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ARTÍCULO DE INVESTIGACIÓN / ORIGINAL RESEARCH PAPER

LEAF TRAITS AND PLASTIC POTENTIAL OF PLANT SPECIES IN A LIGHT-EDAPHIC GRADIENT FROM *RESTINGA* IN SOUTHERN BRAZIL

Características de las hojas y potencial plástico de especies vegetales en un gradiente luminoso y edáfico sobre *Restinga* en el sur de Brasil

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ABSTRACT

Restinga formations grow on sandy spits of coastal plains, an environment whose conditions limit the growth and development of vegetal species. Studies on *restinga* gradients are good examples of how plants acclimate to restrictive environments. This work compares three woody species co-occurring in four vegetations of a *restinga* from Southern Brazil. It pinpoints morpho-anatomical attributes that favor the survival of species faced with spatial variability of soil and light conditions. Results indicate that they respond differently to environmental variables on different scales. The plastic response of morphological attributes is more marked than that of anatomical ones. *Varronia curassavica* and *Dodonaea viscosa* showed more xeromorphic features on the more stressful *restinga* formations while *Symphyopappus casarettoi* varied between xerophyte to mesophyte forms along the gradient. Individual height, fresh and dry leaf masses, leaf area, specific leaf mass and area, leaf density, and water content are particularly noteworthy. These responses are strategies allowing the studied species to survive in *restinga* environment with highly variable soil nutrient, water availability, and light conditions. The environmental conditions are important features that modulate the plant morphology along the gradient.

Keywords: coastal vegetation, leaf morphology, leaf anatomy, light and soil conditions.

RESUMEN

Restinga (o cordón litoral) es una formación que se desarrolla en cordones arenosos de planicies litorales. Este ambiente presenta condiciones limitantes al crecimiento y desarrollo de las especies vegetales. Estudios en gradientes de *restinga* son buenos ejemplos de como las plantas se aclimatan a las condiciones ambientales restrictivas. Este trabajo tuvo como objetivo comparar tres especies leñosas co-ocurrentes en cuatro fisonomías de una *restinga* del sur de Brasil, buscando conocer los atributos morfo-anatómicos que favorecen la sobrevivencia de estas especies frente a la heterogeneidad espacial de las condiciones de suelo y luz. Los resultados indican que las variables ambientales fueron percibidas en diferentes escalas por las especies. *Varronia curassavica* y *Dodonaea viscosa* mostraron características más xeromórficas en las formaciones de *restinga* más estresantes, mientras que *Symphyopappus casarettoi* varió entre formas xerofíticas a mesofíticas a lo largo del gradiente. Atributos morfológicos presentaron respuesta plástica más acentuada que los anatómicos, destacándose la altura de los individuos, las masas foliares frescas y secas, el área foliar, el área y la masa específica foliar, la densidad foliar y el contenido de agua. Tales características representan estrategias que permiten a las especies estudiadas sobrevivir en ambientes de *restinga* con elevada variación en la disponibilidad de nutrientes, agua del suelo y condiciones de luminosidad. Las condiciones ambientales son características importantes que modulan la morfología de la planta de lo largo del gradiente.

Palabras clave: anatomía de la hoja, condiciones de luz y el suelo, morfología de la hoja, vegetación costera.

INTRODUCTION

In nature, environmental conditions vary spatially and temporally and exhibit complex patterns that limit the establishment and development of vegetation (Rossatto *et al.*, 2009). Climate, rainfall, altitude, relief, soil, and light can influence the plant morphological traits (Givnish, 1984). Soil fertility and light can affect directly plant growth (Henriques and Marcelis, 2000). Soil nutrient availability induces different strategies of resource allocation and variations in leaf morphological traits (Boeger *et al.*, 2004; Louw-Gaume *et al.*, 2010; Lü *et al.*, 2012), while incident light regulates plant growth, due to its greater spatial and temporal heterogeneity (Pugnaire and Valladares, 2007). Plants can adjust and grow on large environmental scales (Lambers *et al.*, 1989). Their interaction with distinct abiotic factors is a precursor of adaptation to their growth (Givnish, 1984; Sultan, 1995), through adjustments of morphological, anatomical, physiological (Schlichting, 1986), and reproductive characteristics (Sultan, 2000).

The ability of an organism to alter its phenotype in response to changes in the environment is named phenotypic plasticity (Gratani, 2014). It is an adequate way for sessile organisms to deal with environmental heterogeneity (Sultan, 2000). It influences their adaptation (Pigliucci, 2005) and triggers variations that lead to adaptive divergences and allow for evolution and speciation (Valladares *et al.*, 2007).

Plants are plastic for several important ecological attributes (Sultan, 2000). However, plasticity can adopt a modular form, and affect meristems, leaves, stems, rather than the whole plant (Kroon *et al.*, 2005). Leaves have been considered the most plastic plant organ (Dickison, 2000).

From the ecological viewpoint, these plastic responses and their magnitude can reduce extinction risks (Givnish, 2002). In addition, they allow plants to explore distinct habitats and richer resource niches and to enlarge their geographic distribution (Sultan, 2000; Bradshaw, 2006).

