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Leaf morphoanatomy of the rheophyte *Dyckia distachya* Hassler (Bromeliaceae)

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ABSTRACT: (Leaf morphoanatomy of the rheophyte *Dyckia distachya* Hassler (Bromeliaceae)). This research reports on the leaf morphoanatomy of the rheophyte *Dyckia distachya*. Plants with young and mature leaves of three populations from the Pelotas River and Uruguay River (SC, Brazil), which were maintained in a greenhouse, were utilized in the study. The leaves of *D. distachya* have sheaths, and the blades are lanceolate with serrate margins. The leaf epidermis of this species has a thickened cuticular membrane; thickened and lignified cellular walls, except in the outer periclinal; and silica bodies in the lumen. Tetracytic stomata are found within individual depressions that are protected by peltate scales; both the stomata and scales are restricted to the intercostal zones, on the abaxial surface. These features of the epidermis suggest that this species has the ability to conserve water while gas is exchanged during periods when the water level is low. The mesophyll is formed by the following: the hypodermis, which is made of septate fibers (along the adaxial surface and abaxial costal regions) or sclereids (abaxial intercostal regions); hydrenchyma, the widest tissue; chlorenchyma, located adaxially to the collateral vascular bundles; and aerenchyma, which communicate directly with the stomata. The leaf sheath has neither scales nor stomata. *Dyckia distachya* has both xeromorphic and hydromorphic features, which are associated with survival during periods when the water level is low or is high, respectively.

Key words: leaf histology, bromeliad, Pitcairnioideae, rheophytic environment.

RESUMO: (Morfoanatomia foliar da reófito *Dyckia distachya* Hassler (Bromeliaceae)). Este estudo relaciona a morfoanatomia foliar de *Dyckia distachya* com o habitat reofítico. Foram utilizadas folhas de plantas jovens e adultas provenientes de três populações dos Rios Pelotas e Uruguai (SC, Brasil), cultivadas em casa de vegetação. As folhas de *D. distachya* são constituídas por lâmina e bainha, têm a forma lanceolada e bordos serreados. A epiderme da lâmina foliar possui: membrana cuticular espessa; células com paredes espessas e lignificadas, exceto a periclinal externa; e corpos silicosos no lume. Estômatos tetracíticos, em depressões individuais são protegidos por tricomas peltados; ambos restritos às zonas intercostais, na face abaxial. Características epidérmicas sugerem vantagem quanto à perda hídrica durante as trocas gasosas, em períodos de vazantes. O mesófilo é formado por: hipoderme constituída por fibras septadas (ao longo da face adaxial e regiões costais abaxiais) ou esclereídes (em regiões intercostais abaxiais); hidrênquima, tecido mais amplo; clorênquima localizado adaxialmente aos feixes vasculares colaterais; e aerênquima, em comunicação direta com os estômatos. A bainha foliar não possui tricomas e estômatos. *Dyckia distachya* possui características xeromorfas e hidromorfas que podem ser relacionadas com as necessidades impostas pelos períodos de vazante e cheias do rio, respectivamente.

Palavras-chave: histologia foliar, bromélia, Pitcairnioideae, ambiente reofítico.

INTRODUCTION

Rheophytes are species of plants that occur exclusively beside swift-running streams and rivers that experience frequent and sudden floods (Van Steenis 1981, 1987). Klein (1979), Van Steenis (1981), and Reis *et al.* (2005) discuss the morphological and ecological aspects of this type of plant. Literature covering the anatomy of rheophytes is limited to some works about Asian species, such as species of Asteraceae (Nomura *et al.* 1986, Usukura *et al.* 1994, Tsukaya 2002) and pteridophytes (Kato & Imaichi 1992a, 1992b, Imaichi & Kato 1992, 1993), and works about Brazilian species are limited to one species of Rutaceae (Arioli *et al.* 2008) and one Bromeliaceae (Lobo & Santos 2007).

The family Bromeliaceae is distributed almost exclusively in tropical and warm regions of the Americas, except for *Pitcairnia feliciana* (A. Chev.) Harms and Mildbr., which is found in Africa (Judd *et al.* 1999,

Benzing 2000); in Brazil, there are 40 genera and 1200 species (Souza & Lorenzi 2005). This family is comprised of three subfamilies: Pitcairnioideae, Tillandsioideae, and Bromelioideae (Smith & Downs 1974). The genus *Dyckia* belongs to the Pitcairnioideae (Dahlgren 1985), which is comprised of 103 species (Smith & Downs 1974) that are dispersed throughout South America, especially in the central and southern regions of the country (Reitz 1983). In Santa Catarina, in southern Brazil, there are 12 species (Reitz 1983), among which *D. brevifolia* Baker, *D. distachya* Hassler, and *D. ibiramensis* Reitz are herbaceous rheophytes (Klein 1979).

According to Reitz (1983) and Reis (2005), *Dyckia distachya* (gravata) is a rupicolous rheophyte adapted to extreme variations of high (e.g., floods) and low water periods, and is characteristic and exclusive to islands or rocky edges of riverbanks that are next to rapids of the Uruguay River and Pelotas River in southern Brazil. Currently, Brazilian plant populations are facing

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extinction due to hydroelectric power plants and *Dyckia distachya* is on the Official List of Brazilian Endangered Species (MMA 2008).

The adaptations that allow a plant to survive in a particular environment are the result of continuous selective pressure and may be expressed structurally (Eames & MacDaniels 1947, Metcalfe 1983, Fahn & Cutler 1992). Such adaptations can be seen in rheophytes because the environment they grown in can be dry or wet, due to frequent changes in the level of water.

