

Ecophysiology and Crassulacean Acid Metabolism of Tropical Epiphytes

Katia Silvera and Eloisa Lasso

Abstract Epiphytes are plants that germinate and grow upon other plants without contact with mineral soil and without parasitizing their host plant. Therefore, they derive nutrients and water from the environment. Epiphytes are primarily tropical in distribution and may be the most species-rich life form in very wet rainforest sites, constituting about 10 % of all vascular plants. Nearly 80 % of all vascular epiphytes belong to one of three families: Orchidaceae (orchids), Bromeliaceae (bromeliads), and Polypodiaceae (ferns). Orchids in particular, are the most species rich in epiphytes. In this review, information on the ecophysiology of vascular epiphytes is presented, in an attempt to find patterns that explain the ecophysiological adaptations of canopy living. We highlight the ecophysiology of orchids and bromeliads, and whenever possible, provide insight into other epiphytic families. We discuss morphological, anatomical and physiological novelties that epiphytes have evolved to face the challenges of living in the canopy, including adaptations to increase water capture, to facilitate water storage or to reduce water loss. Because epiphytes are particularly susceptible to climate change, and can be monitored as a component of forest health, we also consider their distribution and physiological responses to climate change as a key aspect of conservation programs.

Keywords Epiphytes • Crassulacean acid metabolism (CAM) • Bromeliaceae • Orchidaceae • Conservation

K. Silvera (✉) • E. Lasso
Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Ancón,
Republic of Panama
e-mail: katia.silvera@ucr.edu

E. Lasso
e-mail: e.lasso@uniandes.edu.co

K. Silvera
Department of Botany and Plant Sciences, University of California Riverside, Riverside,
CA 92521, USA

E. Lasso
Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, Colombia

Introduction

Epiphytes are plants that germinate and grow all or most of their lives attached to other plants without contact with mineral soil (Benzing 1990), and can grow attached to trunks or branches of host trees and shrubs from the understory floor all the way to tree crowns. Unlike mistletoes, epiphytes do not parasitize their hosts, and instead take nutrients and water from the environment (Benzing 1990). They occur on the branches of trees in many biomes, but vascular epiphytes are particularly abundant in tropical forests and can grow so profusely that they substantially increase the mass that tropical tree branches must support (Fig. 1a; Niklas, this volume); epiphytic biomass can be as much as 50 % of the tree leaf biomass (Lüttge 1989), especially in primary montane forests (Nadkarni et al. 2004). In tropical forests, epiphytes form conspicuous masses that are known to support large amounts of animal life including ant nests, arthropods and amphibians (Stuntz et al. 2002), in addition to contributing to the hydrology and nutrient cycling of the ecosystem.

The diversity of epiphytes in tropical forest canopies is also astonishing, constituting about 10 % of all vascular plants. Epiphytes are a conspicuous element of humid tropical forests and may be the most species-rich life form in very wet rainforest sites (Gentry and Dodson 1987). Within this diversity, there are similarities between different species of epiphytes and certain characteristics that are particular to the epiphytic syndrome allowing these species to live in the canopy. With few exceptions, epiphyte species are generally long-lived perennials, have small body size, tend to have small seeds that can be dispersed by wind, and have relatively slow growth. Wind-dispersed seeds allow epiphytes to colonize new trees rapidly. To face the challenges of access to water supply and nutrients, many epiphytes have evolved several morphological adaptations such as leaf succulence, water absorbing trichomes and presence of water absorbing spongy tissue (Benzing 1990; Hietz et al. 1999). Thus the particular growth form and habitat of epiphytes leads to certain physiological outcomes, especially in vascular epiphytes, that appear to facilitate their proclivity for growth in tropical forest canopies.

In this review, information on the ecophysiology of epiphytes is presented, with emphasis on vascular epiphyte literature, in an attempt to find patterns that explain the ecophysiological adaptations of living in the canopy. We emphasize vascular epiphytes because they are the most conspicuous and unique forms of epiphytes in tropical forest, and are particularly abundant in the tropics compared to temperate and boreal forests where non-vascular epiphytes prevail. We also constrain our discussion to epiphytes that germinate in the canopy (Fig. 1a, sometimes called primary epiphytes), and do not consider “nomadic vines”, which refer to climbing plants that germinate on the ground and later become epiphytes by losing contact with the ground while climbing host plants (Hao, this volume; Zotz 2013a). Nearly 80 % of all vascular epiphytes belong to one of three families: Orchidaceae (orchids),

Fig. 1 Epiphytic communities from tropical rainforests. **a** Epiphytic community of bromeliads and orchids in a tropical montane cloud forest of Panama. Photo by Gaspar Silvera.

b *Anthurium* and *Phylodendron* epiphytes in a seasonal tropical forest of Panama. Photo by Gaspar Silvera. **c** Orchid epiphyte in a seasonal lowland forest of Panama. Photo by Katia Silvera



Bromeliaceae (bromeliads), and Polypodiaceae (ferns), and about 85 % of these are orchids and 8 % are bromeliads (Zotz 2013b). Thus, the ecophysiology of orchids and bromeliads will be the main focus of this review, and whenever possible, we will provide insight into other epiphytic families. We will discuss morphological, anatomical and physiological novelties that epiphytes have evolved to face the challenges of living in the canopy. Because epiphytes are particularly susceptible to climate change, and can be monitored as a component of forest health, we also consider their distribution and physiological responses to climate change as a key aspect of conservation programs.

