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EPIPHYTES: PHOTOSYNTHESIS, WATER BALANCE AND NUTRIENTS

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Resumo:

“Epífitas: Balanço Hídrico e Nutrientes.”

Epífitas são plantas adaptadas à vida no dossel, podendo ser facultativas, hemiepífitas ou obrigatórias dependendo do período de vida que a espécie passa sobre o dossel e se também ocorre como planta de solo. As plantas epífitas estão sujeitas às mesmas pressões ambientais das enraizadas no solo, tais como demanda por água, luz e nutrientes, embora a flutuação desses componentes ambientais tenda a ser maior no hábito epifítico. As epífitas não apresentam nenhuma via fotossintética exclusiva embora a via CAM seja relativamente bem freqüente neste grupo, principalmente entre orquídeas. Em geral epífitas apresentam crescimento lento e alta eficiência no uso da água, que pode ser um fator menos competitivo para estas espécies em ambientes onde condições mais favoráveis acentuam a competição. Ou ainda, a fase ativa de crescimento vegetativo de algumas epífitas se dá na estação chuvosa e as plantas podem gastar até 1000g de água por grama de material orgânico produzido, enquanto plantas de alta eficiência no uso da água podem apresentar taxas de 100:1. Esta variedade de estratégias de crescimento demonstra, que assim como em plantas enraizadas no solo, o uso mais parcimonioso da água não necessariamente representa o melhor mecanismo para conciliar economia de água e crescimento.

Abstract:

Epiphytes are plants adapted to living in the canopy and can be classified as facultative, hemiepiphytes or obligatory depending on the period spent in the canopy and if the species also occur as soil-rooted plants. Epiphytes are subjected to the same environmental pressures as soil-rooted plants, such as demand for water, light and nutrients, although environmental fluctuations tend to be more frequent. Epiphytes do not show any exclusive photosynthetic pathway, even though CAM is relatively common within this group, specially among orchids. In general, epiphytes are slow growing plants with high water use efficiency. This trait can be less competitive in environments with more favorable conditions where competition is more pronounced. Yet, among other epiphytes the vegetative growth phase coincides with the rainy season. These plants can spend as much as 1000g of water per gram of organic matter produced, whereas among plants with high water use efficiency typical rates are 100:1. This variety of strategies demonstrates that, as in soil-rooted plants, a more parsimonious use of water does not necessarily represent the best mechanism to compromise water economy and growth.

Introduction

Epiphytism occurs among both vascular and non-vascular plants. The former includes flowering plants and pteridophytes, and the latter bryophytes, algae, and lichens. Vascular epiphytes comprise the group of plants that do not depend on soil for water and nutrient uptake and are particularly abundant in the wet tropics (Gentry & Dodson, 1987; Lüttge, 1989; Benzing, 1990). Epiphytes which use woody vegetation exclusively for support, *i.e.* no contact with the soil, at some stage in their life cycle are considered autotrophs, or true epiphytes. Those attached to the host tree by haustoria (the invasive vascular appendage of a parasitic plant through which water, nutrients and sometimes photosynthate are taken up) are heterotrophs. There are over 23,000 species of vascular epiphytes distributed among 84 families, which comprise about 10% of all vascular plants (Kress, 1986). They can be subdivided by parameters such as type of nutrition, life-form, or capacity to endure periodic drought.

Water stress is one of the major constraints for epiphytes even in wet climates. Depending on water shortage survival strategies, epiphytes are classified as (1) stress tolerant or poikilohydes, those able to endure severe cytoplasmic desiccation to resume growth upon rewetting, such as most lichens; and (2) stress avoiders or homoiohydes, which have developed physiological and morphological means, such as high stomata resistance and sclerophylly to conserve and/or store water to avoid desiccation. Most vascular epiphytes are homoiohydes. In addition, there are epiphytes restricted to mesic (moist) sites, the so-called hydrophytes and mesophytes.

Epiphytes are, then, generally restricted to humid environments, reaching their greatest diversity and abundance in wet regions of the tropics (Gentry & Dodson, 1987; Lüttge, 1989; Benzing, 1990). The wide range of life-forms of vascular epiphytes is often associated with water stress (Griffiths, 1989; Kluge *et al.*, 1989b). Hemiepiphytic stranglers such as *Clusia* germinate within the canopy and later develop feeder roots which grow downwards and penetrate soil. Eventually the phorophyte (support plant, usually a tree) dies from shading or competition for water and nutrients (Whitmore, 1986; Borland *et al.*, 1992). Tank bromeliads exhibit another life form, in which plants accumulate both water and debris in impounding rosulate shoots. Conversely, the so-called atmospheric bromeliads rely solely on dry and wet atmospheric deposition. These bromeliads acquire water and nutrients via specialised epidermal hairs, or trichomes (Benzing, 1970; Benzing, 1976; Owen & Thomson, 1991; Reinert & Meirelles, 1993; see also section below: Bromeliads). The well-known bromeliad Spanish moss (*Tillandsia usneoides*) has evolved a life form similar to some lichens. The high surface area to volume ratio in *T. usneoides* is believed to be more effective in trapping aerosol minerals than conserving water (Schlesinger & Marks, 1977).

