

Leaf morpho-anatomical and physiological plasticity of two *Vriesea* species (*Bromeliaceae*) in Atlantic Coast restingas (Brazil)**Plasticidade morfoanatômica e fisiológica foliar de duas espécies de *Vriesea* (*Bromeliaceae*) em restingas da costa atlântica (Brasil)**

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ABSTRACT

Environmental variations may lead to structural and functional responses among Bromeliaceae and knowledge of these responses can allow better understanding about ecological processes and more effective planning of handling and conservation programs in protected areas. Because of the diverse habitats occupied by *Vriesea*, this study aimed at assessing the morpho-anatomical plasticity and photosynthetic pigment contents in *V. neoglutinosa* and *V. procera* occurring in the Open *Clusia* and Dry Forest formations of a restinga vegetation area in Espírito Santo State, Brazil. In general, plants in Dry Forest formation showed higher growth measurements and lower leaf inclination. In Open *Clusia* formation, both species showed leaves with higher scale density, whereas *V. neoglutinosa* also showed higher stomatal density. The chlorenchyma thickness of *V. procera* was greater in Dry Forest. We did not find differences in leaf blade thickness and water-storage parenchyma for both species between the two environments. We found abundant oil substances in guard and subsidiary cells of Open *Clusia* samples. In both species, individuals from the Dry Forest formation showed higher

chlorophyll *a* and *b* and total chlorophyll contents, whereas *V. neoglutinosa* samples from the Open *Clusia* formation showed higher carotenoid contents. Of the characteristics assessed, photosynthetic pigment contents showed higher plasticity. We found that morphostructural and functional plasticity in both *V. neoglutinosa* and *V. procera* is possibly influenced by variations in irradiance and in nitrogen and organic matter contents in the soils of the evaluated plant formations.

Keywords: Anatomy, Irradiance, Morphology, Photosynthetic Pigment, Tillandsioideae.

RESUMO

Variações ambientais podem levar a respostas estruturais e funcionais entre bromeliaceae e o conhecimento dessas respostas pode permitir um melhor entendimento sobre os processos ecológicos e um planejamento mais eficaz de programas de manejo e conservação em áreas protegidas. Em função dos diversos habitats ocupados por vriesea, este estudo teve como objetivo avaliar a plasticidade morfo-anatômica e os conteúdos de pigmentos fotossintéticos em *v. Neoglutinosa* e *v. Procera* ocorrendo nas formações de *clusia* aberta e floresta seca de uma área de vegetação de restinga no estado do espírito santo, brasil. Em geral, as plantas da formação floresta seca apresentaram maiores medidas de crescimento e menor inclinação foliar. Na formação de *clusia* aberta, ambas as espécies apresentaram folhas com maior densidade de escama, enquanto *v. Neoglutinosa* também apresentou maior densidade estomática. A espessura do clorênquima de *v. Procera* foi maior na floresta seca. Não encontramos diferenças na espessura do limbo foliar e no parênquima de armazenamento de água para as duas espécies entre os dois ambientes. Encontramos substâncias de óleo abundantes em células de guarda e subsidiárias de amostras de *clusia* aberta. Em ambas as espécies, indivíduos da formação floresta seca apresentaram maiores teores de clorofila *a* e *b* e clorofila total, enquanto que as amostras de *v. Neoglutinosa* da formação *clusia* aberta apresentaram maiores teores de carotenóides. Das características avaliadas, os teores de pigmentos fotossintéticos apresentaram maior plasticidade. Verificamos que a plasticidade morfoestrutural e funcional em *v. Neoglutinosa* e *v. Procera* é possivelmente influenciada por variações na irradiância e nos teores de nitrogênio e matéria orgânica nos solos das formações vegetais avaliadas.

Palavras-chave: Anatomia, Irradiância, Morfologia, Pigmento Fotossintético, Tillandsioideae.