Taxonomic and Ecological Distribution of Epiphytes

Vascular epiphytes are present in 27,614 species, 913 genera and 73 families (Zotz 2013b), and are found worldwide in almost all kinds of ecosystems, especially in tropical and subtropical regions. The real diversity, however, is in tropical rainforests and cloud forests where they can represent more than 50 % of the total vascular flora of plant species in a given area (Benzing 1990; Gentry and Dodson 1987). Neotropical montane forests, in particular, are exceptionally rich in epiphytes (Benzing 1989, 1990).

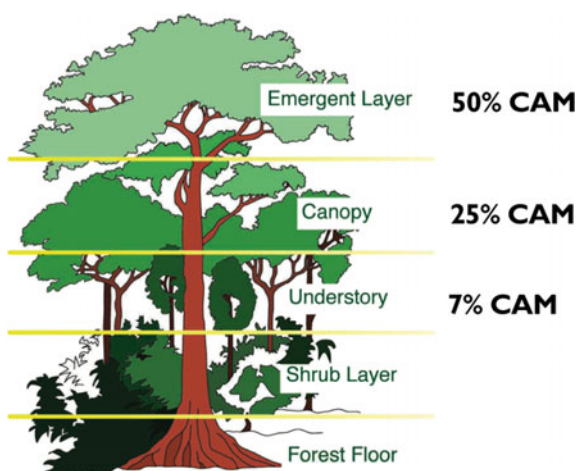
Microclimatic gradients within the canopy of individual host trees provide a variety of niches that can be exploited by different species (Hietz and Briones 1998). Distribution of epiphytes varies greatly within different forests, and has distinct patterns both across environmental gradients, as well as vertically within host trees. To understand the distribution of epiphytes, Burns and Zotz (2010) proposed examining epiphyte assemblages that form different meta-communities as species interaction networks between epiphytes and their host tree. In “classical” meta-communities, epiphytes are restricted to the canopy and are referred to as obligate epiphytes, as in the case of orchids and bromeliads of tropical regions. These meta-communities of epiphytes from different host trees are then linked together by seed dispersal. This differs from temperate zones, where epiphytes are composed of species that can live on the forest floor and occasionally grow as epiphytes.

Distribution of epiphytes also varies horizontally, and this variation occurs between different host trees and among different forest types. Studies that address species composition along altitudinal gradients have revealed that species richness patterns are influenced by the mid-domain-effect (Cardelús et al. 2006), a peak of abundance at mid-elevation. A study focusing on the distribution of CAM in orchids of Panama and Costa Rica found that species richness was highest at sites between 1,000 to 1,500 m altitude, consistent with a peak of abundance at mid-elevation known as the “mid-altitudinal bulge” (Silvera et al. 2009). Almost all epiphytic taxa show hump-shaped curves of distribution with altitude, but their

relative contributions change with elevation (Cardelús et al. 2006; Krömer et al. 2005). The mechanism behind this distribution has been explained by the interaction between temperature and water gradients caused by increasing altitude (Peet 1978; Silvera et al. 2009; Whittaker and Niering 1975). Mid elevation sites of around 1,000 m in tropical forests commonly have the highest incidence of cloud cover.

Vertical stratification of epiphytes in tropical forests has been linked to physiological strategies related to microclimate constraints (Graham and Andrade 2004; Reyes-Garcia et al. 2008). Vertical distribution of epiphytes is influenced by eco-physiological adaptations, such as the ability to acclimate to varying levels of photon flux density (PFD) and humidity (Benzing 1990). For example, species of *Phylodendron* tend to clump at lower sites within branches or trunks of host trees (Fig. 1b) where humidity levels are higher and PFD levels are lower, and because part of the life cycle may be dependent on nutrient uptake from roots that are in contact with mineral soil (Putz and Holbrook 1986). On the other hand, epiphytic species that utilize Crassulacean Acid Metabolism (CAM), a water-saving mode of photosynthesis (Ting 1985), tend to clump in areas of higher PFD and exposed sites within branches of the host tree. For example, a study of vertical stratification of epiphytes in a lowland forest of Panama found that >50 % of all epiphytes clustered at intermediate canopy heights (Zotz and Schultz 2008). In a lowland forest of central Panama, the percentage of CAM epiphytes increases with canopy height (Fig. 2; Zotz and Ziegler 1997). In a lowland forest of the Atlantic slope of Panama, total biomass was largest at intermediate heights within the forest, but the relative contribution of CAM species was higher in the upper canopy (Zotz 2004). In another study by Hietz et al. (1999) the proportion of epiphytic species showing CAM decreased with increasing elevation and precipitation along an altitudinal gradient from tropical dry forest to humid montane forest of eastern Mexico.

