Pak. J. Bot., **50(5): 1877-1884, 2018.**

MORPHO-ANATOMICAL PLASTICITY OF *STYLOSANTHES VISCOSA* (FABACEAE) IN RESPONSE TO DIFFERENT SOIL AND LIGHT CONDITIONS OF RESTINGA ENVIRONMENTS

JÉSSICA STÉFANI DIRKSEN AND JOÃO CARLOS FERREIRA DE MELO JÚNIOR*

[1] *Department of Biological Sciences, Laboratory of Morphology and Plant Ecology, Institucional Research Program in Environmental Science, University of the Region of Joinville, Joinville, Santa Catarina, Brazil*
**Correspondence author's email: joao.melo@univille.br*

Abstract

Structural plasticity is an important ability of plants to acclimate to different environmental conditions, especially in limiting environments such as restingas. The objective of this study was to evaluate the morpho-anatomical plasticity of *Stylosanthes viscosa* (L.) Sw. (Fabaceae) populations based on the hypothesis that edaphic and luminous factors cause different structural adjustments, such that, in the *restinga*, herbaceous plants would be more xeromorphic than shrub-tree plants. The study area included formations of herbaceous and shrub-arboreal *restinga* of Acaraí State Park, located in São Francisco do Sul, Santa Catarina, Brazil. Morpho-anatomical attributes of 10 individuals per formation were compared with the t-test. Principal components analysis was used to evaluate the influence of environmental factors on *S. viscosa* (L.) Sw. populations. In both formations, organic matter content had the greatest influence on adjustments exhibited by the species, with greater emphasis on plant height, stem diameter, fresh mass, dry mass, leaf area and specific leaf area. Morphological attributes exhibited greater plasticity than anatomical attributes. The population of the herbaceous *restinga* was observed to be more xeromorphic, exhibiting greater investment in mechanical tissues, as opposed to the shrub-arboreal *restinga* population, which exhibited greater investment in photosynthetic tissues. The results demonstrate the strong influence that soil and light have on the morpho-anatomical plasticity of *S. viscosa* (L.) Sw. in *restinga* environments.

Key words: Biodiversity conservation, Structural adjustments, Functional morpho-anatomy, Coastal plain

Introduction

The Fabaceae comprises about 650 genera and around 19,000 species, and has a cosmopolitan distribution (Souza & Lorenzi, 2012). It is one of the richest families of the Brazilian flora (Queiroz, 2009) and occurs in all Brazilian biomes. It is considered the second most diverse family in the Atlantic Forest with 939 species (Forzza, 2010). It possesses high ecological and economic importance, with several species serving as food for animals, including humans, through direct and indirect consumption of their resources (Lewis, 1987). In the sandy of littoral plain of southern Brazil, the species *Canavalia rosea* (Sw.) DC., *Dalbergia ecastaphyllum* (L.) Taub., *Lonchocarpus sericeus* (Poir.) Kunth ex DC., *Senna pendula* (Humb. & Bonpl. Ex Willd.) HS Irwin & Barneby, *Sophora tomentosa* L., and *Stylosanthes viscosa* Sw. are important components of different *restinga* formations (Melo Júnior & Boeger, 2015). The genus *Stylosanthes* Sw., characterized by herbaceous-shrub plants, belongs to the subfamily Papilionoideae, and is widely distributed throughout the world (Costa, 2006), with ca. 80 described species (Anon., 2014). They are mostly perennial species with robust root systems, which affords them drought tolerance, great ability to colonize low fertility soils, and the ability to maintain a symbiotic relationship with nitrogen fixing bacteria (Andrade & Karia, 2000).

The species *Stylosanthes viscosa* (L.) Sw. has prostrate, erect or ascending growth, with a sub-shrub habit (20-140 cm tall), a hairy-silky-viscous stem, and a vigorous root. It has a Neotropical distribution, occurring from Mexico to the state of Santa Catarina in southern Brazil (Américo, 2015). It inhabits regions with different physical and climatic characteristics, including arid and semi-arid environments, such as restingas and coastal dunes (Sawkins *et al.*, 2001). Ecological studies on *S. viscosa* (L.) Sw. remain scarce in Brazil. Among this scarce literature, there is the study carried out by Ramalho & Rosa (2010), who discussed the plant-pollinator interaction and concluded that the species' tiny flowers are able to attract medium- to large-sized bees, such as *Xylocopa cearensis* Ducke. In the context of recovery of soils degraded by mining, Neri *et al.*, (2011) highlighted *S. viscosa* (L.) Sw. as one of the key species for the beginning of ecological succession.

Stylosanthes viscosa (L.) Sw. can be found in the restingas of southern Brazil, where it inhabits sandy soils of varying salinity, nutrition and water availability conditions (Melo Júnior & Boeger, 2015). This ecosystem is associated with the Atlantic Forest (Scarano, 2002), and is characterized by a diverse set of biological communities of distinct floristic and structural composition (Miranda & Hanazaki, 2008).

Plant species that inhabit restingas are subjected to extreme environmental conditions, such as high temperatures, constant wind, high salinity and nutrient deficiency (Scarano *et al.*, 2001; Scarano, 2002; McLachlan & Brown, 2006). These conditions can cause mechanical damage and abrasion of leaves, surface osmotic pressure differences, and damage chemical processes and water flow rates (Mc Lachlan & Brown, 2006). Restinga vegetation tends to produce adaptive responses for establishment and growth under variations in the extreme conditions offered by the environment. This ability is attributed to phenotypic plasticity, which is characterized by the ability of a plant to acclimatize itself to the environment through morphological, phenological and/or physiological adjustments, without the necessary occurrence of genetic changes (Bradshaw, 1965; Price *et al.*, 2003).

The *restinga* environment has become an important model for functional studies because it possesses great physico-climatic variation among formations and between seasons, such that on a small spatial scale there can be communities that range physiognomically from herbaceous to forest (Melo Júnior & Boeger, 2016; Melo Júnior & Boeger, 2017). In this sense, we acknowledge there are several studies, carried out in southern Brazil, which attempted to better understand the strategies used by the *restinga* vegetation in response to the extreme conditions to which they are subjected. Examples of this type of study include: Boeger & Gluzezak, 2006; Bachtold and Melo Júnior, 2015; Todorovski *et al.*, 2015; Melo Júnior & Boeger, 2016; Silva and Melo Júnior, 2016; Liberato & Melo Júnior, 2016*;* Amorim & Melo Júnior, 2016; Matilde-Silva and Melo Júnior, 2017; Melo Júnior & Boeger, 2017; and Amorim & Melo Júnior, 2017.

