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Original Paper

Structural adjustment of *Schwartzia brasiliensis* (Marcgraviaceae) in two restinga formations

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Abstract

This study investigated the foliar plasticity in *Schwartzia brasiliensis* in restinga formations (shrub and shrub-tree restinga) in southern Brazil. In each area, 10 individuals were selected and leaves in sunlight were collected for an analysis of functional leaf traits, including: fresh and dry leaf mass, leaf area, specific leaf area, succulence, stem diameter, plant height and tissue thickness. Environmental variables were measured considering soil mineral nutrition, water availability and photosynthetically active radiation. Phenotypic plasticity index was calculated for studied attribute. We compared means with a Student's t-test and the weight of environmental variables with a PCA. Results showed that the main leaf traits that differentiated the populations were leaf dry mass, specific leaf area, lamina thickness and plant height, while the main predictor environmental variables were gravimetric humidity, solar radiation, soil CEC, phosphorus content and salinity. In the shrub restinga, there is greater investment in mechanical support as a water saving strategy due to greater exposure to solar radiation. In the shrub-tree restinga, there is greater investment in photosynthetic production, since the shade provided by the treetops of other species attenuates the radiation effect. Despite the low plastic potential, the populations present structural adjustments that respond to the environmental heterogeneity.

Key words: ecological anatomy, environmental heterogeneity, functional leaf traits.

Resumo

Este estudo investigou a plasticidade foliar em populações de *Schwartzia brasiliensis* (Marcgraviaceae) ocorrentes em duas formações de restinga (arbustiva e arbustiva-arbórea) do Parque Estadual Acaraí, São Francisco do Sul/SC, analisando as respostas morfoanatômicas e ecofisiológicas observadas. Em cada área foram selecionados 10 indivíduos e coletadas de cada 25 folhas de sol para a avaliação de atributos funcionais: massas frescas e seca, área foliar, área específica foliar, suculência, espessura de tecidos, diâmetro do tronco e altura da planta. As variáveis ambientais foram mensuradas considerando os nutrientes minerais do solo, a disponibilidade hídrica e a radiação fotossinteticamente ativa. Índice de Plasticidade Fenotípica foi calculado para cada atributo estudado. Médias foram comparadas por meio do teste t de Student e o peso das variáveis ambientais por meio de PCA, ambos realizados em ambiente R. Os resultados mostraram que os principais atributos foliares que diferenciaram as populações foram a massa seca foliar, área específica foliar, espessura do limbo e altura da planta, enquanto as principais variáveis ambientais preditoras foram a umidade gravimétrica, a radiação solar, a CTC do solo, teor de fósforo e a salinidade. Na restinga arbustiva há maior investimento na sustentação mecânica como estratégia de economia de água face a grande exposição à radiação solar. Na restinga arbustiva-arbórea, há maior investimento em produção fotossintética, pois o sombreamento gerado por outras espécies atenua o efeito da radiação. Apesar do baixo potencial plástico, possivelmente provocado pelo efeito da microescala espacial, as populações apresentam ajustes estruturais que respondem à heterogeneidade ambiental da restinga.

Palavras-chave: anatomia ecológica, heterogeneidade ambiental, atributos funcionais foliares.

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Introduction

Plants can modify their phenotype in response to environmental changes, which is known as phenotypic plasticity (Gratani 2014). Since the role of leaves is intrinsically connected to the environment, at the interface between the habitat and organism (Peppe *et al.* 2011), leaves are influenced by environmental changes and, therefore, their responses serve as ecological indicators of the influence of abiotic conditions on plant growth in heterogeneous environments (Chagas *et al.* 2008).

Considering the marked environmental variation at a spatial microscale in restinga, this environment is an ecologically important formation that can help explain functional patterns of plant development and growth (Melo Júnior & Boeger 2017), such as resource acquisition, maintenance, and storage (Reich *et al.* 2003). In addition, studies in restinga provide data for developmental models that correlate functional characteristics of plants with active environmental factors (Queseda *et al.* 2009).

Restinga is a pioneer formation composed of an extensive mosaic of structurally unique floristic communities that are distributed on coastal plains along sandy ridges, resulting from the deposition of marine sediments, and secondarily shaped by wind (Melo Júnior & Boeger 2017). It is an ecosystem influenced by strong winds, low levels of soil fertility, low water availability and high salinity (Melo Júnior & Boeger 2015). Species diversity is directly correlated with soil composition and gradually increases in the sea-continent direction (Melo Júnior & Boeger 2015). Restinga can present a considerable set of exclusive species along its distribution, but also has different levels of species co-occurrence between mosaics (Melo Júnior *et al.* 2018).