In heterogeneous environments, plants with a larger plastic potential can promote the formation of ecotypes, especially in environments with an edaphic gradient (Fuzeto and Lomônaco, 2000; Cardoso and Lomônaco, 2003), such as *restinga*.

Restinga is a pioneer plant formation distributed in mosaics on coastal plains along sand dunes originated by marine sediment deposition and secondarily modeled by wind action (Bigarella, 2001; IBGE, 2012). This formation occurs along the whole Brazilian coastline, on quaternary deposits formed by marine transgressions and regressions (Araújo and Henriques, 1984; Veloso *et al.*, 1991). *Restinga* belongs to the Mata Atlântica domain (Rizzini, 1997). Its plant communities depend more on soil conditions than on climate (Brasil, 1999). They are distributed from the high tide line to the forests close to the Serra do Mar elevations (Rizzini, 1997) and include from herbaceous, creeping,

and psammophyllous plants, with low diversity on dunes, to ombrophilous dense forests, with higher plant diversity (Fernandes, 2006). Some plant species are established from the tide line to the dense forest and compete in an efficient way for the available resources.

Restinga plants are known to survive in severe environmental conditions and with limited nutrient supply (Fernandes, 2006). They are considered halophytes-psammophytes due to their tolerance to salinity and movement of dunes (Bigarella, 2001). They usually grew in soil with low availability of water and organic matter and under intense sunlight (Waechter, 1985). These conditions vary along the edaphic gradient toward the forest. The few studies that addressed the functional responses of dune plants to the environmental conditions showed the development of xeromorphic traits related to water economy. Small and vertical leaves, thick cuticles, stomata on both leaf surfaces, and water-storage parenchyma on leaf and stem are present among halophyte-psammophyte plants. All allow for a higher efficiency of the physiological processes to occupy and survive in *restinga* ecosystems (Boeger and Gluzezak, 2006; Arruda *et al.*, 2009).

The processes by which plants decode environmental signals (Schmitt *et al.*, 2003) must be studied to understand their plasticity in different natural habitats, since their morphological and anatomical responses provide information on their plastic potential in different conditions of soil and light conditions.

The main objective of this study is to evaluate comparatively the morpho-anatomical traits of three species along a light-edaphic gradient in a *restinga* from Southern Brazil. We assume that, independently from the phylogenetic relationships among them, the environmental conditions modulate the convergent plastic responses of plants in order to survive and grow in this limited environment. Herein, we test the hypothesis that the more restrictive environment of the *restinga* enhances the xeromorphic characters of the species.

MATERIALS AND METHODS

Study site

Study area is located at Grande beach, São Francisco do Sul County, Santa Catarina, Brazil (48° 33' W e 26° 17' S). This area is a Conservation Unity of Integral Preservation, named Acaraí State Park, and classified as extremely high priority by the Project for the Conservation and Sustainable Use of Brazilian Biodiversity (PROBIO, 2003). Its 6,667 ha of coastal plains include dunes, *restinga*, the low-land forest of Praia Grande, the hydrological complex of the Acaraí and Perequê rivers, and the Capivarú lagoon (FATMA, 2008). Climate is classified as mesothermic and Cfa, in Köppen's classification. It is strongly influenced by marine humidity. Annual mean rainfall is 2,372 mm. Annual mean temperature is 21.3 °C (12.9 °C to 33.6 °C, EPAGRI,

2014). The following *restinga* vegetations, adapted from FATMA (2008), and associated to an edaphic gradient constitute the study areas (Fig. 1):

1. Herb *restinga* (Rh) – composed of psammophilous and halophyte species, predominantly rhizomatous, cespitose, and creeping herbaceous plants growing on dunes and antidunes. Soil is sandy, quartzarenic neosol with low water and nutrient retention capacity and low fertility.
2. Shrub *restinga* (Ra) – Formed by dense 0.5 to 1.5 m high shrub mosaics. Its non-hydromorphic, sandy, strongly acid spodosol has a low nutrient content.
3. Shrub-tree *Restinga* (Raa) – This vegetation arises when dunes are more inland and stable. It is composed by shrubs and trees between 2 and 5 m high. Pedological conditions are similar to Ra.
4. Transition Forest (Ft) – A forest formation with a continuous stratum between 15 and 20 m high, on spodosol + hydromorphic organosol. Soil has a high concentration of organic matter and water content. This area is a transition to dense ombrophilous forest *stricto sensu*.

Measurement of environmental variables

Soil characterization included: a) nutritional status and salinity performed by the Laboratório de Análise do Solo e Planta of the Instituto Agronômico de Campinas/SP-Brasil based on five homogenized samples from each physiognomy collected 15 cm deep, according to a methodology recommended by EMBRAPA (2013); b) litter production; and c) gravimetric humidity measured on five samples from each physiognomy (EMBRAPA, 2013). The PAR (photosynthetically active radiation) on leaves was measured on the canopy of each individual with a light meter (Li-250A LICOR, USA), making up 50 measurements/species.

