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Comparative Ecophysiology and Anatomy of Terrestrial and Epiphytic *Anthurium bredemeyeri* Schott in a Tropical Andean Cloud Forest

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ABSTRACT

Water relations and anatomy of a casual epiphyte were studied at La Carbonera, a tropical cloud forest. *Anthurium bredemeyeri* growing as an epiphyte and in its terrestrial form were studied to find differences due to their different habits. Both forms maintained relatively high leaf conductances (0·12 to 0·15 mol m^{-2} s^{-1}) when leaf water potential was relatively high (above −0·5 MPa). A lowering of the leaf water potential (below −0·5 MPa) during the dry season, significantly affected leaf conductances in both terrestrial and epiphytic forms, the latter one to a greater degree. In terms of anatomy, a reduction in stomatal density was observed in the epiphyte, although no other differences were observed. The results show how the epiphyte was affected to a greater degree by a decrease in water availability during the dry season compared to the terrestrial form.

Key words: *Anthurium bredemeyeri*, epiphyte, water relations, anatomy.

INTRODUCTION

Since epiphytes grow on other plants, and their roots have no contact with the ground, they are exposed to a limited access to water and nutrient supply. As a consequence, epiphytes are only abundant where the evaporative demand is low and rainfall is frequent (Sinclair, 1983*a* *b*; Kluge, Avadhani, and Goh, 1989). Epiphytes account for about 10% of all species of vascular plants. The term epiphyte includes true epiphytes, hemi-epiphytes, semi-epiphytic climbers, and casual epiphytes (Kress, 1989). We will focus on casual epiphytes, defined as species in which some individuals of a population are true epiphytes while others are terrestrial plants.

The particular tropical cloud forest we are considering, La Carbonera (Merida, Venezuela), shows distinct wet and dry seasons. Although the soil in the dry season may not be dry enough to produce obvious water stress in terrestrial plants, it is probably sufficient to affect epiphytes growing high on tree canopies where their 'soil' substrate is limited to the water-storing humus which may accumulate on tree branches. This study compares the water relations and anatomical characteristics of *Anthurium bredemeyeri* Schott growing in both terrestrial and epiphytic habits of a cloud forest, to determine the degree to which these plants may be affected by seasonal or diurnal decreases in water availability. The study of some ecophysiological parameters such as leaf water potential and leaf conductance together with some microclimatic parameters will tell us if the terrestrial form, the epiphyte or both are affected in any way in terms of the water balance. These parameters, together with anatomical characteristics, will indicate whether the epiphytes adapt physiologically or anatomically (i.e. greater stomatal control, water storage tissues, increased epidermal layer, decrease in stomatal density, etc.) to the conditions present in the sites they occupy.

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MATERIALS AND METHODS

Site characteristics and plant material

The study site was in the San Eusebio Forest at La Carbonera Forest Reserve (2400 m) in the Venezuelan Andes (8° 39′ N, 71° 24′ W). The area receives an annual mean precipitation of 1640 mm with a wet season between March and November and a dry season between December and March. The mean annual temperature is 14·9 °C with a mean monthly maximum and minimum of 20 °C and 8·5 °C, respectively.

This area corresponds to a high montane cloud forest type vegetation (2250–2550 m), with mostly evergreen trees (Sarmiento, Monasterio, Azocar, Castellanos, and Silva, 1971). There are 40–60 tree species with *Podocarpus rospigliosii*, *Weinmania jahnii*, *Eschweilera monosperma*, *Clusia* sp. and several species of Lauraceae as dominants. Epiphytes (Bromeliaceae, Orchidaceae) are also abundant in this region (Sarmiento *et al.*, 1971). Terrestrial and epiphytic *Anthurium bredemeyeri* Schott (Araceae) was chosen for this study. This species has a succulent stem with adventitious roots. Petioles are approximately 35 cm long; simple, alternate leaves are from ellipsoidal to oblong–lanceolate and are 10–30 cm long and 5–16 cm wide.