Fig. 2 Proportion of epiphytic CAM species in different strata of a lowland forest of Central Panama. The percentage of CAM epiphytes increases with canopy height. Percent CAM species was extrapolated from published work (Zotz and Ziegler 1997)



Physiological Adaptations of Epiphytes

There are also numerous ecophysiological adaptations that appear to contribute to epiphyte success in the canopy. Epiphytes often grow in the canopies of very wet tropical forests, with abundant precipitation and high soil water availability, but even in such humid forests, the canopy can dry out quickly and therefore has been described as “the desert in the rainforest”. Many epiphytic species use CAM, one of three metabolic pathways found in vascular plants for the assimilation of atmospheric CO₂. CAM plants take up CO₂ from the atmosphere predominantly at night, improving the ability of plants to acquire carbon in water-limited and CO₂-limited environments (Winter and Smith 1996a). Thick leaf cuticles are also observed in many epiphyte species. Many epiphytic species also exhibit less negative osmotic potential compared to their terrestrial congeners (Hao et al., this volume), consistent with careful management of internal water resources. Finally, varying degrees of tolerance to shade and desiccation have been observed in epiphytes compared to related terrestrial species. These characteristics allow epiphytes to survive long periods of drought stress, especially in tropical forests with prolonged dry seasons.

Why not Rooting in Soil Leads to Certain Physiologies

The epiphytic habitat represents a highly dynamic environment, subject to temporal and spatial variations in light, nutrient and water supply. Among these abiotic factors, sporadic or seasonal periods of water shortage are perhaps some of the most common challenges even for epiphytes occurring in humid tropics (Zotz and Thomas 1999). Epiphytes do not take water or nutrients from the host plants. The vast majority of epiphytic plants do not have contact with mineral soil, and therefore must obtain nutrients and water from the microenvironment where they live. Because water availability is a limiting factor for growth and survival of epiphytic species living in the canopy (Lüttge 1989; Zotz and Hietz 2001), and represents a strong selective pressure, epiphytes have evolved myriad physiological and morphological adaptations (Benzing 1990; Hietz et al. 1999), in addition to acquiring necessary nutrients from debris or organic soil from the canopy. These adaptations can be divided into adaptations to increase water capture, to facilitate water storage or to reduce water loss.

To maximize water uptake from rain pulses, dew, or moisture in the air and to survive long periods of drought stress, especially in tropical forests with prolonged dry seasons (Benzing 1990; Hietz et al. 1999), epiphytes have evolved specialized absorptive tissues and organs, and a diversity of growth forms. Bromeliads, for example, possess specialized absorptive trichomes—a key innovation associated with the transition from terrestrial to epiphytic life form (Crayn et al. 2004). In orchids, the functional equivalent to bromeliad trichomes is the “velamen”, a

multilayered spongy epidermis that allows orchids to absorb atmospheric moisture and nutrients through the roots (Benzing 1987).

Adaptations related to water storage include leaf succulence, composed of abundant hydrenchyma, an enlarged specialized spongy tissue that allows plants to store water. Often hydrenchyma is the main reservoir for maintaining a stable water status in photosynthetic tissues (Freschi et al. 2010). A thick leaf cuticle, on the other hand, is thought to minimize cuticle conductance and therefore water loss during dry periods. A study of 15 vascular epiphytic species evaluated for water permeability of astomatous isolated cuticular membranes showed a lower leaf cuticular permeability to water in comparison to terrestrial forms (Helbsing et al. 2000). Additionally, epiphytes tend to have lower stomatal densities compared to terrestrial plants, thus reducing water loss. Stomatal density can vary from 1–30 stomata/mm² in some bromeliads (Martin 1994) to 30–62 stomata/mm² in aroids (Lorenzo et al. 2010), to more than 180 stomata/mm² in epiphytic *Clusia* species (Holbrook and Putz 1996). In terrestrial plants, stomata densities can reach 600 stomata/mm² (Larcher 2003). Finally, many epiphytic species utilize CAM. This metabolic pathway is present in ~19 % of epiphytic species in a lowland forest (Zotz 2004), ~50 % of tropical epiphytic orchid species (Silvera et al. 2005; Winter and Smith 1996b) and approximately 25–38 % of epiphytic bromeliad species (data estimated from Zotz 2004 and Crayn et al. 2004). Many epiphytic species use combinations of these adaptive traits, which allow them to tolerate limited water supply in the canopy. Below we highlight key adaptations from two of the largest epiphytic plant families: Orchidaceae and Bromeliaceae, and summarize generalities found in other epiphytic families.