The aim of this study was to increase ecological knowledge about *S. viscosa* (L.) Sw. through the evaluation of plastic responses of this plant to different environmental conditions of *restinga* formations on the coastal plain of Santa Catarina state, southern Brazil. The hypotheses of the study were: I) the limiting conditions of different *restinga* environments cause the expression of different phenotypes in *Stylosanthes viscosa* (L.) Sw.; and II) populations of *Stylosanthes viscosa* (L.) Sw. that inhabit herbaceous *restinga* will be more xeromorphic than those of shrub-arboreal *restinga*.

Materials and Methods

Study area: The study was carried out in Acaraí State Park (PEA), an integral protection conservation unit of the municipality of São Francisco do Sul, located on the northeast coast of Santa Catarina state, Brazil (26º17'S, 48º33'W), as shown in (Fig. 1.) This conservation unit is considered to be the largest continuous *restinga* remnant in the state, and is classified as an extremely high priority area for the biodiversity conservation (Probio, 2003). The climate is heavily influenced by sea moisture, being classified as mesothermic, with hot summers and without a defined dry season (Cfa of Köeppen). Average rainfall is ca. 1,874 mm per year (Knie, 2002). Annual average temperature is 21.2°C, January being the warmest month with a temperature around 25.1°C, and July being the coldest, with a temperature of 17.3°C (Climate-Data, 2017). The relief is characterized by a coastal plain with 6,667 ha of the area covered predominantly by compartmentalized vegetation in herbaceous, shrub, shrub-arboreal and transitional forest (Melo Júnior & Boeger, 2015), as well as other less representative formations, such as submontane forest, floodplains and mangroves (Fatma, 2008).

Complements

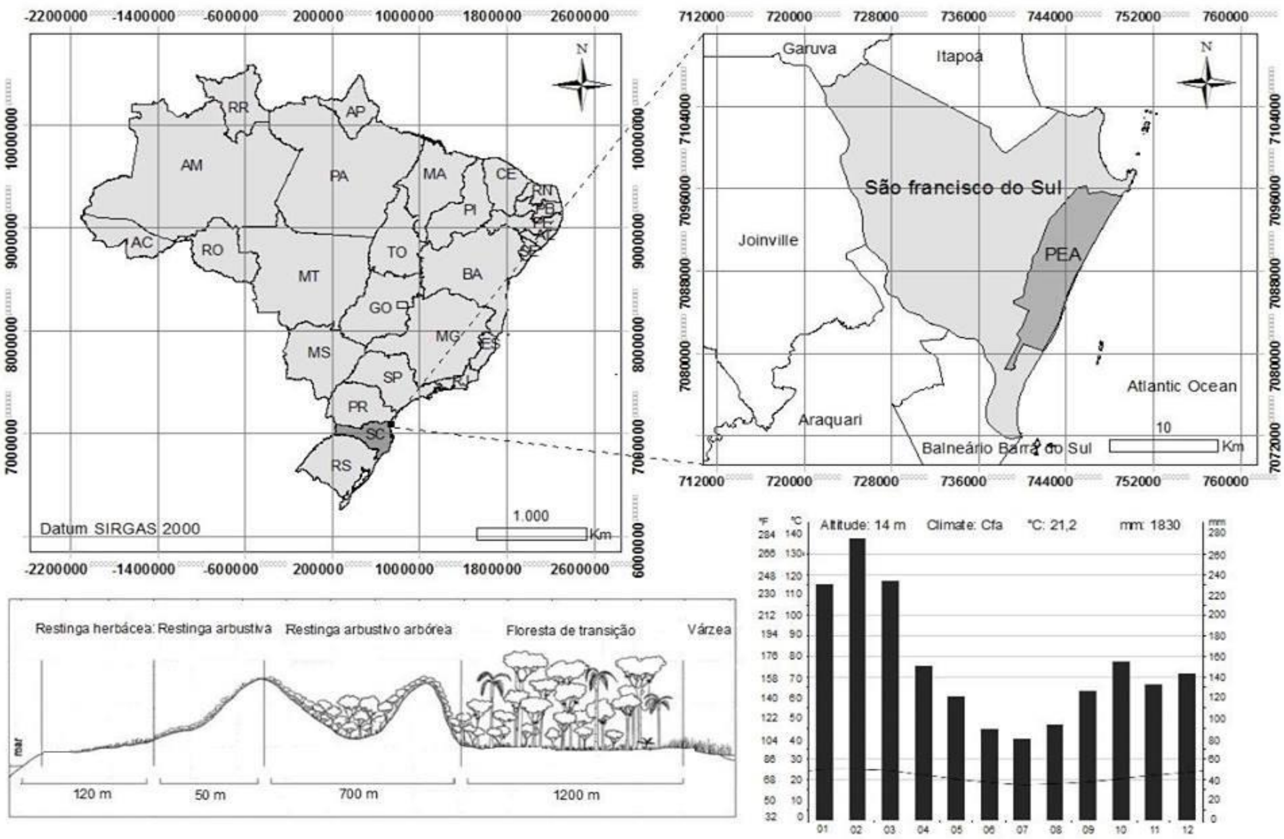

Fig. 1. Location of the study area, plus respective climatic and spatial characteristics of the *restinga* at Parque Estadual Acaraí, São Francisco do Sul, Santa Catarina, Brazil.