Diurnal changes in leaf water potential (Ψ_L), leaf conductance (K_s) and microclimatic variables were measured during both wet and dry seasons. Leaf water potentials were obtained from pressure chamber measurements approximately every 2 h throughout the day in fully expanded leaves ($n = 4$). Leaf conductance ($n = 4$) was determined with a locally constructed steady-state ventilated porometer equipped with a thin-film capacitance humidity sensor and a flow meter assembly to control and measure the inflow of dry air. Leaf and air temperatures were measured with copper–constantan thermocouples (36 gauge) in contact with the lower leaf surface and relative humidity was measured with an Assman aspirated wet–dry bulb psychrometer. These microclimatic variables were used to determine leaf–air vapour pressure difference (*VPD*).

Leaf water potential components were determined from pressure–volume curves (Tyree and Hammel, 1972). Leaves ($n = 5$) from both forms were cut in the late afternoon and the cut end immediately recut under water. The leaves were allowed to saturate fully overnight under a polyethylene cover. The following day the submerged ends were cut, the leaves quickly weighed and the initial balancing pressure determined with a pressure chamber. The leaves were allowed to transpire freely and fresh weight and balancing pressure determinations were continued until several points on the linear portion of the pressure–volume curve had been obtained. Average values of osmotic potential at full turgor (Ψ_π^{100}), at turgor loss (Ψ_π^0) and relative water content at turgor loss (RWC^0) were calculated from these curves (Tyree and Richter, 1981).

Root and leaf samples for anatomical determinations were collected at the study site and placed in FAA for later study. The samples were dehydrated through a series of butyl alcohol treatments described by Johansen (1950), mounted in paraffin, stained with a safranin–fast green combination for sectioning with a sliding microtome. Canada balsam was used for permanent mounting. Free-hand sections were also made for general observations.

RESULTS

Leaf–air vapour pressure difference was not significantly different for terrestrial and epiphytic plants during the wet season (Fig. 1). Both showed a maximum at midday of 0·38 and 0·31 kPa for the terrestrial and epiphytic forms, respectively. Leaf conductance was higher for the epiphyte with the exception of early morning and late afternoon values. Epiphytes reached maximum leaf conductance at mid-morning and then slowly decreased during the rest of the day with a small peak at mid-afternoon. Terrestrial *Anthurium* showed maximum leaf conductance in the early morning, decreasing throughout the day until increasing again in late afternoon. Leaf water potential did not show a defined diurnal pattern for either form. Minimum Ψ_L for the epiphyte occurred at 10.00 h when the stomates were at their maximum opening. At midday, when *VPD* was greatest, Ψ_L became less negative due to stomatal closure. Ψ_L was then maintained at high values due to a low leaf conductance and low *VPD* for the rest of the day. The terrestrial form had the lowest Ψ_L at midday when *VPD* was highest even though leaf conductance had decreased.

