coding regions of chloroplast DNA. Pl. Mol. Bio. 17: 1105–1109.

The Plant Names Project. 1999. International Plant Names Index. Published on the Internet; http://www.ipni.org [accessed 31 July 2003].

Thollesson, M. 2000. Increasing fidelity in parsimony analysis of dorid nudibranchs by differential weighting, or a tale of two genes. Mol. Phyl. Evol. 16: 161–172.

van den Berg, C., W.E. Higgins, R.L. Dressler, W.M. Whitten, M.A.S. Arenas, A. Culham and M.W. Chase. 2000. A phylogenetic analysis of Laeliinae (Orchidaceae) based on sequence data from internal transcribed spacers (ITS) of nuclear ribosomal DNA. Lindleyana 15: 96–114.

Whitten, W.M., N.H. Williams and M.W. Chase. 2000. Subtribal and generic relationships of Maxillarieae (Orchidaceae) with emphasis on Stanhopeinae: combined molecular evidence. Am. J. Bot. 87: 1842–1856.

Williams, N.H., M.W. Chase, T. Fulcher and W.M. Whitten. 2001. Molecular systematics of the Oncidiinae based on evidence from four DNA sequence regions: expanded circumscriptions of *Cyrtochilum, Erycina, Otoglossum,* and *Trichocentrum* and a new genus (Orchidaceae). Lindleyana 16: 113–139.

Withner, C.L. 1988. The Cattleyas: The Cattleyas and their Relatives. Timber Press, Portland, Oregon.

———. 1998. *Brassavola, Encyclia,* and Other Genera of México and Central America: The Cattleyas and their Relatives. Timber Press, Portland, Oregon.

Selbyana 24(2): 180–189. 2003.

FOLIAR ANATOMY OF FIVE *VRIESEA* SECT. *XIPHION* (BROMELIACEAE) SPECIES

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ABSTRACT. The present work aims to extend the knowledge of the genus *Vriesea* Lindley, contributing data on the foliar anatomy of five species: *Vriesea bituminosa* Wawra, *V. longiscapa* Ule, *V. triligulata* Mez, *V. gigantea* Gaudich., and *V. fosteriana* L.B.Sm. Transverse and longitudinal cuts were made manually in fully expanded leaves. The usual histochemical tests were performed. Features typical to the Bromeliaceae were peltate trichomes, single layered epidermis, stomata located only on the abaxial surface of the leaves, a hypodermis with mechanical and water-storing functions, and collateral vascular bundles. Observed differences among the species were number of trichomes in both lamina and sheath, number of cells on the trichome shield, and number of layers of the aquiferous hypodermis. Many of the observed characteristics confirm the xerophytic nature of the leaves. The anatomical organization of the leaves in the studied Bromeliaceae could be related both to environmental pressures as well as to phylogenetic relationships.

RESUMO. O presente trabalho tem como objetivo ampliar o conhecimento acerca do gênero *Vriesea* Lindley fornecendo dados sobre a anatomia foliar de cinco espécies: *Vriesea bituminosa* Wawra, *V. longiscapa* Ule, *V. triligulata* Mez, *V. gigantea* Gaudich. e *V. fosteriana* L.B.Sm. O material botânico foi cortado a mão livre. Testes histoquímicos usuais foram realizados. Os resultados mostraram que as espécies exibem as características típicas da família: folhas hipoestomáticas, epiderme simples dotada de tricomas peltados multicelulares, hipoderme com funções mecânica e de reserva de água, tecido clorofiliano diferenciado em paliçádico e esponjoso do tipo braciforme e feixes vasculares colaterais. Foram notadas diferenças entre as espécies com relação à quantidade de tricomas ao longo da folha; número de células que compõem o escudo dos tricomas e número de camadas da hipoderme aquífera. As características observadas confirmam a natureza xerofítica das folhas. A organização anatômica das folhas das Bromeliaceae estudadas pode ser uma resposta a pressões ambientais assim como refletir relações filogenéticas.

Key words: Bromeliaceae, *Vriesea,* leaf anatomy, epiphytes

INTRODUCTION

Comprising nearly 2700 species (Benzing 2000) in 56 genera (Grant & Zijlstra 1998), the Bromeliaceae family presently represents an extremely diversified group of vascular plants, which has colonized a variety of neotropical habitats (Dahlgren et al. 1985). Specialization related to water-storage, represented by sheath development as well as xeromorphic leaf structure in many species, is a remarkable feature of this family, not yet sufficiently investigated. Family representatives are found both in xeric and mesic environments, from sea level to mountaintops, and account for a considerable portion of the epiphytic vegetation in neotropical forests (Benzing 1990).

Although some anatomic studies have been conducted (Tomlinson 1969, Benzing 1970, 1976, Braga 1977, Souza & Neves 1996, Sajo et al. 1998), the existing data on particular groups are fragmented and little explored, as for example the genus *Vriesea* Lindl. Considering the present infra-generic division of *Vriesea,* the Section *Xiphion* comprises ca. 130 species (Luther & Sieff 1994, 1997a, 1997b, Luther 2001). These species are characterized predominantly by an inflorescence with dull colors; corolla with cream, yellow, or reddish petals; androecium and gynoecium included within the corolla; and stigma with the convolute-blade type morphology (Grant 1993, 1995a, 1995b).

The present work provides data on the foliar anatomy of five species of the *Xiphion* section of *Vriesea,* which are discussed in the light of

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possible plant-environment relationships and as a contribution to the systematics of the family.

MATERIAL AND METHODS

The following species were examined: *Vriesea bituminosa* Wawra, *V. longiscapa* Ule, *V. triligulata* Mez, *V. gigantea* Gaudich., and *V. fosteriana* L.B.Sm. Plant material for the first three species was collected at Serra de Macaé de Cima (Costa 1993), and exsiccates are deposited at the Rio de Janeiro Botanical Garden Herbarium (RB). For the fourth species, material was collected by T. Strehl, in January 1994, at Santo Antônio da Patrulha Municipality, Rio Grande do Sul; and exsiccates are deposited at Herbarium Alarich Schulz (HAS); and finally *V. fosteriana* material comes from Espírito Santo State and is deposited at Museu Nacional Herbarium (R).

