Trees (2026) 40:10
https://doi.org/10.1007/s00468-025-02716-9

ORIGINAL ARTICLE

Leaf anatomy as evidence of water-use strategies in two seasonally dry Brazilian vegetations: a comparison of co-occurring species

Larissa C. Doria[1] · Tayeme Piva[2] · Carina Araujo[1] · Raiane Beu[3] · Juliana L. S. Mayer[1] · Rivete S. Lima[4] · Carmen R. Marcati[5]

Received: 19 May 2025 / Accepted: 22 December 2025 / Published online: 10 January 2026
© The Author(s) 2026

Abstract

Water-use strategies, i.e., the ratio of carbon gain to water loss, reflect how efficiently a plant assimilates carbon minimizing water loss. Leaf anatomical traits are crucial in shaping these strategies. Here, we look at evidence of water-use strategies from assessing leaf anatomical traits in two co-occurring species from the Cerrado (Brazilian savanna) and the Caatinga (a seasonally dry tropical forest in Brazil). We tested whether these species exhibit convergent anatomical adaptation or distinct structural responses, and whether individuals of the same species would exhibit distinct responses to water-use strategies between sites. We collected leaves from fully sun-exposed branches of individuals of the co-occurring species *Tabebuia aurea* and *Tocoyena formosa*, and performed light and scanning electron microscope observations of leaf anatomical traits to assess differences between sites. Leaf anatomical traits explained differences between sites only for *Tabebuia aurea*: individuals from the Cerrado exhibit thicker leaves and spongy and palisade parenchyma, and higher frequency of peltate trichomes, while those from the Caatinga show thicker abaxial and adaxial epidermis and a greater proportion of intercellular air space in the mesophyll. No differences are observed between individuals of *T. formosa*. Therefore, there is no convergent leaf anatomical response of species driven by environmental constraints. The variation in individuals of *T. aurea* between sites reflects contrasting functional adjustment aligning in opposite directions along the conservative-acquisitive strategy spectrum: Caatinga individuals show anatomical traits associated with an acquisitive strategy, while Cerrado individuals exhibit traits linked to a more conservative water-use strategy.

Key message

There is no convergent leaf anatomical adaptation between species driven by site. Leaf traits variance in *T. aurea* reflects contrasting functional adjustment in opposite directions between the Cerrado and Caatinga.

Keywords Caatinga · Cerrado · Functional adjustment · Leaf anatomy · Seasonally dry vegetations · Water-use efficiency

Communicated by Laura Varone.

✉ Larissa C. Doria
larissachacondoria@gmail.com; lcdoria@unicamp.br

[1] Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas - UNICAMP, P.O. Box 6109, Campinas 13083-970, SP, Brazil

[2] Postgraduate Program in Biological Sciences (Botany), Institute of Biosciences, São Paulo State University - UNESP, P.O. Box 510, Botucatu 18618-970, SP, Brazil

[3] Graduate Program in Ecology, Institute of Biological Sciences, University of Brasília, Brasília DF 70904-970, Brazil

[4] Department of Systematic and Ecology, Center for Exact and Natural Sciences, Federal University of Paraíba - UFPB, João Pessoa 58059-900, PB, Brazil

[5] Department of Forest Science, Soil and Environment, School of Agricultural Sciences, São Paulo State University - UNESP, Botucatu, Botucatu 18610-034, SP, Brazil

Introduction

Leaf anatomy is a key adaptive trait shaping plant fitness and survival across different environments, as it directly influences photosynthesis and water-use efficiency (WUE) (Terashima et al. 2011; Tomás et al. 2013; Trueba et al. 2022; Petrík et al. 2022). In broad terms, WUE is defined as the ratio of carbon gain (photosynthesis) to water loss (transpiration) and reflects how efficiently a plant optimizes carbon assimilation while minimizing water loss (Bramley et al. 2013). The prominent effort in genetically modifying leaf structures, such as increasing leaf thickness and internal air volume, which potentially improves WUE, underscores the significant role of leaf anatomy in enhancing WUE (Tholen et al. 2012; Flexas et al. 2013, 2021).

Water-use strategies strongly shape plant species' responses to environmental constraints and are therefore expected to be finely tuned to different environmental filters, such as differences in precipitation, temperature, and soil nutrients (Xu and Li 2006; Tambussi et al. 2007; Hatfield and Dold 2019). Several anatomical and functional traits contribute to WUE, particularly those linked to leaf and stem efficiency. As such, species with low wood density, high leaf water potential, and deciduous habits are typically associated with lower WUE, while species with high wood density and lower leaf water potential exhibit more variable WUE (Wright et al. 2021). Leaf anatomy gives evidence of water use efficiency due to variable mesophyll porosity that will affect mesophyll diffusion conductance to CO2, which will ultimately affect water use efficiency in plants (Tomás et al. 2013; Carriquí et al. 2015; Trueba et al. 2022). For instance, the presence of bundle sheath extensions appears to facilitate water transport from leaf minor veins to the mesophyll to evaporation sites in the leaf. This structural feature is linked to improved water distribution within the leaf and enhanced water-use efficiency (Scoffoni et al. 2008; Buckley et al. 2011).

In terms of abiotic factors, water use efficiency has been proven to be influenced by soil composition (Gonzalez-Dugo et al. 2009; Quemada and Gabriel 2016). The relationship occurs via the response of stomatal closure to drought stress that reduces evapotranspiration and consequently the mass flow of soil solution (nutrients) to the root surface. Consequently, the delivery rate of mineral elements decreases, limiting plant nutrition and growth (Shao et al. 2008; Grzebisz et al. 2013). For example, phosphorus concentration directly regulates CO2 responsiveness to photosynthesis, which in turn affects WUE (Lewis et al. 1994; Campbell and Sage 2006). Additionally, a good nitrogen nutritional status enhances crop tolerance to drought, while a moderate increase in nitrogen supply improves water use efficiency in semiarid environments (Cossani et al. 2012).

The Cerrado and Caatinga are two seasonally dry ecosystems in Brazil (Pennington et al. 2000), both experiencing at least five consecutive dry months annually (Nimer 1972; Silva et al. 2008). The Caatinga is the largest seasonally dry tropical forest (SDTF) of the Americas, located in northeast Brazil (Albuquerque et al. 2012). It operates at the end of the aridity of SDTF with average annual rainfall between 300 and 800 mm and a mean annual temperature of 26 °C (Nimer 1972; Sampaio 1995; Santos et al. 2014). It has only recently been proposed a vast species checklist for the vegetation, with a high number of endemic species (Fernandes et al. 2022). The Cerrado is a savanna-like ecosystem in the central Brazilian plateau that receives approximately 1500 mm of annual rainfall, with mean temperatures of 23 °C (Silva et al. 2008). It is the world's richest savanna, home to over 7000 vascular plant species, 44% of which are endemic (Mendonça et al. 1998; Klink and Machado 2005). A notable characteristic of the Cerrado is the deep, nutrient-poor, aluminum-rich soils, which may affect numerous plant metabolic processes (Haridasan 2000; Coutinho 2002).

Here, we investigate key leaf anatomical traits in two co-occurring species from the Caatinga and Cerrado to assess whether their anatomical characteristics provide some pieces of evidence of their water-use strategies. Specifically, we aim to understand whether the two environments' constraints drive a convergent anatomical adaptation or whether the two species will present distinct structural responses. Additionally, based on variation in leaf anatomy, we aim to test whether individuals of the same species from the two different sites will exhibit distinct functional responses to water-use efficiency. We also discuss how variations in soil fertility might influence leaf anatomical traits and, consequently, water-use strategies.