Epiphytic Orchids

Of all epiphytic families, the Orchidaceae has been the most successful in colonizing tree crowns and exposed sites (Fig. 1c). One important characteristic that allows epiphytic orchids to colonize the canopy is the presence of roots that serve several key functions. Orchid roots have the capability of photosynthesizing due to presence of chlorophyll, orchids roots are surrounded by spongy velamen that serves to quickly absorb and accumulate water and nutrients, and orchid roots enable the plant to anchor itself securely in branches, thus providing mechanical protection and stability (Benzing 1990). Orchids also use a different strategy during the dry season by having access to stored water and nutrients from the pseudobulb, a storage organ derived from a thickening of the stem between leaf nodes. Orchids generally have long-lived thicker leaves with lower photosynthetic capacity per unit area compared to ferns and bromeliads (Cardelús and Mack 2010). Although thick leaves in orchids are typically associated with $\delta^{13}\text{C}$ values in the CAM range, some thin-leaved orchids are also capable of CAM photosynthesis, as demonstrated by acid titration (Silvera et al. 2005).

CAM Photosynthesis in Epiphytic Orchids

In contrast to C_3 and C_4 plants, CAM has evolved multiple independent times within vascular plants, and is widely distributed throughout semi-arid tropical and subtropical environments, including epiphytic habitats in tropical regions (Silvera et al. 2009). Several studies indicate that CAM photosynthesis may be widespread among tropical epiphytic plants, particularly in the largest family of vascular plants, the Orchidaceae with approximately 30,000 species (Earnshaw et al. 1987; Silvera et al. 2009, 2005; Winter et al. 1983). It is estimated that up to 50 % of tropical epiphytic orchid species exhibit different degrees of CAM (Silvera et al. 2005) with a gradient of species showing C_3 to weak CAM to strong CAM modes. The largest proportion of CAM epiphytic orchid species are usually distributed at lower altitudinal sites (Silvera et al. 2009). Additionally, the multiple origins of CAM and its strong positive correlation with epiphytism has been linked to the rapid degree of speciation in the Orchidaceae (Silvera et al. 2009). This is particularly true within the Subfamily Epidendroideae, which represents the largest epiphytic clade within flowering plants (Fig. 3)

Epiphytic Bromeliads

The Bromeliaceae family has approximately 3350 species that cover a wide range of habitats; from very humid forest to extremely xeric sites, and from lowland sites to near 5000 m altitude (Crayn et al. 2015). About half of the species are epiphytes. The epiphytic bromeliads show a morphological progression from tank life forms, to atmospheric or nebulophyte life forms (Zotz 2013b). The term “nebulophyte” has been used in the literature to characterize epiphytic bromeliads with long thin leaves and low leaf succulence, a morphology that maximizes fog-catching (Martorell and Ezcurra 2007; Reyes-Garcia et al. 2012). Tank species have large rosette type leaves that are arranged in such way that can hold large amounts of water after rain events. Tank bromeliads receive nutrient inputs from rain, mist, dust, and nutrient released from ground-rooted plants through leaching or decomposition, as well as from remains of animals and/or organic matter (Benzing 1990; Romero et al. 2010). These “continuously supplied” (Benzing 1990) tank epiphytes tend to have thick leaf cuticles, high stomatal control, and are more restricted to the upper canopy, all characteristics that allow them to resist photoinhibition and avoid desiccation (Reyes-Garcia et al. 2012). Species with large tanks, however, can be subjected to long periods of desiccation. Accumulated water can dry out after 1–2 weeks (Zotz and Thomas 1999), and thus tank species rely on the ability to switch from C_3 to CAM in order to survive these water shortage episodes (Benzing 2000). The tank structure or “phytotelmata” can intercept and retain debris and water, and form a nice microcosm where a diverse community of invertebrate and vertebrate animals thrive (Benzing 2000). Organism debris living inside of the tank can provide

