Rodriguésia 75: e00022024. 2024
http://rodriguesia.jbrj.gov.br
DOI: http://dx.doi.org/10.1590/2175-7860202475068

Original Papers

Elucidating the ecological strategies of evergreen trees in Dry Forests: *Sarcomphalus joazeiro* (Rhamnaceae) produces different wet- and dry-season leaf cohorts

Fernanda Moreira Gianasi[1,2,4,13], *Paola Ferreira Santos*[1,5], *Fernanda de Oliveira*[1,2,6], *André Maciel da Silva*[1,2,7], *Cléber Rodrigo de Souza*[2,8], *Vinícius Andrade Maia*[2,9], *Marinês Ferreira Pires Lira*[1,10], *Evaristo Mauro de Castro*[1,11], *Nathalle Cristine Alencar Fagundes*[3] & *Rubens Manoel dos Santos*[1,2,12,13]

Abstract

Seasonally Dry Tropical Forests experience pronounced precipitation seasonality, intense solar radiation, and high temperatures, which often translate into high levels of deciduousness during the dry season. In these environments, deciduous species coexist with some evergreen species that are able to maintain their canopy leaves throughout the dry season. To understand the strategies behind this behavior, we analyzed leaf anatomical traits of 13 individuals of *Sarcomphalus joazeiro* during both the wet and dry seasons in a seasonal deciduous forest. We hypothesized that wet-season leaves would differ anatomically and functionally from dry-season leaves. Specifically, we expected wet-season leaves to show a more acquisitive resource-use strategy compared to dry-season leaves, which we expected to be more conservative. We assessed the effects of season and climatic variables on 25 leaf anatomical traits using generalized linear mixed models (LMM). Leaf traits varied between the wet and dry seasons and interacted with climatic variables, which together suggest that *S. joazeiro* produces season-specific leaf cohorts. This adaptation allows the species to adjust to the contrasting conditions of light intensity, temperature, and evaporative demand in each season.
Key words: acquisitive/conservative tradeoff, *Caatinga* Domain, functional traits, leaf anatomy, Seasonally Dry Tropical Forests.

Resumo

As Florestas Tropicais Sazonalmente Secas apresentam sazonalidade pronunciada de precipitação, intensa radiação solar e altas temperaturas, que muitas vezes se traduzem em altos níveis de deciduidade durante a estação seca. Nestes ambientes, espécies caducifólias coexistem com algumas espécies perenes que conseguem manter as folhas do dossel durante toda a estação seca. Para entender as estratégias por trás desse comportamento, analisamos características anatômicas foliares de 13 indivíduos de *Sarcomphalus joazeiro* durante as estações chuvosa e seca em uma floresta estacional decídua. Nossa hipótese é que as folhas da estação chuvosa seriam diferentes anatômica e funcionalmente das folhas da estação seca. Especificamente, esperávamos que as folhas da estação chuvosa apresentassem uma estratégia de utilização de recursos mais aquisitiva em comparação com as folhas da estação seca, que esperávamos que fossem mais conservativas. Avaliamos os efeitos da estação e das variáveis climáticas em 25 características anatômicas foliares usando modelos lineares mistos generalizados (LMM). As características foliares variaram entre as estações chuvosa e seca e interagiram com variáveis climáticas, que juntos sugerem que

See supplementary material at <10.6084/m9.figshare.26932432>

[1] Federal University of Lavras, Department of Biology, Graduate Program in Applied Botany, Lavras, MG, Brazil.
[2] Federal University of Lavras, Department of Forest Sciences, Phytogeography and Evolutionary Ecology Laboratory, Lavras, MG, Brazil.
[3] State University of Minas Gerais, Campus Ituiutaba, Ituiutaba, MG, Brazil. ORCID: <https://orcid.org/0000-0002-6518-6104>.
[4] ORCID: <https://orcid.org/0000-0001-9638-7024>. [5] ORCID: <https://orcid.org/0000-0003-3063-5771>. [6] ORCID: <https://orcid.org/0000-0003-0141-7951>.
[7] ORCID: <https://orcid.org/0000-0003-3469-2810>. [8] ORCID: <https://orcid.org/0000-0002-4122-2748>. [9] ORCID: <https://orcid.org/0000-0001-8906-4921>.
[10] ORCID: <https://orcid.org/0000-0003-0660-5775>. [11] ORCID: <https://orcid.org/0000-0002-1385-8503>. [12] ORCID: <https://orcid.org/0000-0002-4075-462X>.
[13] Author for correspondence: fergianasi@gmail.com; rubensmanoel@ufla.br

S. joazeiro produz coortes de folhas específicas para a estação. Esta adaptação permite que a espécieajuste-se às condições contrastantes de intensidade de luz, temperatura e demanda evaporativa em cada estação.

Palavras-chave: tradeoff aquisitivo/conservativo, Domínio da Caatinga, características funcionais, anatomia foliar, Florestas Tropicais Sazonalmente secas.

Introduction

Seasonally Dry Tropical Forests (SDTF) can be described as a heterogeneous set of forest formations that receive less than 1,800 mm of highly seasonal rainfall annually (Pennington *et al.* 2009; Dryflor *et al.* 2016; Allen *et al.* 2017). These forests occur in disjunct nuclei across different phytogeographic domains in areas of highly fertile calcareous soils, ranging from shrub-dominated physiognomies in the most xeric areas, where the dry season is longer than six months, to relatively tall forests in the most humid and fertile areas (Santos *et al.* 2012; Dexter *et al.* 2015; Allen *et al.* 2017). The proportion of canopy deciduousness in SDTFs also responds to this precipitation gradient, whereby semideciduous seasonal forests occur in the regions with the highest precipitation and deciduous seasonal forests, in the driest regions (Pennington *et al.* 2009; Apgaua *et al.* 2014).

Among the different SDTF physiognomies, Deciduous Seasonal Forests (DSF) exhibit the highest proportion of canopy deciduousness during the dry season. These forests occur in regions with highly fertile soils, strong precipitation seasonality, strong solar radiation, and high temperatures (Santos *et al.* 2012; Apgaua *et al.* 2014; Terra *et al.* 2018). In Brazil, this formation predominates in the Caatingas Phytogeographic Domain (Santos *et al.* 2012), where environmental filtering imposes strong selective pressure (Gianasi *et al.* 2020).

During drought, a high vapor pressure deficit induces stomatal closure to avoid water loss by transpiration, which consequently reduces photosynthesis and increases the carbon cost of leaf maintenance, rendering deciduousness advantageous to the plant (Vico *et al*. 2017). However, some evergreen species that preserve most of their canopy cover during the dry season (*i.e.*, less than 10% of leaf loss) are able to coexist with deciduous species even in these highly seasonal environments (Eamus 1999; Silva *et al.* 2004; Loiola *et al.* 2012; Souza *et al.* 2015). While deciduous species prevent drought by shedding leaves and transpiring at negligible rates during this period, evergreen species tolerate drought by changing anatomical/functional traits, enabling the maintenance of leaf transpiration throughout the year (Eamus 1999; Souza *et al.* 2015).