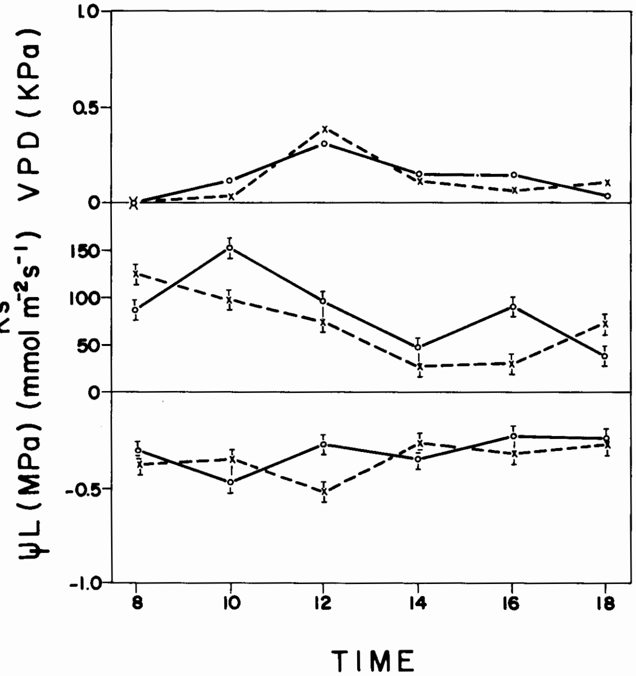

FIG. 1. Daily cycle of vapour pressure difference (*VPD*), leaf conductance (K_s) and water potential (Ψ_L) for terrestrial (×– – –×) and epiphytic (●——●) *Anthurium bredemeyeri* during the wet season (vertical bars are standard errors for $n = 4$).

The results for the dry season showed significant differences between habits (Fig. 2). *VPD* became much greater for the epiphyte showing a maximum of 0·78 kPa as compared to 0·41 kPa for the terrestrial form. Epiphytic *VPD* was always greater throughout the day. With the exception of the 14.00 h value, Ψ_L was also lower for the epiphyte throughout the day. Minimum Ψ_L values were −0·65 MPa and −0·80 MPa for the terrestrial and epiphytic forms, respectively. It is important to note that these minimum Ψ_L values for both wet and dry seasons are far from reaching turgor loss for both habits (Table 1). Leaf conductance, in contrast to the wet season when it

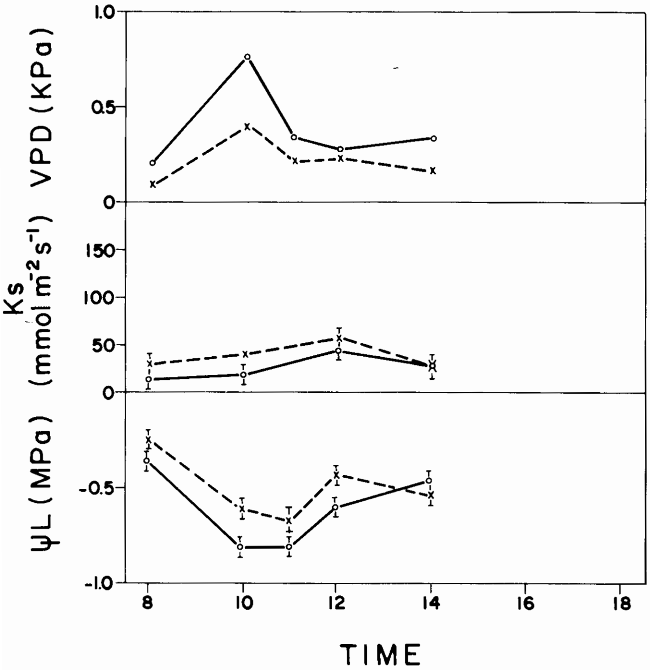

FIG. 2. Daily cycle of vapour pressure difference (VPD), leaf conductance (K_s) and water potential (Ψ_L) for terrestrial (×– – –×) and epiphytic (●——●) *Anthurium bredemeyeri* during the dry season (vertical bars are standard errors for $n=4$).

TABLE 1. *Pressure–volume curve parameters for both habits, epiphytic and terrestrial, during the wet and dry seasons*

Ψ_π^{100} Osmotic potential at full turgor, Ψ_π^0: osmotic potential at turgor loss, and RWC^0: relative water content at turgor loss (mean values ± standard error; $n=5$).

	Ψ_π^{100}	Ψ_π^0	RWC^0
Epiphytic			
Wet season	0·41 ± 0·06	1·30 ± 0·11	0·913 ± 0·043
Dry season	0·63 ± 0·09	1·90 ± 0·10	0·813 ± 0·037
Terrestrial			
Wet season	0·49 ± 0·08	1·20 ± 0·19	0·938 ± 0·028
Dry season	0·57 ± 0·09	1·85 ± 0·21	0·853 ± 0·019

was higher for epiphytes, showed that this latter form closes its stomates to a greater degree. K_s values were lower throughout the day with the exception of the early afternoon values (14.00 h). Comparing the results for both seasons (Figs 1, 2), it can be seen that both plant habits were affected from one season to the other. VPD was higher, K_s and Ψ_L were lower during the dry season. On the other hand, epiphytes seem to be affected to a greater degree than the terrestrial plants.

