

Size-related intraspecific variability in physiological traits of vascular epiphytes and its importance for plant physiological ecology

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Abstract

Intraspecific variation in the physiological characteristics of plant organs due to differences in genotype, environmental heterogeneity, or developmental stage is a generally accepted phenomenon, whereas plant size is much less recognised by ecophysiologicalists as an important source of phenotypic variation. This review argues that size-related intraspecific variability may be found in most plants, but is possibly most pronounced and rather predictable among vascular epiphytes; individuals differing in size by just a few centimetres may show considerable variation in physiological properties such as photosynthetic capacity or *in situ* leaf carbon gain. Unfortunately, the lack of attention given to plant size in ecophysiological experiments may lead to ambiguities in the interpretation of published data. Although the “optimal partitioning theory” provides a useful framework for the interpretation of these size-related changes, the exact mechanism behind the phenomenon is still unclear. For example, it is important to distinguish size effects from those due to age. Regardless of the reason, however, the mere fact that plant size consistently correlates with physiological properties calls for attention to plant size in future studies.

Key words: epiphytes, intraspecific variation, phenotypic plasticity, plant physiological ecology, scaling, plant size

Introduction

Plant physiological ecology (or plant ecophysiology) is concerned with the physiological properties of a species in the context of its natural environment. This study can be undertaken at a mechanistic level, asking how particular physiological attributes contribute to survival, growth and reproduction under the particular circumstances of a given plant. This has been and still is a powerful approach (Larcher 1994). For example, we have reached a detailed understanding of

the biochemistry and ecophysiology of the different photosynthetic pathways (i.e. C₃, C₄ and CAM; Winter & Smith 1996; Ehleringer *et al.* 1997; Lambers *et al.* 1998), ranging from the molecular level of biochemical regulation of the PEP-carboxylase and other key enzymes of C₄ and CAM plants (Cushman & Bohnert 1996) to the explanation of the geographical distribution of whole organisms, e.g. C₃ and C₄ grasses (Ehleringer *et al.* 1997). There is also another, yet not so

prominent facet of physiological ecology, which is concerned with the population, community or evolutionary consequences of biochemical or physiological traits. In this context, it is of particular importance to pay attention to intraspecific variation, the topic of this review. For vascular epiphytes – the plant group in focus – I will show that plant size (measured as plant dry mass or a surrogate such as maximum leaf length or stem height – depending on the particular species) has rarely been acknowledged as a source of intraspecific variability in the past, and that this omission may lower the value of many published results. In the future, ecophysiological studies with vascular epiphytes, i.e. physiological studies in an ecological context, should therefore pay appropriate attention to plant size as an important source of intraspecific variability.

In the last two decades vascular epiphytes, which represent almost 10% of all vascular plants (Benzing 1990), have attracted much interest from physiological ecologists and ecologists, in part due to improved measurement techniques and better field instrumentation, and in part also due to the threatened status of many tropical ecosystems, where vascular epiphytes are most abundant. A growing number of publications deal with epiphyte distributions in time and space (e.g. Pittendrigh 1948; Johansson 1974; Freiberg 1996; Hietz 1997; Zotz 1997b), or provide detailed descriptions of microclimatic gradients within tree crowns (e.g. Andrade & Nobel 1997; Freiberg 1997). These studies have set the stage for physiological investigations showing that the tree canopies of tropical forests offer a large variety of habitats, many of them characterised by a strongly fluctuating supply of water, mostly rather low availability of mineral nutrients, and frequently an excess of light (Lüttge 1989; Benzing 1990). Not surprisingly, these plants are attractive research objects for stress ecophysiologicalists, driven by the conviction that physiological traits assist in understanding the observed differences in species distributions. This is not to deny that other plant features (e.g. morphology) and a multitude of biotic interactions in tropical ecosystem must always be taken into consideration; the physiological competence of a species can only be a necessary, and never a sufficient prerequisite for the establishment and the survival of an organism.