1 INTRODUCTION

The capacity of a genotype to show different phenotypes in response to different environmental stimuli is referred to as phenotypical plasticity (Gianoli & Valladares 2012; Bächtold & Melo Júnior 2015; Amorim & Melo Júnior 2017; Cabral *et al.* 2018; Muniz *et al.* 2018). Environmental parameters, including luminosity, may lead to structural and functional responses among Bromeliaceae individuals so as to provide them with adaptive phenotypical plasticity (Haslam *et al.* 2003; Skillman *et al.* 2005; Cavallero *et al.* 2009). Knowledge of these responses to different environments can allow better understanding about ecological processes and more effective planning of handling and conservation programs in protected areas (Pereira 2002; Almeida *et al.* 2004). In this setting, morpho-anatomical and leaf physiological characteristics, such as leaf inclination in relation to the ground (Valladares *et al.* 2002), succulence (Jones 2011; Amorim & Melo Júnior 2017), density of trichomes (Martin 1985; Batagin *et al.* 2009), stomatal density (Pereira *et al.* 2013, Muniz *et al.*

2018), chlorophyllian tissue thickness (Terashima *et al.* 2006), and photosynthetic pigment content (Martin 1985) have been used as predictors of ecology and the habitat that these plants occupy.

The restinga — coastal ecosystem associated to Atlantic Forest — is not homogeneous and it is distributed through different zones, sheltering species and plant communities with very particular needs (Pereira 1990). The restinga of *Parque Estadual Paulo César Vinha – PEPCV* (Paulo César Vinha State Park), located in Espírito Santo State, Southeastern Brazil, has 11 phytophysiognomies that go from plant formations affected to intense saline spray and high irradiance — predominantly with herb-shrub plants — to formations in humid to flooded soils, made up of tree species (Pereira 1990).

The restinga vegetation has Bromeliaceae as one of the most representative families as far as species richness is concerned (Assis *et al.* 2004; Martinelli 2006; Elias *et al.* 2008). *Vriesea* Lindl., belonging to the Tillandsioideae subfamily (Bromeliaceae), occurs in the subregions Chacoan, Parana and in subregions of the Amazon and Caribbean (Gomes-da-Silva and Souza-Chies, 2018). In Brazil, that genus has a very high endemism rate and occupies several phytogeographic domains such as the Amazon, Caatinga, Cerrado, Atlantic Forest and Pampa (Forzza *et al.* 2010). Among the species, *Vriesea neoglutinosa* Mez has terrestrial habits and is endangered in the Espírito Santo State (Kollmann *et al.* 2007). Samples of this species are assessed in PEPCV in Open *Clusia*, Open *Ericaceae* (Gomes 2004) and Dry Forest formations. Another representative species is *Vriesea procera* (Mart. ex. Schult. & Schult.f.) Wittm., which occurs in seven plant formations, among them, Open *Clusia* and Dry Forest (Gomes 2004). This species has epiphytic habits and is found mostly on phorophytes such as *Jacaranda puberula* (Bignoniaceae) and *Neomitranthes obscura* (Myrtaceae).

Studies on structural (Martin 1985; Lenzi *et al.* 2006; Cavallero *et al.* 2009; Marcondes *et al.* 2018) and functional (Martin 1985; Zorger *et al.* 2019) adaptive aspects of Bromeliaceae species are scarce, and the existing ones usually have a taxonomic nature (Aoyama & Sajo 2003; Arruda & Costa 2003; Proença & Sajo 2004; Souza *et al.* 2005; Ferreira *et al.* 2007; Marcondes *et al.* 2018). Thus, this study aims at assessing the morpho-anatomical plasticity and photosynthetic pigment contents of *Vriesea neoglutinosa* and *Vriesea procera* in Open *Clusia* and Dry Forest formations in *Parque Estadual Paulo César Vinha*, Espírito Santo State, Brazil, so as to identify their adaptive character to different environments.

2 MATERIALS AND METHODS

STUDY AREA

We collected the botanical samples in PEPCV, which comprises a coastal plain of about 1.500 ha, between 20°33' - 20°38'S and 40°23' - 40°26'W in the Municipality of Guarapari, Espírito Santo

State, Brazil. The samples were collected in two plant formations: Open *Clusia* and Dry Forest (Fig. 1). In that region, the climate is Aw tropical (Köppen 1948), with hot and rainy summers and dry winters. The area has annual average temperature of 23.3°C, annual average precipitation of 1.307 mm, and annual average relative humidity of 80% (Fabris 1995).