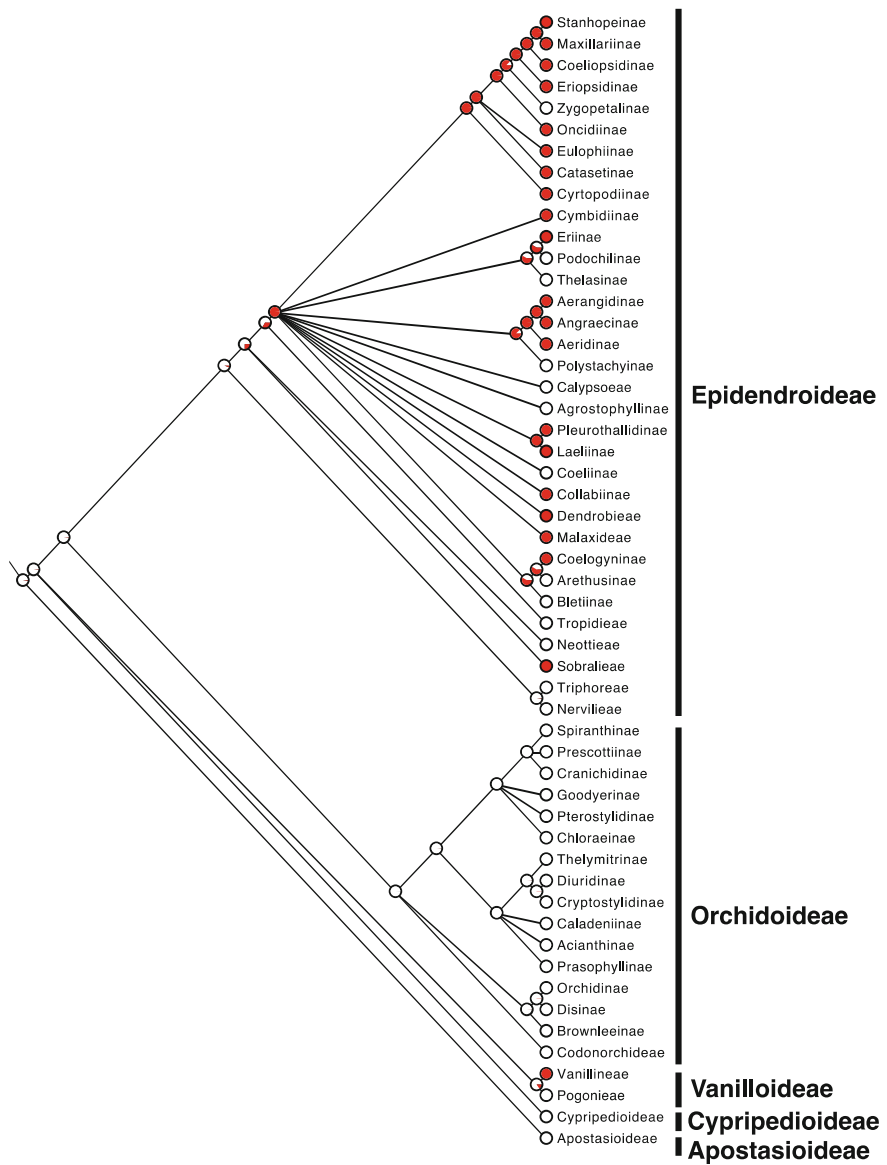


Fig. 3 Cladogram of the relationship among 53 Orchidaceae subtribes. The five orchid subfamilies are represented on the right side. Presence and absence of CAM were mapped onto the cladogram showing lineages with CAM in red. The red area within the pie chart indicates relative support for different ancestor states. This analysis supports the multiple, independent origins of CAM in the epiphytic Subfamily Epidendroideae

nutrition to the bromeliad, as shown by experiments with stable isotopes of nitrogen. Romero et al. (2010) demonstrated that treefrog feces from *Scinax hayii* contributed 27.7 % of the total N to the plant, whereas dead termites contributed 49.6 % of the total N to the plant. They also showed that plants receiving additional N through frog feces and termites had higher photosynthetic rates compared to control plants, but only during the rainy season. Epiphyte nutrient availability is generally less critical than water availability (Laube and Zotz 2003), but can still be a limiting factor when water is available.

In contrast to tank bromeliads, atmospheric life forms or “pulse supplied” epiphytes only have access to water after a precipitation event, and maximize water absorption through abundant leaf trichomes (Benzing 1990). Atmospheric bromeliads receive nutrient inputs from dust, mist and rain through dense surface trichomes. Indeed, the main adaptation of atmospheric bromeliads for living in the canopy is the presence of specialized trichomes for both minerals and water absorption (Benzing et al. 1985), especially because bromeliad roots do not engage in nutrient acquisition nor have mycorrhizal fungi associations (Lesica and Antibus 1990). Trichomes, however, vary in their absorptive capabilities. For example, some tank bromeliads within the subfamily Tillandsioideae have trichomes capable of absorbing large organic molecules such as amino acids (Endres and Mercier 2003), and derive nutrients from predator feces and arthropod carcasses living in their tanks (Romero et al. 2010). Species from the subfamilies Pitcairnioideae and Bromelioideae have trichomes that absorb smaller molecules.

CAM Photosynthesis in Bromeliad Species

The appearance of CAM is considered one of the key innovations associated with the transition from terrestrial to epiphytic life form. In Bromeliads, the epiphytic habit has evolved a minimum of three times (Crayn et al. 2004), and bromeliad epiphytes show great plasticity in the expression of CAM with a range of expressions from C_3 to facultative CAM to full CAM (Andrade et al. 2007; Griffiths and Smith 1983). Some species under stress have shown high levels of recycling of respiratory CO_2 via CAM (Martin 1994; Maxwell et al. 1994). Griffiths and Smith (1983) were able to relate the ecology of different bromeliad species to the occurrence of CAM and C_3 on the island of Trinidad. The authors found that tank bromeliads, which include light demanding C_3 species and CAM species, show a wide range of distribution across rainfall gradients, but are always found in the uppermost part of the canopy. The more xerophytic bromeliads all show CAM and are restricted to sites with the lowest rainfall, whereas the shade-tolerant bromeliads are all C_3 species and are found in a wide geographical range but on sites with high humidity. This study highlights that it is not possible to distinguish C_3 and CAM bromeliad species based only on their stratification within the forest.