Collection and processing of biological material: Formations of herbaceous *restinga* and shrub-arboreal restinga within the park were selected as the study areas for *Stylosanthes viscosa* (L.) Sw. populations. Ten individuals were sampled from each area. From each individual, 10 completely expanded sun leaves devoided of lesions and fixed to the apex of branches at the 3rd and 4th nodes were collected for the evaluation of functional morphological and anatomical attributes. Recorded plant architectural attributes for each sample were plant height (m) and stem diameter (cm), both recorded with the aid of a tape measure during fieldwork. Several leaf attributes were evaluated. Fresh mass (g) was obtained from leaves saturated in water for 12 hours, then weighted in analytical balance (SHIMADZU AUY220). Dry mass (g) was obtained from leaves dried in an air circulation oven (MICROEM EL-003) at 70ºC for 72 hours then weighted in analytical balance (SHIMADZU AUY220). These measures were used to obtain leaf dry matter content (mg.g-1), given by the ratio between the dry mass and the saturated fresh leaf mass. Leaf area (cm^2) was obtained from scanned images created with a desktop scanner coupled to Sigma Scan Pro software (version 5.0, SPSS Inc., Chicago IL, USA). Specific leaf area (cm^2 / g-^{1}) was calculated as the ratio between leaf area and dry mass (Witkowski & Lamont, 1991). Degree of succulence (g.cm-2) was calculated as the ratio between water content (fresh mass - dry mass) and leaf area.

Leaves destined to anatomical studies were fixed in 70% FAA solution (Johansen, 1940) during fieldwork. Considered anatomical attributes were: thickness of foliar tissues (epidermis of adaxial and abaxial faces, including the cuticle, palisade parenchyma, sponge parenchyma, hypodermis and total limb thickness, all measured in micrometric scale); stomatal density (n / mm^2); and density of trichomes (n / mm^2). Tissue biometry was taken from semi-permanent histological slides, which were manually obtained with the aid of a disposable razor and mounted in glycerinated water (Kraus & Arduim, 1997). The middle third of the central leaflet was chosen for tissue sampling. The Dino-Eye software and an Olympus CX 200 photomicroscope were used in the process.

Stomatal and trichome densities were measured under an Olympus CBB light microscope with a coupled light chamber. Thirty fields of 1mm^2 were counted, adopting the technique of modeling the epidermis in the region of the middle third of the leaf with colorless synthetic nail polish (Segatto, 2004). Photomicrographs were obtained by transmitted light optical microscopy for comparative characterization of the foliar anatomy of the two populations of *S. viscosa* (L.) Sw.

Determination of environmental variables: Environmental variables regarding soil mineral nutrition, water availability in the soil, and light radiation on the plants were measured. The soil analysis followed standard methodology recommended by Embrapa (2013). Soil from the two analyzed formations were collected by means of opening ten 15 cm-deep pits that, after homogenization, resulted in two composite samples.

Soil chemical analysis was performed by the Soil Analysis Laboratory of the Agricultural Research and Rural Extension Company of Santa Catarina (EPAGRI). Soil water availability was determined by the gravimetric moisture protocol, which evaluates the difference in mass of freshly collected soil and soil dried in the greenhouse for 72 hours at 105 ºC (Embrapa, 2013). Ten samples were collected from each formation in the vicinity of the sampled plants.

For luminous radiation, photosynthetically active radiation (PAR) was determined from 10 measurements per individual taken at the crown of the plant with the use of a digital luximeter (Li-250A LICOR, USA).

Statistical treatment: Mean values and their respective standard deviations were calculated for all the morpho-anatomical attributes measured on individuals of the *S. viscosa* (L.) Sw. populations of the studied *restinga* formations. After testing for normality, means were compared by Student's t-test with a significance level of 5% (Zar, 1999) using the R software (Borcard *et al.*, 2011). Principal Components Analysis (PCA) was performed in order to verify which environmental variables exert the greatest influence on studied functional attributes. The relationship between environmental variables indicated by the PCA and the structural responses detected in *S. viscosa* (L.) Sw. was verified by linear regression analysis (Legendre & Legendre, 1998) also using the R software. For each attribute, the index of phenotypic plasticity (IPP) was calculated by IPP = (maximum mean value) – (minimum mean value) / (maximum mean value) (Valladares *et al.*, 2006).

Results

As shown in Table 1, chemical analysis revealed that soil of both *restinga* formations have low acidity. The soil of the herbaceous *restinga* had a higher content of phosphorus (P) than the shrub-arboreal restinga, but the latter had higher potassium (K) content. There was no difference between the formations regarding calcium (Ca) content. Base saturation (V) was higher for the soil of the herbaceous formation. Sum of bases (SB), cation exchange capacity (CEC), real acidity (H + Al) that determined the effective CEC of the soil, as well as organic matter content (OM), were higher in the shrub-arboreal restinga formation. Thus, the soil of the shrub-arboreal formation of restinga is potentially more fertile than the soil of the herbaceous formation.

Soil water availability was three-times higher in the shrub-arboreal *restinga* than in the herbaceous *resting*, as shown in (Fig. 2.) On the other hand, the photosynthetically active radiation was higher in the herbaceous *resting*, as shown in Table 1. Together, the first two axes of the PCA explain 95% of the data variation. Organic matter (OM) content was the variable associated with the first principal component, and it had a greater influence on morpho-anatomical attributes. Potassium (K) content was associated with the second principal component, as shown in Table 1. Linear regression analysis showed that organic matter (OM) was most positively correlated with plant height ($F_{1,298}$= 4.918, R^2= 0.89, p<0.001), leaf area ($F_{1.298}$ = 2.352, R^2= 0.79 p<0.001), and leaf dry mass ($F_{1.298}$= 1.132, R^2= 0.62, p<0.001).

Table 1. Mean values of nutritional soil variables, water availability and photosynthetically active functional radiation in *restinga* formations inhabited by *Stylosanthes viscosa* (L.) Sw. (Fabaceae) of Parque Estadual Acaraí, São Francisco do Sul, Santa Catarina, Brazil. Correlation between attributes represented by components 1 (PCA1) and 2 (PCA2) obtained by Principal Component Analysis (PCA).