BOTANICAL SAMPLES

We sampled mature leaves collected from the middle part of the rosette of adult *Vriesea neoglutinosa* Mez and *Vriesea procera* (Mart. ex Schult. & Schult.f.) Wittm. in March, 2010. The exsiccates of the species are at the VIES herbarium, at Federal University of Espírito Santo (UFES), Brazil, under numbers 1984 and 26609.

MORPHOLOGICAL ANALYSIS

We measured length (cm), width (cm), area (cm²), fresh mass (g), dry mass (g), leaf dry mass per area - LMA (g cm⁻²) and leaf fresh mass per area - succulence (g cm⁻²) of three leaves of five individuals. To each plant, we also measured the height from base to the apex of the larger leaf. Leaf length and width and height of individuals were measured using a tape measure. The leaf area was measured using an Area Meter LI-COR 3100 (Lincoln, USA) and dry mass was obtained by drying the sample in an oven at 60°C until constant mass was achieved, and then it was weighed.

Leaf angle in relation to the ground was measured in three leaves of 10 individuals to each species in each plant formation using a clinometer.

ANATOMICAL ANALYSIS

We stored the leaves in 70% ethyl alcohol and performed freehand, cross sections of the middle third of the leaf blade. The sections underwent a staining process using safrablau (Kraus & Arduin 1997) and were set up in glycerin and water (1:1). The water-storage parenchyma, adjacent to both surfaces of the epidermis, chlorenchyma and leaf blade were measured. Stomatal (abaxial surface) and scale (abaxial and adaxial surfaces) density (number per mm⁻²) were also determined by the printing technique, using a universal instant cyanoacrylate ester adhesive on a histological blade so as to obtain the printing of both surfaces of the epidermis. In every analysis, eight measurements of four individuals were performed for each species per plant formation. Measurements were carried out using an image capture system coupled to a Nikon E200 microscope (Tokyo, Japan) through software Tsview v.6.1.3.2 (Tucsen Imaging Technology Co. Limited, Fuzhou, China) and results were documented using a digital Sony camera, model Cyber-shot DSC-S650 7.2 megapixels (Manaus, Brazil) coupled to a Nikon E200 microscope.

HISTOCHEMICAL ANALYSIS

Freehand cuts on fresh material were carried out, and then they underwent histochemical tests using reagent Sudan IV (Johansen 1940) to detect lipophilic compounds and ferric chloride solution (Johansen 1940) to verify phenolic compounds. Controls were obtained by unstained sections analyzed parallelly.

ANALYSIS OF PHOTOSYNTHETIC PIGMENT CONTENT

We collected leaves of five individuals and macerated 500 mg of fresh vegetable material of each individual in 25 mL of 80% acetone (Arnon 1949). The whole process was carried out in a dark chamber using 40 W green light. The samples were kept at low temperatures. The extract reading was carried out using a spectrophotometer Genesys 10 S UV-Vis Thermo Scientific (Madison, USA) at absorbances 480, 645 and 663 nm, and then Hendry & Grime (1993) equations were used for determining the photosynthetic pigment contents:

$$\text{Chlorophyll } a = (12.7.A_{663} - 2.69.A_{645}) \times 1.119$$

$$\text{Chlorophyll } b = (22.9.A_{645} - 4.68.A_{663}) \times 1.102$$

$$\text{Carotenoids} = [(A_{480} + 0.114.A_{663} - 0.638.A_{645}) \times V] / 112.5.FW$$

In which: A_{480} = absorbance at 480 nm; A_{645} = absorbance at 645 nm; A_{663} = absorbance at 663 nm; V = sample volume (mL) and FW = sample fresh weight (g).

MICROENVIRONMENTAL ANALYSIS

Measurements of photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$) incident were carried out for each plant formation (Open *Clusia* and Dry Forest) using a sensor Field Scout Quantum Light Meters (Plainfield, USA). Ten measurements were made at a maximum distance of 10 cm from the leaves sampled. All measurements were made between 10:00 and 11:00 am. The value obtained by the arithmetic mean represented each plant formation.

