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MARÍLIA GRAZIELLY MENDES DOS SANTOS

DINÂMICA FENOLÓGICA E ATRIBUTOS MORFOFUNCIONAIS DE POPULAÇÕES DE UMA ESPÉCIE ARBÓREA NEOTROPICAL (*Maprounea guianensis* AUBL.) EM FLORESTAS ÚMIDAS E SECAS

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Tese apresentada ao Programa de Pós-Graduação em Recursos Genéticos Vegetais, da Universidade Estadual de Feira de Santana como requisito parcial para obtenção do título de Doutor em Recursos Genéticos Vegetais.

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RESUMO

Dinâmica fenológica e atributos morfofuncionais de populações de uma espécie arbórea neotropical (*Maprounea guianensis* Aubl.) em florestas úmidas e secas. 97p. Tese (Doutorado em Recursos Genéticos Vegetais) – Universidade Estadual de Feira de Santana (UEFS), Feira de Santana, BA, 2020.

Este estudo analisou a amplitude da variabilidade dos traços funcionais de *Maprounea guianensis* em florestas úmidas e secas na Chapada Diamantina, contrastantes em características do solo e disponibilidade de água. A tese é apresentada em três capítulos, o primeiro analisou como diferentes condições ambientais afetam o hábito foliar investigando a diversidade fenológica intrapopulacional, sazonalidade e longevidade das folhas; o segundo analisou os traços morfofuncionais quanto às respostas a seca sazonal e a capacidade de adaptação da planta; e o terceiro verificou os efeitos da seca no crescimento vegetativo associando incremento radial, fenologia e potencial hídrico. No primeiro capítulo, foram observadas mensalmente as fenofases de brotação e queda foliar em 62 árvores marcadas entre 2004 e 2012 (84 meses) em sítios de florestas úmida (pluvionebular, ciliar, de planalto) e seca (floresta tropical sazonalmente seca –FTSS). A partir destes dados, calculou-se a longevidade das folhas para identificação do hábito foliar, analisou-se a sazonalidade por estatística circular, a diversidade fenológica e a correlação das fenofases com a precipitação e o fotoperíodo. No segundo capítulo, foram realizadas medidas ecofisiológicas entre janeiro/2017 a abril/2019, em 5 indivíduos/sítio para avaliar potencial hídrico, suculência, espessura e densidade foliar, nas estações seca e chuvosa; densidade básica da madeira e teor de água saturada da madeira foram avaliados no período chuvoso. Precipitação e umidade do solo foram monitorados mensalmente, e análise das propriedades físicas do solo foi realizada. Os traços funcionais foram submetidos à análise de variância. Calcularam-se os índices de plasticidade fenotípica (IPF) em cada sítio comparando as médias por análise de variância. No terceiro capítulo, neste último período, o incremento radial e a fenologia vegetativa e reprodutiva foram acompanhados mensalmente na floresta ciliar e FTSS em 22 indivíduos/sítio. Através de correlação cruzada, o incremento radial foi comparado com a fenologia, dados de precipitação e fotoperíodo. Um teste T analisou a atividade cambial e as fenofases entre os sítios. Os resultados mostraram sazonalidade e baixa diversidade intraespecífica nas fenofases vegetativas. A longevidade das folhas foi mais reduzida na floresta seca e houve variação do hábito sempre verde a decíduo. *M. guianensis* demonstrou baixa capacidade de armazenamento de água em seus tecidos foliares e lenhosos, variações no potencial hídrico e alta plasticidade fenotípica. Precipitação e fotoperíodo foram gatilhos para a atividade cambial, e para o surgimento de brotamento, flores e frutos. Nossos resultados destacam as repostas das plantas aos regimes de seca. Evidenciamos a importância da associação das características funcionais à disponibilidade de água na modulação das estratégias de *M. guianensis* que, devido a sua alta plasticidade consegue modular estratégias de escape ou de tolerância ao período de déficit hídrico

Palavras-chave: Diversidade fenológica. Incremento radial. Longevidade foliar. Plasticidade fenotípica. Potencial hídrico. Resposta à seca.

ABSTRACT

Phenological dynamics and morphofunctional attributes of populations of a neotropical tree species (*Maprounea guianensis* aubl.) In humid and dry forests. 97p. Thesis (PhD in Recursos Genéticos Vegetais) - Universidade Estadual de Feira de Santana (UEFS), Feira de Santana, BA, 2020.

This study analyzed the amplitude of the variability of the functional traits of *Maprounea guianensis* in wet and dry forests in Chapada Diamantina, contrasting in soil characteristics and water availability. It is presented in three chapters, the first analyzed how different environmental conditions affect the leaf habit, investigating the intrapopulational phenological diversity, seasonality and longevity of the leaves; the second analyzed the morphofunctional traits in terms of responses to seasonal drought and the adaptability of the plant; and the third verified the effects of drought on vegetative growth, associating radial increase, phenology and water potential. In the first chapter, the phenophases of budding and leaf fall were observed monthly in 62 trees marked between 2004 and 2012 (84 months) in sites of humid (cloud, gallery, tableland) and dry (seasonally dry tropical forest - SDTF). From this data, leaf longevity was calculated to identify leaf habit, seasonality was analyzed by circular statistics, phenological diversity and the correlation of phenophases with precipitation and photoperiod. In the second chapter, ecophysiological measurements were carried out between January/2017 to April/2019, in 5 individuals/site to assess water potential, succulence, thickness and density leaf, in the dry and rainy seasons; basic wood density and saturated water content of the wood were evaluated in the rainy season. Precipitation and soil moisture were monitored monthly, analysis of the physical properties of the soil was performed. The functional traits were subjected to analysis of variance. Phenotypic plasticity indices (PPI) at each site were calculated to comparing the averages by the analysis of variance. In the third chapter, in this last period, the radial increase and vegetative and reproductive phenology were followed monthly in the gallery forest and SDTF in 22 individuals/site. Through cross correlation, the radial increment was compared with the phenology and precipitation and photoperiod data. A T test analyzed exchange activity and phenophases between sites. The results showed seasonality and low intraspecific diversity in vegetative phenophases. The longevity of the leaves was more reduced in the dry forest, and there was a variation in the evergreen to deciduous habit. *M. guianensis* demonstrated low water storage capacity in its leaf and woody tissues, variations in water potential and high phenotypic plasticity. Precipitation and photoperiod were triggers for foreign exchange activity, and for the appearance of budding, flowers and fruits. Our results highlight the plants responses to drought regimes. We show the importance of associating functional traits to the water availability in *M. guianensis* strategies, which, due to their high plasticity, can modulate escape or tolerance strategies to the water deficit period.

Keywords: Leaf longevity. Phenological diversity. Phenotypic plasticity. Radial increment. Response to drought. Water potential.

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INTRODUÇÃO GERAL

As respostas das plantas à variação na disponibilidade de recursos e condições ambientais é, em grande parte, modulada por características morfológicas e fisiológicas (de MATTOS et al., 2004). Algumas espécies demonstram uma plasticidade nestas características, alterando as suas expressões fenotípicas para se adaptarem às condições ambientais (GANIE et al., 2014; SULTAN, 1987). A identificação dos *trade-offs* dos traços morfofuncionais ajuda a compreender como estas estratégias permitem a sobrevivência e distribuição da planta em gradiente climático ou geográfico (GOULART et al., 2005; WRIGHT et al., 2007; TOLEDO et al., 2012; DORMAN et al., 2013; NEVES et al., 2017).

Dentre as condições limitantes para a sobrevivência das plantas em florestas tropicais, a seca é considerada um dos fatores mais comuns e significativos (YANG et al., 2013). Para sobreviver aos períodos de estresse estas plantas modulam estratégias a partir de traços como fenologia, idade foliar, potencial hídrico, densidade da madeira, atributos morfológicos das folhas (espessura, suculência, densidade) e incremento radial (LARJAVAARA; MULLER-LANDAU, 2010; TOLEDO et al., 2012; ROSSATTO et al., 2013; BRAGA et al., 2016; MORAES et al., 2017; ROSADO; de MATTOS, 2017). Um exemplo claro destes ajustes é observado na fenologia, que é conhecida como o estudo dos eventos biológicos cíclicos e da sua relação com os fatores bióticos e abióticos, podendo apresentar variações mesmo entre populações (WILLIAMS-LINERA; MEAVE, 2002, ENGEL;MARTINS, 2005). Na fenologia vegetativa pode-se distinguir o hábito sempreverde do decíduo, com o primeiro sendo definido pela retenção de folhas funcionais no dossel da planta ao longo do ano, e o segundo por uma planta sem folhas durante parte do ciclo anual (KIKUZAWA; LECHOWICZ, 2011). Há ainda alguns termos intermediários que descrevem peculiaridades intermediárias, como p. ex. o hábito brevidecíduo quando há um breve período no ano em que as folhas velhas estão caindo ao mesmo tempo em que novas folhas estão surgindo (BORCHERT et al., 2002). Assim, a espécie pode assumir uma estratégia de tolerância a seca ao reter as folhas funcionais ao longo do ano, ou assumir uma estratégia de escape da seca com a deciduidade total das folhas (MARKESTEIJN; POORTER, 2009; KIKUZAWA; LECHOWICZ, 2011).

Em regiões tropicais e subtropicais, o regime pluviométrico e a disponibilidade de água no solo vêm sendo avaliados em estudos sobre o desenvolvimento e a atividade reprodutiva de espécies dessas regiões. Estes estudos destacam as informações sobre o potencial hídrico, por ser uma medida integradora dos processos de absorção e perda de água por transpiração, e por estimar a água disponível no solo, podendo assim refletir o balanço hídrico da planta

(BORCHERT, 1994; PALHARES et al., 2010; ROSSATTO et al., 2013; NEVES et al., 2017). Caracteres morfológicos foliares e a densidade da madeira também são bons descritores do status hídrico da planta e podem influenciar nos padrões fenológicos (ROSADO; de MATTOS, 2007; TOLEDO et al., 2012; MORAES et al., 2017).

O fotoperíodo também é um fator ambiental importante na variação dos traços morfofuncionais, muitas vezes foi reconhecido como gatilho para o brotamento foliar e para o surgimento de flores e frutos em florestas tropicais (MORELLATO et al., 2000; TALORA; MORELLATO, 2000; GOULART et al., 2005; MÜLLER; SCHMITT, 2018). Por ser um dadpoiso consistente algumas espécies se baseiam nos sinais do fotoperíodo para detectar a chegada de uma próxima estação produtiva ou estressante (WAY et al., 2015).

Pesquisas anteriores vêm mostrando os efeitos da seca na fisiologia das plantas (BORCHET, 1994; FRANCO et al., 2004; ENGELBRECHT et al., 2007; ARANDA et al., 2012; LIMA et al., 2012; SOUZA et al., 2015; BRUM et al., 2017; BANKS et al., 2019; PEARSE et al., 2019), porém são poucos os estudos em florestas tropicais que abordam as consequências do déficit hídrico no seu crescimento radial (LISI et al., 2008; CARDOSO et al., 2012; TOLEDO et al., 2012; CALLADO et al., 2013), não sendo encontrados registros de estudos desta natureza na região da Chapada Diamantina. Nestas investigações, a fenologia pode fornecer informações úteis por ser frequentemente associada a estágios específicos da atividade do cambio (MATTOS; SALIS, 2007; TOLEDO et al., 2012). Assim, uma espécie pode evitar o estresse hídrico nos meses de seca com a queda de folhas, ao mesmo tempo em que o incremento radial diminui (TOLEDO et al., 2012).

O incremento radial também está intimamente relacionado à fisiologia da planta. Madeiras com alta densidade além de impedir o armazenamento de água nos tecidos do caule também retardam o crescimento radial devido aos custos de construção do tecido. Contudo, ao mesmo tempo em que esta característica é prejudicial em um contexto, também pode ser altamente benéfica em outro, visto que caules mais densos são mais resistentes e fornecem a sustentação necessária para a sobrevivência da planta exposta a uma seca severa (LARJAVAARA; MULLER-LANDAU, 2010; TOLEDO et al., 2012).

Maprounea guianensis Aubl. é amplamente distribuída em todo o Brasil em cerrado e floresta (FLORA DO BRASIL, 2020 – em construção). A espécie tem se destacado no contexto econômico por apresentar importantes agentes farmacêuticos (triterpenos e ferulatos de alquila) (DAVID et al., 2004), e por mostrar grande potencial antibacteriano e antifúngico nas suas folhas e caules (MARQUES, 2011). Na Chapada Diamantina, Bahia, onde é conhecida como *folha miúda* (FUNCH 2008), é uma das poucas espécies arbóreas encontradas em sítios de florestas úmidas (floresta pluvionebular, floresta ciliar e floresta de planalto) e secas (floresta tropical sazonalmente seca) (FUNCH et al., 2008; NEVES et al., 2016), o que favorece a escolha da espécie para investigação da resposta da planta à variação ambiental e frente às mudanças no clima.

Este estudo analisou a amplitude da variabilidade de traços funcionais de *M. guianensis* em florestas úmidas e secas na Chapada Diamantina, contrastantes em características do solo e disponibilidade de água. Esperamos compreender as condições que permitem a ampla distribuição da espécie da espécie em diferentes tipos de florestas encontrando *trade offs* entre os traços morfofuncionais que reflitam em plasticidade fenotípica. A tese é dividida em três capítulos: no primeiro analisamos como diferentes condições ambientais afetam o hábito foliar de *M. guianensis* investigando a diversidade fenológica intrapopulacional, sazonalidade e longevidade das folhas; no segundo analisamos os traços funcionais quanto às respostas a seca sazonal e a capacidade de adaptação da planta; e no terceiro investigamos os efeitos da seca no crescimento vegetativo associando incremento radial, fenologia e potencial hídrico.

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CAPÍTULO 1

PHENOLOGICAL DIVERSITY OF *Maprounea guianensis* Aubl. (EUPHORBIACEAE) IN HUMID AND DRY NEOTROPICAL FORESTS

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ABSTRACT

Phenological diversity, seasonality, and leaf longevity may affect leaf habits, reflecting plant responses to environmental conditions. *Maprounea guianensis* Aubl. is a widespread species in Brazil, associated with different forest types. We investigated how phenological diversity, seasonality, and leaf longevity affect leaf habits of its populations growing in humid and dry forests in the Chapada Diamantina mountains. We made monthly observations of leaf budding and fall in 62 individual trees between 2004 and 2012 (84 months), estimating leaf longevity based on phenophase evaluations. We made use of circular statistics, cross correlations, and the Shannon-Wiener index to evaluate our data. There was little variation in rainfall distribution between the study years, although water availability differed at each site. Phenophase seasonality was found to be negatively correlated with rainfall but positively correlated with photoperiod. Low phenological diversity was observed within each site, but not between sites, and leaf longevity was reduced in the dry forest. Although macroclimatic conditions were similar throughout the range of occurrence of *M. guianensis* in the region, we found that phenological behavior and leaf longevity differed according to micro-site differences, demonstrating the plasticity of the species - which may favor its occupation of different environments.

Keywords: Drought. Intraspecific variation. Photoperiod. Water relations.

RESUMO

Diversidade fenológica, sazonalidade e longevidade das folhas podem afetar os hábitos foliares, refletindo as respostas das plantas às condições ambientais. *Maprounea guianensis* Aubl. é uma espécie difundida no Brasil, associada a diferentes tipos de florestas. Investigamos como a diversidade fenológica, a sazonalidade e a longevidade das folhas afetam os hábitos foliares de suas populações que crescem em florestas úmidas e secas nas montanhas da Chapada Diamantina. Foram feitas observações mensais de brotamento e queda de 62 árvores individuais entre 2004 e 2012 (84 meses), estimando a longevidade das folhas com base em avaliações da fenofase. Utilizamos estatísticas circulares, correlações cruzadas e o índice de Shannon-Wiener para avaliar nossos dados. Houve pouca variação na distribuição das chuvas entre os anos de estudo, embora a disponibilidade de água tenha diferido em cada local. A sazonalidade da fenofase foi correlacionada negativamente com a precipitação, mas positivamente com o fotoperíodo. Baixa diversidade fenológica foi observada dentro de cada local, mas não entre locais, e a longevidade das folhas foi reduzida na floresta seca. Embora as condições macroclimáticas tenham sido semelhantes em toda a faixa de ocorrência de *M. guianensis* na região, verificamos que o comportamento fenológico e a longevidade das folhas diferem de acordo com as diferenças entre os micrositios, demonstrando a plasticidade das espécies - o que pode favorecer a ocupação de diferentes ambientes.

Palavras-chave: Seca. Variação intraespecífica. Fotoperíodo. Relações hídricas.

1.1 INTRODUCTION

Leaf habits, including leaf longevity and seasonality, reflect the phenological patterns of plant populations, and they can be very diverse, depending on resource availability and abiotic filters (KIKUZAWA, 1991). Leaf longevity can be prolonged or reduced by environmental conditions such as water availability through rainfall or from soil water reserves (JOLLY; RUNNING, 2004; KIKUZAWA; LECHOWICZ, 2011; XU et al., 2014), reflecting a plant's conservative/acquisitive strategies - although individual endogenous factors may also play significant roles in adopting such strategies (MOREL et al., 2015). Phenological seasonality, that is, the association between the occurrence of a certain vegetative phenophase and a season (NEWSTRON et al., 1994) is in turn implicit in the definition of leaf habit. As such, plants can show an evergreen habit, defined by the retention of functional canopy leaves throughout the year, or a deciduous habit, characterized by leaflessness during part of the annual cycle (KIKUZAWA, 1991). Intermediate behaviors were also found to be common, such as the brevideciduous habit, with a brief period during the year when old leaves fall (not more than 50%) while new leaves are simultaneously emerging, and a semi-deciduous habit, characterized by leaf fall greater than 50% (KIKUZAWA; LECHOWICZ, 2011).