The coexistence of evergreen and deciduous species in seasonally dry forests is rarely explored in the literature (Eamus 1999; Tomlinson *et al.* 2013; Souza *et al*. 2015). Compared to their deciduous counterparts, evergreen species tend to produce more durable leaves with a less efficient photosynthetic machinery that require a higher carbon investment, a cost that is offset throughout the year by the maintenance of photosynthetic activity year-round (Pringle *et al.* 2011; Tomlinson *et al.* 2013; for more details on the leaf economic spectrum, see Wright *et al.* 2004).

Because evergreen species endure seasonal water deficit while maintaining leaf cover during the dry season, their water use strategy is considered more conservative than that of deciduous species (Tomlinson *et al.* 2013; Lohbeck *et al.* 2015; Vico *et al.* 2017). Indeed, leaves from plants occurring under conditions of high insolation, low water availability, and high temperatures (Santos *et al.* 2012; Terra *et al.* 2018) tend to display effective mechanisms to maintain leaf function in the face of this specific combination of stresses. These include a series of conservative anatomical and physiological adjustments that improve plant water balance and water use efficiency (Eamus 1999; Gratani & Bombelli 2000; Rossatto & Kolb 2009; Mendes *et al.* 2017; Silva *et al.* 2018; Holanda *et al.* 2019).

However, little is known about anatomical trait variation of evergreen species through dry and wet season cycles in water-limited but nutrient-rich SDTFs. Do these species have conservative leaves that remain throughout the year regardless of season, as was found for evergreen species associated with other environments (Pringle *et al.* 2011; Tomlinson *et al.* 2013; Lohbeck *et al.* 2015; Vico *et al.* 2017)? Or do they produce a new set of leaves at every transition between dry and wet seasons, (*i.e.*, distinct leaf cohorts)? If distinct leaf cohorts are produced, how do they compare anatomically and functionally? How do leaf anatomical and functional traits respond to the most limiting environmental conditions of SDTFs (insolation, temperature, and precipitation)?

Here, we focus on an evergreen tree species common in deciduous forests and endemic to the *Caatinga* Domain, *Sarcomphalus joazeiro* (Mart.) Hauenshild (Rhamnaceae). This is an emblematic *Caatinga* species regarded for its ecological importance as a source of shelter and food for wildlife and for the maintenance of important ecosystem services during the dry season (Nadia *et al.* 2007; Diógenes *et al.* 2010; Dantas *et al.* 2014). Despite its high ecological importance and being one of the few evergreen plants in *Caatinga* deciduous forests, no published studies have characterized the morphological or anatomical adaptations behind this species' ecological strategies. How environmental variables influence leaf anatomical traits of evergreen species occurring in deciduous forests remains to be explained.

This study aims to (1) describe morphoanatomical and functional adaptations displayed in the dry and the wet seasons by an evergreen species endemic to Deciduous Seasonal Forests and (2) search for correlations between these adaptations and climatic variables. We hypothesize that *S. joazeiro* produces two well-defined leaf cohorts in response to seasonality, reflecting changes in leaf-level resource use and acquisition strategies. Based on this hypothesis, we predicted that (1) the leaves produced in the wet season are anatomically and functionally different from those produced in the dry season, and that (2) wet-season leaves display a more acquisitive resource-use strategy than dry-season leaves, which are expected to be more conservative.

Materials and Methods

Study area

Leaf samples were collected in Juvenília, northern Minas Gerais, Brazil, at coordinates 14°28'15.45"S and 44°10'21.57"W, and at an altitude of 542 meters above sea level. The soil in the area is classified as eutrophic litolic neossolo (RLe) (Embrapa 2006). The area is covered by Deciduous Seasonal Forests of the *Caatinga* Domain as classified by Brazil's official vegetation classification system (IBGE 2012). According to historical data from the last 26 years from a meteorological station located in Januária, Minas Gerais state (OMM: 83386), the period with the highest precipitation in the region is comprised between November and March (wet season) and the period with lowest precipitation, between April and October (dry season). The average temperature is 25 ºC, with high insolation between July and August and low relative humidity between August and October. The climate of the region is classified as As (tropical with dry summers) in the Köppen-Geiger classification system (Alvares *et al.* 2013; INMET 2016).

Species description

Sarcomphalus joazeiro, popularly known as "juazeiro", is an endemic species of the Deciduous Seasonal Forests of the *Caatinga* Domain, located in the hinterlands of northeastern Brazil and northern Minas Gerais state (Prado & Gibbs 1993; Oliveira-Filho 2006). *S. joazeiro*'s leaves have diagnostic features, including three main visible ribs starting from the base toward the leaf blade, an elliptical shape, a semi-leathery texture, and a size ranging from 3 to 7 cm in length. The species produces yellow-green flowers grouped in small, cymose inflorescences, and globose drupe-type fruits with a trilocular, indehiscent structure. The fruits are yellowish, with a large endocarp covered by a mucilaginous, white, and sweet pulp (Lima 2001). Two vouchers were deposited at the Herbarium ESAL of the Universidade Federal de Lavras under numbers 24199 and 24200.

Anatomical samples

To evaluate the effects of seasonality on *S. joazeiro*'s leaves, we collected healthy, expanded leaves below the fourth branch node from 13 adult individuals of *S. joazeiro* in two seasons: wet in January 2015 and dry in October 2015. Six leaves per tree were collected in each season, packed in plastic containers, and fixed in 70% ethanol. Paradermal sections were made on both sides of the leaf through dissociation, which involves the separation of leaf tissues using a solution of hydrogen peroxide and acetic acid (1:1) at 60 ºC for 48 hours. After this process, the fragments were washed with 50% ethanol, stained with Safranin 1%, and mounted in an aqueous medium with 50% glycerin between the slide and cover slip (Franklin 1945; Kraus & Arduin 1997). Fragments of approximately 1 cm^2 taken from the central region of the leaves were used for transverse sections. These fragments were dehydrated in increasing concentrations of ethanol (70, 80, 90, and 100%). This material was immersed for 24 hours in a pre-infiltration solution composed of 100% ethanol and base resin (1:1), as per the manufacturer's instructions (Historesina Leica kit). For polymerization, the Historesin kit (Leica®

hydroxy-methyl methacrylate) was used, and after this process, the samples were sectioned using a semiautomatic microtome. The sections of about 9 µm were stained with 0.05% Toluidine Blue pH 4.7 (O'Brien *et al.* 1964), and the slides were mounted in a medium with stained glass varnish between the slide and cover slip. All samples were photographed using a ZEISS® optical microscope (model Axio Lab. A1), with an attached digital camera (Axio Cam ERc5s), and with the aid of the image analysis software ImageJ®. One paradermal slide and one cross-sectional slide from each leaf were produced for analysis. From each slide, 5 photographs were taken and measured. All anatomical variables measured and their biological meanings can be consulted in Tab. S1 (available on supplementary material <10.6084/m9.figshare.26932432>).