Furthermore, physical and chemical analysis of soil close to the roots of *V. neoglutinosa* (terrestrial species), in both plant formations, was carried out. Five soil samples were collected in depths of 0 to 20 cm and analyzed by Agronomic Analysis and Consulting Lab — Fullin (Linhares, Espírito Santo, Brazil) according to EMBRAPA (1997) standardized methods. Fe, Zn, Cu, Mn, P, K, and Na were extracted with $\text{HCl } 0.05 \text{ mol L}^{-1} + \text{H}_2\text{SO}_4 \text{ } 0.0125 \text{ mol L}^{-1}$, while Ca and Mg were extracted with $\text{KCl } 1 \text{ mol L}^{-1}$. Fe, Zn, Cu, Mn, Ca and Mg were determined by atomic absorption spectrometer (Model 210 VGP, Buck Scientific, East Norwalk, USA), P was determined by

spectrometer (Model B542, Micronal, São Paulo, Brazil), and K and Na were determined by flame photometer (Model B462, Micronal, São Paulo, Brazil). The texture classification was carried out in compliance with the criteria of the Brazilian Society of Soil Science. The pH was determined using a pHmeterDM-22 (Digimed, São Paulo, Brazil), while the organic matter content (OM) was extracted with $\text{Na}_2\text{Cr}_2\text{O}_7 \cdot 2\text{H}_2\text{O}$ 4 mol L⁻¹+H₂SO₄ 10 mol L⁻¹ oxidation and determined by atomic absorption spectrometer (Model 210 VGP, Buck Scientific, East Norwalk, USA) according to Raij *et al.* (2001). For *V. procera*, no analysis was carried out because it is an epiphyte species.

PLASTICITY INDEX

The plasticity index (IP) represents the variation fraction of a particular type in relation to the different environmental conditions, which can vary from zero to one (Valladares *et al.* 2002). The IP value for each variable analyzed was determined by the difference between the minimum mean value and the maximum mean value divided by the maximum mean value (Valladares *et al.* 2000) obtained from each species in the Open *Clusia* and Dry Forest formations.

STATISTICAL ANALYSIS

The data on quantitative anatomy, growth measurement and leaf angle were analyzed using t-test, with sequential Bonferroni correction (Rice 1989) to prevent error type I, on statistical software program Assistat version 7.6 beta (Campina Grande, Brazil).

3 RESULTS

LEAF MORPHOLOGY

For both species, the individuals from Dry Forest formation presented higher values of leaf area, length, fresh mass and succulence, whereas leaf width and LMA did not differ among individuals of both plant formations. Also for individuals from Dry Forest, higher dry mass values were found only for *V. procera*, while higher height values were found only for *V. neoglutinosa* (Tab. 1).

Open *Clusia* individuals of both species had higher leaf angle values in relation to the ground compared to Dry Forest individuals (Tab. 1).

Table 1. Leaf area, leaf length, leaf width, fresh mass, dry mass, leaf mass per area (LMA), succulence, leaf angle and height of *V. neoglutinosa* and *V. procera* individuals in the Open *Clusia* and Dry Forest formations. Means \pm standard deviation are shown. Differences between plant formations for each species separately are indicated by the highest values when significant (* $p < 0.002$, t-test after Bonferroni correction).

	<i>V. neoglutinosa</i>				<i>V. procera</i>			
	Open <i>Clusia</i>	Dry Forest	P-value	F-value	Open <i>Clusia</i>	Dry Forest	P-value	F-value
Leaf area(cm ²)	199.11 \pm 15.00	291.92 \pm 28.94*	<0.002	40.55	160.34 \pm 13.90	223.17 \pm 12.91*	<0.002	54.87
Leaf length(cm)	37.10 \pm 1.73	51.67 \pm 3.64*	<0.002	65.37	31.70 \pm 1.78	45.40 \pm 2.49*	<0.002	100.40
Leaf width (cm)	4.37 \pm 0.36	4.20 \pm 0.34	0.026	7.38	4.49 \pm 0.14	4.71 \pm 0.12	>0.05	0.62
Fresh mass(g)	8.64 \pm 0.66	14.04 \pm 0.43*	<0.002	234.10	6.24 \pm 0.58	10.75 \pm 0.80*	<0.002	105.35
Dry mass(g)	1.71 \pm 0.27	2.29 \pm 0.35	0.017	8.93	1.25 \pm 0.07	2.20 \pm 0.41*	<0.002	25.76
LMA (g cm ⁻²)	0.009 \pm 0.001	0.008 \pm 0.002	>0.05	0.39	0.008 \pm 0.001	0.010 \pm 0.001	0.037	6.27
Succulence(g cm ⁻²)	8.63 \pm 0.66	14.04 \pm 0.43*	<0.002	234.97	6.23 \pm 0.58	10.74 \pm 0.80*	<0.002	105.18
Leaf angle (°)	50.63 \pm 5.95*	29.10 \pm 8.36	<0.002	43.99	48.10 \pm 4.63*	21.00 \pm 5.25	<0.002	149.60
Height (cm)	40.00 \pm 4.85	59.60 \pm 3.85*	<0.002	50.15	32.60 \pm 0.89	40.20 \pm 4.97	0.010	11.33

