



REVIEW ARTICLE

The physiological ecology of vascular epiphytes: current knowledge, open questions

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Abstract

The current knowledge of the physiological ecology of vascular epiphytes is reviewed here with an emphasis on the most recent literature. It is argued that by far the most relevant abiotic constraint for growth and vegetative function of vascular epiphytes is water shortage, while other factors such as nutrient availability or irradiation, are generally of inferior importance. However, it is shown that the present understanding of epiphyte biology is still highly biased, both taxonomically and ecologically, and it is concluded that any generalizations are still preliminary. Future studies should include a much wider range of taxa and growing sites within the canopy to reach a better understanding how abiotic factors are limiting epiphyte growth and survival which, in turn, should affect epiphyte community composition. Finally, a more integrative approach to epiphyte biology is encouraged: physiological investigations should be balanced by studies of other possible constraints, for example, substrate instability, dispersal limitation, competition or herbivory.

Key words: Epiphytes, intraspecific variation, mortality, nutrient relations, phenotypic plasticity, photosynthesis, water relations.

Introduction

There are an estimated 20 000–25 000 species of vascular epiphytes (Benzing, 1990), which occur mostly in the tropics. Although epiphytic species are found in a large

number of families and orders of ferns, gymnosperms and angiosperms, the monocotyledons are highly over-represented: about 80% of all epiphyte species belong to this group (Kress, 1989). Locally abundant and highly diverse, epiphytes grow (by definition) on other plants, occurring from the forest understorey to the periphery of tree crowns. This variation in growing sites and the numerous different types of inhabited vegetation clearly indicate that there is neither a simple definition of the 'epiphytic habitat' nor of the environmental constraints imposed upon canopy dwelling flora. Published studies hardly encompass this variability. By contrast, the attention of plant physiological ecologists has focused primarily on species from more exposed and supposedly stressful growing sites (Benzing, 2000; Lüttge, 1997; Zotz and Andrade, 2001). Moreover, the majority of these studies has dealt with short-term responses to stress at the level of individual organs. Studying the ecophysiology of epiphytes almost exclusively at this level has severe shortcomings, because the reaction of an organ is certainly only a partial measure of the consequences of stress on entire individuals.

The desire to stimulate a more integrative, and taxonomically and ecologically balanced approach in studies on epiphyte ecophysiology motivated the present review. What is known today on important aspects of epiphyte ecophysiology will be critically summarized, and the validity of the underlying assumptions of many studies will also be questioned, particularly that the major limitations to growth and survival of epiphytes are frequent and severe water stress, low availability of nutrients and photoinhibition, while the biotic constraints are relatively unimportant. The issue of plant size and

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intraspecific variability in physiological parameters, which has been dealt in detail elsewhere (Zotz *et al.*, 2001a) will also be briefly discussed. The available information forces the focus on plant water relations, nutrient relations and photosynthesis, because other fields, for example, the hormone physiology of epiphytes (Zhang *et al.*, 1995; Zotz *et al.*, 2001b), are virtually unexplored.

Finally, although this article will primarily deal with the *ecophysiology* of epiphytes, other ecological topics, such as demographic aspects of epiphyte biology, will also be included to some extent. In the complex ecosystems of tropical forests, which are characterized by a multitude of biotic interactions, a realistic evaluation of the *relative* importance of physiological adaptations for growth and survival can only be achieved by 'putting them into perspective', using an integrative approach in which physiology is studied in conjunction with experiments and observations at the level of morphology, demography or community ecology.

Plant water relations

Scarcity of water is arguably the most important abiotic constraint in the epiphytic habitat. Differences in the evenness of water (and nutrient) availability prompted Benzing to define two functional groups, i.e. 'continuously supplied' and 'pulse supplied' epiphytes (Benzing, 1990). The former encompass tank bromeliads and taxa with access to rooting media with a relatively constant supply of moisture. The latter are comprised of the remaining forms, so-called bark epiphytes, in which rainless periods of a few hours may suffice to cause water stress. Although this dichotomy has some heuristic value, it conceals substantial variability, not only among different taxa within each group, but also within a given species. The efficiency of the tanks of epiphytic bromeliads in bridging rainless periods was analysed as a function of plant size (Zotz and Thomas, 1999; Schmidt and Zotz, 2001). In all three species investigated there was a gradual increase in this efficiency with plant size. For example, while the water reservoir of small individuals of *Vriesea sanguinolenta* was depleted within hours, large conspecifics could draw on externally stored water for more than a week without refill (Schmidt and Zotz, 2001). The low efficiency of small tanks may be the ultimate reason why many tank bromeliads possess an atmospheric juvenile stage, which is assumed to be more drought-tolerant. Unfortunately, the *ecophysiology* of the atmospheric stage has rarely been studied in depth (Adams and Martin, 1986; Schmidt and Zotz, 2001), but certainly warrants more attention. Although the term 'continuously supplied' is thus somehow misleading, possession of a tank undoubtedly alleviates the problems of intermittent water supply by rain, dew or mist, and

in larger individuals in rather wet climates the situation may indeed approach a reliable supply of moisture and nutrients.