Environmental variables	Formation of *restinga*		Principal Component	
	Herbaceous	Shrub-arboreal	PCA1	PCA2
pH	5.6 ± 0.008^{a}	5.1 ± 0.008^{b}	0.2897	0.02626
P (mg/dm^3)	6.09 ± 0.08^{a}	2.60 ± 0.008^{b}	0.2897	-0.01291
K (mg/dm^3)	14.09 ± 0.08^{b}	28.09 ± 0.08^{a}	0.29006	-0.98505
SB	0.43 ± 0.008^{b}	0.54 ± 0.008^{a}	0.29006	0.01848
CEC (%)	1.23 ± 0.008^{b}	2.14 ± 0.008^{a}	0.29002	0.00585
OM (%)	0.1± 0.008^{a}	0.8 ± 0.008^{b}	0.29009	0.01462
V (%)	34.82 ± 0.008^{a}	25.28 ±0.008^{b}	0.29	0.05002
Ca (mg/dm^3)	0.3 ± 0.007^{a}	0.3 ± 0.008^{a}	0.00761	-0.13547
Al (cmolc/dm^3)	0.0 ± 0.00^{b}	0.2 ± 0.008^{a}	0.28998	0.00293
Mg (cmolc/dm^3)	0.1 ± 0.008^{b}	0.2 ± 0.008^{a}	0.28731	-0.05208
H + Al (cmolc/dm^3)	0.8 ± 0.008^{b}	1.6 ± 0.008^{a}	0.29008	-0.05901
Soil water availability	4.81 ± 0.08^{b}	14.19 ± 0.08^{a}	0.29001	0.01891
Photosynthetically active radiation	1512.92 ± 4.60^{a}	608.61 ±236.45^{b}	0.27678	-0.02459
Variance explained by the components			3,445	1,014
Percentage of total variance explained (%)			91	95

Different letters in the same line indicate statistical difference at the $p<0.05$ level

Table 2. Mean values and respective standard deviations of architectural and leaf functional traits of *Stylosanthes viscosa* (L.) Sw. (Fabaceae) in herbaceous shrub-tree *restinga* from Parque Estadual Acaraí, São Francisco do Sul, Santa Catarina, Brazil.

Architectural and morpho-anatomical attributes	Formation of *resting*	
	Herbaceous	Shrub-arboreal
Individual height (m)	5.64 ± 2.55^{b}	49.04 ± 10.37^{a}
Stem basal diameter (cm)	0.34 ± 0.11^{b}	0.57 ± 0.14^{a}
Fresh mass (g)	0.012 ± 0.008^{a}	0.038 ± 0.01^{b}
Dry mass (g)	0.003 ± 0.01^{b}	0.01 ± 0.003^{a}
Leaf area (cm^2)	0.25 ± 0.05^{a}	1.04 ± 0.27^{b}
Specific leaf area (cm^2.g^{-1})	75.49 ± 20.24^{b}	107.62 ± 21.57^{a}
Dry matter content (mg.g^{-1})	3.65 ± 2.55^{b}	3.85 ± 0.66^{a}
Degree of succulence (g.cm^{-2})	0.013 ± 0.02^{b}	0.017 ± 0.002^{a}
Abaxial epidermis thickness (µm)	16.51 ± 3.46^{b}	20.86 ± 4.43^{a}
Adaxial epidermis thickness (µm)	16.14 ± 2.94^{b}	24.22 ± 2.26^{a}
Palisade parenchyma thickness (µm)	94.79 ± 13.01^{b}	108.63 ± 12.53^{a}
Sponge parenchyma thickness (µm)	48.11 ± 6.05^{b}	63.05 ± 7.79^{a}
Palisade / Sponge relationship	2:1	1.7:1
Abaxial hipodermis thickness (µm)	19.44 ± 3.77^{b}	25.10 ± 8.29^{a}
Adaxial hipodermis thickness (µm)	19.71 ± 4.50^{b}	26.57 ± 10.22^{a}
Mesophyll thickness (µm)	214.72 ± 17.15^{b}	268.46 ± 27.35^{a}
Stomatal density (µm)	42.36 ± 6.62^{a}	52.25 ± 8.68^{b}
Trichome density (µm)	18.46 ± 7.86^{b}	30.11 ± 7.24^{a}

Different letters in the same line indicate statistical difference at the $p<0.05$ level

In general, mean values of morpho-anatomical attributes varied significantly among populations of *S. viscosa* (L.) Sw. and higher mean values were observed for shrub-arboreal restinga, as shown in Figure 2. Among the evaluated attributes, morphological variables exhibited greater variation between formations, with emphasis on plant height (eight-times greater) and leaf area (four-times greater), as shown in Table 2.

Plants of the herbaceous restinga showed hypodermis present in the leaves, epidermis with thick cuticle, lower foliar area, lower specific leaf area, high succulence, and a more developed palisade than sponge parenchyma (2:1 ratio), as shown in Figure 2. Plants of the shrub-arboreal restinga had higher densities of stomata and trichomes.

The IPP showed that *S. viscosa* (L.) Sw. is highly plastic regarding nearly all evaluated morphological attributes, as shown in Table 3, with emphasis on plant height, stem diameter, leaf area, fresh mass, and dry mass. On the other hand, anatomical attributes exhibited little variation and, consequently, had low potential plasticity. The mean IPP value for morphological attributes was 0.53, while for anatomical attributes it was 0.23.