Materials and methods

Site and sampling

The Cerrado sampling area has a mean annual temperature of 25 °C and a maximum monthly rainfall of 350 mm during the wet season. The dry season is well-defined, lasting from June to September, with precipitation below 50 mm (data from the Estação Experimental of the School of Agronomic Sciences, São Paulo State University - UNESP). The Caatinga sampling area experiences temperatures above 25 °C throughout the year, with a maximum monthly rainfall of 100 mm in the wet season. The dry season is longer than in the Cerrado, extending from July to December when the precipitation reaches zero (data from the Estação Experimental of São João do Cariri, Paraíba State, Brazil).

In both domains, soils are predominantly sandy. Cerrado soils exhibit higher acidity, likely due to a greater aluminum saturation and higher potential acidity ($H^{+}Al$) in the cation exchange capacity. Additionally, Cerrado soils have lower concentrations of macronutrients (P, K, Ca, Mg) and micronutrients such as manganese compared to Caatinga soils. Additionally, copper and iron concentrations are higher in Cerrado soils than in Caatinga soils (Dória et al. 2016).

We selected the species *Tabebuia aurea* (Silva Manso) Benth. & Hook. f. ex S. Moore and *Tocoyena formosa* (Cham. & Schltdl.) K. Schum., both commonly found in the Cerrado (Ratter et al. 2003) and the Caatinga (Moro et al. 2014). In both sites, the species shed their leaves during the dry season (Barros 2001; Sanz-Veiga et al. 2017). In the Cerrado, samples were collected at the "Palmeira da Serra" Private Reserve, in the city of Pratânia, São Paulo State, Brazil (22 48'35" S, 48 39'57" W). In the Caatinga, the sampling site was in the city of Serra Branca, Paraíba State, Brazil (7 29'14" S, 36 39'51" W).

During the rainy period, we collected five healthy, green, fully expanded leaves from sun-exposed branches, from three individuals for each species and environment. For preservation, the leaves were immediately fixed in FAA 70 solution (37% formaldehyde, acetic acid, and ethanol 70%), and later stored in Ethanol 70%.

Anatomical study

From the five leaves collected per individual, we selected the three healthiest and prepared transverse sections covering regions from the midrib to the leaf blade margins. For light microscopy (LM) analyses, we embedded samples in historesin (Leica Microsystems, Nussloch/Heidelberg, Germany), and sectioned transversely using a rotary microtome (Leica RM2245) at a thickness of 4–6 µm. Sections were stained with 1% toluidine blue in 1% aqueous sodium tetraborate solution (O'Brien et al. 1964), mounted in synthetic resin (Entellan, Merck KGaA, Darmstadt, Germany), and analyzed under LM.

For the three leaf samples per species on each site, we performed three measurements at both the base and the tip of the leaf for each anatomical variable (total leaf thickness, total parenchyma thickness, palisade parenchyma thickness, spongy parenchyma thickness, abaxial and adaxial epidermis thickness) in order to capture the greatest variation. To quantify the proportion of intercellular spaces in the spongy parenchyma, we captured three pictures in 10x magnification, and in each image, we measured the total area of the spongy parenchyma, and the corresponding intercellular space area. Subsequently, all the values were averaged for each individual.

For scanning electron microscopy (SEM), we followed the methodology described by Dória et al. (2018). Dried leaves from each individual per species were dehydrated in an ethanol series (50%, 70%, 96%), air-dried at room temperature, and mounted on aluminum stubs using an electron-conductive carbon sticker. Samples were then coated with platinum/palladium using a sputter coater (Quorum Q150TS Quorum Technologies, Laughton, UK) and examined under a field emission SEM (JEol JSM-7600 F, Tokyo, Japan) at an accelerating voltage of 5 KV. SEM was used to analyze the shape, distribution, and frequency of trichomes on both the abaxial and the adaxial epidermis. To the measurements of trichomes frequency, we selected five areas of $1mm^2$ and counted the number of trichomes exhibited in the area.

All measurements were performed using the software FIJI (ImageJ Distribution) (Schindelin et al. 2012).

Data analyses

To test whether individuals of each species would be differentiated between sites based on leaf anatomical traits, we performed a permutational multivariate analysis of variance (PERMANOVA) with leaf anatomical traits as the response variables, and sites (Cerrado and Caatinga) as predictive variables, using the adonis function in the Vegan package in R. Additionally, to visualize the relationships and distribution of individuals and species between sites, we conducted a principal component analysis (PCA) using leaf measurements as separate points in the PCA. This analysis was performed with the rda function from the Vegan package.

To assess differences between sites in total leaf thickness, palisade and spongy parenchyma thickness, and abaxial and adaxial epidermis thickness, we used linear mixed model with Individuals as a random effect, using the lmer function from the lme4 package in R. Differences in trichome frequency and the proportion of intercellular spaces in the spongy parenchyma between sites were tested using a paired t-test, after checking for normality and homogeneity of variances. A log transformation was applied to the predictive variables to deal with heteroscedasticity and/or non-normality (Zuur et al. 2007).

All statistical analyses were performed in R 2024 version 4.4.2 using R Studio 2024 version 12.0 (R Core Team 2024). All differences were considered significant when $P<0.05$.

Results

Leaf anatomical traits explained differences between sites only for *Tabebuia aurea* ($F=22.1$; $P<0.01$), accounting for 41% of the variance in the data. In contrast, anatomical

Table 1 PERMANOVA results for the effect of sites (Cerrado and Caatinga) on leaf anatomical traits of *Tabebuia aurea* and *Tocoyena formosa*

	Degree of freedoms	Sum of squares	R^2	F	Pr(>F)
Tabebuia aurea					
Vegetation	1	0.81908	0.41613	22.094	**0.001**
Residual	31	1.14925	0.58387		
Total	32	1.96833	1.0000		
Tocoyena formosa					
Vegetation	1	0.06894	0.03872	1.3696	0.265
Residual	34	1.71147	0.96128		
Total	35	1.78041	1.0000		

Values in bold represent differences ($P<0.05$)

traits did not significantly differentiate *Tocoyena formosa* between sites (F = 1.37; $P = 0.265$) (Table 1). The greater variability in anatomical traits for *T. aurea* compared to *T. formosa* is also evident in the distribution of individuals within the PCA space (Fig. 1). Individuals of *T.aurea* (open circles) exhibit a more dispersed distribution in the PCA, with a clear tendency toward site differentiation: those from the Cerrado (green open circles) and the Caatinga (yellow open circles) cluster separately. Conversely, *T. formosa* individuals (filled circles) display a more compact distribution, with no clear separation between sites (Cerrado in green, and Caatinga in yellow) (Fig. 1). When analyzing the association amongst leaf anatomical traits in the PCA, the first axis explains 71% of the total variance, while the second explains 18%. The first principal component has large positive associations with total leaf thickness, and with palisade and spongy parenchyma thickness. Individuals of *T. aurea* are associated with high values of these variables compared to *T. formosa* individuals. The second principal component has negative associations with abaxial and adaxial epidermis thickness. Individuals of *T. formosa* are associated with larger values of adaxial epidermis thickness than individuals of *T. aurea*.