The relationship of leaf water status and gas exchange varies among epiphytes. Some authors found relatively high leaf water potential associated with low leaf conductance in epiphytic ferns (Sinclair, 1983a; b; Kluge *et al.*, 1989b). Goh & Kluge

(1989) obtained similar results with epiphytic orchids. Conversely, Rada & Jaimez (1992), comparing epiphytic and terrestrial forms of *Anthurium bredemeyeri* (Araceae), did not find the same relationship: stomatal conductance was relatively high at high leaf water potentials (up to -0.5 MPa). Additionally, both terrestrial and epiphytic forms showed a decrease in stomatal conductance at low leaf water potentials. Generally the epiphytic form was more affected than the terrestrial by a decrease in water availability during the dry season.

Although epiphytes are often constrained by drought, this does not necessarily restrict annual carbon gain. Zotz & Winter (1994) estimated that annual leaf carbon gain by three epiphytes (Orchidaceae, Polypodiaceae, and Clusiaceae) in Barro Colorado Island, Panama, equals or exceeds that of many deciduous shrubs and trees native to the temperate zone. High leaf carbon gain was attributed to a longer growing season in the tropics. Zotz & Winter (1994) also demonstrated that the decline in net CO₂ uptake was more pronounced in the two C₃ species than in the C₃-Crassulacean acid metabolism (CAM) intermediate Clusiaceae, and that this species showed higher long term water use efficiency (WUE: which refers to the water loss per carbon gain). These findings are similar to those of Griffiths *et al.* (1989a) who found that WUE changed little from the wet to the dry season in two CAM species (Bromeliaceae and Orchidaceae) (for comparative rates of CO₂ uptake see also McWilliams, 1970).

Epiphytism has evolved independently among many lower and higher taxa. This review is restricted to the vascular epiphytes with focus on three taxa: orchids, bromeliads and ferns. Of particular interest are mineral nutrition, and photosynthetic metabolism for these taxa.

Mineral nutrition

In addition to periodic drought, epiphyte growth is often limited by inadequate nutrient supply (Benzing, 1990). Slow-growing oligotrophs generally have evergreen foliage, extended life cycles and vegetative reproduction as several seasons pass until plants reach adult phase. Nevertheless, some epiphytes such as tank-forming bromeliads may have access to considerable amounts of nitrogen, phosphorus and potassium dissolved in the tank water (Benzing & Renfrow, 1974a). Additionally, epiphytes rooted in humus-like soil that occurs on the boles of trees and in the central portion of tree crowns in many wet tropical forests may not be exposed to limited nutrient supply. Humus-like soils are nutrient-rich, even when compared to many fertile temperate soils (Lesica & Antibus, 1990).

Considerable quantities of nutrients leached from the upper canopy are potentially trapped by epiphytic plants (Tukey, 1970; Benzing, 1990; Lesica & Antibus, 1990), however, the mineral composition of rain throughfall available to epiphytes is extremely variable. Variability is dependent on seasonal differences in the airborne deposition and on the type/density of the upper canopy (Schlesinger & Marks, 1977).

Moreover, decomposition within the canopy can be slower than that found in the ground litter (Nadkarni, 1986).

The importance of litterfall as a source of nutrients for epiphytes is open to discussion. Nadkarni & Matelson (1991) argued that nutrient flux through the epiphytic community in a tropical cloud forest in Costa Rica appears to be dissociated from the litterfall pathway. The estimated nutrient input from litterfall retained within the canopy was shown to be small relative to epiphytic productivity. Nadkarni & Matelson (1991) concluded that, of the nutrient sources contributing to epiphytic nutrition, atmospheric deposition and foliar leachate were likely to be important.

Plant nutrition is often dependent on mutualistic associations with other organisms. Mycorrhizal associations (mutualistic interaction between vascular plant roots and fungi, whereby the roots benefit from enhanced water and nutrient uptake and the fungi gain ready access to translocating photosynthates) are likely to favour nutrient uptake in epiphytic plants (Lesica & Antibus, 1990). However, of 16 families of vascular epiphytes surveyed in two Costa Rican wet forests, few members support mycorrhizae (Lesica & Antibus, 1990). Except for Orchidaceae and Ericaceae, mycorrhizal associations do not appear to significantly contribute to the mineral nutrition of epiphytes. Lesica & Antibus (1990) suggested that two factors explain this: (1) many epiphytes inhabit sites that are too dry and exposed for mycorrhizal associations, and (2) net photosynthesis is too low to support symbiotic fungi.