All species are typical tank-bromeliads with epiphytic habit, except *Vriesea fosteriana,* which is rupicolous. Fully expanded leaves (lamina and sheath) were preserved in ethanol 70° GL (Jensen 1962). Transverse and longitudinal sections were then prepared by hand. Sections were stained with a mixture of safranine and Astra blue (Kraus & Arduin 1997). Epidermal analyses were carried out on material dissociated by immersion in Schultze's mixture (Sass 1951). Paradermic sections were then stained with aqueous safranine (Johansen 1940). Stomata were classified according to Metcalfe (1963). Numbers of stomata and trichomes were recorded as the mean obtained from 20 1-mm^2 fields. The number of cells composing the wing corresponds to the mean of counting 15 intact scales. Sections of non-fixed material were used for the following histochemical tests: Sudan IV (Jensen 1962) for cutinized walls and drops of oil, chlorzinc iodine (Strasburger 1924) for cellulosic walls; phloroglucinol (Foster 1949) for lignified walls; iodine in potassium iodide (Johansen 1940) for starch; iron sulfate solution (Johansen 1940) for phenolic compounds, and clove oil/phenol (Netolitzki 1935) for siliceous structures.

RESULTS

In studying the leaf anatomy of *Vriesea* species, we focused on the structure of plant cells in the epidermis and mesophyll. Resulting descriptive data follows.

Epidermis

The structure of the epidermis on the median third and sheath levels was examined in face view (adaxial and abaxial surfaces) and transverse section (FIGURES 1, 2; TABLES 1–3).

Face view at median third level

The epidermis, seen in a face view of the adaxial surface at the median third level, is composed of trichomes and common epidermal cells disposed parallel to the longest axis of the lamina (FIGURE 1A). The common epidermal cells, rectangular with rather sinuous and thickened anticlinal walls, show a siliceous body (FIGURE 1F). The trichomes are distributed randomly along the epidermal tissue (FIGURE 1A, B). Histochemical tests show the presence of phenolic substances in such cells, the reaction being more evident in cells from the central disk. TABLE 1 presents the average proportion of trichome distribution over this leaf region.

On the abaxial surface, the epidermis presents organization in costal and intercostal bands of ordinary epidermal cells. The presence of siliceous bodies can be observed (FIGURE 1B); the stomata are of the tetracytic type with kidney-shaped guard cells, and they are arranged in two or four ranks (TABLE 2). Around the stomatal complex, the epidermal cells show straight, thickened walls, the contents of which present similar histochemical reactions to those from subsidiary cells. The stomata may occur either isolated or in groups of two to five, among which the trichomes are located. Trichomes appear restricted to intercostal bands (FIGURE 1B) in an average that varies from 13.8 (*Vriesea gigantea* and *V. longiscapa*) to 20.9 (*V. trigulata*) (TABLE 1).

Face view at sheath level

In face view of the epidermis at sheath level, features generally are similar to those described, except for a remarkable absence of stomata on either side of the leaf and the presence of trichomes that show rather different morphological features from those of the median third (FIGURE 2A–E). In this region, the scales average a larger number of wing cells compared to the median third (TABLE 3). In both regions, the scales have only one ring of eight cells. The wing cells have elongated forms with unevenly thickened radial walls in the portion facing the cell interior, granting varied forms to the lumen, especially in *Vriesea gigantea* and *V. triligulata* (FIGURE 2B, C). These scales are randomly distributed. The common epidermal cells, with strongly thickened and sinuous anticlinal walls, contain a siliceous spherical body at a rate of one per cell, rarely two.