Plant size – demographic and physiological aspects

Most available information on growth rates of epiphytes indicates slow growth (Benzing 1981; Zotz 1995, 1998; G. Schmidt & G. Zotz, unpubl. data). Leaving aside vegetative propagation, individual plants develop from seeds which in some species are very small or even dustlike. The juvenile stage, typically with rather high mortality rates, may often last for up to ten years (e.g. Zotz 1998), but after reaching maturity plants may continue to grow. For example, model calculations indicate that the epiphytic orchid, *Dimerandra emarginata*, which begins to produce fruits when exceeding a shoot length of 5 cm, needs about 20 additional years to reach its maximum size (Zotz 1995). Thus, the ontogeny of this and many other epiphytes (Benzing 1981; Zotz 1995; G. Schmidt & G. Zotz, unpubl. data) is characterised by a continuous change in plant size over decades. Simultaneously, virtually all demographic parameters change, e.g. mortality rates, fecundity, or relative growth rate (Zotz 1998). This is not something peculiar to epiphytes but is generally found in plants (Samson & Werk 1986). Thus, for plant population ecologists, treating plant size as a covariable is a matter of course; publishing “average” mortality rates or reproductive values of “the members” of a species would – for obvious reasons – be meaningless.

Among plant ecophysiologicalists, however, the need to consider plant size is much less self-evident. Certainly, at the level of entire individuals we appreciate that ontogenetic changes in traits related to resource acquisition, allocation or partitioning are probably wide-spread, if not general among plants (Coleman *et al.* 1994). Indeed, almost 30 years ago Evans (1972) even coined a new term, i.e. “ontogenetic drift”, for the dramatic change of phenotypic features such as root to shoot ratios or leaf area ratios during plant development. However, the understanding that plant size should be standardised or treated as a covariate in physiological studies is generally not applied at the level of individual organs. On the other hand, many if not most ecophysiological studies focus on particular plant organs, for example, when the CO₂ or H₂O gas exchange of individual leaves is measured or when the nutrient up-

take of individual roots is investigated. In view of the possible plasticity of physiological traits (see for example Larcher 1994), it is normal practice to provide in-depth descriptions of environmental conditions or the fertilising regime during cultivation and measurement. Size, on the other hand, is normally not mentioned, as revealed by a recent review (Schmidt *et al.* 2000). Almost 80% of the 125 articles on epiphyte physiology covering the last 80 years gave no information about the size of the organisms which were studied. Of the remainder, only one third actually provided unambiguous information on the dimensions of the plants studied. The obvious conclusion from this finding is that researchers (and reviewers) tend to assume size-related differences in plant physiological traits are irrelevant. How can this attitude be explained? It seems reasonable to assume that our view of plants as modular organisms is at fault. This concept can be taken to imply that individual organs of the same type, leaves for example, behave physiologically in the same way under identical or at least very similar environmental conditions, irrespective of the size of the entire plant.

This is not to say that size-related physiological differences in epiphytes have been completely ignored in the past. Studies by Adams & Martin (1986a,b) and Reinert & Meirelles (1993) focused on physiological and morphological changes from juvenile to adult individuals in two bromeliads. However, both studies used rather unusual epiphyte species, namely the two heteroblastic species *Tillandsia deppeana* (Adams & Martin 1986a,b) and *Vriesea geniculata* (Reinert & Meirelles 1993). In these taxa, early juveniles are atmospheric, while later stages have broad leaves which form a water-impounding tank. Apart from many morphological differences (Adams & Martin 1986a), larger individuals of *Tillandsia deppeana* show significantly higher rates of CO₂ exchange and transpiration, and differ strongly in stomatal behaviour after the onset of drought (Adams & Martin 1986b). Conceptually, however, these studies did not represent much progress, because in both cases the authors treated the differences between “juvenile” and “adult” as step-like changes in plant form. The situation resembles that of *Hedera helix*, the classical example of a heteroblastic plant, where leaves of juvenile and adult phase vary, not only morphologically,

but also show different responses in CO₂ gas exchange and other physiological processes (Bauer & Bauer 1980; Bauer & Thöni 1988). In all of these cases, the use of the terms “juvenile” and “adult” implies that the subsequent phases are regulated by temporal factors and imply no direct relation to plant size *per se*.

