Selbyana 14: 80–88

WATER ACQUISITION STRATEGY SHIFTS IN THE HETEROPHYLOUS SAXICOLOUS BROMELIAD, VRIESEA GENICULATA (WAWRA) WAWRA

FERNANDA REINERT* AND S. T. MEIRELLES

Departamento de Ecología, Instituto de Biología, Universidade Federal do
Rio de Janeiro Ilha do Fundao, Rio de Janeiro—RJ 21941 Brazil

ABSTRACT. *Vriesea geniculata* produces two distinct morphological forms during its life cycle. Juveniles exhibit non-impounding rosettes composed of succulent narrow leaves bearing numerous elaborated trichomes. Adults possess an impounding rosette featuring flat broad leaves with nearly glabrous blades. Trichomes with a 4+8+16+32+64 shield cell pattern cover 80% of juvenile foliage. Trichomes with a reduced shield cell arrangement (4+8+32) cover less than 14% of leaf base in the adult form. Stomatal density increases distally while trichome density increases towards the leaf base in both life forms. There are no adaxial stomata. Both atmospheric and tank forms show C_3 photosynthesis.

The Bromeliaceae, with more than 2,000 species, is widely distributed in the Neotropics, from exposed areas to tropical rain forest understories, both at high altitudes in the Andes and at sea level (Medina *et al.* 1977, Gilmartin 1983, Utley & Burt-Utley 1983, Smith 1989). This wide range of distribution is partially explained by the high structural and physiological diversity found within the Bromeliaceae (Medina *et al.* 1977, Griffiths & Smith 1983, Utley & Burt-Utley 1983). The family is characterized by species with water-impounding or non-impounding leaf rosettes with different degrees of succulence bearing various types and densities of foliar trichomes. The so-called terrestrial species produce a well developed root system functioning in water and nutrient uptake, whereas epiphytes basically produce roots which primarily attach the plant to a substrate. Bromeliads also differ in relation to CO_2 fixation patterns, showing either Crassulacean Acid Metabolism (CAM) or the C_3 pathway, which may be related to modes of water and nutrient procurement (Pittendrigh 1948, Griffiths & Smith 1983).

Some members of the Tillandsioideae subfamily exhibit two distinct developmental forms, which represent the extremes of the range of adaptation to epiphytism within the Bromeliaceae. Juvenile foliage has some of the characteristics of adult atmospheric epiphytes, and adult leaves are morphologically similar to adult tank-forming epiphytes (Adams & Martin 1987). This heterophyllous condition was reported long ago by Morren (1873), Mez (1904) and Lieske (1914). It was seven decades later, however, that Adams and Martin (1986a, 1986b) studied structural and functional aspects of heterophylly in the epiphytic *Tillandsia deppeana* Steudel. Heterophylly is also present in two other genera of Tillandsioideae, *Vriesa* and *Guzmania* (Lieske 1914).

The present study aims to investigate some structural and physiological aspects of the heterophyllous species, *Vriesea geniculata* (Wawra) Wawra, a saxicolous bromeliad that colonizes steep granite outcrops along the Southeast coast of Rio de Janeiro, Brazil. Individuals are distributed among different sized vegetation islands on bare rock. Sympatric species include members of the Cactaceae, Orchidaceae, Melastomataceae, and Veloziaceae. Adult *V. geniculata* produce rosettes up to 2 m in diameter that bear inflorescences of similar height from November to February. Juveniles produce a non-impounding rosette featuring small succulent narrow leaves densely covered with trichomes. Conversely, adults produce an impounding rosette composed of flat broad leaves covered with wax-bearing trichomes mainly within the tank. Soil water and nutrients are rarely available under natural conditions, and must be obtained through the leaves. The sclerified root system is predominantly mechanical, affixing the plant to the substrate. Bearing two different strategies of water and nutrient uptake, each life-form will be under very different microenvironmental conditions (Utley & Burt-Utley 1983, Martin *et al.* 1985, Smith *et al.* 1986a).

MATERIAL AND METHODS

Samples of *Vriesea geniculata* were collected in Pedra da Urca (22°57′13″S and 43°59′13″W) and Pedra de Itacoatiara (22°58′39″S and

---

* Present address: Agriculture and Environmental Science 30, University of Newcastle Upon Tyne NE1 7RU, UK.

Part of this work was supported by CNP*q*, Brazil.

43°01′31″W), both in the State of Rio de Janeiro. The climate of both sites is wet tropical with low precipitation in June and July (Nimer 1989).