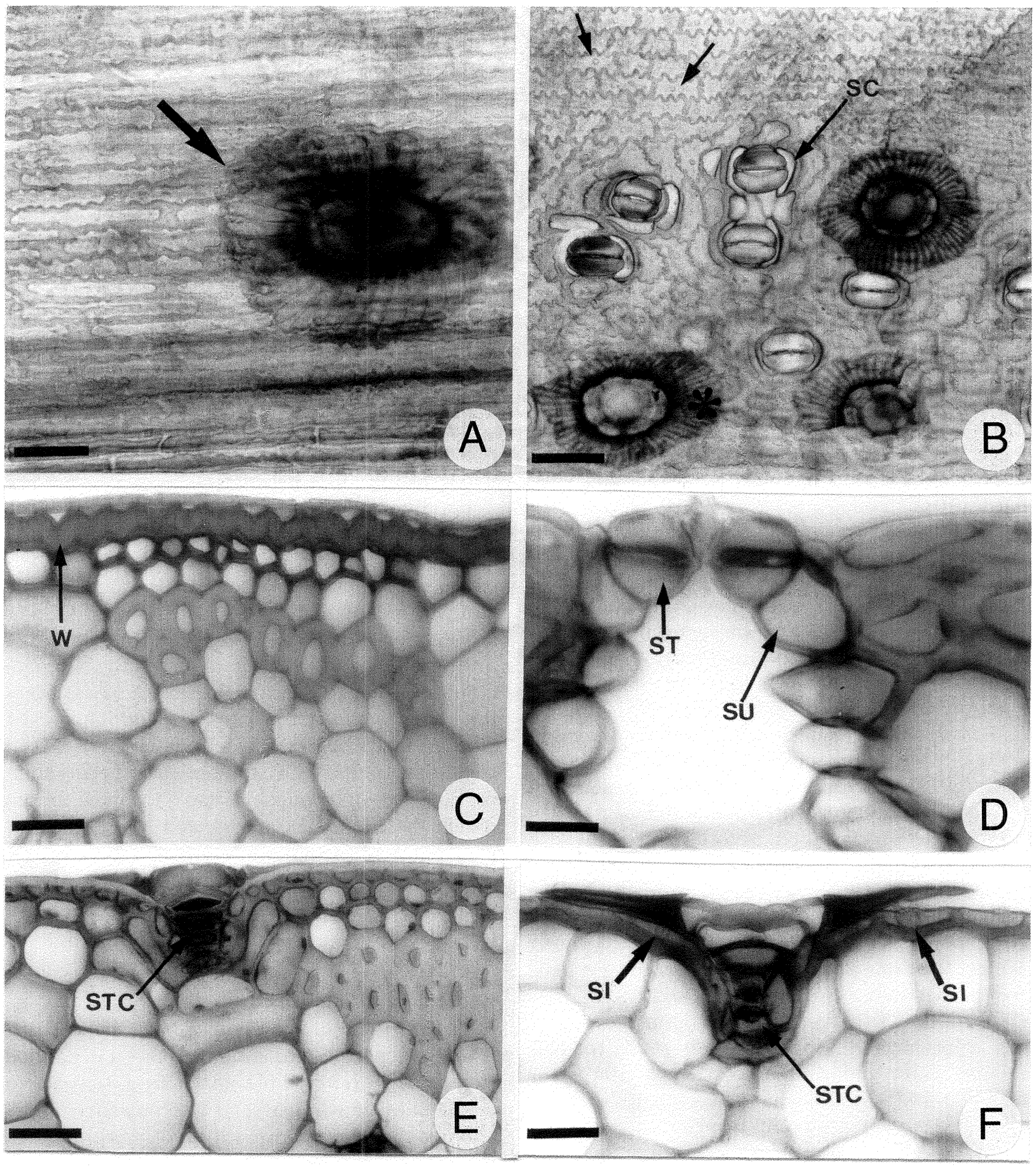

FIGURE 1. Foliar epidermis of *Vriesea* (*Xiphion*) species in face view and transverse section (bar = 25 μm). **A.** *V. longiscapa,* adaxial surface, trichome shield (arrow). **B.** *V. fosteriana,* abaxial surface, stomatal complex (SC), trichome shield (*), ordinary epidermal cells with silica bodies (arrows). **C.** *V. triligulata,* adaxial surface, inner periclinal wall (W). **D.** *V. fosteriana*: stomatal cell (ST), subsidiary cell (SU). **E.** *V. bituminosa,* trichome stalk cells (STC). **F.** *V. fosteriana,* trichome stalk cells (STC) and silica body (SI).

Transverse section at median third and sheath levels

The epidermis, in a transverse section of the lamina at the median third level, is shown to be single layered (FIGURE 3B) and covered by a cuticle layer that ranges from thin in *Vriesea longiscapa* to very thick in the others. The outer periclinal walls are thin, whereas the inner ones are strongly thickened, as in *V. triligulata* (FIGURE 1C), and weakly lignified. Because of the evident wall thickening, the epidermal cells show reduced lumen, which tend to different shapes in the species studied (TABLE 2). Similar characteristics can be observed at the sheath lev-

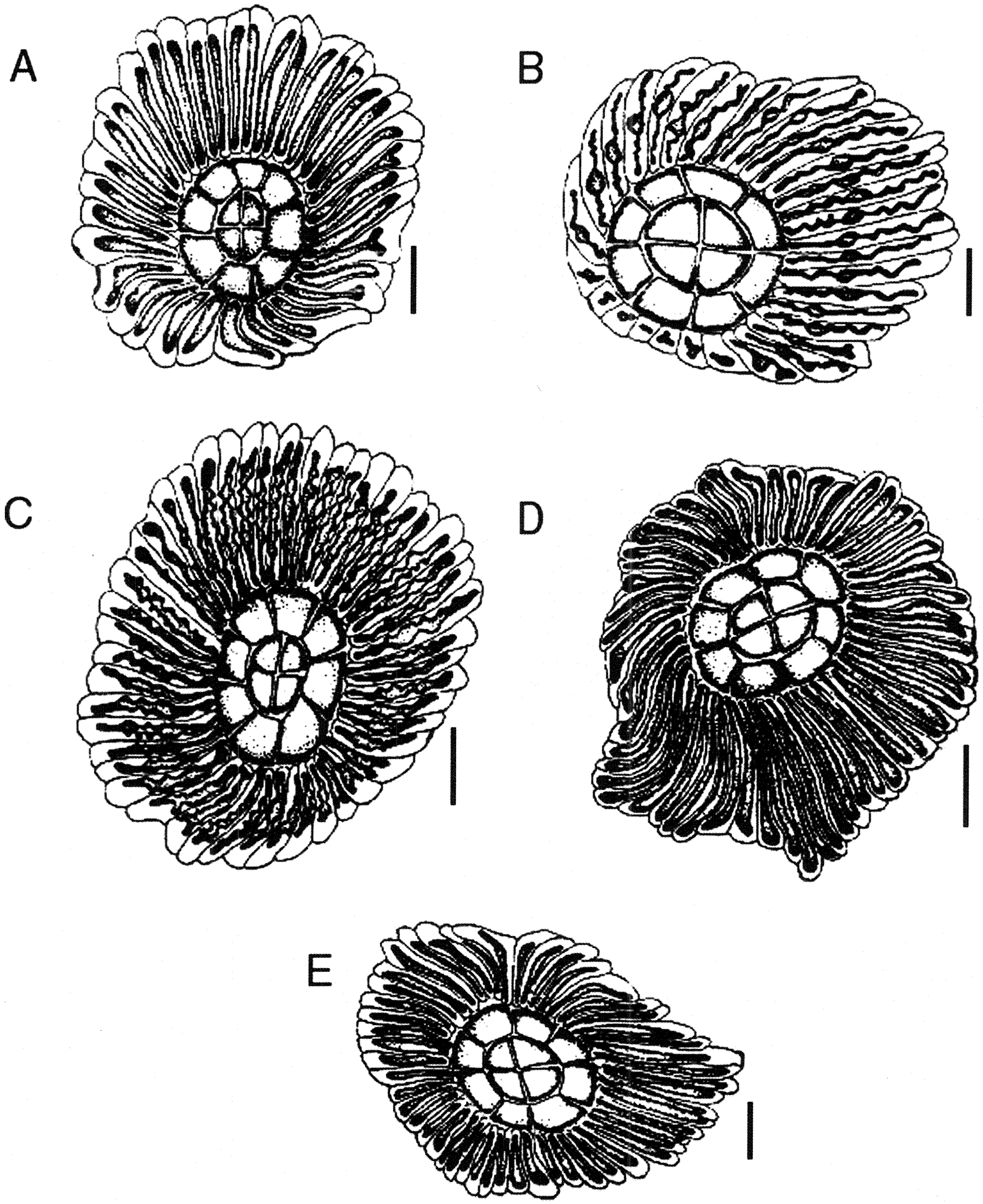

FIGURE 2. Drawings showing trichome shields of sheath leaf of *Vriesea* (*Xiphion*) species. **A.** *V. longiscapa.* **B.** *V. triligulata.* **C.** *V. gigantea.* **D.** *V. fosteriana.* **E.** *V. bituminosa* (bar = 25 μm).

el, except, however, for the presence of a very thin cuticular layer.