Mutualistic associations on leaf surfaces seem to be relatively frequent in atmospheric bromeliads. Leaf surfaces are relatively rich in organic substrates and can support a diverse flora of bacteria and free-living fungi (Ruinen, 1970; 1974; Vance & Nadkarni, 1990). Brighigna *et al.* (1992) studying N_2 -fixing bacteria in several atmospheric and tank *Tillandsia* noted that the layer of absorbing trichomes offers a favourable environment for microbes and serves as an avenue for nutrient uptake from the phyllosphere. Puente & Bashan (1994) confirmed the presence of N_2 -fixing bacteria on *T. recurvata* adding to the debate regarding the significance of bacteria in the phyllosphere for the nitrogen nutrition of epiphytes.

Ant-fed plants represent another type of mutualistic association whereby epiphytes benefit from the interaction with these insects by acquiring nutrients, avoiding predators, and/or seed (spore) dispersal (Thompson, 1981; Benzing, 1990; Gay, 1993). Several ant-house epiphytes, all tropical, are found in the Asclepidaceae, Bromeliaceae, Orchidaceae, Polypodiaceae, and Rubiaceae (Gay, 1993). Gay (1993) suggests that "the ant interaction with *Lecanopteris* may not affect survival of strong individuals, but may be critical for less healthy ones, and especially for immature plants".

Carnivory occurs in two epiphyte families, Lentibulariaceae and Nepenthaceae, as an alternative strategy for nutrient acquisition. There is still controversy surrounding carnivory in bromeliads (Givnish *et al.*, 1984; Owen & Thomson, 1991),

Catopsis berteroniana exhibits some suggestive characteristics including a denser lubricating leaf wax cover at leaf base than on the blade, that supposedly prevents colliding animals from escaping; bright yellow rosettes which would enhance animal attraction; and higher content of animal remains in the tank than most phytotelm bromeliads (Fish, 1976 *apud* Benzing, 1990). Nevertheless, to date, no secretory glands nor digestive secretions have been identified in these plants to further support carnivorous nutritional mode in Bromeliaceae (Benzing, 1990).

The study of nitrogen demand and partitioning in plants and its potential sources are essential for the understanding of nutrition in epiphytes. Zotz & Winter (1994) showed that long term nitrogen-use efficiency (estimated as annual CO₂ gain per leaf nitrogen content) was similar in epiphytic Orchidaceae, Polypodiaceae, and Clusiaceae. These findings suggest that it is possible to estimate annual leaf carbon gain from leaf nitrogen content using the same conversion factor for the three species and possibly other species. Zotz & Winter (1994) suggested that leaf nitrogen has to be treated as a long-term investment and be considered in the context of the entire growing season or leaf life span.

More recently, the natural abundance of stable nitrogen isotopes ($\delta^{15}\text{N}$; nitrogen isotope composition, $^{15}\text{N}/^{14}\text{N}$) has been used in the study of nitrogen nutrition. The major nitrogen pools have different isotope signatures, for example, atmospheric N₂ is enriched in ^{15}N compared to epiphytic biomass (Stewart *et al.*, 1995; Reinert *et al.*, 1996). ^{15}N represents only 0.37% of the total atmospheric N₂, whereas the natural abundance of ^{13}C in relation to ^{12}C in the plant photosynthate ($\delta^{13}\text{C}$; carbon isotope composition, $^{13}\text{C}/^{12}\text{C}$), widely used among plant physiologists, is considerably larger (1.1%). Individual steps in a biochemical reaction can have large isotope fractionation, but these are frequently masked by the complexity of nitrogen pathways, some of which have opposite fractionation effects (Handley & Raven, 1992). Consequently, in nature, the net fractionation of the nitrogen isotopes is small, generally no more than -10‰ to +20‰ in any one system and often within a 1‰ difference (Handley *et al.*, 1991; Handley & Raven, 1992). The low abundance of ^{15}N and the small net fractionation effect on nitrogen pools complicate the use of nitrogen isotope signature in the study of biological processes; more detailed research is required.