The leaf anatomy of 39 plants was examined, including juvenile, intermediate and adult forms. Leaves were divided into six regions: apex (A), middle (M) and base (B) for both abaxial (AB) and adaxial (AD) surfaces. Epidermal sections were cut by hand with a razor blade and stained with eosin. The number of stomata and trichomes were counted and the area occupied by the latter was measured in 1 mm^2 with a light microscope and an ocular graticule. In order to determine the trichome shield patterns, the leaf surface was scraped with a razor blade and trichomes stained with eosin. The area of trichomes was estimated geometrically assuming an elliptical base and using a light microscope with an ocular micrometer scale. Thirty trichomes were examined in each of the six regions of the leaf. Because of their small size, seedlings were only divided into base and apex. The adult and intermediate leaf areas were estimated using the triangle area formula. Since the juveniles have linear leaves, we considered only their leaf length.

Micrographs of foliar surfaces were taken with a Scanning Electron Microscope JEOL 25-S-II. Samples were prepared according to Sabatini *et al.* (1962). For light microscopy, fresh sections of longitudinal tissue were obtained with a razor blade and stained in Safrablau (Bukatsch 1972).

Plant material for $\delta^{13}C$ determination was collected in both localities in June 1988. Samples were dried at 60–70°C and ground in an electric mill. Samples were combusted in an oxygen atmosphere. Carbon isotope analysis was carried out using a DELTA E Finnigan Mat triple collector according to Moreira (1988).

Colorimetric determination of daily acid fluctuation in seedlings were carried out following Medina (1961). Ten samples were collected in November 1987 and May 1988. Adult plants were not used because of their large size. Samples were maintained under a 12 hr photoperiod of natural sun light.

Leaf samples from ten plants at each of the three stages of development were collected in December 1987 and July 1988 at dawn and dusk for acid titration analysis. Plants were macerated and then acid titrated to pH 7 with a pH meter with 0.01 M NaOH.

Five juvenile plants and two leaves of five intermediates and adults were collected in September and December 1989 were used for chlorophyll analysis. Samples were separately homogenized in 80% acetone. The homogenates were vacuum filtered and analyzed spectrophotometrically, according to Arnon (1949).

Voucher specimens were deposited at Jardim Botânico, Rio de Janeiro, Brazil (RB 283950 and RB 285577).

RESULTS

The anatomical description is similar to that of the whole family (Tomlinson 1969, Smith & Downs 1974, 1977). Epidermal peels showed rectangular cells with sinuous walls arranged in longitudinal files. Between the two epidermis, there is a hypodermis (FIGURES 1A, 2A). The ontogeny of this tissue was not studied and it is not possible to state whether it is a true hypodermis (ground tissue) as observed in other species of the Bromeliaceae (Tomlinson 1969), or if it represents an exception and is derived from the epidermis, and is therefore a multiple epidermis. The hypodermis is often differentiated into three layers of mechanical tissue consisting of thick-walled cells and an inner, colorless thin-walled water storage tissue. The colorless tissue cells are larger in adults than in juveniles. The mechanical tissue is interrupted by stomatal chambers abaxially in the blade region of adult leaves. The water storage tissue has about six cell layers in both abaxial and adaxial surfaces within the leaf base. In the abaxial surface of the rest of the leaf, it is restricted to the costal bands. In juveniles, the hypodermis is not well differentiated into mechanical tissue. The colorless water storage tissue is well developed adaxially (FIGURE 1A, B). In the blade of the adult leaves, the chlorenchyma is anticlinally extended and adaxially more compact above air-lacunae as a "cap" (FIGURE 1B). The intercostal chlorenchyma surrounds and fills the air–lacunae with a reticulum of loosely packed lobed cells. The leaf base is not provided with chlorenchyma and the well-developed air-lacunae are surrounded and filled with a somewhat parenchymatous tissue. Air-lacunae are very pronounced throughout the adult leaves, while they are scarcely developed in the atmospheric foliage. At this first stage, the chlorenchyma is longitudinally extended and somewhat more compact than that of adult leaves. The costal chlorenchyma buttresses the vascular tissue. Vascular bundles are shown to be in series, equidistant from each surface in adults, and closer to the abaxial surface in juveniles. Larger veins are irregularly alternate with smaller ones. The veins are buttressed on the outside by a fibrous sheath extension (FIGURE 1A, B). There are loose buttressing fibers transversally extended in the water storage tissue of adult leaves (FIGURE 1B). Transverse commisures of tracheal elements sheathed with somewhat sclerotic parenchyma cross the air–lacunae.