Lacking such a buffer, alternative adaptations among epiphytes experiencing intermittent water supply are, for example, poikilohydry, leaf, stem and root succulence (Ng and Hew, 2000), 'shootlessness' (Benzing *et al.*, 1983) or drought-deciduousness (Benzing, 1990). The crassulacean acid metabolism (CAM), in particular, is very common among epiphytes. Following Winter and Smith, it can be expected that a majority of all CAM taxa worldwide are epiphytic (Winter and Smith, 1996). The proportions of local epiphyte floras with CAM nicely reflect the degree of moisture availability (available data only allow a comparison among epiphytic orchids): numbers increase from about 25% CAM species in New Guinean and Australian rain forests (Earnshaw *et al.*, 1987; Winter *et al.*, 1983), to 40% in the moist lowland forest of Barro Colorado Island, Panama (Zotz and Ziegler, 1997), to 62% in relatively dry, open forests in Australia (Winter *et al.*, 1983), to 100% in a Mexican dry forest (Mooney *et al.*, 1989). Similarly, a significant decrease in the number of CAM species was reported with altitude (and presumably improved water supply) in a study in Mexican forests from 700–2400 m above sea level (Hietz *et al.*, 1999). Consistent with this relative increase in CAM species from wetter to drier forests there is an increase of the proportion of CAM species from shaded to exposed sites within a forest (Griffiths and Smith, 1983; Zotz and Ziegler, 1997). Thus, even in relatively moist forests or forest strata the percentage of CAM species among epiphytes is higher than the average proportion among vascular plants (*c.* 6%, Winter and Smith, 1996), which highlights the importance of this water-saving pathway in the epiphytic habitat.

All these studies have one common shortcoming: they use stable isotope ratios to distinguish photosynthetic pathways, which does not allow the detection of intermediate and facultative CAM species (Borland and Griffiths, 1996). Possibly, there are many species with seeming C₃-like $\delta^{13}\text{C}$ values, but with at least some capacity for nocturnal acidification associated with CO₂ uptake or recycling of respiratory CO₂. For example, Lüttge compiled a list of $\delta^{13}\text{C}$ values of 12 *Clusia* species, which are known to be C₃/CAM intermediates from gas exchanges studies (Lüttge, 1999). It is obvious that most of these taxa would have been assumed to be C₃ species using carbon isotope data alone, because a $\delta^{13}\text{C}$ value below -20‰ is normally interpreted as evidence for C₃ photosynthesis. The importance of such a flexible use of CAM for plant water relations has been quantified in a comparative long-term field study with three epiphyte species differing in phenology and photosynthetic pathway (Zotz and Winter, 1994a): the water use efficiency of the C₃-CAM species *Clusia uvitana* was more than twice

that of two C_3 species. Another study found weak CAM activity in three ferns previously considered C_3 (Holtum and Winter, 1999). Although no net CO_2 uptake was measured at night, at least during drought, CAM-cycling contributed substantially to the total CO_2 balance. However, it may be questioned whether every species with measurable nocturnal PEP-carboxylase activity should be called a 'C₃-CAM intermediate' or even 'CAM plant', as done by Holtum and Winter (Holtum and Winter, 1999). This highlights a problem with the definitions of C_3 -, C_3 -CAM intermediate, and CAM plants. How shall these three groups be delimited, when there is really a continuum between alternative ways of CO_2 fixation (PEP-carboxylase versus Rubisco)?

With the possible exception of the genus *Clusia* (Ball *et al.*, 1991b; Lüttge, 1999; Roberts *et al.*, 1998), the ecological importance of these 'shades' of CAM for vascular epiphytes as a group is still unclear and more detailed studies are needed. Moreover, little is known about intraspecific variability of CAM, in particular in relation to plant size. Assuming more frequent periods of water stress in smaller plants, it was expected that these would take up proportionately less CO_2 during the day than larger conspecifics, leading to a more positive $\delta^{13}C$ pattern. Surprisingly, these expectations were not fulfilled in an isotope study with bromeliads in a montane forest in Mexico (P Hietz and W Wanek, unpublished results). The $\delta^{13}C$ values of the two CAM species *Tillandsia butzii* and *T. juncea* showed no size-related changes. Possibly, there was little daytime CO_2 gas exchange irrespective of plant size, which would explain this result. In contrast, Hietz and Wanek found a significant negative correlation of tissue $\delta^{13}C$ and plant size in the C_3 species *T. punctulata* and several other broad-leaved congeners, indicative of increased water stress and a lower ratio of intracellular to ambient CO_2 (c_i/c_a) in juveniles (P Hietz and W Wanek, unpublished results). Similar results were also found in an earlier isotope study with the orchid, *Dimerandra emarginata*, a species with weak CAM activity (Zotz and Ziegler, 1999). Estimates of stomatal limitations based on carbon isotope data may even underestimate possible size-related differences, because leaf thickness is expected to increase with plant size, and a possibly greater mesophyll resistance (Parkhurst, 1994) could lead to actually lower c_i/c_a in larger plants. However, direct *in situ* gas exchange measurements with well-watered *Vriesea sanguinolenta* (Bromeliaceae) yielded results, which were by and large consistent with the isotope studies: smaller plants showed somehow lower c_i/c_a (Schmidt and Zotz, 2001).