Considered as an area of interest for conservation, the restinga remnant on the coastal plain of the municipality of São Francisco do Sul, Santa Catarina State, is partly protected as a conservation unit called Parque Estadual Acaraí (PEA) (Melo Júnior & Boeger 2017). In addition, it is a RAPELD site of the PPBio Atlantic Forest, making the area of great interest for long-term ecological research. This ecosystem suffers from human impacts, including degradation from the privatization of public areas, buildings and large tourism projects (Rocha *et al.* 2003; Thomazi *et al.* 2013). Due to these disturbances, restinga is highly vulnerable and appropriate measures need to be taken for its preservation and protection (Melo Júnior & Boeger 2017). Thus, it is necessary to understand patterns and ecological processes of the floristic diversity in restinga based on studies of functional nature, such as evaluating the plastic potential of the species.

Schwartzia brasiliensis (Choisy) Bedell *ex* Gir.-Cañas (Marcgraviaceae) is endemic to the eastern region of Brazil (Giraldo-Cañas 2004). In southern Brazil, it is typical of restinga and occurs in shrub and shrub-tree formations (Melo Júnior & Boeger 2017). According to Melo Júnior & Borger (2016), plant species in different restinga formations exhibit structural adjustments that are triggered by the peculiar spatial heterogeneity in the ecosystem and mainly influenced by light intensity and soil fertility. Therefore, this study investigated the structural adjustments of populations of *S. brasiliensis* (Marcgraviaceae) in two restinga formations in PEA under different soil, water and light conditions by analyzing the plant diameter and height, leaf morphoanatomy and ecophysiology of individuals.

Material and Methods

Study area

The study was conducted in the restinga in Parque Estadual Acaraí (PEA), in the municipality of São Francisco do Sul, on the northern coast of Santa Catarina State (Fig. 1). PEA is an integral protection conservation unit that is 6,667.00 hectares (N 7,080,088.14m and E 747,199.28m [UTM]) (Melo Júnior & Boeger 2015). The coastal region of Santa Catarina State has a predominantly humid mesothermal climate with a hot summer (Cfa), according to the Köppen classification, an average annual temperature of 20.6 °C and total annual rainfall of 1,847.68 mm (Marques 2013).

In the park, the shrub restinga is composed of a dense mix of shrubs and climbers, terrestrial bromeliads and cacti (Melo Júnior & Boeger 2017). The shrub-tree restinga has an upper layer composed of species that reach 5 m in height and an herbaceous layer (Melo Júnior & Boeger 2017).

Selection, collection and processing the biological material

Schwartzia brasiliensis is one of the five most important species in the structure of the PEA communities and its frequency is adequate for sampling in both restinga formation areas (Melo