The nitrogen isotope signature of leaf material of phorophytes and their epiphytes (some of them bromeliads) was used to investigate potential sources of nitrogen for the latter (Stewart *et al.*, 1995). Epiphytes generally showed lower $\delta^{15}\text{N}$ values than host trees. Among the possible sources of nitrogen (canopy derived leachates, N₂ fixation in the phyllosphere, and atmospheric nitrogen) these authors suggested that epiphytes uptake nitrogen derived from ^{15}N depleted atmospheric deposition since rainfall isotope composition can be as low as -12‰. The bromeliads *Tillandsia stricta* and *Neoregelia cruenta* were shown to have relatively low $\delta^{15}\text{N}$ values (-11.2‰ and -2.7‰, respectively) and nitrogen contents (2.9 and 6.1 mg/g, respectively) (Reinert *et al.*, 1996). Virginia &

Delwiche (1982) suggested that long-lived plants would preferably retain the lighter isotope of nitrogen, ^{14}N , from senescing leaves, leading to a progressive depletion in ^{15}N in the plant (low $\delta^{15}\text{N}$ values). This process would be further accentuated in nitrogen limiting environments, commonly experienced by epiphytes. It is not clear to date to what extent the relatively low $\delta^{15}\text{N}$ values shown by epiphytes are a consequence of ^{15}N depleted sources or fractionation occurring during nitrogen transformations in the plant. The nitrogen isotope composition of soil and leaf material has been used to make inferences about the nitrogen cycle mainly in crop fields. Results suggest that $\delta^{15}\text{N}$ can be further used as a tool to differentiate between nitrogen sources in natural environments (Vitousek *et al.*, 1989; Schulze *et al.*, 1994) and to clarify nutritional processes in epiphytes, providing that sources and sinks are carefully evaluated.

C_3 and CAM photosynthesis

Photosynthesis in the vascular epiphytes occurs via the C_3 and CAM pathways (Benzing, 1990). The environmental conditions that probably favour the C_4 pathway, such as high irradiance, temperature and moderate drought, do not usually occur in the forest canopy. Conversely, the high humidity and low light intensity generally characteristic of the dense tropical forest, and arid microsites of open canopy forest would favour the C_3 and CAM pathways, respectively. A crucial point regarding the distribution of the photosynthetic pathways among vascular epiphytes is the sequence of evolutionary events leading to the emergence of epiphytism and the C_4 and CAM pathways in the plant kingdom. However, this subject alone warrants an entire review, and as such is beyond the scope of the present discussion (see Smith, 1934; Benzing & Renfrow, 1971; Medina, 1974; Cockburn *et al.*, 1979; Gilmartin, 1983; Gilmartin & Brown, 1986; Griffiths, 1989; Hermans & Westhoff, 1990; Ehleringer *et al.*, 1991; Griffiths, 1992; Pilon-Smith, *et al.*, 1992; Lepiniec *et al.*, 1993; Slocombe *et al.*, 1993; Lepiniec *et al.*, 1994; Cushman & Bohnert, 1996; Winter & Smith, 1996).

CAM Vascular Epiphytes

Crassulacean acid metabolism (CAM) occurs in some 30 families and comprises approximately 30,000 species (Ting, 1985; Griffiths, 1988a). The most remarkable feature of CAM plants is the fact that stomata remain open during the night, allowing CO_2 uptake, fixation and storage as malic acid in the cellular vacuoles to be remobilised in the next light period. This trait determines high WUE (less water being spent per carbon gain), because the vapour pressure deficit (VPD) is usually lower during the night (e.g. 0.4 KPa compared to 3 KPa: Griffiths, 1988a). Organic acids can be accumulated in the cellular vacuoles during the night at concentrations up to 625mM in the epiphyte *Aechmea nudicaulis* and up to 1.6 M in the hemiepiphyte *Clusia minor* (Smith *et al.*, 1985; Borland *et al.*, 1992). Not surprisingly, the majority of known CAM plants grow in arid micro-environments such as exposed epiphytes in the humid tropics (Ting, 1985; Griffiths, 1988a).

The so-called facultative CAM plants perform C_3 photosynthesis under favourable conditions and CAM is only active under stress, such as drought or salt exposure. Maxwell *et al.* (1992) reported a shift from C_3 to CAM in *Guzmania monostachia* (an epiphytic bromeliad, widely distributed in Trinidad: see Pittendrigh, 1948; Griffiths & Smith, 1983) in response to drought stress. *G. monostachia* is the only CAM facultative bromeliad reported so far. Similarly, differences between day/night temperatures maximize acid accumulation in hemiepiphytic *Clusia* (Haag-Kerwer *et al.*, 1992). The obligate CAM plants, on the other hand, perform CAM irrespective of environmental conditions. Often obligate CAM plants restrict stomatal conductance and increase respired CO_2 fixation. Kluge *et al.* (1989a) reported that in the epiphytic fern *Pyrrhosia* the rate of CO_2 recycling was increased under water stress. Similar results were obtained for several bromeliads (Griffiths, 1988b; Martin, 1994; Reinert, 1995). Expression of the CAM pathway can also be associated with plant ontogeny. Holthe *et al.* (1987) showed a gradual expression of CAM during leaf development in the saxicolous *Peperomia scandens* (Piperaceae). Fully expanded leaves photosynthesised via C_3 pathway and progressively increased CAM activity until full CAM was performed. The CAM pathway is expressed in many vascular epiphytes and has been further reviewed elsewhere (Kluge & Ting, 1978; Osmond, 1978; Cockburn, 1985, Ting, 1985; Griffiths, 1988a, Winter & Smith, 1996).