The goal of this study, which was based on plant samples from Brazil, was to analyze the morphoanatomical characteristics of the leaves of *D. distachya*, and relate these characteristics to the rheophytic habitat in which they live. This type of research on endangered species and their relationship to the environment is extremely important for conservation programs that use the data to help make decisions about their initiatives.

MATERIALS AND METHODS

Nine rosettes of *Dyckia distachya* Hassler (Bromeliaceae) were used in this study. The plants were kept in a greenhouse and came from distinct populations located on the shores of the Pelotas River and Uruguay River (Santa Catarina, Brazil). Exsiccate of *D. distachya* (access numbers 36278 and 36279) were deposited in the Flor Herbarium in Florianópolis, Santa Catarina.

Completely expanded leaves were paradermally, transversally, and longitudinally sectioned in the middle of the sheath and blade within the central portion of each part. Cross sections of the leaf margin were also made. In order to determine the origin of the tissues, different regions of young leaves and/or primordial leaves were sectioned.

Temporary, semipermanent, and permanent slides were made for studies using light microscopy. Sections were manually made using a razor blade for mounting temporary slides with water and semipermanent slides with glycerinated-gelatin (Kaiser 1880, cited in Kraus & Arduin 1997).

The histochemical tests performed were the following: reactive of Steimetz, for suberin, lignins, cutin, cellulose, mucilage starch, and phenolic compounds (Costa 1982); Sudan IV, for oils and cutin (Costa 1982); acid floroglucin, for lignin (Costa 1982); tionin, for mucilage (Purvis et al. 1964, cited in Kraus & Arduin 1997); chloridric acid, for calcium oxalate crystals (Johansen 1940); and phenol, for silica (Johansen 1940). Small samples, for permanent slides, were fixed in 2.5% glutaraldehyde, in phosphate 0.1 M sodium buffer, pH 7.2, dehydrated in ethanol graded series and included in hydroxyethylmethacrylate (Historesin, Leica), according to the manufacturer's guidelines. Sections that were 8 µm thick were obtained using a Leica RM 2125 RT microtome and stained with aqueous 0.25% Toluidine Blue (Ruzin 1999) or with basic fuchsin/astra blue (Alquini & Brito 1996). A Zeiss-Jena light microscope with a camera lucida was used for

drawing. Macroscopic images were taken using a Leica MPS 30 DMLS light microscope and Sony P92 digital camera.

For studies using scanning electron microscopy (SEM), samples were fixed, dehydrated and immersed in hexamethyldisilazane (HMDS), replacing the critical point of CO₂, which reduced the superficial tension through the subliming process, avoiding the collapse of the structures (Bozzola and Russel 1991). The dry samples were mounted on aluminum stubs and coated with 20 nm of gold using a Baltec CED030 sputter coater, and they were then observed using a Phillips XL30 SEM. The chemical elements that constituted the crystals were identified using an X-ray detector of Si-Li with a Super Ultra Thin Window, with a Link-Oxford EDX system, coupled to the SEM.

The leaf index (LI) was calculated by the equation $LI = L/W$, where L is the length and W is the width of the leaf blade (Van Steenis 1987). To do so, the dimensions of the leaf blade were measured: length (L = longitudinal axis, from the base until the apex) and width (W = cross axis, from margin to margin, at the middle region). The stomata were counted using light microscopy and semipermanent slides. The dimensions of the guard cells were measured by recording the length (longitudinal axis between the two poles of the cell) and width (cross axis, in the middle portion of the cell) of the cells on the epidermal surface. The thickness of the cuticular membrane, epidermis, mesophyll, and tissues that make the mesophyll, were determined in cross sections using permanent slides.

For all quantitative analyses, a minimum number of samples was determined through the equation:

$$n = (t^2 \cdot s^2) / d^2$$

where " t " is given in Student's table at 0.05 level of significance, " s " is the standard deviation, and $d = E/100 \times \mu$ ($E = 15$, at 15% significance level; μ is the mean (Sokal & Rohlf 1969).

RESULTS AND DISCUSSION

The leaves of *D. distachya* are comprised of a blade and sheath (Fig. 1A) and have a spiral phyllotaxis. The plant has short internodes and the leaves form a rosette (Fig. 1B).

The leaf blade is symmetrical and the margins have a slightly convex curvature in relation to the leaf axis. According to the classification of Hickey (1979), the leaves of *D. distachya* have parallelodromous venation. The leaf blades of *Dyckia distachya* have narrow and elongated shapes with acute apices, serrated margins, and truncate bases. Spines are found at both the apex and along the margins.

The leaf blades have an area of $9.99 \pm 2.06 \text{ cm}^2$, are $7.26 \pm 0.84 \text{ cm}$ long, and $1.33 \pm 0.18 \text{ cm}$ wide. The leaf index is 5.52 ± 0.8 which is characteristic of a stenophyll. According to Van Steenis (1981, 1987), rheophytes are generally stenophylls with high leaf indexes (over 4). The author suggests that this is a functional feature

to help the leaf resist flowing water. It is important to note that leaves of many Bromeliaceae are lanceolate (narrow and elongated) (Benzing 1980). For this reason, additional comparative studies among species of the Bromeliaceae are necessary to determine if stenophylly is more common within rheophytic species compared to non-rheophytic species.

The leaf blade is dorsiventral and hypostomatic and it consists of the epidermis, sclerenchyma, hydrenchyma, chlorenchyma, aerenchyma, and vascular bundles. The

adaxial surface is practically flat, whereas the abaxial surface is convex (Fig. 1C), showing saliences and hollows (Fig. 1D, E), which correspond to the costal zones and intercostal zones (Fig. 2A), respectively.