Bromeliads can also be heteroblastic, changing their growth forms during their lifetime by starting as an atmospheric life form and developing water holding tanks

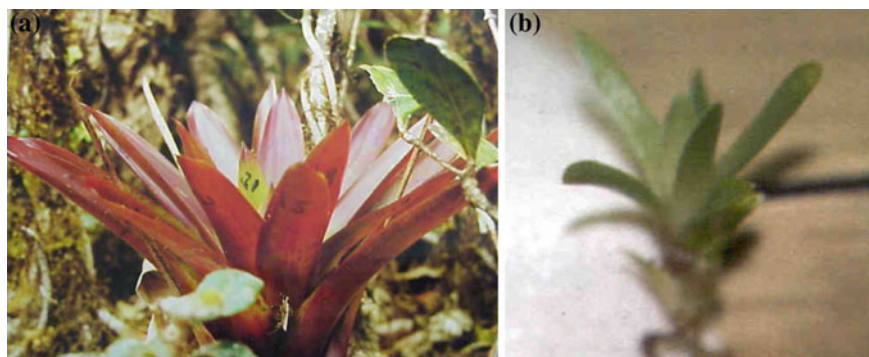


Fig. 4 Bromeliad species *Werauhia sintenisii*. **a** Adult or tank form and **b** juvenile or atmospheric form of the heteroblastic bromeliad species *Werauhia sintenisii*. Production of anthocyanins for photoprotection in the adult form is common in epiphytic bromeliads. Photos by Eloisa Lasso

as adults (Fig. 4, Benzing 2000; Zotz et al. 2011). A study by Beltrán et al. (2013) demonstrated that heteroblastic species shift anatomically and physiologically from C_3 to CAM during their development to increase the survival of juveniles that are more susceptible to drought stress given their lack of tank. In other words, species were able to display features of facultative CAM when exposed to drought stress irrespective of developmental stage. The only obvious difference between the adult and the juvenile was the size of the hydrenchyma, in which juveniles presented thicker hydrenchyma with higher water storage (Beltrán et al. 2013). Zotz et al. (2011) reported that the juvenile atmospheric form of *Werauhia sanguinolenta* showed higher trichome density compared to the adult form. Recent work by Meisner et al. (2013) reported similar size-related variations when studying the functional relevance of water storage tissue, stomata and trichome densities, and transpiration and nutrient uptake rates in seventeen homoblastic and heteroblastic species from Panama, thus questioning the functional relevance of heteroblasty in bromeliads.

Epiphytic Ferns and Aroids

Few species of epiphytic ferns have been studied regarding their adaptation to water scarcity. Even in humid cloud forest, fern species have xeric adaptations including coriaceous leaves, low rates of water loss, leaf scales and high cell wall elasticity. Some ferns species are poikilohydric, and can tolerate high water deficit and recover without any physiological damage (Hietz and Briones 1998), whereas others display a variety of strategies for coping with the xeric conditions in the tree crown, including succulence of leaves and rhizomes, early closure of stomata upon water loss, osmotic adjustment, low rates of cuticular water loss, water-absorbing leaf scales and low cell-wall elasticity (Hietz and Briones 1998). Fern distribution

in the canopy is correlated with the relative water content at which stomata close, leaf thickness, and stomatal density and size (Hietz and Briones 1998).

Canopy species of *Anthurium* and *Philodendron* present morpho-physiological adaptations to the canopy environment, such as litter-trap growth, thick cuticles, and ramification (Jacome et al. 2004). Ontogenetic and size-related changes in anatomy and ecophysiology relate to performance and survival of *Anthurium scandens* epiphytes in the field (Lorenzo et al. 2010). For example, stomatal conductance did not change with ontogenetic phase and was highly dependent on water availability at the root level. Nevertheless, adult epiphytes had lower epidermal conductance to water loss as well as higher values of leaf succulence and sclerophylly, and showed higher retranslocation rates of leaf nitrogen during senescence, all traits that confer higher resistance to low resources in comparison to seedlings living in the shaded humid understory (Lorenzo et al. 2010).

