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.

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 phytosociological groups 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 Neomitrantes 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 (cm$^2$), 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 Mater 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 (Tucson 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 (µmol m\(^{-2}\) 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 HCl 0.05 mol L\(^{-1}\) + H\(_2\)SO\(_4\) 0.0125 mol L\(^{-1}\), while Ca and Mg were extracted with KCl 1 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 Na₂Cr₂O₇·2H₂O 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 ± 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).

|                      | *V. neoglutinosa* |                      | *V. procera* |                      |
|----------------------|-------------------|---------------------|--------------|---------------------|
|                      | Open Clusia       | Dry Forest          | P-value      | F-value             | Open Clusia       | Dry Forest          | P-value      | F-value             |
| Leaf area (cm²)      | 199.11 ± 15.00    | 291.92 ± 28.94*     | <0.002       | 40.55               | 160.34 ± 13.90    | 223.17 ± 12.91*    | <0.002       | 54.87               |
| Leaf length (cm)     | 37.10 ± 1.73      | 51.67 ± 3.64*       | <0.002       | 65.37               | 31.70 ± 1.78      | 45.40 ± 2.49*      | <0.002       | 100.40              |
| Leaf width (cm)      | 4.37 ± 0.36       | 4.20 ± 0.34         | 0.026        | 7.38                | 4.49 ± 0.14       | 4.71 ± 0.12        | >0.05        | 0.62                |
| Fresh mass (g)       | 8.64 ± 0.66       | 14.04 ± 0.43*       | <0.002       | 234.10              | 6.24 ± 0.58       | 10.75 ± 0.80*      | <0.002       | 105.35              |
| Dry mass (g)         | 1.71 ± 0.27       | 2.29 ± 0.35         | 0.017        | 8.93                | 1.25 ± 0.07       | 2.20 ± 0.41*       | <0.002       | 25.76               |
| LMA (g cm⁻²)         | 0.009 ± 0.001     | 0.008 ± 0.002       | >0.05        | 0.39                | 0.008 ± 0.001     | 0.010 ± 0.001      | 0.037        | 6.27                |
| Succulence (g cm⁻²)  | 8.63 ± 0.66       | 14.04 ± 0.43*       | <0.002       | 234.97              | 6.23 ± 0.58       | 10.74 ± 0.80*      | <0.002       | 105.18              |
| Leaf angle (°)       | 50.63 ± 5.95*     | 29.10 ± 8.36        | <0.002       | 43.99               | 48.10 ± 4.63*     | 21.00 ± 5.25       | <0.002       | 149.60              |
| Height (cm)          | 40.00 ± 4.85      | 59.60 ± 3.85*       | <0.002       | 50.15               | 32.60 ± 0.89      | 40.20 ± 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 ± 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).