As discussed in detail (Schmidt and Zotz, 2001), size-related changes in anatomy and leaf physiology may be interpreted in the context of 'drought avoidance' versus 'drought tolerance'. In terms of plant water relations, there is an inevitable disadvantage of smaller plants

because of a less favourable surface-to-volume ratio (Schmidt *et al.*, 2001; Schmidt and Zotz, 2001; Zotz and Thomas, 1999). Furthermore, larger plants do better in bridging rainless periods via a more efficient tank, and avoid large tissue water deficits by fast stomatal closure after tank water depletion (drought avoidance). In contrast, the drought-related reduction in stomatal conductance of smaller plants is relatively less pronounced, which leads to higher water deficits (drought tolerance). Remarkably, residual transpiration *after* stomatal closure was lower in small conspecifics (Schmidt and Zotz, 2001). This finding sheds new light on a recent study on cuticular properties of vascular epiphytes (Helbsing *et al.*, 2000). These authors studied the water permeabilities of isolated astomatal cuticular membranes of 15 species of vascular epiphytes, using large individuals only, and observed the lowest cuticular permeances to water currently known for vascular plants. Assuming similar size-related differences in residual transpiration as described above, leaf cuticles of smaller plants may be even more efficient barriers for water loss. However, there is also an alternative explanation for size-related differences in residual transpiration unrelated to any change in cuticular properties: leaves of larger individuals commonly have higher stomatal densities, and an increased importance of peristomatal transpiration (Muchow and Sinclair, 1989) could also be the reason for the observation made by Schmidt and Zotz (Schmidt and Zotz, 2001).

While desiccation tolerance is commonly found in non-vascular organisms (bryophytes, lichens, algae), only a rather small number of vascular plants, both ferns and angiosperms, have been described as 'resurrection plants' (Bewley and Krochko, 1982). None of the angiosperms is epiphytic: all known vascular poikilohydric epiphytes are ferns (Härtel, 1940; Stuart, 1968; Hietz and Briones, 1998). Benzing mentioned that there could be some poikilohydric gesneriads, but unfortunately presented no evidence (Benzing, 1990).

Strictly speaking, most of the above studies did not study *plant* water relations, but only one aspect of it, leaf water relations. Focusing on leaves alone may lead to a skewed picture of plant functioning, for example, in multi-stemmed orchids, where leaves may only account for 10% or less of the entire plant biomass (Zotz, 1999). For example, translocation of water between organs may be an important mechanism to maintain near-constant water contents in leaves even during times of drought, while allowing substantial fluctuations in the water content of stems or roots. Clearly, a more integrated approach is needed in these studies with vascular epiphytes to allow the scaling up from organs to plants.

Most studies on the water relations of vascular epiphytes focus on water loss. Relatively little is known on water uptake (Biebl, 1964), although rapid water

uptake after the occasional rain may be as important for the plant's water balance as are low rates of water loss between rain events (Zotz and Tyree, 1996). Many drought-adapted ground-rooted plants have low osmotic potential (Ψ_{π}) to promote the uptake of strongly bound water from the soil. In epiphytes known values of Ψ_{π} are high even compared to mesophytic terrestrial plants (Benzing, 1990; Gessner, 1956). In the absence of soil, water is either abundantly available during short pulses, in which case low Ψ_{π} is unnecessary to drive water uptake, or practically unavailable even for plants with very negative Ψ_{π} . Alternatively, Benzing suggested that low Ψ_{π} results in early turgor loss and stomatal closure thus minimizing water loss at the onset of drought (Benzing, 1990). Hemiepiphytic taxa allow direct comparisons between individuals of the same species and, indeed, the osmotic potential of leaves of epiphytic individuals of five hemiepiphytic *Ficus* species was higher than that of ground-rooted conspecifics (Holbrook and Putz, 1996), although the latter had better access to water.

Plant nutrient relations

With no root contact to the soil, epiphytes lack access to what is by far the most important nutrient source of ground-rooted plants. Sources for epiphytic plants are atmospheric inputs (rain, dust and intercepted mist), nutrients released from ground-rooted plants through leaching or decomposition, dinitrogen fixation, and, to a lesser extent, remains of animals as well as mineral and organic matter imported by them (Benzing, 1990).

Nutrient scavenging in epiphytes is assisted by unusual morphological structures, but many of these (phytotelmata, litter-trapping leaf arrangement, bromeliad trichomes, orchid velamen radicum) may primarily promote water uptake. Animals associated with epiphytes are mostly ants (Stuntz *et al.*, 2001). In many cases these live in cavities formed by plant organs, or nests of colonies provide the rooting substrate for the plants (Davidson and Epstein, 1989). Epiphytes may benefit substantially from an increased nutrient supply: using differences in stable isotopic composition it was estimated that *Dischidia major* (Rubiaceae) derives almost 30% of its nitrogen from the debris deposited by ants inhabiting its cavities (Treseder *et al.*, 1995).

The importance of mycorrhizae for nutrient uptake has been shown for many ground-rooted plants, and mycorrhizal associations are prominent in dystrophic peat soils. Mycorrhizae have also been reported from many epiphytes, even when orchids and ericoids are excluded (Gemma and Koske, 1995; Lesica and Antibus, 1990; Richardson and Currah, 1995), but to date no systematic comparisons of infection rates among epiphytic and ground-rooted plants have been conducted, and the relative importance of this trait for epiphyte nutrient acquisition is open to debate.

Under favourable climatic conditions, however, most prominently in tropical cloud forests, branches may be covered by a veritable soil layer, sometimes decimetres in depth. Although canopy soils are essentially of organic origin, their N and P content, with an average N:P ratio of 13, was often found to be higher than that on the forest floor (Table 1). Consequently, one may assume

Table 1. Nitrogen and phosphorus concentrations in canopy soils

The sampling methods varied somewhat, but 'canopy soil' or 'fine earth' generally refers to the heavily decomposed fraction with no or few recognizable plant remains.