To CAM or not to CAM? That Is the Question

CAM is an ecophysiological adaptation to water limitation influencing the distribution of plants within their natural environments. One way to predict extinction threats is to understand the evolutionary history of drought resistance mechanisms in plants. CAM photosynthesis is one of the best examples of convergent evolution in vascular plants; estimates report that the CAM pathway is found in approximately 7 % of vascular plants from 35 families and 343 genera (Holtum et al. 2007; Silvera et al. 2010; Smith and Winter 1996). It is estimated that over 57 % of all epiphytes are capable of performing CAM (Benzing 1987; Lüttge 2004). Epiphytes that utilize different levels of CAM photosynthesis are plastic in their responses to environmental cues, and with elevated CO₂, CAM plants have an average increase in biomass of 35 % without the downward acclimatization of photosynthesis that is typically observed in many C₃ species (Drennan and Nobel 2000). CAM evolution is accompanied by a series of anatomical and biochemical modifications from common C₃ photosynthesis that allows CAM species to have a competitive advantage in drought prone epiphytic habitats (Silvera et al. 2010). As a consequence, CAM species have a higher water use efficiency (WUE) when compared to C₃ species due to reduced amount of water lost per unit carbon assimilated. The possibility that the habitats and growth potential for selected CAM species may be favored, relative to C₃ species, is important considering current trends of increased atmospheric CO₂ and associated climate change patterns, along with predicted increases in arid and semi-arid land area (Cushman and Borland 2002; Yang et al. 2015).

CAM has contributed to the exploitation of epiphytic habitats through mid elevation tropical humid environments, which is especially true for the Orchidaceae (Silvera et al. 2009). Studies using leaf carbon isotopic composition ($\delta^{13}\text{C}$) of epiphytic orchids have shown a bimodal distribution with the majority of species exhibiting values of approximately -28‰ , typically associated with the C₃

pathway, and a second peak of distribution at values around -15‰ , which is associated with strong CAM. The presence of weak CAM, as evidenced by acid titrations, can also contribute to a second peak of abundance within the C_3 photosynthesis isotopic cluster (Silvera et al. 2005). These data suggest that among CAM orchids, there may be preferential selection for species to exhibit strong CAM or weak CAM, rather than intermediate metabolism (Silvera et al. 2005). The role of weak CAM as an intermediate state between C_3 and strong CAM, or as an evolutionary reservoir for CAM adaptive radiations is an unknown and interesting question for further studies.

Nutrient Limitation

Even though roots of epiphytes are not in touch with mineral soil, nutrient alterations of mineral soil can have an effect on epiphytic communities by altering the edaphic factors of soils used by the host trees. Experimental evidence in support of the hypothesis that epiphytes are nutritionally linked to their host tree is, however, contradictory to date. Nutritional links between host trees and epiphytes in high mountain trees are expected to be more nutrient limited than those in lowland forests (Grubb 1977). Cardelús and Mack (2010) explored epiphytic nutrient status along an elevation gradient in Costa Rica and found no relationship between foliar chemistry and elevation for any of the epiphytic groups studied, which included ferns, orchids and bromeliads. In contrast, a long-term fertilization experiment in the elfin forest of Puerto Rico showed that nutrient addition to soil stimulated tree leaf litter production (Walker et al. 1996), and increased nutrient content of litterfall (Yang et al. 2007), which in turn affected epiphytes growing on those trees. Epiphytic bromeliads growing on fertilized trees clearly responded to nutrient augmentation received by their host trees, and accumulated more nutrients in their vegetative body thus increasing their growth rate, fruit production and lifetime fitness (Lasso and Ackerman 2013). These studies together with Benner and Vitousek (2007), and Boelter et al. (2014), suggest that epiphytes are nutrient limited, and that a nutritional link exists between host trees and their epiphytes. This may be especially true for tank bromeliads since their impounding leaf rosette traps litter and leachates from their host trees. However, epiphytes with different nutrient acquisition mechanisms may not be strongly linked to their host tree. Different epiphyte groups use diverse nutrient uptake mechanisms, which ultimately provide an explanation for the coexistence and maintenance of species richness in tropical forest canopies (Cardelús and Mack 2010).

Vascular epiphytes of lowland tropical forests are nutrient limited, mainly by P and sometimes by N, or P and N simultaneously (Wanek and Zotz 2011; Zotz and Asshoff 2010; Zotz and Richter 2006). Epiphytes living in tropical montane cloud forests are more likely nutrient limited because there is constant input of water and excessive rain that may wash out nutrients from the tank, leaf surface or even the layer of canopy soil where epiphytes grow. Additionally, lower temperatures in

tropical mountain cloud forest reduce decomposition rate, potentially decreasing the release of nutrients from canopy soil. Benner and Vitousek (2007) documented a dramatic increase in the abundance and species richness of canopy epiphytes in a forest fertilized annually with phosphorus (P) for 15 years, but found no response in forest fertilized with nitrogen (N) or other nutrients, suggesting that P is also the main limitation in highland forests. Studies of two bromeliad species, *Werauhia sanguinolenta* from the lowlands of Panama (Zotz and Richter 2006) and *Werauhia sintenissi* from the cloud mountain forest in Puerto Rico (Lasso and Ackerman 2013) also point to phosphorous limitation for growth and reproduction at all altitudes. The accumulation of P, Zn, Al, Fe, Na in the foliar tissue of *Werauhia sintenissi* growing in plots fertilized regularly for 10 years with macro and micro nutrients (Lasso and Ackerman 2013), suggest luxury consumption and storage not only of P, as reported before for *Vriesea sanguinolenta* (Wanek and Zotz 2011), but also for other nutrients.