Climatic data

We obtained the climatic variables used in the analyses from the historical database of the National Institute of Meteorology (INMET 2018). We used data from the weather station closest to the collection site (50 km; OMM: 83408), which has been active since 12/01/1927 and is located in Carinhanha, Bahia state. We selected four ecologically relevant climatic variables with the largest time series available (40 years; 1978-2018): average relative humidity (UMID), average total insolation (MIT), average total precipitation (PREC), and average compensated temperature (TCOMP). Climate seasonality is presented in Figure 1.

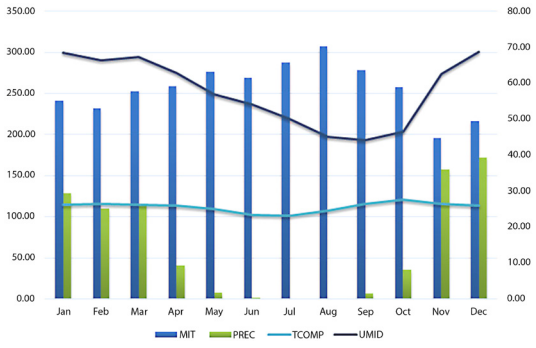

Figure 1 – Climate seasonality. Historical data (1978–2018) of four climatic variables: MIT = average total insolation; PREC = average total precipitation; TCOMP = average compensated temperature; UMID = average relative humidity.

Data analysis

We fitted linear mixed models (LMM) to evaluate the effects of seasonal (categorical) variables (month) on leaf anatomical variables (described in Tab. S1, available on supplementary material <10.6084/m9.figshare.26932432>). The "lmer" function (Bates *et al.* 2015) of the "lme4" package was used to obtain the models and to assess statistical significance (Kuznetsova *et al.* 2017). One model was generated for each anatomical variable, totaling 21 models. The tree individuals were included as a random factor to deal with the dependence between within-tree observations. Type II Wald chi-square test was used to determine the validity of each fitted model against the null model. The "MuMIn" package (Bartón 2018) was used for R^2 calculation. All analyses were performed in R version 4.3.3 (R Core Team 2024).

Results

Leaf anatomy

The individuals of *Sarcomphalus joazeiro* exhibited significant variations in all leaf anatomical traits analyzed between the wet and dry seasons (January and October, respectively), except for hypodermis thickness. The analyzed leaves had a rounded shape with significantly larger leaf areas in the wet season. The average numbers of adaxial and abaxial epidermal cells were higher in the dry season (Fig. 2a-b). The leaves were hypostomatic with tiny anomocytic stomata (Fig. 2c) located close to the ribs. Stomatal density, mean stomatal diameter and stomatal index were significantly higher in the wet season compared to the dry season (Fig. 2c-d). Trichomes were found on both leaf surfaces, with higher average density on the adaxial surface in the wet season and on the abaxial surface in the dry season. The thickness of both adaxial and abaxial cuticles was also greater in dry-season leaves (Fig. 3a-b). The adaxial and abaxial epidermises were uniseriate and thicker in wet-season leaves. The species displayed uniseriate hypodermis just below the adaxial epidermis, without significant differences between wet and dry seasons. The leaf blade was thicker in dry-season leaves. The dorsiventral mesophyll of *S. joazeiro* leaves presented palisade mesophyll with only one layer and spongy mesophyll (Fig. 3b) with idioblasts, prismatic oxalate crystals, and three to four cell layers (Fig. 3a-b). The average midrib area was larger in the wet season, with vascular bundles showing fiber caps, xylem internal to

the phloem, and the presence of idioblasts with prismatic oxalate crystals. The average number of vessel elements, average xylem area, and average phloem area were also higher in the wet season. The lamellar-type collenchyma, with four to five cell layers, was restricted to just below the adaxial and abaxial epidermises of the central vein. The average adaxial and abaxial collenchyma area and the average diameter of vessel elements were greater during the wet season (Fig. 3c-d).

Effect of seasonality on leaf anatomy

The historical climate data of the region (Fig. 1) indicates intense seasonality between January and October. January has a much higher average total precipitation and relative humidity, while October has a higher average total insolation. Accordingly, all anatomical variables analyzed, except for hypodermis thickness, also varied significantly between January and October (Tab. S2, available on supplementary material <10.6084/m9.figshare.26932432>). These results indicate that the region's strong climatic seasonality has an important effect on *Sarcomphalus joazeiro*'s leaf anatomy.

The following anatomical traits had higher values in the leaves collected in January (*i.e.*, wet season): abaxial collenchyma area (ACOAB), adaxial collenchyma area (ACOAD), leaf area (af) (Fig. 4a), phloem area (Aflo) (Fig. 4b), midrib area (AN), xylem area (AX) (Fig. 4c), abaxial cuticle thickness (CAB), diameter of xylem vessel elements (DEVX), stomatal diameter (DME) (Fig. 4d), abaxial and adaxial numbers of epidermal cells (EPAB and EPAD) and number of xylem vessel elements (NEVX).

The following anatomical traits had higher values in the leaves collected in October (*i.e.*, dry season): abaxial epidermis thickness (CEAB) (Fig. 5a), adaxial epidermis thickness (CEAD) (Fig. 5b),