Location	Vegetation type	N (%)	P (%)	Comments	Source
Colombia	Humid montane forest	1.43	0.119	Fine earth on trunk foot <3m	(Hofstede <i>et al.</i> , 1993)
		1.08	0.066	Fine earth on basal 1/3 of large branches	
El Salvador	Six humid montane forests 1950–2280 m	1.69 ± 0.45	0.195 ± 0.04	Canopy soil <2 mm fraction	(Klinge, 1963)
	3 pine–oak forests 1000–2100 m	1.29 ± 0.56	0.2 ± 0.1	<2 mm fraction	
Togo	Humid montane forest	2.54	0.35	<2 mm fraction	(Klinge, 1963)
Venezuela	Two humid montane forests	2.1, 2.3	0.20, 0.27	Canopy soil	(Rabatin <i>et al.</i> , 1993)
		0.6, 0.5	0.16, 0.10	Terrestrial soil	
New Guinea	Lowland rain forest	1.43	0.062	Canopy soil	(Grubb and Edwards, 1982)
Venezuela	Seasonally inundated savanna	0.78	0.031	Behind palm leaf base	(Putz and Holbrook, 1989)
		0.27	0.03	Terrestrial soil	
Costa Rica	Humid montane forest	2.16	n.d.	Canopy soil	(Vance and Nadkarni, 1990)
		1.44	n.d.	Terrestrial H horizon	
		0.98	n.d.	Terrestrial A1 horizon	
Florida, USA	Swamp forest	1.9	0.11	In bromeliad tank	(Benzing, 1980)
Panama	Moist lowland forest	2.1	0.14	In bromeliad tank	(Zotz, unpublished data)
		0.5	0.07	Terrestrial A1 horizon	

n.d. = not determined.

that epiphytes rooting in such soils or storing it in their tanks are no more nutrient-limited than ground-rooted plants.

Benzing concludes that 'circumstantial evidence favours the presumption that nutrient insufficiency is a major constraint', but this is 'based wholly on the absence of mineral soil in the tree crown, the often dilute and transitory nature of canopy solutions, and the frequent capacity of resident vegetation to utilize alternative nutrient pools' (Benzing, 1990). In other words, in spite of the generally held notion of nutrient deficiency in epiphytes, a direct experimental proof is missing even for lowland conditions: virtually all the results described in the following paragraphs give circumstantial evidence only.

In a comparison between epiphytes and trees, significantly lower nitrogen concentrations in epiphytes were found in only two out of six tropical forests (2-sided *t*-test computed from the mean and SD in that paper) (Stewart *et al.*, 1995). When averages for epiphytes and trees were compared for all six forests, N concentration in epiphytes tended to be lower although differences were not significant (paired *t*-test, $P=0.066$). Although leaf N is often closely correlated with photosynthesis (Field and Mooney, 1986), bulk leaf N is not an unambiguous measure of N deficiency when comparing species. For example, species with rigid leaves will have a high proportion of total dry matter in cell walls and thus rather low nitrogen concentrations even under high supply. Recently, Roderick *et al.* presented a common relationship for changes in leaf N in respect to changes in specific leaf area (SLA) for a large number of plant species from different vegetation types (Roderick *et al.*, 2000). When comparing the data set of more than 140 terrestrial plants (Roderick *et al.*, 2000; Schulze *et al.*, 1994) with available data of 41 epiphytes (Fig. 1), almost all of the latter fall in the lower range, and in some cases the nitrogen concentrations at a given SLA are lower than any other (terrestrial) plant. This, however, is not necessarily a sign of nutrient deficiency: Roderick *et al.* showed that leaves of individuals of species from more fertile sites and of cultivated plants that were fertilized increased in SLA and in leaf nitrogen concentration but did remain within the correlation found for cultivated and wild plants (Roderick *et al.*, 2000). If some epiphytes have lower nitrogen content per SLA than others, this could rather suggest different patterns of nitrogen utilization (compare also Stuntz and Zotz, 2001). The hypothesis that epiphytes differ from ground-rooted plants in their N/SLA relationship should be tested with a larger number of species from different habitats. These data do not allow many comparisons among epiphytes, but CAM plants did not appear to differ from C_3 plants, and bromeliads tended to have rather low N concentrations at a given SLA.

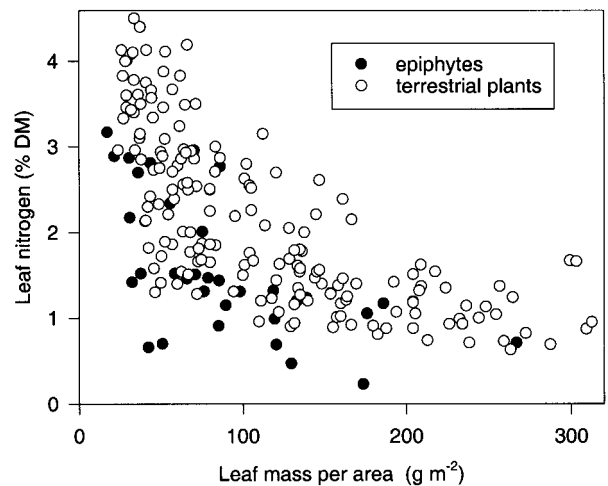


Fig. 1. Relationship between leaf nitrogen concentration and leaf weight per area in a large range of ground-rooted plants (open circles, data from Roderick *et al.*, 1999; Schulze *et al.*, 1994) and 41 species of vascular epiphytes (closed symbols, Putz and Holbrook, 1989; Zotz and Winter, 1994a; Zotz and Hietz, unpublished data).

Possibly, their strong reliance on atmospheric nitrogen sources may have led to the evolution of very efficient nitrogen use.