Plant material

The selected species for this study were *Varronia curassavica* Jacq. (Boraginaceae), *Dodonaea viscosa* Jacq. (Sapindaceae) and *Symphyopappus casarettoi* B.L.Rob. (Asteraceae). These species occur in all the vegetations described. Vouchers were deposited at the JOI (Herbarium of University of Joinville Region) for reference, under the following numbers: *Varronia curassavica* (J.C. Melo 14103, JOI), *Dodonaea viscosa* (J.C. Melo 1054, JOI) and *Symphyopappus casarettoi* (J.C. Melo 881, JOI). As indicated in the *Lista de Espécies da Flora do Brasil* (2015), these species are typically characterized as shrub, tree and shrub, respectively.

Measurements

Five individuals were selected in each physiognomy. Their height, life form, and habitat were registered. Thirty canopy leaves, between 3rd and 6th nodes from apex were collected for morphometric to analyze leaf fresh mass (g), leaf dry mass (g), leaf thickness (mm), leaf area (cm²), specific leaf area (leaf area/leaf dry mass, cm² g⁻¹), leaf density (specific leaf mass.1/leaf thickness, mm³ mg⁻¹), and water content (g). Leaf area was estimated from images created with a flatbed scanner calibrated with Sigma Scan PRO software (version 5.0, SPSS Inc., Chicago, IL, USA). Water content was calculated by the difference between weight of fresh and dry leaf mass (Vaierett *et al.*, 2007).

Stomata density (mm²) was determined by clear nail polish prints from the median region of epidermal surface of leaves (Boeger and Gluzezak, 2006), using light microscope Olympus with 10x magnification and camera lucida.

Ten leaves were fixed in FAA 50 and later conserved in ethanol 70 % (Johansen, 1940). The fixed samples were sectioned with a razor blade, clarified in sodium hypochlorite 10 %, stained with toluidine blue 1 % and mounted in glycerin 30 % (O'Brien and McCully, 1981). For anatomical studies, leaf samples from the median region of leaf blades were embedded in methacrylate-glycol (JB-4) and sectioned with

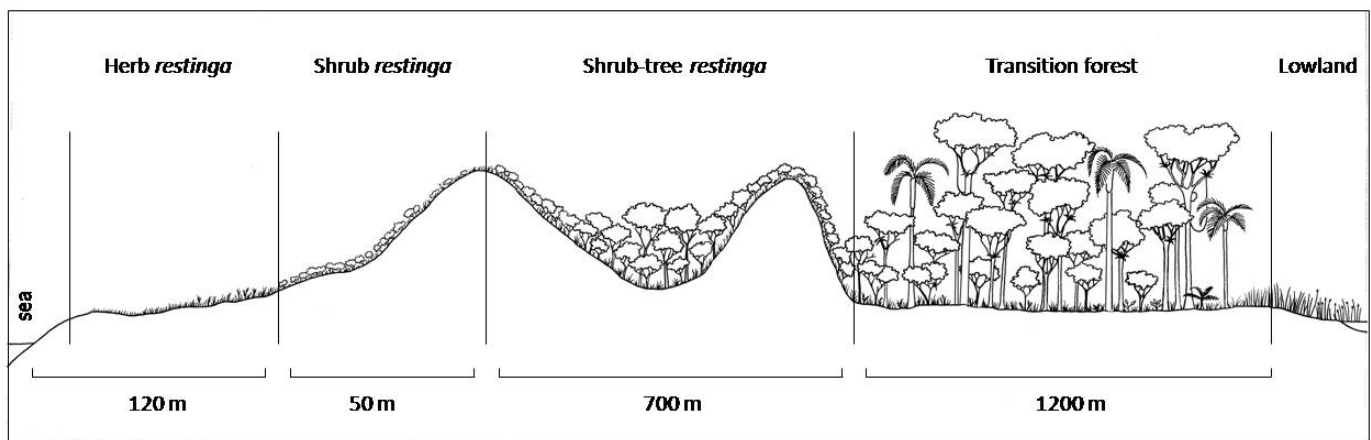


Figure 1. *Restinga* vegetation from the Icarai State Park. São Francisco do Sul county, SC, Brazil.

a rotary microtome Leica. Transverse sections were stained with toluidine blue 0.05 % (Feder and O'Brien, 1968) and mounted on synthetic resin (Paiva *et al.*, 2006). Palisade parenchyma (PP), spongy parenchyma (SP), and water storage parenchyma (WSP) were measured (µm) in transverse sections of median regions of leaf blades. Palisade parenchyma/spongy parenchyma ratio (PP/SP) was also calculated. All measurements were made with an optical microscope Olympus CBB and micrometric ocular. The mean values and respective standard deviations were calculated for all quantitative biological and environmental variables, for all species from the four *restinga* vegetations. Principal Component Analysis (PCA) evaluated the edaphic gradient. Mean values of morphological and anatomical traits were compared by ANOVA using Tukey's test, with a 5 % significance level, with software Statistica, version 7.0 (Statsoft Inc., USA). For each morphological and anatomical quantitative feature, the phenotypic plasticity index (PPI, *sensu* Valladares *et al.*, 2006) was calculated, according to the following formula: $PPI = (value\ of\ maximum\ mean - value\ of\ minimum\ mean) / (value\ of\ maximum\ mean)$. This index varies from zero to one, with values closer to zero being less plastic and values closer too one, more plastic. The Pearson's correlations were used to verify the relations between environmental and morpho-anatomical traits (Legendre and Legendre, 1998).