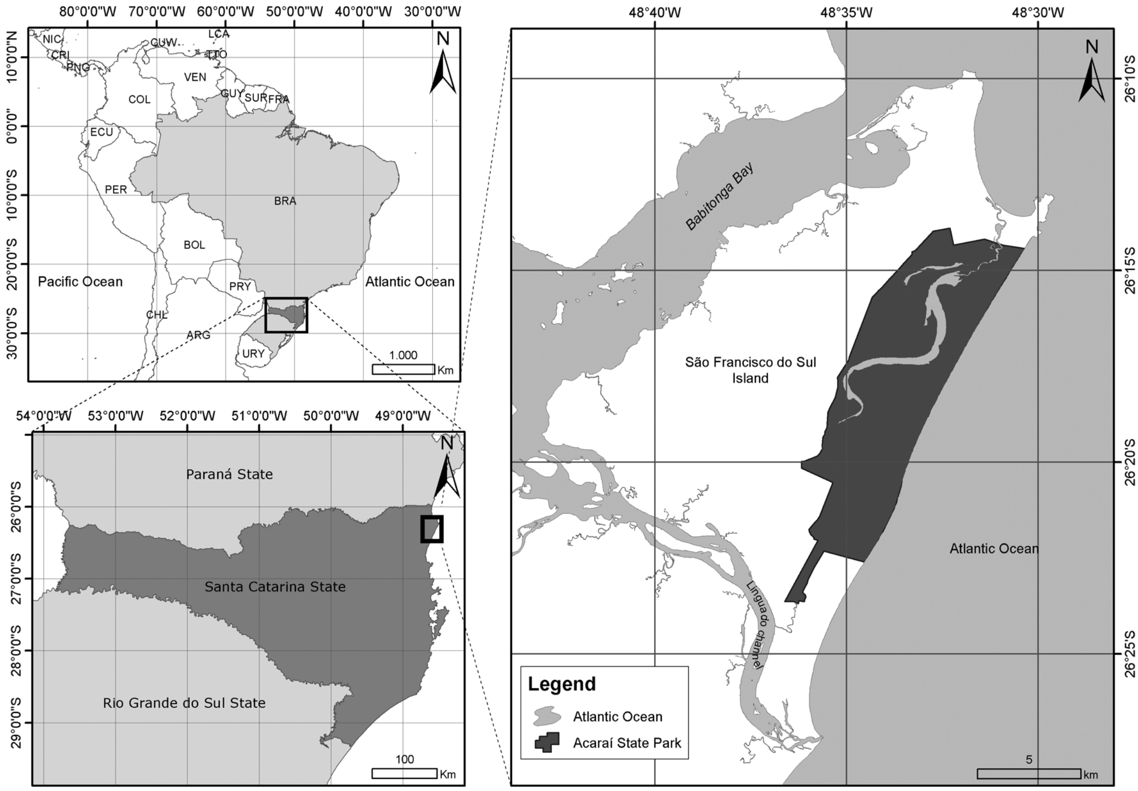

Figure 1 – Location of Parque Estadual Acaraí, São Francisco do Sul, Santa Catarina, Brazil. Source: Melo Júnior (2015).

Júnior & Boeger 2015). Ten adult individuals were selected in each area, the shrub restinga (sR) and shrub-tree restinga (stR), and 30 leaves that were completely expanded in the sun were collected between the 3rd and 4th nodes at the branch apices. The basal trunk diameter (cm) and height (m) were measured for all individuals. After collecting the samples, the leaves were weighed on an analytical scale to obtain the fresh mass (g). Subsequently, and after being dried in a ventilation oven at 70 ºC, the leaves were weighed to obtain the dry mass (g). Leaf area (cm^2) was determined with the software Sigma Scan Pro 5.0 after scanning the leaves on a flatbed scanner. Specific leaf area (SLA, $cm^2.g^1$) was obtained by dividing the leaf area by the dry mass. The middle third of five leaves per individual was used for the anatomical sections. For this, the leaves were fixed in 70% FAA, rinsed with alcohol, embedded in paraffin following standard techniques used in plant anatomy for sectioning with a rotary microtome, stained with toluidine blue and mounted on permanent slides (Kraus & Arduin 1997; Paiva *et al.* 2006). Using the software DinoCapture 2.0 and an Olympus photomicroscope, the following anatomical traits were measured: thickness of the palisade and spongy parenchyma (µm), lamina thickness (µm) and epidermal + cuticle thickness on both surfaces (µm).

Environmental variables

Soil samples were collected at the base of 10 individuals in each area; half was used to obtain information on gravimetric moisture, while the other half was homogenized to obtain a composite sample per formation and sent for nutritional analysis, following the standard methodology recommended by EMBRAPA (2013). The height of the litter on the soil was measured with a ruler. The soil chemical analysis was performed by the Epagri Soil Laboratory and the following parameters were evaluated: organic matter (MO), potential hydrogen (pH), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), aluminum (Al), hydrogen (H), base sum (SB), cation exchange capacity (CEC), base saturation (V) and salinity. For each sample individual, photosynthetically active radiation (PAR) measurements were taken with a luxmeter.

Statistical analysis

For all structural traits studied, in each population of *S. brasiliensis*, means and standard deviations were calculated for all biological traits studied and a comparison of means was performed using a Student's t-test, with a confidence level of 0.05, in the R environment (Crawley 2007). Calculating the weight of each environmental variable on the structural/ecophysiological responses detected was done with a principal component analysis (PCA), (Legendre & Legendre 1998) and Pearson's correlation was used to verify the degree of correlation between the variables, both in the same statistical environment.

Results

The soil of the shrub restinga (sR) showed a low level of nutrients compared to that of the shrub-tree restinga (stR). The greatest differences expressed were for the contents of phosphorus (P) and calcium (Ca), the cation exchange capacity (CEC) and salinity (Tab. 1). The pH of the soils is alkaline with no differences between the two formations. In the stR, the contents of macronutrients (P), (Ca) and magnesium (Mg) were higher, and potassium (K) and aluminum (Al) were lower, in relation to the sR formation. The CEC and gravimetric humidity had higher values for the soil in the stR formation. The sodium (Na) concentration, base sum (SB), base saturation (V), acidity that determines the effective CEC of the soil (H + Al), litter and organic matter (OM) content were higher in the sR formation (Tab. 1).

