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ANATOMICAL, MORPHOLOGICAL, AND PHYSIOLOGICAL CHARACTERISTICS OF SUN AND SHADE LEAVES OF THE OITIZEIRO TREE (MOQUILEA TOMENTOSA BENTH)

CARACTERÍSTICAS ANATÔMICAS, MORFOLÓGICAS E FISIOLÓGICAS DE FOLHAS DE SOL E DE SOMBRA DE OITIZEIRO (MOQUILEA TOMENTOSA BENTH)

CARACTERÍSTICAS ANATÓMICAS, MORFOLÓGICAS Y FISIOLÓGICAS DE HOJAS DE SOL Y DE SOMBRA DE OITIZEIRO (MOQUILEA TOMENTOSA BENTH)

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ABSTRACT
The oitizeiro (Moquilea tomentosa), is a native and endemic Brazilian plant species found in the restinga vegetation that is well-adapted to elevated temperatures. It is known for its economic importance, as it is commonly used for landscaping, food and recovery of degraded areas. This study aimed to analyze and compare the anatomical, morphological, and physiological characteristics of sun and shade leaves of oitizeiro trees sampled in the São Luís and Bacurituba cities, Maranhão state, Brazil. The parameters evaluated included chlorophyll indices, leaf length and width, estimated leaf area, and leaf anatomy. Leaf length, width, and estimated area were higher in shade leaves compared to sun leaves. Chlorophyll a, chlorophyll b, and total chlorophyll indices were higher in the shade leaves collected in Bacurituba. For plants collected in São Luís, the chlorophyll a index was higher in shade leaves, and no difference was found in chlorophyll b and total chlorophyll. The differences in leaf size, chlorophyll content, and anatomy found between sun and shade leaves demonstrate that Moquilea tomentosa exhibits a high phenotypic plasticity, which suggests it

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is highly adaptable to varying light intensities and highlights its potential use in the recovery of degraded areas.

Keywords: Leaf Thickness. Oiti. Phenotypic Plasticity. Degraded Area Recovery. Morphophysiological Responses.

RESUMO
O oitizeiro (Moquilea tomentosa) é uma planta nativa e endêmica da flora brasileira, característica da restinga, que se adapta muito bem a temperaturas mais elevadas. Se destaca pela importância econômica, sendo muito utilizada em paisagismo, na alimentação e recuperação de áreas degradadas. Este trabalho objetivou analisar e comparar características anatômicas, morfológicas e fisiológicas de folhas de sol e de sombra de oitizeiro, coletadas em São Luís e Bacurituba, Maranhão. Foram avaliados: índice de clorofilas, comprimento e largura das folhas, estimativa de área foliar, anatomia foliar. O comprimento, largura e estimativa de área foliar nas plantas de sombra foram maiores que nas folhas de sol. O índice de clorofila a, b e total foi maior em folhas de sombra coletadas em Bacurituba, e nas plantas coletadas em São Luís o índice de clorofila a foi maior nas plantas de sombra, não havendo diferença para o índice de clorofila b e total. A diferença no tamanho das folhas, conteúdo de clorofila e alterações constatadas na anatomia entre as folhas de sol e sombra demonstram que esta espécie apresenta alta plasticidade fenotípica, sugerindo elevada capacidade de adaptação em ambientes com diferentes intensidades luminosas, podendo ser utilizada na recuperação de áreas degradadas.

Palavras-chave: Espessura Foliar. Oiti. Plasticidade Fenotípica. Recuperação de Áreas Degradadas. Respostas Morfofisiológicas.

RESUMEN
El oitizeiro (Moquilea tomentosa) es una especie nativa y endémica de la flora brasileña, característica de ecosistemas de restinga, que presenta alta adaptación a temperaturas elevadas. Se destaca por su importancia económica, siendo ampliamente utilizada en paisajismo, alimentación y en la restauración de áreas degradadas. El presente estudio tuvo como objetivo analizar y comparar las características anatómicas, morfológicas y fisiológicas de hojas expuestas al sol y a la sombra de oitizeiro, recolectadas en los municipios de São Luís y Bacurituba, estado de Maranhão, Brasil. Se evaluaron el índice de clorofila, la longitud y el ancho foliar, la estimación del área foliar y la anatomía de las hojas. La longitud, el ancho y la estimación del área foliar fueron mayores en las hojas de plantas desarrolladas a la sombra en comparación con aquellas expuestas al sol. El contenido de clorofila a, b y total fue superior en hojas de sombra recolectadas en Bacurituba; mientras que en las plantas recolectadas en São Luís, el contenido de clorofila a fue mayor en hojas de sombra, sin observarse diferencias significativas en los contenidos de clorofila b y total. Las diferencias en el tamaño foliar, el contenido de clorofila y las modificaciones anatómicas observadas entre hojas de sol y de sombra evidencian una elevada plasticidad fenotípica de la especie, lo que sugiere una alta capacidad de adaptación a ambientes con diferentes intensidades lumínicas, destacando su potencial para la restauración de áreas degradadas.