The stomatal apparatus consists of four sub-

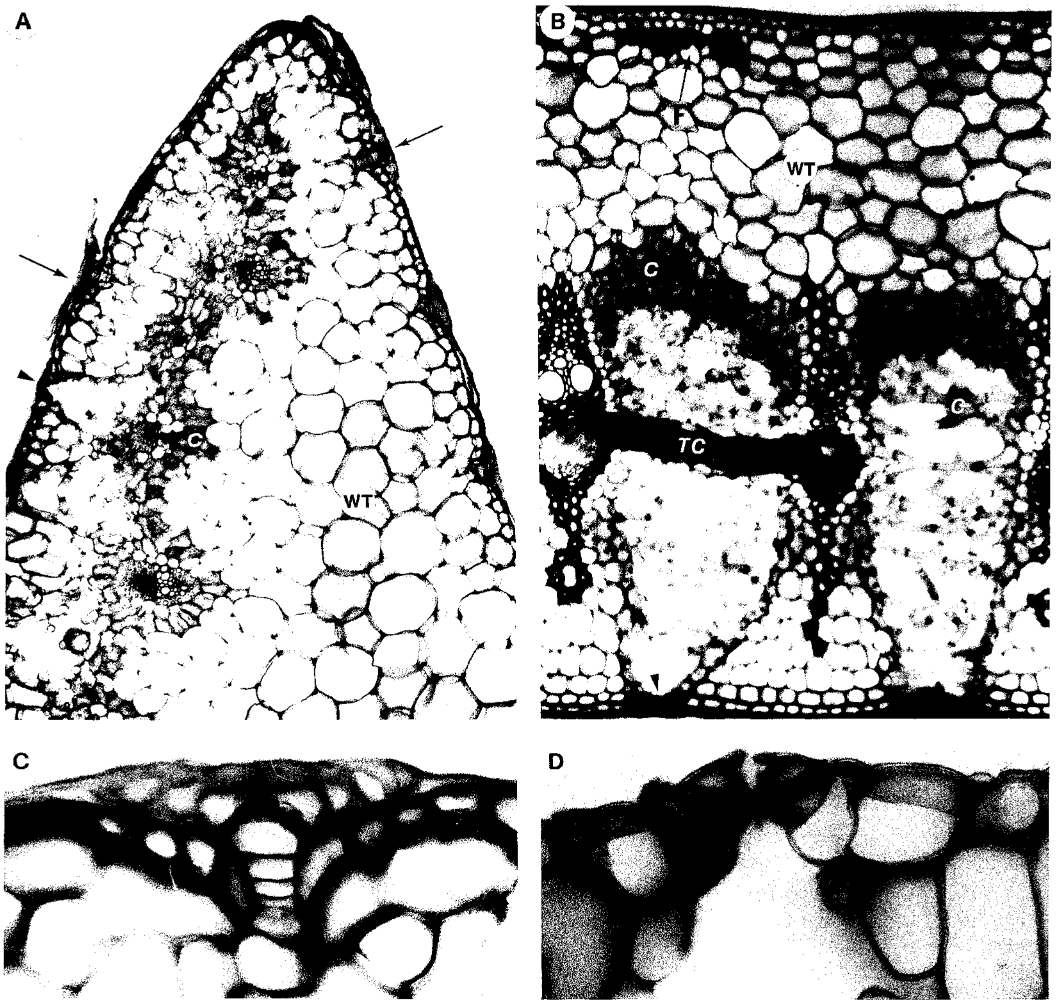

FIGURE 1. Transverse section of middle portion of the leaf of *Vriesea geniculata*. A, juvenile—16×. B, adult—16×. C, juvenile trichome—50×. D, stomata—50×. Trichome (long arrow), stomata (short arrow), water tissue (WT), transverse commisures (TC), fibers (F) and chlorenchyma (C).

sidiary cells and guard-cells not deeper than those of the normal epidermis with ledges of wall material on the upper side appearing like horns in transverse section (FIGURE 1D). The substomatal cavities join directly into the air-lacunae (described above) and are surrounded by chlorenchyma. Stomata and trichomes are restricted to longitudinal series in intercostal bands of adult leaves, while in juveniles, trichomes appear both in costal and intercostal bands (FIGURE 2B).

The trichomes of *Vriesea geniculata* possess a uniseriate stalk of four cells, the dome cell plus three lower ones (FIGURE 1C), with typical tillandsioid anatomy (Tomlinson 1969). The central part of the peltate scale varies little among life stages. Isomorphic central disc cells are surrounded by eight ring cells. Those of juveniles possess a second concentric ring, usually consisting of sixteen cells but ranging from 12 to 19 cells. Between the outermost ring and the marginal wing is the inner wing whose cells are often irregularly divided, and less elongated than those of the marginal wing and comprise at most 32 cells. The marginal wing of the trichomes of the juveniles is irregularly shaped, having some cells more elongated than others, mainly on the adaxial surface of the leaf usually with 64 cells (with a range from 36 to 72) (FIGURE 2A, C). Juvenile plants thus have a 4 + 8 + 16 + 32 + 64 shield cell pattern. Peltate scales in the leaf base of adult plants have neither the second ring nor the inner wing. The marginal wing cells are shorter than