The scales on both sides of the leaf, in the median third and sheath regions, are inserted at an inferior level to that of the other epidermal cells, with a group of five to seven cells supporting the shield and constituting the foot of the trichome (FIGURE 1E, F). The transverse section shows that the periclinal walls of the shield cells present thickened primary walls, especially

TABLE 1. Average number of trichomes and stomata (mm²) from the leaf median third and sheath level of *Vriesea* (*Xiphion*) species.

	Trichomes median third level		Trichomes sheath level		
Vriesea species	Adaxial surf.	Abaxial surf.	Adaxial surf.	Abaxial surf.	Stomata median third level
V. bituminosa	4.5	13.9	—	—	41.2
V. fosteriana	10.2	15.4	16.72	12.04	42.1
V. gigantea	7.7	13.8	19.73	15.3	46.4
V. longiscapa	7.4	13.8	9.56	8.12	25.7
V. triligulata	10.3	20.9	17.24	13.28	38.0

those of the central disk, the lumen of which is restricted to a narrow slot. Under the shield, the dome cell has a roughly triangular section, while other cells have rectangular sections. Thin primary cell walls generate a strong reaction for the presence of lipid substances.

Stomata, covered by cuticle that invades part of the substomatal chamber, may occur at the same level of other epidermal cells (*Vriesea triligulata, V. longiscapa, V. fosteriana*), slightly above them (*V. bituminosa*), or below them (*V. gigantea*) (TABLE 2). The stomatal cells have reduced lumen with strongly thickened periclinal walls (FIGURE 1D). The surrounding sub-epidermal cells of the stomatal complex send out projections towards the pore and partially obliterate the stomatal opening. These projections have primary walls.

Mesophyll

The structure of the mesophyll, including the vascular system, was examined in transverse section at median third and sheath levels (FIGURE 3, TABLE 4).

Median third level

The mesophyll shows a tendency to the dorsiventral structure (FIGURE 3A, B). Below the epidermis there is a hypodermis with a differentiated mechanical portion whose cell walls (two or three layers) may appear strongly thickened as in *Vriesea fosteriana* (FIGURE 3A) and *V. triligulata* (FIGURE 3C) and thinner in *V. gigantea, V. bituminosa* (FIGURE 3B) and *V. longiscapa.* Under this stratum, three to seven layers of non-chlorophyllous cells with relatively thin walls constitute a water-storing tissue (TABLE 4). Among these cells are groups of lignified fibers (FIGURE 1C), consisting of a varied number of elements remarkably developed in portions related to large-sized vascular bundles (FIGURE 3B). The chlorophyllous parenchyma, with extremely thin-walled cells, occupies the median-lower region of the mesophyll and is differentiated into palisade parenchyma and spongy parenchyma with stellate cells (FIGURE 3A, B, TABLE 4). This organization is loosely differentiated in *V. longiscapa* and very clear in the other species. Idioblasts containing raphides are observed in the spongy parenchyma of *V. gigantea.* In the portion turned to the abaxial surface of the lamina, the stellate parenchyma cells touch the substomatal chambers (FIGURE 3B).

Sheath level

In the sheath, subjacent to the abaxial face of the epidermis, occurs a layer (simple in *Vriesea longiscapa* and double in the other species) of narrow-lumen cells with extremely thickened walls and numerous simple pits. These cells show a strong reaction to phenolic substances, and negative reaction to lignin. The subepider-

TABLE 2. Other epidermic cells features distinguishing the five *Vriesea* (*Xiphion*) species studied.

Vriesea species	No. stomata ranks FV, MTL	Lumen shape in common epid. cells TS, MTL	Stomatal cell position in common epidermal cells TS, MTL	Subepid. cell section shape M, SL
V. bituminosa	4	pentagonal	slightly above epid. cells	circular
V. fosteriana	2	rectangular	same level	elongated
V. gigantea	4	pentagonal	above epid. cells	elongated
V. longiscapa	2	rectangular	same level	thickened
V. triligulata	2	triangular	same level	circular

Note: FV = face view. TS = transverse section. M = mesophyll. MTL = median third level. SL = sheath level.

TABLE 3. Average number of cells that integrate the trichome shield wings of *Vriesea* (*Xiphion*) species.

	Median third level		Sheath level	
Vriesea species	Adaxial surf.	Abaxial surf.	Adaxial surf.	Abaxial surf.
V. bituminosa	30.0	32.3	40.5	55.6
V. fosteriana	40.6	46.0	51.7	52.6
V. gigantea	45.0	—	62.2	56.8
V. longiscapa	32.0	32.0	37.3	42.7
V. triligulata	30.0	32.3	34.6	54.7

mal cell sections have different shapes (TABLE 2). The subepidermal tissue makes this leaf region extremely hard, with very resistant foliar sheaths. It is evident that in this leaf region, the intercellular spaces of the spongy parenchyma are well developed. The stellate cells produce a continuous lacuna system from the sheath to the top of the lamina.

Vascular system

Along the whole extension of the leaf, the vascular system is represented by collateral vascular bundles in a parallel disposition (FIGURE 3A, B). Surrounding the large-sized vascular bundles are two distinct bundle sheaths. The outermost, the endodermis, consists of a single layer of parenchymatous cells (FIGURE 3B). These cells are chlorophyllous in the third median of the lamina and lack chloroplasts in the sheath where they contain starch grains. Adjacent and internal to the endodermis is a fibrous pericycle. In large vascular bundles, these fibers may separate xylem and phloem (FIGURE 3B). The walls of the pericycle fibers are thickened, strongly lignified, and pitted. In the middle-sized and small-sized vascular bundle fibers of the mesophyll, walls are weakly lignified and thin with an ample lumen, disposed in such a way as to form extensions that interrupt the endodermis and reach the two portions of the aquiferous hypodermis (FIGURE 3A, B).

DISCUSSION

The Bromeliaceae are an angiosperm family predominantly neotropical, distributed along ecosystems with a range of temperature, precipitation, soil composition, and light incidence (Benzing 1990). Their success in dealing with these habitats may be related to development of anatomical and morphological characteristics that enable water retention and carbon assimilation and their progressive shift to the epiphytic habit (Schimper 1884, Tomlinson 1969, Medina 1990).