The potential importance of plant size became clear when Zotz (1997a) reported a *continuous* size-related increase in photosynthetic capacity (*PC*, both area based and dry mass based) measured with an oxygen electrode, in the epiphytic orchid, *Dimerandra emarginata*. All plants were growing under similar conditions and all leaves were of similar age (Zotz 1997a). In contrast to the above studies, changes in size were not interpreted as shifts between ontogenetic phases or changes in plant form or architecture. After a seedling stage, which lasts for at least 3–4 years, during which there is no visible stem (Zotz 1998), the basic plant form and leaf shape does not change; all adult *D. emarginata* plants are characterised by their sympodial architecture, usually with the production of one new stem per year. The relevance of these laboratory measurements of *PC* for the behaviour of the plants under natural conditions was indicated by a second study, this time in the field (Zotz & Ziegler 1999). Using $\delta^{13}\text{C}$ ratios, Zotz & Ziegler (1999) found a continuous increase in carbon isotope discrimination from small to larger plants, indicating that stomatal limitation decreases continuously with increasing plant size. Subsequent studies with a number of additional epiphyte species showed that the above observation was not exceptional; indeed, Schmidt *et al.* (2000) found similar increases in *PC* in eight of nine species studied (including the major taxa of vascular epiphytes, i.e. orchids, bromeliads, aroids and ferns). Thus, nine of ten species studied so far show significant increases in *PC* associated with increasing plant size (Fig. 1). Intraspecific variability was considerable and overlap of *PC* values between species substantial; in the case of the bromeliad *Guzmania monostachya*, for example, area-based *PC* increased five-fold from the smallest to the largest specimen measured (dry mass based *PC* increased similarly).

To compare the relative magnitude of intraspecific and interspecific variation, Schmidt *et al.* (2000) calculated the deviation

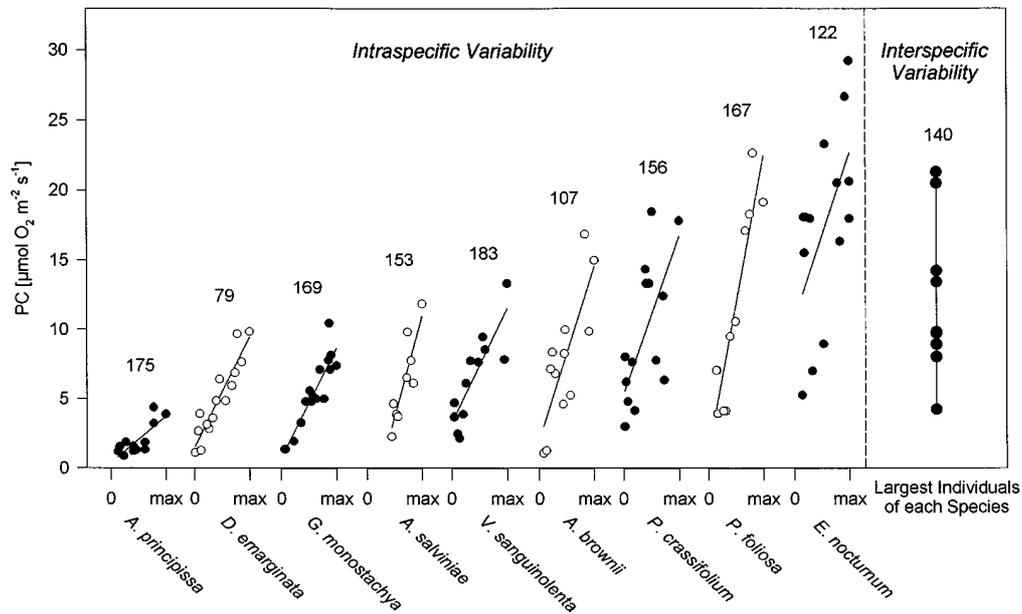


Fig. 1. Comparison of inter- and intraspecific variability of PC in vascular epiphytes. Left panel: intraspecific variability of photosynthetic capacity (PC , $\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$) in nine species. For each species, the relationship of area-based PC and plant size (0 to maximum) are given (solid lines are linear regressions). Each circle symbolizes a single leaf of a different plant. Leaves are of similar age. Right panel: interspecific variability of PC with each point representing one species. "Species values" were calculated as the average PC of the largest individuals (80–100% of maximal size) of each species. Numbers above individual plots are percent deviation of the extremes from the mean (figure modified after Schmidt *et al.* 2000).

of the extreme values from the mean (in percent) for each species, i.e. "intraspecific variation", and compared these measures of variability with the variation of PC among the larger individuals of each species (defined as "interspecific variation"). Surprisingly, intraspecific variation exceeded interspecific variation in most cases; or in other words: for this physiological trait small individuals of a particular species are generally much more similar to small members of another species than to larger conspecifics!