On the adaxial surface of the mature leaves, and the costal zones of the abaxial surface, there are only ordinary epidermal cells. There are stomata and scales (Fig. 1D, E) in the intercostal zones of the abaxial surface between the ordinary epidermal cells. The epidermis is unistratified (Fig. 2B, C). On both surfaces of the blade there is a thick cuticular membrane, which could be seen after performing histochemical tests that showed lipophilic substances throughout this layer and anticlinal and inner periclinal cell walls that were thickened and lignified. From the surface (Fig. 2D), the epidermal cells tend to be rectangular with the longer axis in the apex-base direction of the leaf, and have sinuous anticlinal walls. The features of the epidermal cells of *D. distachya* correspond to the features commonly observed in the Bromeliaceae, as described by Tomlinson (1969).

The stomata are orientated longitudinally and randomly distributed in the depressions of the intercostal zones (Fig. 1E). Esau (1959) reported that in parallel-veined leaves, as in monocotyledons and conifers, the stomata are displayed in parallel files. Tomlinson (1969) reported that the stomata of Bromeliaceae are often restricted to epidermal furrows. In the leaf blades of *D. distachya* there are 176.05 ± 35.62 stomata/mm².

The *D. distachya* guard cells are slightly elevated and curved in relation to the surrounding epidermal cells (Fig. 3A-D). This is similar to *D. floribunda* described by Chodat & Vischer (1916, cited in Tomlinson 1969). The guard cells are 20.01 ± 1.97 µm long and 8.31 ± 1.32 µm wide; the stomatic pore is 11.14 ± 1.73 µm long and 5.10 ± 1.30 µm wide. The epidermal depression of each stoma makes it difficult to identify the type of stoma as well as obtain good images of a stoma using light microscopy. However, the stomata are tetracytic because an analysis (of the epidermal surface, cross section, and longitudinal section) showed that there are four subsidiary cells, two lateral and two polar ones, placed below the guard cell (Fig. 3E, F). Chodat & Vischer (1916, cited in Tomlinson 1969) noted the occurrence of two lateral subsidiary cells flanking the guard cells in *D. floribunda*. On the other hand, Krauss (1949) analyzed the ontogeny of the leaves of *Ananas comosus* (L) Merr. (Bromeliaceae) and reported that the stomata consist of four subsidiary cells (two lateral and two polar); the same as what was found for *D. distachya* in this study. Tetracytic stomata occur in many monocotyledons (Tomlinson 1969). Another aspect worth pointing out is the partial obstruction of the substomatic chamber by the subsidiary cells (Fig. 3 C)—a fact that is bound to be relevant to how the plant controls transpiration.

Moreover the specialized characteristics of the stomata and other epidermal features are associated with how the plant manages water (Ziegenspeck 1939, cited in Tomlinson 1969). For example, the stomata are protected

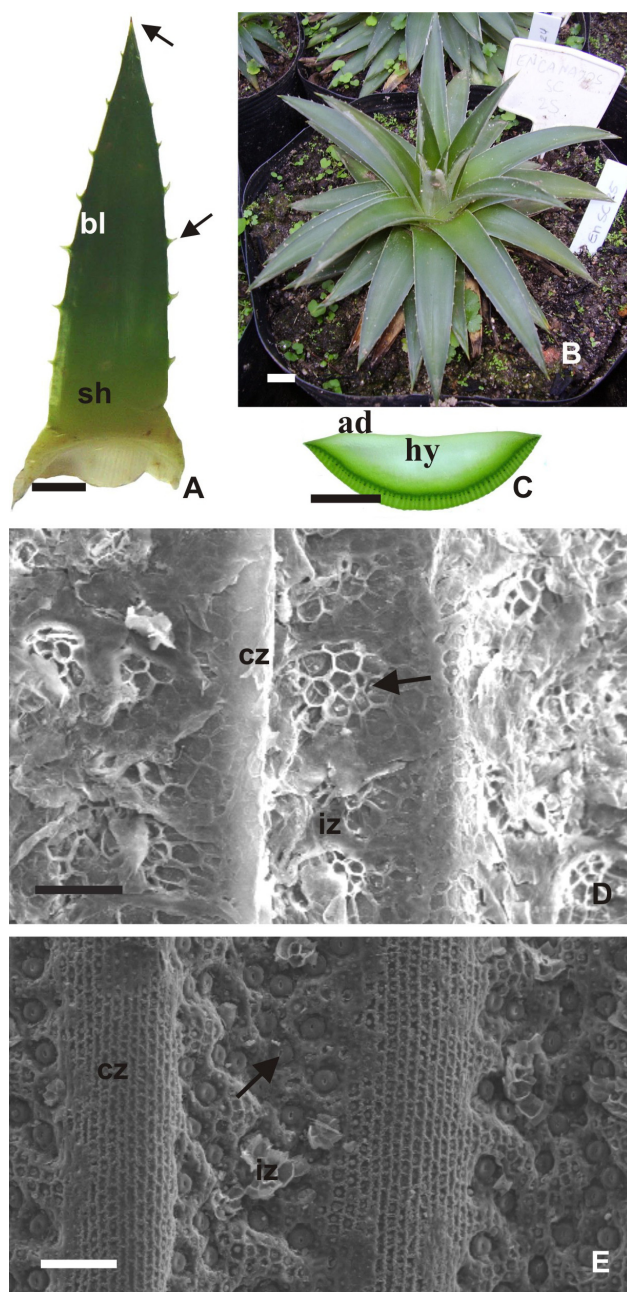


Figure 1. *Dyckia distachya* Hassler. A. Leaf morphology: blade (bl), sheath (sh), spines (arrows). B. Rosette form of plant. C. Leaf blade in cross section: hydrenchyma (hy) adaxial side (ad), the most abundant leaf tissue. D, E. Electronmicrographs showing costal zones (cz) and intercostal zones (iz). D. Adaxial surface with trichomes (arrow). E. Abaxial surface with stomata (arrow), without scales of trichomes. Scale bars (A–C) = 1 cm, (D–E) = 100 µm.