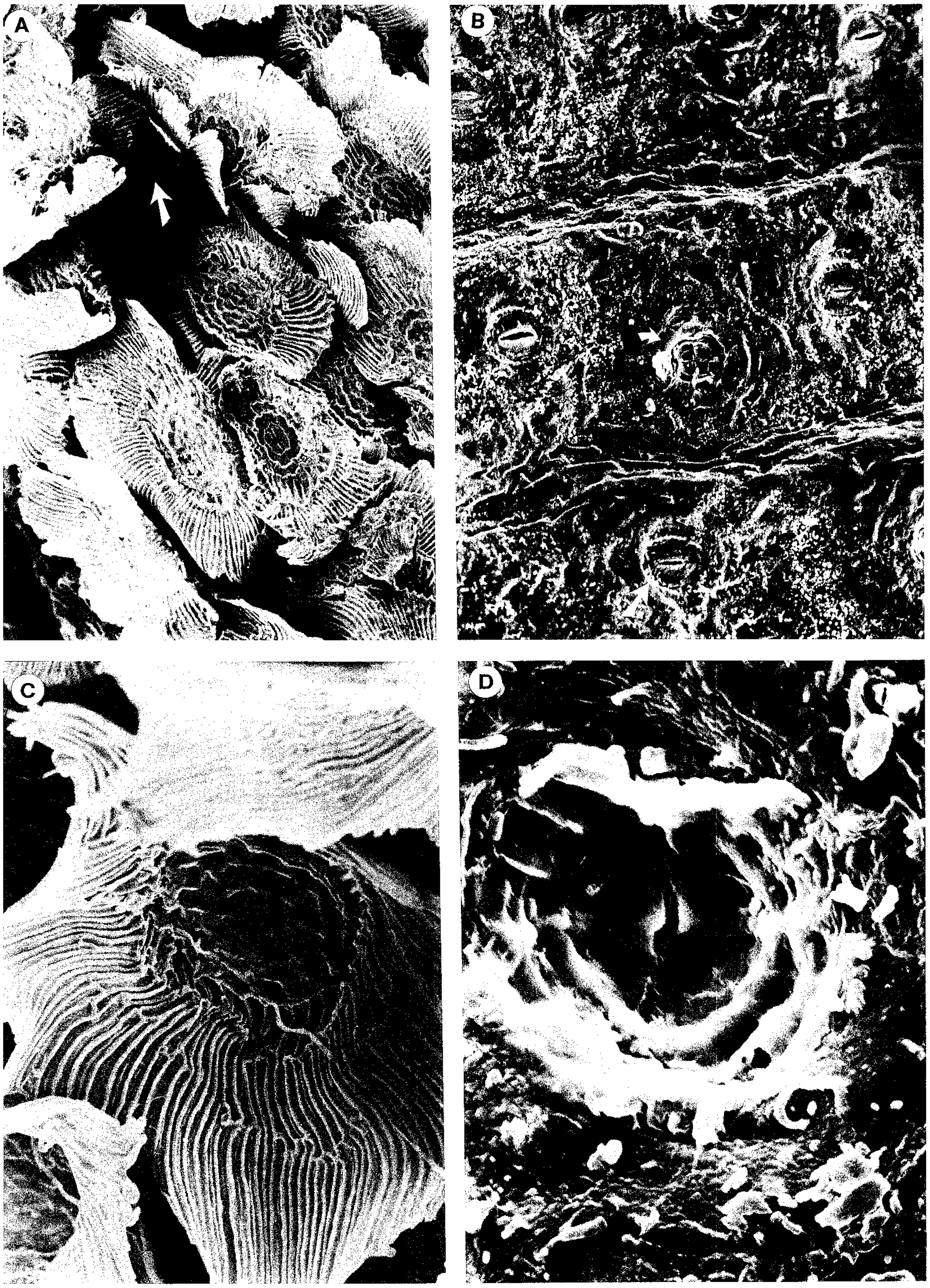

FIGURE 2. Scanning electron micrographs. A, basal portion of a juvenile leaf on the adaxial surface—100×. B, middle portion of adult leaf on adaxial surface—200×. C, trichome of the apical portion of a juvenile plant on the adaxial surface—450×. D, degenerated trichome from the apical portion of an adult leaf on the adaxial surface—1,000×. Stomata (long arrow), and trichome (short arrow).

Table 1. Number of trichomes on 1 mm^2 of leaf of *Vriesea geniculata* in the three life forms (percentage of trichome cover in parentheses).