The sinuosity of the ordinary anticlinal cell walls of the epidermis observed in the study species is a common feature of many bromeliad species in all three subfamilies (Tomlinson 1969). Sinuosity may protect internal tissues, maintaining leaf structure during periods of change in water availability, winds, and rain (Haberlandt 1928, Krauss 1949). Spherical silica bodies are common in Bromeliaceae species (Tomlinson 1969).

In many species of the family, stomata show modifications related strictly to their water budget. They are generally restricted to the abaxial surface of the leaves and located at the same level, or in depressions of different depths in relation to the epidermis (Tomlinson 1969, Sajo et al. 1998). Adaxial stomata were recorded for *Tillandsia* L. spp. (Souza & Neves 1996), *Catopsis berteroniana* (Schult. f.) Mez (Tomlinson 1969), and *Brewcaria* L.B. Sm., Steyerm. & H. Rob. spp. (H. Robinson pers. comm.). Stomata placement exclusively on the abaxial surface of the leaves has been interpreted as a strategy to minimize water loss caused by convection currents or even light breezes that could remove water vapor from the leaf surface (Nobel et al. 1975, Nobel 1991, Mauseth 1988). This may prove to be especially beneficial in the subject species, which have stomata not covered by trichomes. For *Ananas comosus* (L.) Merr., species of *Navia* Mart. ex Schult. f. and *Vriesea splitgerberi* (Mez) L.B. Sm. & Pittendr., Krauss (1949), Robinson (1969), and Braga (1977), respectively, noted that ordinary epidermal cells that surround the stomatal complex show straight walls, thicker than the others. This characteristic also is observed in the studied species, except for *V. bituminosa.* Krauss (1949) suggests that these modified epidermal cells may help protect the stomata from longitudinal stresses applied on the leaves. Peltate trichomes are typical of Bromeliaceae species (Tomlinson 1969). Many of the tank-tillandsioids, among them *Vriesea,* have trichomes that exhibit a moderately high absorptive capacity (Pittendrigh 1948). Such plants have enlarged leaf sheaths, which usually keep a large water supply together with organic debris. In mesic environments, the tank-bromeliads have leaf sheath surfaces sufficiently permeable to allow the plant to acquire needed nutrients for growth up to the adult phase and to produce fruits and seeds a few years after sprouting (Benzing et al. 1978).

Among the Bromeliaceae, the number of trichomes along the leaf may vary depending on leaf surface (more trichomes on the abaxial surface) and on leaf region (more trichomes near the sheath). Although trichomes were generally similar in the five species investigated, some

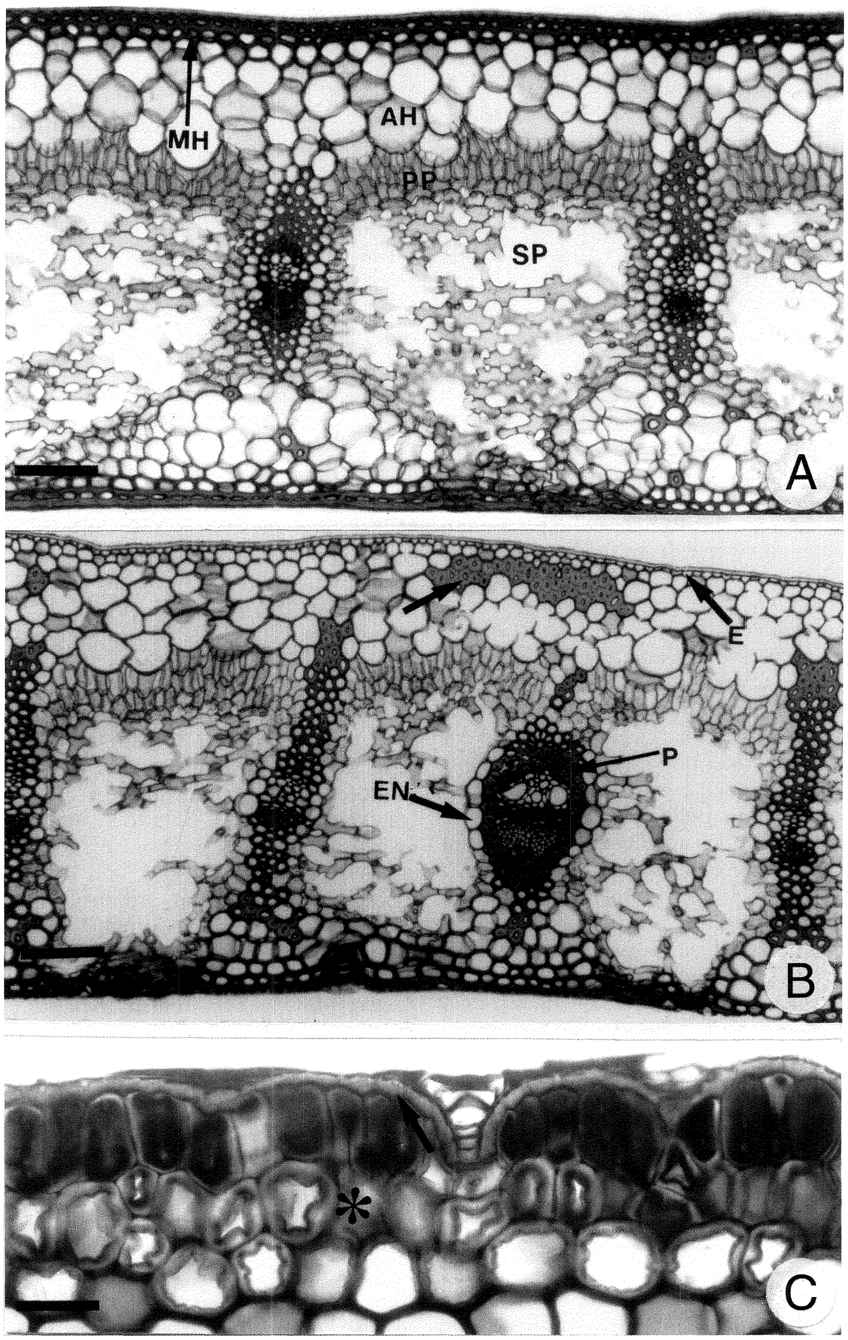

FIGURE 3. Transverse section of foliar lamina and sheath of *Vriesea* (*Xiphion*) species (bar = 100 μm). **A.** *V. fosteriana,* mechanical hypodermis (MH), aquiferous hypodermis (AH), palisade parenchyma (PP), and spongy parenchyma (SP). **B.** *V. bituminosa,* epidermis (E), fiber group (arrow), pericyclic fibers (P), endodermis (EN). **C.** *V. triligulata,* detail of mechanical hypodermal cells with primary thick wall.