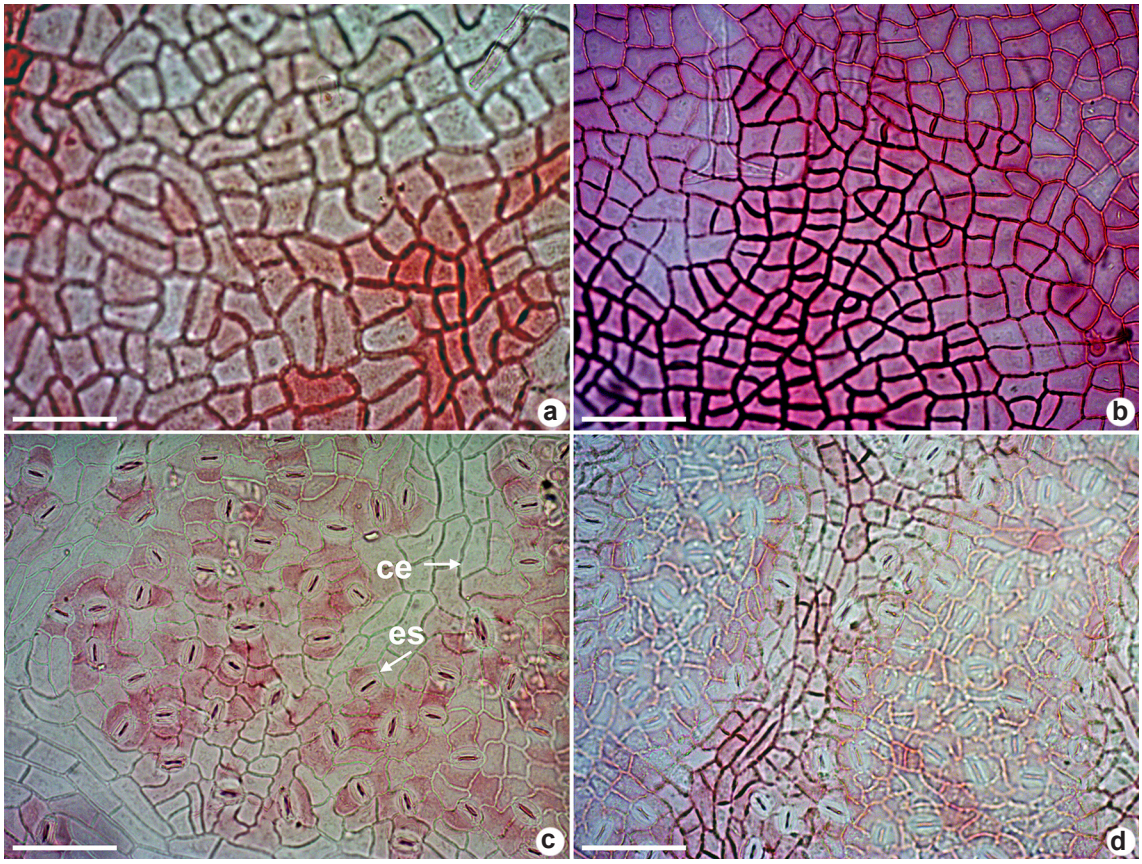

Figure 2 – a-d. Paradermal sections of *Sarcomphalus joazeiro* leaves – a. adaxial epidermal cells of wet-season leaves; b. adaxial epidermal cells of dry-season leaves; c. abaxial epidermal cells of wet-season leaves; d. abaxial epidermal cells of dry-season leaves. The arrow indicates epidermal cells (ce) and stomata (es). Scale bar = 50 µm.

adaxial cuticle thickness (CAD) (Fig. 5c), stomatal density (EAB) (Fig. 5d), leaf thickness (ETL) (Fig. 6a), trichomes on abaxial surface cells (TAB) (Fig. 6b), spongy parenchyma thickness (TE) (Fig. 6c) and palisade parenchyma thickness (TP) (Fig. 6d).

Discussion

Our results suggest that *Sarcomphalus joazeiro* produces two well-defined leaf cohorts in response to seasonality, reflecting changes in leaf-level resource use and acquisition strategies. Leaves produced in the wet season are anatomically and functionally more acquisitive compared to those produced in the dry season.

Functional and anatomical leaf traits, including those involved in phenology and leaf longevity, can serve as a proxy for the ecological strategies of plants (Jonasson 1989; Kikuzawa 1995; Eamus 1999; Givnish 2002; Westoby *et al.* 2004). Leaf longevity is closely tied to photosynthetic capacity, integrates ecological processes, and reflects responses to environmental factors such as solar radiation, nutrient availability, and drought (Gratani & Bombelli 2000). The results from *S. joazeiro* indicate that evergreen species in water-limited but nutrient-rich environments produce relatively shorter-lived leaves compared to evergreen species in seasonal environments with less fertile soils.

Cerrado savannas adjacent to the *Caatinga* region also experience seasonal droughts, but other environmental factors, such as low soil fertility and natural fires, play an additional role in the physiological and morphological traits of Cerrado plants (Bieras & Sajo 2009; Cianciaruso *et al.* 2013; Souza *et al.* 2015; Miatto *et al.* 2016). Even under these conditions, coexisting evergreen and deciduous tree species show similar photosynthetic

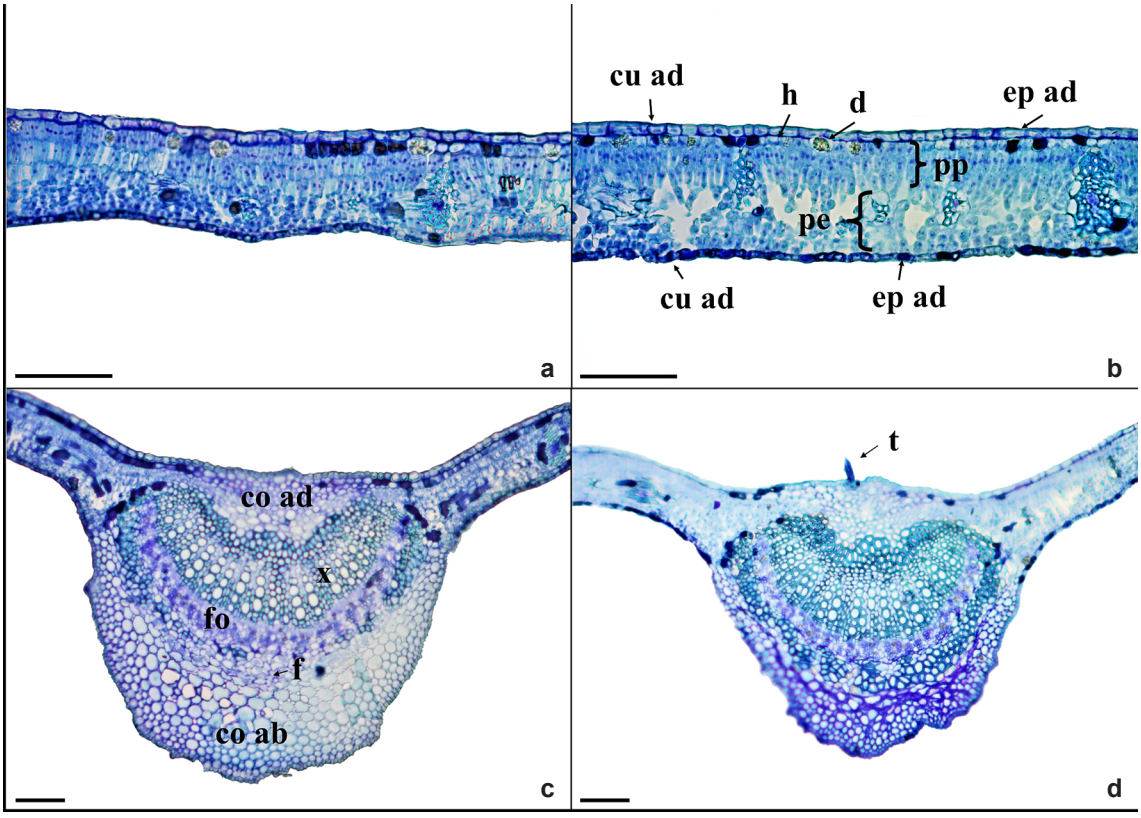

Figure 3 – a-d. Cross-sections of *Sarcomphalus joazeiro* leaves – a. mesophyll of wet-season leaves; b. mesophyll of dry-season leaves; c. midrib of wet-season leaves; d. midrib of dry-season leaves. (cu ad = adaxial cuticle; h = hypodermis; d = druses; ep ad = adaxial epidermis; pp = palisade parenchyma; pe = spongy parenchyma; cu = abaxial cuticle; ep = abaxial epidermis; co ad = adaxial collenchyma; coab = abaxial collenchyma; fo = phloem; x = xylem; t = trichomes). Scale bar = 100 µm.

