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LEAF MORPHO-PHYSIOLOGY AND DISTRIBUTION OF EPIPHYTIC AROIDS ALONG A VERTICAL GRADIENT IN A BRAZILIAN RAIN FOREST

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ABSTRACT. Nearly 80% of all epiphytic species belong to only four families: Bromeliaceae, Orchidaceae, Polypodiaceae, and Araceae. Adaptations to life in the canopy have been examined extensively for the first three families but not for Araceae. To contribute to the understanding of the vegetative basis for epiphytism in the Araceae, the author studied influences of leaf structure on leaf water relations. Four species representing a hypothetical transition from ground to canopy were selected for study: *Rhodospatha oblongata* (secondary hemiepiphyte), *Anthurium longifolium* (shade epiphyte), *Philodendron alternans* (primary hemiepiphyte), and *Philodendron crassinervium* (sun epiphyte). Investigations were performed at Reserva Botânica das Águas Claras, Rio de Janeiro state, southeastern Brazil (22°30′S; 42°30′W). The abiotic conditions along a vertical profile inside the forest indicated increasing drought and exposure toward the canopy. Structural and physiological traits were analyzed of adult plants of all species occurring at different heights on trees. Additionally, young individuals were studied to detect adaptations to establishment in the epiphytic strata. The results showed that higher heights in the forest were conquered with the aid of anatomical and physiological mechanisms, such as increasing leaf succulence, sclerophylly, and epidermal resistance to water loss.

Key words: Araceae, epiphyte, anatomy, physiology

INTRODUCTION

Epiphytes are present in numerous families (Kress 1986), but nearly 80% of all vascular epiphytes belong to just four, Bromeliaceae, Orchidaceae, Polypodiaceae, and Araceae (Gentry & Dodson 1987). Since the end of the 19th century (Schimper 1888), studies of bromeliads, orchids, and polypoids (Lüttge 1989) created a vegetative basis for epiphytism in these families (Benzing 1990). Results indicate clear structural and physiological mechanisms for life in the canopy. These include macro and micro strategies for water and nutrient impoundment (Benzing 1976, Kluge et al. 1989, Sanford & Adanlawo 1973); crassulacean acid metabolism (CAM) (Zotz & Winter 1994); xeromorphism (Coutinho 1962, Medina 1974), deciduousness (Benzing et al. 1982); and resurrection capacity (Stuart 1969).

Although equally frequent in the canopy as other epiphytes, aroids were not as intensively studied (Benzing 1990). This could be explained by the absence of conspicuous, major adaptive modifications to live on trees. Some possible adaptive features which emerge from the literature are the lianescent habit (Gill & Tomlinson 1975), leaf morphological plasticity (Ray 1990, 1992), deciduousness (Croat 1988), leaf macro-impoundments (Sheridan 1994), and the presence of velamen (Benzing 1986, Rada & Jaimez 1992).

There is little doubt about the existence of a primitive shade terrestrial ancestor for epiphytic aroids (Schimper 1888). Thus, these plants possibly went from ground to trees (Lüttge et al. 1986). Benzing (1990) states about aroids that, despite living in the canopy, "water and nutrition balance exhibit no obvious modifications for arboreal life, but they have not been examined closely." In fact, aroids can be considered as mesophytes and even hygrophytes (Croat 1988). By making a fine adjustment through morpho-physiological studies, it is possible, however, to elect more resistant aroids to epiphytic conditions. Considering the lack of CAM among aroids (Kluge & Ting 1978, Carter & Martin 1994), structural characters could have influenced epiphytism in the family (Holbrook & Putz 1996b). Thus, an analysis of anatomical and physiological traits may help explain the success of aroids in the canopy.

MATERIALS AND METHODS

Study Site and Microclimate

The study was performed on a private property, Reserva Botânica das Águas Claras (22°30′S, 42°30′W), situated in Silva Jardim county, Rio de Janeiro state, Brazil. The reserve is in the Atlantic Rain Forest domain, and the vegetation studied belongs to the low-montane type (Velloso et al. 1991). Although at only 50 m above sea level, the site is bordered on the west side by mountains of > 900 m elevation in the Serra do Mar hills. Polar and south Atlantic air masses interact with the topography, provoking high annual rainfalls of ca. 2223 mm (Nimer 1989), with a mid-year reduction of 80%. Mean monthly air temperature varies from 19° to 25°C (Mantovani 1999). The low temperature and short dry period (never longer than 30 days) do not characterize a clear dry season. The result is a hot and humid climate (Nimer 1989) without a water deficit in the soil (Projeto Radam-Brasil 1983).