Epiphytes and Climate Change

Potential Responses or Indicators of Climate Change

Atmospheric CO₂ levels are predicted to double that of pre-industrial levels by 2050 (IPCC Assessment Report). With increasing levels of atmospheric CO₂, tropical forests are expected to increase carbon uptake, which may lead to faster growth. In the case of epiphytes, this may translate into higher biomass and subsequently higher loads on tree branches, which might lead to increased structural damage of host trees. Tropical species, including epiphytes, are likely to shift upslope rather than latitudinally with climate change mostly because of the very steep temperature gradient found per meter elevation as compared to temperate zones (5.2–6.5 °C decrease per 1000 m elevation, Colwell et al. 2008). To estimate the potential responses of epiphytes to climate change, it is crucial to estimate the effects of increasing levels of CO₂ in epiphytic CAM species, and on species with facultative CAM. Whether these species would have an advantage with increased photosynthetic flexibility remains unknown.

Are Epiphytes Really Indicators of Climate Change?

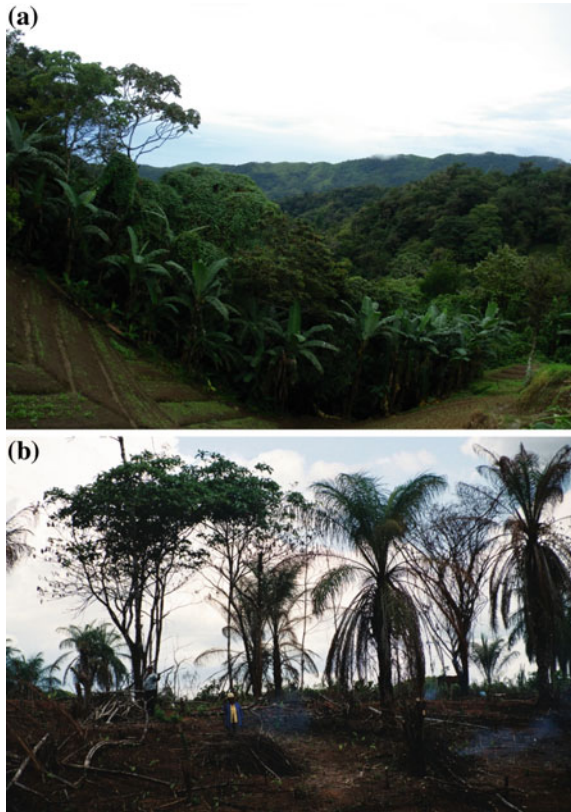
Epiphytes are one of the most sensitive plant growth forms to disturbance and microclimate changes due to their lack of access to permanent water sources and nutrients, which forces them to be tightly dependent on seasonal precipitation, fog or dew. For this reason, epiphytes are thought to be exceptionally sensitive to air quality and climate, and considered indicators of climate change and forest health. In addition, epiphytes are an important component of watersheds because of their

ability to intercept cloud and fog water thus increasing net water inputs. Managing and implementing conservation programs for epiphytes is highly dependent on understanding which factors influence epiphytic diversity in species-rich regions, and the physiological responses of epiphytes to environmental change. Climate change, through its effect on temperature, is likely to have an effect, albeit small, on evaporation rates, which in turn can have an effect on communities of animals living in water reservoirs inside epiphytic bromeliads. Examining patterns of epiphytic community distribution among different climate areas may provide an early indication of vegetation responses to climate change.

Undoubtedly, the major threat to epiphytic diversity is deforestation (Fig. 5). It is estimated that about 21,000 square km of forest is deforested annually in South America, which harbors one of the richest epiphytic communities in the world, most of it in the Amazonian Basin. Conservation of tropical rainforest is key to conservation of epiphytes.

Fig. 5 Epiphytic habitat loss due to deforestation.

a Deforestation for agricultural plantations. Photo by Katia Silvera, and **b** Deforestation due to slash-and-burn agricultural practices. Photo by Gaspar Silvera



Concluding Remarks

Because most studies on epiphytes are species or genus specific, we need an array of experiments using broad species samples, in order to estimate how communities will change over time. As Zotz (2004) pointed out, when studying epiphytic communities it is important to distinguish prevalence of vascular epiphytes in terms of species numbers or biomass, because many orchid species occur in very low numbers and their contribution to community biomass can be low. Because of this inherent bias, interpretations of whether CAM is prevalent in tropical moist forests compared to semiarid regions remain biased by number of species (Zotz 2004). Most of the ecophysiological studies conducted on epiphytic plants have focused on water relations of leaves, which provide a skewed view of plant function across communities. Integration of studies using different organs is lacking and necessary to understand how species will respond to climate change.

Epiphytes, as indicators of climate change, may be the first to respond to global changes; therefore how we implement conservation strategies to forests is key to mitigate changes to tropical forests.

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