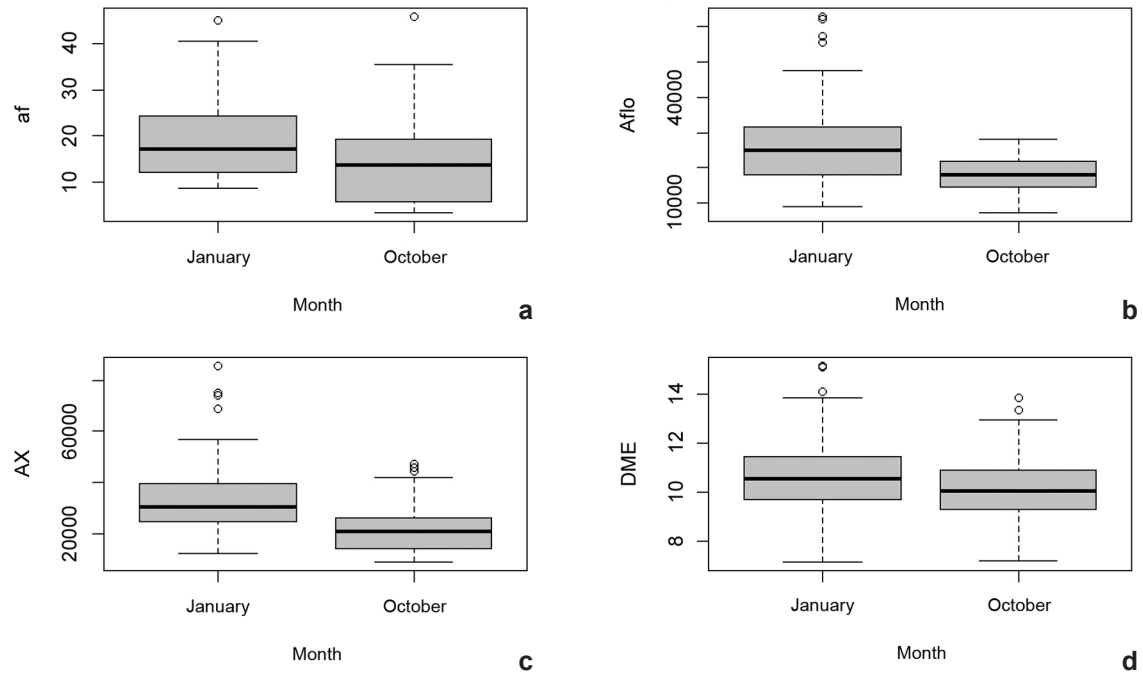

Figure 4 – a-d. Boxplots showing the variation in *Sarcomphalus joazeiro*'s leaf anatomical variables in two different months (January and February). All variables showed significant differences between months – a. leaf area; b. phloem area; c. xylem area; d. stomatal diameter. (af = leaf area; Aflor = phloem area; AX = xylem area; DME = stomatal diameter).

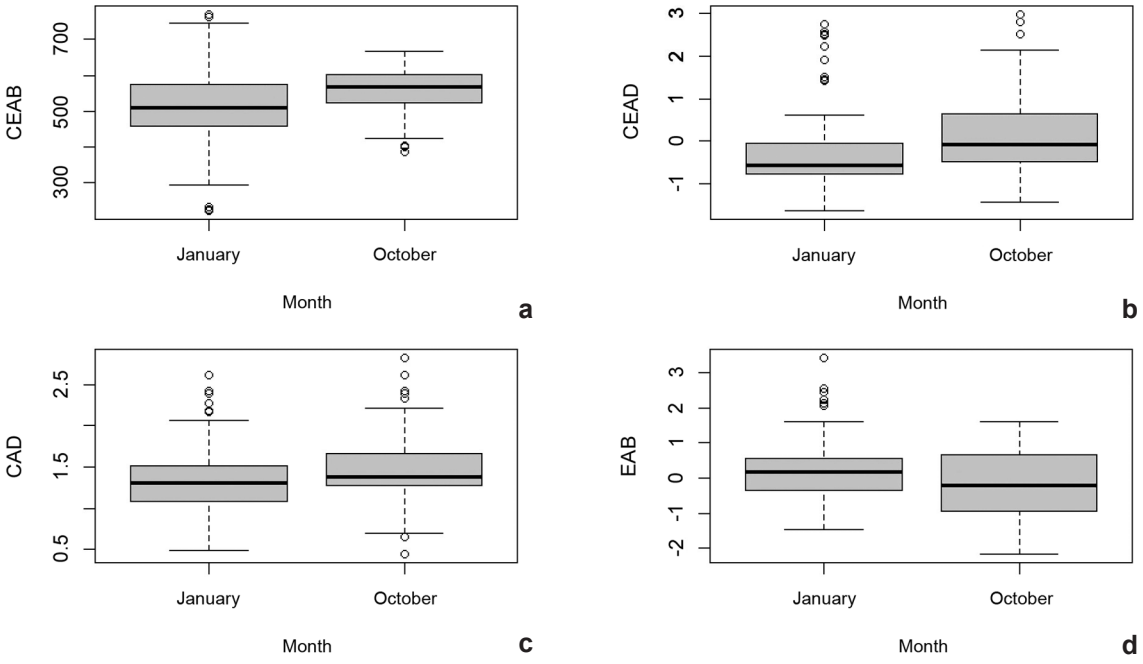

Figure 5 – a-d. Boxplots showing the variation in *Sarcomphalus joazeiro*'s leaf anatomical variables in two different months (January and February). All variables showed significant differences between months – a. abaxial epidermis thickness; b. adaxial epidermis thickness; c. adaxial cuticle thickness; d. stomatal density. (CEAB = abaxial epidermis thickness; CEAD = adaxial epidermis thickness; CAD = adaxial cuticle thickness; EAB = stomatal density).

rates. Evergreen Cerrado species usually maintain their leaves for periods longer than 11 months and do not exhibit leaf exchange in response to seasonality, which indicates a predominance of conservative resource-use strategies (Franco *et al*. 2005; Cianciaruso *et al*. 2013). Plants experiencing milder seasonality tend to have longer leaf longevity, which is expected to lead to lower variation in leaf morphophysiological traits. In contrast, in the strongly seasonal *Caatinga* deciduous forests, the evergreen *S. joazeiro* changes leaves more than once a year, allowing for the maximization of fitness through anatomical and functional adaptations and performance adjustments according to existing climatic conditions.