|                | V. neoglutinosa | V. procera |
|----------------|-----------------|------------|
|                | Open Clusia     | Dry Forest | P-value | F-value | Open Clusia | Dry Forest | P-value | F-value |
| Thickness(µm)  |                 |            |          |         |             |            |          |         |
| Ws abaxial     | 35.28 ± 4.10    | 36.20 ± 4.37 | >0.05   | 0.09    | 31.08 ± 3.54 | 31.42 ± 0.81 | >0.05   | 0.04    |
| Ws adaxial     | 21.76 ± 3.19    | 23.20 ± 1.82 | >0.05   | 0.61    | 21.66 ± 0.57 | 19.77 ± 1.53 | >0.05   | 5.35    |
| Ws total       | 57.06 ± 6.42    | 59.41 ± 3.23 | >0.05   | 0.43    | 52.74 ± 4.09 | 51.20 ± 2.28 | >0.05   | 0.43    |
| Chlorenchyma   | 49.84 ± 6.75    | 62.89 ± 3.40 | 0.013   | 11.94   | 58.40 ± 2.48 | 77.74 ± 2.53* | <0.002 | 119.25  |
| Leaf blade     | 115.82 ± 5.91   | 122.15 ± 6.24 | >0.05   | 2.17    | 102.31 ± 6.26 | 116.80 ± 4.14 | 0.008   | 14.92   |
| Density (nº mm⁻²) |                 |            |          |         |             |            |          |         |
| Stomatal       | 63.36 ± 1.66*   | 48.55 ± 1.91 | <0.002  | 136.99  | 45.00 ± 1.93 | 54.78 ± 3.49 | 0.003   | 24.06   |
| Scale adaxial  | 12.66 ± 0.52*   | 8.19 ± 0.32  | <0.002  | 215.57  | 15.11 ± 1.01* | 8.26 ± 0.35  | <0.002  | 162.73  |
| Scale abaxial  | 16.36 ± 1.55    | 13.53 ± 0.67 | 0.015   | 11.27   | 25.71 ± 2.55 | 25.42 ± 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 ± 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). |
|---|---|---|---|---|---|---|---|---|
| | **V. neoglutinosa** | | | **V. procera** | | | | |
| | Open *Clusia* | Dry Forest | P-value | F-value | Open *Clusia* | Dry Forest | P-value | F-value |
| Content(µmol.g⁻¹MF) | | | | | | | | |
| Chlorophyll *a* | 0.11 ± 0.02 | 1.47 ± 0.16* | <0.002 | 365.53 | 0.18 ± 0.07 | 1.75 ± 0.45* | <0.002 | 59.20 |
| Chlorophyll *b* | 0.02 ± 0.01 | 0.50 ± 0.05* | <0.002 | 414.92 | 0.06 ± 0.02 | 0.60 ± 0.18* | <0.002 | 44.21 |
| Chlorophyll *a/b* | 6.36 ± 2.75 | 2.95 ± 0.06 | 0.025 | 7.64 | 3.25 ± 0.49 | 2.96 ± 0.15 | >0.05 | 1.53 |
| Total chlorophyll | 0.11 ± 0.03 | 1.76 ± 0.19* | <0.002 | 381.39 | 0.21 ± 0.09 | 2.10 ± 0.56* | <0.002 | 55.02 |
| Carotenoids | 1.08 ± 0.20* | 0.23 ± 0.004 | <0.002 | 93.01 | 1.43 ± 0.86 | 0.23 ± 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 *Clusia* | Dry Forest |
|-----------------------|---------------|------------|
| PAR ($\mu$mol m$^{-2}$ 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 (cmol$_c$ dm$^{-3}$) | 0.3           | 0.2        |
| Mg (cmol$_c$ dm$^{-3}$) | 0.1           | 0.1        |
| Al (cmol$_c$ 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        |
### 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               | *V. neoglutinosa* | *V. procera* |
|-------------------------|-------------------|--------------|
| **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         |
### 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 Rhodospatia 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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REFERENCES

Abreu, M.F.; Andrade, J.C. & Falcão, A.A. 2006. Protocolos de análises químicas. Pp. 121-1581. In: Andrade, J.C. & Abreu, M.F. (Eds). Análise Química de Resíduos Sólidos para Monitoramento e Estudos Agroambientais. Campinas, IAC.

Aimi, S.C.; Araujo, M.M.; Tonetto, T.S.; Tabaldi, L.A.; Saldanha, C.W.; Farias, J.G. & Oliveira, G.G. 2017. Shading as a conditioning factor to forest species planting: a study with Apuleia leioarpa. Bosque 38: 371-379.

Albuquerque, E.S.B. & Neves, L.J. 2004. Anatomia foliar de Alpinia zerumbet (Pers.) Burtt & Smith (Zingiberaceae). Acta Botanica Brasílica 18: 109-121.

Almeida, L.P.; Alvarenga, A.A.; Castro, E.M.; Zanela, S.M. & Vieira, C.V. 2004. Crescimento inicial de plantas de Cryptocaria aschersoniana Mez. submetidas a níveis de radiação solar. Ciência Rural 34: 83-88.

Amorim, M.W. & Melo Júnior, J.C.F. 2017. Plasticidade morfoanatômica foliar de Tibouchina clavata (Melastomataceae) ocorrente em duas formações de restinga. Rodriguésia 68: 545-555.

Aoyama, E.M. & Sajo, M.G. 2003. Estrutura foliar de Aechmea Ruiz & Pav. subgênero Lamprococcus (Beer) Baker e espécies relacionadas. Revista Brasileira de Botânica 26: 461-473.

Arnon, D.I. 1949. Copper enzymes in isolated chloroplasts: polyphenoloxidase in Beta vulgaris. Plant Physiology 24: 1-15.

Arruda, R.C.O. & Costa, A.F. 2003. Foliar anatomy of five Vriesea Sect. Xiphion (Bromeliaceae) species. Selbyana 24: 180-189.