by scales (Fig. 1 D, 3 B, 4 A). In other *Dyckia* species, Strehl (1983) observed stomata totally covered by scales on the abaxial surface of the leaves. Mature leaves of *Dyckia distachya* have scales only on the abaxial surface; however, in young leaves, there are also some scales on the adaxial surface. Tomlinson (1969) reported that some bromeliads have scales restricted to the intercostal bands or in furrows associated with stomata. The scales of *D. distachya* are densely arranged in the intercostal zones; however, their shields are projected on the costal

zones (Fig. 1 D). The scales are multicellular, peltate, and comprised of a stalk and shield (Fig. 4 A-C). The stalk (Fig. 4 C) is formed by three cells, one smaller cell at the base and the others more elongated, perpendicular to the surface of the organ, and derived from periclinal divisions. The peltate scales of *Ananas comusus* (Bromeliaceae) originate from the cells of the protoderm (Krauss 1949). The shield is formed by cells that are parallel to the leaf surface and comprised of two parts: the disc, which is the central part close to the connection

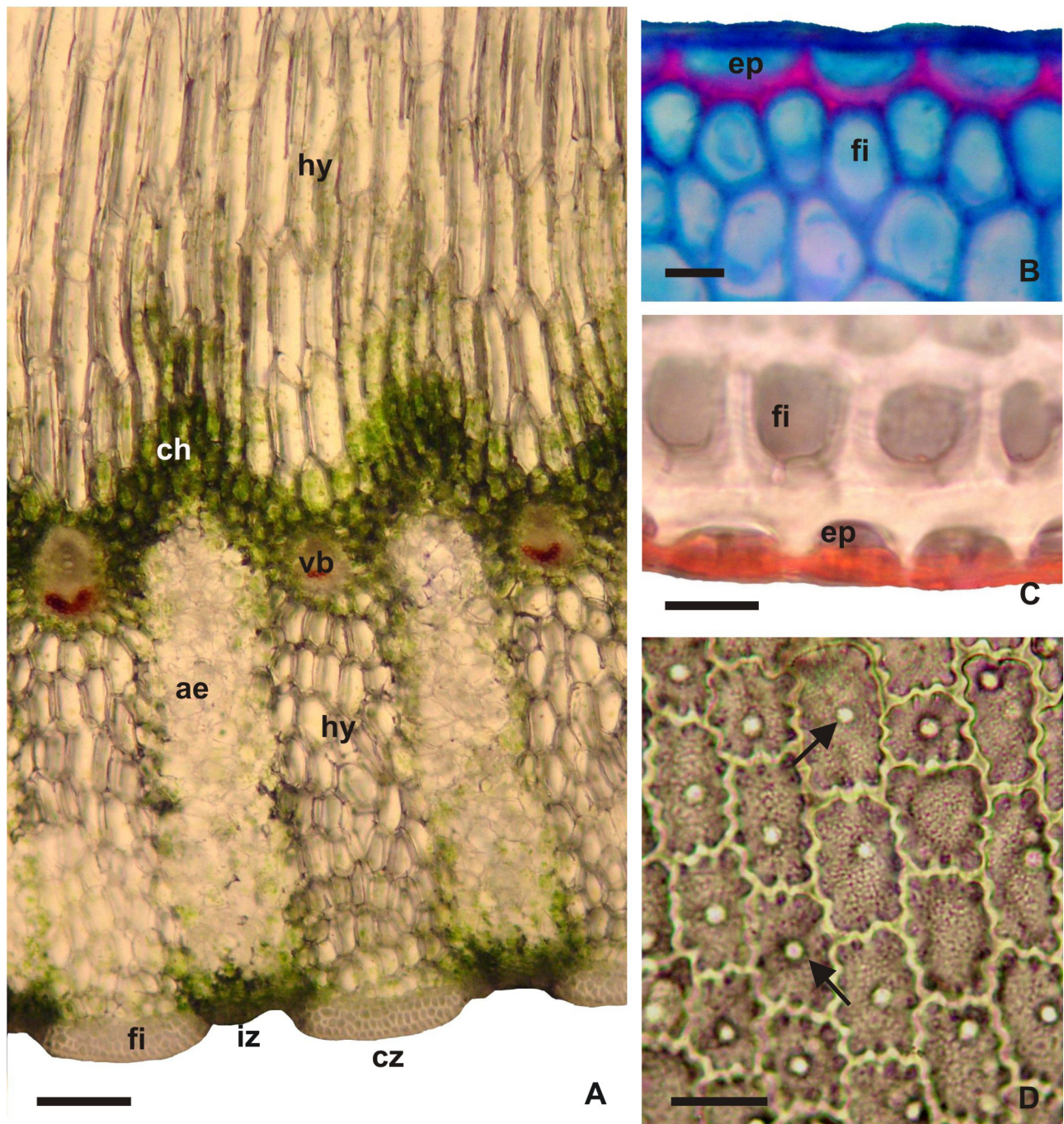


Figure 2. *Dyckia distachya* Hassler. A–C. Photomicrographs of leaf blade cross sections. A. General aspects showing saliences of the costal zones (cz) and hollows of the intercostal zones (iz), vascular bundles (vb), hydrenchyma (hy), chlorenchyma (ch), aerenchyma (ae) and fibers (fi). B, C. Detail of the adaxial (B) and abaxial (C) leaf tissues: epidermis (ep) and fibers (fi). D. Epidermis of adaxial leaf surface with silica bodies (arrows). Scale bars (A) = 200 μ m, (B, C) = 10 μ m, (D) = 20 μ m.

with the stalk; and the wing which is comprised of asymmetric peripheral expansions that are formed by radially elongated cells (Fig. 4 A, B). Tomlinson (1969) reported that peltate scales, typical of Bromeliaceae, have a long uniseriate stalk, totally immersed in the epidermis, and a distal expansion that is perpendicular to this tissue. The analysis of a primordial leaf and very young leaves of *D. distachya* showed that the differentiation of the scales occurs in the acropetal direction of the leaf blade.