Limiting factors such as high temperatures, vapor pressure deficit, and solar radiation also influence photoinhibition, which further plays a role in the leaf anatomical traits of *S. joazeiro*. The outer tissues of the leaf and its appendages play an important role in photoinhibition through light interception. Together, the trichomes, epidermis, and cuticle can reflect part of the solar radiation and even filter damaging UV rays (Karabourniotis *et al*. 2021). In the more energy-expensive dry-season leaves, we observed more protective structures such as more abundant trichomes and thicker adaxial cuticles.

Leaves collected during the dry season, characterized by higher energy costs for the plant, showed investments in protective structures like trichomes and thicker adaxial cuticles. The thicker cuticles act towards limiting non-stomatal water loss and gas exchange, providing protection against extreme temperatures, radiation, pathogens, herbivores, and mechanical stress. These adaptations ensure leaf durability and maintenance of photosynthetic activities during the dry season until new leaves are flushed in the wet season.

Regarding the anatomical traits actively involved in photosynthesis, we observed an increase in palisade parenchyma thickness and a significant increase in spongy parenchyma thickness in dry-season leaves compared to wet-season leaves. A thicker palisade parenchyma could contain a greater number of CO_2 fixation sites, while a thicker spongy parenchyma could result in easier diffusion of CO_2 to these sites (Ennajeh *et al*. 2015). This indicates a trade-off for structural mechanisms that enhance photosynthesis per unit leaf area, enabling more efficient water use.

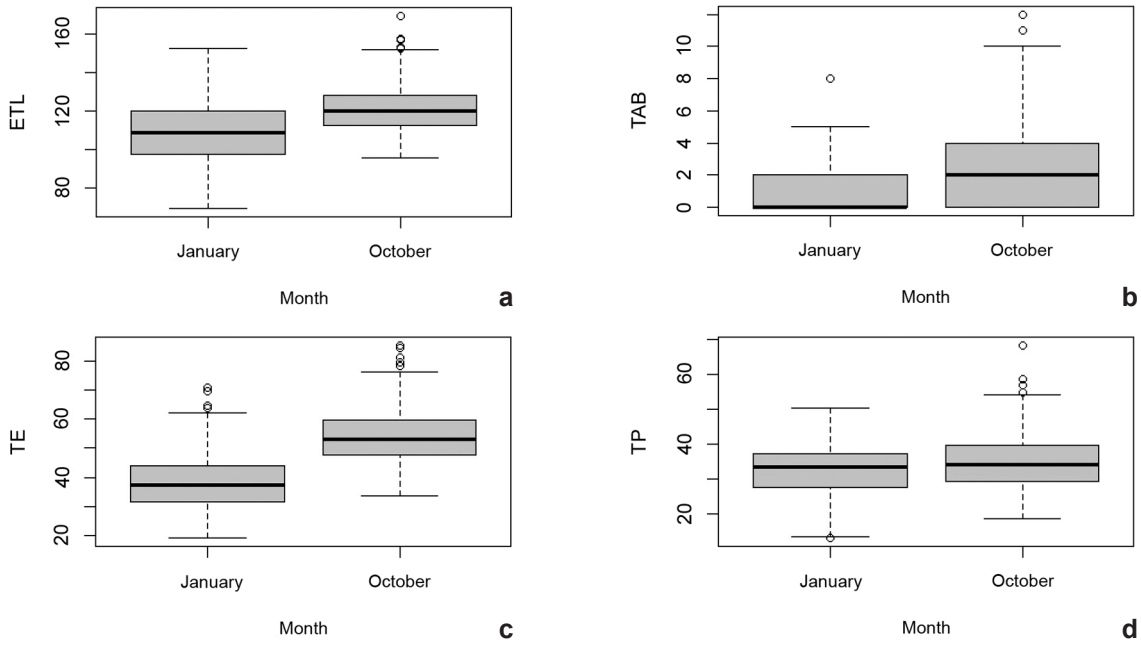

Figure 6 – a-d. Boxplots showing the variation in *Sarcomphalus joazeiro*'s leaf anatomical variables in two different months (January and February). All variables showed significant differences between months – a. leaf thickness; b. trichomes on the abaxial surface cells; c. spongy parenchyma thickness; d. palisade parenchyma thickness.

The hydraulic components of leaves, including midrib area, vessel elements, xylem and phloem areas, and diameter of the vessel elements, play a crucial role in water transport and stomatal conductivity. The leaf can fully perform its function when supplied with sufficient water for photosynthesis. The lack of coordination between CO_2 capture for photosynthesis and transpiration during stomatal opening can lead to hydraulic dysfunction due to embolism or the collapse of vessel elements. Therefore, ideal leaf function must be coordinated with the structural development of anatomical variables associated with water transport (Gebauer *et al*. 2022). The adjustments in these traits observed between wet and dry seasons optimize photosynthesis and water relations in response to varying environmental conditions.

The reduction in leaf area during the dry season contributes to dissipating heat, neutralizing overheating effects, and reducing transpiration rates. Our findings also emphasize the importance of leaf veins, vessel elements, and xylem in water transport processes and the adaptation of leaf anatomy to optimize water use and photosynthesis.

In conclusion, the variability of *S. joazeiro*'s leaf anatomical traits between wet and dry seasons and their interactions with climatic variables suggest the production of season-specific leaf cohorts to be an adaptation of evergreen tree species occurring in Deciduous Seasonal Forests. These cohorts are tailored to suit the conditions of light intensity, temperature, and evaporative demands in each season. Wet-season leaves exhibit traits associated with acquisitive strategies, while dry-season leaves bear more conservative traits, demonstrating the plant's ability to adapt its leaf production to maximize fitness under different seasonal stresses.

Acknowledgement

This study received partial financial support from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) under Finance Code 001. The authors extend their gratitude to CAPES, CNPq, FAPEMG, and UFLA, for their financial assistance. Special thanks are given to Universidade Federal de Lavras (UFLA), Departamento de Ciências Florestais, and Laboratório de Anatomia Vegetal UFLA, for providing material support. Poderiam acrescentar a seguinte frase nos agradecimentos: The authors wish to express their gratitude to the Research Productivity Grant Program of the State University of Minas Gerais (PQ/UEMG) for awarding a research productivity grant to N. C. A. F.

Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

References

Allen K, Dupuy JM, Gei MG, Hulshof C, Medvigy D, Pizano C, Salgado-Negret B, Smith C, Trierweiler A & Bloem SJ (2017) Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes. Environmental Research Letters 12: 1-15.

Alvares CA, Stape JL, Sentelhas PC, Moraes JLG & Sparovek G (2013) Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22: 711-728.

Apgaua DMG, Santos RM, Pereira DGS, Menino GCO, Pires GG, Fontes MAL & Tng DYP (2014) Beta-diversity in seasonally dry tropical forests (SDTF) in the Caatinga Biogeographic Domain, Brazil, and its implications for conservation. Biodiversity and Conservation 23:217-232. DOI: 10.1007/s10531-013-0599-9

Bartón K (2018) MuMIn: Multi model inference. R package version 1.43.17.75. Avaliable at < https://cran.r-project.org/web/packages/MuMIn/index.html>. Access on 10 March 2024.

Bates D, Mächler M, Bolker BM & Walker SC (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-48. DOI: 10.18637/jss.v067.i01

Bieras AC & Sajo MDG (2009) Leaf structure of the cerrado (Brazilian savanna) woody plants. Trees - Structure and Function 23: 451-471. DOI: 10.1007/s00468-008-0295-7

Cianciaruso MV, Silva IA, Manica LT & Souza JP (2013) Leaf habit does not predict leaf functional traits in cerrado woody species. Basic and Applied Ecology 14: 404-412. DOI: 10.1016/j.baae.2013.05.002

Dantas FCP, Tavares MLR, Targino MDS, Costa AP & Dantas FO (2014) *Ziziphus joazeiro* Mart. - Rhamnaceae: características biogeoquímicas e importância no bioma Caatinga. Vol. 25. Revista Principia - Divulgação Científica e Tecnológica do IFPB, João Pessoa. Pp. 51-57. DOI: 10.18265/1517-03062015v2n25p51-57

Dexter KG, Smart B, Baldauf C, Baker TR, Balinga MPB, Brienen RJW, Fauset S, Feldpausch TR, Silva LF, Muledi JI, Lewis SL, Lopez-Gonzalez G, Marimon-Junior BH, Marimon BS, Meerts P, Page N, Parthasarathy N, Phillips OL, Sunderland TCH, Theilade I, Weintritt J, Affum-Baffoe K, Araujo A, Arroyo L, Begne SK, Neves EC, Collins

M, Cuni-Sanchez A, Djuikouo MNK, Elias F, Foli EG, Jeffery KJ, Killeen TJ, Malhi Y, Maracahipes L, Mendoza C, Monteagudo-Mendoza A, Morandi P, Santos CO, Parada AG, Pardo G, Peh KSH, Salomão RP, Silveira M, Sinatora-Miranda H, Slik JWF, Sonke B, Taedoumg HE, Toledo M, Umetsu RK, Villaroel RG, Vos VA, White LJT & Pennington RT (2015) Floristics and biogeography of vegetation in seasonally dry tropical regions. The International Forestry Review 17: 10-32. DOI: 10.1505/146554815815834859

Diógenes FE, Oliveira A, Coelho MF, Maia SSS & Azevedo RAB (2010) Pré-tratamento com ácido sulfúrico na germinação de sementes de *Ziziphus joazeiro* Mart.: Rhamnaceae. Revista Brasileira de Plantas Medicinais 12: 188-194.

Dryflor, Banda-RK, Delgado-Salinas A, Dexter KG, Linares-Palomino R, Oliveira-Filho A, Prado D, Pullan M, Quintana C, Riina R, Rodríguez MGM, Weintritt J, Acevedo-Rodríguez P, Adarve J, Álvarez E, Aranguren BA, Arteaga JC, Aymard G, Castaño A, Ceballos-Mago N, Cogollo Á, Cuadros H, Delgado F, Devia W, Dueñas H, Fajardo L, Fernández Á, Fernández MÁ, Franklin J, Freid EH, Galetti LA, Gonto R, González-MR, Graveson R, Helmer EH, Idárraga Á, López R, Marcano-Vega H, Martínez OG, Maturo HM, McDonald M, McLaren K, Melo O, Mijares F, Mogni V, Molina D, Moreno ND, Nassar JM, Neves DM, Oakley LJ, Oatham M, Olvera-Luna AR, Pezzini FF, Dominguez OJ, Ríos ME, Rivera O, Rodríguez N, Rojas A, Särkinen T, Sánchez R, Smith M, Vargas C, Villanueva B & Pennington RT (2016) Plant diversity patterns in neotropical dry forests and their conservation implications. Science 353: 1-125.

Eamus D (1999) Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. Trends in Ecology & Evolution 14: 11-16. <https://doi.org/10.1016/S0169-5347(98)01532-8>.

Embrapa (2006) Sistema brasileiro de solos. Embrapa, Rio de Janeiro. Pp. 84-85.

Ennajeh M, Vadel AM, Cochard H & Khemira H (2015) Comparative impacts of water stress on the leaf anatomy of a drought-resistant and a drought-sensitive olive cultivar. The Journal of Horticultural Science and Biotechnology 85: 289-294.

Franco AC, Bustamante M, Caldas LS, Goldstein G, Meinzer FC, Kozovits AR, Rundel P & Coradin VTR (2005) Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. Trees - Structure and Function 19: 326-335. DOI: 10.1007/s00468-004-0394-z

Franklin G (1945) Age of the Baker's Hole Coombe Rock. Nature 1: 3924.

Gebauer R, Urban J, Volařík D, Matoušková M, Vitásek R, Houšková K, Hurt V, Pantová P, Polívková T & Plichta (2022) Does leaf gas exchange correlate with petiole xylem structural traits in Ulmus laevis seedlings under well-watered and drought stress conditions? Tree Physiology 42: 2534-2545. DOI: 10.1093/treephys/tpac082

Gianasi FM, Souza CR, Fagundes NCA, Maia VA, Morel JD, Santos PF & Santos RM (2020) Environmental filtering both indirectly and directly drives the Dry Tropical Forest species composition and functional composition. Ecological Research 36: 107-118. DOI: 10.1111/1440-1703.12178

Givnish TJ (2002) Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. Silva Fennica 36: 703-743.

Gratani L & Bombelli A (2000) Leaf anatomy, inclination, and gas exchange relationships in evergreen sclerophyllous and drought semideciduous shrub species. Photosynthetica 37: 573-585.

Holanda AER, Souza BC, Carvalho ECD, Oliveira RS, Martins FR, Muniz CR, Costa RC & Soares AA (2019) How do leaf wetting events affect gas exchange and leaf lifespan of plants from seasonally dry tropical vegetation? Plant Biology 21: 1097-1109. DOI: 10.1111/plb.13023

IBGE - Instituto Brasileiro de Geografia e Estatística (2012) Manual técnico da vegetação brasileira, 2ª ed. IBGE, Rio de Janeiro. Pp. 120-129.

