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Comparative leaf ecophysiology and anatomy of seedlings, young and adult individuals of the epiphytic aroid *Anthurium scandens* (Aubl.) Engl.

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ABSTRACT

Usually dry and oligotrophic, canopies can impose stressful conditions on plant survival. Adaptations to life in the canopy have been examined extensively for Bromeliaceae, Orchidaceae and Polypodiaceae, but not for Araceae. These four families comprise nearly 80% of all vascular epiphytic species. Recent data indicate that ontogenetic and size-related changes in anatomy and ecophysiology affect the performance and survival of epiphytes in the field. Therefore, to better understand how Araceae species have successfully adapted to the epiphytic habitat, we studied the holoepiphyte *Anthurium scandens* in relation to stomatal and epidermal conductance, leaf succulence, sclerophylly, leaf nitrogen content and retranslocation, and quantitative anatomy. Analyses were performed for leaves of seedlings, young and adult individuals. First, results showed that the stomatal conductance of young and adult individuals was similar, with maximal daily conductance varying from 20 mmol m^{-2} s^{-1} in the dry period to 100 mmol m^{-2} s^{-1} after four continuous rainy days. We concluded that stomatal conductance is highly dependent on water availability at the root level for both ontogenetic phases. Second, in comparison to young and adult individuals, seedlings had higher epidermal conductance to water loss as well as lower values of leaf succulence and sclerophylly. Third, although both young and adult individuals had similar leaf nitrogen content in green mature leaves, higher retranslocation rates of leaf nitrogen during senescence were found in adult individuals. Fourth, young and adult individuals presented leaves with similar quantitative anatomy, but with higher values in comparison to seedling leaves, with the exception of the higher adaxial and abaxial thickness of epidermal cells. Finally, in addition to mesophytic anatomical characters, results showed that leaves of *A. scandens* seedlings had lower succulence, sclerophylly and resistance to water loss, indicating a higher potential susceptibility to stressful abiotic conditions in comparison to young and adult individuals. Based on these findings, we suggest that this higher susceptibility of seedlings to abiotic stress helps explain the establishment and distribution of *A. scandens* in the more mesic micro-sites of the canopies.

1. Introduction

Epiphytes play an important role in the biodiversity of tropical forests (Gentry and Dodson, 1987). There are around 20,000–25,000 epiphytic species, which represent 10% of all vascular flora (Benzing, 1990; Rada and Jaimez, 1992). However, nearly 80% of the epiphytic species belong to just four families: Bromeliaceae, Orchidaceae, Polypodiaceae and Araceae. These families, except for Araceae, are well documented in regard to adaptations to life in the canopy (Benzing, 1990).

Usually dry and oligotrophic, canopies can impose stressful conditions on plant survival (Lüttge, 1989). In spite of this, epiphytes exhibit ecophysiological, morphological and anatomical adaptations to survive these harsh canopy conditions. Examples are Crassulacean acid metabolism (CAM) (Martin, 1994), biomass and nutrient allocations (Mantovani and Iglesias, 2009; Zotz, 2004), water and organic debris impoundments, and xeromorphism (Benzing, 1986), which simultaneously improve the water and nutrient use efficiency of epiphytes. However, a few studies in Araceae indicate that the lack of CAM (Winter et al., 1983; Zotz and Ziegler, 1997) points to morphological and anatomical adaptations as a way of explaining the capacity of Araceae to survive under canopy conditions. Previously cited adaptations are as follows: lianescent habit (Gill and Tomlinson, 1975), deciduousness (Croat, 1988), leaf macroimpoundments (Sheridan, 1994), leaf paraheliotropism (Mantovani, 2000), high leaf succulence and sclerophylly, and stomatal and epidermal resistance to water loss (Mantovani, 1999a).

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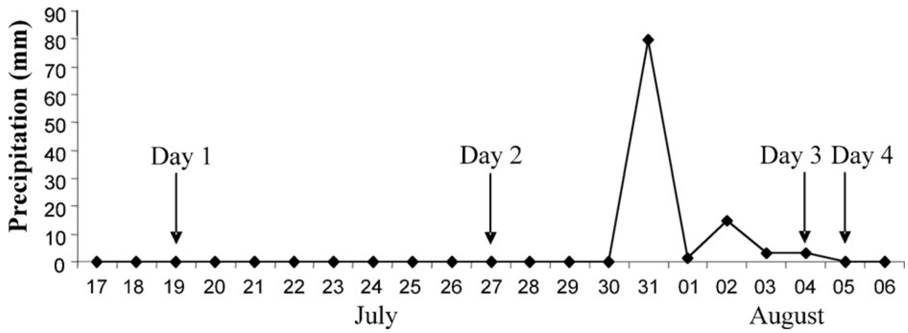

Fig. 1. Daily rainfall (mm) during July and August at the study site. First two measurement days of the stomatal conductance experiment (days 1 and 2) were recorded during a dry period in July. The two last measurement days (days 3 and 4) were performed after three rainy days in August. Arrows indicate measurement days.