In the epidermal cells of *D. distachya*, round silica bodies occur (one per cell) (Fig. 2D). Silica bodies

have been reported in several species of Bromeliaceae (Krauss 1949, Tomlinson 1969, Proença & Sajo 2004). A chemical analysis confirmed the presence of silica bodies (Fig. 4D). A light microscopy analysis using phenol, which reacted positive to the presence of silica, revealed the irregularity of the surface of such bodies, which look like druses. This corroborates Linsbauer's (1911, cited in Krauss 1949) descriptions which reported that silica bodies in *Ananas comusus* and in species of *Dyckia* are conglomerates of tiny silica crystals (i.e., they have a rough surface). Prychid *et al.* (2004) explained that among the monocotyledons, the most frequent type of silica body is spherical, with a surface similar to a druse, rough or spinous, and generally one per cell. The silica bodies are highly refractive (Krauss 1949). Baumert (1907, cited in Krauss 1949) believes that the role of such bodies is to disperse light due to their structure and location in the leaf epidermis.

Sclerenchyma occurs adjacent to the epidermis, on the adaxial surface of the leaf blade of *D. distachya* (Fig. 4 E), with approximately two (2.16 ± 0.37) continuous layers of septate fibers (Fig. 4F). This tissue also occurs on the abaxial surface, but discontinuously, is restricted to the costal zones, and has 3 to 5 (3.32 ± 0.62) layers. At the intercostal zone, the presence of sclereids can be found contouring the areas of the stomata. Tomlinson (1969) mentioned the presence of a sclerotic hypodermis with mechanical functions in the Bromeliaceae. In *D. distachya*, an analysis of young leaves, compared to leaves in other stages of development, revealed that this tissue originated from the meristematic cells of the plant body (i.e., their origin is distinct from the epidermis and, therefore, could be considered the hypodermis). According to Tomlinson (1969) Bromeliaceae leaves with distinct costal and intercostal zones have a discontinuous sclerotic hypodermis that is interrupted by substomatal chambers. Cross and longitudinal sections of young leaves revealed that the differentiation of this subepidermal sclerenchyma is posterior to the differentiation of the epidermal tissue. There is evidence that the apex in the young leaves is the first region to complete the histologic differentiation process because it is comprised only of the epidermis and fibers. Because the differentiation of the epidermal cells and fibers involves the thickening of the cell wall, it becomes impracticable for the cells to divide and laterally expand at the apex of the leaf blade. This explains the very pungent shape of the apex as well as the general shape of the leaf blade, since after the differentiation of the peripheral tissues it is not possible to enlarge the inner tissues. The septate fibers and the sclereids of *D. distachya* have thickened and lignified walls. Tomlinson (1969) described the occurrence of such cell types in other species of *Dyckia*. In the case of septate fibers of *D. distachya*, each fiber is a multicellular unit, shaped (enclosed) by a thickened and lignified cell wall; however, with nucleate cells that are separated by thin septa. According to Mauseth (1988), after the elongation of the original cell, it goes through mitosis and