Ψ_π^{100} and Ψ_π^0 were similar for both plant forms, but there were important differences in Ψ_π^0 between seasons, decreasing from − 1·30 MPa (wet season) to − 1·90 MPa (dry season) for the epiphyte and from − 1·20 MPa to − 1·85 MPa from wet to dry season for the terrestrial plants (Table 1). RWC^0 also decreased between seasons from 0·913 to 0·813 for the epiphyte and from 0·938 to 0·853 for the terrestrial plants from wet to dry, respectively.

With respect to anatomical features, Figs 3 and 4 show leaf and root sections for both habits. Cells on both the adaxial and abaxial surface of the leaf epidermis showed variable sizes for both forms, from approximately 35 to 39 μm wide and 38 to 75 μm in length. The mesophyll showed only one layer of palisade parenchyma having crystals (druses) for both forms. Raphides were also found in the epiphyte. Spongy parenchyma occupied nearly 85% of the leaf with very large intercellular spaces. There were 8 to 9 vascular bundles with a diameter of approximately 362 μm surrounded by fibres. Stomata were found only on the abaxial surface. Although the cuticle for both terrestrial and epiphyte were similar,

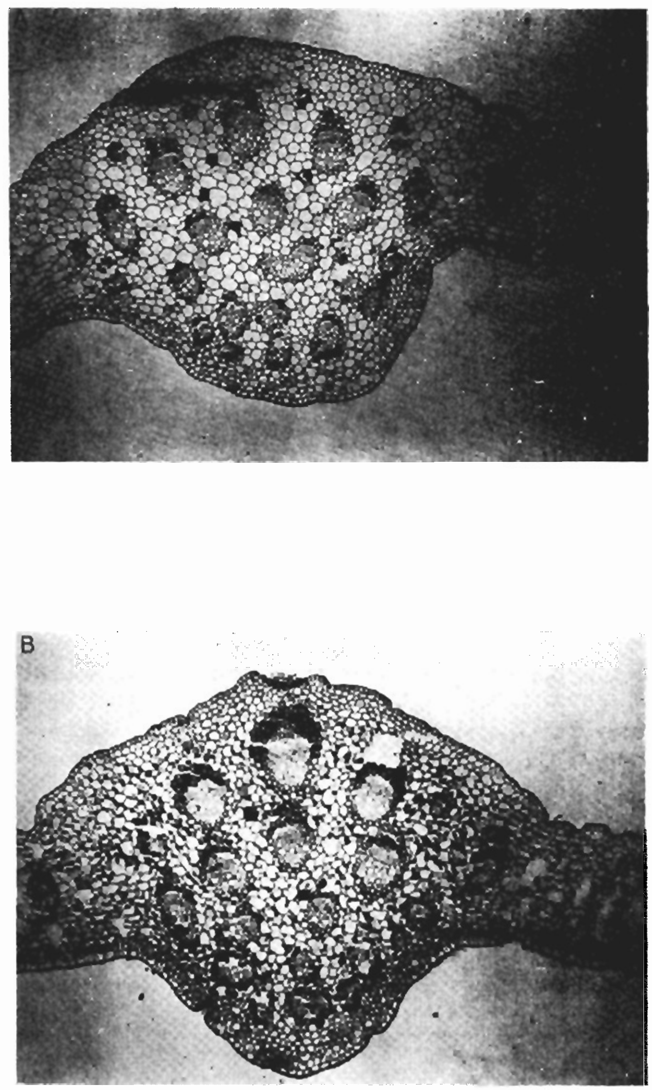

FIG. 3. Anatomical cross-sections of leaf midveins of terrestrial (A) and epiphytic (B) *Anthurium bredemeyeri*.