RESULTS

The principal component analysis showed that the first two components explained 98 % of the total variance of

environmental attributes (Table 1, Fig. 2). The principal component 1, represented by levels of P, K, Na, H+Al, and organic matter content, litter thickness and gravimetrical humidity explains 71.9 % of soil variation among vegetation, while the sum of bases and Ca and Mg concentrations, related to principal component 2, explains 26.4 % of the total variance.

Table 1. Correlation of soil chemical attributes in the studied vegetation at components 1 and 2 obtained by principal component analysis (PCA).

	Principal components	
	1	2
pH	-0.30	0.28
P	0.35	0.12
K	0.36	0.08
Na	0.34	0.21
Ca	-0.13	0.49
Mg	-0.08	0.52
H + Al	0.36	0.09
Sum of bases (BS)	0.01	0.54
ion exchange capacity (IEC)	0.36	0.11
base saturation (V)	-0.35	0.17
Organic matter content (OM)	0.36	0.08
Variance explained by components	7.41	3.40
Percentage of total variance explained (%)	67.391	30.942

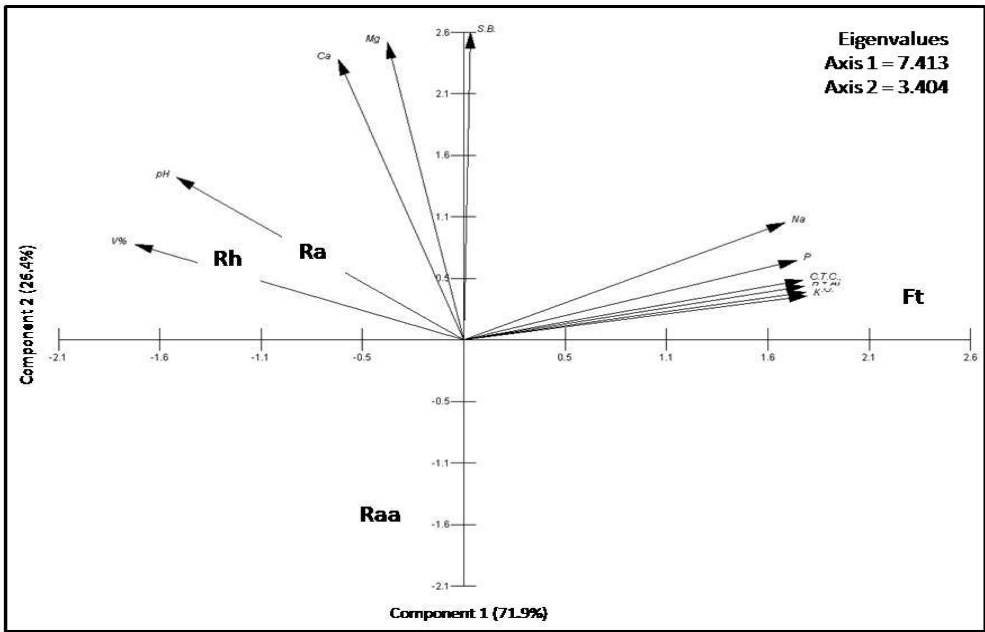


Figure 2. Principal component analysis of edaphic attributes from study *restinga* vegetation, showing an environment gradient. Legend: Rh = herb *restinga*; Ra = Shrub *restinga*; Raa = Shrub-tree *restinga* and Ft = transition forest.

Soil chemical analysis showed that pH decreases (become more acidic) gradually from Rh to Ft (Table 2). Soil is initially slightly acid and becomes extremely acid in Ft. Base saturation is inversely related to soil gradient. The values of P and K were higher in Ft. Lower concentrations of P and K were found in Raa and Rh soils, respectively. Very high values of Na were observed in Ft. In addition, Ca was inversely proportional to Na in all vegetations, except Raa, where the values of Na and Ca were the lowest. Aluminum

concentration (H + Al), ion exchange capacity (IEC), litter thickness, and organic matter were directly proportional to the gradient, with higher values in Ft for all variables. Water soil, represented by gravimetric humidity, is low in Rh but it increases along the gradient to reach 76.2 % in Ft, which has a hydromorphic soil.

The PAR of each species differed according to vegetations as a function of height, life form, and habitat of the sampled individuals (Table 3). A well-defined light gradient (Rh

Table 2. Mean values of soil chemical attributes, salinity, litter thickness, and gravimetric humidity in the studied vegetation. Legend: Rh = herb *restinga*; Ra = Shrub *restinga*; Raa = Shrub-tree *restinga*, and Ft = transition forest; BS = base sum; IEC = ion exchange capacity; V = base saturation.