At this stage one might still doubt the ecological relevance of these findings, since neither PC nor $\delta^{13}\text{C}$ values are *direct* measures of physiological activities in the field. However, preliminary *in situ* measurements of the CO_2 gas exchange of ten specimens of the epiphytic tank bromeliad, *Vriesea sanguinolenta*, covering the whole size range, confirm our tentative reasoning that carbon gain under field conditions is strongly size-dependent (G. Schmidt & G. Zotz, unpubl. data).

This result was expected considering the close correlation of PC and the maximum *in situ* rate of CO_2 uptake (A_{max} , compare Schmidt *et al.* 2000) on the one hand, and the well-established correlation between A_{max} and 24-h carbon gain (Zotz & Winter 1993) on the other. Work is now in progress to evaluate by means of a model the importance of these findings for the next level of integration, i.e. whole-plant carbon gain and growth. Finally, we are also investigating whether other physiological properties, not directly related to carbon gain, also change with plant size. First results suggest that they do; for example, pronounced and consistent differences were found in ABA production in roots and hormone transport in the xylem in small, medium-sized and larger plants of *Dimerandra emarginata* (V. Thomas *et al.*, unpubl. data).

Accepting that consistent, size-related differences in the physiological properties of plant organs are widespread among vascular

epiphytes, the question of the mechanisms arises. A detailed hypothesis to explain such effects was first proposed by Zotz (1997a) and builds on the optimal partitioning theory of Bloom *et al.* (1985). Zotz (1997a) argued that – in contrast to most other cormophytes – bark-dwelling epiphytes cannot trap soil as a vast external water reservoir. Consequently, even very short periods without rain can cause water stress (Benzing 1990). Hence, size-related changes in surface/volume-ratios (= changes in transpiring surface to plant tissue water) can have profound consequences for plant water relations and this in turn could influence other physiological parameters. The optimal partitioning theory predicts that plants respond to limiting environmental factors by shifting their partitioning of resources to tissues and processes in such a way as to make all resources equally limiting. Thus, if daily gas exchange is generally more restricted in smaller plants (Zotz & Ziegler 1999), the investment of resources in the photosynthetic apparatus should differ from that in larger plants. For example, because nitrogen is in short supply in most plant communities (Chapin 1980), we can expect plants to invest only as much nitrogen in their photosynthetic apparatus as needed given other limitations. In view of the well-established correlation of leaf nitrogen and both short-term CO₂ uptake (A_{max} , Field & Mooney 1986) and long-term carbon gain (Zotz & Winter 1994b), effects on physiological parameters such as PC can be expected. Furthermore, the economic analogy of Bloom *et al.* (1985) implies that smaller plants should store excess nitrogen in long-lived organs like stems for higher productivity in the future, whereas larger plants should maximise their carbon gain by improving their current photosynthetic machinery. In short, seemingly identical environmental conditions impose different levels of stress on conspecifics differing in size, and this leads to significant and consistent changes in physiological properties.

It must be conceded that, at present, alternative explanations, e.g. that the “size effect” actually represents an “age effect”, cannot be excluded, although available evidence tends to indicate otherwise. For example, growth rates in *Dimerandra emarginata* show considerable variability (Zotz 1998), which implies a weak correlation between plant size and age. Thus, the tight correlation between

plant size and various physiological traits can hardly be due to an age effect. However, further experimental studies are clearly needed to provide unambiguous evidence on this point. Preliminary results of such experiments, where water and nutrient availability were manipulated, are consistent with the notion of a pure size effect (G. Schmidt & G. Zotz, unpubl. data).