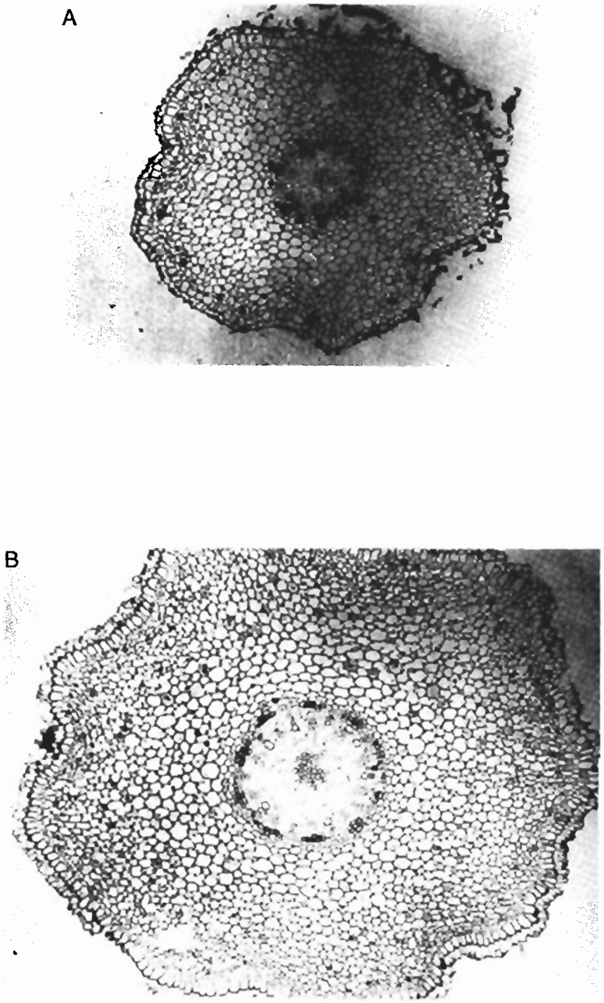

FIG. 4. Anatomical cross-sections of roots of terrestrial (A) and epiphytic (B) *Anthurium bredemeyeri*.

stomatal density was significantly lower in the epiphyte as compared to the terrestrial plants (Table 2). There were no significant differences in mean stomatal length between forms.

Roots showed a pluristratified epidermis with 2 to 3 runs of cells (Fig. 4) and below it a hypodermis of densely packed cells. The mean diameter for the vascular bundles was 200 μm in terrestrial plants and 260 μm in epiphytes.

TABLE 2. *Anatomical features for epiphytic and terrestrial habits (mean values ± standard errors; stomatal density (stomata mm^{-2})* n = *8; mean stomatal length* (μm) n = *12; cuticular thickness* (μm) n = *3)*.

	Epiphytic	Terrestrial
Stomatal density	65·4 ± 4·9	75·0 ± 1·0
Mean stomatal length	43·4 ± 1·1	44·5 ± 1·8
Cuticular thickness	6·8 ± 0·3	6·8 ± 0·8

There was also a greater number of vascular bundles in the epiphyte (15–16) as compared to the terrestrial plants (10–12).

DISCUSSION

Sinclair (1983*a*, *b*), studying the relationship between leaf water potential and leaf conductance in two epiphytic ferns, found that when water potential was high, maximum leaf conductance was approximately 0·1 mol m^{-2} s^{-1}. Kluge *et al.* (1989) found even lower K_s (0·03 mol m^{-2} s^{-1}) for another fern, *Asplenium nidus*. These same authors working with a CAM epiphyte, *Pyrrosia longifolia*, obtained similar values for nocturnal K_s as those of *A. nidus*. Goh and Kluge (1989) working with orchid epiphytes also obtained relatively low K_s values comparable to those of Kluge *et al.* (1989). *Anthurium bredemeyeri* showed relatively high leaf conductances for both terrestrial and epiphyte forms when leaf water potential was more or less stable at high values (above −0·5 MPa).