A different way to assess N availability is to compare individuals of a species growing under different conditions. By selecting only species growing in humid montane as well as in the drier premontane forests in central Veracruz, Mexico, Hietz *et al.* found that leaf N was significantly higher in epiphytes from the humid montane forests (Hietz *et al.*, 1999). This may result from several factors. As the precipitation, and probably tree litter production, are higher in the more humid forests, this should increase the N input for the canopy community. Decomposition rates will often be limited by substrate humidity, which further reduces the available N. Finally, since water uptake will be lower in the drier forests, the possibility of nutrient uptake is also reduced (Schmidt, 2000). Whatever the cause, even if N concentrations are lower in the drier forests, this need not limit growth if the scarcity of water overrides that of nitrogen. Richardson *et al.* found leaf nitrogen contents in tank bromeliads unchanged with altitude in three humid montane forests, but concentrations of P, K, Ca, Mg, Fe, and Mn were lowest in the most humid dwarf cloud forest (Richardson *et al.*, 2000). Although the results of this study should be interpreted with caution due to the low number of replicates and the fact that the bromeliad species were not controlled at different altitudes, it is notable that bromeliad growth rates were highest in the dwarf forest. This strongly suggests that tissue nutrient concentrations did not limit growth in the other two forests, but lower precipitation may have.

Facultative epiphytes and hemiepiphytes, which grow with or without contact to the soil depending on their

ontogenetic stage, offer further options for study. While soil contact invariably led to improved water supply in hemiepiphytes, leaf N showed no consistent pattern: it was significantly lower in epiphytic *Clusia* spp. and *Anthurium* spp., but higher in *Ficus* spp., and did not change in *Aechmea lingulata*, *Tillandsia utriculata* and *Didymopanax pittieri* (Table 2). The fact that tank bromeliads have very low N concentrations irrespective of growing site may result from generally low nutrient requirements (see above), or alternatively from insignificant water and nutrient uptake by roots when growing on soil.

A recent study on size-related differences in bromeliad N nutrition showed that in *Catopsis* and broad-leaved *Tillandsia* (comprising mainly *T. multicaulis* and *T. depeana*, which could not be distinguished as juveniles) the C/N ratio increased from about 40 in small plants (c. 10% maximum size) to 60 and 80 in large plants (c. 90–100% maximum size) of *Catopsis* and *Tillandsia*, respectively (corresponding to N concentrations of about 1.12, 0.75 and 0.56% dry weight), but remained constant in three other species (P Hietz and W Wanek, unpublished results). In broad-leaved *Tillandsias* water appears to be the main limiting resource for juveniles (indicated by higher $\delta^{13}\text{C}$ values), whereas N became relatively more important later on. This contrasts with a study by Schmidt *et al.*, who found a consistent increase in leaf N with plant size in a number of species, including bromeliads (Schmidt *et al.*, 2001).

Direct experimental manipulations of nutrient supply in the field are rare. Castro-Hernández *et al.* found moderate to substantial increases in relative growth rates in *Tillandsia guatemalensis* under greenhouse and outdoor conditions when fertilizing with N-P-K, but virtually no effect from phosphate or nitrate alone (Castro-Hernández *et al.*, 1999). However, considering that plants were irrigated (and water is likely to be the main limiting resource under natural conditions), this and other mainly horticultural experiments do not prove nutrient limitations under field conditions. In a different field experiment Schmidt showed that moderate shading, meant to improve the plant water status, increased

both the photosynthetic capacity and leaf N of smaller individuals of *Dimerandra emarginata* and *Polystachya foliosa* (Orchidaceae) (Schmidt, 2000). A parallel greenhouse experiment with different levels of irrigation and fertilization suggested that photosynthetic capacity as well as leaf N were controlled by water rather than by nutrient supply.

Rather little information is available for nutrients other than N, although studies on tropical rain forest trees suggest that soil P is more often limiting tree growth than N, at least in the lowlands (Vitousek and Howarth, 1991). There are some indications that this could also be true for epiphytes. For example, when treating field-grown *Tillandsia pauciflora* and *T. usneoides* with nutrient solutions, the N:P ratios decreased dramatically from 23.6 to 3.6 and from 40.4 to 3.4, respectively (Benzing and Renfrow, 1974). However, the N:P ratios of these and other field-grown epiphytes (Ball *et al.*, 1991a; Benzing and Davidson, 1979; Putz and Holbrook, 1989; Zimmerman, 1990) do not appear to be particularly low (12.1 ± 10.5 , $n=41$), but variation is substantial (3.1–68.3). Omitting one extreme case (*T. usneoides* with an N:K ratio of 39.4; Benzing and Renfrow, 1974), average N:K ratios were 1.16 ± 1.67 , $n=37$, ranging from 0.29 to 10.5. A field study by Benzing and Davidson tried to correlate nutrient contents and growth (Benzing and Davidson, 1979). A population of *T. pauciflora* from a nutrient-poor *Taxodium ascendens* forest in Florida, which had significantly lower concentrations of Ca, Mg and mostly also P and Mn, but not of N, than populations in more vigorously growing forests, had significantly lower reproductive output as well as lower asexual propagation with offshoots. This provides at least one clear example of nutrient limitations in the field.

In conclusion, the notion that epiphytes are nutrient-stressed does not appear to be generally valid, at least not in regard to nitrogen. Even where nutrients are scarce, this may not be of much importance if the prime limiting factor is water. It should be pointed out, however, that this statement is only valid for vegetative function. Investment in reproduction can be substantial in epiphytes (Benzing and Davidson, 1979; Zotz, 1999), and

Table 2. Nitrogen concentrations (% dry matter) in leaves of epiphytic and ground-rooted individuals of primary hemiepiphytes

Significance indicates significantly lower or higher concentrations in epiphytes (*t*-test, $P < 0.05$); n.s. = not significant.