Palabras clave: Espesor Foliar. Oiti. Plasticidad Fenotípica. Restauración de Áreas Degradadas. Respuestas Morfofisiológicas.

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1 INTRODUCTION

Plant morphology is determined by genetics but can also be influenced by environmental factors (Sommer, 2020). Soil, water, light, and temperature conditions can influence plant development and productivity, resulting in the rise of morphological and physiological mechanisms that increase survival in the environment (Silva *et al.*, 2005).

Luminosity is one of the main factors driving plant growth, as it can affect photosynthetic rates, respiration, the number and dimensions of mesophyll cells, cuticle thickness, the density of stomata and phenological traits, such as the leaf's longevity (Campos; Uchida, 2002; Montanari *et al.*, 2004). As a primary resource, light is essential for leaf development, accumulation of photosynthetic products, survival, and individual growth (Chen *et al.*, 2023; Wei *et al.*, 2023). Although excess light can hinder plant growth, development and production, plants that continuously growth under low light conditions can also exhibit reduced photosynthetic capacity and, consequently, reduced growth rates (Yong; Hew, 1995).

When discussing light intensity, it is important to consider the variations in the structure of leaves, as these are the plant's organs whose anatomy is the most responsive to variations in a habitat's light intensity (Dikson, 2000), and which exhibits the most morphological and physiological plasticity. Light availability tends to be heterogeneous within a plant's canopy, with some leaves being exposed to direct sunlight and others being found under varying levels of shading (Théroux-Rancourt *et al.*, 2023). Although plants respond differently to varying light conditions, light intensity drives changes in leaf structure, resulting in different leaf categories which are named sun leaves and shade leaves (Dardengo *et al.*, 2017).

For each sun leaf, there may be four or five shade leaves under a certain level of shading, and these shade leaves contribute significantly to the carbon intake and dynamics in forests (He *et al.*, 2018). Shade leaves usually exhibit lower photosynthetic rates but require lower light levels to maintain a positive carbon net balance, as they have a lower light compensation point. Additionally, maximum temperatures of shade leaves found in the canopy of a tropical forest are much lower than that of sun leaves (Rey-Sánchez *et al.*, 2016; Fauset *et al.*, 2018).

Understanding how luminous radiation affects plant cultivation is important to elucidate how plants respond morphologically, physiologically, and anatomically, as it can optimize the cultivation of species of economic interest, reduce extractivism, and thus contribute to the success of plant reintroduction and maintenance projects. Furthermore, there is a lack of studies linking light intensity and plant cultivation to describe and understand not only tissue structure and distribution but also the physiology and ecology of these species. The present study adds to the body of knowledge regarding plant dynamics and strategies in various ecological niches with varying light intensities. This is noteworthy when one considers the scarcity of studies in this topic, especially within the state of Maranhão.

The oitizeiro tree (Moquilea tomentosa Benth - Chrysobalanaceae family) is a Brazilian native and endemic species, found in the restinga forest vegetation of Northern and Northeastern Brazil. It is a tree species well-adapted to elevated temperatures (Rizzini; Mors, 1995). The species has been gaining significance regarding its different means of utilization, which include landscaping, owing to its wide canopy that provides a good amount of shading (Rizzini; Mors, 1995; Souza; Lorenzi, 2012), the recovery of degraded areas, as a food item, since the pulp of its fruit is highly nutritive, and in traditional medicine, due to its antibacterial and antioxidant properties (Miranda *et al.*, 2002; Silva; Peixoto, 2009; Silva *et al.*, 2012).

As such, the present study aims to characterize leaf morphoanatomy and physiology of oitizeiro trees at varying degrees of light incidence on the leaves, based on specimens collected in the São Luís and Bacurituba cities, Maranhão state, Brazil.

2 METHODOLOGY

Sampling was carried out in the cities of São Luís and Bacurituba. Both cities are located within the equatorial tropical region, with a warm, semi humid climate characterized by four to five dry months per year (Alvares *et al.*, 2013). In São Luís, plant specimens were collected at the following geographic coordinates: 02 31 47 S, and 44 18 10 W. The local climate is tropical, with a short dry season and most months exhibiting a significant amount of rainfall, an average annual temperature of 26.8°C, and an average annual rainfall of 2156 mm. According to Köppen and Geiger, the climate is classified as Am. The Bacurituba city is located in the Northern Maranhão Mesoregion, Western Coast Microregion, Maranhão Lowlands, with the following geographic coordinates: 02 42 21 S and 44 44 16 W. According to Köppen's classification, the region exhibits a tropical (AW'), humid climate, with two well-defined seasons: a rainy season which lasts from January to June and exhibits monthly rainfall averages of more than 255 mm, and a dry season, which lasts from July to December.