Orchids

The Orchidaceae occurs in extremely diverse habitats. Predominantly distributed in the tropics, orchids also inhabit arctic tundra and alpine meadows while *Habenaria repens* grows as an aquatic plant (Benzing & Ott, 1981). Orchids can tolerate low pH when growing in marshes, or severe drought when growing epiphytically (Benzing & Ott, 1981). The CAM pathway is well represented among epiphytes mainly because some 14,000 orchids (73%) are epiphytic, whereas non-orchid CAM epiphytes comprise about 9,000 species (Dresser, 1993; Atwood, 1986). Further surveys of the photosynthetic mode in epiphytic orchids are necessary to estimate the number of CAM orchid species. Generally, thick-leaved orchids perform CAM whereas those with thin leaves exhibit C_3 photosynthesis, as exemplified by the two Singaporean species, *Phalaenopsis grandiflora* and *Paphilopedilum barbatum*, respectively (Goh & Kluge, 1989).

Plectrorhiza trisentata and *Dendrobium speciosum* (Australian CAM epiphytic orchids native to subtropical forest) monitored over 24h periods throughout a year showed different responses to summer water shortage. *P. trisentata* (wiry-stemmed twig epiphyte) showed reduced leaf conductance and nocturnal acid accumulation, whereas *D. speciosum* with an absorptive spongy root ball maintained similar leaf conductance and nocturnal acidification values throughout the year (Wallace, 1981 *apud* Benzing, 1990). These findings suggest a close coupling between stomatal control, photosynthetic pathway, and water storage capacity to counter drought-stress in canopy habitats.

Some orchids have very reduced shoots and photosynthesis takes place in the green roots. The significance of the shootless life-form of some orchids is controversial. Rolfe (1914 *apud* Benzing & Ott, 1981) claimed that it is an adaptation against drought, others (Ruinen, 1953 *apud* Benzing & Ott, 1981; Johansson, 1977) attributed this condition to a parasitic mode of nutrition, and finally Benzing & Ott (1981) suggested that the shootless condition is primarily related to nutrient economy. Roots of leafless orchids lack stomata but possess a velamen (spongy, multilayered rhizodermis composed of dead cells that surround the cortex of aerial and some terrestrial roots: Benzing, 1990) through which gas exchange takes place. Goh *et al.* (1983) observed that dark CO₂ assimilation and acid accumulation was lower in aerial roots than in leaves of epiphytic CAM orchids. Cockburn *et al.* (1985) used a microsyringe to sample air inside the roots of the shootless *Chiloschista usneoides* to learn how CO₂ loss through the velamen is prevented during phase III of CAM (light phase). They concluded that the loss of CO₂ is minimized by the balance between acid decarboxylation and CO₂ refixation by Rubisco, such that the internal concentration of the gas approximates that of the atmosphere.

The function of the velamen is controversial though it is thought to be involved in water uptake (Benzing *et al.*, 1983; Goh & Kluge, 1989). Walter (1951 *apud* Goh & Kluge, 1989) and Sinclair (1983b) reported 1h and 3 days, respectively, to complete rehydration following the irrigation of the aerial roots. On the other hand, Dycus & Knudson (1957) argued that velamina are associated primarily with water conservation by insulating the living core of the root. Sanford & Adanlavo (1973) examined 73 species of epiphytic orchids in West Africa and noted a strong correlation between the number of cell layers in the velamen and the habitat exposure of the microsite. These results reinforce the water conservation role of the velamen. Among shootless orchids such as *Chiloschista usneoides*, the water-absorbing function of the velamen would conflict with the photosynthetic function of the roots, since water-saturated velamina do not take up CO₂ (Cockburn *et al.*, 1985). However, the pneumathodes in the roots do not fill with water so that gas exchange can take place while the root is wet.