Species	Epiphytic (mean \pm SD (<i>n</i>))	Terrestrial (mean \pm SD (<i>n</i>))	Significance	Source
<i>Clusia uvitana</i>	0.6 \pm 0.1 (13)	0.9 \pm 0.1 (25)	Lower	(Zotz and Winter, 1994a, b)
<i>Clusia rosea</i>	1.29 \pm 0.12 (18)	1.69 \pm 0.16 (12)	Lower	(Ball <i>et al.</i> , 1991a)
<i>Didymopanax pittieri</i>	1.68 \pm 0.3 (20)	1.73 \pm 0.2 (19)	n.s.	(Feild <i>et al.</i> , 1997)
<i>Ficus pertusa</i>	2.7 \pm 0.24 (5)	2.12 \pm 0.28 (5)	Higher	(Putz and Holbrook, 1989)
<i>Ficus trigona</i>	2.81 \pm 0.24 (5)	1.59 \pm 0.26 (5)	Higher	(Putz and Holbrook, 1989)
<i>Aechmea lingulata</i>	0.84 \pm 0.15 (12)	0.87 \pm 0.15 (24)	n.s.	(Ball <i>et al.</i> , 1991a)
<i>Tillandsia utriculata</i>	0.65 \pm 0.01 (6)	0.65 \pm 0.02 (6)	n.s.	(Ball <i>et al.</i> , 1991a)
<i>Anthurium acaule</i>	1.87 \pm 0.07 (6)	2.44 \pm 0.1 (6)	Lower	(Ball <i>et al.</i> , 1991a)
<i>Anthurium cordatum</i>	2.33 \pm 0.15 (6)	2.78 \pm 0.14 (6)	Lower	(Ball <i>et al.</i> , 1991a)

nutrient availability could be ultimately limiting when it comes to fruit production. Future studies on epiphyte nutritional demand should therefore look for trade-offs between nutrient investment in vegetative growth and reproduction, and attempt to isolate the effects of water and nutrients, not only considering nitrogen, as other nutrients may be of similar or even greater importance.

Photosynthesis, gas exchange and carbon gain

Leaf carbon gain of vascular epiphytes is expected to be limited most prominently by both relatively low leaf nutrient contents (associated with low photosynthetic capacities [PC], compare Field and Mooney, 1986) and by frequent water shortage (leading to reductions in leaf conductance or even complete stomatal closure). Indeed, a recent review of maximum rates of net photosynthesis in this plant group (Stuntz and Zotz, 2001) yielded mostly low values (average: $2.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), but there were some noteworthy exceptions. Values of PC (determined under non-limiting conditions in the oxygen electrode) of $20 \mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$ or more clearly challenge the notion that *all* epiphytes have a very low potential for carbon gain and growth. A major problem in the interpretation of older data from the literature is the lack of information on the size of the study organisms used. It has been shown recently for members of all major epiphyte groups (orchids, bromeliads, aroids, and ferns) that photosynthetic capacity is a function of plant size (Schmidt *et al.*, 2001). For example, area-based PC in the bromeliad *Guzmania monostachya* increased 5-fold from the smallest to the largest specimen measured (dry mass based PC increased similarly, Schmidt *et al.*, 2001). Thus, low literature values could be in part an artefact of the use of small specimens. Moreover, (shade-adapted) greenhouse plants are highly represented in the available data set. It is concluded that epiphytes as a group show low photosynthetic capacities, but with much higher variability and probably overall higher values than currently acknowledged.

Irrespective of differences in PC, epiphytic plants will be affected by intermittent water supply (so-called 'continuous supplied' taxa are no exception, see above). There are a number of studies on the response of CO_2 gas exchange to drought, both in the laboratory (Adams and Martin, 1986; Martin and Schmitt, 1989; Maxwell *et al.*, 1994; Nowak and Martin, 1997) and under field conditions (Schmidt and Zotz, 2001; Zotz *et al.*, 2001b; Zotz and Tyree, 1996). Depending on the species, plants were able to maintain a positive carbon balance in the absence of irrigation for several days to weeks. Here again, however, past studies have rarely paid adequate attention to plant size, which makes interspecific comparisons virtually impossible. Although differences in

CO_2 exchange between different ontogenetic stages of a species (atmospheric versus tank form) had been known for years (Adams and Martin, 1986), differences of similar magnitude between individuals of the same life stage but varying size have only been described recently (Schmidt and Zotz, 2001). Interestingly, smaller individuals sustained gas exchange for longer periods during drought, thus allowing larger relative water deficits. This 'go for broke' strategy resembles that of tree saplings (Bond, 2000) and is assumed to improve the growth potential needed for establishment, but with a greater risk of a fatal outcome. However, at variance with small epiphytes, juvenile trees show generally *higher* rates of net photosynthesis and transpiration compared to larger conspecifics.

One possibility of *quantifying* the effects of abiotic limitations of epiphytes in an integral manner is a comparison of the *in situ* CO_2 gas exchange of the epiphytic stage of hemiepiphytes and co-occurring ground-rooted conspecifics. Zotz and Winter listed pertinent data for five species of *Chusia* and *Ficus* (Zotz and Winter, 1996). The average diel leaf carbon gain in epiphytes ranged from 5–73% of ground-rooted individuals, percentages being lowest in the dry season, again emphasizing the water factor. But even in the rainy season integrated 24 h carbon gain of epiphytes averaged only about 50% of ground-rooted plants.