The leaves used in the present study were obtained from trees in good phytosanitary condition and an average height of three and a half meters. Outer (sun) and inner (shade) mature leaves were collected at a height between 1.5 and 2.0 m above the ground, between

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08 AM and 09 AM, to a total of 30 leaves under each radiation regime and at each sampling location.

For morpho-physiological analyses, the following parameters were assessed: leaf length and width (obtained using a millimeter ruler), chlorophyll a, chlorophyll b, and total chlorophyll indices (obtained using a chlorophyll content meter of the Clorofilog CFL 1030, Falker model), and estimated leaf area, measured using the equation LA = 0,667 L.W, in which LA = estimated leaf area (cm2); L = greatest leaf length (cm); W = greatest leaf width (cm).

For anatomical analyses, three specimens were sampled, fixed in 50% FAA, and later transferred into 70% ethanol after 48 hours. Transversal sections of the petiole, blade, and midrib were performed, as well as paradermal sections of the leaves' adaxial and abaxial sides. Sodium hypochlorite at 2% was used to lighten sections (Kraus; Arduim, 1997). Sections were colored using a solution made of safranine and Toluidine blue 1%, after which slides were mounted using 50% glycerin, visualized through an optical microscope, and photographed. Four fields of six individuals per treatment were used to measure cell and tissue thickness, and stoma size. In these analyses, treatments were compared in relation to tissue composition, cuticle thickness, stomata density, and cell shape. Thickness was measured with the use of a micrometer eyepiece coupled to a light microscope. Measurements were obtained using the ImageJ software.

Data analyses included an analysis of variance and a comparison of means between sun leaves and shade leaves using the T-student Test with a 5% probability.

3 RESULTS AND DISCUSSIONS

In oitizeiro leaves collected in Bacurituba, leaf length, width and estimated area were higher in shade leaves compared to sun leaves by 22.2%, 21%, and 39.6%, respectively. For plants collected in São Luís, shade leaves were 38.9% longer and 53% wider, with an estimated leaf area 60% higher than sun leaves (Table 1).

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Table 1

Length (cm), width (cm), and estimated leaf area (cm²) of sun and shade leaves of oitizeiro (Moquilea tomentosa Benth.) collected in São Luís and Bacurituba, Maranhão

São Luís	Length (cm)	Width (cm)	Estimated leaf area (cm²)
Sun leaves	10.90 b (1.26)	3.67 b (0.53)	26.58 b (1.93)
Shade leaves	14.01 a (1.57)	4.65 a (0.50)	44.02 a (2.12)
Bacurituba	Length (cm)	Width (cm)	Estimated leaf area (cm²)
Sun leaves	7.75 b (1.16)	2.77 b (0.49)	14.23 (2.04)
Shade leaves	12.69 a (1.97)	4.25 a (0.69)	35.85 (3.85)

Source: means followed by different letters in the column differ from each other by the t-test ($\alpha < 0.05$).

Differences in development of leaf surface coverage between shade leaves and sun leaves of both locations are results from leaf adaptations, reflecting the species' phenotypic plasticity, with the surface area being smaller in sun leaves due to the direct contact with elevated levels of solar radiation, even though photosynthetic capacity is not affected (Terashima *et al.*, 2001). This reflects the development of thick leaves, which provide support to excessive radiation, thus maintaining a high photosynthetic rate. Shade leaves are larger due to adaptations to low luminosity conditions, with a higher investment in leaf expansion to maximize the use of the incident light on the leaf's surface. In order to reach their maximum photosynthetic capacity, shade leaves have a larger contact surface with their entire photosynthesizing apparatus, which captures the remaining light rays coming from the tree's canopy to produce energy and support the plant's development. This pattern was also observed in a study by Mendes *et al.* (2001) on Myrtus communis (common myrtle), in which fully developed leaves from sun plants had a smaller contact surface compared to shade plants.

A common trait of species with high adaptation potential is the capacity to change leaf structure in response to varying levels of light intensity, which grants them a great plasticity to their leaf structure in relation to different light regimes (Yang *et al.*, 2023).

Chlorophyll a, chlorophyll b, and total chlorophyll indices were higher in shade leaves compared with sun leaves for plants collected in the city of Bacurituba. For plants collected in São Luís, the chlorophyll a index was higher in shade leaves, and there were no significant differences in the chlorophyll b and total chlorophyll indices (Table 2).