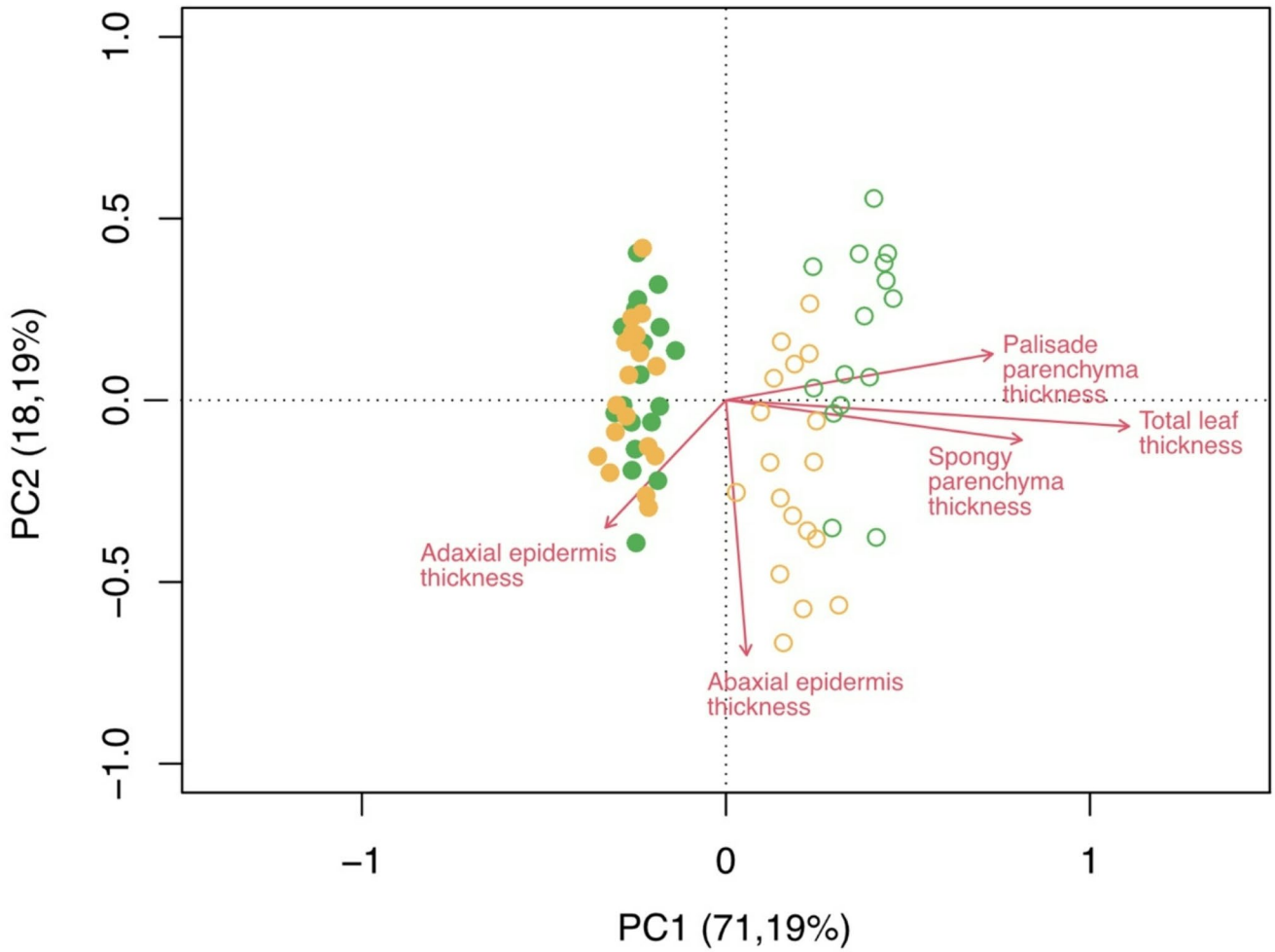


Fig. 1 Principal component analysis of leaf anatomical traits of *Tabebuia aurea* and *Tocoyena formosa* from the Cerrado and Caatinga on the first two axes. Open circles represent measurements of leaf anatomical trait of *T. aurea* and filled circles represent those of *T. formosa* in the Cerrado (green) and the Caatinga (yellow)

Consistent with the results of multivariate analysis, pairwise t-tests revealed no significant differences between anatomical traits for *T. formosa*, except for a slight difference in spongy parenchyma thickness. In contrast, *T. aurea* exhibited significant differences in all analyzed leaf anatomical traits, as detailed below.

Tabebuia aurea

Individuals from the Cerrado have thicker leaves ($P<0.01$, $X^2=9.94$), with increased palisade parenchyma thickness ($P<0.01$, $X^2=6.82$) and spongy parenchyma thickness ($P<0.05$, $X^2=5.98$) compared to individuals from the Caatinga (Fig. 2A and B and 3; Supplementary Information,