Air temperature, air humidity, and light intensity were measured along a vertical path to characterize the different plant niches and the ascendent path of plants from ground to canopy. Previous observations revealed that these parameters experienced higher diurnal amplitude during summer. Thus, by the end of summer 1997, light, temperature, and humidity were measured, at noon, for the cardinal points ($N = 4$) at each 2 m from the forest floor up to 12 m. Light intensity was quantified, using a luximeter with 1 lux resolution, held in horizontal position. Air temperature, with 0.1°C resolution, was measured by a digital Fluke thermometer, model 52, equipped with copper-constantan thermocouples. Air relative humidity was quantified by a Omega digital psycrometer, model RH-10, with 0.1% resolution.

Study Plants

Considering a hypothetical ascending path for aroids in forests, four species were chosen to represent a transition from ground to canopy: *Rhodospatha oblongata* Poepp. (secondary hemiepiphyte), *Anthurium longifolium* (Hoff-sgg.) G. Don (shade epiphyte), *Philodendron alternans* Schott (primary hemiepiphyte), and *P. crassinervium* Lindl. (sun epiphyte) (sensu Putz & Holbrook 1986). These species occupy different canopy positions in the forest with regard to height. The lower height for adults (flowering plants) was similar for all species (ca. 1 m above the forest floor). The maximum heights observed were 8 m for *R. oblongata* and *A. longifolium,* 15 m for *P. alternans,* and 25 m for *P. crassinervium.* Adult plants could be found under deep shade inside the forest or in more exposed positions, such as along river banks, treefall gaps, or treetops for *P. crassinervium.* Thus, the selected species had shade and sun plants, but the light intensity reaching their respective habitats varied from species to species.

Anatomy and Physiology

The anatomy and physiology of four species were compared. Young shade plants, representing distinct life forms, also were compared. Such comparisons are useful in describing strategies for plant establishment. For example, *Rhodospatha oblongata* (secondary hemiepiphyte) begins as a terrestrial plant, though *Philodendron alternans* (primary hemiepiphyte) is at first an epiphyte. Shade and sun adult plants of the four species were compared anatomically and physiologically, in search of structural plasticities.

The anatomical parameters considered were leaf, cuticle, and hypodermis thickness; lignified elements, because of their influence on sclerophylly (Turner 1994); and epidermal water conductance (Araus et al. 1991). Five expanded leaves from different individuals for each young plant or adult in shade and sun (15 leaves per species) were collected in the field, immediately stored in humidified plastic bags, and brought to the laboratory for anatomical measurements. For each leaf, one transversal hand-section was made, and five measurements per section ($N = 25$ per condition) were made to quantify leaf, cuticle, and hypodermis thickness. The thickness of these anatomical traits was quantified using an Aus Jena microscope equipped with an ocular micrometer. Data were calculated as mean ± standard deviation. The presence of lignified elements was detected in fresh materials by the phloroglucin test (Vieira 1995). Leaf anatomical plasticity was quantified as the percentage of leaf thickness increase of sun leaves in relation to shade leaves (sensu Ashton & Berlyn 1992). The greater the difference between shade leaf and sun leaf thickness, the greater the leaf anatomical plasticity of the plant.

The physiological parameters measured were leaf succulence, sclerophylly, and leaf epidermal conductance. These parameters can confer distinct capacities for survival in the canopy (Benzing 1990). Succulence and sclerophylly were quantified for ten leaves for each young plant and for shade and sun adult plants (2 leaves per plant; 10 leaves per condition; 30 leaves per species). Leaf succulence (*LS*) was quantified by the following formula (Mantovani 1999):

$$LS = \frac{MFW - DW}{A}$$

where MFW = maximum fresh weight, DW = dry weight, and A = leaf area. Sclerophylly (S) was measured using specific leaf dry weight as an index by the formula (Medina et al. 1990):

$$S = \frac{DW}{A}$$

The leaf epidermal conductance was measured as in Araus et al. (1991). Completely turgid leaves (1 leaf per plant; 5 leaves per condition; 15 leaves per species) were kept under constant conditions (30.1 ± 0.3°C; 63.2 ± 0, 8% of air relative humidity; $N = 5$) for 24 hours. Leaf water content after this period was measured as relative water content after 24 hours (*RWC* 24 h) by the formula (Meidner and Sheriff 1986):

$$RWC\ (24\ \mathrm{h}) = \frac{FW - DW}{MFW - DW}$$

where *FW* is the fresh weight after 24 hours, *DW* is the dry weight, and *MFW* the maximum fresh weight at the beginning of the experiment.