POS	Side	Juvenile ($N = 30$)	Intermediate ($N = 30$)	Adult ($N = 30$)
Base	AB	19.3 ± 6.7 (84%)	16.3 ± 4.7 (47%)	15.4 ± 9.1 (14%)
	AD	12.4 ± 4.7 (83%)	13.9 ± 2.4 (70%)	16.5 ± 8.4 (14%)
Middle	AB	18.3 ± 6.8 (66%)	10.7 ± 2.4 (13%)	6.8 ± 4.3 (2%)
	AD	13.3 ± 3.4 (87%)	9.9 ± 2.2 (52%)	2.9 ± 1.6 (1%)
Apex	AB	15.5 ± 6.9 (56%)	6.9 ± 1.3 (1%)	4.9 ± 2.4 (2%)
	AD	12.2 ± 3.8 (79%)	8.8 ± 2.5 (28%)	4.3 ± 3.0 (0%)
Total		15.2 ± 6.3	10.8 ± 4.1	8.5 ± 7.8

POS = Leaf position; AB = Abaxial surface; AD = Adaxial surface.

Table 2. Number of stomata on 1 mm^2 of leaf of *Vriesea geniculata* in the three life forms.

POS	Side	Juvenile	Intermediate	Adult
Base	AB	5.78 ± 7.13	7.12 ± 3.36	4.44 ± 7.18
	AD	0	0	0
Middle	AB	19.77 ± 7.71	18.92 ± 2.95	26.83 ± 5.19
	AD	0	0	0
Apex	AB	19.05 ± 6.09	22.23 ± 5.90	37.61 ± 11.46
	AD	0	0	0
Total		7.29 ± 9.96	8.45 ± 9.99	11.59 ± 16.13

POS = Leaf position; AB = Abaxial surface; AD = Adaxial surface.

Table 3. Correlation analysis between the logarithm of foliar area and (1) percentage of trichome cover, (2) number of trichomes, and (3) number of stomata on the leaf surface of *Vriesea geniculata.*

POS	Side	Covered area (1)	Trichome number (2)	Stomata number (3)
Base	AB	$r = -0.66$*	$r = -0.27$**	$r = -0.34$**
	AD	$r = -0.74$*	$r = -0.13$**	—
Middle	AB	$r = -0.81$*	$r = -0.74$*	$r = 0.61$*
	AD	$r = -0.78$*	$r = -0.85$*	—
Apex	AB	$r = -0.84$**	$r = -0.84$*	$r = 0.75$*
	AD	$r = -0.84$*	$r = -0.80$*	—

POS = Position; AB = Abaxial surface; AD = Adaxial surface; * = $P < 0.01$; ** = $P > 0.01$. Stomata are absent in the adaxial surface.

those of juvenile plants, round-shaped with a 4 + 8 + 32 shield cell pattern (with the wing varying from 27 to 38 cells). Trichomes are nearly absent or degenerated in the rest of the leaf (Figure 2B, D, Table 1). The transitional leaves produce both types of trichomes in different ratios and patterns of distribution according to the stage of development, but no transitional trichome was observed.

The atmospheric form exhibits trichome cover of approximately 83% on the adaxial leaf surface and 68% on the abaxial surface (Table 1, Figure 2A). This number decreases from base to apex in the tank-forms (14%) (Table 1, Figure 2B). The peltate scales on the leaf base of adult plants have a reduced wing with an average area of 0.10 ± 0.06 mm^2, while those of the juveniles are 0.21 ± 0.15 mm^2 (Figure 2D, C).

Numbers of abaxial stomata decrease from apex to base in all three life stages, although this pattern is most pronounced in adults (average 37.61% in the tip and 4.44% in the leaf base).