TABLE 4. Variability in the number of cell layers of the mesophyll (hypodermis and chlorophyllous parenchyma), at the leaf median third level observed among *Vriesea* (*Xiphion*) species.

Vriesea species	Hypodermis water-storage tissue	Chlorophyllous parenchyma	
		Palisade	Spongy
V. bituminosa	4–5	2–3	10–12
V. fosteriana	3–4	2–3	12–14
V. gigantea	5–6	3–4	10–12
V. longiscapa	3–4	1–2	5–6
V. triligulata	4–5	1–2	6–8

morphological differences were observed in the middle of the leaf when compared to leaf morphology near the sheath. Other studies have reported similar results in relation to structure and distribution of trichomes (Benzing 1970, Benzing et al. 1978). In our study, the leaf sheath has trichomes with wider shields, more numerous and wider wing cells, and denser cytoplasm. Wing cells with differential distribution of the radial wall thickness, such as those in *Vriesea triligulata* and *V. gigantea,* are illustrated by Tomlinson (1969) for *Tillandsia circinnata* Schltdl. and *Glomeropitcairnia penduliflora* (Griseb.) Mez.

The strong reaction of trichome cells to phenolic substances test-observed for the study species may be related to protection against herbivory. In addition, trichomes may be linked to reduced transpiration, at least for some Pitcairnioideae, in which they cover the stomata as a roof (Robinson 1969). When full of air, trichomes are highly reflective and reduce the amount of incident sunlight on the leaf. For example, some populations of *Tillandsia fasciculata* Sw. reflect 42–47% of incident visible light from leaf surface, while mesophytic tank species reflect no more than 28% of incident light (Benzing et al. 1978). This might explain the small number of trichomes observed at the central portion of the leaves of the five studied species when compared to the xerophytic tillandsias described by Souza and Neves (1996).

The cuticle layer of the leaf has functions that are essential for plant survival (Mauseth 1988, Kerstiens 1996, Grubb et al. 1994). The marked thickening and occasional sclerification of the epidermal cell walls, especially from the internal periclinal wall, is a typical bromeliad characteristic reported in all subfamilies (Braga 1977, Souza & Neves 1996, Sajo et al. 1998). During the present study, the presence of lignin was identified with higher intensity in the foliar epidermal cells of *Vriesea triligulata,* both in the median third and sheath; the other species had less lignin. Prime characteristics for efficient moisture conservation inside the leaves of xerophytic species are precise stomatal control and impermeable (though not necessarily thick) cuticle (Turner 1994).

Under the epidermis of the subject species, in the median third level and sheath, layers of nonchlorophyllous cells were observed, forming that what Tomlinson (1969) calls hypodermis. In bromeliads, this hypodermis has mechanical and water-storing functions. Linsbauer (1911) identified an epidermal-hypodermal complex, whose typical function was mechanical, with lignification reaching the first subepidermal layers. This organization provides support to the leaves and protects the internal tissues against herbivory and possibly against intense luminosity. At this same leaf level, the degree of thickening of hypodermal cells adjacent to the epidermis varied. This variation was observed within the same species and among different species. Pita (1997) described a similar characteristic for the median third level of the leaves of *Dyckia* Schultes f. and *Encholirium* Mart. ex Schultes f. species (Pitcairnioideae), in which she also noted quite reduced lumen cells with much thickened and strongly lignified walls.

At the sheath level, the cells of the mechanical hypodermis, mainly those from the abaxial surface, are in permanent contact with the accumulated water in the tank formed by the leaf sheaths. The presence of phenolic compounds saturating the cell walls may be beneficial in preventing leaf decay or organismal attack. Pits on cell walls also demonstrate the benefits of such tissue in water and nutrient transport from the tank to the internal layers of the hypodermis. Water-storing tissues in bromeliads has been reported by many authors (Krauss 1949, Tomlinson 1969, Robinson 1969, Sajo et al. 1998).

For *Vriesea gigantea, V. fosteriana,* and *V. bituminosa,* the palisade parenchyma exhibits its typical form with high and narrow cells, which may be an adaptation to the intense light in the environment where they occur. Light has proved to be a major determinant of the degree of development of such tissue (Nobel et al. 1975, Nobel 1991, Mott & Michaelson 1991). Among the study species, *V. longiscapa* occurs in a mesic habitat (on low parts of trunks, rarely in the canopy), with epiphytic habit. This can explain the loose differentiation of the organization of the palisade parenchyma. The leaf sheath has only stellate parenchyma cells, which may be responsible for the transport gases found inside leaves, much like an aerenchyma [large intercellular spaces] (Matsukura et al. 2000).

The collateral vascular bundles are surrounded by parenchymatous cells and fibers forming bundle sheaths. Although ontogenetic tests have not been performed for the identification of the origin of these layers, for the purpose of this study, the cells were called endodermis (parenchymatous sheath) and pericycle (fibrous sheath). This follows nomenclature from Van Fleet (1961), Esau (1965), Flores (1975), and Menezes et al. (2000).

Our results indicate that the *Vriesea* species analyzed exhibit the features cited by Tomlinson (1969) as typical to the Bromeliaceae: peltate trichomes, single-layered epidermis, stomata located only on the abaxial surface of the leaves, a hypodermis with mechanical and water-storing functions, and collateral vascular bundles. Many of the characteristics observed confirm the xerophytic nature of the leaves, previously mentioned by other authors. Xerophytic leaves may allow establishment of these plants in environments inhospitable for other plants. The analyzed species presented characteristics typical of groups phylogenetically related (e.g., trichomes typical of the subfamily Tillandsioideae). Well developed spongy parenchyma with stellate cells also are present in a number of species, such as the nidularioid-complex, subfamily Bromelioideae. Despite the xeric habitat (rocky outcrops and high altitude fields), species of *Alcantarea* E. Morr. ex Mez are similar to species of *Vriesea* (Arruda unpubl. data). The *Vriesea* studied here, however, have an anatomical organization distinct from related atmospheric-tillandsias. In contrast with some *Tillandsia* investigated by Souza and Neves (1996), the analyzed *Vriesea* present stomata only on the abaxial surface, dorsiventral mesophyll with large development of spongy parenchyma, and stomata not covered by trichomes. This suggests that the anatomical organization of the leaves in Bromeliaceae could be related to environmental pressures as well as to phylogenetics. Sajo et al. (1998) suggested that the occurrence of similar structures in taxa with more remote relationships may be the result of similar environmental conditions or conservation of characteristics from a common ancestor.