On the other hand, leaf conductance was significantly affected by a lowering of leaf water potential (Fig. 2) for both the terrestrial plant and the epiphyte, although the latter was affected to a greater degree. When Ψ_L dropped below −0·5 MPa, the plants seemed to respond by closing their stomata (reaching maximum K_s of approximately 0·05 mol m^{-2} s^{-1} for both habits) although the stomata never closed completely. Sinclair (1983*a*, *b*) found that for both ferns stomatal closure occurred at high water potentials (−0·5 to −0·75 MPa). Stomatal closure due to lowering of Ψ_L has been reported to have a wide range depending on the species and environment in which they exist; from −1·2 to −3·0 MPa for different plants (Ritchie and Hinckley, 1975) and as high as −0·7 MPa for some crop plants (Hsiao, 1973); but values as high as these found for epiphytes have not been reported.

Although, from our results, it seems that K_s is controlled by leaf water potential, it is necessary to separate it from the effect of leaf–air *VPD* since some authors have found that *VPD* has an effect on stomatal control (Schulze, Lange, Buschbom, Kappen, and Evenari, 1972; Schulze, Lange, Evenari, Kappen, and Buschbom, 1975; Meinzer, Goldstein, and Jaimes, 1984). With respect to osmotic potential at turgor loss and relative water content, again our results agree with those of Sinclair (1983*a*). We found that RWC^0 for the epiphyte was 0·913 and 0·813 for wet and dry seasons, respectively (Table 1), both being relatively high compared to those cited in the literature for terrestrial plants (Hsiao and Acevedo, 1974). It is important to note that from our results, both epiphyte and terrestrial plants seem slightly to adjust osmotically from one season to the other, observed in the lowering of all measured water potential components (Table 1).

If we compare ground-rooted plants and epiphytes in terms of ecophysiology and anatomy a few characteristics stand out. First of all, epiphytes were affected to a greater degree by a decrease in water availability during the dry season. This is observed in the larger decrease in leaf conductance and in the lower leaf water potentials in the epiphyte during the dry season. This was expected as the 'soil' substrate on the tree branches must dry faster than the ground substrate where the terrestrial plants grow. This is not to say that the terrestrial plant is not affected. Reduction in stomatal density (Table 2) is also an indicator of the manner in which the epiphyte has adjusted to prevent greater water loss through transpiration. Putz and Holbrook (1986) found that stomatal densities in five species of hemi-epiphytic *Ficus* were significantly lower than in ground-rooted individuals of the same species.

As mentioned in the Introduction, there seems to be two main limitations to epiphytic growth: water and nutrients. However, nutrients do not seem to be a limitation to those epiphytes which grow on well developed canopy 'soils' as in this case. The lack of access to mineral soil does not appear to be a major impediment to many canopy-dwelling species (Benzing, 1989). *Ficus* species growing on palms in Venezuela show no visible evidence of nutrient deficiencies considering the high concentration of nutrients in the epiphytic humus (Putz and Holbrook, 1986). These authors obtained specific differences between the epiphytic humus and terrestrial soil samples, the epiphytic humus having a five times higher nitrogen content and ten times higher phosphorus content than the terrestrial soil. Therefore, water availability would seem to be the major limitation to epiphytic growth.

An advantage of the epiphytic habit would be an increase in light for photosynthesis (Lüttge, Ball, Kluge, and Org, 1986; Kluge *et al.*, 1989). Other hypotheses include an avoidance of flooding, fire damage and depredations of terrestrial animals (Putz and Holbrook, 1986). Further studies on all aspects of epiphyte ecophysiology are needed to understand the distribution and success of this plant form, especially in the Tropics.

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