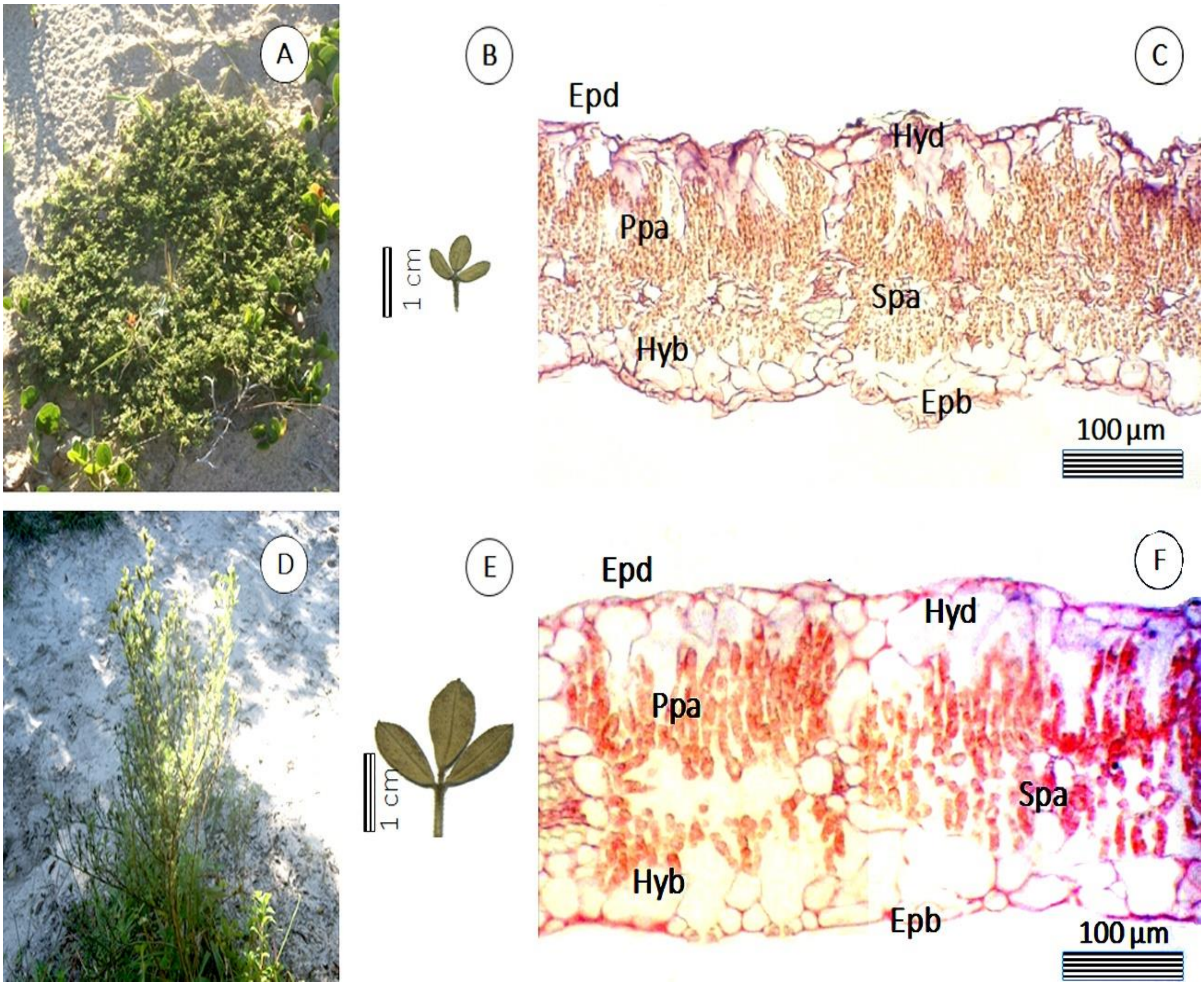

Fig 2. Foliar traits of *Stylosanthes viscosa* (L.) Sw. (Fabaceae) in herbaceous (A, B and C) and shrub-tree *restinga* (D, E and F) formations. Legend: A and D: general view of plant architecture. B and E: external leaf morphology. C and F: leaf anatomical tissues in cross section. Epd: adaxial surface epidermis. Epb: abaxial surface epidermis. Hyd: adaxial hypodermis. Hyb: abaxial hypodermis. Ppa: palisade parenchyma. Spa: spongy parenchyma.

Table 3. Phenotipic Plasticity Index (PPI) of architectural and leaf functional traits of *Stylosanthes viscosa* (L.) Sw. (Fabaceae) of the *restinga* from Parque Estadual Acaraí, São Francisco do Sul, Santa Catarina, Brazil.

Architectural and morpho-anatomical attributes	IPP
Individual height (m)	0.71
Stem basal diameter (cm)	0.88
Fresh mass (g)	0.69
Dry mass (g)	0.65
Leaf area (cm²)	0.74
Specific leaf area (cm².g^{-1})	0.29
Dry matter content (mg.g^{-1})	0.12
Degree of succulence (g.cm^{-2})	0.16
Abaxial epidermis thickness (µm)	0.20
Adaxial epidermis thickness (µm)	0.33
Palisade parenchyma thickness (µm)	0.13
Sponge parenchyma thickness (µm)	0.16
Palisade / Sponge relationship	0.22
Abaxial hipodermis thickness (µm)	0.25
Adaxial hipodermis thickness (µm)	0.16
Mesophyll thickness (µm)	0.23
Stomatal density (µm)	0.38

Discussion

Low soil acidity of the two studied *restinga* formations are consistent with the expected trend for tropical coastal environments due to the recent soil genesis (Casagrande, 2003). In addition, soils of the two areas can be considered to be dystrophic (SB <50), indicating low fertility and low exchangeable bases (Embrapa, 2010), which limit plant growth. Another important finding regarding the soil was phosphorus deficiency (P). This is common for low fertility soils (Embrapa, 2006) and it has great influence on plant growth and development, especially in acid soils of tropical and subtropical regions (Silva & Delatorre, 2009). It also may explain the limited development of the herbaceous restinga plants in comparison to those plants inhabiting the shrub-arboreal restinga. The shrub-arboreal *restinga* also possessed a higher content of potassium (K) (50% higher), which may explain the greater dry mass observed in plants of this area, since this nutrient plays an important role in energy metabolism (Silva & Delatorre, 2009), and consequently dry mass production (Andrade *et al.*, 2010).

Organic matter has a strong influence on soil fertility, both through ion exchange capacity and retention of organic nutrients forms, thus favoring nutrient absorption and easy substitution between cations in solution (Guariguata & Ostertag, 2001). Thefore, it seems likely that better soil nutritional conditions in the shrub-arboreal *restinga* favored plants growth therein, mainly due to the greater amount of organic matter and availability of P, Ca and K for plant allocation. In tropical and subtropical soils, there is a close relationship between OM and the physical, chemical and biological characteristics of the soil (Ciotta *et al.*, 2003), accounting for 30% to 65% of the CEC of mineral soils, and more than 50% of CEC of sandy and organic soils (Mattos *et al.*, 1996). Soil of the shrub-arboreal restinga showed greater OM, and thus had greater cation exchange capacity, than soil of the herbaceous restinga, which likely explains the greater development of plants in the former.

The positive relationship of OM, obtained via PCA, and its correlation with the functional attributes of *S. viscosa* (L.) Sw., indicate its important influence on plant growth, specifically plant height, stem diameter, leaf area, fresh mass, and dry mass. Therefore, greater investment in growth in shrub-arboreal *restinga* correlates with the greater nutritional availability of the soil.