Plants can respond to biotic and abiotic factors through their phenological traits, such as peaks of leaf production and leaf lifespan, which allows them to resist environmental limitations and expand their geographic domains (SULTAN, 2001; SINGH; KUSHWAHA, 2005). Variation on those traits can be analyzed by monitoring species throughout their distribution in different habitats, comparing their specific phenological responses (NIMETTES; VALLADARES, 2004; GOULART et al., 2005; LEMOS FILHO et al., 2008; CAPUZZO et al., 2012; TOLEDO et al., 2012; MORAES et al., 2017). The analysis of phenological trait variability within populations is an important approach that can provide information about how populations are able to persist in diverse habitats subject to very different environmental filters (SEGHIERI; SIMIER, 2002; GOULART et al., 2005; LEMOS FILHO et al., 2008). Many of the studies undertaken in tropical seasonal climates have focused on only a single population (e.g., CODY; PRIGGE, 2003; SOUZA et al., 2012; MENEZES et al., 2017; MÜLLER; SCHMITT, 2018; SILVA et al., 2018; LEÃO-ARAÚJO et al., 2019), especially comparisons between plants subjected to very distinct environments in terms of water availability (such humid forest and seasonal systems) (GOULART et al., 2005); mainly because of time limitations and difficulties encountered during sampling at different sites (REICH, 1995, BRITO et al., 2017).

Plant populations are exposed to wide rainfall ranges in tropical seasonal environments, and thus experience different periods of water stress duration due to droughts – which constitute challenges to leaf functioning (KOZLOWSKI; PALLARDY, 2002; KIKUZAWA; LECHOWICZ, 2011). Some plant populations in dry tropical forests can tolerate droughts by reducing water losses through total or partial deciduousness, allowing them to survive without compromising their hydraulic structures (MARKESTUIN; POORTER, 2009; ROSSATTO et al., 2013; KOOYERS, 2015; NEVES et al., 2016). In humid tropical forest (and sites with the frequent presence of clouds or nearside rivers), the higher relative humidity and greater soil water availability (the usually shallow soils can become saturated) allow canopy maintenance throughout the year (HAMILTON et al., 1995; HOSTETTLER, 2002; SCHAEFER et al., 2012; AUGSPURGUER; SALK, 2017). Although rainfall has been indicated as the main factor regulating the phenological behaviors of woody species in seasonally dry forests (MÉNDEZ-ALONZO et al., 2012; SOUZA et al., 2014; MENDIVELSO et al., 2016), photoperiod changes can also be determinant in plant phenological strategies (RIVERA et al., 2002; BORCHERT et al., 2005; SINGH; KUSHWAHA, 2005).

The great diversity of habitats found in the Chapada Diamantina Mountains (the northeastern extension of the Espinhaço Range, included in the Brazilian semiarid) favors testing hypotheses of populational phenological dynamics (MORAES et al., 2017; NEVES et al., 2017), mainly because the region comprises vegetation mosaics of grasslands, savannas, and diverse types of humid and dry forests (FUNCH et al., 2009), reflecting a high diversity of soils, reliefs, and elevations. Few plant species are widely distributed along the landscapes in many of those vegetation types (FUNCH et al., 2009), with the tree *Maprounea guianensis* Aubl. (Euphorbiaceae) being an exception (FUNCH et al., 2005; COUTO-SANTOS et al., 2015; NEVES et al., 2016). This species can form relatively large populations in both evergreen (CERQUEIRA, 2009; MIRANDA et al., 2011; COUTO-SANTOS et al., 2015) and deciduous forests. Those types of environments do not differ in terms of their macroclimatic conditions along their distribution in the Chapada Diamantina, but rather in terms of soil types, elevation, and relief, which can affect water availability for plants (NEVES et al., 2017). Those varying factors could result in *M. guianensis* individuals experiencing different water restrictions during the dry season according to the type of environment they occupy (NEVES et al., 2017), and those same factors can affect phenological responses.

Given the widespread distribution of *M. guianensis* in both humid and dry forests, we investigated intrapopulational phenological diversity, seasonality, and leaf longevity at four sites (three in humid forests, and one in a dry forest) in the Chapada Diamantina. We examined the roles of abiotic factors (rainfall and photoperiod) in determining leaf phenology at each study site. Specifically, we asked whether the shared regional climatic seasonality was reflected in seasonal phenological habits associated with leaf longevity. We hypothesized that humid sites should show continuous canopy maintenance in contrast to a shorter duration of canopy cover in drier sites. Secondly, we hypothesized that leaf duration will be higher in humid sites given constant canopy maintenance during the year, while leaf longevity in drier sites would be shorter given canopy deciduousness for a long period of time. Our purpose was to understand plant conservative/acquisitive strategies considering responses to macro- and micro-climatic environmental conditions.

1.2 MATERIAL AND METHODS

1.2.1 Species and studied sites

We performed this study using phenological datasets for *Maprounea guianensis Aubl*. (Euphorbiaceae) previously collected by our research group in the Chapada Diamantina Mountain Range during the course of different studies (FUNCH et al., 2002; CERQUEIRA, 2009; MIRANDA et al., 2011; COUTO, 2014; NEVES et al., 2017) (Table 1). This woody specie is widely distributed in Brazil and forms populations in different vegetation types in the Chapada Diamantina (FUNCH et al., 2005; COUTO-SANTOS et al., 2015; NEVES et al., 2016). The forests studied were located between 12º 27' 06" - 12º 33' 39" S and 41º 23' 14" - 41º 35' 52" W, from 500 m - 1000 m, on the eastern border of the Chapada Diamantina Mountains (Table 1, Figure 1).

Table 1: Phenology studies of *Maprounea guianensis* Aubl. in the Chapada Diamantina mountains, Brazil, indicating the study periods,authors, geographic coordinates, elevations (m), soil types, numbers of individuals observed (n), and their relative densities (RD).

Sites	Study Period	Author	Coordinates	Altitude	Soil	n	RD
Cloud forest	Sep/2006 - Aug/2008	Cerqueira 2009	12°27’49”S - 41°28’34”W	940 - 1000	litholic neosol	6	1.70
Gallery forest	Jan/2004 - Dec/2005	Funch 1997; Miranda et al. 2011	12º33’39”S - 41º24’40”W	500	litholic neosol	21	0.91
Tableland forest	Jan/2011 - Dec/2012	Couto-Santos et al. 2015	12º28’31’’S - 41º23’14’’W	600	red-yellow latosol	11	3.32
SDTF	Jan/2010 - Dec/2011	Neves et al. 2017	12º27’06”S - 41º35’52”W	697	litholic neosol	26	14.15

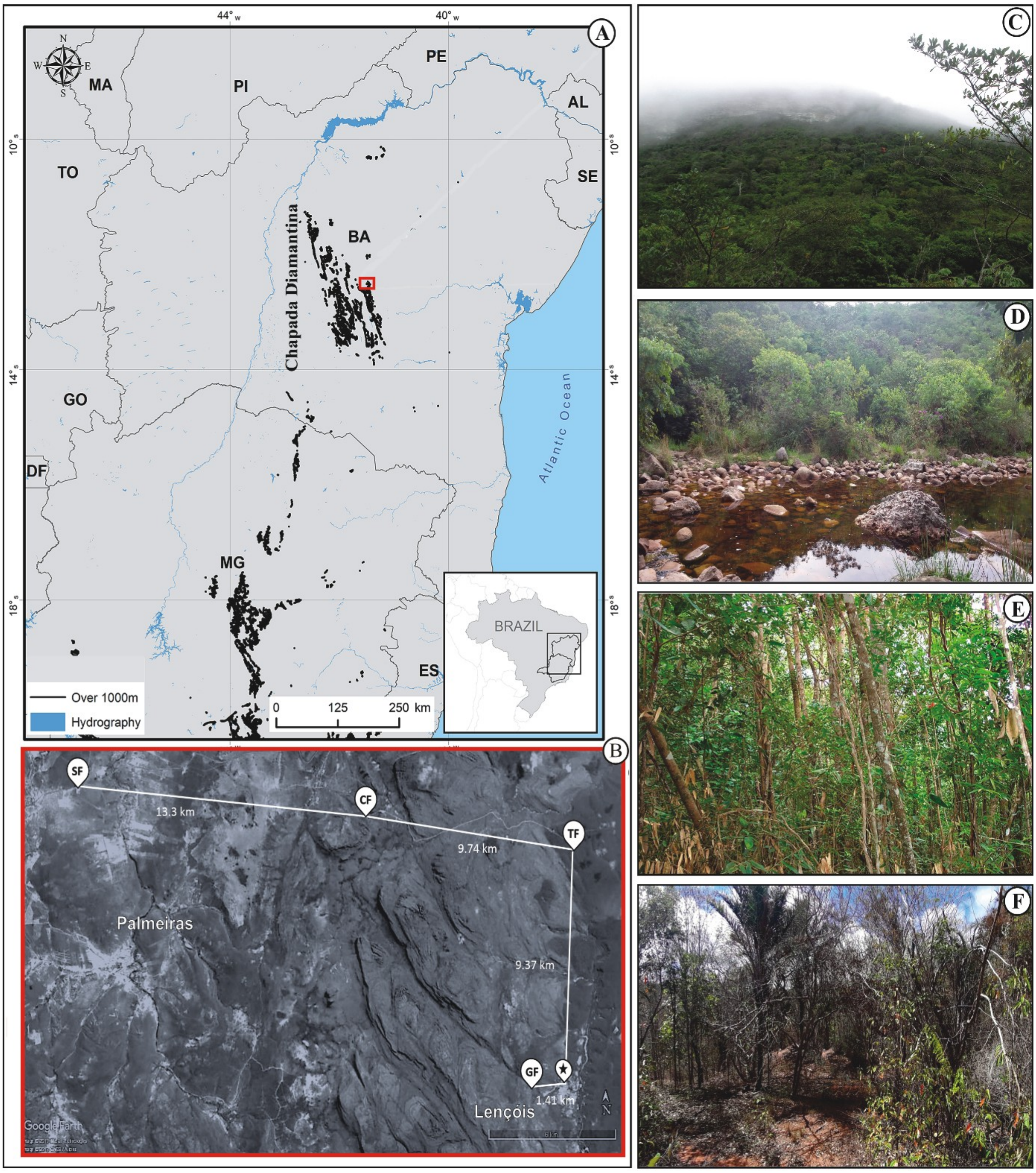

Figure 1: Location of the studied forests in the Chapada Diamantina mountains, Brazil. (A) Chapada Diamantina mountains; (B) - Google Earth image, indicating the distance between the studied forests and the Meteorological Station (National Institute of Meteorology – INMET):/ Seasonally dry tropical forest (SF), Cloud forest (CF), Tableland forest (TF), Gallery forest (GF); Meteorological station (★) (C) - Cloud forest; (D) - Gallery forest; (E) Tableland forest; and (F) Seasonally dry tropical forest.

Although our sampling was performed in different years, we did not find any differences in terms of the annual rainfall in the region (Table 2). Few differences were found between the rainy seasons of the study years, with the exception of the final year (2012) (Table 2). We did not found any differences in terms of the dry season (Table 3), which we believe is the most important period influencing the canopy behavior of the individuals.

Table 2: Independent sampling t-test comparing total precipitation (mm) between *Maprounea guianensis* Aubl. phenological observation periods in the Chapada Diamantina mountains, Brazil.

Year		2005	2006	2007	2008	2010	2011	2012
2004	**p(f)**	0.05 (4.02)	0.72 (0.14)	0.24 (1.44)	0.15 (2.17)	0.19 (1.79)	0.14 (2.27)	0.52 (0.53)
2005	**p(f)**		0.15 (2.21)	0.24 (1.48)	0.51 (0.46)	0.62 (0.81)	0.59 (0.72)	0.11 (2.70)
2006	**p(f)**			0.57 (0.34)	0.63 (0.86)	0.55 (0.59)	0.61 (0.78)	0.86 (0.03)
2007	**p(f)**				0.61 (0.27)	0.76 (0.09)	0.68 (0.18)	0.57 (0.34)
2008	**p(f)**					0.82 (0.05)	0.89 (0.02)	0.33 (1.01)
2010	**p(f)**						0.92 (0.01)	0.57 (0.66)
2011	**p(f)**							0.66 (0.96)

$p < 0.05$ indicates statistical difference using t-Teste

Table 3: Independent samplingt-test comparing dry and rainy periods (mm) between years of phenological observation of *Maprounea guianensis* Aubl. in the Chapada Diamantina mountains, Brazil

Rainy season							
Year	**2005**	**2006**	**2007**	**2008**	**2010**	**2011**	**2012**
2004 p(t)	0.44 (-0.15)	0.43 (0.19)	0.33 (0.44)	0.19 (0.92)	0.09 (1.44)	0.15 (1.14)	**0.03** (2.07)
2005 p(t)		0.35 (0.40)	0.23 (0.77)	0.05 (1.83)	**0.01** (2.73)	**0.02** (2.35)	**0.00** (3.89)
2006 p(t)			0.41 (-0.24)	0.26 (-0.68)	0.13 (1.20)	0.20 (0.90)	0.05 (1.84)
2007 p(t)				0.34 (0.42)	0.17 (1.01)	0.26 (0.67)	0.06 (1.72)
2008 p(t)					0.19 (0.93)	0.35 (0.39)	**0.03** (2.11)
2010 p(t)						0.27 (0.63)	0.14 (1.15)
2011 p(t)							**0.04** (1.93)
Dry season							
Year	**2005**	**2006**	**2007**	**2008**	**2010**	**2011**	**2012**
2004 p(t)	0.11 (-1.31)	0.24 (-0.78)	0.08 (-1.59)	0.28 (-0.61)	0.17 (-1.07)	0.22 (-0.82)	0.16 (-1.07)
2005 p(t)		0.43 (-0.18)	0.40 (0.27)	0.22 (0.81)	0.37 (-0.35)	0.22 (0.83)	0.34 (0.42)
2006 p(t)			0.38 (0.31)	0.30 (0.57)	0.46 (-0.10)	0.30 (0.56)	0.36 (0.39)
2007 p(t)				0.23 (0.78)	0.32 (-0.52)	0.21 (0.86)	0.41 (0.24)
2008 p(t)					0.22 (-0.82)	0.47 (-0.07)	0.33 (-0.45)
2010 p(t)						0.23 (0.81)	0.28 (0.60)
2011 p(t)							0.33 (-0.45)

$p < 0.05$ indicates statistical difference using t-Teste

The humid forest sites have continuous evergreen canopies, where *M. guianensis* can grow to be between 5 and 15 m tall (FUNCH et al., 2002; CERQUEIRA, 2009; COUTO, 2014). The cloud forest site, at Serra da Bacia, experiences consistent mistiness throughout the year, even during dry months, while the gallery forest site along the Lençóis River experiences sporadic and rapid flooding during the rainy season (FUNCH et al., 2002). The dry forest site shows a discontinuous deciduous canopy, with *M. guianensis* growing to between 1 and 12 m tall (NEVES et al., 2016). The region has dry winters and rainy summers, with an Aw climate according to the Köppen climate classification system (ALVARES et al., 2013). Climatic data were obtained from the National Institute of Meteorology (INMET) based on the Lençóis Meteorological Station. Photoperiod data were obtained from the Astronomical Applications Department of the U.S. Naval Observatory website (http://aa.usno.navy.mil/data/docs/RS_OneYear.php) (Figure 2).

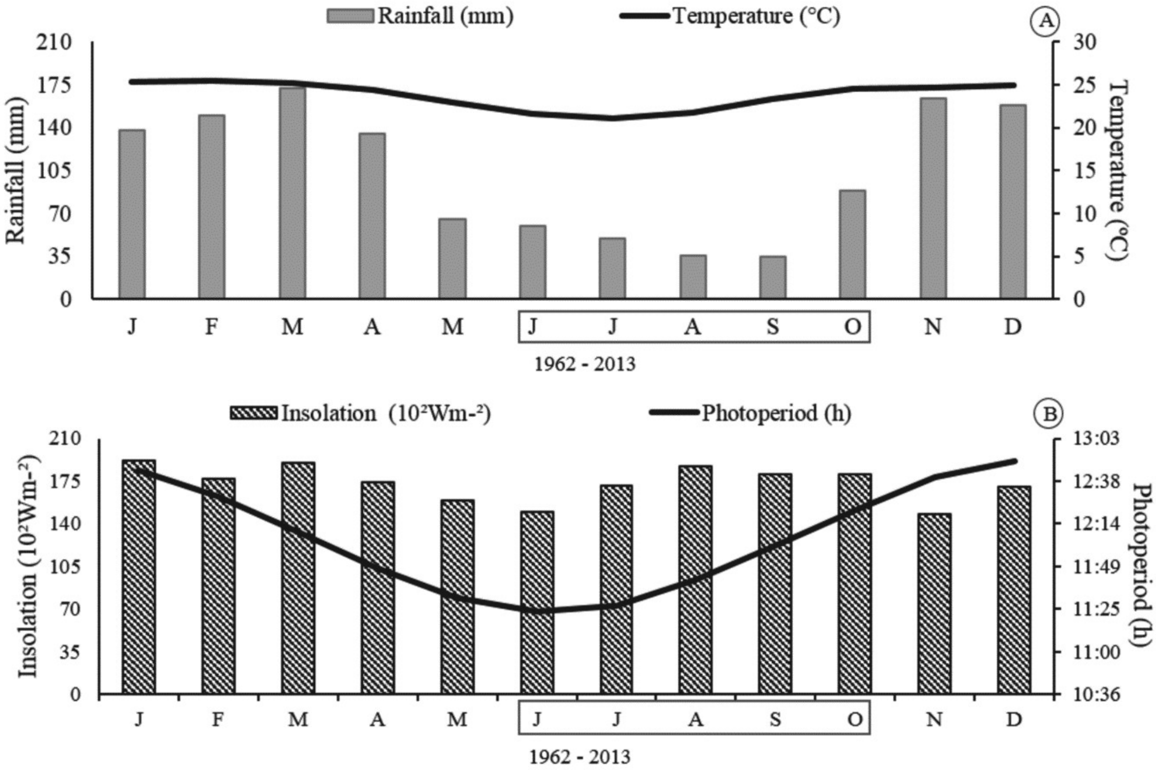

Figure 2. Environmental data for the municipalities of Lençóis and Palmeiras in the Chapada Diamantina mountains, Brazil. (A) Rainfall and temperature (National Institute of Meteorology – INMET station, located in Lençóis); (B) Monthly insolation and photoperiod (Source: National Institute of Meteorology – INMET/ National Institute of Meteorology and Astronomical Applications Department of the U.S. Naval Observatory). Enhanced dry season.