Environmental attributes	Vegetation			
	Rh	Ra	Raa	Ft
pH	5.47	4.73	3.53	3.10
P (mg.dm ⁻³)	2.67	2.00	1.00	25.67
K (mmolc.dm ⁻³)	1.13	1.33	1.30	2.27
Na (mmolc.dm ⁻³)	0.93	1.10	0.83	1.90
Ca (mmolc.dm ⁻³)	9.33	10.33	5.67	7.67
Mg (mmolc.dm ⁻³)	2.67	2.33	1.00	2.00
H + Al (mmolc.dm ⁻³)	9.00	15.00	21.67	291.67
BS (mmolc.dm ⁻³)	14.07	15.10	8.80	13.83
IEC (mmolc.dm ⁻³)	23.07	30.10	30.47	305.50
V (%)	59.67	50.00	29.00	4.33
Organic matter content (g.dm ⁻³)	7.33	14.00	14.67	82.67
litter (cm)	0.1	2.4	3.7	7.9
Gravimetric humidity (%)	4.9	8.3	14.1	76.2

Table 3. Mean values and respective standard deviation (between brackets) of light intensity (PAR), height, life form, and habitat of studied species in the *restinga* vegetation. Legend: Rh = herb *restinga*; Ra = Shrub *restinga*; Raa = Shrub-tree *restinga* and Ft = transition forest.

Species	Vegetation			
	Rh	Ra	Raa	Ft
<i>Varronia curassavica</i>				
PAR (μmol.s ⁻¹ .m ⁻²)	1513.76 (29.75)	722.24 (17.07)	524.44 (19.52)	374.44 (19.52)
Height (m)	0.26 (0.1)	1.06 (0.1)	1.60 (0.2)	1.70 (0.2)
Life form	subshrub	subshrub	shrub	Shrub
Habitat	sammophyllous	edge	understory	understory
<i>Dodonaea viscosa</i>				
PAR (μmol.s ⁻¹ .m ⁻²)	1506.94 (15.89)	1068.28 (55.30)	841.7 (26.66)	1451.86 (21.75)
Height (m)	0.23 (0.1)	1.00 (0.1)	2.40 (0.2)	4.30 (0.3)
Life form	creeping subshrub	small tree	small tree	Tree
Habitat	psammophyllous	Edge	Edge	Gap
<i>Symphyopappus casarettoi</i>				
PAR (μmol.s ⁻¹ .m ⁻²)	1518.1 (24.57)	731.22 (12.31)	546.28 (30.72)	1456.06 (27.53)
height (m)	0.25 (0.1)	1.04 (0.1)	1.32 (0.1)	1.86 (0.1)
Life form	subshrub	Subshrub	shrub	shrub
Habitat	psammophyllous	edge	understory	gap

though Ft) was only observed in *V. curassavica*. *D. viscosa* and *S. casarettoi*, which present high PAR, occurred in gaps where the radiance is high due, for example, to fall of canopy trees.

The phenotypic plasticity index (PPI) evidences morpho-anatomical differences in all species (Table 4). All the morpho-anatomical traits of *V. curassavica* were highly plastic, except spongy parenchyma. Because this species presented the highest values, it can be considered the most plastic species. In *D. viscosa* e *S. casarettoi*, the plastic responses were higher for morphological attributes than anatomical ones, which showed a low plastic potential, except for stomata density in leaves of *S. casarettoi*.

ANOVA shows a different pattern of responses for each species along the edaphic gradient (Tables 5 and 6), supporting the PPI results. *Varronia curassavica* exhibits plastic responses directly proportional to light, humidity, and organic matter content, for the following traits: fresh and dry leaf mass, leaf area, AEF, and water content. Its leaf area is four times higher in Ft than in Rh. Leaf thickness is inversely proportional to the edaphic gradient. Thicker leaves show more developed palisade parenchyma, while thinner ones have more developed spongy parenchyma. The gradual increase of leaf area was inversely proportional to stomata density (Table 5).

Dodonaea viscosa and *S. casarettoi* present similar patterns of structural variation. Their Rh and Ft individuals, on the one hand, and their Ra and Raa individuals, on the other, are alike. Thus, individuals of Rh and Ft show similar mean values for morphological and anatomical characteristics, except for SLA in *S. casarettoi* and leaf density, for both

species. This pattern was also found in individuals from Ra and Raa (Table 5).

The correlations obtained between environmental attributes and morpho-anatomical traits showed strong correlations between luminosity and some morphological traits. Light was inversely correlated to leaf area ($r = -0.68$, $p < 0.002$), water content ($r = -0.70$, $p < 0.001$), fresh leaf mass ($r = -0.69$, $p < 0.002$), and dry leaf mass ($r = -0.63$, $p < 0.002$).

Soil humidity ($r = 0.68$, $p < 0.001$), organic matter content ($r = 0.67$, $p < 0.003$), and litter thickness were positively correlated to individual heights.

DISCUSSION

The results obtained indicate different plastic responses to the variables soil and light throughout the restinga gradient, according to species. The spatial heterogeneity characterized in each physiognomy induced responses on different scales in the studied species. Spatial changes in the light intensity that reaches plants seems to produce more relevant plastic responses in some species (Aranda *et al.*, 2004) whereas soil conditions can be more decisive for others (Poorter, 1999; Valladares, 2003; Hodge, 2006).