The present work is a preliminary contribution to the study of leaf anatomy of *Vriesea* species. The use of anatomical features in the systematics of the genus remains premature, considering the large number of existing species and species-complexes. We suggest that detailed studies will produce better organizing patterns of the internal foliar structure, which may allow the compilation of more significant data for further comprehension of Bromeliaceae biology and systematics.

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LITERATURE CITED

Benzing, D.H. 1970. Foliar permeability and the absorption of mineral and organic nitrogen by certain tank bromeliads. Bot. Gaz. 131(1): 23–31.

———. 1976. Bromeliad trichomes: structure, function, and ecological significance. Selbyana 1(4): 330–348.

———. 1990. Vascular Epiphytes. General Biology and Associated Biota. Cambridge University Press, Cambridge.

———. 2000. Bromeliaceae, Profile for an Adaptive Radiation. Cambridge University Press, Cambridge.

Benzing, D.H., J. Seemann and A. Renfrow. 1978. The foliar epidermis in Tillandsioideae (Bromeliaceae) and its role in habitat selection. Am. J. Bot. 65(3): 359–365.

Braga, M.M.N. 1977. Anatomia foliar de Bromeliaceae da Campina. Acta Amazon. 3 (supl.): 1–74.

Costa, A. "*Vriesea* Lindley (Bromeliaceae) na Reserva Ecológica de Macaé de Cima, Nova Friburgo, RJ, Brasil." Master Dissertation, Museu Nacional/ Univ. Federal do Rio de Janeiro, Brazil, 1993.

Dahlgren, R.M.T., H.T. Clifford and P.F. Yeo. 1985. The Families of the Monocotyledons. Springer-Verlag, Berlin, Heidelberg.

Esau, K. 1965. Anatomy of Seed Plants. John Wiley & Sons, New York.

Flores, E.M. 1975. Algunos aspectos de anatomía foliar comparada de dos especies de Bromeliaceae (*Aechmea mexicana* Baker y *Hechtia glomerata* Zucc.). Rev. Biol. Trop. 23(1): 29–52.

Foster, A.S. 1949. Practical Plant Anatomy. D. van Nostrand Inc., New York.

Grant, J.R. 1993. True tillandsias misplaced in *Vriesea* (Bromeliaceae: Tillandsioideae). Phytologia 75(2): 170–175.

———. 1995a. The resurrection of *Alcantarea* and *Werauhia,* a new genus. Trop. und Subtrop. Pflanz. 91: 1–59.

———. 1995b. Addendum to "The resurrection of *Alcantarea* and *Werauhia,* a new genus" (Bromeliaceae: Tillandsioideae). Phytologia 78(2): 119–123.

Grant, J.R. and G. Zijlstra. 1998. An annotated catalogue of the generic names of the Bromeliaceae. Selbyana 19(1): 91–121.

Grubb, P.G., I.M. Turner and D.F.R.P. Burslem. 1994. Mineral nutrient status of coastal hill dipterocarp forest and *Andinandra belukar* in Singapore: analysis of soil, leaves and litter. J. Trop. Ecol. 10: 283–335.

Haberlandt, G. 1928. Physiological Plant Anatomy. Mc Millan & Co. Ltd., London.

Jensen, W.A. 1962. Botanical Histochemistry. H.H. Freemann & Co., San Francisco.

Johansen, D.A. 1940. Plant Microtechinique. Paul Hoeber Inc., New York.

Kerstiens, G. 1996. Cuticular water permeability and its physiological significance. J. Exp. Bot. 47: 1813–1832.

Kraus, J.E. and M. Arduin. 1997. Manual Básico de Métodos em Morfologia Vegetal. Ed. Universidade Rural, Seropédica.

Krauss, B.H. 1949. Anatomy of the vegetative organs of the pineapple, *Ananas comosus* (L.) Merr. II. The leaf. Bot. Gaz. 110 (3): 333–404.

Linsbauer, K. 1911. Zur physiologischen anatomie der epidermis und des durchlüftungsapparates der Bromeliaceen. Sber. Akad. Wiss. Wien 120: 319–348.

Luther, H.E. 2001. De Rebus Bromeliacearum III. Selbyana 22(1): 34–67.

Luther, H.E. and E.Sieff. 1994. De Rebus Bromeliacearum I. Selbyana 15(1): 9–93.

———. 1997a. De Rebus Bromeliacearum II. Selbyana 18(1): 103–148.

———. 1997b. De Rebus Bromeliacearum: Addenda et corrigenda. Selbyana 18(2): 215.

Matsukura, M., M. Kawai, K. Toyofuku, R.A. Barrero, H. Uchimiya and J. Yamaguchi. 2000. Transverse vein differentiation associated with gas space formation—fate of the middle cell layer in leaf sheath development of rice. Ann. Bot. 85: 19–27.

Mauseth, J.D. 1988. Plant Anatomy. The Benjamim Cunmings Publishing Co. Inc., California.

Medina, E. 1990. Ecofisiologia y evolucion de las Bromeliaceae. Bol. Acad. Nac. Ciênc. 59: 71–100.

Menezes, N.L., D.C. Silva and G.F.M. Pinna. 2000. Folha. Pp. 303–325 *in* B. Apezzato-da -Gloria and S.M. Carmello-Guerreiro, eds. Anatomia Vegetal. Universidade Federal de Viçosa, Viçosa.

Metcalfe, C.R. 1963. Comparative anatomy as a modern botanical discipline with special reference to recent advances in the systematic anatomy of monocotyledons. Adv. Bot. Res. 1: 101–147.