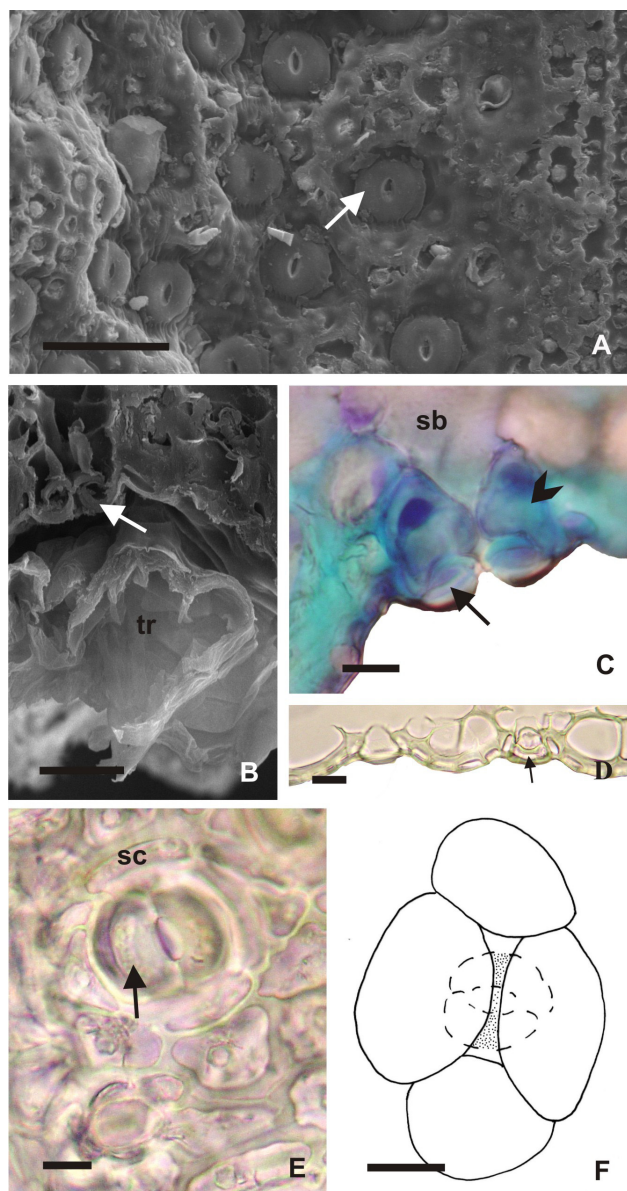


Figure 3. *Dyckia distachya* Hassler. A, B. Electronmicrographs of stomata (arrows). A. Abaxial surface. B. Cross section, covered by trichome (tr). C-E. Photomicrographs of stomata. C. Cross section, the guard cells (arrows) elevated, the subsidiary cells (arrowhead) placed below and the substomatic chamber (sb) with partial obstruction. D. Longitudinal cross section, the guard cells (arrows) elevated. E. Abaxial surface. F. Diagram of stomata from within showing the four subsidiary cells (sc) and two guard cells (arrows). Scale bars (A) = 50 μ m, (B, D, F) = 20 μ m, (C, E) = 10 μ m.

cytokinesis resulting in a chain of cells; the primary cell wall, which separates each new offspring cell, constitutes the septa, which may remain thin or receive secondary deposition. The author also reports that the septate fibers generally remain alive, with an active metabolism, and are important for storing materials (usually starch, oils,

and crystals).

Inside the adaxial fibers, of *D. distachya*, there is hydrenchyma (Fig. 4 E), the most abundant leaf tissue, which is mainly in the middle portion and more scarce near the leaf margins. The cells of this tissue are isodiametric, when peripheral, becoming more elongated