1.2.2 Vegetative phenology and leaf longevity

The phenology of 62 tagged trees of *M. guianensis* were evaluated. Data collection was performed during different periods between 2004 and 2012 through bi-annual phenological studies at each site, totaling 84 months of observations (please refer to Table 1 for details concerning the observation period). The observations were carried at the end of each month, following an average interval of 30 days. The intensities of the budding and leaf fall phenophases were determined using the class interval technique proposed by Fournier (1974), on a scale of from zero to four (with 25 % range increases between the classes). Leaf habit was described according to Kikusawa and Lechowicz (2011). Leaf longevity was estimated through evaluations of the budding and fall leafing peaks of individuals (scores three or four on the Fournier scale).We calculated the average leaf longevity in months between the respective phenophases in the observed phenological cycles (OLIVEIRA et al., 2015).

1.2.3 Intrapopulation phenological diversity

Phenological diversity was evaluated for each forest type using the Fournier categories. The individuals were characterized according to the combinations of their categories (0, 1, 2, 3 and 4) that corresponded to observed phenophases, which were classified as vegetative “phenological states”. After characterization of each sampled individual, phenological diversity under different forest conditions was estimated through the adapted Shannon-Wiener index (GOULART et al., 2005), using the equation proposed by Magurran (1988). In practice, the values assigned by the Shannon-Wiener index are usually between 1.5 and 3.5, but can reach 4.5, with low values indicating low diversity (MAGURRAN, 1988).

1.2.4 Data analyses

The seasonality of the phenological events in each site in each year were evaluated using circular statistical analyses, performed using Oriana 4.02 software (Kovach Computing Services, available at http://www.kovcomp.co.uk). The frequency of each phenophase was calculated based on the total number of individuals accompanied every month. Months were converted into angles at 30° intervals (0° representing January, 30° representing February, and so forth, until 330° representing December). The mean angles and r vector lengths were calculated. Angle significance was tested using the Rayleigh test (z) for circular distributions (ZAR, 2010). The vegetative phenological events with significant mean angles ($p < 0.05$) were transformed into mean dates. Vegetative phenophases whose vector lengths (r) were >

0.5, and which the Rayleigh test indicated as significant, were considered seasonal (MORELLATO et al., 2010). The Watson–Williams F test was used to compare the mean dates ($p < 0.05$) of each phenophase in each of the studied forests. (ZAR, 2010). The normal distributions of the phenological data were evaluated following Shapiro and Wilk test (ZAR, 1996). As normal distributions were not detected, cross-correlation was calculated to evaluate the lag period between the phenophases and monthly rainfall and photoperiod. Only significant results ($p < 0.05$) were considered in those analyses. The cross-correlation analyses were performed using PAST version 2.17c software (HAMMER et al., 2001). We used the independent t-test to compare total rainfall, and the amount of rainfall during dry and wet seasons in different years using Bioestat software. The results for leaf longevity in each site were submitted to analysis of variance (ANOVA), and their means were compared by the Tukey's test ($p < 0.05$), using Sisvar software (version 5.3, Lavras, Minas Gerais, Brazil).

1.3 RESULTS

The *M. guianensis* population in the cloud forest site demonstrated a slow leaf exchange rhythm throughout the year, indicating an evergreen leaf habit (Figue 3A). Low budding intensity and leaf fall (scores one or two on the Fournier scale) did not permit an estimation of foliar longevity in that site. Plants growing in the gallery and tableland forests showed high intensity episodic leaf fall (> 60 %) – although always maintaining green leaves in their crowns, with a leaf longevity of 10 to 11.8 months (semideciduous habit) (Figure. 3B - C, Figure 4). The entire crown was renewed each year in the dry forest site, with clear and separate episodes of budding and total leaf fall (up to 100 %), with a leaf longevity of 7.8 months (deciduous habit) (Figure 3D, Figure 4).

M. guianensis showed seasonal budding and leaf fall events (except in the cloud forest site), with marked episodes during rainfall and drought periods respectively (Figure 5; Table 4). Foliar habits were confirmed at the sampled sites, without variations among the different years in each forest, as indicated by the F test (Table 4).

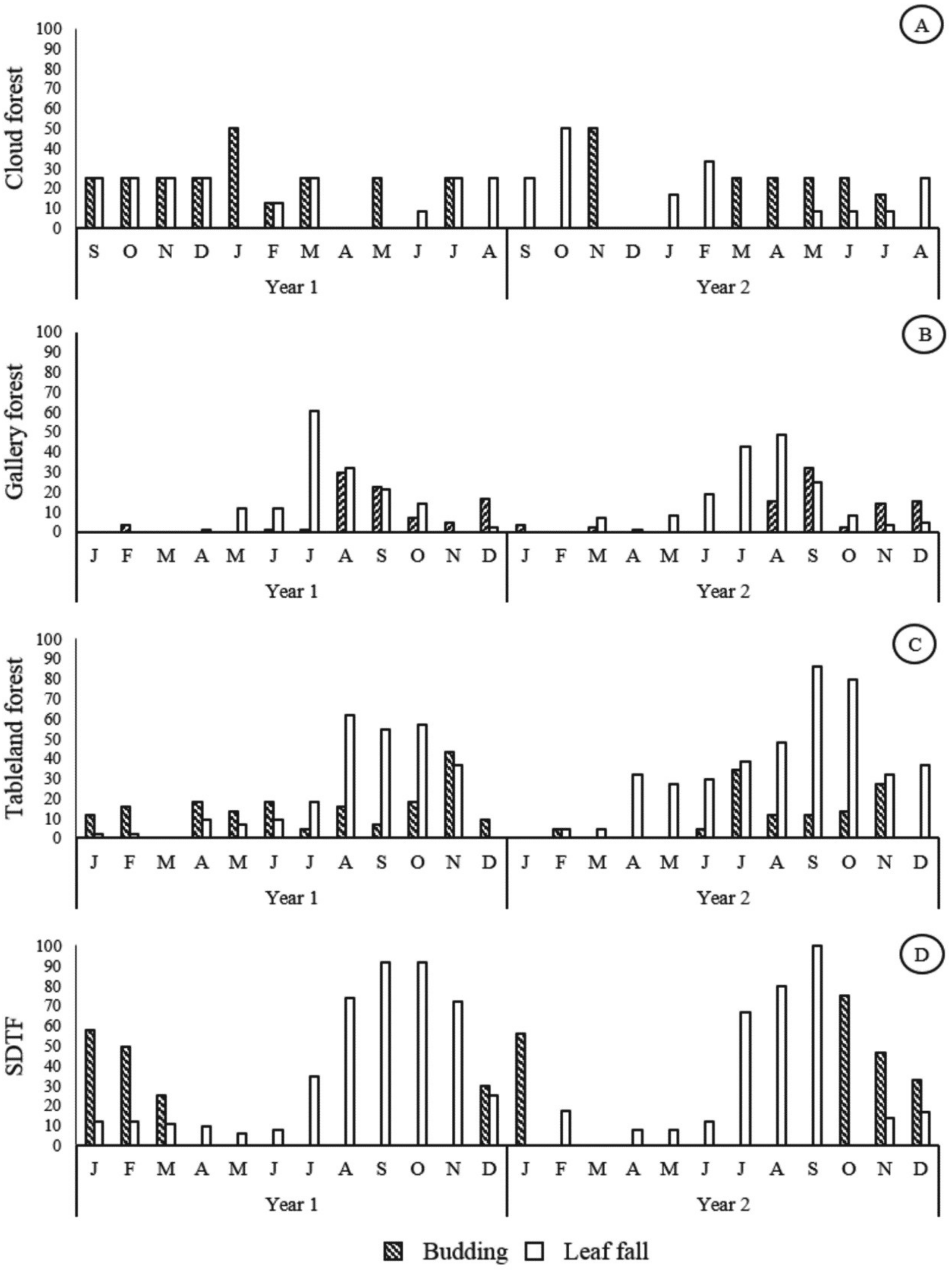

Figure 3: Phenological rhythm of *Maprounea guianensis* Aubl. in the Chapada Diamantina mountains in northeastern Brazil. (A) Cloud forest ; (B) Gallery forest; (C) Tableland forest; (D) Seasonally dry tropical forest

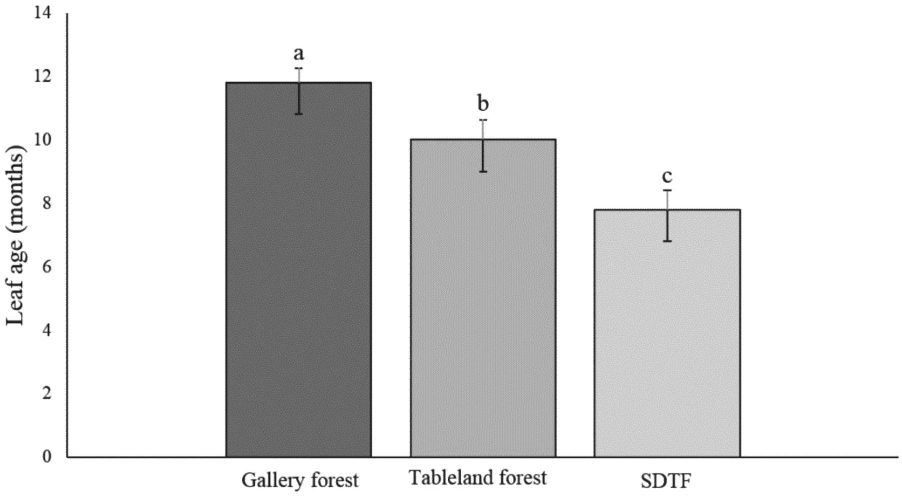

Figure 4: Mean (±SD) values of leaf longevity (in months) of *Maprounea guianensis* Aubl. in the Chapada Diamantina mountains (Gallery forest, Tableland forest, and Seasonally dry tropical forest) in northeastern Brazil. Means followed by same letter indicate no statistically significant differences (p < 0.05).

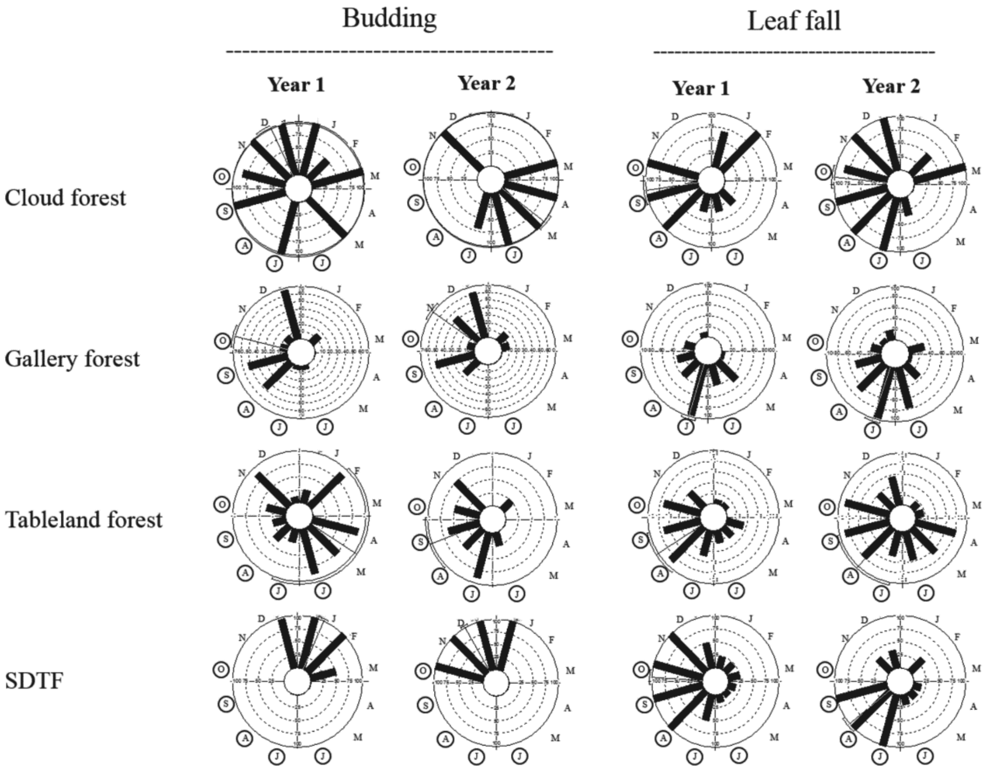

Figure 5: Circular histograms of the rhythms of *Maprounea guianensis* Aubl. in the Chapada Diamantina mountains in northeastern Brazil. (A) Cloud forest ; (B) Gallery forest; (C) Tableland forest; (D) Seasonally dry tropical forest. Enhanced dry season.

Table 4: Circular analysis of the phenological events of *Maprounea guianensis* Aubl. in the Chapada Diamantina mountains, Brazil.

Statistical Parameters	Cloud forest		Gallery forest		Tableland forest		SDTF	
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
				budding				
Mean Angle (mean date)	335.26°(Dec/05)	128.65º(May/10)	284.10°(Oct/14)	305.84º(Nov/05)	124.22°(May/05)	248.62°(Sep/08)	23.74°(Jan/24)	330°(Nov/30)
r	0.21	0.46	**0.54**	**0.52**	0.15	**0.57**	**0.87**	**0.85**
Z	35.05	120.39	60.51	77.95	1.00	9.63	263.00	286.39
P	< 1E-12	< 1E-12	< 1E-12	< 1E-12	0.37*	3.11E-05	< 1E-12	< 1E-12
Watson-Williams – p (F)	0.20 (1.75)		0.94 (0.01)		0.20 (1.72)		0.84 (0.04)	
				leaf fall				
Mean Angle (mean date)	276.21°(Oct/06)	261.66º(Sep/21)	196.79°(Jul/17)	198.98°(Jul/19)	237.37°(Aug/28)	223.31°(Aug/14)	273.61°(Oct/03)	230.35°(Aug/21)
r	0.31	0.28	**0.68**	**0.57**	**0.52**	0.28	**0.58**	**0.51**
Z	71.16	42.95	132.92	127.94	14.08	5.99	141.53	112.76
P	< 1E-12	< 1E-12	< 1E-12	< 1E-12	7.71E-07	0.01	< 1E-12	< 1E-12
Watson-Williams – p (F)	0.29 (1.18)		0.56 (0.65)		0.15 (2.17)		0.62 (1.00)	

r > 0.5 indicates synchrony; $p < 0.05$ indicates statistical differences, using the Watson-Williams test.

* the value may not be reliable due to low concentrations (uniform distribution – $p > 0.05$)

Leaf fall was negatively correlated with rainfall, and positively correlated with photoperiod; leaf budding was positively correlated with photoperiod in all of the study sites (Table 5).

Table 5: Cross correlation analyses of the environmental variables (rainfall and photoperiod) and the Fournier intensities of the budding and leaf fall of *Maprounea guianensis* Aubl. for each study period in the Chapada Diamantina mountains, Brazil, indicating the correlation coefficient (r) and the lag time (numbers of months) with which a given phenological variable follows a given environmental variable.

Study forests	Study periods	Budding				Leaf fall			
		Rainfall		Photoperiod		Rainfall		Photoperiod	
		r (lag)	p	r (lag)	p	r (lag)	p	r (lag)	p
Cloud Forest	Year 1	---	---	---	---	---	---	---	---
	Year 2	---	---	0.78 (4)	< 0.01	-0.64 (1)	0.04	---	---
Gallery Forest	Year 1	---	---	0.80 (1)	< 0.01	0.81 (4)	0.01	-0.59 (0)	0.04
	Year 2	---	---	---	---	-0.64 (1)	0.02	-0.59 (0)	0.04
Tableland Forest	Year 1	---	---	---	---	---	---	0.86 (2)	< 0.01
	Year 2	0.81 (5)	0.02	0.68 (3)	0.04	-0.62 (2)	0.04	0.67 (3)	0.04
SDTF	Year 1	---	---	0.62 (0)	0.03	---	---	0.93 (2)	< 0.01
	Year 2	0.72 (2)	< 0.01	0.72 (0)	< 0.01	-0.73 (1)	0.01	0.81 (3)	< 0.01

Cross correlations coefficient ($p < 0.05$)

Intrapopulation phenological diversity levels were low at each site (Figure 6). Diversity was zero during 65 % of study period in the cloud forest site, with recorded averages ranging from 0.69 to 0.94. In the gallery forest site, the highest diversity values were from 1.59 to 1.79 in the dry season (August and September), with the lowest values (0.0) in the rainy season (January to March). The highest averages for monthly diversity were 1.85 and 1.97 in the tableland forest site. There were higher averages of diversity in the dry forest site in the rainy season (December to January) with values ranging from 0.84 to 1.55, with averages of 0.0 in the dry season (September and October) in the second year (Figure 6).