LEAF ANATOMY

Both species from the Open *Clusia* formation showed higher scale density on the adaxial leaf surface, but scale density on the abaxial surface did not differ between the two plant formations. For *V. neoglutinosa*, stomatal density was higher among individuals of the Open *Clusia* formation, whereas *V. procera* samples did not show significant differences between the formations. Chlorenchyma thickness of *V. procera* was higher among Dry Forest

individuals, whereas for *V. neoglutinosa*, it did not differ significantly between the plant formations. For both species, water-storage parenchyma and leaf blade thickness did not vary significantly between the plant formations (Fig. 2 and Tab. 2).

Table 2. Water-storage parenchyma (Ws), chlorenchyma and leaf blade thickness, and stomatal and scale density of *V. neoglutinosa* and *V. procera* leaves from the Open *Clusia* and Dry Forest formations. Means \pm standard deviation are shown. Differences between plant formations for each species separately are indicated by the highest values when significant (* $p < 0.002$, t-test after Bonferroni correction).

	<i>V. neoglutinosa</i>				<i>V. procera</i>			
	Open <i>Clusia</i>	Dry Forest	P-value	F-value	Open <i>Clusia</i>	Dry Forest	P-value	F-value
Thickness(μm)								
Ws abaxial surface	35.28 \pm 4.10	36.20 \pm 4.37	>0.05	0.09	31.08 \pm 3.54	31.42 \pm 0.81	>0.05	0.04
Ws adaxial surface	21.76 \pm 3.19	23.20 \pm 1.82	>0.05	0.61	21.66 \pm 0.57	19.77 \pm 1.53	>0.05	5.35
Ws total	57.06 \pm 6.42	59.41 \pm 3.23	>0.05	0.43	52.74 \pm 4.09	51.20 \pm 2.28	>0.05	0.43
Chlorenchyma	49.84 \pm 6.75	62.89 \pm 3.40	0.013	11.94	58.40 \pm 2.48	77.74 \pm 2.53*	<0.002	119.25
Leaf blade	115.82 \pm 5.91	122.15 \pm 6.24	>0.05	2.17	102.31 \pm 6.26	116.80 \pm 4.14	0.008	14.92
Density (n $^\circ$ mm $^{-2}$)								
Stomatal	63.36 \pm 1.66*	48.55 \pm 1.91	<0.002	136.99	45.00 \pm 1.93	54.78 \pm 3.49	0.003	24.06
Scale adaxial	12.66 \pm 0.52*	8.19 \pm 0.32	<0.002	215.57	15.11 \pm 1.01*	8.26 \pm 0.35	<0.002	162.73
Scale abaxial	16.36 \pm 1.55	13.53 \pm 0.67	0.015	11.27	25.71 \pm 2.55	25.42 \pm 0.94	>0.05	0.05

HISTOCHEMISTRY

Tests using Sudan IV revealed the presence of more abundant oil substances in the stomatal guard and subsidiary cells among individuals of Open *Clusia* formation (Fig. 3). The test using ferric chloride solution showed accumulation of phenolic compounds in the scale pedicel, round cells of chlorenchyma, and in the xylem and phloem parenchyma cells (data not shown). However, this reaction did not differ between the plant formations.

PHOTOSYNTHETIC PIGMENT CONTENTS

Both species from the Dry Forest formation presented higher contents of chlorophyll *a*, *b* and total chlorophyll. Higher carotenoid contents were found among samples of *V. neoglutinosa* from the Open *Clusia* formation. The Chlorophyll *a/b* ratio did not differ significantly for both species between the plant formations (Tab. 3).