INMET - Instituto Nacional de Meteorologia (2016) Banco de dados meteorológicos. Available at <https://portal.inmet.gov.br/processos>. Access on 18 May 2018.

Jonasson J (1989) Implications of leaf longevity, leaf nutrient re-absorption and translocation for the resource economy of five evergreen plant species. Oikos 56: 121-13.

Karabourniotis G, Liakopoulos G, Bresta P & Nikolopoulos D (2021) The optical properties of leaf structural elements and their contribution to photosynthetic performance and photoprotection. Plants 10: 1455. <https://doi.org/10.3390/plants10071455>.

Kikuzawa K (1995) The basis for variation in leaf longevity of plants. Vegetatio 121: 89-100. <https://doi.org/10.1007/BF00044675>.

Kraus JE & Arduin M (1997) Manual básico de métodos em morfologia vegetal. EDUR, Seropédica. 198p.

Kuznetsova A, Brockhoff PB & Christensen RHB (2017) ImerTest Package: tests in linear mixed effects models . Journal of Statistical Software 82: 1-26. <https://doi.org/10.18637/jss.v082.i13>.

Lima RB (2001) A família Rhamnaceae no Brasil: diversidade e taxonomia. Tese de Doutorado. Universidade de São Paulo, São Paulo. 292p.

Lohbeck M, Lebrija-Trejos E, Martínez-Ramos M, Meave JA, Poorter L & Bongers F (2015) Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession. PLoS One 10: 1-15. DOI: 10.1371/journal.pone.0123741

Loiola MIB, Roque ADA & Oliveira ACP (2012) Caatinga: vegetação do semiárido brasileiro. Ecologia 4: 14-19.

Mendes KR, Granja JAA, Ometto JP, Antonino ACD, Menezes RSC, Pereira EC & Pompelli MF (2017) Croton blanchetianus modulates its morphophysiological responses to tolerate drought in a tropical dry forest. Functional Plant Biology 44: 1039-1051. DOI: 10.1071/FP17098

Miatto RC, Wright IJ & Batalha MA (2016) Relationships between soil nutrient status and nutrient-related leaf traits in Brazilian cerrado and seasonal forest communities. Plant and Soil 404: 13-33. DOI: 10.1007/s11104-016-2796-2

Nadia TL, Machado IC & Lopes AV (2007) Reproductive phenology and pollination system of *Ziziphus joazeiro* Mart. (Rhamnaceae): the role of *Apis mellifera* and autochthonous floral visitors as pollinators. Acta Botanica Brasilica 21: 835-845. DOI: 10.1590/s0102-33062007000400008

O'Brien TP, Feder N & McCully ME (1964) Polychromatic staining of plant cell walls by toluidine blue O. Protoplasma 59: 368-373. DOI: 10.1007/BF01248568

Oliveira-Filho AT (2006) Catálogo das árvores nativas de Minas Gerais. Editora UFLA, Lavras. 423p.

Pennington RT, Lavin M & Oliveira-Filho A (2009) Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. Annual Review of Ecology, Evolution, and Systematics 40: 437-457. DOI: 10.1146/annurev.ecolsys.110308.120327

Prado DE & Gibbs PE (1993) Patterns of species distributions in the dry seasonal forests of South America. Annals of the Missouri Botanical Garden 80: 902. DOI: 10.2307/2399937

Pringle EG, Adams RI, Broadbent E, Busby PE, Donatti CI, Kurten EL, Renton K & Dirzo R (2011) Distinct leaf-trait syndromes of evergreen and deciduous trees in a seasonally dry tropical forest. Biotropica 43: 299-308. DOI: 10.1111/j.1744-7429.2010.00697.x

R Core Team (2024) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <https://www.R-project.org/>. Access on 15 May 2024

Rossatto DR & Kolb RM (2009) An evergreen neotropical savanna tree (Gochnatia polymorpha, Asteraceae) produces different dry- and wet-season leaf types. Australian Journal of Botany 57: 439-443. DOI: 10.1071/BT09045

Santos RM, Oliveira-Filho AT, Eisenlohr PV, Queiroz LP, Cardoso DB & Rodal MJ (2012) Identity and relationships of the arboreal *caatinga* among other floristic units of seasonally dry tropical forests (SDTFs) of north-easter n and Central Brazil. Ecology and Evolution 2: 409-428.

Silva EC, Nogueira RJMC, Azevedo Neto AD, Brito JZ & Cabral EL (2004) Aspectos ecofisiológicos de dez espécies em uma área de caatinga no município de Cabaceiras, Paraíba, Brasil. Iheringia 59: 201-205.

Silva JLA, Souza AF, Caliman A, Voigt EL & Lichston JE (2018) Weak whole-plant trait coordination in a seasonally dry South American stressful environment. Ecology and Evolution 8: 4-12. DOI: 10.1002/ece3.3547

Souza BC, Oliveira RS, Araújo FS, Lima ALA & Rodal MJM (2015) Divergências funcionais e estratégias de resistência à seca entre espécies decíduas e sempre verdes tropicais. Rodriguésia 66: 21-32. DOI: 10.1590/2175-7860201566102

Souza MC, Franco AC, Haridasan M, Rossato DR, Araújo JF, Morellato LPC & Habermann G (2015) The length of the dry season may be associated with leaf scleromorphism in cerrado plants. Anais da Academia Brasileira de Ciências 87: 1691-1699. DOI: 10.1590/0001-376520150381

Terra MCNS, Santos RM, Prado-Júnior JA, Mello JM, Scolforo JRS, Fontes MAL, Schiavini I, Reis AA, Bueno IT, Magnago LFS & Steege H (2018) Water availability drives gradients of tree diversity, structure and functional traits in the Atlantic-*Cerrado Caatinga* transition, Brazil. Journal of Plant Ecology 11: 803-814. DOI: 10.1093/jpe/rty017

Tomlinson KW, van Langevelde F, Ward D, Bongers F, Silva DA, Prins HH, Bie S & Sterck FJ (2013) Deciduous and evergreen trees differ in juvenile biomass allometries because of differences in allocation to root storage. Annals of Botany 112: 575-587.

Vico G, Dralle D, Feng X, Thompson S & Manzoni S (2017) How competitive is drought deciduousness in tropical forests? A combined eco-hydrological and eco-evolutionary approach. Environmental Research Letters 12: 065006. DOI: 10.1088/1748-9326/aa6f1b

Westoby M, Falster DS, Moles AT, Vesk PA & Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology, Evolution, and Systematics 33: 125-159. DOI: 10.1146/annurev.ecolsys.33.010802.150452

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JH, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ & Villar R (2004) The worldwide leaf economics spectrum. Nature 428: 821-827.

Area Editor: Dra. Simone Teixeira
Received on January 19, 2024. Accepted on May 02, 2024.