Epiphytic orchids are classified as either monopodial or sympodial. Monopodial species have axillary flowers (shoot apex grows vegetatively and the inflorescence is produced by the axillary buds) and may form aerial roots. The sympodial group grows vegetatively from the axillary buds, and the inflorescence is terminal. Sympodial growth leads to more pronounced shortening of the individual shoots. All Orchidaceae are thought to be obligate mycotrophs (benefit from mycorrhizal associations) as seedlings and some are facultative as adult plants (Benzing, 1990). Lesica & Antibus (1990) found mycorrhizal associations occurring in almost half of the epiphytic orchids examined in a Costa Rican rain forest.

Most epiphytic orchids have short swollen stems, known as pseudobulbs (in contrast to true bulbs which have thickened leaves). Pseudobulbs are associated with water and carbohydrate storage as well as photosynthesis, although not much carbon gain occurs here for most species (D. Benzing, pers. comm.). The small orchids

Bulbophyllum minutissimum and *B. odoardii* have only rudimentary leaves, so in this case pseudobulbs are the photosynthetic organ (Benzing, 1990). The abscission layer involved in leaf shedding is another morphological adaptation associated with water economy by reducing transpiring surfaces.

Bromeliads

The ecological classification of the bromeliads into 4 types (Pittendrigh, 1948) has at one extreme the obligate terrestrial bromeliads (type I) and at the other, the obligate atmospheric epiphytes (type IV). Soil roots perform the usual functions of plant nutrition in type I bromeliads, whereas in type IV, roots only anchor the plant to the substrate and foliar trichomes replace roots as absorptive organs. Types II (tank-root) and III (tank-absorbing trichome) bromeliads are also largely independent of the substrate and can grow both terrestrially and epiphytically. Holdfast roots of *Tillandsia* exhibit unicellular hairs which augment the adhesion/mechanical role by secreting a cement-like substance (lipopolysaccharid) and hydrophilic mucopolysaccharidic material in the root cap (Brighigna *et al.*, 1990). Peltate leaf hairs, or trichomes, characteristic of the subfamily Tillandsioideae, are composed of an uniseriate chain of living cells (the "stalk") and are capped by a shield, which is a single layer of concentrically arranged empty cells with a high concentration of hygroscopic hemicellulose and pectin in the outer walls (Tomlison, 1969; Benzing *et al.*, 1978). The atmospheric species of *Tillandsia* are characterised by highly specialised trichomes which bear a wide, sometimes asymmetric wing (Benzing *et al.*, 1978; Adams & Martin, 1986a; Reinert & Meirelles, 1993). These trichomes are involved in absorbing airborne ions and water, as exemplified by atmospheric bromeliads such as Spanish moss, *Tillandsia usneoides* (Benzing, 1976; Benzing *et al.*, 1976; Schlesinger & Marks, 1977; Benzing *et al.*, 1978). Shacklette & Connor (1973) carried out an exhaustive survey on the accumulation of more than 30 chemical elements including metals by *Tillandsia usneoides*, growing at several locations in the USA, and demonstrated that this species can be used as an indicator of air pollution. Similarly, a study carried out in the coastal vegetation of Rio de Janeiro, Brazil, showed that the concentration of airborne calcium, magnesium and sodium strongly correlated with that in the foliage of *T. stricta* (Reinert *et al.*, 1996). On the other hand, mineral nutrition of other atmospheric *Tillandsia*, such as *T. circinnata*, may be associated with foliage leachates (Benzing & Renfrow, 1974b). Additionally a strong relationship existed between the concentration of minerals in *Tillandsia usneoides* and the host tree (phorophyte) (Schlesinger & Marks, 1977). Research on nutrients in tank bromeliads suggests that plant mineral uptake is mainly via basal trichomes and tank roots. Nadkarni & Primack (1989) found that mineral uptake through the tanks was considerably higher than through the soil roots in the C₃ tank bromeliad *Guzmania lingulata* (Griffiths *et al.*, 1983). Benzing *et al.* (1992) found that *Tillandsia* species do not appear to be as sensitive as some other plants, such as certain crops, to short exposures to several toxic gases such as ozone and sulphur dioxide.