Mott, K.A. and O. Michaelson. 1991. Amphystomy as an adaptation to high light intensity in *Ambrosia cordifolia* (Compositae). Am. J. Bot. 78(1): 76–79.

Netolitzki, F. 1935. Das tropische parenchyn. *In* K. Linsbauer, ed. Handbuch der Pflanzenanatomie. Gerbuder Borntraeger, Berlin.

Nobel, P.S. 1991. Physicochemical and Environmental Plant Physiology. Academic Press, San Diego.

Nobel, P.S., L.J. Zaragoza and W.K. Smith. 1975. Relation between mesophyll surface area, photosynthetic rate and illumination level during development for leaves of *Plectranthus parviflorus* Henckel. Plant Physiology 55: 1067–1070.

Pita, P.B. "Estudo anatômico dos órgãos vegetativos de *Dyckia* Schultes f. e *Encholirium* Mart ex Schultes f. (Bromeliaceae) da Serra do Cipó, MG." Master Dissertation, Instituto de Biociências, Universidade de São Paulo, 1997.

Pittendrigh, C. 1948. The Bromeliad-Anopheles-Malaria complex in Trinidad. I. The bromeliad flora. Evolution 2: 58–89.

Robinson, H. 1969. A monograph on foliar anatomy of the genera *Connellia, Cottendorfia* and *Navia.* Smiths. Cont. Bot. 2: 1–41.

Sajo, M.G., S.R. Machado and S.M. Carmello-Guerreiro. 1998. Aspectos estruturais de folhas de bromélias e suas implicações no agrupamento de espécies. Pp. 101–111 *in* E.M.C. Leme. *Canistropsis,* Bromélias da Mata Atlântica. Ed. Salamandra, Rio de Janeiro.

Sass, J.E. 1951. Botanical Microtechnique. The Iowa State College Press, Iowa.

Schimper, A. F. W. 1884. Ueber bau und Lebenweise der Epiphyten. Westindiens. Bot. Zbl. 17: 192–195.

Souza, R.C.O.S. and L.J. Neves. 1996. Anatomia foliar de quatro espécies de *Tillandsia.* Bromélia 3(2): 28–39.

Strasburger, E. 1924. Handbook of Practical Botany. George Allen & Nonwin, Ltd., London.

Tomlinson, P.B. 1969. Anatomy of Monocotyledons. III. *in* C.R. Metcalfe, ed. Commelinales-Zingiberales. Clarendon Press, London.

Turner, I.M. 1994. Sclerophylly: primary protective? Func. Ecol. 8: 1–32.

Van Fleet, D.S. 1961. Histochemistry and function of the endodermis. Bot. Rev. 27: 165–220.

Selbyana 24(2): 190–195. 2003.

SPECIES RICHNESS OF VASCULAR EPIPHYTES IN TWO PRIMARY FORESTS AND FALLOWS IN THE BOLIVIAN ANDES

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ABSTRACT. To study the impact of deforestation on vascular epiphyte diversity, we compared species richness in plots in primary forest and adjacent 15-year-old fallows in two different sites in the Yungas of Bolivia, including submontane forest near Sapecho (500–1200 m) and montane forest in the Parque Nacional Cotapata (1500–2500 m). Nearly 500 species of epiphytes (25 families, 110 genera) were recorded, and a 1.0 ha plot composed of eight subplots with a total surface of 0.32 ha of montane forest had up to 175 species. These forests rank among the richest worldwide in terms of epiphyte diversity. Fallows had 60–70% fewer species than neighboring natural forest. Numbers of species of orchids, bromeliads, Hymenophyllaceae, and Grammitidaceae were much lower in fallows than in primary forest, but hemiepiphytic aroids, Polypodiaceae and Aspleniaceae, were similar. Reduction of epiphytic species diversity in fallows can be explained by structural characteristics of the fallow trees, the lack of a dense moss cover, and the drier microclimate in the fallows.

Key words: epiphytes, vascular epiphytes, biodiversity, canopy studies, tropical rain forest, secondary vegetation, Bolivia

INTRODUCTION

The montane forests of the tropical Andes are among the world's richest ecosystems in terms of number of species (Barthlott et al. 1996). Vascular epiphytes, among them orchids, bromeliads, aroids, and ferns, are a key component of these forests, both in terms of species richness (Gentry & Dodson 1987, Ibisch 1996, Nieder et al. 1999) and their roles in water-balance and nutrient cycles (Nadkarni 1984, Coxson & Nadkarni 1995). These forests are now disappearing rapidly, as the result of increasing human pressures in the region. Deforestation in the tropical Andes is ca. 90% or ten times higher than in Amazonia (Henderson et al. 1991). The rapid destruction poses a major threat to the epiphytic vegetation and calls for measures to safeguard their existence.

Very little is known about effects on the epiphyte communities of these forests following deforestation nor about the ecology of the epiphytes in secondary forests (e.g., Hietz-Seifert et al. 1996, Engwald 1999). This investigation is the first one of its kind in the Central Andes. We investigated how the diversity of vascular epiphyte communities of Bolivian montane forests is affected by deforestation. We also documented the epiphyte diversity of secondary forest.

METHODS

Study Sites

The study was conducted in two different sites on the eastern slopes of the Andes in the Department of La Paz, Bolivia, the so-called "Yungas of La Paz" (FIGURE 1). The first study site is near the village of Sapecho (450 m; 15°27′–32′S, 67°18′–23′W), located along the Alto Beni River at the northeastern base of the Serranía Marimonos. Temperature in Sapecho averages ca. 24–25°C during the day, and annual rainfall varies from ca. 1500 mm in the valley to 2000 mm on the slopes. The rainy season of October–May alternates with a marked dry period of June–September (Elbers 1995). The natural forest on the slopes of the Serranía Marimonos is an evergreen or semi-evergreen submontane forest comprised of trees 30–40 m in height and a well developed shrub layer. Tree diversity averages ca. 120 species per ha (Seidel 1995).

Since the 1960s, the population of the Alto Beni region has increased considerably because of colonization by immigrants from the country's altiplano regions. The increased population has led to the conversion of large tracts of forests into agricultural fields. As a result, the lower slopes of the Serranía Marimonos are covered by a mosaic of arable fields and fallow land with trees up to 15 years old and a canopy height of 12–15 m (Krömer 2003). The most common pioneer trees of the fallows are *Cecropia* spp.,

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