Table 3. Chlorophyll *a*, chlorophyll *b*, ratio chlorophyll *a/b*, total chlorophyll and carotenoids of *V. neoglutinosa* and *V. procera* from the Open *Clusia* and Dry Forest formations. Means \pm standard deviation are shown. Differences between vegetation formations for each species separately are indicated by the highest values when significant (* $p < 0.002$, t-test after Bonferroni correction).

	<i>V. neoglutinosa</i>				<i>V. procera</i>			
	Open <i>Clusia</i>	Dry Forest	P-value	F-value	Open <i>Clusia</i>	Dry Forest	P-value	F-value
Content($\mu\text{mol.g}^{-1}\text{MF}$)								
Chlorophyll <i>a</i>	0.11 \pm 0.02	1.47 \pm 0.16*	<0.002	365.53	0.18 \pm 0.07	1.75 \pm 0.45*	<0.002	59.20
Chlorophyll <i>b</i>	0.02 \pm 0.01	0.50 \pm 0.05*	<0.002	414.92	0.06 \pm 0.02	0.60 \pm 0.18*	<0.002	44.21
Chlorophyll <i>a/b</i>	6.36 \pm 2.75	2.95 \pm 0.06	0.025	7.64	3.25 \pm 0.49	2.96 \pm 0.15	>0.05	1.53
Total chlorophyll	0.11 \pm 0.03	1.76 \pm 0.19*	<0.002	381.39	0.21 \pm 0.09	2.10 \pm 0.56*	<0.002	55.02
Carotenoids	1.08 \pm 0.20*	0.23 \pm 0.004	<0.002	93.01	1.43 \pm 0.86	0.23 \pm 0.01	0.014	9.69

MICROHABITAT DESCRIPTION

Photosynthetically active radiation (PAR) was higher in the Open *Clusia* formation compared to Dry Forest formation radiation. Both formations presented sandy and acid soils. Organic matter and nitrogen contents were higher in Dry Forest formation soils than Open *Clusia*. The values referring to PAR and physical and chemical analyses of soils of both plant formations are summarized in Table 4.

Table 4. Photosynthetically active radiation (PAR) and physical and chemical analysis of soil close to *V. neoglutinosa* in the Open *Clusia* and Dry Forest formations (CEC = cation exchange capacity).

	Open <i>Clusia</i>	Dry Forest
PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	2000.0	44.7
Soil analysis		
Textural classification	sand	sand
Organic matter (g dm^{-3})	85	97
N (g dm^{-3})	2.9	3.7
P – Mehlich (mg dm^{-3})	1.0	1.0
K (mg dm^{-3})	8.0	5.0
S (mg dm^{-3})	7.0	5.0
Ca ($\text{cmol}_c \text{dm}^{-3}$)	0.3	0.2
Mg ($\text{cmol}_c \text{dm}^{-3}$)	0.1	0.1
Al ($\text{cmol}_c \text{dm}^{-3}$)	0.4	0.8
Fe (mg dm^{-3})	19.0	16.0
Zn (mg dm^{-3})	0.4	0.5
Cu (mg dm^{-3})	0.1	0.1
Mn (mg dm^{-3})	1.0	14
Bo (mg dm^{-3})	0.3	0.1
Na (mg dm^{-3})	10.0	6.0

pH (H ₂ O)	5.1	4.8
H + Al (cmol _c dm ⁻³)	1.2	1.6
Electrical conductivity (dS m ⁻¹)	0.02	0.04
CEC (pH 7,0) (cmol _c dm ⁻³)	1.6	1.9
CEC effective (cmol _c dm ⁻³)	0.8	1.1
Sum of bases (%)	0.4	0.3

PHENOTYPICAL PLASTICITY

For both species, the variables with higher IP values were chlorophyll *a*, chlorophyll *b* and total chlorophyll contents, carotenoid content and leaf angle, followed by chlorophyll *a/b*, succulence, fresh mass and scale density of the adaxial surface for *V. neoglutinosa* and scale density of the adaxial surface, dry mass, fresh mass and succulence for *V. procera*. The variables with lower IP values for *V. neoglutinosa* were water-storage parenchyma thickness, leaf width and leaf blade, whereas for *V. procera*, the number of scales on the abaxial surface, water-storage parenchyma thickness and leaf width presented the lowest IP values (Tab. 5).