CAM occurs in all three bromeliad subfamilies, however the CAM epiphytes are restricted to Tillandsioideae and Bromelioideae (Medina *et al.*, 1977; Benzing, 1990). The presence of the CAM pathway in all atmospheric *Tillandsia* except for the heterophyllous *T. deppeana* (Adams & Martin, 1986c) is related to improved CO₂ supply and water economy. Smith *et al.* (1986) compared CAM, C₃ and C₃-CAM intermediate type III bromeliads growing epiphytically. The CAM species *Aechmea nudicaulis* showed the highest carbon assimilation rates, followed by the C₃ species *Vriesea amazonica*, and then the C₃-CAM intermediate, *Guzmania monostachia*. Nevertheless, they all showed relatively low rates of photosynthesis (1-3 mmol m⁻² s⁻¹). Several species of the genus *Tillandsia* often occur under a range of light intensities where adjustments at the physiological and molecular levels are required for acclimation to different environments. Plants growing under high light need to maintain a balance between CO₂ uptake (and consequent water loss), leaf temperature and absorption of solar radiation (Björkman, 1981). Dense trichome cover helps prevent water loss and endows the leaf surface with higher reflectance (Griffiths *et al.*, 1983; Martin *et al.*, 1985). Leaves growing under high light intensity usually have a higher degree of overlapping and self-shading than do shade plants. Laboratory-grown *T. usneoides* showed higher nocturnal acid accumulation under high incident photosynthetic flux density (PFD) although field data show similar rates for plants grown under a range of light intensities (Martin *et al.*, 1985; Adams & Martin, 1986b). Generally, the photosynthetic apparatus is protected from relatively high levels of PFD by reduced total chlorophyll content and higher chlorophyll a:b ratios, reflecting a smaller light harvesting chlorophyll a:b-protein complex (Björkman, 1981). However, although some bromeliads tolerate a wide range of light regimes and consequently exhibit wide variation in chlorophyll content, chlorophyll a:b ratios do not appear to vary considerably in bromeliads (Martin, 1994).

Carbon isotope fractionation occurs naturally during stomatal diffusion and fixation of CO₂, which results in different carbon isotope signatures among C₃, C₄ and CAM plants (Farquhar *et al.*, 1989). Measurements of instantaneous carbon isotope discrimination (Δ) can distinguish between carboxylation by Rubisco and PEPC (Evans *et al.*, 1986; Griffiths *et al.*, 1990). *Tillandsia utriculata*, *T. stricta* and *Neoregelia cruenta* showed intermediate Δ values (5-15‰) during phases II and IV of CAM (exogenous CO₂ uptake during the light period) revealing that both Rubisco (C₃ carboxylation) and PEPC (C₄ carboxylation) contribute to the fixation of CO₂ (Griffiths *et al.*, 1990; Reinert, 1995). Δ values for C₃ and C₄ carboxylation are around 30‰ and -1‰, respectively (O'Leary, 1981). Simultaneous activation of both carboxylating enzymes represents an optimisation of carbon uptake per water loss.

Consistent with the well established water-conserving nature of CAM (Kluge & Ting, 1978; Griffiths, 1988b), refixation of CO₂ respired during phase I often represents more than 50% of the total dark fixation of CO₂. The percentage of CO₂ recycling is influenced by nighttime temperature, PFD, and possibly leaf to air VPD (Griffiths, 1988b). The tank bromeliad *Neoregelia cruenta* showed an increase in percentage of recycled

CO₂ from 68% to 75% when subjected to water stress (Reinert, 1995). Nevertheless, exceptions have been reported. Another tank bromeliad *Tillandsia flexuosa* showed a decline from 76% to 73% of CO₂ recycled during the dry season (Griffiths *et al.*, 1989a). These results contrast with Loeschen *et al.* (1993) who recorded no appreciable CO₂ recycling during CAM in twelve epiphytic *Tillandsia* under well-watered conditions. Loeschen *et al.* (1993) suggested that CO₂ recycling during CAM would predominantly occur under sub-optimal conditions and, thus, represent a gradation between CAM and CAM-idling (Ting, 1985).

Regulation of CAM under different VPD

A direct stomatal response to relative humidity (RH) has been shown in a number of bromeliad species (Lange *et al.*, 1971; Lange & Medina, 1979; Grantz, 1990). Increased evaporation rates from (or around) the guard cells under higher VPD would cause guard cells to lose turgor and consequently lower conductance, so that evaporation rate would act as a humidity sensor. Differences in VPD would then be sensed by the guard cells, before any significant change in the water status of the leaf had occurred (Cowan, 1977; Grantz, 1990). The detailed mechanism of stomatal response to RH remains unclear (Monteith, 1995). It has been suggested that some species might have an evaporation region with a thinner cell wall in the guard cell (Appleby & Davies, 1983). Conversely, Grantz (1990) suggested that diversion of the water flux from the guard cell to the stomatal cavity would decrease turgor pressure of the guard cells and subsequently decrease conductance. The mechanism of stomatal response to VPD is subtle, especially in epiphytic plants, where direct uptake of water from air is only believed to occur above 99% RH (Martin & Schmitt, 1989; Martin, 1994). Griffiths *et al.* (1986) showed that stomata responded to variation in VPD under natural conditions. Stomatal conductance of two bromeliads, *Aechmea nudicaulis* and *A. aquilega*, decreased immediately after a drop in RH (when a warm wind started to blow). These results are in agreement with those found for *T. recurvata* (Lange & Medina, 1979), although these were not subsequently confirmed (Schmitt *et al.*, 1989). One of the possible explanations offered by Schmitt *et al.* (1989) for contradictory results was that day-night changes in relative air humidity may be more important in influencing rates of gas exchange than the changes in absolute water content of the air.