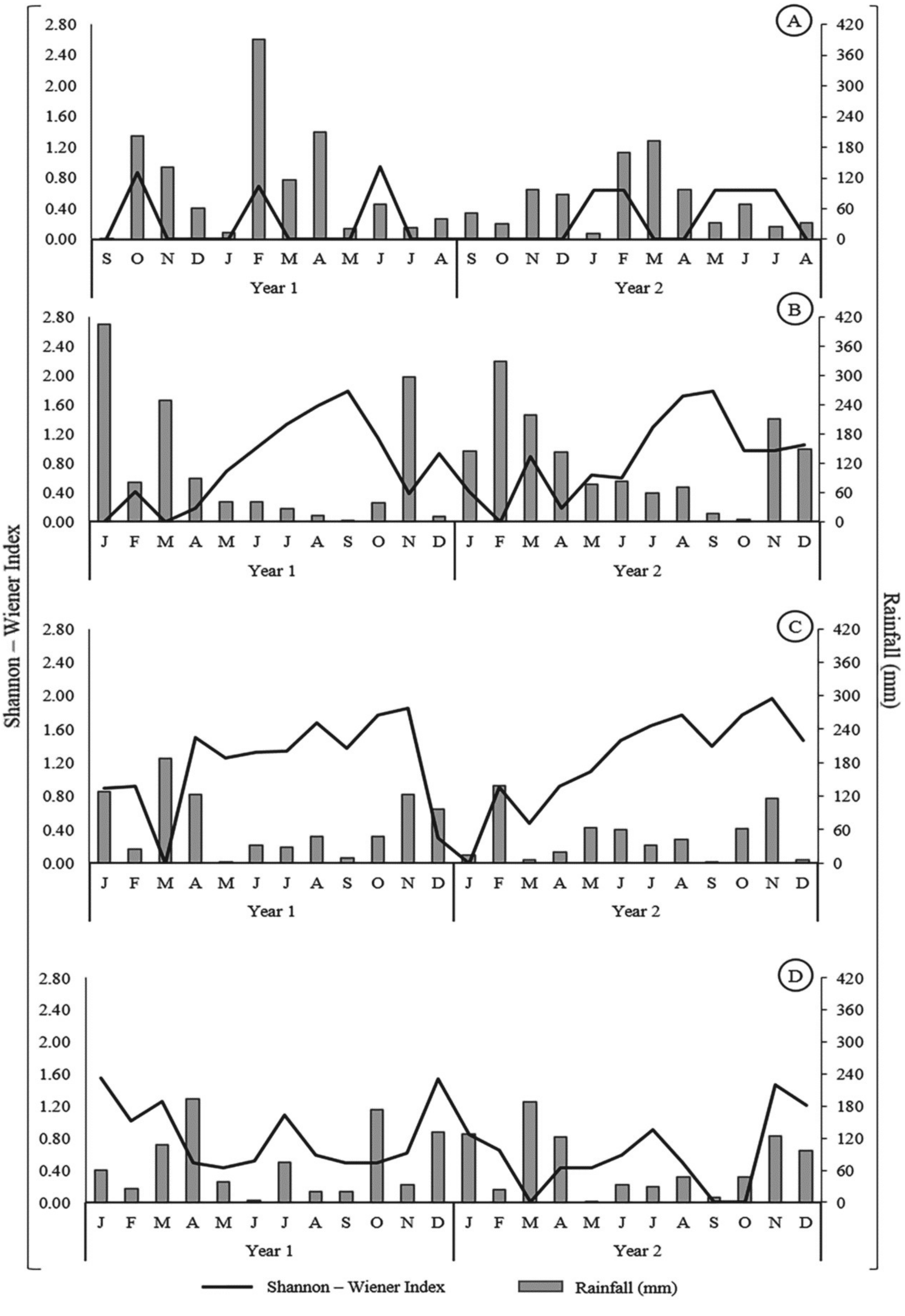

Figure 6: Phenological Diversity (Shannon-Wiener Index) of *Maprounea guianensis* Aubl. and average rainfall in the Chapada Diamantina mountains in northeastern Brazil: (A) Cloud forest; (B) Gallery forest; (C) Tableland forest; (D) Seasonally dry tropical forest

1.4 DISCUSSION

We confirmed our hypothesis that *M. guianensis* shows different leaf longevities according to the environment type, and that canopy maintenance through the year was achieved in humid sites, but not in drier sites. We found that *M. guianensis* showed evergreen to deciduous habit variations with seasonal budding and leaf fall peaks, which could be attributed to distinct and local soil water availability. We also found low phenological diversity within each site, with diversity values being similar for all the study sites.

In environments with pronounced precipitation seasonality, the dry season will determine leaf longevity, reflecting on their habit (ESCUDERO et al., 2008; KIKUZAWA; LECHOWICZ, 2011). That relationship between water availability and leaf habit variations has previously been reported for other tropical species distributed in both wet and dry environments. (BORCHERT, 1980; SINGH; KUSHWAHA, 2005; TOLEDO et al., 2012). The evergreen habit of *M. guianensis* in the cloud forest reflects the presence of cloudiness most of the year, even in the dry season, as has been seen in other studies in similar forest communities (KOPTUR et al., 1988; BERLIN et al., 2000; SUN et al., 2003). Frequent clouds in montane vegetation ensure the moisture necessary for leaf production throughout the year (HOSTETTLER, 2002; ELLER et al., 2013). Under seasonal climates, the plants may experience a dry season, but an evergreen habit can represent an advantageous strategy, as the presence of leaves in the crown for longer periods of time can increase carbon gains in species with low rates of CO_2 assimilation (FONSECA et al., 2017; XU et al., 2014; 2017).

Rapid leaf change during the dry season (with consecutive leaf fall and budding) characterized the seasonality of leaf fall in the gallery and tableland forests, showing that a semideciduous habit is a variation of the evergreen habit (*sensu* KIKUZAWA; LECHOWICZ, 2011). Reductions of leaf transpiration and the use of residual underground water can allow rapid stem rehydration and growth resumption during the dry season (REICH; BORCHERT, 1984). Wright and van Schaik (1994) pointed out this phenological behavior as a survival strategy during periods of greatest evaporative demand, as a fast leaf exchange allows young leaves to be maintained in the crowns, which provides *M. guianensis* with stomatal control and photosynthetic efficiency, even in periods of low water availability. Franco et al. (2005) and Elliott et al. (2006) highlighted this behavior in other species showing rapid leaf exchange as a way to regain a positive water status and allow subsequent budding.

The deciduous habit of *M. guianensis* responded to the climatic seasonality seen in seasonally dry tropical areas, with the exchange of all of its leaves during the period of low water availability (*sensu* KIKUZAWA; LECHOWICZ 2011), a behavior similar to that observed in other dry forest trees (AMORIM et al., 2009; BARBOSA et al., 1989; LIMA et al., 2012). Neves et al. (2017) showed that the pre-dawn water potentials did not differ from noon water potentials in seasonally dry tropical forest species during the dry season - indicating severe water scarcity at that time. Species must withstand dry periods and then exploit humid periods in seasonal environments (LASK et al., 2016). The senescence of leaves in the dry season reduces water losses by the plant and the maintenance costs of old leaves, with recovery and leaf flush with the arrival of the seasonal rains (REICH; BORCHERT, 1984; 1988; DEVI; GARKOTI, 2013).

The negative correlation observed between leaf fall and rainfall reflects this strategy, which has been widely discussed in other studies in dry tropical environments (BORCHERT et al., 2005; LIMA et al., 2012; ROCHA et al,. 2015; NEVES et al., 2016). That correlation was also noted in humid forest sites, confirming water availability as a condition for canopy rhythm throughout the year, and allowing for leaf longevity adjustments that can maximize survival and increase productivity (MELOCHE; DIGGLE, 2001; SEINO, 2001). The correlation between photoperiod and budding demonstrated the importance of that variable, as photoperiod stimulates the development of pre-dormant apical shoots and affects leaf longevity (RICHARDS, 1996; CALLE et al., 2009). No correlation was found between leaf flushing and rainfall in dry forest site, although leaf flushing was largely restricted to the rainy season, representing an adaptation of that phenophase to seasonal water availability (DYER et al., 2012; MÉNDEZ-ALONZO et al., 2012). Deciduous species may show less conservative strategies for water use due to the short repayment interval determined by reductions in leaf longevity, investing little carbon in new leaf construction (LLOYD; FARQUHAR, 1994; FRANCO et al., 2005; TOMLINSON et al., 2013). Reich et al. (1992) pointed out that deciduous species are likely to be favored in environments where annual variations in water availability result in favorable and unfavorable periods of carbon gain.

M. guianensis showed low phenological diversity at each site, which according with study performed by Goulart et al. (2005) suggests a high synchrony of their leaf phases. In general, synchronized leaf flushing during periods of increased water availability represent a mechanism to prevent energy losses during young leaf production during unfavorable periods of the year (VAN SCHAIK et al., 1993). Simulations show that when the favorable period length is equal to 1 year, all plants are expected to be evergreen, because they can carry out photosynthesis throughout the year; when the favorable period length is shorter than 1 year, a deciduous habit will be favored, with shorter leaf life cycles (KIKUZAWA; LECHOWICZ, 2011).

Our results highlight the value of studying associated phenological traits to characterize foliar habits and to understand phenological responses to temporal and spatial variations. Our results showed that *M. guianensis* responded to the environmental conditions at each site, and that photoperiod and precipitation acted as triggers for leaf fall or maintenance. Precipitation was an important environmental filter for canopymaintenance throughout the year, while photoperiod was the variable responsible for the resumption of vegetative growth. Decreases in water availability in gallery and tableland forests, and seasonally dry tropical forests caused reductions in leaf longevity and seasonal phenophases of leaf turnover. In the cloud forest, *M. guianensis* leaf longevity extended through the dry season, with continual formation of new leaves, which maintained and evergreen canopy aspect that allowed continuous photosynthetic activity and maximum carbon gains. The intrapopulation phenological diversity of *M. guianensis* confirmed its evergreen habit in humid forests and its deciduous habit in dry forests, with high synchrony between individuals in each site. Although the basic evergreen/deciduous dichotomy is reasonably clear, some intermediate conditions do exist with differing degrees of deciduousness. Our observations indicate that the phenological behavior and leaf longevity of *M. guianensis* favors its occupation of wide varieties of environments due to the high adaptability of its responses to changing conditions of water availability.

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CAPÍTULO 2

DROUGHT RESPONSES AND PHENOTYPIC PLASTICITY OF *Maprounea guianensis* AUBL. POPULATIONS IN HUMID AND DRY TROPICAL FORESTS

Submetido ao Periódico *Rodriguésia*

ABSTRACT

The wide distribution of *Maprounea guianensis* populations in dry and humid forests in the Chapada Diamantina, northeastern Brazil, has enabled our investigation of its phenotypic plasticity. We analyzed the morphofunctional traits of *M. guianensis* to understand its functional responses and phenotypic plasticity in response to seasonal droughts. Functional traits were measured in five individuals in each forest. Water potential, succulence, thickness and density, were evaluated during the dry and rainy periods; wood basic density and the saturated water content of the wood were evaluated in rainy period. Rainfall was monitored monthly. The functional traits of the plants and the means of the phenotypic plasticity indices (PPI) were submitted to analysis of variance. Our results demonstrated variations in plant functional traits between seasons and between sites. *M. guianensis* demonstrated a low capacity for storing water in its leaf and wood tissues. Those characteristics, associated with soil properties and the regional seasonal rainfall/drought regimes, conditioned water potential variations that were greatest during the rainy season, and showed more negative values in the dry forest. Our results highlight connections between drought regimes and plant responses and demonstrate the importance of functional traits associated with water availability as modulating the strategies of *M. guianensis*.

Key-words: Functional traits. Soil properties. Water availability.

RESUMO

A ampla distribuição de populações de *Maprounea guianensis* em florestas secas e úmidas na Chapada Diamantina, nordeste do Brasil, permitiu investigar a plasticidade fenotípica da espécie. Analisamos as características morfofuncionais de *M. guianensis* em florestas úmidas e secas para entender suas respostas funcionais e plasticidade fenotípica em resposta a secas sazonais. Características funcionais foram medidas em cinco indivíduos de cada floresta. O potencial hídrico, suculência, espessura e densidade foram avaliados durante os períodos seco e chuvoso; a densidade básica da madeira e o teor de água saturada da madeira foram avaliados no período chuvoso. A precipitação foi monitorada mensalmente. Os caracteres funcionais das plantas e as médias dos índices de plasticidade fenotípica (PPI) foram submetidos à análise de variância. Nossos resultados demonstraram variações nas características funcionais das plantas entre estações e entre locais. *M. guianensis* demonstrou baixa capacidade de armazenamento de água em seus tecidos foliares e lenhosos. Essas características, associadas às propriedades do solo e aos regimes regionais de chuvas / seca, condicionaram as variações do potencial hídrico maiores durante a estação chuvosa e apresentaram valores mais negativos na floresta seca. Nossos resultados destacam conexões entre os regimes de seca e as respostas das plantas, demonstrando a importância de características funcionais associadas à disponibilidade de água como modulação das estratégias de *M. guianensis*.

Palavras-chave: Características funcionais. Disponibilidade de água. Propriedades do solo.

2.1 INTRODUCTION

Functional syndromes, which are the combinations of traits that occur during evolutionary processes, increases their fitness and thus favor plant species survival (MARKS; LECHOWICZ, 2006). Each species demonstrates 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). The identification of those strategies remains an important focus of plant ecology (REICH et al., 1997; DIAZ et al., 2004; WRIGHT et al., 2004; CORNWELL et al., 2008; FRESCHET et al., 2010; MORAES et al., 2017; NEVES et al., 2017), especially when considering significant environmental variability.

Any physiological, morphological or phenological characteristics that indirectly affects plant fitness, in relation to its growth, reproduction, or survival, corresponds to a functional trait (VIOLLE et al., 2007). Among those traits, wood density, leaf succulence, thickness and density, and leaf water potential have been examined in studies designed to characterize the ecophysiological performances of plants occupying 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 those studies have reported that plants maintain their water balances by regulating water absorption and losses, with their roots and leaves serving as interfaces with the environment (DOLMAN, 1993; ROSADO, 2006).

In many tropical environments characterized by marked rainfall seasonality, plants exhibit morphofunctional traits designed to deal with periods of low water availability (MIRANDA et al., 2011; MORAES et al., 2017; NEVES et al., 2017). In such environments, plants display strategies such as: deciduousness or discontinuous canopy cover, early closure of their stomata, development of deep roots (ROJAS-JIMENEZ et al., 2007; MARKESTEIJN; POORTER, 2009; MIRANDA et al., 2011; NEVES et al., 2017), and leaf and trunk water storage that allow plants to resist water deficits (ROSADO; DE MATTOS, 2007; LIMA et al., 2012). Water deficits can increase cavitation, especially in plants with low wood densities and thin cell walls (MCDOWELL et al., 2008; CHAVE et al., 2009; LIMA et al., 2012); plants with denser woods and thick cell walls, on the other hand, are better protected against cavitation (MCDOWELL et al., 2008; CHAVE et al., 2009; LIMA et al., 2012).

In dry tropical forests, where rainfall is scarce and irregular and period of drought can last for many months, species coexist with varying morphophysiological traits (TOLEDO et al., 2011), ranging from evergreen species that store water in their woody tissues (low wood density) (NEVES et al., 2010; LIMA et al., 2012), to deciduous and semi-deciduous species having high wood densities and leaf phenologies closely linked to periods of rainfall (LIMA; RODAL, 2010; NEVES et al., 2017). In humid tropical forests with rainfall well-distributed throughout the year (thus with shorter periods of drought), wood density is often more closely related to plant growth. Species with low wood densities, or those that show rapid growth when water is available, may die in the dry season, while species with high wood densities show slow growth, but are more drought tolerant (POORTER et al., 2019).

Leaf thickness, succulence, and density are also indicative of resistance to water stress (OGBURN; EDWARDS, 2012). High values of leaf thickness and succulence are associated with higher water storage capacities, with those leaves serving as alternative sources of water during periods of lower water availability in the external environment, especially among plants that grow on sandy soils (LAMONT; LAMONT, 2000; ROSADO; DE 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). As water deficits increase in the soil, leaf density and succulence also increase, with the leaves becoming thicker (especially when exposed to high light intensities) (WITKOWSKI; LAMONT, 1991; NIINEMETS, 2001; ROSADO; DE MATTOS, 2007). Thus, dry forest species tend to present 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 environments with greater water availability and shorter drought periods, on the other hand, fewer temporal variations of leaf attributes are observed (NIINEMETS, 2001).

Water potential assessments reflect the balance between water availability in the soil and water losses due to evaporative demands (BHASKAR; ACKERLY, 2006; PALHARES et al., 2010). Species growing in humid sites in tropical forests, despite showing variations in water status, are in more favorable conditions to maintain their leaf water potentials (MIRANDA et al., 2011; MORAES et al., 2017) than plants growing in dry environments and subject to greater fluctuations of water availability (NEVES et al., 2017).

Plant water statuses often 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 the soil are highly relevant to 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).

Phenotypic plasticity represents the capacity of plants to alter their genotype expressions, with changes in their physiologies and/or morphologies to adapt to 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 in natural environments (ACKERLY et al., 2000).

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. 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 dry forests (NEVES et al., 2017) and a brevideciduous habit in humid forests (MIRANDA et al., 2011), 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 dry forests (SDTF) would show characteristics associated with water storage, with less dense wood and leaves with high succulence, density, and thickness, which would allow it to maintain a favorable water balance throughout the year – in contrast to individuals growing in humid forest sites, which would be expected to show characteristics such as higher wood densities, lower water storage capacities, lower leaf water retention values, and maintain high water potential values. We also expected the plants growing in the SDTF to show higher trait plasticity, as the dry forest environment is more variable than the humid forest.

2.2 Materials and Methods

2.2.1 Species and Studied Sites

The present study was conducted in a humidity gradient extending from Atlantic Forest remnants (cloud, gallery, and tableland forests) to seasonally dry tropical forest (SDTF) vegetation (12º 27 '06 "- 12º 33 '39" S and 41º 23 '14 "- 41º 35' 52" W), from 500 m - 1000 m a.s.l., on the eastern border of the Chapada Diamantina mountains (Figure 1A - F), where was possible to encounter individuals of *Maprounea guianensis* Aubl. (Euphorbiaceae), a tree, 5-15 m tall (Figure 1G), widely distributed in Brazil. That tree species 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).

Atlantic Forest sites have a continuous evergreen canopy. The cloud forest site (12°27'49" S – 41°28'34" W, at 940 – 1000 m a.s.l., Figure 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., Figure 1C) is situated along the Lençóis River and experiences sporadic and rapid flooding during the rainy season (FUNCH et al., 2002); the tableland forest (12º28'31'' S - 41º23'14'' W, at 500 – 600 m a.s.l., Figure 1D) occurs on clayey yellow-red soils (COUTO et al., 2011); the SDTF site (12º 27'6.46" S - 41º 35'51.81" W, at 657 m a.s.l., Figure 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 dry winters (between June and October). Historical climatic data were obtained from the National Institute of Meteorology (INMET), based on the Lençóis Meteorological Station (Figure. 2).