Table 5. Plasticity index of morphological, anatomical and photosynthetic pigments variables of *V. neoglutinosa* and *V. procera* from the Open *Clusia* and Dry Forest formations. (Ws= water-storage parenchyma; LMA= leaf mass per area).

Variables	Plasticity index	
	<i>V. neoglutinosa</i>	<i>V. procera</i>
Morphological		
Fresh mass	0.38	0.42
Dry mass	0.25	0.43
Leaf area	0.32	0.28
LMA	0.11	0.20
Succulence	0.39	0.42
Leaf length	0.28	0.30
Leaf width	0.04	0.05

Height	0.33	0.19
Leaf angle	0.43	0.56
Anatomical		
Ws adaxial	0.06	0.09
Ws abaxial	0.03	0.01
Ws total	0.04	0.03
Chlorenchyma	0.21	0.25
Leaf blade	0.05	0.12
Stomatal density	0.23	0.18
Scale density abaxial	0.17	0.01
Scale density adaxial	0.35	0.45
Photosynthetic pigment		
Chlorophyll <i>a</i>	0.93	0.90
Chlorophyll <i>b</i>	0.96	0.90
Chlorophyll <i>a/b</i>	0.54	0.09
Total chlorophyll	0.94	0.90
Carotenoids	0.79	0.84

4 DISCUSSION

Bromeliaceae comprises representatives whose leaves have morphological characteristics of xeric environments, which have high adaptive values (Tomlinson 1969; Scatena & Segecin 2005; Proença & Sajo 2007; Monteiro *et al.* 2011). These features can vary according to environmental conditions in order to provide these plants with adaptive plasticity (Cavallero *et al.* 2009; 2011). In our study, the phenotypical plasticity observed in *V. neoglutinosa* and *V. procera* seems to help these individuals settle under distinct irradiance and edaphic conditions in each environment.

In the Dry Forest formation, both species showed higher growth measures concerning most of the features assessed. This corroborates other studies involving Bromeliaceae species, which verified increase in height (Medina *et al.* 1986; Cavallero *et al.* 2009), leaf length (Holcman &

Sentelhas 2013) and area (Cavallero *et al.* 2011) among individuals under lower light incidence. Larger leaves allow the plant to capture more light because they increase the contact area of the leaf with irradiance in individuals under shading. On the other hand, leaves with reduced area, such as those found among individuals in the Open *Clusia* formation, decrease the transpiration surface, which is important for survival in sunny environments (Oliveira *et al.* 2009, Pires *et al.* 2015). The leaves of Dry Forest individuals from both species also presented more succulence. Studies on this feature show that plants can respond differently in environments with similar characteristics. Cavallero *et al.* (2011), for example, verified higher leaf succulence in *Aechmea distichantha* occurring at the edge of forests compared to understory plants. Mantovani (1999), however, assessed four species of *Araceae* and observed higher succulence in the leaves of adult *Rhodosphata oblongata* individuals occurring in the shade, whereas *Anthurium longifolium* and *Philodendrum alternans* presented more succulence under the sun. Also, *Philodendrum crassinervium* did not vary significantly between both environments. In our study, the higher succulence among the species in the Dry Forest formation — more shaded area — can be a result of less water loss through the leaves, keeping the tissues more hydrated.

LMA is a compound variable, resulting from the density and leaf thickness (Niinemets 2001). Although different gradients of resource availability — especially light and temperature (Poorter *et al.* 2009) — can lead to variations in this aspect within the same species, individuals do not show differences in LMA values between Open *Clusia* and Dry Forest formations, which is in part due to lack of leaf blade thickness variation.

Leaf angle is another characteristic that is influenced by solar radiation intensity. In general, sun leaves tend to be more vertically inclined compared to shaded leaves (Valladares & Pearcy 1998; Ishida 1999; Cavallero *et al.* 2011). In both species, the higher leaf inclination in the samples from Open *Clusia* formation reduces the surface of sunlight incidence, which minimizes the degradation effect of excessive light over chlorophyll (He *et al.* 1996), overheating (Liu *et al.* 2003) and dehydration (Mantovani 2000). On the other hand, less inclined leaves such as those of individuals from Dry Forest formation allow more sunlight to be captured and thus higher photosynthetic rates to be achieved (Falster & Westoby 2003).