Size-related variation of physiological parameters in other plant groups

The evidence presented above suggests that the drought-prone habitat of many vascular epiphytes is likely to promote systematic changes in the physiological properties of individual organs with plant size. This does not mean, however, that such a phenomenon is restricted to vascular epiphytes. Size is expected to play a similar, if not even more important, role in the physiology of most poikilohydric organisms. Considering the significance of the length of the wet state for carbon gain and growth (Proctor 1972), size-related changes in the surface-volume ratio should strongly affect the *in situ* performance of lichens, mosses and liverworts. For example, in a study with five lichen species, Larson (1984) found significant effects of thallus size on physiological parameters such as net photosynthesis and respiration rates in most, but not all, species. This lack of consistency in the effect of size further complicates the interpretation of published physiological data where the size of the study organisms is not specified. Unfortunately, Larson's (1984) plea to recognise the importance of size has had relatively little effect; studies with lichens like the one by Gauslaa & Solhaug (1998), which address a physiological question at the population level, are still rather exceptional. The same is true for physiological studies with bryophytes (but see Alpert 1988; Pérez 1991). The effect of plant size on the maximum rates of net photosynthesis and carbon gain in the field was quantified for the first time only recently in a study with the cushion moss, *Grimmia pulvinata* (G. Zotz *et al.*, in prep.). As expected following the argument presented above, the effect of size was pronounced and activity periods and carbon gain differed substantially between small and

large cushions. Consequently, the outcome of comparative studies of *in situ* CO₂ exchange may strongly depend upon the choice of plant size.

The effect of size on the physiological performance of individual organs has also been studied several times in terrestrial phanerogamic plants, but results do not show a consistent pattern. For example, in a field study in the Chihuahuan Desert in southern New Mexico, small mesquite shrubs showed either greater (after high summer rainfall) or lower (after a dry period) stomatal conductance and net assimilation than larger conspecifics (De Soyza *et al.* 1996). Differences in the short-term availability of water were also responsible for size-related differences in stomatal conductance, transpiration and xylem pressure potential in the vine *Cucurbita foetidissima* (Knapp & Fahnestock 1990). When well watered, no differences could be detected in the *in situ* leaf gas exchange of smaller and larger plants, but the onset of drought affected small plants differentially; CO₂ uptake was reduced to zero after midday, while no substantial reductions were measured in larger vines. Although these results may primarily be the consequence of differences in rooting depths, other ontogenetic changes in plant morphology and water storage capacity (root succulence) seem to be important as well (Knapp & Fahnestock 1990). On the other hand, the leaf gas exchange of the shrub *Chrysothamnus nauseosus* in the semi-arid Great Basin showed a consistent pattern (Donovan & Ehleringer 1992); smaller plants had higher rates of photosynthesis, but lower long-term water use-efficiency, as deduced from carbon isotope discrimination. The reverse situation was observed in a terrestrial orchid; the rates of leaf CO₂ exchange in *Spiranthes cernua* were positively correlated with plant size (Wendel & Antlfinger 1996). Finally, in the tallest land plants, i.e. trees, photosynthetic rates have also been shown to decline in larger individuals. While Yoder *et al.* (1994) discuss a possible role of hydraulic conductance in limiting stomatal aperture, others (e.g. Niinemets 1997) show that even at constant internal CO₂ concentrations, photosynthesis is lower in larger trees. In contrast, rates of leaf net photosynthesis of a 35-m tall *Ceiba pentandra* were almost identical to those of small seedlings (Zotz & Winter 1994a). Once again, as in the case of lichens

(Larson 1984) and unlike that of vascular epiphytes, the lack of consistency is striking.

This lack of a consistent pattern is arguably due to the pronounced *intra-individual* variability in plants rooted in soil. Stress is not related to plant size in any consistent fashion; for example, depending on water availability in different strata of the soil and differences in rooting depths, smaller plants may be either at a disadvantage or, alternatively, at an advantage compared to larger conspecifics. Consistent size-related *inter-individual* differences in physiological properties of individual organs can only be expected when the environmental conditions are also consistently different for conspecifics differing in size. This seems to be the case for bark-dwelling vascular epiphytes, and also for lichens, mosses and liverworts.