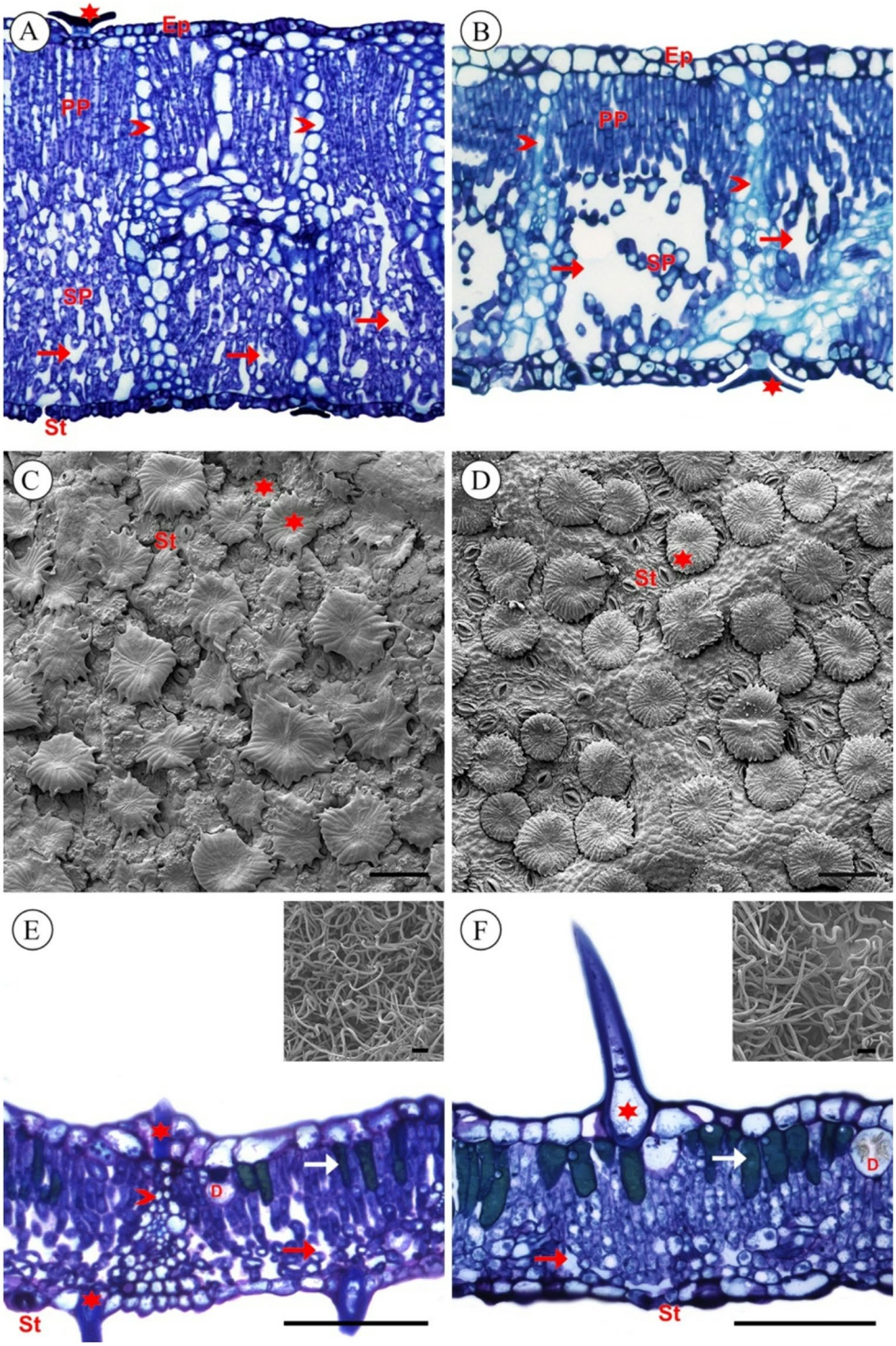


Fig. 2 Leaf anatomical sections of *Tabebuia aurea* and *Tocoyena formosa* from the Cerrado and the Caatinga. (**A**, **B**) Light microscopy of a leaf cross section of *T. aurea* from the Cerrado and the Caatinga, respectively. (**C**, **D**) Scanning electron microscope of the abaxial epidermis of *T. aurea* from the Cerrado and the Caatinga, respectively, showing the peltate trichomes. (**E**, **F**) Light microscopy of a leaf cross section of *T. formosa* from the Cerrado and the Caatinga, respectively. The inserts in both images show the detail of the filiform trichomes in scanning electron microscopy. Ep = epidermis. PP = palisade parenchyma. SP = spongy parenchyma. St = stomata. D = idioblast with druses. Red arrows show the intercellular air space. White arrows show idioblasts with phenolic compounds in palisade parenchyma. Asterisks show the trichomes. Arrowheads show the bundle sheath extension cells. Scale bars: 200 µm (A, B); 100 µm (C – F)

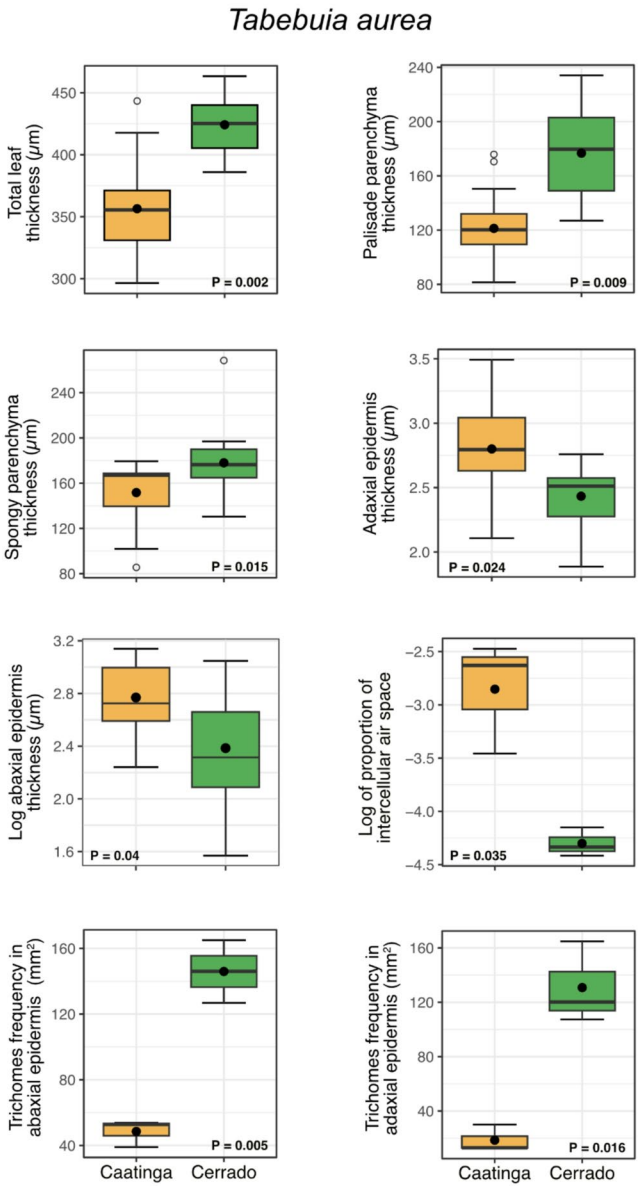


Fig. 3 Differences in leaf anatomical traits of *Tabebuia aurea* occurring in the Cerrado (green) and the Caatinga (yellow). Values in bold ($P<0.05$) represent mean differences between sites. The bottom, middle, and upper lines of the box represent the 25th quartile, the median, and the 75th quartile, respectively. The upper and the bottom ends of the vertical lines indicate the maximum and minimum values of each variable

Table S1). In contrast, Cerrado individuals exhibit a lower proportion of intercellular spaces in the spongy parenchyma ($P<0.04$, t=4.59) and a thinner adaxial epidermis ($P<0.05$, $X^2=4.81$), and abaxial epidermis ($P<0.05$, $X^2=4.23$) (Figs. 2A and B and 3; Supplementary Information, Table S1). Individuals from both sites exhibit heterobaric leaves, characterized by bundle-sheath extensions connecting the adaxial and abaxial epidermis (Fig. 2A, B). In Caatinga individuals, these extensions are lignified (Fig. 2B). Peltate trichome frequency is higher in Cerrado individuals on both the adaxial and abaxial surfaces ($P<0.05$, t = −6.13; $P<0.01$; t = −8.11, respectively) than individuals from Caatinga (Figs. 2C and D and 3; Supplementary Information, Table S1). Additionally, the head of the peltate trichomes in Cerrado individuals appears to be larger, providing increased coverage and shading over a greater portion of the epidermis (Fig. 2C).

Tocoyena formosa

No differences are observed in leaf anatomical traits between Cerrado and Caatinga individuals, except for a slightly thicker spongy parenchyma in Cerrado individuals ($P<0.05$, $X^2=6.28$) (Fig. 4; Supplementary Information, Table S1). The spongy parenchyma is tightly organized with minimal intercellular air spaces (Fig. 2E, F). The frequency of filiform trichomes was not quantified for *T. formosa* due to their high density on both epidermal surfaces, which also hindered the observation of stomatal morphology in both sites (inserts in Fig. 2E, F). Individuals from both sites exhibit heterobaric leaves, characterized by thin bundle-sheath extensions connecting the adaxial and abaxial epidermis (Fig. 2E, F). Also, in individuals from both sites, the first layer of palisade parenchyma contains a high concentration of idioblasts with phenolic compounds and druses (Fig. 2E, F).