Araceae has around 2823 species (Govaerts et al., 2002) with 1349 of these being epiphytic species (Kress, 1986), mainly concentrated in *Anthurium* and *Philodendron* (Coelho and Mayo, 2007; Croat, 1988). While Benzing (1990) states that aroids exhibit no obvious modifications for arboreal life, it is also true that they have not been closely examined. Therefore, in order to better understand epiphytism in Araceae, we characterized the leaf ecophysiology and anatomy of *Anthurium scandens*. This holoepiphytic aroid species is largely distributed along the West Indies and southern Mexico to southern Brazil and from sea level to 2700 m in altitude (Sheffer et al., 1980), occurring in wet to seasonally dry forests (Zotz and Ziegler, 1997). On tree crowns, *A. scandens* occurs from around the first few meters of trunk height to the inner crown of canopies, as a partial-shade-demanding epiphyte (Gonçalves and Waechter, 2002; Rodal and Nascimento, 2002; Viana and Lombardi, 2005), rarely present under drier and more exposed conditions at the outer crown (Sheffer et al., 1980).

Publications have reported that many morphophysiological parameters (photosynthesis, stomatal conductance, leaf nitrogen, leaf anatomy) of epiphytes are a function of plant size and/or ontogenetic phase (Adams and Martin, 1986; Zotz and Tyree, 1996; Zotz et al., 2001; Schmidt et al., 2001). Zotz et al. (2001) argue that, in order to better understand if these size- and ontogenetic-related changes are relevant to plant performance and survival under field conditions, close attention should be paid to the size of organisms under study. In this sense, considering a potential positive effect of size-related changes on epiphyte survival, we studied the ecophysiology and anatomy not only for the adult, but also for the seedlings and young individuals of *A. scandens*.

2. Material and methods

2.1. Study site and micro-climate

The study was conducted in the arboretum of the Research Institute of the Rio de Janeiro Botanical Garden. Field and laboratory analyses were performed from June 2006 to January 2007. The macro-climate in the study site was Am (*sensu* Köppen) (Mantovani and Pereira, 2005), with mean air temperatures of 29 and 22 °C during summer and winter, respectively, and mean annual rainfall around 1075 mm. During the study, there was an extended dry period in July, followed by 4 consecutive rainy days at the beginning of August, which allowed us to perform a stomatal conductance experiment (Fig. 1). From June to October 2006, rainfall, air temperature and humidity at 12:00 and 15:00 h were determined daily through a meteorological station positioned near the study site.

2.2. Plant species

A. scandens is distributed along the West Indies and southern Mexico to southern Brazil and from sea level to 2700 m in altitude (Sheffer et al., 1980). In the arboretum, *A. scandens* is commonly found growing on *Mangifera indica* L. (Anacardiaceae). We chose to study individuals of *A. scandens* growing between 1.50 and 3.00 m in height from 9 adjacent *M. indica* hosts. This decision permitted a more rigorous analysis of potential ontogenetic and size-related effects on ecophysiological and anatomical parameters (Freiberg, 1997; Schmidt et al., 2001). This choice was also made to avoid potential biotic and abiotic effects originating from distinct host species, substrates or canopy positions. Seedlings, young and adult individuals are easily distinguished based on morphological parameters, such as the number and length of shoots, number of leaves and inflorescences for adult plants (Table 1). Seedlings have short stems with 3–5 small leaves, while young and adult reproductive individuals have longer and larger stem lengths, sustaining several larger leaves. Five individuals belonging to each growth phase were chosen for the study. From each individual, one totally expanded leaf was collected and analyzed in relation to epidermal conductance, succulence, sclerophylly and quantitative anatomy. Stomatal conductance and nitrogen content and retranslocation during leaf senescence were studied for young and adult individuals only. Leaves from seedlings were smaller than the porometer cup, and their dry weight was lower than the minimum dry biomass necessary for the analysis.

Table 1
Comparative morphology of seedlings, young and adult individuals of *A. scandens* growing as epiphytes in the arboretum of Rio de Janeiro Botanical Garden. Letters show significant statistical differences ($P < 0.05$). Data are mean ± standard deviation ($n = 5$).

Morphological parameters	Seedling	Young	Adult
Leaf number	4.2 ± 1.3 a	11.4 ± 3.8 a,b	23.8 ± 15.9 b
Highest leaf length (cm)	5.7 ± 2.6 a	9.2 ± 1.5 a,b	10.4 ± 1.6 b
Highest leaf width (cm)	1.5 ± 0.63 a	2.8 ± 0.7 a,b	2.9 ± 0.5 b
Highest shoot length (cm)	2.0 ± 2.8 a	9.2 ± 4.9 a,b	27.8 ± 15.3 b
Percentage of the studied individuals that present ramified shoots (%)	20	60	100
Total sum length of ramified shoots (cm)	2.2 ± 2.7 a	16.9 ± 10.6 a,b	73.2 ± 88.4 b