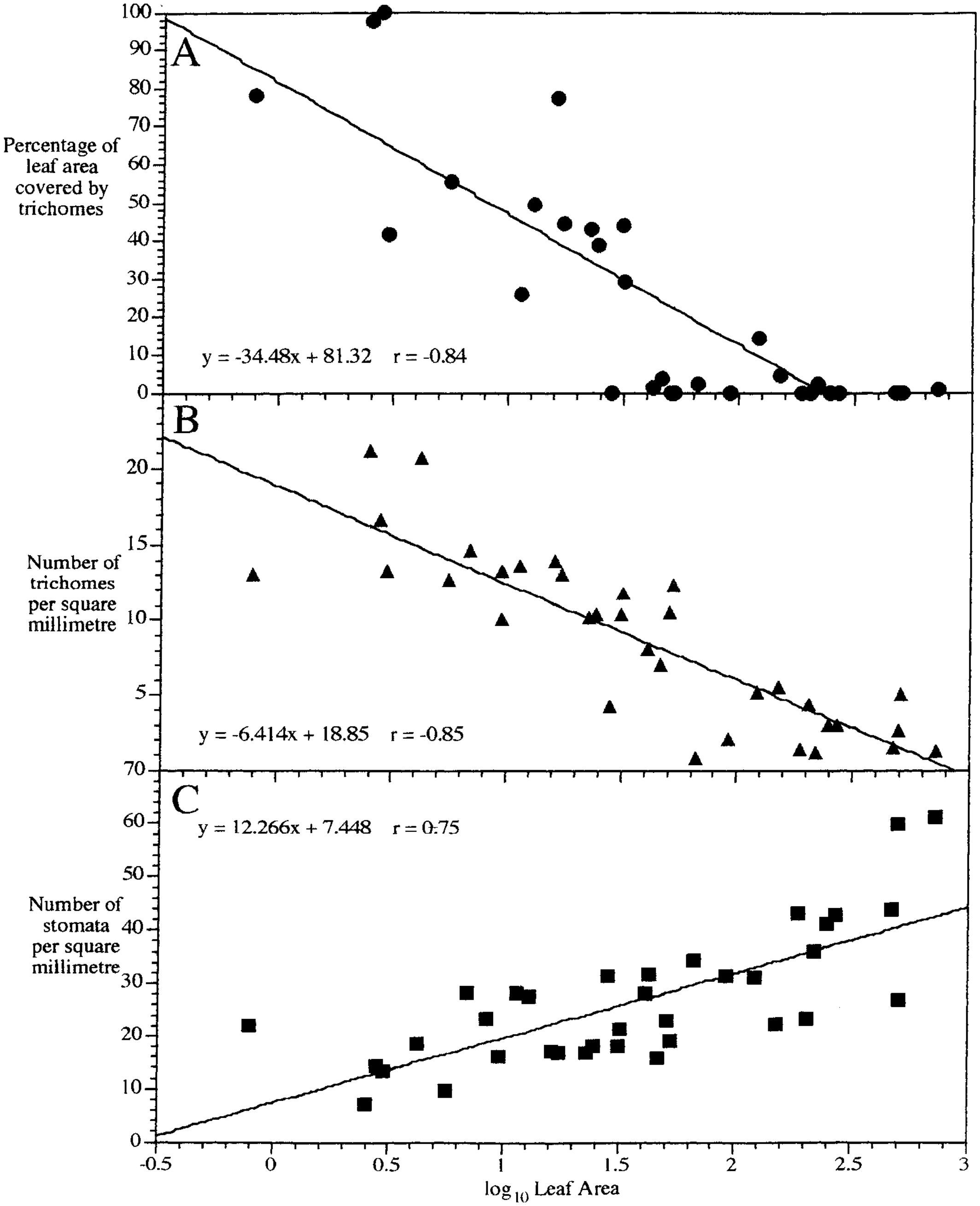

FIGURE 3. Correlation analysis between: A, percentage of trichome cover on the abaxial surface of the leaf apex. B, the number of trichomes on the adaxial surface of the leaf middle region. C, the number of stomata on the abaxial surface of leaf apex.

No adaxial stomata were observed in leaves of any stage (TABLE 2).

A significant relationship existed between the logarithmic foliar area and the degree of trichome cover on leaf surfaces of all six leaf zones examined (TABLE 3; FIGURE 3A, B). There is a significant positive correlation between the logarithm of the foliar area and the stomatal number

TABLE 4. Chlorophyll concentration in leaves of *Vriesea geniculata* in the three stages of development.

	Juvenile	Intermediate	Adult
Mean (μg/DW mg)	263.8	384.6	423.4
SD	237.9	138.6	151.4
N	10	10	10

in the apex of the adaxial surface (TABLE 3, FIGURE 3C).

Neither set of seedlings of November 1987 nor May 1988 showed net CO_2 uptake during the dark period as determined by the colorimetric method or by day night changes in titratable acidity. The $\delta^{13}C$ determinations of juveniles were $-26.7‰$ to $-27.2‰$ ($N = 6$) and for the adults $-24.2‰$ to $-26.0‰$ ($N = 6$). Juveniles showed lower chlorophyll concentrations than adults (TABLE 4).

DISCUSSION

The observed shift in life form during the development of *Vriesea geniculata* is accompanied by morphological changes of the leaf surface (TABLES 1, 2, FIGURE 2A, B). The ecological classification of bromeliads (types III and IV) used here was proposed by Pittendrigh (1948) and used subsequently (Benzing & Renfrow 1971, Griffiths *et al.* 1986, Smith *et al.* 1986a, Smith 1989). The juvenile form exhibits features often present in adult atmospheric type IV tillandsioids (non-impounding rosette of succulent narrow leaves densely covered with shield trichomes). The adult form of *V. geniculata* has the traits of adult type III bromeliads (flat broad leaves overlapping within the base and trichomes almost restricted to the water reservoir). Both forms exhibit a mechanical root system.