Although the edaphic features of *restinga* soils show wide variations in macronutrient and organic matter contents, organic litter thickness, and moisture, we suggest that the different light conditions have more influence on the leaf morpho-anatomy of the studied species (Tables 3 and 5). A growing offer of nutrients, organic matter, and water in soils implies a gradual biomass allocation to plant stems and

Table 4. Plasticity Index values of leaf traits from studied species. Legend: H = height (m); LFM = leaf fresh mass (g); LDM = leaf dry mass (g); LT = leaf thickness (mm); LA = leaf area (cm²); SLA = specific leaf area (cm².g⁻¹); LD = leaf density (mm³.mg⁻¹); LWC = leaf water content (g); SD = stomata density (n.mm⁻²); PP = palisade parenchyma thickness (μm); SP = spongy parenchyma thickness (μm) WSP = water storage parenchyma thickness (μm); PP/SP = palisade parenchyma/spongy parenchyma ratio and/or water storage parenchyma.

Leaf traits	Species		
	<i>Varronia curassavica</i>	<i>Dodonaea viscosa</i>	<i>Symphypappus casarettoi</i>
H	0.91	0.96	0.90
LFM	0.90	0.84	0.90
LDM	0.91	0.83	0.86
LT	0.77	0.44	0.57
LA	0.89	0.81	0.77
SLA	0.83	0.76	0.77
LD	0.86	0.73	0.79
LWC	0.89	0.98	0.92
SD	0.76	0.50	0.78
PP	0.66	0.44	0.36
SP	0.35	0.45	0.36
PP/SP	0.68	0.67	0.29

Table 5. Mean values and respective standard deviations (between brackets) of morphological and anatomical traits of studied species. Legend: LFM = leaf fresh mass (g); LDM = leaf dry mass (g); LT = leaf thickness (mm); LA = leaf area (cm²); SLA = specific leaf area (cm²·g⁻¹); LD = leaf density (mm³·mg⁻¹); LWC = leaf water content (g); SD = stomata density (n·mm⁻²); PP = palisade parenchyma thickness (μm); SP = spongy parenchyma thickness (μm); WSP = water storage parenchyma thickness (μm); PP/SP = palisade parenchyma thickness/spongy parenchyma thickness and/or water parenchyma thickness; Rh = herb *restinga*; Ra = Shrub *restinga*; Raa = Shrub-tree *Restinga* and Ft = transition forest. Different letters in the same roll among vegetation for each species means significant differences, by Tukey test, ($p < 0.05$). (*) = not present.

Morpho-logical traits	Species and Vegetation									
	<i>Varronia curassavica</i>					<i>Dodonaea viscosa</i>				
	Rh	Ra	Raa	Ft	Rh	Ra	Raa	Ft	Rh	Ra
LFM	0.25 (0.06) ^c	0.48 (0.07) ^b	0.50 (0.17) ^b	0.61 (0.15) ^a	0.15 (0.03) ^c	0.25 (0.05) ^a	0.28 (0.06) ^a	0.20 (0.05) ^b	0.14 (0.03) ^c	0.21 (0.05) ^b
LDM	0.07 (0.02) ^c	0.17 (0.03) ^b	0.15 (0.05) ^b	0.19 (0.05) ^a	0.06 (0.01) ^c	0.09 (0.02) ^a	0.10 (0.02) ^a	0.08 (0.02) ^b	0.04 (0.01) ^b	0.06 (0.01) ^a
LT	0.50 (0.08) ^a	0.34 (0.07) ^b	0.30 (0.03) ^c	0.27 (0.03) ^d	0.22 (0.02) ^a	0.18 (0.02) ^b	0.18 (0.02) ^b	0.21 (0.02) ^a	0.42 (0.04) ^a	0.33 (0.04) ^b
LA	4.6 (0.90) ^d	10.7 (1.83) ^c	13.2 (1.96) ^b	17.5 (1.77) ^a	5.7 (0.93) ^b	9.1 (1.52) ^a	10.4 (1.60) ^a	6.5 (0.84) ^b	3.0 (0.45) ^b	4.7 (0.35) ^a
SLA	67.5 (13.06) ^b	65.5 (12.29) ^b	95.2 (28.40) ^a	98.8 (29.33) ^a	97.5 (13.75) ^a	102.2 (14.71) ^a	110.1 (21.84) ^a	90.7 (18.55) ^b	84.5 (13.01) ^a	87.5 (22.58) ^a
LD	0.31 (0.07) ^c	0.48 (0.13) ^a	0.39 (0.14) ^b	0.41 (0.10) ^b	0.49 (0.07) ^c	0.55 (0.08) ^a	0.52 (0.12) ^b	0.55 (0.13) ^a	0.29 (0.05) ^c	0.37 (0.10) ^b
LWC	0.18 (0.05) ^d	0.31 (0.06) ^c	0.35 (0.12) ^b	0.42 (0.11) ^a	0.09 (0.02) ^c	0.16 (0.03) ^a	0.18 (0.04) ^a	0.12 (0.03) ^b	0.10 (0.02) ^c	0.15 (0.04) ^b
SD	279.71 (20.35) ^a	176.79 (13.01) ^b	143.59 (6.83) ^c	83.83 (8.25) ^d	144.42 (7.00) ^a	88.81 (4.01) ^c	81.34 (6.55) ^c	112.88 (4.29) ^b	72.21 (4.01) ^a	37.35 (4.37) ^b
PP	265.47 (7.27) ^a	148.57 (7.27) ^b	142.76 (5.25) ^b	94.62 (4.29) ^c	123.67 (6.12) ^a	78.02 (4.29) ^c	76.36 (3.50) ^c	114.54 (7.63) ^b	179.28 (5.80) ^a	127.82 (4.29) ^b
SP	124.50 (6.78) ^b	102.09 (6.83) ^c	123.67 (2.62) ^b	128.65 (5.87) ^a	52.29 (4.01) ^b	81.34 (6.55) ^a	83.83 (7.27) ^a	51.46 (3.50) ^b	*	*
WSP	*	*	*	*	*	*	*	*	195.05 (8.07) ^a	166.00 (6.78) ^b
PP/SP	2.06 (0.09) ^a	1.46 (0.08) ^b	1.15 (0.03) ^c	0.74 (0.05) ^d	2.37 (0.12) ^a	0.96 (0.05) ^b	0.92 (0.08) ^b	2.24 (0.2) ^a	0.92 (0.05) ^a	0.77 (0.04) ^b
										153.59 (7.87) ^b
										0.89 (0.06) ^a