The photosynthetically active radiation incident on the sampled individuals differed between the two restinga formations; it was about 17% higher in the sR formation compared to the stR formation (Tab. 1).

The results show that the functional attributes that differentiate the populations between the two formations were height, stem diameter, leaf dry mass, specific leaf area and thickness of all leaf tissues (Tab. 2). In the sR, the mean values of all attributes were higher in relation to those observed in the stR, except for height, stem diameter and specific leaf area. Anatomically, the leaves of *S. brasiliensis* in the sR environment are thicker compared to those in the stR environment, as a result of an increase in thickness of all tissues (Tab. 2; Fig. 2).

The Pearson's correlation showed a high rate of positive interactions between the following: leaf area and leaf fresh mass ($r = 0.85$, $p = < 0.0001$); leaf area and leaf dry mass ($r = 0.70$, $p = < 0.0001$); leaf area and succulence ($r = 0.82$, $p = < 0.0001$); lamina and spongy parenchyma thickness ($r = 0.89$, $p = < 0.0001$); leaf fresh mass and leaf dry mass ($r = 0.80$, $p = < 0.0001$); leaf fresh mass and succulence ($r = 0.97$, $p = < 0.0001$); and leaf dry mass and succulence ($r = 0.64$, $p = < 0.0001$).

The principal component analysis (PCA) showed that the first three axes explained 61.49% of the variance in the data between populations (Fig. 3; Tab. 3). Leaf fresh mass, leaf area and succulence were most related to principal axis 1, which explained 28.87%. The main axis 2 explained 22.27% of the variance and was more related to the lamina thickness and spongy parenchyma attributes, and the main axis 3 explained 10.35% and was related to specific leaf area and spongy parenchyma thickness.

Discussion

Our morphological and anatomical results demonstrate that distinct responses of *S. brasiliensis* can be associated with contrasting

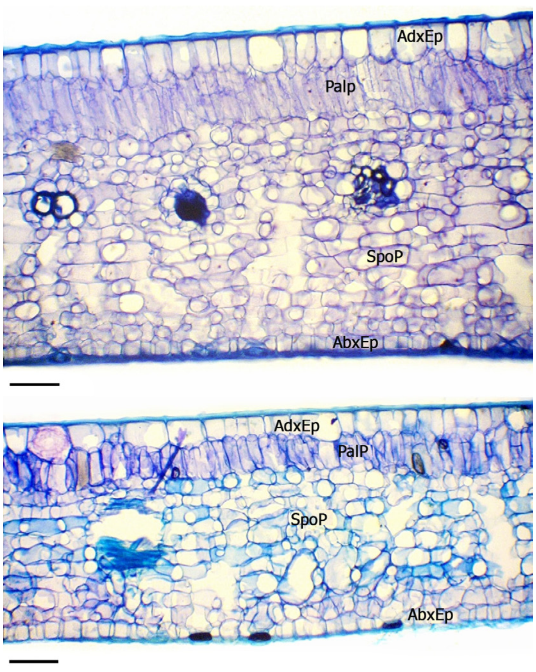

Figure 2 – a-b. Comparison of leaf anatomy of *Schwartzia brasiliensis* in shrub restinga (a) and shrub-tree restinga (b) formations in Parque Estadual Acaraí, São Francisco do Sul, SC. AdxEp = adaxial epidermis; PalP = palisade parenchyma; SpoP = spongy parenchyma; AbxEp = abaxial epidermis.

Table 1 – Analysis of soil fertility, water availability and photosynthetically active radiation of the schrubby and shrub-woody restingas of Acaraí State Park, São Francisco do Sul/SC. H + Al = potential acidity; CTC = cation exchange capacity; V = base saturation; MO = organic matter.