Assis, A.M.; Thomaz, L.D. & Pereira, O.J. 2004. Florística de um trecho de floresta de restinga no município de Guarapari, Espírito Santo, Brasil. Acta Botanica Brasílica 18: 191-201.
Bächtold, B.A. & Melo Júnior, J.C.F. 2015. Plasticidade morfológica de Calophyllum brasiliense Camb. (Calophyllaceae) em duas formações de restinga no sul do Brasil. Acta Biológica Catarinense 2: 21-32.

Batagin, K.D.; Almeida, C.V.; Tanaka, F.A.O & Almeida, M. 2009. Alterações morfológicas foliares em abacaxizeiros cv. IAC “Gomo-de-mel” micropropagados e aclimatizados em diferentes condições de luminosidade. Acta Botanica Brasilica 23: 85-92.

Benzing, D.H. 2000. Bromeliaceae: profile of an adaptative radiation. Cambridge, Cambridge University Press.

Cabrál R.D.C.; Melo Junior, J.C.F. & Matilde-Silva, M. 2018. Plasticidade morfoanatômica foliar em Smilax campestris (Smilacaceae) em gradiente ambiental de restinga, SC, Brasil. Hoehnea 45: 173-183.

Cavallero, L.; Galetti, L.; López, D.; McCargo, J. & Barberis, I.M. 2011. Morphological variation of the leaves of Aechmea distichanletha Lem. plants from contrasting habitats of a Chaco forest: a trade-off between leaf area and mechanical support. Revista Brasileira de Biociências 9: 455-464.

Cavallero, L.; López, D. & Barberis, I.M. 2009. Morphological variation of Aechmea distichantha (Bromeliaceae) in a Chaco forest: habitat and size-related effects. Plant Biology 11: 379-391.

Demmig-Adams, B.; Gilmore, A.M. & Adams, W.W. 1996. In vivo functions of carotenoids in higher plants. The FASEB Journal 10: 403-412.

Elias, C.; Fernandes, E.A.N.; França, E.J.; Bacchi, M.A. & Tagliaferro, F.S. 2008. Native bromeliads as biomonitors of airborne chemical elements in a Brazilian restinga forest. Journal of Radioanalytical and Nuclear Chemistry 278: 423–427.

Embrapa. 1997. Manual de métodos de análise de solo. Rio de Janeiro, EMBRAPA - Centro Nacional de Pesquisa de Solo.

Fabris, L.C. 1995. Composição florística e fitossociológica de uma faixa de floresta arenosa litorânea do Parque Estadual de Setiba, Município de Guarapari, ES. Dissertaçao de Mestrado. Universidade Estadual Paulista, Rio Claro.

Falster, D.S. & Westoby, M. 2003. Leaf size and angle vary widely across species: what consequences for light interception. New phytologist 158: 509-525.

Ferreira, L.M.S.L.; Bellintani, M.C & Silva, L.B. 2007. Anatomia Foliar de Orthophytum mucugense Wand. e Conceição (Bromeliaceae). Revista Brasileira de Biociências 5: 825-827.
Ferreira, M.M.M.; Ferreira, G.B.; Fontes, P.C.R. & Dantas, J.P. 2006. Índice SPAD e teores de clorofila no limbo foliar do tomateiro em função de doses de nitrogênio e da adubação orgânica, em duas épocas de cultivo. *Ceres* **53**: 83-92.

Forzza, R.C.; Costa, A.; Siqueira Filho, J.A. & Martinelli, G. 2010. Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/2010/FB006414 (acesso em 14/04/2011).

Gianoli, E.; Valladares, F. 2012. Studying phenotypic plasticity: the advantages of a broad approach. *Biological Journal of the Linnean Society* **105**: 1-7.

Gomes, J.M.L. 2004. *Bromeliaceae do Parque Estadual Paulo César Vinha, Guarapari, ES: taxonomia e ecofisiologia*. Dissertação de Mestrado. Universidade Federal do Espírito Santo, Vitória.

Gomes-da-Silva, J., & Souza-Chies, T.T. 2018. What actually is *Vriesea*? A total evidence approach in a polyphyletic genus of Tillandsioideae (Bromeliaceae, Poales). *Cladistics* **34**, 181-199.

Gurevitch, J.; Scheiner, S.M. & Fox, G.A. 2009. *Ecologia Vegetal*. Porto Alegre, Artmed.