Table 6. Results of variance analyses (ANOVA) of morphological (N = 500) and anatomical (N = 125) traits of studied species, post hoc by Tukey test, ($p < 0.05$).

Morphological traits	<i>Varronia curassavica</i>	<i>Dodonaea viscosa</i>	<i>Symphycarpus casarettoi</i>
LFM	F _{3,496} = 299.2, $p < 0.0001$	F _{3,496} = 275.6, $p < 0.0001$	F _{3,496} = 284.4, $p < 0.0001$
LDM	F _{3,496} = 297.9, $p < 0.0001$	F _{3,496} = 217.6, $p < 0.0001$	F _{3,496} = 252.3, $p < 0.0001$
LT	F _{3,496} = 331.6, $p < 0.0001$	F _{3,496} = 233.4, $p < 0.0001$	F _{3,496} = 302.2, $p < 0.0001$
LA	F _{3,496} = 429.4, $p < 0.0001$	F _{3,496} = 373.6, $p < 0.0001$	F _{3,496} = 380.2, $p < 0.0001$
SLA	F _{3,496} = 192.6, $p < 0.0001$	F _{3,496} = 45.7, $p < 0.0001$	F _{3,496} = 67.2, $p < 0.0001$
LD	F _{3,496} = 132.9, $p < 0.0001$	F _{3,496} = 34.4, $p < 0.0001$	F _{3,496} = 170.7, $p < 0.0001$
LWC	F _{3,496} = 280.7, $p < 0.0001$	F _{3,496} = 281.6, $p < 0.0001$	F _{3,496} = 280.7, $p < 0.0001$
SD, PP, SP, WSP, PP/SP	F _{3,121} = 227.7, $p < 0.001$	F _{3,121} = 49.1, $p < 0.0001$	F _{3,121} = 34.5, $p < 0.0001$

branches, represented by higher plants as we move from the dunes towards the forest.

Plasticity indices (PPI) show that the morphological attributes present more significant plastic than anatomical responses. This supports the idea that according to the level of incident light, species have different abilities to respond to luminosity variations and develop leaves with distinct, modularized morphological and anatomical features (Aranda *et al.*, 2004; Kroon *et al.*, 2005). Thus, environmental variations do not provoke a uniform response in each individual, but induce changes in certain functional unities (Kroon *et al.*, 2005), as shown, mainly, by the morphological attributes of the species studied.

The leaf morphological responses (smaller leaf areas, thicker limb, and higher stomatal density) presented by the plants from the herbaceous physiognomy, which is naturally more open due to a higher number of small height species, and by those from the forest physiognomy, where populations of *D. viscosa* and *S. casarettoi* are present in border areas or clearings, corroborate the morphological response of plants exposed to high light radiation (Boardman, 1977; Pyykko, 1979; Sultan, 1987; Ackerly *et al.*, 2000; Gratani *et al.*, 2006), as reduced leaf areas, and can be interpreted as a strategy to conserve water and control excessive transpiration (Boeger and Gluzezak, 2006). Such strategies were observed similarly in forest populations due to occur in gaps with luminous condition similar to that found in open areas of sandbanks, showing the effect of different levels of light on the development of leaf traits.

On the other hand, in the more shaded environments of Ft, the leaves of *V. curassavica* present higher leaf area and reduced leaf thickness and stomatal density, which represent a trade-off to maximize light capture capacity in low light intensity environments (Pearcy, 2007) and a better photosynthetic yield and biomass allocation, despite the increase in transpiration surface (Givnish, 1988; Niinemets and Fleck, 2002; Santos *et al.*, 2010). In addition to the light factor, greater nutrient and water supply induce an increase in leaf area (Nicotra *et al.*, 2007), as observed in individuals of *V. curassavica* growing in Ft.

Anatomically, these attributes reflect more developed palisade parenchyma in leaves with smaller areas and more developed spongy parenchyma in leaves with wider areas, in the studied species. This mesophyll organization is directly influenced by the balance between carbon gain and water loss (Givnish and Vermeij, 1976). A better profit of diffuse light in shady environments is associated with thin leaves with more developed spongy parenchyma, which was reported in other studies on understory species (Cao, 2000; Boeger *et al.*, 2004; Boeger *et al.*, 2006).

