Gallery forest	0.831 ± 0.026 c	59.793 ± 3.097 b
Tableland forest	0.933 ± 0.031 b	59.331 ± 2.043 c
SDTF	0.994 ± 0.020 a	42.573 ± 0.653 d

Means followed by same letter indicate no significant differences ($p < 0.05$).

of the vegetation (Stadtmüller 1987; Holder 2006). Additionally, some authors claim that the crown foliage can intercept a substantial proportion of the water present in a fog through leaf water uptake processes (Eller *et al.* 2013, 2016; Oliveira *et al.* 2014). The proximity of plants to watercourse in gallery forests, and occasional flooding, can provide the humidity necessary for maintaining plant water balances. Other possible alternatives for obtaining water in humid sites include the development of root systems that can reach subsoil water stores (Xu *et al*. 2017).

SDTF plants were exposed to periods of very severe water deficit, and showed very low Ψ_{AM}, Ψ_{MD}, and $\Delta\Psi$ values during the dry season - indicating significant water restrictions. Additionally, the ability of the wood architecture of those plants to achieve very low water potential values - narrower

Table 4 – Mean, maximum value (Max), minimum value (Min), and phenotypic plasticity indexes (PPI) of morphofunctional traits of *Maprounea guianensis* in the gallery and tableland sites in the municipality of Lençóis, and in the cloud and SDTF forests in the municipality of Palmeiras, in the Chapada Diamantina mountains, Bahia state, Brazil.

Traits	**Mean**	**Max (clou)**	**Min (clou)**	**Max (gall)**	**Min (gall)**	**Max (tabl)**	**Min (tabl)**	**Max (SDTF)**	**Min (SDTF)**	**PPI (clou)**	**PPI (gall)**	**PPI (tabl)**	**PPI (SDTF)**
LTH (mm)	0.14	0.16	0.11	0.17	0.11	0.18	0.13	0.17	0.11	0.34	0.31	0.27	0.37
SUC (g.cm^2)	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.38	0.21	0.13	0.64
LDE (mg.mm^{-2})	0.05	0.06	0.04	0.07	0.05	0.06	0.05	0.05	0.05	0.28	0.30	0.30	0.03
Ψ_{PD} (MPa)	-1.73	-0.71	-0.20	-1.12	-0.21	-1.03	-0.24	-10.00	-0.31	0.72	0.81	0.77	0.97
Ψ_{MD} (MPa)	-2.30	-1.35	-0.38	-2.00	-0.81	-1.95	-0.72	-10.00	-1.22	0.72	0.60	0.63	0.88
Δ_{Ψ} (Mpa)	0.63	0.96	0.42	0.82	0.61	0.82	0.49	0.91	0.00	0.56	0.26	0.40	1.00
Mean										0.50 a	0.41 a	0.41 a	0.65 a
Standard Error										± 0.08	± 0.10	± 0.10	± 0.16

clou = cloud forest; gall = gallery forest; tabl = tableland forest; SDTF = Seasonally Dry Tropical Forest; LTH = leaf thickness; SUC = succulence; LDE = leaf density; Ψ_{PD} = before dawn water potential; Ψ_{MD} = after midday water potential; Δ_{Ψ} = daily amplitude of water potential. Phenotypic plasticity index values from 0 to 1; values closer to 1 show higher plasticity, values closer to 0 show lower plasticity. Mean followed by same letter indicate no statistically significant differences ($p < 0.05$).

and more numerous pots - allows it to quickly absorb water from the soil (when available) and reduce the propensity for cavitation (Borchert 1994; Chave *et al*. 2009; Lima *et al*. 2012). Those characteristics are traditionally associated with fluctuations in plant water potentials due to differences in water transport efficiency and the capacity for replacing water losses incurred during the day (Meinzer 2003; Oliveira *et al*. 2014). The absence of nocturnal recuperation of water losses incurred during the day was clearly observed in the SDTF population, where $\Delta\Psi$ values reached zero during the dry period - in contrast to what occurred during the rainy period, with higher Ψ_{PD} and Δ_{Ψ} values suggesting the satisfactory nocturnal recuperation of their water status (Lemos Filho & Mendonça Filho 2000; Miranda *et al.* 2011).

Considering functional traits, the SDTF was observed to be distinct in relation to the humid sites. The leaf SUC and LDE values of the plant population in the SDTF site were generally observed to be greater than those of the more humid sites (although still low as compared to other species in the region) (Couto-Santos 2014; Moraes *et al*. 2017; Costa 2019), possibly due to less investments in leaf production by *M. guianensis*, a deciduous to semideciduous species with short leaf lifetimes (Santos *et al*. 2020); plants of that species growing in the SDTF shed all of their leaves as a survival strategy (Neves *et al*. 2017; Miranda *et al*. 2011).

Those characteristics, together with high density wood with a low saturation capacity, limit storage water by *M. guianensis* under dry conditions. However, it was the characteristics of the soil, and the low seasonal precipitation in the dry periods that resulted in a low water potential during that time. A previous study compared the clayey SDTF soils with other sites in the Chapada Diamantina, and demonstrated that the soils there were more compact, limiting water infiltration and the development of plant root systems, and causing marked decreases in their water potentials during dry periods (Neves *et al*. 2016; Neves *et al*. 2017). The interference of soil compaction on water availability for plants and high resistance to root penetration was postulated by Junior & Estanislau (1999) and Beutler & Centurion (2004) as affecting agricultural species.

We found that wood density showed the least plasticity among the plant traits monitored, with similar characteristics among the different populations. Of all the functional traits evaluated in this study that differed between wet and dry forest sites, water potential appeared as the main functional trait modulating species` responses to seasonal differences in water availability. *M. guianensis* demonstrated the largest differences in water potential in response to the marked seasonality in the STDF. As such, although the t-test did not demonstrate any differences between the means of the PPI in the different sites, the STDF plants did demonstrate the greatest PPI, principally in relation to their water potential values. Previous studies carried out in dry forests likewise confirmed that precipitation determined variations in intraspecific characteristics, indicating phenotypic plasticity for the species studied (Falcão *et al*. 2015; Chaturvedi *et al.* 2018; Zorger *et al.* 2019).

The present study demonstrated that local environmental aspects (especially seasonal rainfall, drought regimes, and soil characteristics) influenced variations in the functional traits of *M. guianensis* populations, reflecting phenotypic plasticity. That observed plasticity in functional leaf traits is also linked with phenological features, as Santos *et al*. (2020) reported canopy and leaf longevity plasticity among populations under the same conditions studied here. Our results highlight the connections between drought regimes and plant responses, demonstrating the importance of functional traits associated with water availability (especially leaf water potential) in modulating the adaptive strategies of *M. guianensis*, making the factors associated with its wide distribution more apparent.

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