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Table 2

Chlorophyll a, chlorophyll b and total chlorophyll indices and standard deviation (in parentheses) in sun and shade leaves of oitizeiro (Moquilea tomentosa Benth.) collected in Bacurituba and São Luís, Maranhão

São Luís	Chlorophyll a	Chlorophyll b	Total chlorophyll
Sun leaves	39.74 b (2.01)	11.93 a (3.69)	54.67 a (5.31)
Shade leaves	44.36 a (3.53)	13.18 a (4.62)	54.00 a (8.00)
Bacurituba	Chlorophyll a	Chlorophyll b	Total chlorophyll
Sun leaves	35.47 b (3.03)	10.44 b (2.23)	46.91 b (4.67)
Shade leaves	39.74 a (2.17)	14.15 a (2.63)	53.89 a (3.14)

Source: means followed by different letters in the column differ from each other by the t-test ($\alpha < 0.05$).

These results agree with those obtained by Scalon *et al.* (2003) when studying the growth of Bombacopsis glabra (Pasq.) A. Robyns (castanha-do-maranhão) seedlings under different light conditions, in which seedlings growing at 50% shade showed a higher total chlorophyll index and a lower chlorophyll a/b rate. Comparable results were obtained in leaves collected from the outer canopy (sun leaves) and inner canopy (shade leaves) of Java plum trees (Syzygium cumini), in which the existing level of shading was sufficient to alter chlorophyll content, thus altering the rate between chlorophyll a and b (Souza *et al.*, 2008).

One of the photosynthetic traits of sun leaves is the lower concentration of chlorophyll molecules per chloroplast, especially chlorophyll b, since these plants do not need to invest in the production of light-harvesting pigments in environments with high luminosity (Salisbury; Ross, 1991; Lichtenthaler; Babani, 2004). The increased proportion of chlorophyll b is an important characteristic of shaded environments because this molecule captures the energy from other wavelengths and transfers it to chlorophyll a molecules, which effectively participate in the photochemical reactions of photosynthesis, representing an adaptation mechanism to lower light intensity conditions (Scalon *et al.*, 2003).

In addition to these changes, differences in luminosity may have complex effects on a plant's physiology, involving other factors such as reduced temperature inside the tissues, changes in relative air humidity and soil humidity (Costa *et al.*, 1998; Zhang *et al.*, 2003; Da Matta, 2004).

The composition of the photosynthesizing apparatus is highly sensitive to changes in the quantity and spectral quality of light energy (Murchie; Horton, 1997). The synthesis of chlorophyll molecules is influenced by several factors, including solar radiation, and the quantities and rates of the pigments present in the leaves vary with the species, the growth environment, and a leaf's age, even within a single plant. As seen in leaves from plants collected in Bacurituba, a leaf's capacity to assimilate light depends on the chlorophyll content per unit of leaf area, which is proportional to the amount of incident light that is absorbed, that is, the higher the chlorophyll content, the higher the capacity to absorb incident light (Stirbet *et al.*, 2011).

The anatomical analyses revealed differences in leaf tissue thickness depending on the light intensity under which leaves grew (Table 3). Sun leaves exhibited a 28% thicker blade compared with shade leaves in both sampling locations. The greatest thickness of leaf blades reflected the fact that the mesophyll, composed mainly of palisade and spongy parenchyma, was 35% and 32% thicker in the sun leaves collected in São Luís and Bacurituba, respectively. Leaf cuticle was 40% thicker in sun leaves compared to shade leaves. No difference was found in stomata length and width.

Table 3

Measurements obtained from sun and shade leaves of oitizeiro (Moquilea tomentosa Benth.) collected in São Luís and Bacurituba, Maranhão

Analyzed Parameters	São Luís - Sun leaves	São Luís - Shade leaves	Bacurituba - Sun leaves	Bacurituba - Shade leaves
Leaf blade thickness	0,207 a	0,149 b	0,205 A	0,139 B
Mesophyll thickness	0,182 a	0,118 b	0,172 A	0,116 B
Cuticle thickness	0,005 a	0,003 a	0,005 A	0,003 B
Stomatal length	0,016 a	0,015 a	0,017 A	0,016 A
Stomatal width	0,012 a	0,012 a	0,013 A	0,013 A

Source: means followed by the same letters in the row do not differ from each other according to the t-test ($\alpha < 0.05$). Lowercase letters refer to comparisons among Bacurituba means. Uppercase letters refer to comparisons among São Luís means.

Results concerning the thickness of sun leaves were similar to those obtained by Morais *et al.* (2004) in experiments with Coffea arabica, in which leaves of coffee tree plants cultivated in fully sunny conditions presented thicker cell walls and cuticles in both adaxial and abaxial sides. These structures participate in the thermal isolation of the mesophyll, protecting it from the excessive heat, which is especially important for sun leaves and represents a characteristic adaptation caused by the luminosity stimulus.

The oitizeiro tree presents hypostomatic leaves. The adaxial epidermis of leaves collected in Bacurituba and São Luís exhibits polyhedral cells from a paradermal view, with

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straight walls lacking stomata (Fig. 1a, 1c, 2a, and 2c). The abaxial epidermis exhibits polyhedral epidermic cells, with diacytic stomata (Fig. 1b, 1d, 2b, and 2d) in the same level as epidermic cells. Stomata density is higher in sun leaves, as observed by Mendes *et al.* (2001) in sun leaves of Myrtus communis.