Environment variables	**Restinga**	
	Shrub	**Shrub-tree**
pH	5,3	5,4
SMP index	6,4	6,7
P (mg/dm³)	7,7	5,3
K (mg/dm³)	31,2	34,2
Al (cmolc/dm³)	0,5	0,3
Ca (cmolc/dm³)	0,9	2,8
Mg (cmolc/dm³)	0,9	1,2
H+ Al (cmolc/dm³)	2,6	2
CTC (cmolc/dm³)	4,51	16,52
V (%)	42,33	40,9
MO (g/dm³)	1,8	1,2
Bases sum	1,91	1,39
Salinity (mg/dm³)	65,6	53,4
Litter (cm)	9,40	8,20
Gravimetric humidity (g)	3,33	6,98
Photosynthetically active radiation (μmol $m^{-2}s^{-1}$)	508,40	421,30

Table 2 – Leaf morphoanatomical and architectural traits of *Schwartzia brasiliensis* in the restinga formations of Acaraí State Park, São Francisco do Sul-SC. Values represent means ± standard deviations and t-test results with significance level of $p \leq 0.05$.

Traits	**Shrub**	**Shrub-tree**	**t**	**p**
Height (m)	1,479 (± 0,26)	2,534 (± 0,55)	27,04	< 0,0001
Stem diameter (cm)	9,016 (± 2,30)	9,42 (± 2,45)	2,03	0,043
Leaf fresh mass (g)	2,34 (± 0,62)	2,31 (± 0,58)	0,61	0,54
Leaf dry mass (g)	0,67 (± 0,20)	0,61 (± 0,17)	3,61	0,0003
Leaf area (cm²)	40,79 (± 10,06)	39,97 (± 9,74)	0,93	0,35
Specific leaf area (cm²)	62,41 (± 11,17)	69,99 (± 49,82)	2,35	0,02
Succulence (g)	1,67 (± 0,48)	1,7 (± 0,45)	0,63	0,52
Adaxial epidermis (μm)	92,73 (± 14,61)	82,62 (± 12,72)	8,27	< 0,0001
Abaxial epidermis (μm)	54,61 (± 8,97)	47,65 (± 4,50)	11,1	< 0,0001
Palisade parenchyma (μm)	125,31 (± 54,33)	108,45 (± 50,28)	9,68	< 0,0001
Spongy parenchyma (μm)	366,78 (± 21,70)	343,91 (± 16,78)	4,81	< 0,0001
Leaf lamina thickness (μm)	639,42 (± 64,20)	582,63 (± 61,48)	10,12	< 0,0001

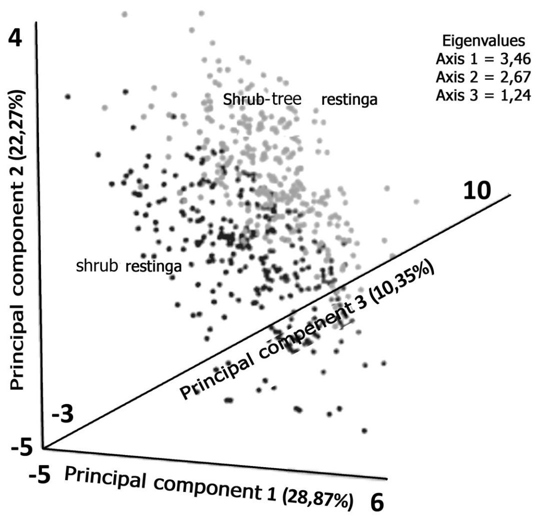

Figure 3 – Principal component analysis (PCA) of leaf morphoanatomical and architectural traits of populations of *Schwartzia brasiliensis* in two restinga formations in Parque Estadual Acaraí, São Francisco do Sul, SC. The first three axes explained 61.49% of the variance of the data.

characteristics of the restinga formations, such as soil nutritional status, water availability and light conditions. The plasticity index was very low for the majority of the traits analyzed, but the height of individuals stood out.

Potassium was one of the elements that showed well differentiated values between the two restinga formations and was higher in the shrub-tree formation (Tab. 1). This nutrient is important for the metabolism of the species, since it mitigates the adverse effect of high salinity by reducing the rate of sodium transport in the xylem and its accumulation in aerial organs (Rodrigues *et al.* 2012). The nutrients adsorbed by the soil particles can become available to plants and can be replaced by other cations (Ca2+ + Mg2+ + K+ + H+ + Al3+); therefore, they are called exchangeable. Cation exchange capacity (CEC) corresponds to the total amount of cations retained at the surface of the soil in the exchangeable condition (Ronquim 2010). The shrub-tree restinga had higher values of K, Ca and Mg in relation to the shrub restinga, showing that the stR soil is more fertile for plants due to the CEC being occupied with these essential cations. The shrub restinga had higher values of H + Al, which shows that its CEC is occupied by potentially toxic cations, resulting in a dystrophic soil (Ronquim 2010). This is reflected in the shorter individuals with smaller diameters (Tab. 2).