Size and other sources of intraspecific variability

Although focussing on vascular epiphytes, one of the goals of this review is to draw attention to the importance of size and intraspecific variation for ecophysiological work with plants in general. However, intraspecific variation is caused not only by the size of an organism (it can be noted in passing that size-related differences are fully acknowledged among animal physiological ecologists; Schmidt-Nielsen 1984), but may also be due to differences in genotype, past and present environmental conditions, developmental stage, and any combination thereof.

Frequently, as criticised by the zoologist Bennett (1987) more than ten years ago, intraspecific variation is not sufficiently taken into account in ecophysiological research, a fact that Bennett called the "tyranny of the golden mean". He wrote "The framework of physiological studies implicitly emphasizes the description and analysis of central tendency. Depending on the data, this involves the calculation of mean values or the development of least-squares regression equations. After these values are determined, they take on a life of their own and become the only point of analysis and comparison. The complete breadth of biological variation determined in the investigation then is forgotten. Measures of variability ... are calculated and reported only to stipulate confidence limits

about the mean or slope of regression line. ... The variability inherent in the original data is seen only as 'noise', through which the 'true' value of the central tendency can be glimpsed with appropriate statistical techniques" (Bennett 1987).

Clearly, his warning against a typological approach in the physiological ecology of animals equally applies to plant ecophysiology as well. Moreover, if physiological parameters such as photosynthetic capacity, *in situ* CO₂ exchange, or leaf transpiration rates do not only show much variation between individuals, but are all *continuous* functions of plant size, then lumping together several study organisms of different size is likely to yield spurious conclusions because these averages are biologically meaningless. Worse still, the choice of the size of the study organisms may determine the outcome of comparative studies. For example, simply by choosing the appropriate size for the study plants of the nine species shown in Fig. 1, one could "prove" that all species with the exception of the orchid *Aspasia principissa* have the same PC of, e.g. 10 μmol O₂ m⁻² s⁻¹. Obviously, additional information on the population structure of all the species in a comparative ecophysiological study is needed; Schmidt *et al.* (2000) called this a "demographic approach" to physiological ecology.

The following example illustrates how this demographic approach may work. Analysing the spatial distributions of two bromeliads, *Guzmania monostachya* and *Tillandsia fasciculata*, both Pittendrigh (1948) in Trinidad, and Zotz (1997b) in Panama observed that the former tends to grow in the inner canopy of host trees whereas the latter generally occurs at more exposed sites. Hypothesizing that differences in drought tolerance may have caused this pattern, Zotz & Andrade (1998) and Zotz & Thomas (1999) studied various aspects of plant water relations of the two species. The differences between large individuals of both species proved to be rather small. Water loss in small individuals, on the other hand, differed substantially; small *Guzmania* plants lost as much water on the first day of a drought cycle as similarly small *Tillandsia* plants during the first week (Zotz & Andrade 1998). Thus, while the results derived from small individuals were totally consistent with the above hypothesis, the measurement of large individuals alone or

of individuals of unspecified size could have led to possibly misleading conclusions.

In contrast, problems of interpretation may arise when information on size is missing. For example, Bergstrom & Tweedie (1998) studied nitrogen utilization in the epiphytic fern, *Pyrrosia rupestris*. Repeated sampling of six individuals within a single tree crown revealed a larger variation in the δ¹⁵N tissue values in this species than in a comparative study across six different rainforest sites with more than 40 species of epiphytes (mostly with only one sample per species; Stewart *et al.* 1995). However, neither Bergstrom & Tweedie (1998) nor Stewart *et al.* (1995) paid attention to plant size. Without information on possible size-related intraspecific variability in the δ¹⁵N tissue values an unambiguous interpretation of this surprising finding is hardly possible. In summary, ignoring plant size and other sources of intraspecific variation not only hampers the interpretability and repeatability of ecophysiological studies but possibly masks interesting biological phenomena.