The distribution of trichomes and stomata on leaf surfaces appears to be directly related to the different strategies of water acquisition of each life form (TABLE 3, FIGURE 3). As reported for *Tillandsia deppeana* (Adams & Martin 1986b), the leaf anatomy of *Vriesea geniculata* enables us to speculate about juvenile and adult nutrition mechanisms. The adult phase exhibits a high density of stomata, well developed chlorenchyma, and a lack of trichomes in the blade region of the leaf; while within the base, there are higher trichome and lower stomata densities and a lack of chlorenchyma (FIGURE 1A, B). This suggests that plant water and nutrient procurement occur in the leaf base, while CO_2 uptake is in the blade region. On the other hand, juveniles show a similar distribution of stomata, trichomes, and chlorophyllous tissue along the leaf. This suggests that the nutritional and water uptake functions occur over all the leaf surface (Adams & Martin 1986b). In addition, there is a significant negative correlation between the logarithm of the foliar area and the area covered by trichomes (TABLE 3, FIGURE 3A). The well developed flexible wing, covering nearly the whole leaf surface, is essential for the development of the atmospheric habit (FIGURE 2A). When the leaf surface is dry, shoots appear silver-grey and are very reflective because of considerable light-scattering. Stomata are relatively uncovered when the leaf surface is dry and gas exchange with the atmosphere will depend on relative humidity (Benzing 1976, Lange & Medina 1979, Benzing & Ott 1981, Smith *et al.* 1986b). A possible ecological role of the different shield cell pattern of trichomes in juvenile and adult forms of *V. geniculata* remains unclear.

The root system of juvenile plants produced absorbing hairs and was not sclerified when they were placed in well–watered soil (Reinert and Meirelles, unpubl. data). This suggests that the root system has an absorption capacity under good water supply conditions. The results obtained in the present study with *Vriesea geniculata* are similar to those reported in *Tillandisia deppeana* (Adams & Martin 1986a, 1986b).

The $\delta^{13}C$ values for both juvenile and adult plants are in the range of C_3 plants (Smith & Epstein 1971, Ting 1985, Griffiths 1988). In addition, indirect measurements of gas exchange, acid titration (colorimetric test) and indicate no net CO_2 uptake (data not shown) in dark conditions. The results strongly suggest that both forms exhibit C_3 metabolism. *V. geniculata* often grows sympatrically on steep granite outcrops with *Tillandsia araujei,* which is an extreme high-light adapted atmospheric CAM plant (Medina *et al.* 1977). Both seedlings grow on the exposed rock surfaces, but despite the same habit, they exhibit different photosynthetic pathways.

Chlorophyll concentrations were lower in the atmospheric form on a dry weight basis (TABLE 4). These results are in accordance with data obtained for *Tillandisia deppeana* (Adams & Martin 1986b) and with those reported by Benzing and Renfrow (1971). Benzing and Renfrow studied chlorophyll levels within thin and thick adult leaves of several tillandsioid bromeliads and found higher chlorophyll concentrations in thinner leaves. Generally thinner leaves are related to mesic environments and thicker leaves to xeric habitats. The low concentration of chlorophyll in the juvenile plant of *Vriesea geniculata* could reflect a mechanism for protection of the photosynthetic apparatus.

Literature Cited

Adams W. W., III and C. E. Martin. 1986a. Morphological changes accompanying the transition from juvenile (atmospheric) to adult (tank) forms in the mexican epiphyte *Tillandsia deppeana* (Bromeliaceae). Amer. J. Bot. 73: 1207–1214.

——— and ———. 1986b. Physiological consequences of changes in life-form of the Mexican epiphyte *Tillandsia deppeana* (Bromeliaceae). Oecologia (Berlin) 70: 298–304.

——— and ———. 1987. Heterophylly and its relevance to evolution within the Tillandsioideae. Selbyana 9: 121–125.

Arnon D. L. 1949. Copper enzymes in isolated chloroplasts Polyphenoloxidase in Beta vulgaris. Plant Physiol. 24: 1–15.

Benzing D. H. 1976. Bromeliad trichomes: structure, function and ecological significance. Selbyana 1: 330–348.

——— and D. W. Ott. 1981. Vegetative reduction in epiphytic Bromeliaceae and Orchidaceae: its origin and significance. Biotropica 13: 131–140.

——— and A. Renfrow. 1971. The significance of habitat preference and phylogeny among tillandsioid bromeliads. Bot. Gaz. 132: 19–30.

Bukatsch F. 1972. Bemerkungen zur doppelfarbung Astrablau-Safranin. Mikrokosmos, Sttutgart 61: 255.

Gilmartin A. J. 1983. Evolution of Mesic and Xeric Habits in *Tillandsia* and *Vriesea* (Bromeliaceae). Syst. Bot. 8: 233–242.

Griffiths H. 1988. Crassulacean acid metabolism: a re-appraisal physiological plasticity in form and function. Adv. Bot. Res. 15: 43–92.

———, U. Luttge, K. H. Stimmel, C. E. Crook, N. M. Griffiths, and J. A. C. Smith. 1986. Comparative ecophysiology of CAM and C_3 bromeliads. III—environmental influences on CO_2 assimilation and transpiration. Plant. Cell and Environment 9: 385–393.