Light variation was statistically significant among the two restinga formations and is considered one of the main predictors of leaf variation (Melo Júnior & Boeger 2016; Stiegel & Mantilla-Contreras 2018). Light is a fundamental resource for photosynthesis; thus, solar intensity and the heterogeneity within the canopy can limit plant performance, generating specific morphological adaptations according to the light gradient (Valladares & Niinemets 2008; Gratani 2014).

Schwartzia brasiliensis develops more spongy parenchyma in both formations, with a ratio of approximately 3:1 in relation to the palisade parenchyma. Due to its occurrence under the canopy, a more developed spongy parenchyma is expected, since this tissue better optimizes diffuse light from shading (Lee *et al.* 1990). This pattern has been recorded in several shrub and tree species in forest and restinga systems (Fermino Junior 2004; Amorim & Melo Júnior 2017). On the other hand, individuals from the sR had thicker leaves as a result of a thicker epidermis, more layers of spongy and palisade parenchyma and a lower SLA. SLA is one of the leaf traits affected by light. It tends to increase in shade in order to enhance light harvesting at the expense of a decrease in leaf thickness, showing that leaf tissue anatomy is relevant in the process of light absorption (Gratani 2014). In the shrub-tree restinga, the individuals are subject to more shade due to the denser canopy. This attenuates the effect of solar radiation and reduces evapotranspiration, which is reflected in a lower biomass investment in individuals in this formation.

Water stress is one of the constraints in restinga, due to short periods of precipitation, low capacity of water retention by the substrate, salinity, high soil temperatures and high rates of evapotranspiration caused by wind (Melo Júnior & Boeger 2017). As a result, plant species respond by increasing the number of parenchyma cells and succulence (Cordazzzo *et al.* 2006). This can be seen in *S. brasiliensis* in the shrub restinga, where the leaves are thicker due to a greater development of the parenchyma and epidermis. This also reflects a water retention strategy (Melo Júnior & Boeger 2016), since this formation is subject to lower water availability and a higher degree of exposure to solar radiation compared to shrub-tree restinga.

Considering the theory about acquisitive and conservative strategies (Mathur *et al.* 2018),

Table 3 – Principal Component Analysis (PCA) of leaf morphoanatomical and architectural traits of populations of *Schwartzia brasiliensis*, occurring in two restinga formations of Acaraí State Park, São Francisco do Sul, SC.

Traits	Comp. 1	Comp. 2	Comp. 3
Height (m)	0,12	0,32	0,33
Stem diameter (cm)	0,029	0,045	0,15
Leaf fresh mass (g)	- 0,52	0,13	0,034
Leaf dry mass (g)	- 0,46	0,012	- 0,16
Leaf area (cm²)	- 0,47	0,16	0,071
Specific leaf area (cm²)	0,032	0,072	0,51
Succulence (g)	- 0,48	0,16	0,11
Adaxial epidermis (µm)	- 0,094	- 0,37	- 0,20
Spongy parenchyma (µm)	- 0,068	- 0,42	0,50
Palisade parenchyma (µm)	- 0,12	- 0,38	- 0,039
Abaxial epidermis (µm)	- 0,034	- 0,24	- 0,43
Leaf lamina (µm)	- 0,12	- 0,55	0,29

it is suggested that because the shrub restinga population is in a formation where soil nutrient levels and water availability are lower, and solar radiation is higher, individuals invest in biomass (Tab. 2) to withstand the stress caused by the combination of these abiotic factors, demonstrating a conservative strategy. In the shrub-tree restinga, the individuals are not exposed to these factors at the same intensity and demonstrate an acquisitive strategy, as evidenced by the attributes of height and stem diameter that were greater in this population. If on one hand, the individuals from the shrub restinga invest more in survival, those from the shrub-tree restinga invest more in growth, possibly as a result of an environment with richer soil. On the other hand, based on the other morphological traits, the individuals in the shrub restinga are more adapted to harsher conditions, such as higher salinity and poorer soils, which culminates in shorter plants.

Environmental heterogeneity is a determining factor in the expression of structural variation in *S. brasiliensis*. The populations exhibited structural adjustments in response to soil nutritional differences, water and light regime in the restinga formations, where the population of *S. brasiliensis* in the shrub restinga is subject to more limiting conditions compared to that in the shrub-tree restinga.

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