The existence of significant differences was determined for anatomical and physiological traits by ANOVA and Tukey, both with $\alpha = 0.05$ (Zar 1996). Anatomical and physiological traits were compared for young plants, adult shade plants, and adult sun plants of each species. Significant differences were tested among young, adult shade, and adult sun plants from different species for succulence and sclerophylly. Data are expressed as mean ± standard deviation.

RESULTS

Microclimatic Gradient

The behavior of temperature, humidity, and light in a forest on a typical summer day can be seen in FIGURE 1. The host tree held individuals of *Anthurium longifolium, Philodendron alternans,* and *P. crassinervium*; *Rhodospatha oblongata* plants were growing on adjacent trees. At the forest floor, light was 560 ± 141 lux, increasing from 4 to 8 m, when mean light intensity was 1.5 to $3 \cdot 10^3$ lux. At 12 m above the ground, light was already 142 times higher (78.9 ± $26.8 \cdot 10^3$ lux). Air temperature increased 0.5°C per meter, beginning at 25 ± 0.1°C near the ground and finishing at 30.1 ± 0.6°C at 12 m. Air relative humidity behaved in the opposite direction, decreasing 2.5% for each meter ascended in the forest, beginning with 80.3 ± 0.7% at ground level and finishing at 54.7 ± 1.2% at 12 m. As might be expected, the vertical path in the forest was characterized by an increasing drought and exposition toward the canopy.

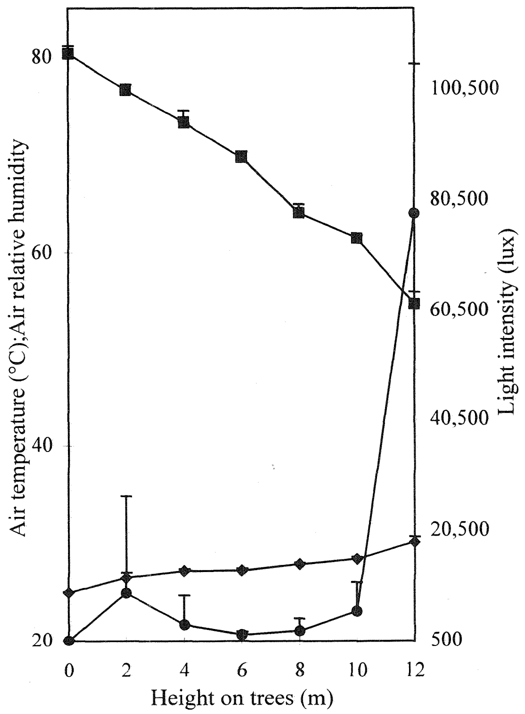

FIGURE 1. Relationship of plant height on trees to light intensity, air temperature, and air relative humidity throughout a 12 m section of the Águas Claras forest. A vertical microclimatic gradient of light = ●, air temperature = ◆, air relative humidity = ■. Exposition and drought are higher at higher points in the canopy; (x ± SD, $N = 4$).

Anatomical Traits

Leaf anatomy of young, adult shade, and adult sun plants of the four study species revealed structural differences. Dimensions of leaf, cuticles, and hypodermis are shown in TABLE 1. The ascendent path of *Rhodospatha oblongata* was matched by an increase of leaf and cuticle thickness; as young plants at ground level had thinner characters than did adult plants. Conversely, the young shaded plant of *Philodendron alternans,* born as an epiphyte, showed thicker leaves with thicker cuticles than did the terrestrial adult shade plant. The adult sun leaves of *P. alternans* showed not only thicker leaf and cuticle but also an adaxial hypoderm. *Anthurium longifolium* and *P. crassinervium* adult sun leaves showed the thickest structures in comparison to young and adult shade leaves. Analysis of structural data reveals that the thickest cuticles were observed in plants able to occupy the higher points in the canopy. Adaxial and abaxial cuticles of the sun leaf of *P. alternans* were respectively 7 and 4.5 μm thick; in the sun leaf of *P. crassinervium,* they were 12.5 and 6.4 μm thick.