Discussion

The two co-occurring species in the Cerrado and Caatinga show distinct structural responses in leaf anatomy. While *Tabebuia aurea* demonstrates greater plasticity, showing remarkable differences in leaf anatomical traits, *Tocoyena formosa* appears more conservative, with no differences between sites. This response pattern has also been observed in the variation of wood anatomy characters, which show no differentiation between cerrado and caatinga individuals of *T. formosa* at the same sites, highlighting the more conservative anatomical behavior of *T. formosa* compared to *T. aurea* (Dória et al. 2016). Despite its conservative anatomical behavior, *T. formosa* exhibits a broad distribution across South America, ranging from Suriname to Paraguay, similar to *T. aurea*. In Brazil, it occurs in diverse regions, including the Amazon Rainforest, Caatinga, Cerrado, and Atlantic Forest (Oliveira 2015; Borges 2020; Lohmann 2020). This result reinforces the complexity of plant responses to environmental constraints, and suggests that, although variations in leaf and wood anatomy are important traits influencing the ecological success of species across different environments (Hacke et al. 2001; Fradera-Soler et al. 2021;

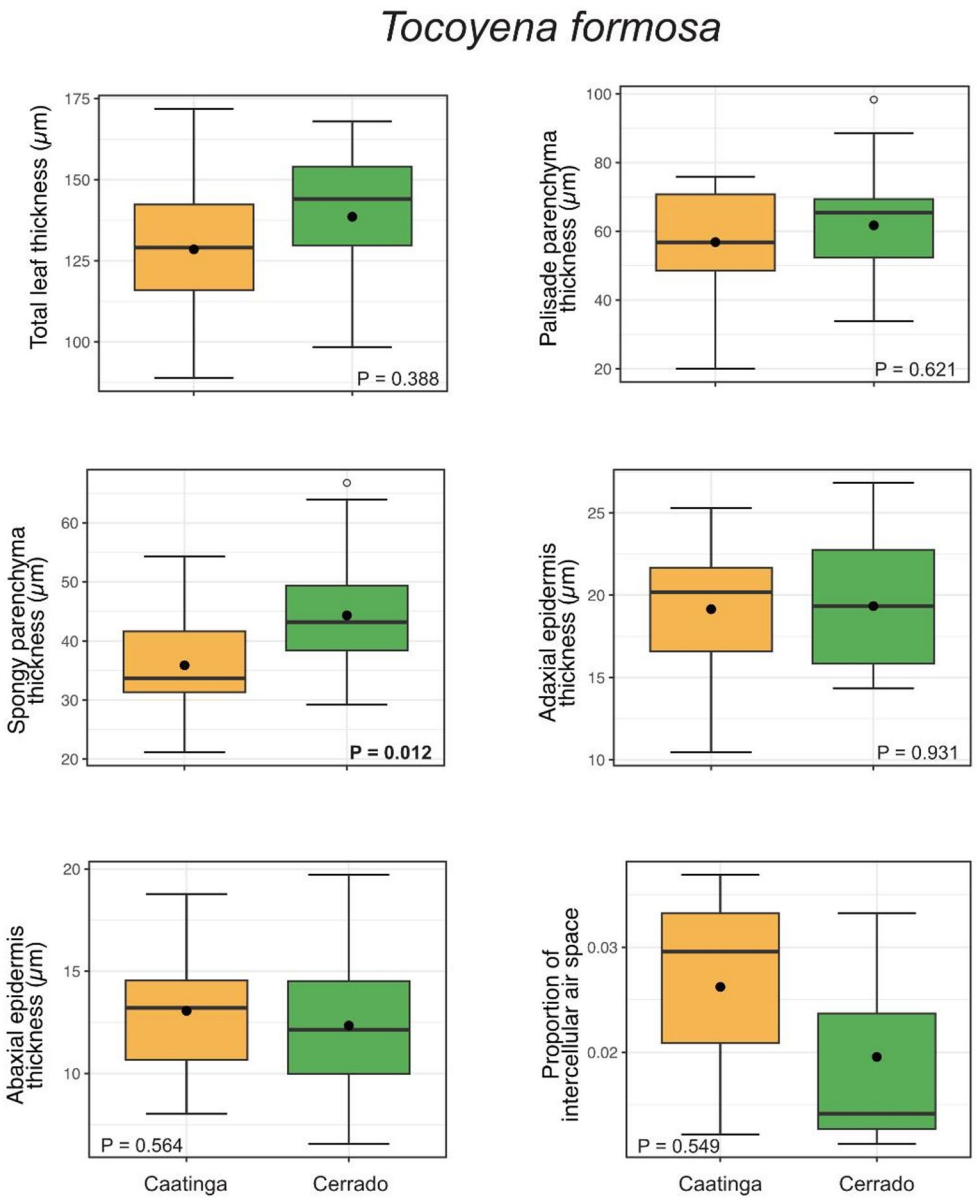


Fig. 4 Differences in leaf anatomical traits of *Tocoyena formosa* occurring in the Cerrado (green) and the Caatinga (yellow). Values in bold ($P<0.05$) represent mean differences between sites. The bottom, middle and upper lines of the box represent the 25th quartile, the median and the 75th quartile, respectively. The upper and bottom ends of the vertical lines indicate the maximum and minimum values of each variable

Liu and Zheng 2024), they represent just two of multiple contributing factors. *T. formosa* likely invests in alternative adaptive strategies, such as physiological responses, to cope with varying environmental conditions.

Although *T. formosa* individuals do not show marked differences in leaf morphology between sites, both populations exhibit peculiar anatomical traits associated with adaptation to drought. In addition to the bundle-sheath extensions, the high concentration of phenolic compounds in the palisade parenchyma is considered a drought-response adaptation to abiotic stress. Phenolic compounds are multifunctional and have strong antioxidant properties, which protect cells from oxidative damage (Reginatto et al. 2014; Varela et al. 2016).

Based on the observed leaf anatomical differences in *T. aurea*, we can infer that individuals from the two sites adopt different strategies to enhance water-use efficiency. Individuals from Cerrado invest in thicker leaves, with a thicker spongy and palisade parenchyma, and a higher frequency of trichomes with larger heads covering a greater proportion of the epidermis than Caatinga individuals. In contrast, individuals from Caatinga exhibit a thicker abaxial and adaxial epidermis, a greater proportion of intercellular air spaces, and lignified bundle-sheath cell extensions connecting the adaxial and abaxial epidermis compared to Cerrado individuals.

Thicker leaves and increased palisade parenchyma thickness have been associated with enhanced water-use efficiency (Guerfel et al. 2009), primarily due to the formation of a thicker leaf-air boundary layer, which increases resistance to water loss and reduces transpiration, ultimately

improving WUE (Mo et al. 2016). Similarly, the higher frequency of trichomes with larger heads observed in Cerrado individuals is also linked to a thicker boundary layer, further contributing to increased WUE (Klich 2020; Bramley et al. 2013). Although trichomes are well-known for their role in reflecting photossynthetically active radiation (PAR) - blue, green, and red light - thereby balancing energy input and reducing heat stress (Ehleringer et al. 1976; Bickford 2016), they also play a significant role in WUE by decreasing transpiratory water loss through increased leaf–air boundary layer resistance (Mo et al. 2016; Galdon-Armero et al. 2018). For instance, Chen et al. (2022) observed that in *Shepherdia sp.*, trichome density doubled under drought conditions, followed by an 85% reduction in stomatal conductance (gs) compared to well-watered plants, highlighting the role of trichomes in water conservation. There is also evidence that leaf trichomes play a role in heavy metal detoxification (Broadhurst et al. 2004; Karabourniotis et al. 2020). This is particularly relevant for Cerrado individuals, since the Cerrado soils at the sampling site show high levels of heavy and toxic metals, including manganese and aluminum (Dória et al. 2016).

Regarding the WUE of *T. aurea* individuals from the Caatinga, the data indicate that they invest in larger intercellular air spaces than individuals from Cerrado. Mesophyll conductance (g_m), which quantifies the diffusion of CO_2 from substomatal cavities to the carboxylation sites in the chloroplasts, is strongly dependent on the proportion of intercellular air spaces (Evans et al. 2009). The greater proportion of intercellular air spaces facilitates faster CO2 carboxylation, and ultimately, enhances plant productivity (Flexas et al. 2013). Additionally, *T. aurea* individuals from the Caatinga exhibit lignified cells in the bundle-sheath extensions, which may contribute to greater compartmentalization of the leaf mesophyll compared to Cerrado individuals. Increased mesophyll compartmentalization has been associated with patchy stomatal closure under drought conditions and higher photosynthetic capacity per unit of leaf mass (Liakoura et al. 2009; Kamakura et al. 2011; Inoue et al. 2010).