The midrib of leaves exhibits a single-layer epidermis, followed by several layers of plate collenchyma. Xylem and phloem are distributed in a single collateral bundle in the form of a closed arc, and there is no difference in the quantity and caliber of xylem and phloem vessels between sun and shade leaves. The bundles are surrounded by a sheath of sclerenchyma cells, followed by several layers of parenchyma with cells of varying sizes (Fig. 1e-f, 2e-f).

In a transversal section, the petiole of leaves of the oitizeiro tree exhibits convexity on the adaxial side, with a single-layer epidermis, followed below by several layers of collenchyma. Internally, there are parenchyma cells of varying sizes. The vascular bundle of the petiole is similar to that of the midrib in relation to the number and size of conducting elements (Fig. 1g-h, 2g-h). In sun leaves, there are two smaller vascular bundles on the upper portion of the petiole (Fig. 1g and 2g).

The leaf blade of M. tomentosa is composed by the upper epidermis, palisade parenchyma, vascular bundles, spongy parenchyma, and lower epidermis (Fig. 3). A transversal section evidences a single-layer epidermis surrounded by the cuticle in both sun and shade leaves, showing that the cuticle of sun leaves is thicker (Fig. 3e-f, Table 3). The palisade parenchyma of sun leaves is thicker, with few intercellular spaces, and a large quantity of chloroplasts in its cells (Fig. 3a), while in shade leaves the parenchyma exhibits flatter cells and a smaller number of cell layers compared with sun leaves (Fig. 3b). These results were similar for samples from both locations.

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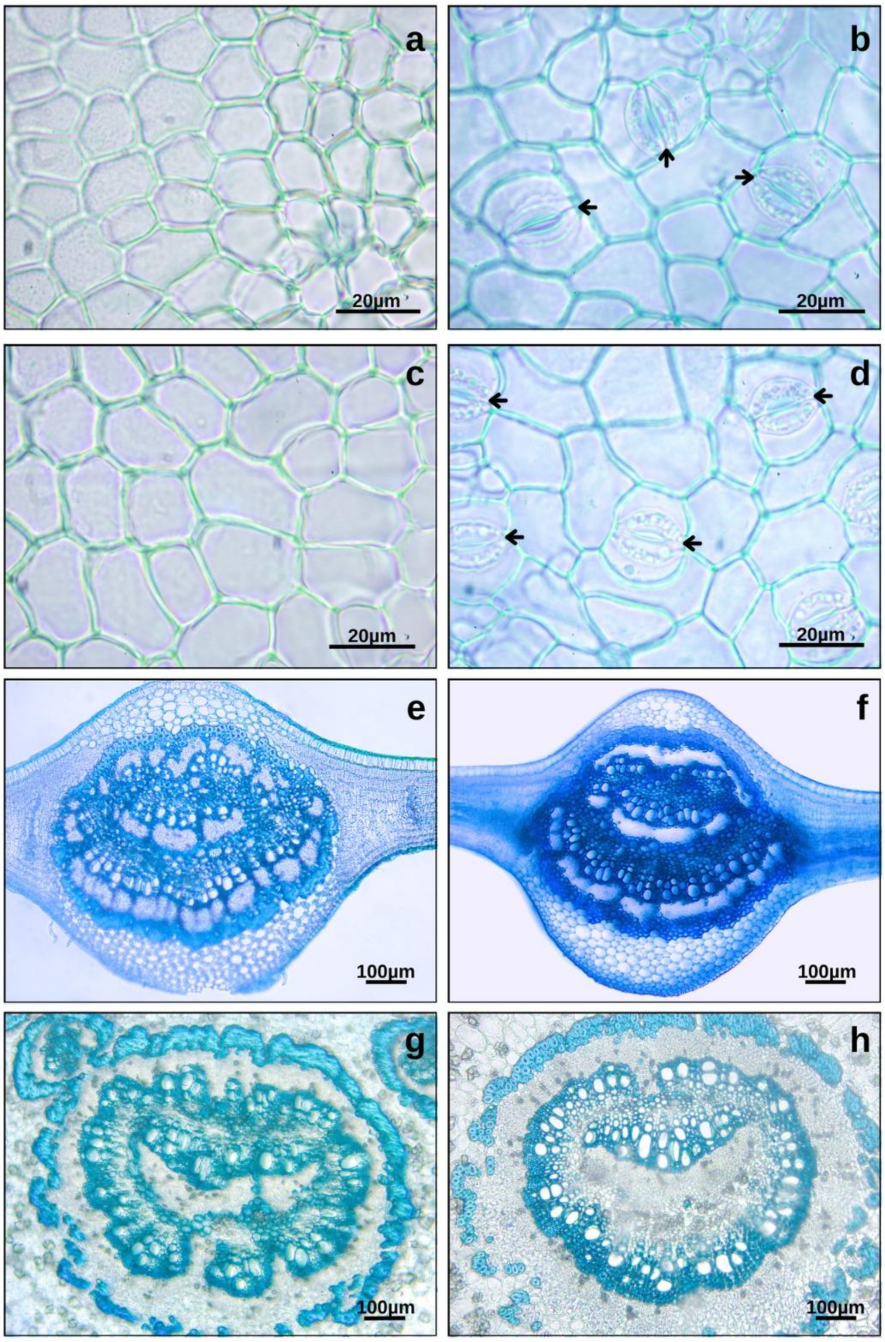
Figure 1