The positive relationship between higher nutritional availability and the general architecture of *S. viscosa* (L.) Sw. is demonstrated by the values for plant height and stem diameter, in which higher OM values were the higher values of these attributes (F= 4918, gl= 1.598, R^2= 0.89, p<0.0001 and F= 486.2, gl= 1.598, R^2= 0.50, p<0.0001, respectively). The positive relationship between plant height and OM content can be explained by the greater availability of exchangeable cations, which improves soil fertility. Working with different sources of OM, Lima *et al.,* (2011) observed an increase in height of individual plants of *Jatropha curcas* L. (Euphorbiaceae), with increased fertility. Values obtained for stem diameter corroborate those found by Amorim & Melo Jr (2017), who observed higher values in phytophysiognomies with higher OM.

Leaf area is an important attribute, as it allows inferences about water economy, given that leaves carry out transpiration processes responsible for gas exchange with the environment (Pereira *et al.*, 1997). Leaf area was also positively related with OM availability (F= 2352, gl= 1.598, R^2= 0.80, p<0.0001), corroborating data obtained by Liberato & Melo Jr. (2016) and Amorim & Melo Jr. (2017). These two studies observed a greater development of vegetative structures in *restinga* plants when exposed to higher concentrations of OM. Mean values of dry and fresh mass (F= 1132, gl= 1.598, R^2= 0.65, p<0.0001; and F= 789, gl= 1.598, R^2= 0.57, p<0.0001) corroborate data obtained by Todorovski *et al.,* (2015) and Matilde-Silva & Melo Júnior (2017). These studies report a directly proportional relationship between dry and fresh mass and the increase of aerial structures in in restinga plants grown on more fertile soils.

Together, the other morpho-anatomical attributes show the existence of a clearly defined xeromorphic pattern in *S. viscosa* (L.) Sw. plants grown in the herbaceous *restinga*. A number of studies have shown that plants living in sandy soils have leaves with xeromorphic characteristics (Turner *et al.*, 1995; Medina *et al.*, 1990), represented by thicker leaves with a coriaceous texture, thick cuticle, palisade parenchyma, sclerenchyma and hypodermis (Boeger & Wisniewski, 2003). Thus, the observation of these functional characteristics in the population of *S. viscosa* (L.) Sw. from herbaceous *restinga* confirms the hypothesis that the more restrictive environmental conditions in this formation produce a higher degree of xeromorphism when compared to plants of the shrub-arboreal formation.

The pattern of morphological attributes indicates that plants of the shrub-arboreal *restinga* population have a greater investment in photossintetic production, as represented by the greater amount of photosynthetic tissue, which is probably due to the greater availability of resources (Vendramini *et al.*, 2002). Plants of the herbaceous restinga population, on the other hand, show greater investment in mechanical tissue, due to the water and nutrient availability of the soil (Turner, 1994), in order to optimize the use of available resources.

Specific leaf area (SLA) is an important ecological predictor for describing leaf biomass allocation, reflecting the trade-off between rapid biomass production and efficient nutrient conservation (Poorter & Garnier, 1999). The plants of herbaceous restinga had lower SLA than shrub-arboreal *restinga* plants, which may represent a resource conservation strategy, since leaves with lower SLA tend to have greater longevity (Agrawal & Fishbein, 2006). These observations are consistent with patterns expected for xeromorphic environments. Xeromorphic characteristics are advantageous for plants in environments such as restinga, because they reduce water loss, eliminate light excess and decrease the action of herbivorous insects (Matilde-Silva *et al.*, 2017).

Mesophyll thickness, although varying little between the different restinga formations, can signal a secondary function related to defense against herbivory due to a greater carbon supply in the soil that is transformed into compounds for leaf protection (Sanches *et al.*, 2005). Thus, the greater leaf mesophyll thickness in plants of the shrub-arboreal restinga is likely to compensate for the lower investment in mechanical tissues, which can serve to hinder insect attack (Corrêa, 2007; Guerra *et al.*, 2010), consequently promoting greater leaf longevity.

Stomata distribution and density vary among species (Al Afas *et al.*, 2006) and environmental conditions (Neejad & Van Meeteren, 2005). In the present study, greater stomatal density in plants of shrub-arboreal restinga may be related to their greater investment in photosynthesis. Additionally, higher trichome density in plants of shrub-arboreal restinga can aid greater investment in photosynthesis by reflecting excessive sunlight and maintaining longer periods of gas exchange. Secondarily, it can also inhibit loss of photosynthetic leaf area due to herbivory, considering that trichomes are able to block or hinder access to the limb or foliage nervures (Woodman, 1991; Abdala-Roberts, 2005).

Values of phenotypic plasticity index that are higher for morphological attributes, than for anatomical attributes, indicate that *S. viscosa* (L.) Sw. has greater plasticity in attributes related to individual growth and leaf size increase, and therefore serve to acclimate individuals to different environments in response to varying conditions of edaphic nutrition and light radiation.

References

Abdala-Roberts, L.V. and P. Tabla. 2005. Artificial defoliation induces trichome production in the shrub *Cnidoscolus aconifolius* (Euphorbiaceae). *Biotropica*, 37: 251-257.

Agrawal, A.A and M. Fishbein. 2006. Plant defense syndromes. *Ecol*., 87: 132-149.

Al Afas, N., N. Marron and R. Ceulemans. 2006. Clonal variation in stomatal characteristics related to biomass production of 12 Poplar (Populus) clones in a short rotation coppice culture. *Environ. Exp. Bot*., 58: 279-286.

Américo, F.K.A 2015. Germinação e armazenamento de sementes de *Stylosanthes* sw. em diferentes ambientes. Website: http://tede.uefs.br/162/2/0fabianaKrico [accessed 10 November 2016]. Feira de Santana (BA): Universidade Estadual de Feira de Santana; 50p.

Amorim, M.W and J.C.F. Melo Júnior. 2016. Plasticidade morfológica de Myrcia splendens (S.w) CD. (Myrtaceae) ocorrente em Mata Atlântica e Cerrado. *Iheringia*, 71:261-268.

Amorim, M.W and J.C.F. Melo Júnior. 2017. Plasticidade morfoanatômica foliar de *Tibouchina Clavata* (Pers.) Wurdack (Melastomataceae) ocorrente em duas formações de Restinga. *Rodriguésia*, 68: 545-555.

Andrade, M.J.B. 2010. Cultura do Feijoeiro. In: Scorsolini-Comin, F. (Org.). Aperfeiçoamento em Agronegócio. *INEPAD*, 2: 48-62.

Andrade, R.P and C.T. Karia. 2000. O uso de *Stylosanthes* em pastagens no Brasil. In: Simpósio de Forragicultura e Pastagem. *Lavras*, 273-309.