These findings suggest that each population of *T. aurea* invests in distinct water-use strategies shaped by their respective environments. While Cerrado individuals seem to prioritize anatomical traits that enhance the leaf-air boundary layer thickness – potentially reducing transpirational water loss but also limiting CO2 diffusion - individuals from the Caatinga tend to exhibit traits that facilitate greater CO2 assimilation, potentially optimizing carbon fixation under water-limited conditions. Such anatomical distinctions offer insight into the functional adjustment of *T. aurea* to environmental conditions, positioning along the spectrum of conservative-acquisitive strategies in the two sites (Westoby 1998; Grime 2001; Diaz et al. 2016). Given the longer and more intense dry season in the Caatinga, one might expect individuals from this biome to exhibit more conservative leaf anatomical traits aimed at water conservation. Nevertheless, seasonally dry tropical forests (STDFs), such as the Caatinga, undergo seasonal cycles alternating between high and low water stress conditions (Pennington et al. 2009). During the dry season, *T. aurea* individuals shed their leaves, thereby avoiding hydraulic failure and limiting photosynthetic activity. This behaviour enables the species to concentrate physiological activity during the rainy season, when environmental conditions favor the development of acquisitive traits in SDTFs (Chesson et al. 2004; De Lima et al. 2021). This is evidenced here by the higher proportion of intercellular air spaces in the spongy parenchyma in *T.aurea* individuals from the Caatinga, suggesting a strategy suited to maximizing photosynthetic capacity via faster carboxylation of CO2.

Conversely, *T. aurea* individuals from the Cerrado appear more conservative on leaf anatomical traits aimed at water conservation and retention, such as thicker leaves and palisade and spongy parenchyma, and a higher frequency of trichomes. Although the Cerrado experiences a defined rainy season lasting approximately five months, plants are still subject to strong selective pressures from the low nutrient availability in the Cerrado soils. Such soil environmental constraints expose these plants to conditions far from their physiological optimum, which influences carbon allocation patterns, that in turn shape water-use strategies (Bucci et al. 2005). For instance, the high clay content of Cerrado soil can limit water availability even during wet periods, as clay particles reduce soil permeability and water retention capacity. Furthermore, essential macronutrients such as potassium (K) and magnesium (Mg) - which are present in low concentrations in Cerrado soils (Dória et al. 2016) - are required in large quantities by plants and play a critical role in photosynthesis (Trankner et al. 2018). Deficiency in K and Mg triggers a cascade of anatomical, physiological, and biochemical responses that ultimately reduce photosynthetic carbon assimilation (Jákli et al. 2017). Anatomically, K deficiency induces structural adaptations in the leaf that decrease mesophyll conductance, thereby limiting chloroplastic CO_2 concentration and constraining photosynthetic efficiency. Additionally, the high aluminum content in the Cerrado soils increases the water stress by further restricting plant capacity to acquire both water and essential nutrients (Kochian et al. 2015). Such impedance potentially occurs, for instance, via Al-induced disruption of root cells, which also disrupts the uptake and transport of important nutrients, including potassium (K+), magnesium (Mg2+), and calcium (Ca2+) (Zhang et al. 2017; Ofoe et al. 2023).

Conclusion

Our findings highlight an absence of a convergent anatomical response of species driven by environmental constraints in the Brazilian savanna (Cerrado) and in a seasonally dry tropical forest in Brazil (Caatinga). *Tabebuia aurea* demonstrates greater anatomical plasticity reflected in a contrasting functional adjustment to local environmental conditions. Such contrasting response align in opposite directions along the conservative-acquisitive strategy spectrum: Caatinga individuals of *T.aurea* show anatomical traits associated with an acquisitive water-use strategy, while Cerrado individuals exhibit traits linked to a more conservative strategy. The interplay between water availability and poor soil nutrient content in the Cerrado might play a crucial role in shaping these anatomical strategies by impose additional selective pressures. On the other hand, *Tocoyena formosa* exhibits limited trait adjustment in leaf anatomical traits between sites, while still maintaining adaptations for drought resistance in both environments.

Acknowledgements L.C.D. was supported by a grant from the CNPq - Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil (The National Council for Scientific and Technological Development) (PROC. no. 206433/2014-0).

Author contributions The conception of ideas, methodology design, statistical analyses and writing of the first draft of the manuscript were performed by Larissa C. Dória. The sample collection was performed by Larissa C. Dória, Tayeme Piva, Rivete Lima and Carmen R. Marcati. The data collection was performed by Larissa C. Dória, Tayeme Piva, and Carina Araujo. All authors critically commented on previous version of the manuscript, read and approved the final manuscript.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). This work was supported by the CNPq - Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil (The National Council for Scientific and Technological Development) (PROC. no. 206433/2014-0).

Data availability The datasets generated during and/or analysed during the current study are available in the manuscript and in the supplementary information, and from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Albuquerque UP, Araújo EL, El-Deir ACA et al (2012) Caatinga revisited: ecology and conservation of an important seasonal dry forest. Sci World J 205182. https://doi.org/10.1100/2012/205182

Barros MG (2001) Pollination ecology of *Tabebuia aurea* (Manso) Benth. & Hook. and *T. ochracea* (Cham.) Standl. (Bignoniaceae) in central Brazil Cerrado vegetation. Rev Bras Bot 24:255–261. https://doi.org/10.1590/S0100-84042001000300003

Bickford CP (2016) Ecophysiology of leaf trichomes. Funct Plant Biol 43:807–814. https://doi.org/10.1071/FP16095

Borges RL (2020) Tocoyena in Flora do Brasil. Jardim Botânico do Rio de Janeiro. https://floradobrasil2020.jbrj.gov.br/FB74808

Bramley H, Turner NC, Siddique KHM (2013) Water use efficiency. In: Kole C (ed) Genomics and Breeding for Climate-Resilient Crops, vol 2. Springer, Berlin Heidelberg, pp 225–268. https://doi.org/10.1007/978-3-642-37048-9_6

Broadhurst CL, Chaney RL, Angle JS, Maugel TK, Erbe EF, Murphy CA (2004) Simultaneous hyperaccumulation of nickel, manganese, and calcium in alyssum leaf trichomes. Environ Sci Technol 38:5797–5802. https://doi.org/10.1021/es0493796

Bucci SJ, Goldstein G, Meinzer FC, Franco AC, Campanello P, Scholz FG (2005) Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plant water potential in Neotropical savanna trees. Trees 19:296–304. https://doi.org/10.1007/s00468-004-0391-4

Buckley TN, Sack L, Gilbert ME (2011) The role of bundle sheath extensions and life form in stomatal responses to leaf water status. Plant Physiol 156:962–973. https://doi.org/10.1104/pp.111.175638

Campbell CD, Sage RF (2006) Interactions between the effects of atmospheric CO_2 content and P nutrition on photosynthesis in white lupin (*Lupinus albus* L). Plant Cell Environ 29:844–853. https://doi.org/10.1111/j.1365-3040.2005.01464.x

Carriquí M, Cabrera HM, Conesa M et al (2015) Diffusional limitations explain the lower photosynthetic capacity of ferns as compared with angiosperms in a common garden study. Plant Cell Environ 38:448–460. https://doi.org/10.1111/pce.12402

Chen J, Sun Y, Kopp K, Oki L, Jones SB, Hipps L (2022) Effects of water availability on leaf trichome density and plant growth and development of Shepherdia ×utahensis. Front Plant Sci 13:855858. https://doi.org/10.3389/fpls.2022.855858