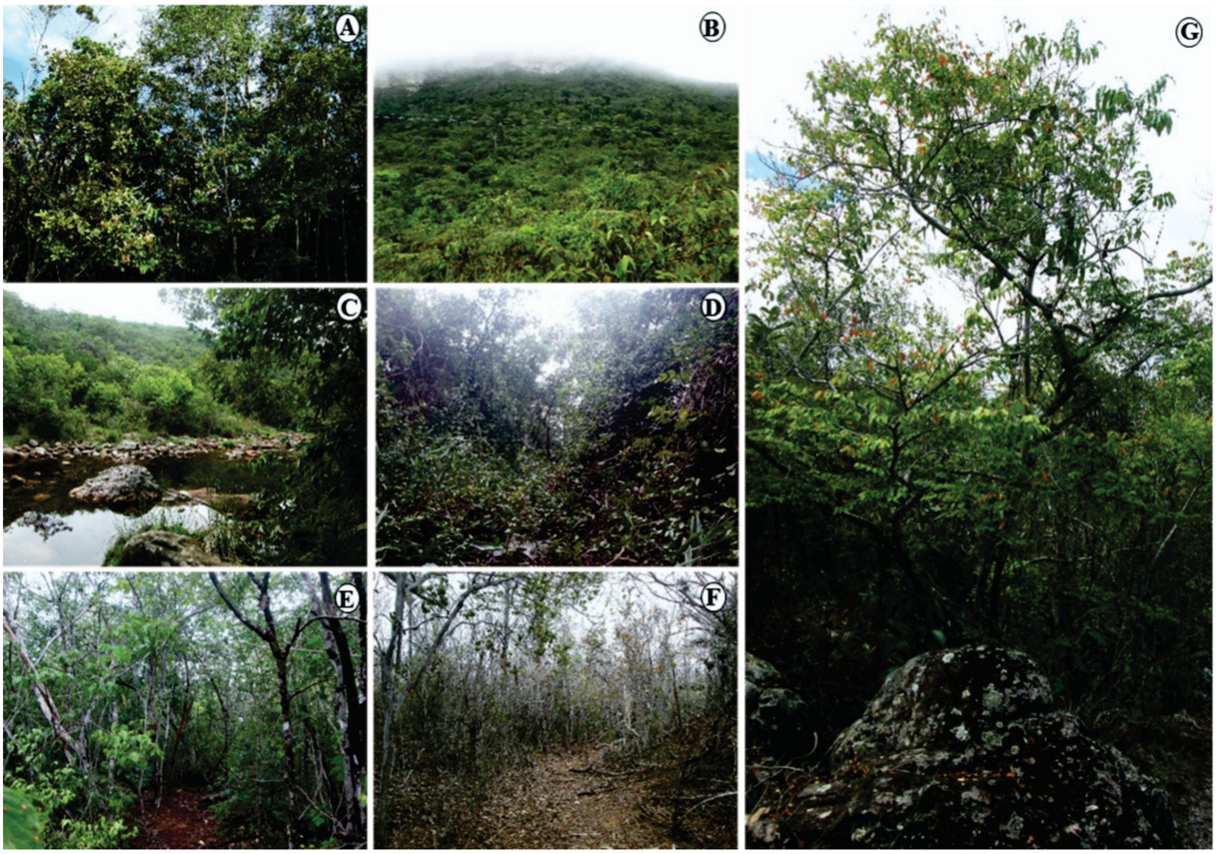

Figure 1. Figure 1 - Views of the study areas and focal species: (A) cloud forest; (B) cloud forest with mist; (C) gallery forest; (D) tableland forest; (E) Seasonally dry tropical forest during the rainy period; (F) Seasonally dry tropical forest during the dry period; (G) *Maprounea guianensis* Aubl.

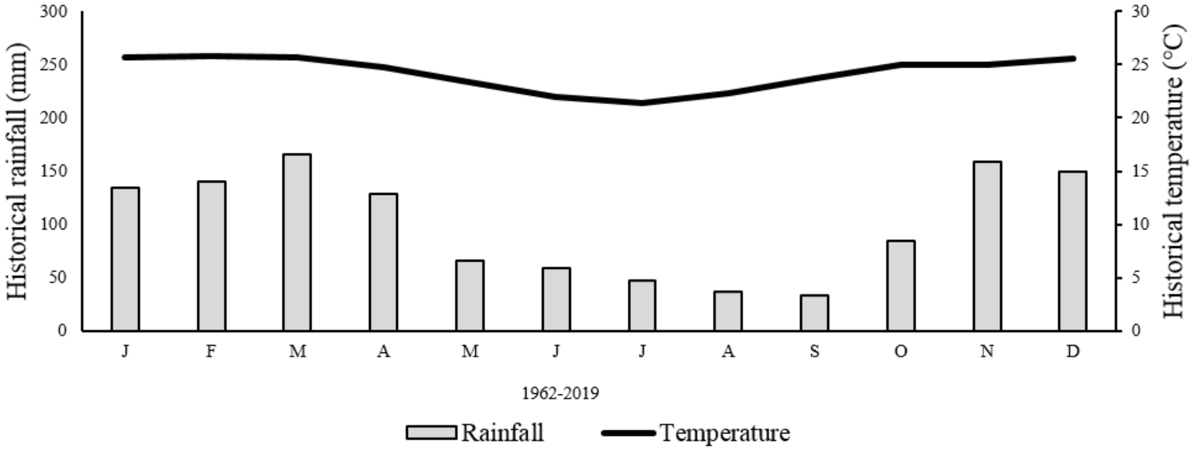

Figure 2: Historical environmental data of the study sites in the municipalities of Lençóis and Palmeiras, in the Chapada Diamantina mountains, Bahia State, Brazil: rainfall and temperature (source: Instituto Nacional de Meteorologia).

2.2.2 Environment variables

Environmental data used in the analysis of morphofunctional traits were collected near the marked individuals. Rainfall data were obtained using pluviometers installed at each site. Equivalent rainfall measurements were assumed for the gallery and tableland forests due to their proximity (9.53 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; soil analyses were performed by the Soil, Water and Plant Analysis Laboratory, Embrapa Semiarid – PE.

2.2.3 Functional traits

At each site, five adult individuals (approximately 10 meters tall and distant 4 meters one from another) were marked for measurements of their functional traits. Two measurements were taken in the rainy season (March/2018 and 2019) and two in the dry season (September/2017 and 2018), with the same individuals being sampled 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. 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). (0.23 cm²). 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 (to 0.001 g, using a precision electronic balance (MARTE – AY220: 0.0001g); the disks were then placed in a drying oven at 55º C 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). To better visualize the dispersion and asymmetry of the data, we present the results of leaf traits in the form of Box Plots, using BioEstat 5.3 software (AYRES et al., 2007). 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 (Δ_Ψ) were calculated using the formula $\Delta_\Psi = \Psi_{PD} - \Psi_{MD}$. Wood basic density (WBD) sampling was performed in March/2018; 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 basic density (WBD = 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).

2.2.4 Data 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 the physical soil analysis data of the four sites. Posteriorly, their means were compared by the Tukey test ($p < 0.05$), using Sisvar software (version 5.6, Lavras, Minas Gerais, Brazil) (FERREIRA, 2011).

2-factor analysis of variance (ANOVA) was used to determine the temporal and spatial characteristics of *M. guianensis* in the different habitats studied, with each evaluation month being considered a treatment. The means were compared by Tukey test, using Sisvar 5.6 open source software, at a 5% level of probability (ZAR, 2010).

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 – 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 were tested using 1-factor analysis of variance (ANOVA).

2.3 RESULTS

The t-test showed variations between rainfall volumes in the dry and humid forests for the second rainy season (dry forest x cloud forest) and for all the dry seasons (dry forest x humid forests) ($p < 0.05$) (Figure 3; Table 1).

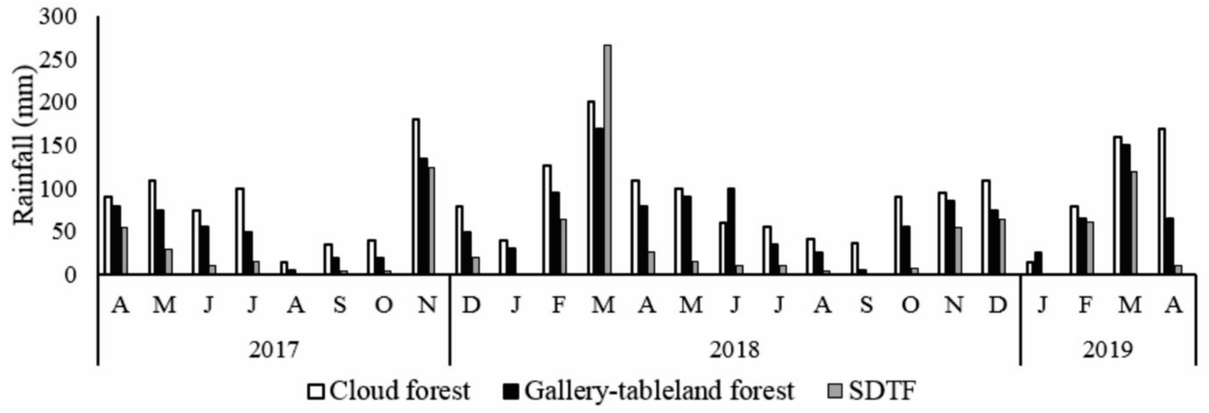

Figure 3: Rainfall data of the study sites in the municipalities of Lençóis and Palmeiras, in the Chapada Diamantina mountains, Bahia State, Brazil: Cloud forest; Gallery-tableland forest; Seasonally dry tropical forest (SDTF).

Table 1: Independent t-test comparing rainfall volumes in 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, tableland and cloud forests, and in the seasonal dry tropical forest (SDTF) in the Chapada Diamantina mountains, Bahia State, Brazil

		Rain 1		*Rain 2*	
		Gallery-tableland forest	**SDTF**	**Gallery-tableland forest**	**SDTF**
Cloud forest	p (t)	0.194 (0.904)	0.218 (0.810)	0.180 (0.962)	**0.049 (1.815)**
Gallery-tableland forest	p (t)		0.424 (0.196)		0.161 (1.040)

		Dry 1		*Dry 2*	
		Gallery-tableland forest	**SDTF**	**Gallery-tableland forest**	**SDTF**
Cloud forest	p (t)	0.118 (1.278)	**0.020 (2.982)**	0.260 (0.674)	**0.003 (5.239)**
Gallery-tableland forest	p (t)		**0.041 (2.312)**		**0.041 (2.312)**

$p < 0.05$ indicates statistical difference

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 (Table. 2).

Table 2: Means (± SE) of the physical parameters of each soil type in the gallery, tableland and cloud forests, and in the seasonal dry tropical forest (SDTF) 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.

Leaf traits varied between the dry and humid forest populations, and between seasons (Figure. 4; Figure.5). 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 (Figure. 4; Figure. 5).

Water potentials varied between the populations of dry and humid forests and between seasons (Figure. 6). The water potential data showed the highest Ψ_{PD} and Ψ_{MD} values in the rainy season. In terms of spatial variations, the Δ_{Ψ} indicated significant differences between the dry and humid forest populations, with smaller values in humid forests during the rainy season. The lowest Δ_{Ψ} (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 (Figure. 6).

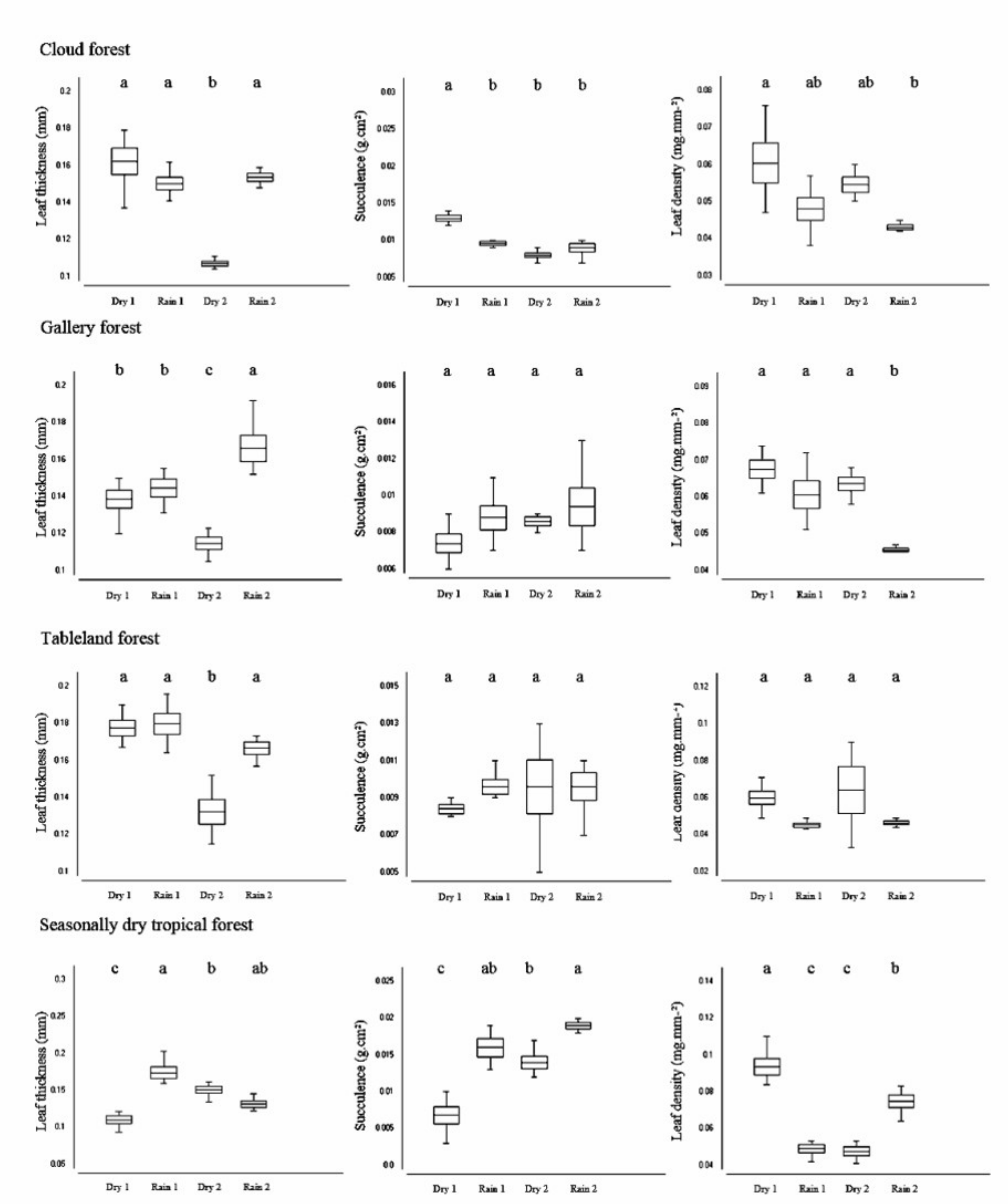

Figure 4. Box plot chart comparing the data of leaf thickness (mm), succulence (g.cm²), and leaf density (mg.mm-²) of *Maprounea guianensis* Aubl. between seasons (dry and rain) in the cloud forest, gallery forest, tableland forest, and seasonally dry tropical forest located in the Chapada Diamantina mountains, Bahia State, Brazil. Horizontal lines represent the arithmetic means (middle line) ± standard error (upper and lower lines); outer horizontal lines represent the minimum and maximum values. Means followed by same letter indicate no statistically significant differences (*$p < 0.05$*)

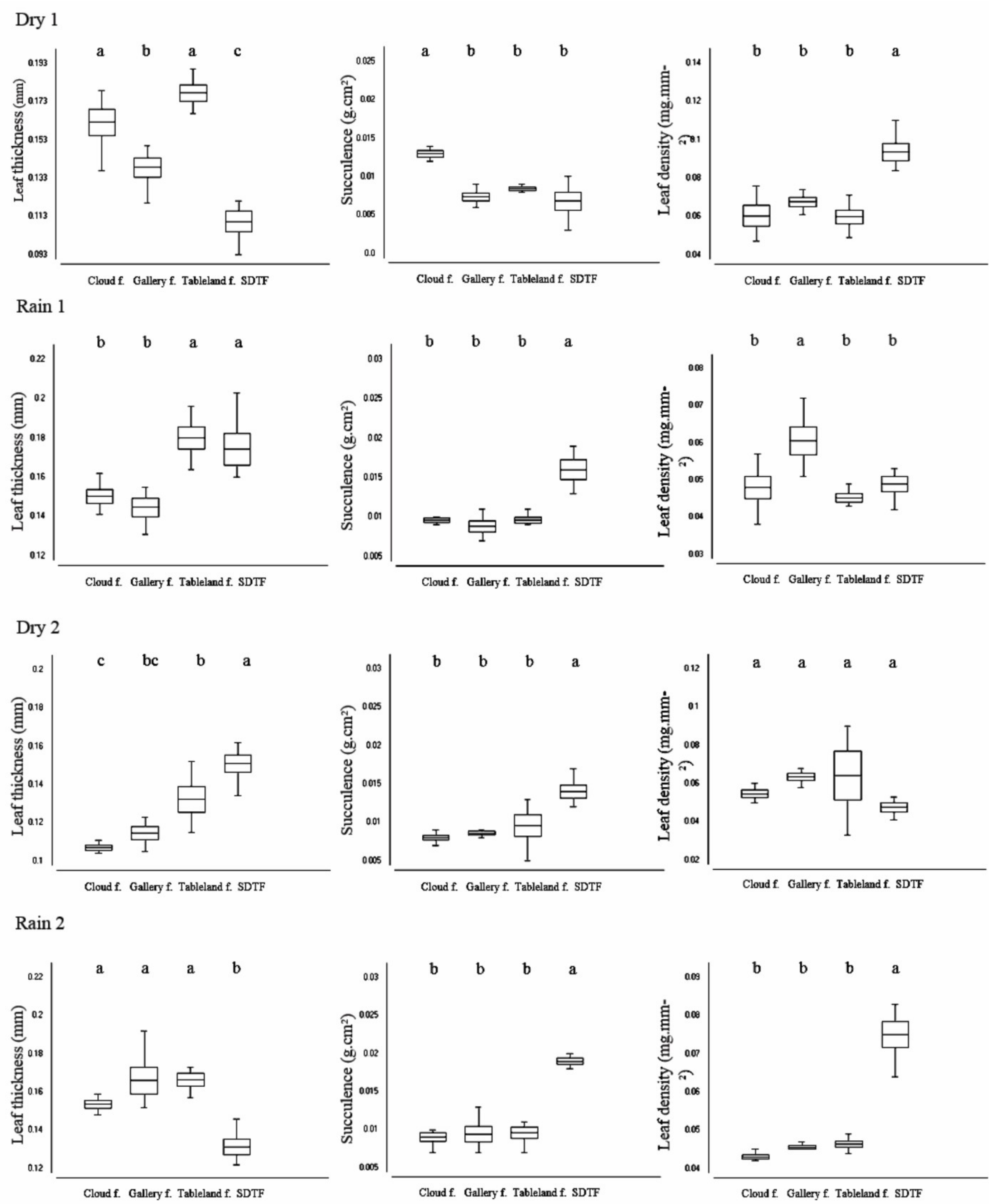

Figure 5: Box plot chart comparing the data of leaf thickness (mm), succulence (g.cm²), and leaf density (mg.mm-²) of *Maprounea guianensis* Aubl. between sites: cloud forest, gallery forest, tableland forest, and seasonally dry tropical forest in the Chapada Diamantina mountains, Bahia State, Brazil. Horizontal lines represent the arithmetic means (middle line) ± standard error (upper and lower lines); outer horizontal lines represent the minimum and maximum values. Means followed by same letter indicate no statistically significant differences ($p < 0.05$)