György, E. 2009. Anatomic adaptive strategies of some *Cormophytes* with individuals growing in light and shade conditions. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* **37**: 33-39.

Haslam, R.; Borland, A.; Maxwell, K. & Griffiths, H. 2003. Physiological responses of the CAM epiphyte *Tillandsia usneoides* L. (Bromeliaceae) to variations in light and water supply. *Journal of Plant Physiology* **160**: 627-634.

He, J.; Chee, C.W. & Goh, C.J. 1996. Photoinhibition of *Heliconia* under natural tropical conditions: the importance of leaf orientation for light interception and leaf temperature. *Plant, Cell and Environment* **19**: 1238-1248.

Hendry, G.A.F.; Grime, J.P. 1993. *Methods in comparative plant ecology*. London, Chapman & Hall.

Hetherington, A.M. & Woodward, F.I. 2003. The role of stomata in sensing and driving environmental change. *Nature* **424**: 901-908.

Holman, E. & Sentelhas, P.C. 2013. Bromeliads production in greenhouses associated to different shading screens. *Horticultura Brasileira* **31**: 386-391.
Ishida, A.; Toma, T. & Marjenah. 1999. Leaf gas exchange and chlorophyll fluorescence in relation to leaf angle, azimuth, and canopy position in the tropical pioneer tree, *Macaranga conifer*. *Tree Physiology* 19: 117-124.

Jesus, R.S.; Anjos, G. L.; Ferreira, P.M.; Jesus, A.R.; Sousa, G.S. & Santos, A.R..S. 2020. Características agronômicas de ora-pro-nóbis cultivadas em ambientes de luz e adubação orgânica. *Brazilian Journal of Development* 6: 15048-15063.

Johansen, D. 1940. *Plant microtechnique*. New York, McGraw-Hill.

Jones, L.A. 2011. Anatomical adaptations of four Crassula species to water availability. *Bioscience Horizons* 4: 13-22.

Kollmann, L.J.C.; Fontana, A.P.; Simonelli, M. & Fraga, C.N. 2007. As angiospermas ameaçadas de extinção no Estado do Espírito Santo. Pp.105-140. In: Simonelli, M. & Fraga C.N. (Orgs.). *Espécies da Flora Ameaçadas de Extinção no Estado do Espírito Santo*. Vitória, Gráfica JEP.

Köppen, W. 1948. *Climatología: com un estudio de los climas de la Terra*. Mexico, Fondo de Cultura Económica.

Kramer, T. & Koslowski, T. 1979. *Physiology of woody plants*. New York, Academic Press.

Kraus, J.E. & Arduin, M. 1997. *Manual básico de métodos em morfologia vegetal*. Rio de Janeiro, Editora Universidade Rural.

Larcher, L. 2004. *Ecofisiologia Vegetal*. São Carlos, Rima.

Lenzi, M.; Matos, J.Z. & Orth, A.I. 2006. Variação morfológica e reprodutiva de *Aechmea lindenii* (E. Morren) Baker var. *lindenii* (Bromeliaceae). *Acta Botanica Brasilia* 20: 487-500.

Leonardo, F.A.P.; Pereira, W.E.; SILVA, S.M. & Costa, J.P. 2013. Teor de clorofila e índice spad no abacaxizeiro cv. Vitória em função da adubação nitrogenada. *Revista Brasileira de Fruticultura* 35: 377-383.

Liu, L.-X.; Xu, S.-M. & Woo, K.C. 2003. Influence of leaf angle on photosynthesis and the xanthophyll cycle in the tropical tree species *Acacia crassicarpa*. *Tree Physiology* 23: 1255–1261.

Lu, Z.; Radin, J.W.; Turcotte, E.L.; Percy, R. & Zeiger, E. 1994. High yields in advanced lines of Pima cotton are associated with higher stomatal conductance, reduced leaf area and lower leaf temperature. *Physiologia Plantarum* 92: 266-272.
Mantovani, A. 1999. A method to improve leaf succulence quantification. Brazilian Archives of Biology and Technology 42: 9-14.

Mantovani, A. 2000. Leaf orientation in epiphytic Aroids: effect on water and temperature balances of the leaves. Leandra 15: 91-103.

Mantovani, A. & Iglesias, R.R. 2005. Quando aparece a primeira escama? Estudo comparativo sobre o surgimento de escamas de absorção em três espécies de bromélias terrestres de restinga. Rodriguésia 56: 73-84.