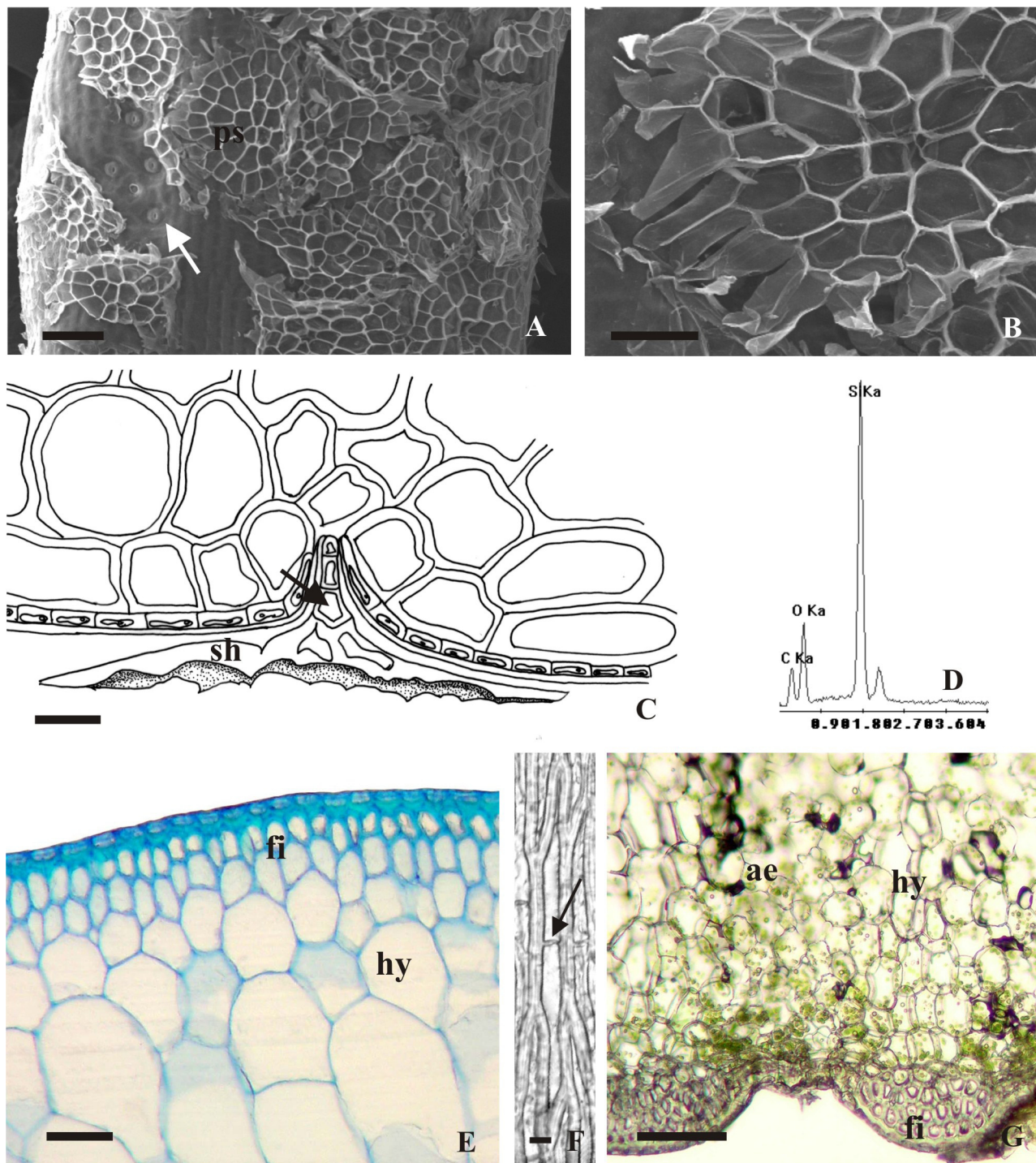


Figure 4. *Dyckia distachya* Hassler. A, B. Electronmicrographs of abaxial surface of young leaf. A. Peltate scales (ps) protecting the stomata (arrow). B. Detail of the peltate scale. C. Diagram of peltate scale in cross-section composed by stalk (arrow) and shield (sh). D. Diagram of chemical microanalysis (EDX-MEV) of a silica body: C (27,69%), O (36,92%), Si (35,39%). E. Photomicrograph of the adaxial leaf tissues in cross section hydrenchyma (hy) and fibers (fi). F. Photomicrograph of the leaf fibers in longitudinal cross section, septa (arrow). G. Photomicrograph of the abaxial leaf tissues in cross section: hydrenchyma (hy), aerenchyma (ae), and fibers (fi). Scale bars (A, G) = 100 µm, (B, E) = 50 µm, (C) = 30 µm, (F) = 10 µm.

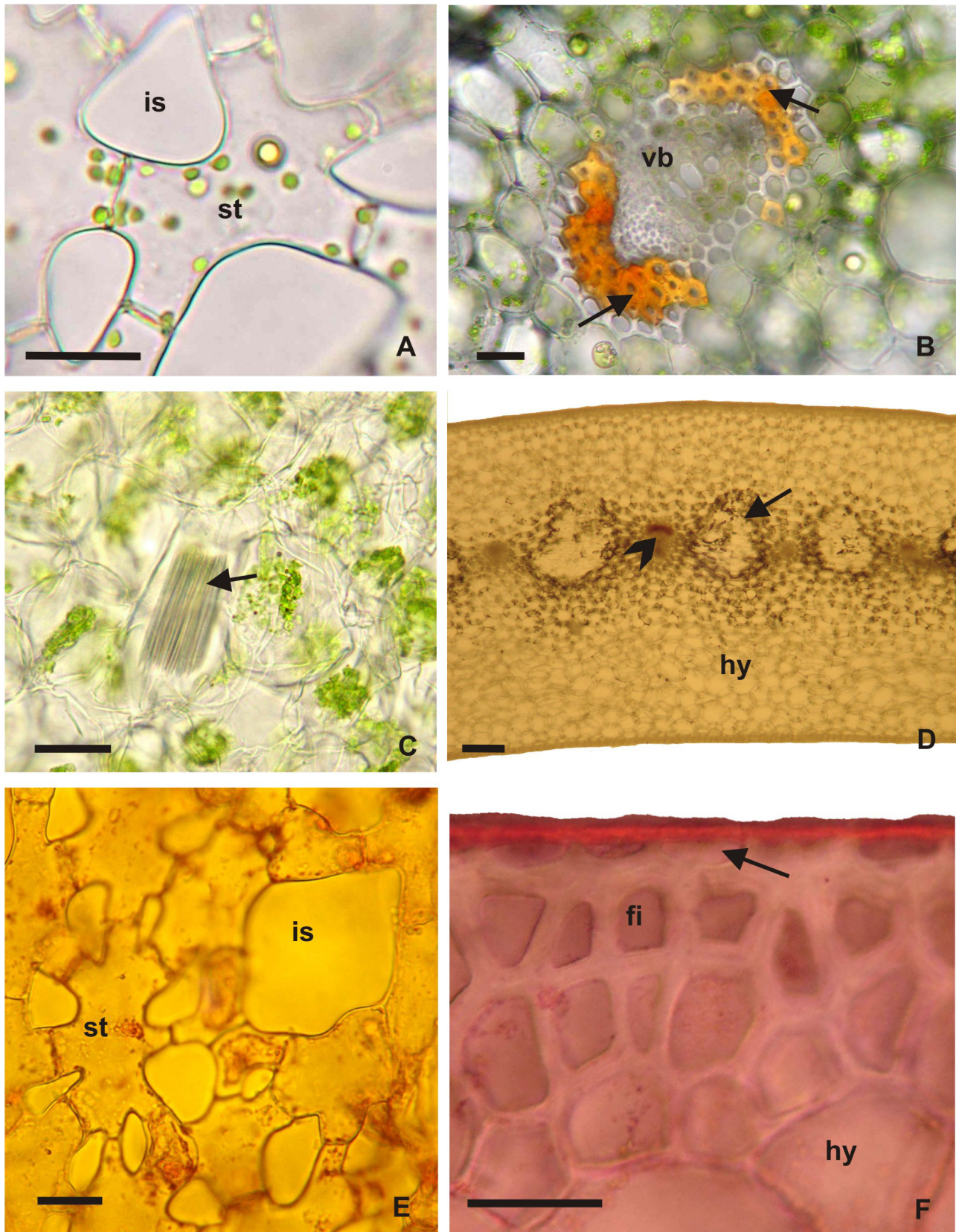


Figure 5. *Dyckia distachya* Hassler. A–C. Photomicrographs of leaf blade cross section. A. Detail of aerenchyma: stellate cell (st), intercellular space (is). B. Collateral vascular bundle (vb) enclosed by fibrous sheath (arrows). C. Detail of chlorenchyma: idioblast with raphids (arrow). D–F. Leaf sheath cross section. D. General aspects: hydrenchyma (hy), aerenchyma (arrow), vascular bundle (arrowhead). E. Details of aerenchyma: stellate cell (st), intercellular space (is). F. Details of adaxial tissues: epidermis (arrow), fibers (fi), hydrenchyma (hy). Scale bars (A, B, E) = 20 µm, (C) = 30 µm, (D) = 150 µm, (F) = 50 µm.

towards the center; they have thin walls and mucilaginous content; the inner cells of this tissue may be chlorophyll. The hydrenchyma cells cause the leaves to be succulent - a remarkable feature of the Bromeliaceae (Krauss 1949). Tomlinson (1969) reinforced the fact that most terrestrial bromeliads, which are usually spinous xerophytes, store water in tissue that has thin cell walls, lacks chlorophyll, and contains mucilage. Krauss (1949) reported that the mucilaginous substances, besides absorbing water, may also retain water due to their colloidal nature. Eames & MacDaniels (1947) attributed the importance of the sclerenchyma to the prevention of water loss and also protection against intense light as well as sustaining the structure of the leaves.