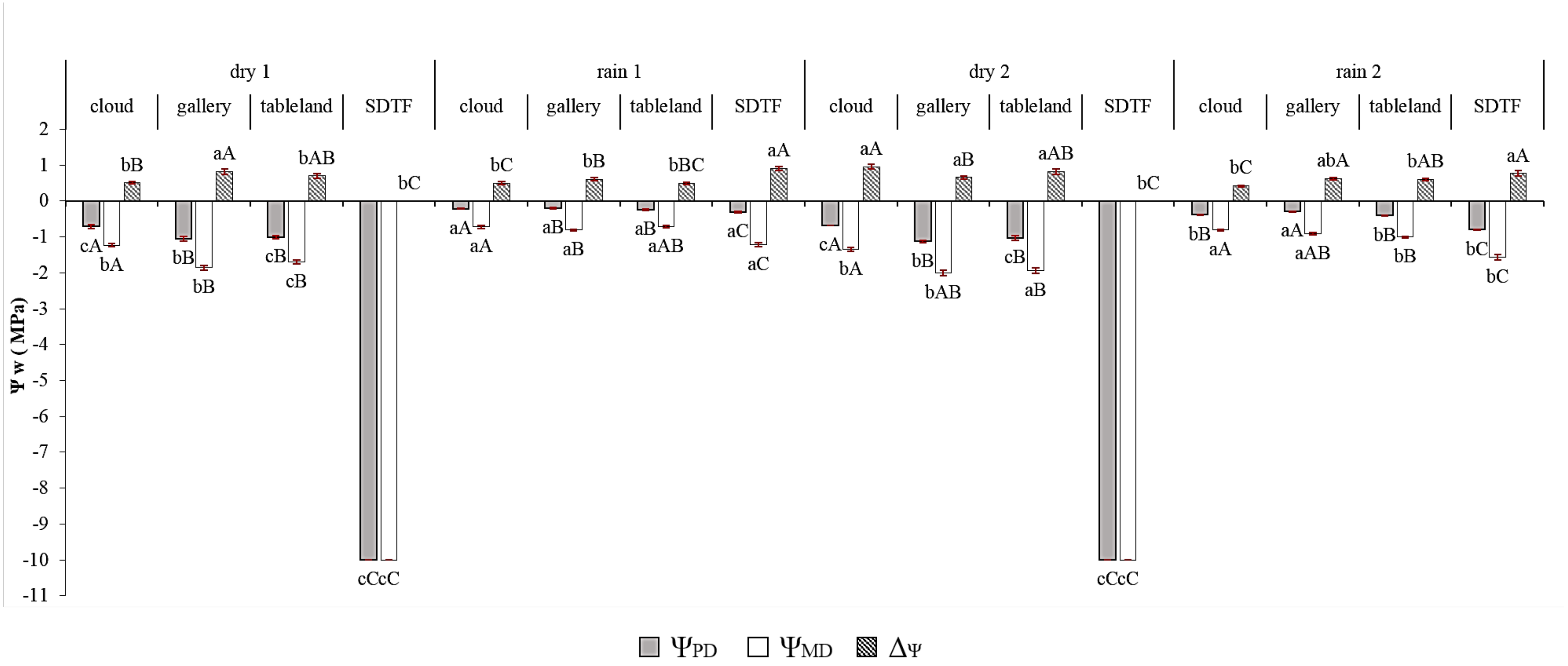

Figure 6: Means ± standard error of the predawn (Ψ_{PD}) and after midday (Ψ_{MD}) water potential values and the amplitudes of variation of the water potential (Δ_{Ψ}) of *Maprounea guianensis* Aubl. in the cloud forest, gallery forest, tableland forest, and seasonally dry tropical forest located in 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 ($p < 0.05$).

Wood basic density was high in all populations, although there were differences between them, from 0.74 g/cm^{-3} in the cloud forest to 0.98 g/cm^{-3} in the SDTF. The Saturated water contents were low, and differed between populations, with the lowest percentage (42.37%) observed in SDTF and the highest (67%) in the cloud forest (Table 3).

Table 3 - Mean (± SE) values of wood basic densities and the saturated water content in the wood of *Maprounea guianensis* Aubl. in the gallery, tableland and cloud forests, and in the seasonal dry tropical forest (SDTF) in the Chapada Diamantina mountains, Bahia State, Brazil. Means followed by same letter indicate no significant differences ($p < 0.05$).

Sites	**Wood basic density (g.cm-³)**	**Saturated water content (%)**
Cloud forest	0.738d	67.058a
Gallery forest	0.812c	60.118b
Tableland forest	0.922b	56.353c
SDTF	0.985a	42.372d

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

In general, *M. guianensis* showed greater phenotypic plasticity in the SDTF, and lower plasticity in humid forests (Table 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 (Table 4). Water potential values (Ψ_{PD}, Ψ_{MD}, and $\Delta\Psi$) showed high PPI, highlighting the population of SDTF site, with the highest $\Delta\Psi$ (PPI) (Table 4).

Table 4 - Mean, maximum value (Max), minimum value (Min), and phenotypic plasticity indexes (PPI) of morphofunctional traits of *Maprounea guianensis* Aubl. in the gallery, tableland and cloud forests, and in the seasonal dry tropical forest (SDTF) 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	0.3	0.3	0.03
Ψ_{PD} (MPa)	-1.73	-0.71	-0.2	-1.12	-0.21	-1.03	-0.24	-10	-0.31	**0.72**	**0.81**	**0.77**	**0.97**
Ψ_{MD} (MPa)	-2.3	-1.35	-0.38	-2	-0.81	-1.95	-0.72	-10	-1.22	**0.72**	**0.6**	**0.63**	**0.88**
Δ_{Ψ} (Mpa)	0.63	0.96	0.42	0.82	0.61	0.82	0.49	0.91	0	**0.56**	0.26	0.4	**1**
Mean										**0.50 a**	**0.41 a**	**0.41 a**	**0.65 a**
Standard Error										**± 0.08**	**± 0.10**	**± 0.10**	**± 0.16**

Cloud forest (clou), gallery forest (gall); tableland forest (tabl), Seasonally Dry Tropical Forest (SDTF), leaf thickness (LTH), succulence (SUC), leaf density (LDE), before dawn water potential (ΨPD), after midday water potential (ΨMD); daily amplitude of water potential (ΔΨ). Phenotypic plasticity index values from 0 to 1; values closer to 1 show higher plasticity, values closer to 0 show lower plasticity. Means followed by same letter indicate no statistically significant differences ($p < 0.05$).

2.4 DISCUSSION

M. 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 in water potential, physical soil properties, and rainfall regimes (with seasonal droughts). Populations under 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 seen in the dry forest led to greater fluctuations in plant water potentials and demonstrated 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. *M. 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). The high values of water potential observed here show the high capacity for water regulation of the populations in humid sites, suggesting no water restrictions in the that soil.

SDTF plants were exposed to periods of very severe water deficit, showed very low Ψ_{AM}, Ψ_{MD}, and $\Delta\Psi$ values – indicating significant water restrictions. 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, 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 basic 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 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.

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., 2015). 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 (MIRANDA et al., 2011; LEMOS FILHO; MENDONÇA FILHO, 2000). Additionally, the SUC and LDE values of the species were considered low in comparison to other species examined in the same region (MORAES et al., 2017; OLIVEIRA, 2019), likewise indicating a low water retention capacity of their leaves.

Rosado et al. (2012) recognized the practicality of studying the morphological traits of the species in the different environments in which they are distributed to better understand their characteristics, but those authors also highlighted the importance of analyzing physiological traits (such as water potential) as essential for describing plant responses.

The physical properties of the soils were different in the different sites, which, according to Perkins et al. (2013), will influence water availability for the plants. Tableland forests differed from the others due to their clayey soils, which favor water retention and allowed the *M. guianensis* populations growing there to maintain positive water balances. The cloud and gallery forests have sandy soils with low water retention capacities due to the relatively large spaces between the sand particles that allow rapid drainage and the entrance of air into the soil (BRADY; WEIL, 2013; PERKINS et al., 2013).

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 of the vegetation (STADTMÜLLER, 1987; HOLDER, 2006). The proximity of plants to watercourses 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).

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 and Estanislau (1999) and Beutler and Centurion (2004) as affecting agricultural species. 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 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 (unpublished data); 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.

In the present study, water potential appeared as the principal functional trait modulating the species` response to seasonal differences in water availability. Leaf traits such as SUC, LTH, and LDE were not found to be good indicators of phenotypic plasticity. Alpert and Simms (2002) noted that phenotypic plasticity is associated with (among other factors) resource availability (water and nutrients) and the response times of the plants to changing environmental conditions. *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., 2014; CHATURVEDI et al., 2018; ZORGER et al., 2019).

The present study demonstrated that local environmental parameters (especially seasonal rainfall, drought regimes, and soil characteristics) influenced variations in the functional traits of *M. guianensis* populations, reflecting phenotypic plasticity. Our results highlight the connections between drought regimes and plant responses, demonstrating the importance of functional traits associated with water availability (especially water potential) in modulating the adaptive strategies of *M. guianensis*.

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CAPÍTULO 3

INFLUÊNCIA DA SECA NO INCREMENTO RADIAL DE *Maprounea guianensis* AUBL. EM FLORESTAS TROPICAIS ÚMIDA E SECA

RESUMO

Para sobreviverem a seca, as plantas desenvolvem *trade-offs* morfofuncionais que lhes permite assumir estratégias de escape ou de tolerância ao déficit hídrico. Nesta pesquisa, investigamos os efeitos da seca no crescimento radial e na fenologia de *Maprounea guianensis* em floresta ciliar e floresta tropical sazonalmente seca (FTSS), na Chapada Diamantina, Brasil. Marcamos 22 indivíduos/sítio, acompanhando mensalmente o incremento radial e a fenologia vegetativa e reprodutiva. Calculou-se a amplitude diária do potencial hídrico (Δ_{Ψ}) em cinco indivíduos/sítio em períodos secos e chuvosos. Dados de precipitação e fotoperíodo foram coletados e comparados com o incremento radial mensal e a fenologia através de correlação cruzada. Utilizando o mesmo teste, comparou-se a relação do incremento radial com as fenofases. Um teste T comparou o incremento radial e as fenofases entre os sítios. Os resultados mostraram correlação: das variáveis ambientais com o incremento radial e a fenologia, e do incremento radial com as fenofases. No período de seca *M. guianensis* diminuiu o incremento radial e perdeu (total ou parcialmente) suas folhas. Na floresta ciliar manteve padrão semidecíduo e balanço hídrico positivo, assumindo estratégia de tolerância a seca, enquanto na FTSS teve redução drástica do $\Delta\Psi$ (com 0 MPa) e da copa com mais de 80% em senescência, assumindo estratégia de escape da seca. Os recursos para reprodução não limitaram o incremento radial que, por sua vez, foi maior na floresta ciliar. Nossos resultados mostram que a seca limita o crescimento de *M. guianensis* e destaca a importância de compreender a resposta das plantas frente às mudanças climáticas.

Palavras-chave: Chapada Diamantina, Dendrômetros, Fenodinâmica, Floresta tropical, Potencial hídrico.

ABSTRACT

In order to survive drought, plants develop morphofunctional *trade-offs* that allow them to assume strategies for escape or tolerance to water deficit. In this research, we investigated the effects of drought on the radial growth and in phenology of *Maprounea guianensis* in galerry and seasonally dry tropical forest (SDTF), in Chapada Diamantina, Brazil. We marked 22 individuals/site, monitoring the radial increment and the vegetative and reproductive phenology monthly. The daily amplitude of water potential (Δ_Ψ) was calculated in five individuals/site in dry and rainy periods. Precipitation and photoperiod data were collected and compared with the monthly radial increment and phenology through cross-correlation. Using the same test, the relationship between radial increment and phenophases was compared. A T test compared the radial increment and phenophases between sites. The results showed a correlation: of the environmental variables with the radial increase and the phenology, and of the radial increase with the phenophases. During the dry season, *M. guianensis* decreased the radial increment and lost (totally or partially) its leaves. In the galerry forest, it maintained a semi-deciduous pattern and a positive water balance, assuming a drought tolerance strategy, while in the SDTF it had a drastic reduction in Δ_Ψ (with 0 MPa) and the canopy with more than 80% in senescence, assuming an escape strategy from drought. The resources for reproduction did not limit the radial increment, which, in turn, was greater in the galerry forest. Our results show that drought limits the growth of *M. guianensis* and highlights the importance of understanding the response of plants to climate change.

Keywords: Chapada Diamantina, Dendrometers, Phenodynamics, Rainforest, Water potential.

3.1 INTRODUÇÃO

A periodicidade do crescimento radial em árvores tropicais tem sido um atributo de crescente interesse em questões climáticas e de conservação de espécies (ROZENDAAL; ZUIDEMA, 2011; CARDOSO et al., 2012; VLAM et al., 2014; ZUIDEMA et al., 2013; BRANDES et al., 2015; MOREL et al., 2015; VENEGAS-GONZÁLEZ et al., 2015; VASCONCELLOS et al., 2016). A avaliação dessas informações pode indicar as estratégias de colonização e sobrevivência de espécies vegetais e são necessárias para o estabelecimento de práticas eficazes de manejo florestal, em planos de recuperação de áreas degradadas (WORBES 1999; 2002; CALLADO, 2010; ROZENDAAL; ZUIDEMA, 2011).

A atividade cambial pode ser indiretamente acessada por meio de dendrômetros, uma opção não destrutiva e eficiente para medidas contínuas do crescimento em diâmetro do tronco que permite avaliar pequenas mudanças no seu crescimento em intervalos reduzidos (BOTOSSO; TOMAZELLO FILHO, 2001). Este crescimento pode mostrar diferentes respostas aos fatores endógenos e ambientais (CALLADO et al., 2001; TOLEDO et al., 2012). Dentre os fatores ambientais, a precipitação (LISI et al., 2008; TOLEDO et al., 2012; BRANDES et al., 2015; KANIESKI et al., 2017; KLISZ et al., 2019) e o fotoperíodo (BORCHERT, 1999; CALLADO et al., 2001; 2004) se mostram relevantes para explicar as variações sazonais no incremento radial. Com base nas condições ambientais, o comportamento sazonal do câmbio vascular pode exibir diferença interespecífica (CALLADO et al., 2013) ou intraespecífica (RAJPUT; RAO 2000; RAO; RAJPUT, 2001; TOLEDO et al., 2012; COSTA et al., 2013). É possível ainda observar espécies que mantém o mesmo ritmo cambial sob regimes pluviométricos distintos (FAHN, 1995; CALLADO et al., 2001; 2013) ou que mostrem adaptações a sazonalidade local (MARCATI et al., 2006; 2008).

Ccaracterísticas do solo e sua disponibilidade hídrica também alteram o crescimento e desenvolvimento vegetativo das plantas (NEVES et al., 2017). Através de medidas de potencial hídrico é possível estimar a água disponível no solo para as plantas que, perante um déficit de água pode ou não regular o seu potencial hídrico, refletindo no seu crescimento (WELCKER et al., 2011; RÜGER et al., 2012). Toledo et al. (2012) investigaram diferenças no incremento radial do caule entre populações de *Plathymenia reticulata* Benth. localizadas em ambientes de savana e floresta ecotonal considerando o seu status hídrico, e encontraram relação entre o incremento radial e o potencial hídrico.

A fenologia foliar pode fornecer informações úteis sobre os processos de crescimento estando frequentemente associada com estágios específicos do incremento radial (MATTOS;

SALIS, 2007; TOLEDO et al., 2012). Espécies perenes e decíduas podem se diferenciar tanto no hábito foliar como no aumento do diâmetro, por exemplo, com crescimento radial e brotamento iniciando simultaneamente (ROSSATTO et al., 2009; ROSSATO et al., 2013). Embora a fenologia reprodutiva seja menos estudada (CALLADO et al. 2001, 2004; O'Brien et al., 2008; SILVA, 2018), a locação de recursos envolvidos na produção e desenvolvimento de flores e frutos pode acarretar na diminuição ou até na parada do incremento radial (GUREVITCH et al., 2006; TAIZ et al., 2015).

Uma interpretação mais ampla do incremento radial e da sua relação com a variação de padrões fenológicos, poder ser obtida comparando espécies ou populações que crescem em habitats contrastantes (CALLADO et al., 2013; 2014). Mesmo sob um gradiente de umidade, as florestas tropicais sempre passam por um período de seca (mais ou menos severos), sendo este período um dos estressores abióticos mais importantes para o desenvolvimento das plantas, por controlar o seu ritmo de crescimento e a sua distribuição (ARANDA et al., 2012; YANG et al., 2013; ASNER et al., 2016; COPELAND et al., 2016). Para sobreviverem no período de estresse hídrico as plantas podem assumir *trade-off*s morfofuncionais importantes que lhe permite escapar ou tolerar a seca (MARKESTEIJN; POORTER, 2009; WRIGHT et al., 2010). Uma das estratégias de escape é a deciduidade total das folhas a fim de reduzir a desidratação com a perda de água por transpiração (KOOYERS, 2015). Deste modo, as plantas decíduas lançam suas folhas apenas nas épocas em que a água é mais abundante (PEARSE et al., 2019). Em contrapartida, a tolerância à seca é uma estratégia associada a espécies perenes. Essas plantas compreendem processos fisiológicos distintos que lhe permite manter o seu crescimento e desenvolvimento mesmo sob condições desfavoráveis (ROSADO et al., 2013).