Marcondes, J.P.B.A.C. & Tardivo, R.C.; Kowalski, V.K. & Costa, M.E. 2018. O gênero Catopsis (Bromeliaceae: Tillandsioideae) no estado do Paraná: aspectos taxonômicos e anatômicos. Rodriguésia 69: 649-662.

Marques, A.R.; García, Q.S. & Fernandes C.W. 1999. Effects of sun and shade on leaf structure and sclerophyll of Sebastiania myrtilloides (Euphorbiaceae) from Serra do Cipó, Minas Gerais, Brazil. Boletim de Botânica da Universidade de São Paulo 18: 21-27.

Marques, A.R.; García, Q.S.; Rezende, J.L.P. & Fernandes, G.W. 2000. Variations in leaf characteristics of two species of Miconia in the Brazilian cerrado under different light intensities. Tropical Ecology 41: 47-60.

Martin, C.E.; McLeod, K.W.; Eades, C.A. & Pitzer, A.F. 1985. Morphological and physiological responses to irradiance in the CAM epiphyte Tillandsia usneoides L. (Bromeliaceae). Botanical Gazette 146:489-494.

Martinelli, G. 2006. Manejo de populações e comunidades vegetais: um estudo de caso na conservação de Bromeliaceae. Pp. 479-503. In: Rocha, C.F.D; Bergallo, H.G.; Sluys M.V. & Alves, M.A.S. (Orgs.). Biologia da conservação: essências. São Carlos, Rima.

Maxwell, C.; Griffiths, H.; Borland, A.M.; Broadmeadow, M.S.J. & McDavid, C.R. 1992. Photoinhibitory responses of the epiphytic bromeliad Guzmania monostachia during the dry season in Trinidad maintain photochemical integrity under adverse conditions. Plant Cell and Environment 15: 37-47.

Medina, E.; Olivares, E. & Diaz M. 1986. Water stress and light intensity effects on growth and nocturnal acid accumulation in a terrestrial CAM bromeliad (Bromelia humilis Jacq.) under natural conditions. Oecologia 70: 441-446.
Monteiro, R.F.; Forzza, R.C. & Mantovani, A. 2011. Leaf structure of Bromelia and its significance for the evolution of Bromeliioideae (Bromeliaceae). Plant Systematics and Evolution 293: 53-64.

Muniz, L.F.; Bombo, A. B.; Filartiga, A.L. & Appezzato-da-Glória, B. 2018. Can climate and soil conditions change the morpho-anatomy among individuals from different localities? A case study in Aldama grandiflora (Asteraceae). Brazilian Journal of Biology 78: 706-717.

Nascimento, E.A.; Oliveira, L.E.M.; Castro, E.M.; Delú Filho, N.; Mesquita, A.C. & Vieira, C.V. 2006. Alterações morfofisiológicas em folhas de cafeeiro (Coffeea arabica L.) consorciado com seringueira (Hevea brasiliensis Muell. Arg.). Ciência Rural 36: 852-857.

Niinemets Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. Ecology 82: 453-469.

Oguchi, R.; Hikosaka, K. & Hirose, T. 2005. Leaf anatomy as a constraint for photosynthetic acclimation: differential responses in leaf anatomy to increasing growth irradiance among three deciduous trees. Plant, Cell and Environment 28: 916-927.

Oliveira, G.X.S.; Filho, M.A.C.; Pereira, F.A.C.; Coelho, E.F.; Paz, V.P.S. & Neto, M.T.C. 2009. Relações entre transpiração máxima, evapotranspiração de referência e área foliar em quatro variedade de mangueira. Revista Brasileira de Fruticultura 31: 20-27.

Papini, A.; Tani, G.; Falco, P.D. & Brighigna, L. 2010. The ultrastructure of the development of Tillandsia (Bromeliaceae) trichome. Flora 205: 94-100.

Pereira, O.J. 1990. Caracterização fitofisionômica da restinga de Setiba, Guarapari, Espírito Santo. Pp.207-219. In: Anais do II Simpósio de Ecossistemas da Costa Sul e Sudeste Brasileira. São Paulo, Aciesp v.III.

Pereira, O.J. 2002. Restingas. Pp.38-41. In: Araújo, E.L.; Moura, A.N.; Sampaio E.V.S.B., Gestinari, L.M.S. & Carneiro, J.M.T. (Eds.). Biodiversidade, conservação e uso sustentável da flora do Brasil. Recife, Imprensa Universitária.