For a few epiphyte species, long-term leaf carbon gain has been estimated from repeated *in situ* measurements of diel CO_2 exchange or by modelling carbon gain under field conditions (Table 3). There was surprisingly little variation in annual leaf carbon gain (average *c.* $1000 \text{ g CO}_2 \text{ m}^{-2} \text{ a}^{-1}$), at least when related to leaf area. It should be pointed out, however, that this data set is highly biased. All five species were studied in the same type of forest, i.e. the moist lowland forest of Barro Colorado Island, Panama, and comprise species from rather exposed sites in the upper canopy. Epiphytes, however, occupy sites of very variable light exposure and the highest percentage is found at intermediate levels (Johansson, 1974). Leaf carbon gain at these sites or from other forest types is expected to differ substantially from these results.

Photoprotection in epiphytes has received much attention in the last years. Many species live at exposed sites all year long. Others experience a substantial increase in radiation load (PFD), when host trees in seasonal forests shed their leaves at the onset of each dry season (Zotz and Winter, 1994a). In the latter case, high PFD coincides with a sudden decrease in water availability. Consequent reductions in leaf conductance may intensify the probability of photoinhibition. The large percentage of taxa with CAM at exposed sites is not only relevant for plant water relations, but CAM may also confer at least some photo-protection due to the

Table 3. Annual leaf carbon budgets of five epiphyte species from a moist tropical lowland forest

Both area-based and dry mass-based values are given.

Species	Family	Net leaf carbon budget		Source
		g CO ₂ m ⁻² a ⁻¹	g CO ₂ g ⁻¹ a ⁻¹	
<i>Catasetum viridiflavum</i>	Orchidaceae	1090	26.3	(Zotz and Winter, 1994a)
<i>Caularthron bilamellatum</i>	Orchidaceae	1500	8.1	(Herz and Zotz, unpublished data) ^a
<i>Clusia uvitana</i>	Clusiaceae	1060	6.1	(Zotz and Winter, 1994a)
<i>Polypodium crassifolium</i>	Polypodiaceae	840	7.4	(Zotz and Winter, 1994a)
<i>Vriesea sanguinolenta</i>	Bromeliaceae	1400	11.6	(Schmidt and Zotz, unpublished data) ^a

^a Estimates derived from leaf gas exchange models.

maintenance of carbon fluxes through decarboxylation (Griffiths *et al.*, 1989). But even in the absence of CAM, there seems to be an extraordinary capacity for non-photochemical quenching among epiphytes growing at exposed sites (Griffiths and Maxwell, 1999; Maxwell *et al.*, 1994; Ruban *et al.*, 1993). For example, in a field study on epiphytic bromeliads (Griffiths and Maxwell, 1999) the average rapidly relaxing non-photosynthetic quench (qE) of eight species at saturating light was 0.75. Noticeably, qE in shade-tolerant species acclimated to full light was much lower. Whether the increased probability of photoinhibition in this group is of ecological relevance is unclear. Although understory epiphytes may suffer drastic changes in light conditions after gap formation in their immediate vicinity, they will normally experience high light only for short periods during so-called sunflecks. Sunflecks exceeding about 10 min may cause photoinhibition in some ground-rooted understory herbs (Le Gouallec *et al.*, 1990), but most studies emphasize the positive effect of transiently increased light for the carbon gain of terrestrial understory plants (Chazdon and Pearcy, 1991). Up to 65% of daily carbon gain may occur during sunflecks. A similarly high effect for epiphytic plants remains to be shown. Although rather speculative, it is conceivable that water shortage is of overriding importance for epiphytes, substantially reducing the importance of sunflecks for carbon gain in this group due to, for example, relatively low ratios of intracellular to ambient CO₂ at low light, very slow induction times after an increase in PFD due to stomatal limitations, or very fast loss of induction after a sunfleck.

All the preceding information on the CO₂ gas exchange and carbon gain of epiphytes referred to individual organs, mostly leaves. Assuming that most researchers use the most productive distal leaf portions, published information is certainly not representative for the entire foliage of an individual. Moreover, the poor correlation between net photosynthesis of leaves and plant growth (Körner, 1991) makes any conclusion of the performance of individuals based on these gas exchange

measurements subject to doubt. In order to scale up from organ to the whole plant, data on the carbon budgets of supports (stems, pseudobulbs), roots or fruits (Benzing and Pockman, 1989) are also needed. This information is almost entirely missing.

Mortality

Water stress, nutrient deficiencies, low or excessive PFD may lead to reduced rates of CO₂ exchange, decreased vegetative growth and low fecundity. Whether moderate stress has much consequence on community composition depends on the intensity of competition (Crawley, 1997). For epiphytes, mostly low plant densities suggest that competition is rather low, although experimental data are missing (Benzing, 1990). Accordingly, only severe stress with fatal consequences is expected to have a substantial influence on the structure of epiphyte communities, although decreased fecundity as a result of moderate stress could also be important.

Similar to most other plant groups (Harper, 1977), the majority of the studies on epiphyte population dynamics report higher mortality rates in seedlings and juveniles (Ackerman *et al.*, 1996; Hietz, 1997; Tremblay, 1997; Zotz, 1998). Evidence points to drought as the prime cause of high juvenile mortality, possibly as a consequence of less favourable surface to volume ratios, but it should be pointed out that finding dried-out plants is no proof of death from water loss, as these could have equally succumbed to, for example, pathogens. On the other hand, the dependence of seedling survival on substrates differing in water-holding capacity (Laman, 1995) make alternative explanations unlikely.