For *Rhodospatha oblongata, Anthurium longifolium,* and *Philodendron alternans,* leaf anatomical patterns showed a tendency of increas-

TABLE 1. Anatomical traits of young, adult shade, and adult sun leaves of the plants studied. Data are mean ± standard deviation ($N = 25$; except for thickness of central vein of *Philodendron crassinervium,* where $N = 15$). Letters indicate significant differences between conditions for each species. Symbols: 1°H = primary hemi-epiphyte; 2°H = secondary hemi-epiphyte; T = terrestrial; E = epiphyte; na = not applicable; no = not observed.

		Thickness of anatomical traits (μm)				
Species	Habit	Leaf	Adaxial cuticle	Abaxial cuticle	Adaxial hypodermis	Abaxial hypodermis
Rhodospatha oblongata						
Young	T	136.2 ± 7.26^{a}	1.34 ± 0.28^{a}	1.27 ± 0.26^{a}	no	no
Adult shade	2°H	153 ± 7.07^{b}	2.12 ± 0.38^{b}	1.45 ± 0.34^{a}	no	no
Adult sun	2°H	170.4 ± 5.58^{c}	1.99 ± 0.26^{c}	1.43 ± 0.31^{a}	no	no
Anthurium longifolium						
Young	E	280.8 ± 26.25^{a}	2.57 ± 0.39^{a}	2.16 ± 0.35^{a}	no	no
Adult shade	E	354.6 ± 50.27^{b}	3.65 ± 0.87^{b}	3.18 ± 0.61^{b}	no	no
Adult sun	E	458.4 ± 21^{c}	4.04 ± 1.01^{b}	3.80 ± 0.59^{c}	no	no
Philodendron alternans						
Young	E	448.80 ± 43.48^{a}	3.15 ± 0.62^{a}	2.85 ± 0.63^{a}	no	no
Adult shade	1°H	348 ± 10.31^{b}	2.29 ± 0.39^{b}	2.27 ± 0.44^{b}	no	no
Adult sun	1°H	675.73 ± 38.2^{c}	7.22 ± 1.47^{c}	4.45 ± 1.05^{c}	27.69 ± 3.76^{b}	no
Philodendron crassinervium						
Young	E	273 ± 12.42^{a}	6.54 ± 0.77^{a}	3.13 ± 0.85^{a}	37.24 ± 6.55^{a}	41.99 ± 9.55^{a}
Adult shade	E	291.20 ± 7.68^{b}	5.36 ± 0.47^{b}	1.86 ± 0.38^{b}	24.60 ± 7.10^{b}	29.27 ± 5.29^{b}
Adult sun	E	414.80 ± 12.29^{c}	12.51 ± 1.71^{c}	6.42 ± 1.28^{c}	37.5 ± 4.86^{a}	40.26 ± 6.44^{a}
central vein		12200 ± 1000	na	na	no	no

ing leaf and cuticle thickness along the vertical path inside the forest. Although living at higher sites in the canopy, leaves of *P. crassinervium* did not show the greatest leaf thickness, in spite of having adaxial and abaxial hypodermis. The explanation may be that, as indicated by the specific name *crassinervium,* the central vein occupies 25% of the leaf surface, is extremely thick and succulent, and has chlorophyll and active stomata on both sides of the leaf; and the intercostal leaf region is hypostomatous. Thus, when considering the central vein of *P. crassinervium* in the anatomical analysis, the ascendent path in the forest still was followed by an increase of leaf and cuticle thickness.

The phloroglucin test revealed that lignified structures were represented by only a few perivascular fibers. Lignified epidermis and hypodermis, sclereids, and isolated fibers were not observed.

Although shade and sun leaves were anatomically different for all species, leaf anatomical plasticity was different for each species. Aroids capable of living higher in the canopy showed a higher plasticity in comparison to aroids with lower height amplitudes (TABLE 2). *Philodendron alternans,* living from the first meter above ground up to 15 m of height (14 m of amplitude) showed sun leaves 48.5% thicker than shade ones. *Rhodospatha oblongata* and *Anthurium longifolium,* with 7 m of amplitude showed an increase of 10% and 22.7% respectively in the

TABLE 2. Leaf anatomical plasticity and height amplitude for epiphytic aroids. Plasticity was quantified as percentage of leaf thickness increase of sun in relation to shade leaves; i.e., the higher the difference between shade and sun leaf thickness, the higher the leaf anatomical plasticity of the plant. Height amplitude was measured as the difference between maximum and minimum height of the plants on trees of Águas Claras forest.