Maprounea guianensis Aubl. (Euphorbiaceae) é uma espécie arbórea, amplamente distribuída no Brasil com destaque econômico (apresenta agentes farmacêuticos e potencial antibacteriano e antifúngico) e ambiental (única espécie arbórea que ocorre em florestas seca e úmida na Chapada Diamantina) (DAVID et al., 2004; MARQUES, 2011; MIRANDA et al., 2011, COUTO-SANTOS et al., 2015, NEVES et al., 2017). Um dos fatores que favorece a sua ampla distribuição é a capacidade de ajustar seus traços morfofuncionais para se adaptar a diferentes condições de regime de chuva e característica do solo. Pesquisas anteriores mostram que a espécie apresenta mecanismo para escapar do período de déficit hídrico quando em floresta seca (com folhas de curta duração, caules resistentes de alta densidade e baixo potencial hídrico - assumindo um hábito decíduo) e mecanismos que lhe permite tolerar esse período quando em florestas úmidas (com maior longevidade foliar e balanço hídrico positivo ao longo do ano – assumindo um hábito sempre verde) (SANTOS 2020, dados não publicados).

Assim, o principal objetivo deste estudo foi investigar a influência da seca no crescimento de *M.* guianensis em sítios de floresta úmida e seca na Chapada Diamantina, nordeste do Brasil. Esperamos observar diferentes estratégias de sobrevivência a seca, com correlação entre o crescimento radial, a fenologia (foliar e reprodutiva) e o potencial hídrico, considerando o papel da pluviosidade em cada sítio e o fotoperíodo da região. Esperamos encontrar diferentes estratégias para enfrentar o período de déficit hídrico e, consequentemente, diferentes ritmos de crescimento entre as florestas seca e úmida.

3.2 MATERIAL E MÉTODOS

3.2.1 Espécie experimental e sítios estudados

O gênero *Maprounea* Aubl pertence à família Euphorbiaceae e compreende cinco espécies distribuídas na América do Sul e na África. Dentre as espécies encontradas no Brasil, *Maprounea guianensis* Aubl. se destaca por ser amplamente distribuída na região da Chapada Diamantina – Bahia, em sítios úmidos e secos, apresentando porte arbóreo de 5 – 15m de altura (FUNCH et al., 2005; CERQUEIRA, 2009; MIRANDA et al., 2011; COUTO-SANTOS et al., 2015; NEVES et al., 2017) (Figura 1 A). Neste trabalho, foram acompanhadas duas populações de *M. guianensis* em: (i) um sítio úmido de floresta ciliar (12º33’38.6” S - 41º24’40” W, 500 m) com solo franco-arenoso (SANTOS 2020, dados não publicados) e uma faixa relativamente estreita (15-25m) de vegetação distribuídas nas margens do rio Lençóis que lhes propicia elevada disponibilidade hídrica (MIRANDA et al., 2011) (Figura 1 B).; (ii) um sitio seco de floresta tropical sazonalmente seca (FTSS) (12º 27’6.46” S - 41º 35’51.81” W, 657m) de solo franco argiloso arenoso (SANTOS 2020, dados não publicados), e baixa disponibilidade hídrica (NEVES et al., 2016) (Figura 1 C). A região apresenta clima do tipo Aw, com inverno seco e verão chuvoso, segundo a classificação climática de Köppen (ALVARES et al., 2013).

3.2.2 Variáveis ambientais

Os dados de precipitação mensal de cada sítio foram coletados mensalmente a partir da instalação de pluviômetros, e os dados do fotoperíodo da região foi obtido através do site do observatório Astronomical Applications Department of the U.S. Naval (http://aa.usno.navy.mil/data/docs/RS_OneYear.php).

Figura 1. Apresentação dos sítios e da espécie estudada, e das fenofases observadas na floresta ciliar e na floresta tropical sazonalmente seca (FTSS), situadas na Chapada Diamantina, Bahia, Brasil. **(A)** *Maprounea guianensis* Aubl. – folhas em senescência; **(B)** floresta ciliar; **(C)** FTSS; **(D)** fenofases foliares – brotamento, folha jovem e folha madura; **(E)** inflorescência; **(F)** frutos imaturos; **(G)** fruto maduro.

3.2.3 Traços Funcionais

Foram marcados 22 indivíduos adultos de *Maprounea guianensis* em cada sítio para o acompanhamento mensal do incremento radial e da fenologia. O incremento radial foi acompanhado com a instalação de faixas dendrométricas (precisão de 0,2 mm) para mensurar o crescimento contínuo em diâmetro ao longo do tempo. As faixas foram confeccionadas conforme indicações de Botosso e Tomazello Filho (2001), afixados na altura do DAP (diâmetro a altura do peito = 1,30 m do solo). Os valores obtidos da variação da circunferência foram convertidos em incremento radial assumindo uma seção transversal circular do caule (PALERMO, 2002). Os dendrômetros foram instalados em junho de 2016, sendo os seis primeiros meses desconsiderados nas análises devido ao tempo de ajuste das faixas dendrométricas.

Nesses mesmos indivíduos, observou-se as fenofases vegetativas: brotamento (BR), folha jovem (FJ), folha madura (FM) e queda foliar (QD); e as reprodutivas: floração (FA), fruto imaturo (FI) e fruto maduro (FM), utilizando um método semi-quantitativo (Figura 1: D-G). Para tanto, considerou-se cinco categorias de classes (0 a 4) em intervalos de 25%, sendo as intensidades das fenofases mensuradas mensalmente como a razão da soma das categorias multiplicada por 100 e o número máximo de Fournier (4) multiplicado pelo número de indivíduos (FOURNIER, 1974; SAN MARTIN-GAJARDO; MORELLATO, 2003). Utilizamos a classificação de Kikuzawa e Lechowicz (2011) para definir os hábitos fenológicos foliares, e Newstrom et al. (1994) para os padrões reprodutivos, considerando os critérios de frequência e duração.

Para avaliar o potencial hídrico (Δ_Ψ) utilizou-se uma a câmara de pressão de Scholander (PMS InstrumentCo – Modelo 1000 – USA). Foram tomadas duas medidas nos períodos secos (setembro/2017 e setembro/2018) e duas nos períodos chuvosos (março/2018 e março/2019), em cinco indivíduos marcados em cada sítio. Para tanto, foram coletados de cada indivíduo, três ramos de aproximadamente 20 cm, localizados no terço médio da copa, acondicionando-os em sacos plásticos e armazenando-os em caixa térmica para minimizar as perdas de água. As medidas foram tomadas em dois horários: antes do amanhecer Ψ_{AM} (entre 4:00 e 5:00 h), para avaliar o valor máximo do potencial no início do dia; e após o meio dia Ψ_{MD} (entre 12:30 e 13:30 h), para avaliar o menor potencial diário. Com estes dados calculou-se a amplitude diária de potencial hídrico (Δ_Ψ) a partir da fórmula: $\Delta_\Psi = \Psi_{AM}-\Psi_{MD}$ (LEMOS FILHO; MENDONÇA FILHO, 2000).

3.2.4 Análise dos dados

A normalidade da distribuição dos dados de incremento radial e fenologia foram testadas com base no teste de Shapiro e Wilk (ZAR, 1996), apontando distribuição não normal. Com isso, foi feito teste de correlação cruzada afim de analisar a relação (lag temporal) das do incremento radial e das fenofases com as variáveis ambientais (precipitação em cada sítio e fotoperíodo da região), assim como para verificar a relação do incremento radial com as fenofases. Foram considerados apenas os resultados significativos ($p < 0,05$) e que apresentaram algum significado biológico. Para a execução dos testes utilizou-se o software PAST versão 2.17 (HAMMER et al., 2001).

Para verificar diferenças no incremento radial e da atividade fenológica entre os sítios foi feito um teste-T independente com o software Bioestat 5.3 (ZAR, 1996; ZAR, 2010).

Os dados da Δ_{Ψ} foram submetidos à análise de variância (ANOVA) sendo cada mês de avaliação considerado como um tratamento. Utilizou-se o teste de Turkey para comparar as médias, considerando 5% de probabilidade, usando software Sisvar 5.6 a fim de investigar a variação temporal e espacial da Δ_{Ψ} de *M. guianensis* nos sítios estudados (ZAR, 2010).

3.1 RESULTADOS

A avaliação contínua do incremento radial permitiu observar a periodicidade, ritmo e taxa de crescimento das populações de *M. guianensis* que diferiu entre os sítios de estudo (Tabela 1). Observou-se maior incremento radial no período chuvoso (principalmente nos meses de março e novembro), com taxas de 0,05 e 0,06 mm na FTSS, chegando a 0,10 mm na floresta ciliar (Figura 2; 3 A-B). O incremento radial acumulado foi maior na floresta ciliar (0.74 mm) em relação aos dados registrados na FTSS (0.21 mm), sendo possível inferir que o câmbio vascular foi reativado no período chuvoso com taxas de incremento contínuas e graduais (Figura 2; 3 C-D).

Tabela 1: Teste-T independente comparando o ritmo do incremento radial e da fenologia entre as populações de *Maprounea guianenses* Aubl. da floresta ciliar e floresta tropical sazonalmente seca (FTSS), situadas na Chapada Diamantina, Bahia, Brasil. I.M. – incremento médio; I.A. – incremento acumulativo; bro – brotamento; jov – folha jovem; mad – folha madura; que – queda; flo – floração; f.ima – fruto imaturo; f. mad – fruto maduro.

	Floresta ciliar X FTSS								
	I.M	I.A.	bro	jov	mad	que	flo	f.ima	f.mad
t	-2.1033	-7.3189	-0.3865	-0.1293	-3.1776	3.3101	0.4455	-1.3415	-3.1776
p	**0.0205**	**< 0.0001**	0.3503	0.4488	**0.0014**	**0.001**	0.3294	0.0926	**0.0014**

Nível de significância $p < 0,05$

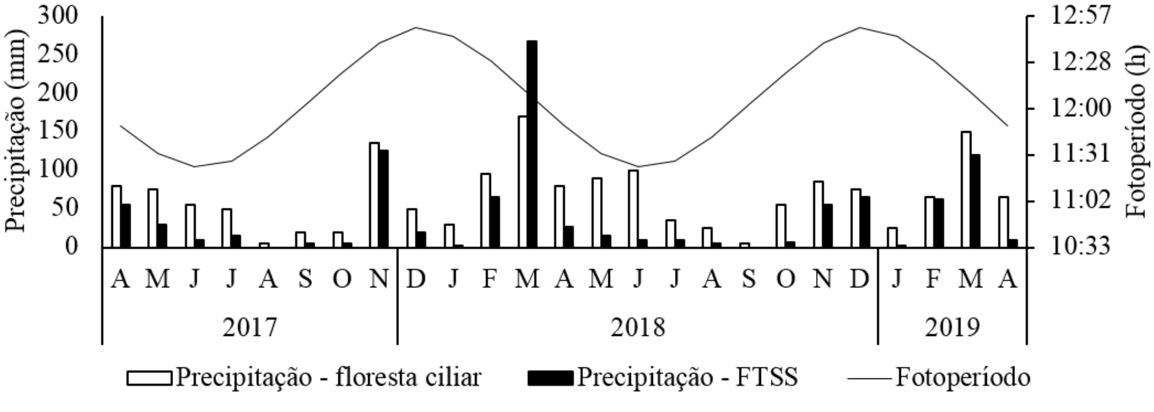

Figura 2. Dados de precipitação pluviométrica nos sítios de floresta ciliar e floresta tropical sazonalmente seca (FTSS); e fotoperíodo da região da Chapada Diamantina, Bahia, Brasil (Fonte: Astronomical Applications Department of the U.S. Naval).

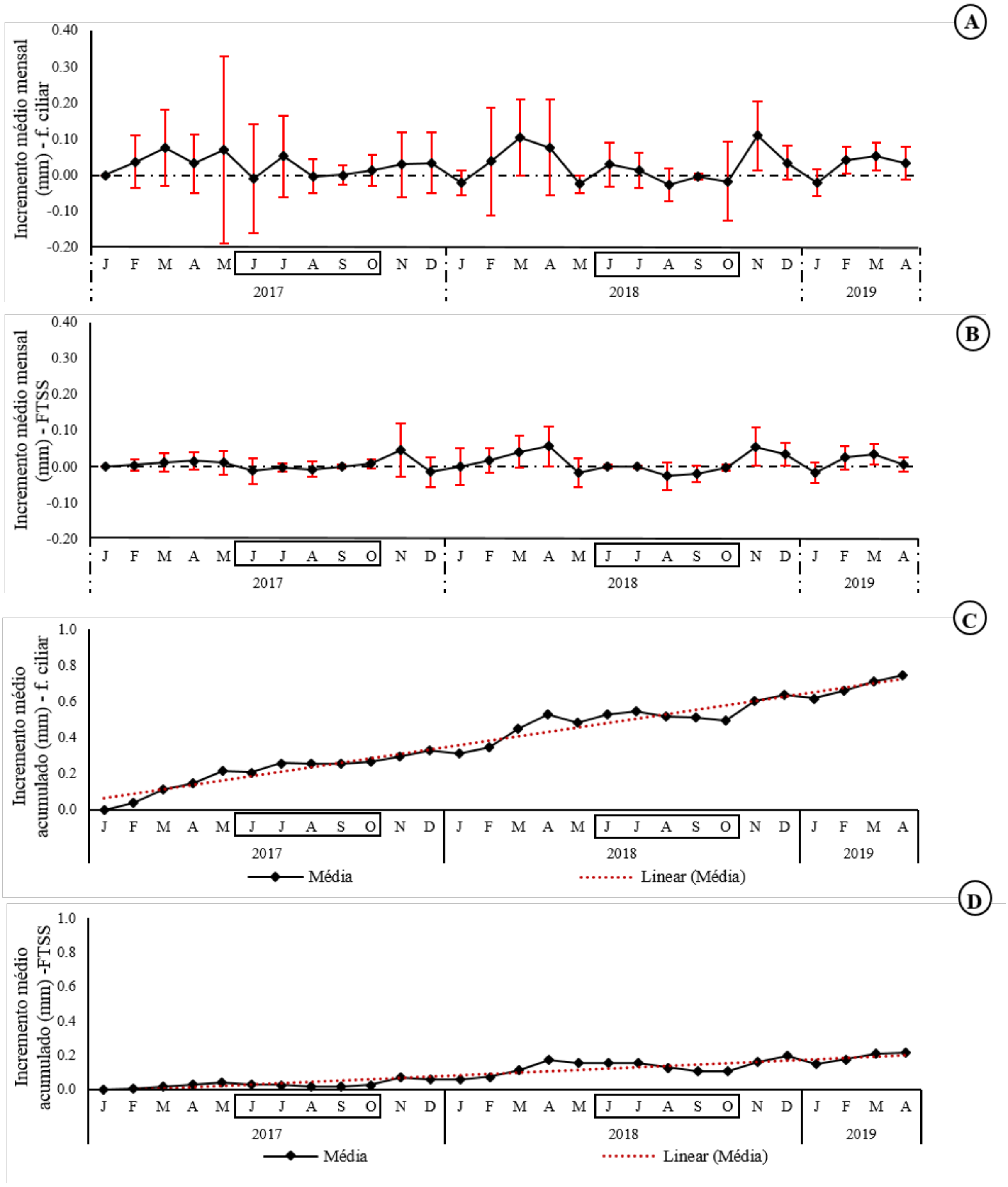

Figura 3. Ritmo cambial de *Maprounea guianensis* Aubl. em floresta ciliar e floresta tropical sazonalmente seca (FTSS), Chapada Diamantina, Bahia, Brasil: **(A)** incremento médio mensal na floresta ciliar **(B)** incremento médio mensal na FTSS; **(C)** incremento médio acumulado na floresta ciliar **(D)** incremento médio acumulado na FTSS. Período seco destacado.

O teste T mostrou ainda diferença da queda foliar e das folhas maduras entre os sítios (Tabela 1). A queda foliar foi mais marcada no período de menor disponibilidade hídrica; com taxas > 50 % na floresta ciliar (contudo sempre mantendo folhas verdes nas copas -hábito semidecíduo), enquanto na FTSS as taxas de queda foliar chegaram a > 80% com registro da troca de todas as folhas da copa em grande parte dos indivíduos (hábito decíduo) (Figura 4: A-B).

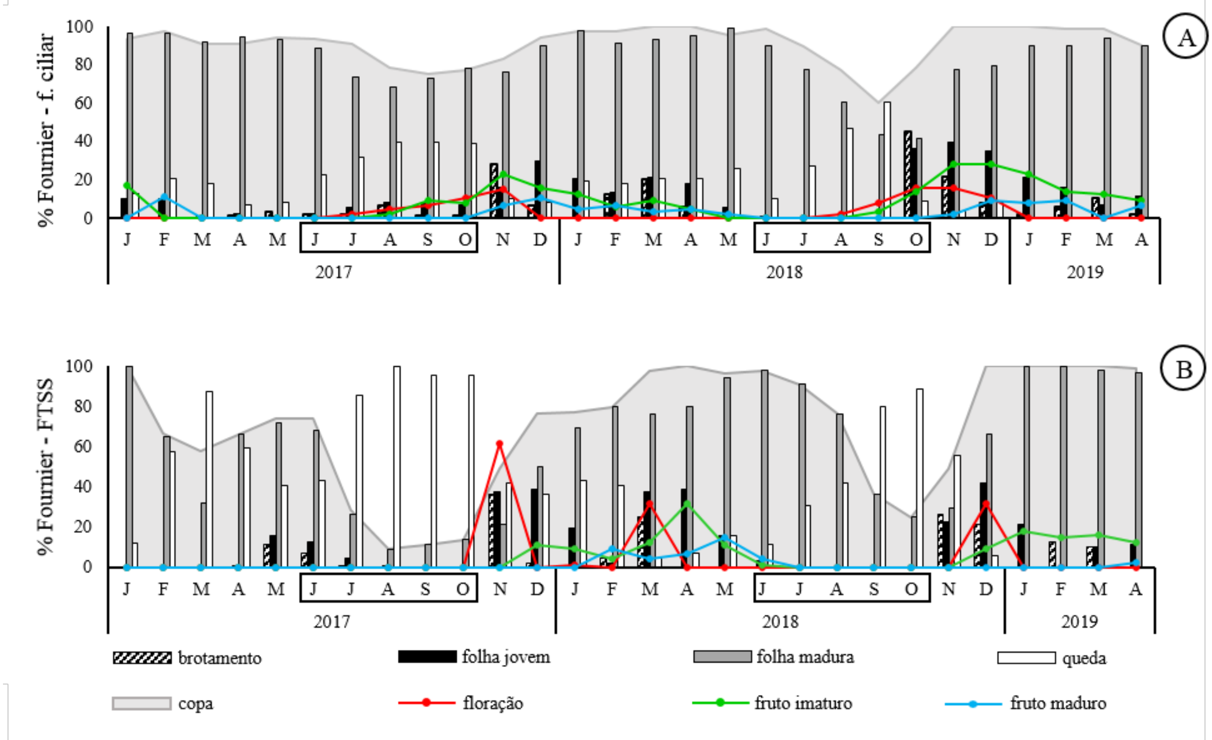

Figura 4: Ritmo fenológico de *Maprounea guianensis* Aubl. na Chapada Diamantina, Bahia, Brasil: **(A)** floresta ciliar; **(B)** Floresta tropical sazonalmente seca (FTSS). Período seco destacado

Nas duas populações observou-se floração rápida seguida de frutificação intermediária sem registro de diferença entre floração e fruto imaturo entre os sítios (Figura 4: A – B; Tabela 1). A floração ocorreu principalmente no período chuvoso, enquanto o fruto imaturo foi mais expressivo durante ou logo após as chuvas. Os frutos maduros também ocorreram no período chuvoso, no entanto não foram observados na FTSS no ano de 2017, fato que pode ter refletido na diferença registrada no teste T para esta fenofase (Figura 4: A – B; Tabela 1).