Anonymous. 2014. International Plant Names Index. 2014. Website: http://www.ipni.org/ [acessed 10 January 2017].

Bachtold, B.A and J.C.F. Melo Júnior. 2015. Plasticidade morfológica de *Calophyllum brasiliense* Camb. (Calophyllaceae) em duas formações de restinga no sul do Brasil. *Acta Biologica Catarinense*, 2: 21-32.

Boeger, M.R.T and C. Wisniewski. 2003. Comparação da morfologia foliar de espécies arbóreas de três estádios sucessionais distintos de floresta ombrófila densa (Floresta Atlântica) no sul do Brasil. *Revista Brasileira de Botânica*, 26: 61-72.

Boeger, M.R.T and R.M. Gluzezak. 2006. Adaptações estruturais de sete espécies de plantas para as condições ambientais da área de dunas de Santa Catarina, Brasil. *Iheringia*, 61: 73-82.

Borcard, D. F. Gillet and P. Legendre. 2011. Numerical Ecology with R. New York, Dordrecht London Heidelberg.

Bradshaw, A.D. (Ed.). 1965. Evolutionary significance of phenotypic plasticity in plants. In: Caspary EM, Thoday JM Advances in Genetics. *Academic Press*: pp. 115-155.

Casagrande, J.C., D.A. Santos. R.M. Reis-Duarte. 2003. O desenvolvimento do sistema radicular na Floresta de Restinga do Parque Estadual da Ilha Anchieta, Ubatuba, SP. 54º Congresso Nacional de Botânica e 3ª Reunião Amazônica de Botânica, Belém, SBB, 13-18 jul, Anais.

Ciotta, M.N., C. Bayer, S.M.V. Fontoura, P.R. Ernani and J.A Albuquerque. 2003. Matéria orgânica e aumento da capacidade de troca de cátions em solo com argila de atividade baixa sob plantio direto. *Ciência Rural*, 33: 1161- 1664.

Climate-Data. 2017. Clima: São Francisco do Sul. Website: http://pt.climate-data.org/location/28141/ [accessed 10 November 2016].

Corrêa, P. 2007. Defesas foliares em resposta à herbivoria em espécies lenhosas de restinga, Ipojuca-PE. Website: http://ww2.pgb.ufrpe.br/br/defesas-foliares-em-resposta-herbivoria-restingaipojuca-pe [accessed 18 November 2016].

Costa, N.M.S. 2006. Revisão do gênero *Stylosanthes* Sw. Website: www.bdpa.cnptia. embrapa.br/ costa./ 20nm.de.%%20 Facets =autoria [accessed 04 February 2017].

Embrapa. 2013. Sistema brasileiro de classificação de solos. (1rd Ed). Brasília, Brasil.

Embrapa. 2006. Centro Nacional de Pesquisa de Solos. Sistema Brasileiro de Classificação de Solos, EMBRAPA Solos. (2rd Ed) Brasília, Brasil.

Embrapa. 2010. Conceitos de fertilidade do solo e manejo adequado para as regiões tropicais. Boletim de Pesquisa e Desenvolvimento. (1rd Ed). Campinas, Brasil.

Fatma. 2008. Plano de manejo do Parque Estadual do Acaraí. FATMA, Curitiba.

Forzza, R.C., J.F.A. Baumgratz, A. Costa, M. Hopkins, P.M. Leitman, L.G. Lohmann, G. Martinelli, M.P. Morim, M.A.N. Coelho and A.L. Peixoto. 2010. Introdução: As angiospermas do Brasil. 1: 78-89.

Guariguata, M.R. and R. Ostertag. 2001. Neotropical Secondary Forest Succession: changes in structural and functional characteristics. *Forest Ecol. Manag*., 148: 185-206.

Guerra, P.C, J. Becerra and E. Gianoli. 2010. Explaining differential herbivory in sun and shade: the case of *Aristotelia chilensis* saplings. *Arthropod-Plant Interations*, 4: 229- 235.

Johansen, D.A. 1940. Plant microtechnique. *McGraw-Hill*, 423.

Knie, J.L.W. 2002. Atlas ambiental da região de Joinville: complexo hídrico da Baía da Babitonga. (2rd Ed). Florianópolis, Brasil.

Kraus, J.E. and M. Arduin. 1997. Manual básico de métodos em morfologia vegetal. Universidade Federal Rural do Rio de Janeiro, *Seropédica*: 198.

Legendre, P. and L. Legendre. 1998. Numerical ecology. (2rd Ed).. Netherlands: Elsevier Science.

Lewis, G.P. 1987. Legumes of Bahia. Royal Botanic Gardens Kew. *Great Britaisn*: 369.

Liberato, I. and J.C.F. Melo Júnior. 2016. Morphological plasticity of *Ilex theezans* Mart. ex Reissek (Aquifoliaceae) in two restinga vegetation of Santa Catarina coastal plain. *Acta Biológica Catarinense*, 3: 91-101.

Lima, R.L.S., L.S. Severino, G.B. Ferreira, V. Sofiatti, L.R. Sampaio and N.E.M. Beltrão. 2011. Casca de mamona associada a quatro fontes de matéria orgânica para a produção de mudas de pinhão-manso. *Rev. Ceres,* 58: 232-237.

Matilde- Silva, M. and J.C.F. Melo Júnior. 2017. Plasticidade da folha e lenho de cinco espécies lenhosas em duas áreas de restinga no Sul do Brasil. *Iheringea*, 72(2): 173-180.

Matilde-Silva, M and J.C.F. Melo Júnior. 2016. Composição florística e estrutural de uma comunidade herbáceo-arbustiva de restinga em Balneário Barra do Sul, Santa Catarina. *R. Bras. Bioci*., 14: 207-214.

Matilde-Silva, M., M..R.T Boeger, J.C.F Melo Júnior and B.F.S. Santos. 2017. Antiherbivory defense mechanisms along an environmental gradient in restinga. *Acta. Bot. bras.,* 1-14.

Mattos, A.T., M.P.F, Fontes, C.P, Jordão and L.M, Costa. 1996. Mobilidade e formas de retenção de metais pesados em adsorção de cobre em solos 489 latossolo vermelho-amarelo. *Rev. Brasil. Ciênc. Solo,* 20: 379-386.