Species	Plasticity (%)	Height amplitude (m)
Rhodospatha oblongata	10.0	7
Anthurium longifolium	22.7	7
Philodendron alternans	48.5	14
Philodendron crassinervium (intercostal)	29.8	24
Philodendron crassinervium (central vein)	96.4	24

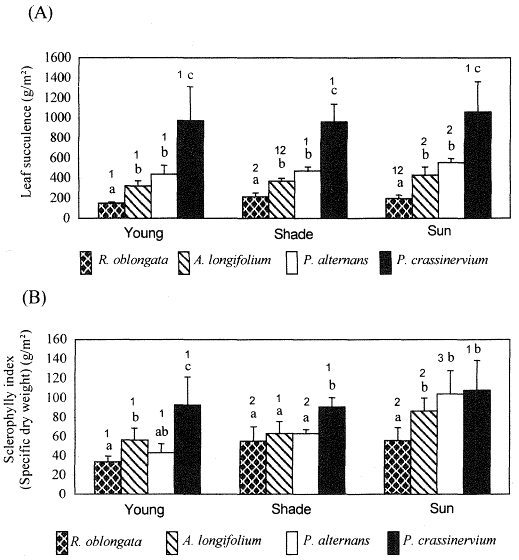

FIGURE 2. Succulence (*A*) and sclerophylly (***B***) of young, adult shade, and adult sun leaves of hemiepiphytic and epiphytic aroids. Note the increase of leaf succulence values following the ascendent path in the forest (represented by the species). For sclerophylly, this pattern was clearly found only for young individuals. Bars indicate standard deviation (*N* = 10); different letters = significative differences between species; different numbers = significative differences between conditions in same species.

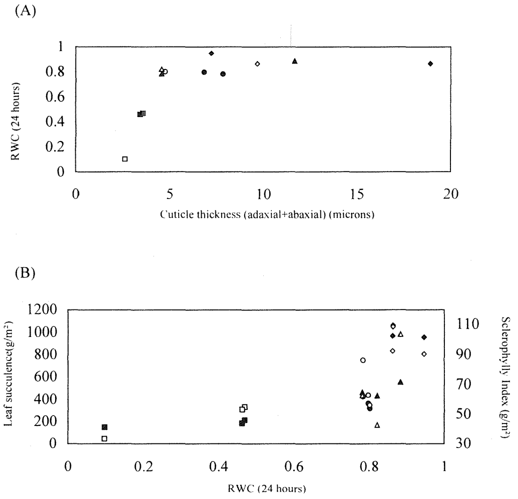

FIGURE 3. Relationship between leaf anatomical and physiological traits of hemiepiphytic and epiphytic aroids. *Rhodospatha oblongata* = □, ■; *Anthurium longifolium* = ○, ●; *Philodendron alternans* = △, ▲; and *Philodendron crassinervium* = ◇, ◆. ***A.*** Relationship of cuticle thickness to relative water content (RWC). Open symbols = values for young plants; closed symbols = values for adult plants. Note influence of cuticular thickness promoting higher water loss resistance. ***B.*** Relationship of RWC to leaf succulence and sclerophylly. Open symbols = sclerophylly; closed symbols = leaf succulence; all symbols are mean values. Note parallelism among leaf succulence, sclerophylly, and water loss resistance, with higher values found for plants occupying higher points on the canopy.

thickness of sun leaves. Considering only the intercostal region of shade and sun leaves of *P. crassinervium,* the plasticity was ca. 30%, although this species showed a height amplitude of 24 m. The search for maximum plasticities between shade and sun leaves, must consider that the central vein of the sun leaf is 96% thicker than the intercostal region of the shade leaf. These data indicate a possible relationship in epiphytic aroids between the capacity to reach higher sites in the canopy with higher levels of leaf anatomical plasticity.

Physiological Traits

The epiphytic young individuals of *Anthurium longifolium, Philodendron alternans,* and *P. crassinervium* had more succulent leaves than the terrestrial young plants of *Rhodospatha oblongata* (FIGURE 2). Thus, establishment in the canopy was accompanied by an increase of leaf succulence, which also could be seen when young and adult leaves of the secondary hemiepiphyte *R. oblongata* were compared. The young plant of this species, occurring at the forest floor, had lower mean leaf succulence values than the adult shade plants that occurred 1–8 m above the ground.