Details of the adaxial epidermis of sun leaves (a), abaxial epidermis of sun leaves (b) adaxial epidermis of shade leaves (c), abaxial epidermis of shade leaves (d), midrib of sun leaves (e), midrib of shade leaves (f), petiole of sun leaves (g) and petiole of shade leaves (h) of the oitizeiro tree (Moquilea tomentosa Benth.) collected in Bacurituba city, Maranhão state, Brazil. Black arrows: stoma



Source: research authors themselves.

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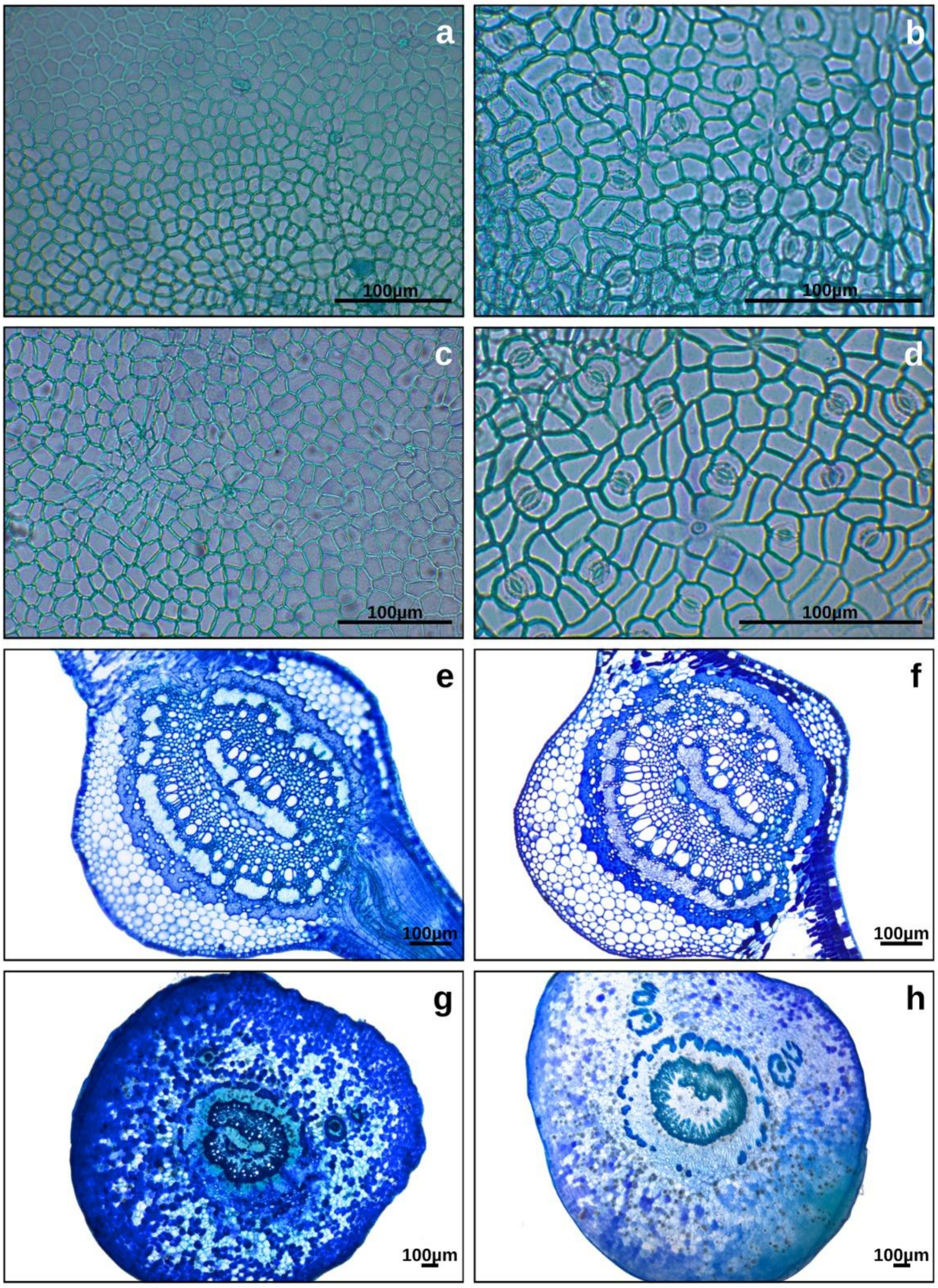
Figure 2