Pereira, D.C.; Barros, C.F. & Scarano, F.R. 2009. In situ variation in leaf anatomy and morphology of Andira legalis (Leguminosae) in two neighbouring but contrasting light environments in a Brazilian sandy coastal plain. Acta Botanica Brasilica 23: 267-273.

Pereira, T.A.P., Silva, L.C., Azevedo, A.A., Francino, D.M.T., Coser, T.S. & Pereira, J. D. 2013. Leaf morpho-anatomical variations in Billbergia elegans and Neoregelia mucugensis (Bromeliaceae) exposed to low and high solar radiation. Botany 91: 327-334.
Pires, M.F.; Pereira, M.P.; Castro, E.M.; Barbosa, S. & Pereira, F.J. 2015. Micromorfometria foliar de Schinus molle L. (Anarcardiaceae) em diferentes alturas na copa. Cerne 21: 17-25.

Poorter, H; Niinemets, Ü; Poorter, L.; Wright, I.J. & Villar, R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytologist 182: 565–588.

Proença, S.L. & Sajo, M.G. 2004. Estrutura foliar de espécies de Aechmea Ruiz & Pav. (Bromeliaceae) do Estado de São Paulo, Brasil. Acta Botanica Brasiliaca 18: 319-331.

Proença, S.L. & Sajo, M.G. 2007. Anatomia foliar de bromélias ocorrentes em áreas de cerrado do Estado de São Paulo, Brasil. Acta Botanica Brasiliaca 21: 657-673.

Rice, W.R. 1989. Analysing tables of statistical tests. Evolution 43: 223-225.

Scatena, V.L. & Segecin, S. 2005. Anatomia foliar de Tillandsia L. (Bromeliaceae) dos Campos Gerais, Paraná, Brasil. Revista Brasileira de Botânica 28: 635-649.

Silva, A.B.; Pasqual, M.; Castro, E.M.; Miyata, L.Y.; Melo, L.A. & Braga, F.T. 2008. Luz natural na micropropagação do abacaxizeiro (Ananas comosus L. Merr). Interciencia 33: 839-843.

Skillman, J.B.; Garcia, M.; Virgo, A. & Winter, K. 2005. Growth irradiance effects on photosynthesis and growth in two co-occurring shade- tolerant neotropical perennials of contrasting photosynthetic pathways. American Journal of Botany 92: 1811-1819.

Souza, G.M.; Estelita, M.E.M. & Wanderley, M.G.L. 2005. Anatomia foliar de espécies brasileiras de Aechmea subg. Chevaliera (Gaudich. ex Beer) Baker, Bromeliioideae-Bromeliaceae. Revista Brasileira de Botânica 3: 603-613.

Terashima, I.; Hanba, Y.T.; Tazou, Y.; Vyas, P. & Yano, S. 2006. Irradiance and phenotype: comparative eco-development of sun and shade leaves in relation to photosynthetic CO2 diffusion. Journal of Experimental Botany 57: 343-354.

Tomlinson, P.B. 1969. Commelinales-Zingiberales. Vol 3, Pp. 1-446. In: Metcalf, C.R. Anatomy of the Monocotyledons. Oxford, Clarendon Press.

Valladares, F. & Pearcy, R.W. 1998. The functional ecology of shoot architecture in sun and shade plants of Heteromeles arbutifolia M. Roem., a Californian chaparral shrub. Oecologia 114: 1-10.
Valladares, F.; Balaquear, L.; Martínez-Ferri, E.; Perez-corona, E. & Manrique, E. 2002. Plasticity, instability and canalization: is the phenotypic variation in seedlings of sclerophyll oaks consistent with the environmental unpredictability of Mediterranean ecosystems? *New Phytologist* **156**: 457-467.

Valladares, F.; Wright, S.J.; Lasso, E.; Kitajima, K. & Pearcy, R.W.. 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology* **81**: 1925-1936.

Zorger, B.B., Arrivabene, H.P. & Milanez, C.R.D. 2019. Adaptive morphoanatomy and ecophysiology of *Billbergia euphemiae*, a hemiepiphyte Bromeliaceae. *Rodriguésia* **70**, 1-10.

**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. neoglutenosa* 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 bybraciforms 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. neoglutenosa* 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.