On the abaxial surface, inside the fibers, at the costal zone, hydrenchyma occur (Fig. 4G); however, the cells are slightly different compared to the adaxial hydrenchyma. The cells of the abaxial hydrenchyma are isodiametric, containing mucilage and some chloroplasts. This tissue probably receives a limited amount of light because of the position of the adaxial vascular bundles and abaxial fibers. Alternating with the hydrenchyma, there is aerenchyma that is restricted to the intercostal zone and directly linked with the stomata and chlorenchyma (Fig. 2A). The aerenchyma tissue is formed by stellate cells, which comprise an interlaced net with ample intercellular spaces (Fig. 5A). Haberlandt (1928) reported that gaseous exchanges, in organs permanently submerged or that grow in very wet soils, may be totally dependent on aerial spaces formed in their tissues. According to Fahn (1974), the formation of channels containing stellate cells by the aerenchyma is very common in hydrophytes. The intercellular spaces may form a connected system along the entire plant, resembling honeycombs (Cutter 1978). The authors highlight that in aquatic plants this system may also provide mechanical resistance and promote sustentation. Lambers *et al.* (1998) reinforced the importance of a continuous system of aerial spaces for plants of flooded soils because it allows the oxygen to be transported from the stems to the roots. Thus, the presence of aerenchyma may be relevant to the adaptation of *D. distachya* when it is submerged in water. On the other hand, the presence of aerenchyma in leaves of Bromeliaceae has been reported by Krauss (1949), Tomlinson (1969), and Benzing (1980).

The vascular bundles (Fig. 5 B) are collateral and enclosed in a sheath of septate fibers; even *in vivo* samples are red-orange. The presence of phenolic compounds in the sheath of septate fibers was verified by histochemical tests. The vessel elements are reduced in diameter and length, and the perforation plates are well inclined. Such features are classically related to dry environments (Fahn and Cutler 1992). The vascular bundles inside the leaf blades of *D. distachya* are surrounded by chlorenchyma, however the chlorophyll also occurs in other tissues. The chlorenchyma cells are isodiametric with thin walls and they may contain mucilage. Idioblasts with calcium oxalate raphids occur in the chlorenchyma cells (Fig. 5

C), but they may also be found in other parenchymatous tissues of the leaf blade. Raphids are abundant in Bromeliaceae (Tomlinson 1969).

The leaf sheath is concave and whitish, which occurs because the sheaths overlap and receive little light. The predominant tissue in the leaf sheath of *D. distachya* is hydrenchyma (Fig. 5D), which is comprised of isodiametric cells that have thin walls and lack intercellular spaces. At the central region of the sheath there is aerenchyma alternating with the vascular bundles (Fig. 5D). The aerenchyma is comprised of stellate cells (Fig. 5E); this tissue helps circulate gases between the leaf blade, the stem, and the roots. The vascular bundles are collateral, contoured by parenchyma, made of cells smaller than the hydrenchyma, and contain starch grains. The epidermis is unistratified (Fig. 5F) and lined by a thickened cuticular membrane. There are neither stomata nor scales. The epidermal cells are longitudinally elongated, have sinuous anticlinal walls, and lack silica bodies. Under the epidermis, on both leaf surfaces, sclerenchymatous tissue is found (Fig. 5F) with approximately two layers of septate fibers.

The features observed in the leaves of *D. distachya* are similar to those described by several authors (Krauss 1949, Benzing 1980, Tomlinson 1969, Proença & Sajo 2004, Scatena & Segecin 2005, Sousa *et al.* 2005) for Bromeliaceae species, and these features may favor the survival of this species in a rheophytic habitat. When the water level of a river is low, the vegetation along its margins is submitted to intense light from the sun and subjected to xeric conditions. Some anatomical features of the leaf of *D. distachya* are related to conserving water during these periods. The thick cuticular membrane and the presence of silica bodies in the majority of the epidermal cells help in the reflection and refraction of light. The deep location (individual depressions and intercostal furrows) of the stomata and their protection by peltate scales help conserve water by creating a microclimate. To help maintain the hydric balance, the achlorophyll and mucilaginous hydrenchyma store water. The hydrenchyma also minimizes solar irradiation, aiding in the reduction of the temperature of the plant and blocking excess light, thus, guaranteeing the optimal amount of light for the inner tissues. During periods when the water level is high (e.g., during a flood), when *D. distachya* is submersed in water, the limiting factors are related to the strength of the water current and the diffusion of gasses within the plant. The stenophylly and the fact that the leaf has layers of septate fibers and subepidermal sclereids aid in the plants ability of withstand strong water currents. The first guarantees a hydrodynamic shape and the second reinforces the structure of the leaves. The ability that the leaves have to store and circulate gases, which are factors controlled by the aerenchyma in the leaf mesophyll, is a hydromorphic characteristic and is needed during periods of flooding. The presence of mucilage also contributes to helping the plant store water at an optimal level because it prevents

the apertures of the stomata from opening and absorbing water that is not needed.

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