Details of the adaxial epidermis of sun leaves (a), abaxial epidermis of sun leaves (b) adaxial epidermis of shade leaves (c), abaxial epidermis of shade leaves (d), midrib of sun leaves (e), midrib of shade leaves (f), petiole of sun leaves (g) and petiole of shade leaves (h) of the oitizeiro tree (Moquilea tomentosa Benth.) collected in São Luís city, Maranhão state, Brazil



Source: research authors themselves.

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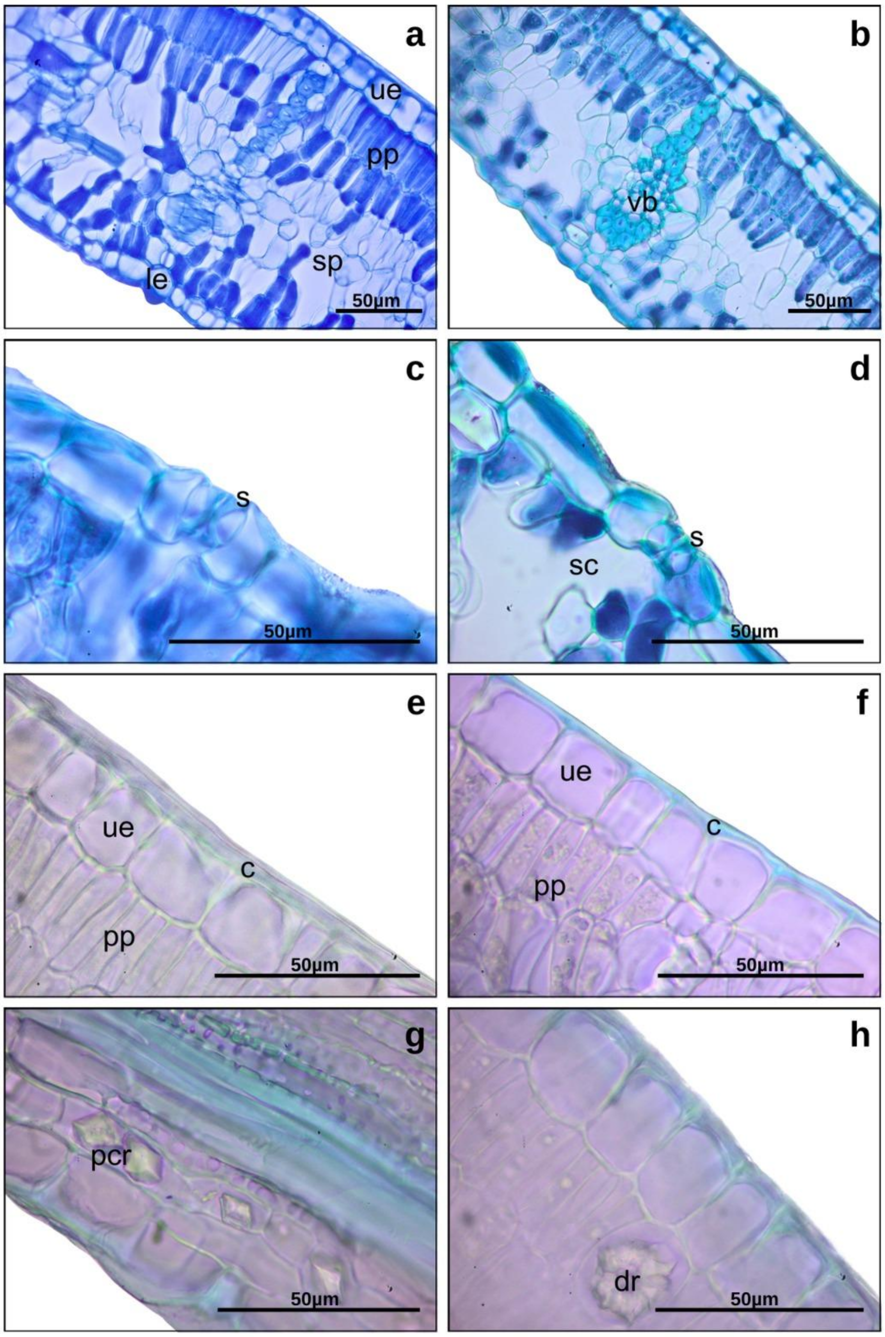
Figure 3

Transversal section of sun leaves (a, c, and e) and shade leaves (b, d, f and h) of the oitizeiro tree (Moquilea tomentosa Benth.). ue: upper epidermis, ct: cuticle, le: lower epidermis, pp: palisade parenchyma, sp: spongy parenchyma, fv: vascular bundle, pcr: prismatic crystals, dr: druse, s: stoma, sc: substomatal chamber



Source: research authors themselves.