Mc Lachlan, A. and A. Brown. 2006. The ecology of sandy shores. Academic: 373.

Medina, E., V. Garcia and E. Cuevas. 1990. Sclerophylly and oligotrophic environments: relationships between leaf, structure, mineral nutrient content, and drought resistance in tropical rain forest of the upper Rio Negro region. *Biotropica*, 22: 51-64.

Melo Júnior, J.C.F. and M.R.T. Boeger. 2016. Leaf traits and plastic potential of plant species in a light-edaphic gradient from a restinga in southern Brazil. *Acta. Biol. Colomb*., 21: 51-62.

Melo Júnior, J.C.F. and M.R.T. Boeger. 2015. Riqueza, estrutura e interações edáficas em um gradiente de restinga do Parque Estadual do Acaraí, Estado de Santa Catarina, Brasil. *Hoehnea*, 42: 207-232.

Melo Júnior, J.C.F. and M.R.T. Boeger. 2017. Functional Traits of Dominant Plant Species of the Brazilian Sandy Coastal Plain. *Int. J. Curr. Res.,* 9: 45585-45593.

Miranda, T.M. and N. Hanazaki. 2008. Conhecimento e uso de recursos vegetais de restinga por comunidades das ilhas do Cardoso (SP) e de Santa Catarina (SC), Brasil. *Acta. Bot. Bras*., 22: 203-205.

Neejad, A.R. and U. Van Meeteren. 2005. Stomatal response characteristics of *Tradescantia virginiana* grown at high relative air humidity. *Physiol. Plantarum*, 125: 324-332.

Neri, A.V., M.P. Soares, J.A.A.M. Neto and L.E. Dias. 2011. Espécies de Cerrado com potencial para recuperação de áreas degradadas por mineração de ouro, Paracatu MG. *Revista Árvore,* 35: 907-918.

Pereira, A.R., N.A. Villa Nova and G.C. Sediyama. 1997. Evapotranspiração. *Fealq*: 183.

Poorter, H. and E. Garnier. 1999. Ecological significance of inherent variation in relative growth rate and its components. In: *Handbook of functional plant ecology*, (Eds.): F. Pugnaire & F. Valladares. *CRC Press*: 81-120.

Price, T.D., A. Qvarnstrom and D.E. Irwin. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. B*., 270: 1432-1440.

Probio. 2003. Áreas prioritárias para a conservação, utilização sustentável e repartição de benefícios da biodiversidade brasileira. Brasília: Ministério do Meio Ambiente.

Queiroz, L.P. 2009. Leguminosas da Caatinga. *UEFS*: 467.

Ramalho, M. and J.F. Rosa. 2010. Ecological interaction between the tiny keel flowers of *Stylosanthes viscosa* Sw. (Faboideae) and the large bee *Xylocopa* (Neoxylocopa) *cearensis* Ducke, 1910 (Apoidea, Hymenoptera), in tropical sand dune. *Biota Neotrop*., 10.

Sanches, L., G.S. Suli, N. Prinate-Filho, G. Vourlitis and J.S. Nogueira. 2005. Índice de área foliar em floresta de transição Amazônia Cerrado. *Rev. Ciência Nat*., 1: 37-40.

Sawkins, M.C., B.L. Maass, B.C. Pengelly, H.J. Newbury, B.V. Ford-Lloyd, N. Maxted. and R. Smith. 2001. Geographical patterns of genetic variation in two species of *Stylosanthes* Sw. using amplified fragment length polymorphism. *Mol. Ecol*., 10: 1947-1958.

Scarano, F.R., H.M. Duarte, K.T. Ribeiro, P.J.F.P. Rodrigues, E.M.B. Barcellos, A.C. Franco, J, Brulfert, E, Deleâens and U, Luèttge. 2001. Four sites with contrasting environmental stress in southeastern Brazil: relations of species, life form diversity, and geographical distribution to ecophysiological parameters. *Bot. J. Linn. Soc.*, 136: 345-364.

Scarano, F.R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats to the brazilian atlantic rainforest. *Ann. Bot.,* 90: 517-524.

Segatto, F.B., D.A. Bisognin, M. Benedetti, L.C. Costa, M.V. Rampelotto and F.T. Nicoloso. 2004. Técnica para o estudo da anatomia da epiderme foliar de batata. Ciênc. Rural, 34: 1597-1601.

Silva, A.A. and C.A. Delatorre. 2009. Root architecture modification in response to phosphorus and nitrogen availability. *R. Ciênc. Agrovet*., 8: 152-163.

Silva, K.R. and J.C.F. Melo Júnior and M.R.T. Boeger. 2016. Variações fenotípicas em *Andira fraxinifolia* Benth. (Fabaceae) em duas fitofisionomias de Restinga. *Hoehnea*, 43: 237-245.

Souza, V.C. and H. Lorenzi. 2012. Botânica sistemática: guia ilustrado para identificação das famílias de Angiospermas da flora brasileira, baseado na APG III. (3rd Ed). Instituto Plantarum, Nova Odessa, Brasil.

Todoroviski, E.C.D., J.C.F. Melo Júnior, M.W. Amorim and M. Matilde-Silva. 2015. Potencial plástico de *Nectandra oppositifolia* Nees. (Lauraceae) em fisionomias de floresta ombrófila densa e restinga. *Natureza on line*, 13: 70-76.

Turner, I.M. 1994. A quantitative analysis of leaf form in woody plants from the word's major brodleaved forest types. *J. Biogeograph.*, 21:413-419.

Valladares, F., D. Sanches-Gomez and M.A. Zavala. 2006. Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *J. Ecol.*, 94: 1103-1116.

Vendramini, F., S. Díaz, D.E. Gurvich, P.J. Wilson, K. Thompson and J.G. Hodgson. 2002. Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytol.*, 154: 147-157.

Witkowski, E.T.F. and B.B. Lamont. 1991. Leaf specific mass confounds leaf density and thickness. *Oecologia*., 88: 486-493.

Woodman, R.L. and G.W. Fernandes. 1991. Differential mechanical defense-herbivory, evapotranspiration, and leaf-hairs. *Oikos.*, 60: 11-19.

Zar, J.H. 1999. Biostatistical analysis. *Upper Saddle River*, 663.

(Received for publication 4 August 2017)