The presence of photosynthesizing water-storage parenchyma in *S. casarettoi* has been interpreted as a xeromorphic response to the conditions of radiation and

lower water availability in *restinga* vegetations. Xeromorphic features as water-storage tissue in psammophilous, halophytic plants are interpreted as attributes of resistance to environmental pressures related to water saving, which favor the permanence of some species in the *restinga* environment (Boeger and Gluzezak, 2006; Arruda *et al.*, 2009).

SLA, which is the ratio between leaf area and dry mass, is often used to assess plant growth because it is positively related to the relative growth rate between species (Pérez-Harguindeguy *et al.*, 2013). It is also an important indicator of strategies of habitat preferences and of productivity of plants related to environments under stress (Niklas and Christianson, 2011), as *restingas*. The three studied species presented considerable SLA variation, a phenomenon reported as common in co-occurring species (Pérez-Harguindeguy *et al.*, 2013).

Individuals under higher levels of light, either because they are more isolated in Ra or occur in border areas of the other *restinga* vegetation, presented lower SLA values, which indicates a strategy to diminish the excessive temperature to which they are submitted and the transpiration it entails (Soares *et al.*, 2012). On the other hand, the individuals in more shaded environments, since they are covered by the canopy in Ft or are less exposed to light due to neighboring plants, presented higher SLA values. This reflects a greater investment in photosynthetic than in support tissues, corroborating the results of other studies on sciophytic species (Boeger *et al.*, 2006; England and Attiwill, 2006). Thus, both dry mass and leaf area contribute to SLA in different manners, according to the conditions of each physiognomy and to the species concerned (Pérez-Harguindeguy *et al.*, 2013).

Unlike leaf area, the stomatal density value for these three species was proportional to the quantity of light received in each *restinga* physiognomy and, in some cases, they corresponded to environments with higher water stress. Stomatal density variations are reported as a mechanism that controls stomatal conductance to regulate water loss through transpiration (Morais *et al.*, 2003). An increase in stomata number per leaf area unit may be due to high luminosity (Duz *et al.*, 2004; Pearce *et al.*, 2006; Santos *et al.*, 2010) and to soil water scarcity (Klich, 2000; Moratelli *et al.*, 2007; Melo Jr. *et al.*, 2012).

Leaf density shows the relation between leaf dry mass, area, and thickness (Witkowski and Lamont, 1991). It is considered as a plant acclimation to the luminous intensity received (Wright *et al.*, 2004) and reflects a higher investment in the production of mechanical tissues, in addition to photosynthesizing tissue compaction (Niinemets, 2001), which limits gas diffusion within the leaf (Niinemets, 1999).

Although higher densities are expected in environments poor in nutrients or humidity or with high luminosity (Witkowski and Lamont, 1991), in the present study, leaf

density did not vary accordingly among species and among *restinga* vegetation. This can be explained by the variation observed in leaf thickness and dry mass, characters that often vary independently in the same plant, between species and in response to resource gradients (Witkowski and Lamont, 1991).

Higher water content was observed in the lower, shaded plants of the three species throughout the *restinga* gradient, which differs from our expectancies and most data reported for other species growing in such an environment (Boeger and Gluzezak, 2006; Pereira *et al.*, 2009). Nevertheless, some *restinga* species with water storage tissues and exposed to high solar radiation can present low water content (Boeger and Gluzezak, 2006). This phenomenon was observed in the populations of *V. curassavica*, *D. viscosa*, and *S. casarettoi* occurring under high luminosity in *restinga* vegetation. The plants of *D. viscosa* and *S. casarettoi* with higher water content were observed in the shadiest vegetations. In *V. curassavica*, water content was proportional to the gradient owing to a greater availability of water in the soil. Plants probably present distinct transpiration rates according to the availability of light (Markesteijn *et al.*, 2007). Thus, higher water storage in the leaves of low plants may serve as an alternative source for photosynthesis in conditions of water restriction (Lamont and Lamont, 2000). Nonetheless, in plants more exposed to light, be they low or not, low water potential can be compensated for by a reduction of leaf area reduction, a thicker palisade tissue increase, and dew absorption through stomata to maintain photosynthetic capacity (Zagdanska and Kozdoj, 1994; Lüttge, 1997).

Species with a higher plastic potential tend to allocate resources more effectively and occupy environments more aptly (Bradshaw, 2006). Low PPI values in leaf anatomy suggest that a low plastic response indicates a greater canalization and a regulatory action for anatomical structure plasticity (Pigliucci, 1996; Weinig, 2000). On the other hand, the different strategies used by the three species point out that a greater plasticity, represented by morphological attributes, equalizes the conditions of high luminosity, nutrient scarcity, and water availability, which vary along the *restinga* vegetation, and regulates resource allocation and photosynthetic production to levels that allow their survival in this restricting environment.

CONCLUSION

The results of this study manifest that the species were able to develop structural responses, to a greater or lesser extent, to physical-climatic variations imposed by the environment. Environmental heterogeneity, which translates into a great variation in nutrient and water availability in the soil and by distinct light conditions, transforms *restinga* into a model environment to study plasticity, since some species are distributed along the whole gradient.

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