No significant differences were found concerning the cellular composition of the leaf blade, petiole, and midrib between the different solar radiation exposure conditions in both locations, except for the presence of idioblasts with druses scattered irregularly in the collenchyma, both in the midrib and the petiole, found in larger quantities in sun leaves (Figure 3G-H). Sun leaves tend to have more idioblasts than shade leaves (Taiz *et al.* 2017)

Such difference in leaf thickness is mostly due to the larger quantity of mesophyll cells, a characteristic also seen in other studies (Millaneze-Gutierre *et al.*, 2003), such as that of Espindola Junior *et al.* (2009), who observed differences in how parenchyma cells were distributed in leaves of Piper hispidinervium. The authors suggested that the spacing of epidermal cells may be associated with a high light intensity, due to increased photosynthetic activity. Similarly, Morais *et al.* (2004) demonstrated that the leaves of coffee trees cultivated in fully sunny conditions presented thicker cell walls and cuticles in both the abaxial and adaxial sides, which reflects the role they play in isolating the mesophyll from excessive heat.

Changes in the morphological and anatomical characteristics of leaves exposed to different light intensities have been observed in several species, such as Piper hispidinervium, Myrtus communis, Hymenaea courbaril, and Coffea arabica (Santiago *et al.*, 2001; Mendes *et al.*, 2001; Campos; Uchida, 2002; Morais *et al.*, 2004). Some plants may develop adaptive responses to the conditions they are exposed to, driving changes in leaf structure characteristics. Under intense incident solar radiation, plants may exhibit smaller, thicker leaves (James; Bell, 2001). Reducing leaf surface also reduces water loss in plants, and thicker leaves allow for a greater utilization of solar radiation and a higher water storage, thus favoring the maintenance of a plant's water balance (James; Bell, 2001).

Even species of the restinga vegetation with water storage tissues but exposed to a high degree of solar radiation can exhibit low water content. When exposed to high rates of radiation, these plants present phenotypic plasticity, making up for the low water potential through adaptive strategies that enable their survival in limiting environments with low water and nutrient availability, and high luminosity, thus regulating photosynthetic rates and resource allocation (Melo; Boeger, 2016).

Adaptive diversity, which includes responses related to the mass per unit of area in response to light and leaf size, is mediated by genes, and is seen among individuals of the same species, and among leaves of the same individual. Such anatomical differences, together with the analyzed morphological changes, show that the leaves of oitizeiro trees respond to varying levels of incident light. The amount and intensity of radiation can drive changes in leaf area, thickness, in the quantity and size of intercellular spaces, the number and layers of the mesophyll, as well as changes in the distribution of photoassimilates, as

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reported by, Kappel and Flore (1983), Almeida (1985), Givnish *et al.* (2004) and Guerra *et al.* (2015), when characterizing the phenotypic plasticity of plant species.

Radiation, environmental air temperature and transpiration determine leaf temperature, which in turn affects photosynthetic capacity by altering the carboxylation rates. The portion of a canopy illuminated by the sun receives direct and diffuse radiation, while shaded leaves receive only diffuse radiation for photosynthesis; as such, temperature in shaded leaves tends to be a few degrees lower than that of sun leaves (Spayd *et al.*, 2002).

Changes in leaf temperature can significantly affect carbon assimilation and transpiration in various plant species (Amissah *et al.*, 2015; Martins *et al.*, 2014). For instance, the shading provided by the canopy was found to be effective to mitigate photoinhibition and improve the efficiency of water use in Olea europaea (Sofo *et al.* 2009), Citrus (Alarcon *et al.*, 2006), and Actinidia deliciosa var. deliciosa (Montanaro *et al.*, 2009).

Variations in light intensity may change morphological, physiological, and biochemical aspects of plants, leading them to develop sophisticated strategies with fascinating evolutionary differences. However, more studies are needed to better elucidate differences between leaves and plants of different ages, and differences in the canopy's exposure to light, in addition to detecting early symptoms of stress long before damage becomes visible in sun and shade plants. Furthermore, additional studies would be useful to analyze proteins in plants cultivated in the sun and in the shade, which would help elucidate the role of various protein complexes that help plants adapt to sunny and shaded conditions. Understanding the mechanisms underlying an efficient photosynthesis with fluctuating light conditions can open doors to increasing cultivation yields and may reveal fundamental principles of energy in conversion systems.

5 CONCLUSION

The differences in leaf size, chlorophyll content, and leaf anatomy variations found between sun and shade leaves of M. tomentosa demonstrate that the species exhibits a high phenotypic plasticity, suggesting it is highly adaptable to life in environments of varying light intensities.

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