In contrast, some atmospheric bromeliads are known to be quite sensitive to *high* humidity. When their flexible trichome shields are moistened, they spread, holding a continuous film of water against the leaf surface, thus impeding gas exchange (Benzing *et al.*, 1978). Excessive humidity is the most plausible reason why atmospheric bromeliads are scarce or absent in cloud

forests, even in exposed canopy positions where light should not be limiting, but experimental evidence is required to eliminate alternative possibilities such as pathogen attack.

Most vascular epiphytes are tropical plants. In subtropical or temperate regions, or on tropical mountains low temperatures may limit their growth and survival. For example, it was reported how freezing temperatures wiped out several populations of *Encyclia tampensis* in Florida (Larson, 1992). On the other hand, it was shown that epiphytic orchids survived severe frost in Mexican montane forests (Halbinger, 1941). To some extent, vascular epiphytes can certainly endure frost and severe drought, but possibly not both stresses simultaneously. This can be deduced from their global distribution: epiphytes are found both in habitats with occasional subzero temperatures and in arid tropical scrublands, but their extension into the temperate zone is restricted to humid climates with mild winters such as the west coast of North America or New Zealand. Again, experimental studies on the interaction of frost and drought are missing. Remarkably, some species of hemiparasitic mistletoes, which share the same microenvironment with true epiphytes, are much more tolerant to frost and are even found in boreal forests (Benzing, 1990).

Whether photoinhibition can ever be lethal for entire epiphytes under natural conditions is unclear. Shade-demanding species will probably not establish themselves at exposed sites primarily due to drought, but photo-damage may occur when a newly created gap in the forest canopy drastically increases light levels at formerly shaded sites. In that case shade-demanding species would be expected to disappear from the gap margins, but it remains unclear whether mortality would be caused by drought, excessive light or a combination of both. By contrast, tree or branch fall is certainly a major cause of mortality for epiphytes. Epiphytes attached to a fallen tree or branch in a gap may remain vigorous for some time, but the chances for survival of those fallen to the shady ground are low (Matelson *et al.*, 1993). Studies on epiphyte demography therefore correctly classify fallen epiphytes as deaths. The probability of falling with a branch strongly depends on branch size and decreased from 29% for branches <1 cm diameter to 0% for branches >16 cm in a Mexican humid montane forest (Hietz, 1997). Substrate instability is a major cause of mortality for larger individuals in particular, which rarely die of other causes (Zotz, 1998). Another biotic cause of mortality was only recently acknowledged: herbivory. Schmidt and Zotz observed that some sub-populations of the bromeliad *Vriesea sanguinolenta* were wiped out almost completely by a *Rhiodinid* caterpillar (Schmidt and Zotz, 2000). Whether herbivore attack is a frequent cause of mortality in this and other vascular epiphytes remains an open question.

Conclusions and recommendations for future studies

This review has shown that the current understanding of epiphyte biology is highly biased. First, there is a strong taxonomic bias, with most research on epiphyte physiology focusing on very few groups, particularly bromeliads, the genus *Clusia* and, to a lesser extent, orchids. Secondly, plants occurring at rather extreme sites in the periphery of the forest canopy were much more likely to be studied than those in the more mesic mid- and understorey. This may have led to a distorted view of a 'typical' epiphyte, considering that the majority of taxa occur at intermediate levels of exposure or in the understorey (Johansson, 1974). Future studies should therefore include a much broader spectrum of species, both taxonomically and ecologically.

Possibly even more important, is critically to reconsider whether the most appropriate questions have been asked. A majority of published studies on epiphyte ecophysiology deal with only one particular aspect (e.g. carbon gain/loss) of one particular organ (mostly leaves), and at one particular time scale (mostly short term). The integration of various processes within the organism (Clifford *et al.*, 1995; Yong and Hew, 1995), and particularly long-term trade-offs between vegetative and reproductive function, have received much less attention. As pointed out repeatedly throughout this review, there is still a long way to go towards linking the physiology of single organs to the compartment of entire individuals, let alone to the structure and dynamics of populations and communities. Although it is tempting to interpret 'reasonable' correlations (e.g. the prevalence of species exhibiting crassulacean acid metabolism in the drier parts of the forest canopy, Griffiths and Smith, 1983) as evidence for an underlying mechanism, caution should be taken: a correlation does not prove a causal relationship, and the spatial distributions within tree crowns may be influenced similarly or even more prominently by, for example, varying germination requirements (Tremblay *et al.*, 1998), or quite different ecophysiological characteristics of juveniles (Schmidt and Zotz, 2001; Zotz and Andrade, 1998). Clearly, experiments including the entire life cycle of epiphytes are needed to identify mechanisms, but unfortunately experimental studies that exceed more than just a few days or weeks are rare (Ackerman *et al.*, 1996; Benzing, 1978; Laman, 1995).

In order to obtain a more balanced picture of the ecology of vascular epiphytes, more ecophysiological work alone will not suffice. We have to check the underlying assumptions of many ecophysiological studies, particularly the one that abiotic factors are of primary importance for epiphyte growth and survival, while biotic interactions such as competition, herbivory and

pathogens are not. This notion has some foundation in ecological theory because harsh physical conditions often coincide with plants with long-lived leaves, well-protected against herbivore and pathogen attack (Coley *et al.*, 1985). However, exposure to harsh physical conditions is by no means universal among epiphytes, and the few data of biotic interactions available are not at all unequivocal, urging the use of a more integrative approach in studies on epiphyte biology in the future.

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