Chesson P, Gebauer RLE, Schwinning S et al (2004) Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141:236–253. https://doi.org/10.1007/s00442-004-1551-1

Cossani CM, Reynolds MP (2012) Physiological traits for improving heat tolerance in wheat. Plant Physiol 60:1710–1718. https://doi.org/10.1104/pp.112.207753

Coutinho LM (2002) O bioma do Cerrado. In: Klein AL (ed) Eugene warming e o Cerrado brasileiro: Um século depois. UNESP, Imprensa Oficial do Estado, São Paulo, pp 77–92

De Lima ALA, Rodal MJN, Castro CC et al (2021) Phenology of Hogh-and low-density wood deciduous species responds differently to water supply in tropical semiarid regions. J Arid Environ 193:104594

Díaz S, Kattge J, Cornelissen JHC et al (2016) The global spectrum of plant form and function. Nature 529:167–171. https://doi.org/10.1038/nature16489

Dória LC, Podadera DS, Batalha MA, Lima RS, Marcati RM (2016) Do woody plants of the Caatinga show a higher degree of xeromorphism than in the cerrado? Flora 224:244–251. https://doi.org/10.1016/j.flora.2016.08.011

Dória LC, Podadera DS, del Arco M et al (2018) Insular woody daisies (*Argyranthemum*, Asteraceae) are more resistant to drought-induced hydraulic failure than their herbaceous relatives. Funct Ecol 32:1467–1478. https://doi.org/10.1111/1365-2435.13085

Ehleringer J, Björkman O, Mooney HA (1976) Leaf pubescence: effects on absorptance and photosynthesis in a desert shrub. Science 192:376–377. https://doi.org/10.1126/science.192.4237.376

Evans JR, Kaldenhoff R, Genty B, Terashima I (2009) Resistances along the CO_2 diffusion pathway inside leaves. J Exp Bot 60:2235–2248. https://doi.org/10.1093/jxb/erp117

Fernandes MF, Cardoso D, Pennington RT, de Queiroz LP (2022) The origins and historical assembly of the Brazilian Caatinga seasonally dry tropical forests. Front Ecol Evol 10:723286. https://doi.org/10.3389/fevo.2022.723286

Flexas J, Scoffoni C, Gago J, Sack L (2013) Leaf mesophyll conductance and leaf hydraulic conductance: an introduction to their measurement and coordination. J Exp Bot 64:3965–3981. https://doi.org/10.1093/jxb/ert319

Flexas J, Clemente-Moreno MJ, Bota J et al (2021) Cell wall thickness and composition are involved in photosynthetic limitation. J Exp Bot 72:3971–3986

Fradera-Soler M, Rudall PJ, Prychid CJ, Grace OM (2021) Evolutionary success in arid habitats: morpho-anatomy of succulent leaves of *Crassula* species from southern African. J Arid Environ 185:104319. https://doi.org/10.1016/j.jaridenv.2020.104319

Galdon-Armero J, Fullana-Pericas M, Mulet PA, Conesa MA, Martin C, Galmes J (2018) The ratio of trichomes to stomata is associated with water use efficiency in *solanum lycopersicum* (tomato). Plant J 96:607–619. https://doi.org/10.1111/tpj.14055

González-Dugo MP, Neale CMU, Mateos L et al (2009) A comparison of operational remote sensing-based models for estimating crop evapotranspiration. Agric For Meteorol 149:1843–1853. https://doi.org/10.1016/j.agrformet.2009.06.012

Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties, 2nd edn. Wiley, Chichester

Grzebisz W, Gransee A, Szczepaniak W, Diatta J (2013) The effects of potassium fertilization on water-use efficiency in crop plants. J Plant Nutr Soil Sci 176:355–374. https://doi.org/10.1002/jpln.201200287

Guerfel M, Baccouri O, Boujnah D, Chaïbi W, Zarrouk M (2009) Impacts of water stress on gas exchange, water relations, chlorophyll content and leaf structure in the two main Tunisian Olive (*Olea Europaea* L.) cultivars. Sci Hort 119:257–263. https://doi.org/10.1016/j.scienta.2008.08.006

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126:457–461. https://doi.org/10.1007/s004420100628

Haridasan M (2000) Nutrição mineral de Plantas Nativas do Cerrado. Rev Bras Fisiol Veg 12:54–64. https://doi.org/10.1590/S0103-31312000000100006

Hatfield JL, Dold C (2019) Water-use efficiency: advances and challenges in a changing climate. Front Plant Sci 10:103. https://doi.org/10.3389/fpls.2019.00103

Inoue S, Takemiya A, Shimazaki K (2010) Phototropin signaling and stomatal opening as a model case. Curr Opin Plant Biol 13:587–593. https://doi.org/10.1016/j.pbi.2010.08.005

Jákli B, Tavakol E, Tränkner M, Senbayram M, Dittert K (2017) Quantitative limitations to photosynthesis in K deficient sunflower and their implications on water-use efficiency. J Plant Physiol 209:20–30. https://doi.org/10.1016/j.jplph.2016.11.010

Kamakura M, Kosugi Y, Takanashi S, Matsumoto K, Okumura M, Philip E (2011) Patchy stomatal behavior during midday depression of leaf CO_2 exchange in tropical trees. Tree Physiol 31:160–168. https://doi.org/10.1093/treephys/tpq102

Karabourniotis G, Liakopoulos G, Nikolopoulos D, Bresta P (2020) Protective and defensive roles of non-glandular trichomes against multiple stresses: structure–function coordination. J Forestry Res 31:1–12. https://doi.org/10.1007/s11676-019-01034-4

Klich MG (2020) Leaf variations in elaeagnus angustifolia related to environmental heterogeneity. Environ Exp Bot 44:171–183. https://doi.org/10.1016/S0098-8472(00)00056-3

Klink CA, Machado RB (2005) A conservação do Cerrado Brasileiro. Megadiversidade 1:147–155. https://www.researchgate.net/publication/228342037_A_conservacao_do_Cerrado_brasileiro

Kochian LV, Piñeros MA, Liu J, Magalhaes JV (2015) Plant adaptation to acid soils: the molecular basis for crop aluminum resistance. Annu Rev Plant Biol 66:571–598. https://doi.org/10.1146/annurev-arplant-043014-114822

Lewis JD, Griffin KL, Thomas RB, Strain BR (1994) Phosphorus supply affects the photosynthetic capacity of loblolly pine grown in elevated carbon dioxide. Tree Physiol 14:1229–1244. https://doi.org/10.1093/treephys/14.11.1229

Liakoura V, Fotelli MN, Rennenberg H, Karabourniotis G (2009) Should structure–function relations be considered separately for homobaric vs. heterobaric leaves? Am J Bot 96:612–619. https://doi.org/10.3732/ajb.0800166

Liu S, Zheng J (2024) Adaptive strategies based on shrub leaf-stem anatomy and their environmental interpretations in the Eastern Qaidam basin. BMC Plant Biol 24:323. https://doi.org/10.1186/s12870-024-05026-3

Lohmann LG (2020) Tabebuia in Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro. https://floradobrasil2020.jbrj.gov.br/FB114257

Mendonça RC, Felfili JM, Walter BMT, Silva Júnior MC, Rezende AV, Filgueiras TS, Nogueira PE (1998) Flora vascular do Cerrado. In: Sano SM, Almeida SP (eds) Cerrado: ambiente e flora. Embrapa-CPAC, Planaltina, pp 289–556. https://www.bdpa.cnptia.embrapa.br/consulta/busca?b=ad&biblioteca=vazio& busca=(autoria%3A%22MENDON%C3%87A%2 C+R.+C.+de%22)