In shade conditions, the young epiphytic individuals *Anthurium longifolium* and *Philodendron alternans* had leaves more sclerophyllous than did *Rhodospatha oblongata.* All three had leaves less tough than *P. crassinervium.* This pattern changed during plant growth, as shade and sun adult leaves came to have similar specific dry weight, instead of showing terrestrial (*R. oblongata* and *P. alternans*) and epiphytic (*A. longifolium* and *P. crassinervium*) life forms. Sclerophyll mean values, however, were similar for succulence and showed a tendency to follow plant maximum height on trees (FIGURE 3). The same tendency could be found in relation to leaf epidermal conductance.

Relative water content (*RWC*) of leaves after 24 hours under constant conditions was higher among epiphytes that occur at higher sites in trees (FIGURE 3A). During dehydration, leaves lost water by both adaxial and abaxial surfaces. To quantify the cuticular efficiency for preventing water loss, the author plotted the values of relative water content after 24 hours against the sum of adaxial plus abaxial cuticular thickness. A general relationship is seen between cuticular thickness and epidermal conductance, with the higher values of relative water content (after 24 hours) occurring on leaves with the higher sum of cuticular thickness. The thickest cuticles were found on leaves from aroids occupying higher points in the canopy.

The direct relationship of the anatomical and physiological parameters is shown in FIGURE 3B, where leaf succulence and sclerophylly are plotted against *RWC* (24 hours). The more succulent and sclerified leaves also showed the higher water loss resistance values. The presence of these three physiological traits was observed in leaves of the aroids able to survive in higher points of the canopy. It may mean that an ascending path inside the Águas Claras forest, toward more exposed and dry conditions, was followed by an increase of leaf succulence, sclerification, and resistance to water loss.

DISCUSSION

Anatomically and physiologically, aroids in general are considered mesophytic plants, less drought resistant than xeromorphic epiphytes (Benzing 1973). The data presented here suggest that epiphytic aroids do not represent a strictly homogenous group. It is possible to elect species with distinct survival capacities.

Anatomical studies of epiphytes find the occurrence of water parenchyma, thick cuticle, lignified epidermis and hypodermis, and sunken stomata for Bromeliaceae (Braga 1977), Cactaceae and Gesneriaceae (Coutinho 1962, Johansson 1974), Peperomiaceae (Kaul 1977), and other families (Oliver 1930). These anatomical traits have adaptive values for survival in the canopy (Benzing 1990). Few studies have been made of structural adaptations by epiphytic aroids (Rada & Jaimez 1992). The vertical microclimatic gradient along the forest of Águas Claras imposes on epiphytic plants an increasing drought and exposition toward the canopy. In this study, the establishment and growth of aroids that occurred with morpho-physiological modifications, such as increasing succulence, sclerophylly, and water loss resistance, were matched by anatomical characters.

Although cuticle efficiency in the prevention of water loss does not necessarily depend on its thickness (Schönrerr 1982), lower epidermal conductance values were achieved in this study by aroid leaves covered by the thickest cuticles. Schreiber and Riederer (1996), analyzing several plant species from different habitats, found in leaves from hemiepiphytic aroids of *Philodendron* and *Monstera* higher cuticular efficiency in preventing water loss. In comparisons of cuticle thickness and aroid distribution in Águas Claras, the ascendent path inside the forest matched an increasing cuticle thickness and epidermal resistance to water loss.

Holbrook and Putz (1996a) found similar results studying terrestrial and epiphytic plants of *Ficus* (Moraceae) in the Pluvial Forest of Monteverde, Costa Rica. They reported that the higher resistance to epidermal water loss was exhibited by leaves of epiphytic plants. Similarly, adult epiphytic leaves of *Rhodospatha oblongata,* 1–8 m above the ground, showed a higher resistance to water loss than young terrestrial leaves. Differences of epidermal conductance for epiphytic and terrestrial plants of *Philodendron alternans* were negligible, in spite of the distinct life forms.