Higher scale density among individuals from the Open *Clusia* formation — area under high solar radiation — forms a reflective surface that protects the plant from excessive solar radiation (Benzing 2000). Furthermore, the scales can allow water and nutrient absorption (Benzing 2000; Papini *et al.* 2010), which contributes to survival under dry and/or oligotrophic substrates (Mantovani & Iglesias 2005) and represents a relevant strategy for the plants in this study.

As far as stomatal density is concerned, several studies have shown that individuals under higher solar radiation have higher stomatal density values (Marques *et al.* 2000; Nascimento *et al.* 2006; Batagin *et al.* 2009; György 2009; Pereira *et al.* 2009). The results found on *V. neoglutinosa* in the Open *Clusia* formation corroborate this trend. A higher number of stomata per area can be an advantage because it decreases leaf temperature due to the increase in stomatal conductance (Lu *et al.* 1994). Moreover, increased stomatal density can decrease leaf transpiration (Larcher 2004; Gurevitch *et al.* 2009) due to its association to smaller stomata, which improves stomatal opening and closing control (Hetherington & Woodward 2003).

Several studies, on different taxa, report that sun leaves are thicker than shaded leaves because of the higher elongation or higher number of cell layers of chlorenchyma (Marques *et al.* 1999; Oguchi *et al.* 2005; Silva *et al.* 2008). However, the results obtained do not corroborate this statement regarding the species in the present study and, differently from what was expected, Dry Forest *V. procera* individuals had increased chlorenchyma thickness.

Abundance of oil substances in guard and subsidiary cells of individuals in the Open *Clusia* formation can be explained by their higher exposure to solar radiation. According to Wattiez & Sternon (1942) apud Albuquerque & Neves (2004), these oils protect tissues against transpiration and excessive heat. They also help to control osmotic function, speeding up water movement through cell walls and, consequently, transporting enzymes and soluble matter. These functions can be considered an advantage to plants grown under high irradiance.

In shaded plants, higher chlorophyll contents result in higher capture of solar radiation (Aimi *et al.*

2017). Under shaded conditions, chlorophyll *a*, *b* and total chlorophyll of Bromeliaceae samples are usually higher (Martin 1985; Medina *et al.* 1986; Maxwell *et al.* 1992). Further, higher organic matter and nitrogen contents in soils usually result in higher concentrations of chlorophyll in leaves (Soratto *et al.* 2004; Ferreira *et al.* 2006; Leonardo *et al.* 2013; Jesus *et al.* 2020). Under high irradiance conditions, chlorophyll concentrations tend to be lower because this pigment is constantly produced and degraded in presence of light (Kramer & Kozlowski 1979). The results obtained from *V. neoglutinosa* and *V. procera* individuals from the Open *Clusia* and Dry Forest formations reinforce this theory. In the Open *Clusia* samples, higher carotenoid contents provide the plant with photoprotection to dissipate the exceeding energy (Demmig-Adams 1996).

V. neoglutinosa and *V. procera* individuals occurring in the Open *Clusia* and Dry Forest formations of PEPCV restinga showed structural and functional plasticity, which seems to be related to solar radiation conditions and organic matter and nitrogen contents in the soil of each formation.

Among the variables analyzed, the physiological ones (photosynthetic pigment content) showed higher plasticity index.

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LEGENDS FOR FIGURES

Figure 1. Map of Brazil and Espírito Santo State with the location of the PEPCV and the species in the studied plant formations.

Figure 2. Cross sections of *Vriesea* leaf blade of restinga. A-B. *V. neoglutinosa* sampled in the Open *Clusia* and Dry Forest formations, respectively. C-D. *V. procera* sampled in the Open *Clusia* and Dry Forest formations, respectively. (Ac) aerenchyma constituted by brachiforms cells, (Cp) chlorenchyma, (Ep) Epidermis, (Fi) fibers, (Sc) scale, (St) stomata, (Vb) vascular bundle, (Wp) water-storage parenchyma. Bars = 30 μm .

Figure 3. Paradermal sections of the leaf blade (abaxial surface) of *V. neoglutinosa* from Open *Clusia* (A) and Dry Forest (B) formations that underwent histochemical test using sudan IV. Notice the oil drops inside the stomata and common epidermal cells. Bars = 10 μm .