——— and J. A. C. Smith. 1983. Photosynthetic pathways in the Bromeliaceae of Trinidad: relations between life-forms, habitat preference and the occurrence of CAM. Oecologia 60: 176–184.

Lange O. L. and E. Medina. 1979. Stomata of the CAM plant *Tillandsia recurvata* respond directly to humidity. Oecologia 40: 357–363.

Lieske R. 1914. Die Heterophyllie epiphytischer, rosettenbildender Bromeliaceen. Jb. Wiss. Bot. 53: 502–510.

Martin C. E., K. W. Mcleod, C. A. Eades, and A. F. Pitzer. 1985. Morphological and physiological responses to irradiance in the CAM epiphyte *Tillandsia usneoides* L. (Bromeliaceae). Bot. Gaz. 146: 489–494.

Medina E. 1961. Sobre la influencia de la temperatura y la luz en las velocidades de los procesos de asimilacion en plantas terrestres. Acta Cient. Ven. 12: 166–171.

———, M. Delgado, J. H. Troughton, and J. D. Medina. 1977. Physiological ecology of CO_2 fixation in Bromeliaceae. Flora Bd. 66: 137–152.

Mez C. 1904. Physiologische Bromeliaceen-Studien 1. Die Wasserokonomie der extrem atmosphari-schen Tillandsien. Jb. Wiss. Bot. 40: 157–229.

Moreira M. Z. 1988. Inferências ambientais a partir dos isotopos estáveis (C^{13} e O^{18}) e idades de árvores naturais da floresta amazônica. Master dissertation. ESALQ/USP, Piracicaba, SP. 102 pp.

Morren É. 1873. Exposition de Liége. Belgique Hort. 23: 137–138.

Nimer E. 1989. Climatologia do Brasil. 2nd ed. IBGE, Rio de Janeiro. 422 pp.

Pittendrigh C. S. 1948. The bromeliad-Anopheles-malaria complex in Trinidad. 1—the bromeliad flora. Evolution 2: 58–89.

Sabatini D. D., K. Bensch, and R. J. Barrnett. 1962. New means of fixation for electron microscopy and histochemistry. Anat. Rec. 142–274.

Smith B. N. and S. Epstein. 1971. Two categories of $^{13}C/^{12}C$ ratios for higher plants. Plant Physiol. 47: 380–384.

Smith J. A. C. 1989. Epiphytic bromeliads. Pp. 109–138 *in* U. Luttge, ed., Vascular plants as epiphytes: evolution and ecophysiology. Springer-Verlag, Berlin.

———, H. Griffiths, and U. Luttge. 1986a. Comparative ecophysiology of CAM and C_3 bromeliads. I. The ecology of the Bromeliaceae in Trinidad. Plant, Cell and Environ. 9: 359–376.

———, ———, ———, C. E. Crook, N. M. Griffiths, and K. H. Stimmel. 1986b. Comparative ecophysiology of CAM and C_3 bromeliads. IV—plant water relations. Plant, Cell and Environ. 9: 395–410.

Smith L. B. and R. J. Downs. 1974. Bromeliaceae Part 1 Pitcairnioideae. Fl. Neotrop. monogr. 14. Hafner Press, New York.

——— and ———. 1977. Bromeliaceae Part 2 Tillandsioideae. Fl. Neotrop. Monogr. 14. Hafner Press, New York.

Ting I. P. 1985. Crassulacean acid metabolism. Ann. Rev. Plant. Physiol. 16: 595–622.

Tomlinson P. R. 1969. Anatomy of the monocotyledons—III Commelinales—Zingiberales. C. R. Metcalfe, ed. Oxford University Press. 446 pp.

Utley J. F. and K. Burt-Utley. 1983. Bromeliads (Pina Silvestre, Pinuelas, Chiras, Wild Pineapple). *In*: D. H. Janzen, ed., Costa Rican natural history. University of Chicago Press.

ACKNOWLEDGMENTS

We are indebted to the Department of Ecology and the Department of Biochemistry (UFRJ) for supporting our research, especially to R. Chaloub for his advice and discussions during the course of this study. For manuscript review we thank M. Richardson, I. Ting, H. Griffiths and L. Salles. The authors are grateful to Moreira and M. A. Perez (CENA/USP) for ^{13}C determination and to M. Vanier for electron micrographs. The authors would also like to thank the following colleagues for the stimulating discussions, and for technical and field assistance: C. Russo, G. Faria, Sole-Cava, B. Zinsmeister, M. Cavalcanti, L. Klackzco, L. D'Avila, R. Arruda, M. Serra, C. Grillo, E. Arcoverde, R. Heath, D. DeMason, E. Costa, I. Reinert Adilson Jr., and the colleagues at Newcastle Upon Tyne.