The aroids in the Águas Claras study did not develop tissues like typical water parenchyma (Haberlandt 1928) or water storage tracheids (Zimmermann 1983). Some leaves of Orchidaceae and Peperomiaceae possess a large hypodermis that occupies > 50% of the mesophyll, an important water reservoir (Benzing 1990). The hypodermis observed on adult leaves of *Philodendron alternans* and *P. crassinervium* occupied only 7% and 19% of their respective leaves in a transversal section. Kluge and Ting (1978) stated that the absence of a typical water parenchyma is not a limiting factor for high leaf succulence. Chlorenchymatic tissues also are able to store water. Coutinho (1962) reported the presence of epiphytes with thick leaves occupied only by chlorenchyma. Terrestrial young plants of *Rhodospatha oblongata* showed less succulent leaves than the epiphytic young individuals of *Anthurium longifolium* and *P. alternans.* These data show the importance of leaf succulence for aroid establishment on the canopy. For adult plants, leaf succulence followed aroid distribution on trees, with the lowest leaf succulence found on *R. oblongata* (at lower heights) and the highest on *P. crassinervium* (at greater heights). Holbrook and Putz (1996b) reported similar results for primary hemiepiphytic *Ficus,* whose leaves were more succulent in the epiphytic than the terrestrial phase.

Anatomical and physiological parameters for aroid life on the canopy were clearly demonstrated by *Rhodospatha oblongata* and *Anthurium longifolium.* Although occupying the same vertical strata in the forest (1–8 m above ground), they showed different leaf anatomy and physiology, with the highest values of leaf succulence, sclerophylly, and resistance to water loss shown by the epiphytic *A. longifolium.*

Leaf sclerophylly was higher on leaves with high succulence and water loss resistance. Sclerophylly originates in response to water and nutritional deprivation (Medina et al. 1990), a common phenomenon in canopies (Benzing 1990). The epiphytic rooting media of the study aroids showed a higher water loss than the ground soil, while leaves of the epiphytic plants had the lower total nitrogen content (unpubl. data).

Water and nutrient deficits impair plant growth, promoting the development of xeromorphic structures (Arens 1958, Jensen 1986), common features of sclerophyll leaves (Fahn & Cutler 1992). Sclerophylly improves resistance against water loss (Chiudina et al. 1997) and herbivory (Turner 1994, Turner et al. 1993); and it develops longer leaf life-span (Reich et al. 1992). Sclerophylly plays a role in resource economy under canopy conditions, by promoting longevity of plant organs (Benzing 1990). Epiphytic plants of *Philodendron crassinervium* had a leaf productivity 85% lower than the terrestrial *Rhodospatha oblongata,* whose leaves were 60% higher in sclerophylly than were leaves of the terrestrial plant (unpubl. data).

Anatomical differences between shade and sun leaves have been correlated to better light distribution inside the leaf (Vogelmann & Martin 1993) and to a lower diffusive resistance for CO_2 (Nobel 1976), which leads to a higher water-use efficiency (Nobel 1980). Phenotypic plasticity, the capacity of an individual to change its morpho-anatomy and/or physiology in response to environmental changes (Bradshaw 1965), varies from plant to plant. Although known for terrestrial plants in the tropics (Roças et al. 1997, Strauss-Debenedetti & Berlyn 1994, Vieira 1994, 1995), studies about leaf anatomical plasticities for epiphytic plants are few (Martin et al. 1985).

The capacity of some aroids to produce leaves with distinct morphology throughout their life cycle is a well-reported phenomenon (Ray 1990, 1992). No correlations, however, are reported between external (morphological) and internal (anatomical) plasticities in the Araceae. Bazzaz (1996) states that a higher plasticity increases the capacity of plants to live under heterogenous conditions. Results of this study show a direct relationship between height amplitude and leaf anatomical plasticity for aroids. The influence of the latter on water balance helped to promote the vertical stratification observed.

Although occurring on a cellular/organic level, these morpho-physiological modifications have their major influence on the whole-plant level. In the canopy, competition capacity is not based on a high productivity rate but on strategies that lead to an economy of resources. Plant productivity should be reduced at the expense of production and maintainance of long-lasting new organs for several seasons. Such a reduction is determined through modifications in the anatomy and physiology. Along the ascending path of aroids inside the forests, high leaf productivity was progressively substituted by low production of more resistant leaves. This conservative life strategy, based on a well-modulated anatomy and physiology, can account for the success of aroids in the canopy.

The Araceae family occupies various biotopes from submerged to terrestrial, hemiepiphytic, and epiphytic habitats, which make the family a natural laboratory for studies on plant adaptation. These data may be useful in possibly creating a vegetative basis of epiphytism in the Araceae.

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