As variáveis ambientais influenciaram no incremento radial e na fenologia. O incremento radial foi correlacionada positivamente com a precipitação e negativamente com o fotoperíodo (Tabela 2). Na Figura 3: C-D mostra a relação positiva entre a precipitação e o aumento do incremento radial, observando que a cada chuva há um aumento no incremento radial e que nos meses de menor pluviosidade o incremento radial mantem-se estável ou reduz, provavelmente resultado da retração da casca por desidratação, além da redução da atividade do câmbio.

As duas populações mostraram correlação positiva da precipitação com as fenofases de brotamento, folha madura, floração e fruto imaturo, e correlação negativa com queda foliar. Houve ainda correlação positiva da precipitação com folha jovem na FTSS e com fruto maduro na floresta ciliar foliar (Tabela 2). Em relação ao fotoperíodo, as duas populações mostraram correlação positiva com folha jovem, queda, floração e fruto imaturo, e mostraram correlação negativa com folha madura. Houve ainda correlação positiva do fotoperíodo com brotamento na FTSS, com fruto maduro na floresta ciliar, e correlação negativa com fruto maduro na FTSS (Tabela 2).

Tabela 2: Coeficiente de correlação (r) e o tempo de atraso (números de meses) com os quais o incremento radial e as variáveis fenológicas de *Maprounea guianenses* Aubl. seguem a precipitação total e o fotoperíodo em floresta ciliar e floresta tropical sazonalmente seca (FTSS), situadas na Chapada Diamantina, Bahia.

Fenofases/ Incremeto	**Floresta ciliar**				**FTSS**			
	Precipitação							
	2017		**2018**		**2017**		**2018**	
	r (lag)	***p***	**r (lag)**	***p***	**r (lag)**	***p***	**r (lag)**	***p***
Incremento radial	0.58 (0)	0.04	0.61 (0)	0.03	0.86 (0)	<0.01	0.59 (0)	0.04
Brotamento	0.62 (0)	0.02	-	-	0.86 (0)	<0.01	0.61 (0)	0.04
Folha jovem	-	-	-	-	0.59 (0)	-	0.61 (0)	0.03
Folha madura	-	-	0.69 (3)	0.03	-	-	0.80 (3)	<0.01
Queda	-0.60 (0)	0.04	0.70 (0)	0.03	-	-	-0.85 (3)	<0.01
Floração	-	-	0.78 (3)	<0.01	0.86 (0)	<0.01	0.78 (0)	<0.01
Fruto imaturo	-	-	0.61 (1)	0.04	1 (1)	<0.01	-	-
Fruto maduro	-	-	0.58 (0)	0.02	**	**	-	-
	Fotoperíodo							
Incremento radial	-0.66 (2)	0.03	-0.64 (2)	0.04	-0.88 (4)	0.04	-0.65 (0)	0.02
Brotamento	-	-	-	-	-	-	0.71 (1)	0.01
Folha jovem	0.67 (0)	0.01	0.81 (0)	<0.01	-	-	0.64 (2)	0.04
Folha madura	-0.71 (2)	0.02	-0.88 (2)	<0.01	-0.80 (1)	<0.01	-0.62 (0)	0.03
Queda	0.82 (2)	<0.01	0.78 (3)	0.01	0.89 (2)	<0.01	0.88 (1)	<0.01
Floração	0.74 (1)	<0.01	0.77 (1)	<0.01	1 (2)	<0.01	-	-
Fruto imaturo	0.76 (0)	<0.01	0.84 (0)	<0.01	1 (2)	<0.01	0.64 (2)	0.04
Fruto maduro	0.77 (1)	<0.01	0.56 (0)	0.04	**	**	-0.75 (2)	0.01

** não houve fruto maduro neste ano (Nível de significância $p < 0,05$)

O incremento radial ainda mostrou correlação positiva (*p* < 0,05) com as fenofases de brotamento nos dois sítios (floresta ciliar 2017: r = 0.81, lag = 0, p=<0.01; FTSS 2017: r = 0.85, lag = 0, p=<0.01; FTSS 2018: r = 0.69, lag = 1, p=<0.01) e com folha jovem na floresta ciliar (ano 2018: r = 0.59, lag = 1, p=<0.02)

Os valores do potencial hídrico variaram (*p* < 0,05) entre os sítios e entre os períodos de seca e chuva. O Δ_Ψ não se diferenciou entre os sítios nos períodos chuvosos, porém mostrou uma grande variação entre eles no período seco, chegando a 0 MPBa na FTSS. Entre as estações na floresta ciliar, *M. guianensis* teve maiores médias de Δ_Ψ no período seco, enquanto na FTSS as maiores médias foram registradas nos períodos chuvosos (Figura 5).

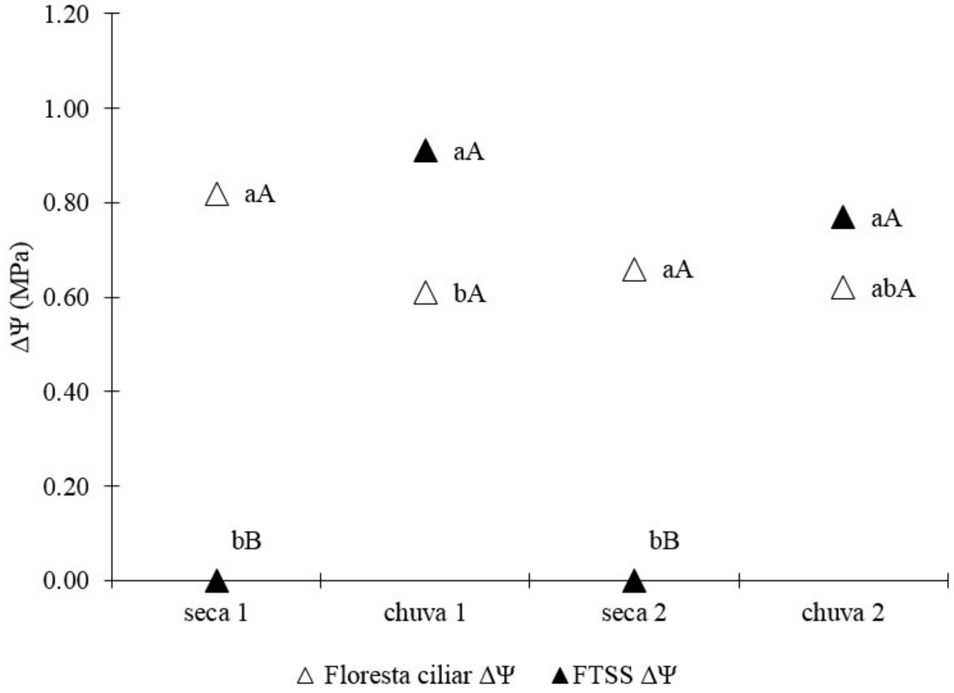

Figura 5: Valores da amplitude da variação do potencial hídrico (Δ_Ψ) de *Maprounea guianensis* Aubl.nos sítios situados na Chapada Diamantina, Bahia, Brasil. Letras minúsculas comparam as médias entre os períodos (seca e chuva). Letras maiúsculas comparam as médias entre os sítios no mesmo período. Médias seguidas da mesma letra não diferiram entre si com p < 0,05.

3.4 DISCUSSÃO

A avaliação do incremento radial, das fenofases e do potencial hídrico permitiu a caracterização do ritmo de crescimento como resposta ao ambiente de origem (sítio úmido e seco) e a capacidade de regulação hídrica da espécie. Nossos resultados mostraram que a seca sazonal limitou o crescimento em circunferência do tronco de *M. guianensis* e foi um gatilho para a queda foliar. Foi observado uma população decídua que se diferenciou da sempre verde pelo conjunto de traços funcionais relacionados as estratégias de sobrevivência a seca. Segundo Bigler (2016) a capacidade de uma espécie de se adaptar a seca facilita o equilíbrio entre os custos e os benefícios da manutenção dos traços funcionais e morfológicos. Esse *trade-off* pode mudar ao longo de gradientes ambientais, mesmo a nível intraespecífico, e também é observado em espécies que querem investir na produção de frutos (STAUDHAMMER et al., 2013; DORMAN et al., 2013).

O incremento radial e os eventos fenológicos de *M. guianensis* tiveram forte influência da precipitação, e consequentemente, apresentaram o mesmo ritmo sazonal. O incremento radial foi maior durante e logo após os períodos chuvosos, paralelo ao período em que as copas das árvores estavam se recuperando com novos brotamentos e folhas jovens. Segundo Kozlowski e Pallardy (2008) isso ocorre, em grande parte, devido a reativação do meristema cambial em decorrência de hormônios produzidos por gemas foliares em desenvolvimento. O fotoperíodo também é reconhecido como gatilho do brotamento em florestas tropicais (TALORA; MORELLATO, 2000). Neste estudo observamos a relação do fotoperíodo com as fenofases vegetativas, no entanto, somente a população da FTSS mostrou correlação deste fator com o brotamento, assim, o principal papel do fotoperíodo foi atuar juntamente com a precipitação na determinação da troca foliar.

Apesar das duas populações apresentarem o mesmo ritmo no incremento radial, *M. guianensis* registrou maior incremento radial médio acumulativo na floresta ciliar. Segundo Chave et al. (2009), a densidade de madeira é negativamente relacionada ao incremento radial, uma vez que, espécies de madeira densa apresentam crescimento mais lento, devido aos custos de construção deste tecido. SANTOS (2020, dados não publicados) observou que as árvores de *M. guianensis* presentes na FTSS apresentam madeiras mais densas do que a população da floresta ciliar o que estaria limitando o seu crescimento. No entanto, esta característica é importante para a sobrevivência dos indivíduos que estão expostos a uma seca mais severa (LARJAVAARA; MULLER-LANDAU, 2010). Sendo assim, a variação deste traço funcional é uma vantagem para a espécie, favorecendo a sua adaptação às condições do ambiente (CHAVE et al., 2009; UBUY et al., 2018).

Com a chegada do período seco, as plantas precisam desenvolver estratégias de sobrevivência, seja por ajustes fisiológicos ou morfológicos (SOUZA et al., 2015). Foi neste período que *M. guianensis* registrou redução no incremento radial e a deiscência (total ou parcial) das suas folhas. O mesmo comportamento foi observado por Toledo et al. (2012), ao investigarem diferenças no incremento radial de *Plathymenia reticulata* Benth. em savana e ecótipos florestais, e por Cardoso et al. (2012) ao estudarem a espécie *Citharexylum myrianthum* Cham. Estes autores afirmaram que a produção hormonal diminui com a queda das folhas e, consequentemente, o incremento radial também é reduzido, podendo ainda permanecer inativa até que ocorra a reativação do meristema cambial.

O *trade-off* entre as características que influenciam no crescimento da planta está diretamente associado ao tipo de estratégia de resposta à seca (MARKESTEIJN; POORTER, 2009; SOUZA et al., 2015). Na floresta ciliar apesar de *M. guianensis* ter diminuído o crescimento em circunferência do tronco e a queda foliar, observou-se uma estratégia de tolerância a seca com um hábito semidecíduo, mantendo mais da metade das folhas na copa. O mesmo hábito fenológico foi registrado neste estudo e por Miranda et al. (2011). A capacidade de *M. guianensis* em tolerar a seca está associado a disponibilidade de água no solo. Lier (2010) afirma que através das medidas de $\Delta\Psi$ pode-se estimar a água disponível no solo para a utilização da planta em suas funções fisiológicas. Neste ambiente, *M. guianensis* manteve altos valores de $\Delta\Psi$, mesmo no período de seca, sendo possível considerar que os indivíduos avaliados não sofreram grandes restrições de água. Por sua vez, na FTSS *M. guianensis* teve maior dificuldade em manter o balanço hídrico favorável para o crescimento ao longo do ano, mostrando uma redução drástica do $\Delta\Psi$ com 0 MPa nas épocas mais secas e, consequentemente manteve uma estratégia de escape da seca, diminuindo o incremento radial, perdendo todas as suas folhas (hábito decíduo) e restringindo o brotamento para a época chuvosa. Andreacci et al. (2017) afirmam que esse comportamento é característico de algumas espécies de regiões sazonais com estação seca bem definida, onde com a reidratação dos indivíduos inicia-se o brotamento das folhas, indicando a água como fator limitante para espécie.

Assim como os traços foliares, o custo de reprodução das plantas também desempenha um importante papel na história de vida de um indivíduo por influenciar toda sua trajetória de crescimento, desde os padrões fenológicos e processos fisiológicos (OBESO, 2002; THOMAS, 2011). Neste estudo observamos que *M. guianenis* concentrou a floração e frutificação principalmente nos meses chuvosos, mostrando a forte correlação dessas fenofases com a precipitação. Apesar dessas fenofases não apresentarm correlação com o incremento radial, o uso de recursos para a reprodução não limitou o incremento radial na espécie que manteve o crescimento em circunferência do tronco mesmo durante o período em que os indivíduos apresentaram flores e frutos. Estas observações são semelhantes aos registros de Staudhammer et al. (2013) que ao investigar o *trade-off* entre o estado reprodutivo e o incremento radial de *Bertholletia excelsa* Humb. & Bonpl e observou que os efeitos da alocação de recursos para a produção de frutos não são tão importantes para a espécie, cujos indivíduos continuavam a aumentar em tamanho e maturidade. Nossos resultados mostraram ainda que o surgimento de flores e frutos também tiveram relação significativa com o fotoperíodo, já reconhecido como gatilho para o desencadeamento desses eventos em muitas espécies (MORELLATO et al., 2000; TALORA; MORELLATO, 2000; MÜLLER; SCHMITT, 2018).

O presente estudo mostrou que a sazonalidade da precipitação e do fotoperíodo refletiram no incremento radial e na fenologia. A seca foi um fator limitante do crescimento de *M. guianensis* que, quando em período de maior demanda hídrica, mostrou menor crescimento em circunferência do tronco e queda foliar (parcial e total) nos dois sítios. A alta plasticidade fenótipica de *M. guianensis* (Santos 2020, dados não publicados) permitiu o *trade-off* entre os traços morfofuncionais para o desenvolvimento de estratégias de sobrevivência a seca. Em meio ao recente cenário de mudanças climáticas globais, nossos resultados mostram a importância de compreender a resposta das plantas a seca, sabendo que os *trade-off*s associados às características morfofuncionais determinam a aptidão das plantas em gradientes climáticos e ambientais.

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CONSIDERAÇÕES FINAIS

O estudo das populações de *M. guianensis*, localizadas em florestas tropicais secas e úmidas na Chapada Diamantina, revelou que a disponibilidade hídrica de cada sítio (precipitação e úmidade do solo) foi significativa para os traços morfofuncionais. O fotoperíodo atuou na manutenção das copas como um gatilho para a retomada da produção foliar e para o surgimento de flores e frutos. A seca sazonal foi significativa para as estratégias de sobrevivência da espécie que demonstrou baixa capacidade de armazenamento de água em seus tecidos foliares e lenhosos. As variações no potencial hídrico foram importantes para a adaptação aos diferentes ambientes, favorecendo um alto nível de plasticidade fenotípica.

Nas florestas úmidas *M. guianensis* conseguiu manter um balanço hídrico positivo, assumindo uma estratégia de tolerância aos períodos de seca. Características particulares de cada sítio (precipitação mensal, fontes alternativas de água e tipos de solo) condicionaram diferentes comportamentos na fenologia vegetativa. Na floresta pluvionebular, com maiores índices pluviométricos e alta umidade do solo, a longevidade das folhas se estendeu durante a estação seca e o brotamento foi contínuo, mostrando hábito sempre-verde. Nas florestas ciliar e de planalto, a redução da disponibilidade de água na estação seca, com redução da longevidade foliar, e eventos marcados de queda e brotamento condicionaram o hábito brevidecíduo. Na FTSS os períodos de seca muito mais extremos e o solo compactado não permitiram a recuperação do potencial hídrico fazendo com que a população assumisse uma estratégia de escape da seca com eventos de queda foliar mais intensos, sendo observado na maior parte dos indivíduos a deciduidade total das folhas, caracterizando o hábito decíduo. A espécie apresentou baixa diversidade fenológica em cada sítio de floresta amostrado e eventos vegetativos e reprodutivos sazonais.

A seca também influenciou no incremento radial que acompanhou a manutenção das copas dos indivíduos, apresentando um aumento no crescimento cambial nos períodos chuvosos, no mesmo momento em que surgiam novos brotamentos foliares e folhas jovens. Com a diminuição das chuvas, ocorriam a queda das folhas e a diminuição do crescimento cambial. Na floresta ciliar foi observado maior incremento radial acumulativo, podendo este fato estar associado as características do tronco que se diferenciaram por ser menos densos na população da floresta ciliar em relação a população da FTSS.

Finalizando, nossos resultados mostram as conexões entre os regimes de seca e as respostas das plantas, com alta plasticidade fenotípica para *M. guianensis* que demosntrou diferentes estratégias de sobrevivência perante a seca sazonal dos sítios.