Mo Y, Yang R, Liu L et al (2016) Growth, photosynthesis and adaptive responses of wild and domesticated watermelon genotypes to drought stress and subsequent re-watering. Plant Growth Regul 79:229–241. https://doi.org/10.1007/s10725-015-0128-9

Moro MF, Lughadha EN, Filer DL, Araújo FS, Martins FR (2014) A catalogue of the vascular plants of the Caatinga phytogeographical domain: a synthesis of floristic and phytosociological surveys. Phytotaxa 160:1–118. https://doi.org/10.11646/phytotaxa.160.1.1

Nimer E (1972) Climatologia Da região Nordeste do Brasil. Rev Bras Geogr 34:3–51

O'Brien TP, Feder N, McCully ME (1964) Polychromatic staining of plant cell walls by toluidine blue o. Protoplasma 59:368–373. https://doi.org/10.1007/BF01248568

Ofoe E, Thomas RH, Asiedu SK, Wang-Pruski G, Fofana B, Abbey L (2023) Aluminum in plant: benefits, toxicity and tolerance mechanisms. Frontiers in Plant Science 13:1085998. https://doi.org/10.3389/fpls.2022.1085998

Oliveira JA (2015) Tocoyena in Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. http://floradobrasil2015.jbrj.gov.br/FB74808

Pennington RT, Prado DE, Pendry CA (2000) Neotropical seasonally dry forests and quaternary vegetation changes. J Biogeogr 27:261–273. https://doi.org/10.1046/j.1365-2699.2000.00397.x

Pennington RT, Lavin M, Oliveira-Filho A (2009) Woody plant diversity, evolution, and ecology in the tropics: perspectives from

seasonally dry tropical forests. Annu Rev Ecol Evol Syst 40:437–457. https://doi.org/10.1146/annurev.ecolsys.110308.120327

Petrík P, Petek-Petrik A, Kurjak D et al (2022) Interannual adjustments in stomatal and leaf morphological traits of European Beech (Fagus sylvatica L.) demonstrate its climate change acclimation potential. Plant Biol 24:1287–1296. https://doi.org/10.1111/plb.13401

Quemada M, Gabriel JL (2016) Approaches for increasing nitrogen and water use efficiency simultaneously. Global Food Secur 9:29–35. https://doi.org/10.1016/j.gfs.2016.05.004

R Core Team (2024) R: A Language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Ratter JA, Bridgewater S, Ribeiro JF (2003) Analysis of the floristic composition of the Brazilian Cerrado vegetation III: comparison of the Woody vegetation of 376 areas. Edinb J Bot 60:57–109. https://doi.org/10.1017/S0960428603000064

Reginatto MA, Castagna A, Furlan A, Castro S, Ranieri A, Luna MV (2014) Physiological responses of a halophytic shrub to salt stress by Na_2SO_4 and nacl: oxidative damage and the role of polyphenols in antioxidant protection. Ann Botany 6:plu042. https://doi.org/10.1093/aobpla/plu042

Sampaio EVSB (1995) Overview of the Brazilian Caatinga. In: Bullock SH, Mooney HA, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge, pp 35-63

Santos MG, Oliveira MT, Figueiredo KV et al (2014) Caatinga, the Brazilian dry tropical forest: can it tolerate climate changes? Theoretical Experimental Plant Physiol 26:83–99. https://doi.org/10.1007/s40626-014-0008-0

Sanz-Veigas PA, Jorge LR, Benitez-Vieyra S, Amorim FW (2017) Pericarpial nectary-visiting ants do not provide fruit protection against pre-dispersal seed predators regardless of ant species composition and resource availability. PLoS ONE 11:e0151149. https://doi.org/10.1371/journal.pone.0188445

Schindelin J, Arganda-Carreras I, Frise E et al (2012) Fiji: Na open-source platform for biological-image analysis. Nat Methods 9:676–682. https://doi.org/10.1038/nmeth.2019

Scoffoni C, Pou A, Aasamaa K, Sack L (2008) The rapid light response of leaf hydraulic conductance: new evidence from two experimental methods. Plant Cell Environ 31:1803–1812. https://doi.org/10.1111/j.1365-3040.2008.01884.x

Shao HB, Song WY, Chu LY (2008) Advances of calcium signals involved in plant anti-drought. CR Biol 331:587–596. https://doi.org/10.1016/j.crvi.2008.03.012

Silva FAM, Assad ED, Evangelista BA (2008) Caracterização climática do bioma Cerrado. In: Sano SM, Almeida SP, Ribeiro JF (eds). Cerrado: ecologia e flora. Embrapa Informação Tecnológica, Brasília, pp 69–88. https://www.infoteca.cnptia.embrapa.br/infoteca/bitstream/doc/570911/2/CERRADO-Ecologia-e-flora-VOL-1.pdf

Tambussi EA, Bort J, Araus JL (2007) Water use efficiency in C3 cereals under Mediterranean conditions: a review of physiological aspects. Ann Appl Biol 150:307–321

Terashima I, Hanba YT, Tholen D, Niinemets Ü (2011) Leaf functional anatomy in relation to photosynthesis. Plant Physiol 155:108–116. https://doi.org/10.1104/pp.110.165472

Tholen D, Boom C, Zhu X-G (2012) Opinion: prospects for improving photosynthesis by altering leaf anatomy. Plant Sci 197:92–101. https://doi.org/10.1016/j.plantsci.2012.09.005

Tomás M, Flexas J, Copolovici L, Niinemets Ü et al (2013) Importance of leaf anatomy in determining mesophyll diffusion conductance to CO_2 across species: quantitative limitations and scaling up by models. J Exp Bot 64:2269–2281. https://doi.org/10.1093/jxb/ert086

Tränkner M, Tavakol E, Jákli B (2018) Functioning of potassium and magnesium in photosynthesis, photosynthate translocation and photoprotection. Physiol Plant 163:414–431. https://doi.org/10.1111/ppl.12747

Trueba S, Théroux-Rancourt G, Earles JM et al (2022) The three-dimensional construction of leaves is coordinated with water use efficiency in conifers. New Phytol 233:851–861. https://doi.org/10.1111/nph.17772

Varela MC, Arslan I, Reginato M, Cenzano AM, Luna MV (2016) Phenolic compounds as indicators of drought resistance in shrubs from Patagonian shrublands (Argentina). Plant Physiol Biochem 104:81–91. https://doi.org/10.1016/j.plaphy.2016.03.014

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199:213–227. https://doi.org/10.1023/A:1004327224729

Wright CL, Lima ALA, de Souza ES, West JB, Wilcox BP (2021) Plant functional types broadly describe water use strategies in the Caatinga, a seasonally dry tropical forest in northeast Brazil. Ecol Evol 11:11808–11825. https://doi.org/10.1002/ece3.7949

Xu H, Li Y (2006) Water-use strategy of three central Asian desert shrubs and their responses to rain pulse events. Plant Soil 285:5–17. https://doi.org/10.1007/s11104-005-5108-9

Zhang C, Chen WQ, Liu G, Zhu DJ (2017) Economic growth and the evolution of material cycles: an analytical framework integrating material flow and stock indicators. Ecol Econ 140:265–274. https://doi.org/10.1016/j.ecolecon.2017.05.004

Zuur AF, Ieno EN, Smith GM (2007) Analysing ecological data. Springer Science, New York. https://doi.org/10.1007/978-0-387-45972-1

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.