Tillandsia stricta showed a more dramatic decrease in CO₂ exchange under high VPD than under high PFD regimes in the range naturally experienced by the coastal vegetation of Brazil. Total daily CO₂ uptake dropped about 3-fold in response to a 4-fold increase in VPD and decreased less than 1.5-fold with changes from high to low PFD. Total daily CO₂ uptake was reduced from 33 mmol m⁻² s⁻¹ under low VPD to 11 mmol m⁻² s⁻¹ under high VPD, and no phase II of CAM was observed. Stomatal conductance decreased from values close to 250 mmol m⁻² s⁻¹ to less than 10 mmol m⁻² s⁻¹, representing a 50-fold decrease which was not reflected by an equivalent reduction in transpiration, which decreased less than 9-fold (Reinert, 1995).

Ferns

There are two major types of epiphytic ferns. Nest ferns are typically stress-avoiders; they establish their own water-collecting system around the roots. These ferns accumulate humus around the roots by a nest of fronds which act as a sponge, allowing constant water supply and no demand for additional adaptations to reduce water loss. *Asplenium nidus* (Aspleniaceae) is a typical example commonly found throughout Singapore and Malasia (Kluge *et al.*, 1989b). Xeromorphic ferns, in contrast to nest ferns, grow directly on the phorophyte's bark. These ferns have no means of accumulating water between rainfalls and exhibit characteristics common to other xeric epiphytes such as thick cuticles, water storage cells, and reduced transpiring surfaces.

Winter *et al.* (1983), studying the distribution of the photosynthetic modes in Australian epiphytes, found that in Polypodiaceae the CAM species of the genus *Pyrrhosia* occupy the most exposed sites of any epiphytic fern and that among Aspleniaceae all species showed C₃ photosynthesis. Gas exchange measurements showed that *P. longifolia* and *Drymoglossum piloselloides* invariably exhibited CAM photosynthesis regardless of the laboratory growing conditions, and are therefore considered to be constitutive CAM plants (Ong *et al.*, 1986). Conversely, *Asplenium nidus* showed relatively high transpiration rates and daytime CO₂ uptake, closely following available PFD at the site (Kluge *et al.*, 1989b) and consistent with $\delta^{13}\text{C}$ values of -26‰, characteristic of C₃ photosynthesis (O'Leary, 1981). The lower relative CO₂ assimilation rate measured under natural conditions for *A. nidus* of 0.5 mmol m⁻² s⁻¹, when compared to the CAM cycling epiphytic fern *P. adnacens* (2.5 mmol m⁻² s⁻¹), is probably due to low PFD (maximum 40 μE m⁻² s⁻¹), insufficient to allow maximum photosynthetic rates. *P. confluens* showed an extremely flexible response to varying light conditions in relation to nocturnal acid accumulation and assimilation rates, which indicates a possible C₃-CAM intermediate status (Winter *et al.*, 1983). Griffiths *et al.* (1989b) working on sun and shade-adapted populations of *P. piloselloides* showed that shade fronds were less succulent, had higher chlorophyll content, lower chlorophyll a:b ratios, and reduced dark respiration rates and compensation point, typical of shade plants. Griffiths *et al.* (1989b) concluded that CO₂ from dark respiration and photorespiration is sufficient to alleviate photoinhibition in sun and shade plants when compared to plants artificially deprived of CO₂.

Conclusion

Whether puzzled by intriguing questions on how epiphytes acquire nutrients, how they overcome periods of water shortage, how epiphytism evolved in different taxa, or simply perplexed when faced with the beauty of huge trunks carpeted with hundreds of epiphytes and telephone wires festooned with air-plants, epiphytism has struck naturalists, botanists, and more recently the journalist, Andrew Revkin (1990), who on observing the Amazon Forest wrote:

“The forest’s layered look has been determined by the location of the crucial fuels that it needs to thrive. The architecture of the forest has resulted from a sort of tug-of-war between the need to absorb water and nutrients from the earth below while competing with neighbouring plants for the light coming from the sun above. (...) Evolution has solved the dilemma in several ways. (...) Myriad epiphytes -air plants-grow high in the canopy, their dust-fine seeds having lodged in the crooks of the tree branches.”

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