Conclusions and recommendations for future studies

Plant size may influence physiological properties of plant organs in virtually all plants. However, trends are often highly inconsistent between species and seasons. The *consistent* size-related patterns observed in vascular epiphytes are probably due to the particularities of the epiphytic habitat. Even if size-related changes really prove to be a general phenomenon in this group, the attention given to plant size will depend upon the scope of the particular study (Fig. 2). For example, it will not be feasible, nor even necessary, to include the whole range of different sizes in a study on the effect of excess light on the photosynthetic apparatus of exposed epiphytes (e.g. Griffiths & Maxwell 1999), nor will the demonstration of nutrient uptake by the leaf scales of bromeliads (e.g. Benzing *et al.* 1976) necessarily merit the inclusion of all sizes. However, even in these cases, it seems essential to standardise plant size and to be precise in the description of the material used. Recognising the potential variation of physiological traits due to plant size, future comparability of published results depends upon such a detailed specification of size.

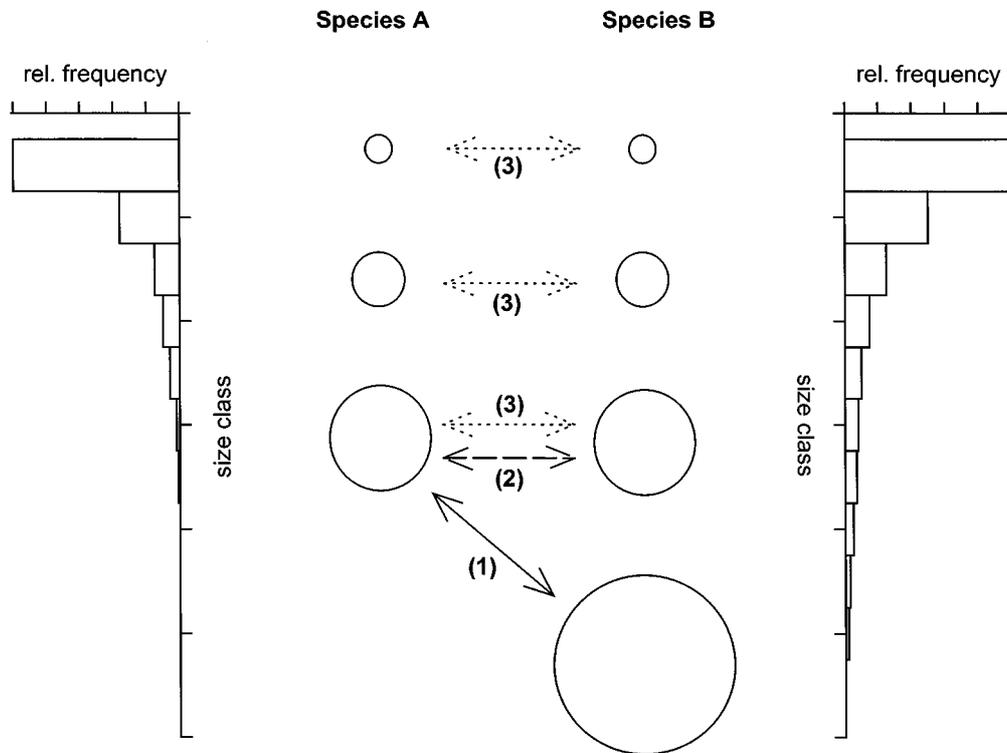


Fig. 2. Possible design of a comparative ecophysiological study with size-related physiological differences. Depending on the scope of the study, one may compare the largest individuals (indicated by large circles) of either species (1), individuals of similar size of one (2) or several size classes (3). Information on the population structure (lateral histograms) and growth rates should strongly influence the experimental design.

In many other cases it will be essential to study plants of various sizes (Fig. 2). Appropriate statistical analysis may include regression analysis with continuous variation of size (Zotz 1997a), or ANOVA, using several size classes (Knapp & Fahnestock 1990). This much more laborious approach could be perceived as a nuisance. In contrast, I argue that the study of the mechanisms behind phenotypic plasticity should be considered an important opportunity to understand the interplay of resource availability and biotic response in vascular epiphytes. Which mechanisms lead to size-related changes among conspecifics? Do the size-related anatomical, morphological and physiological changes lead to differential survivorship and growth and ultimately increase fitness, i.e. are they adaptive, or are they simply the consequences of allometric constraints? Identifying constitutive and plastic

components of plant adaptations is clearly essential to the understanding of the ecology and the evolution of the entire group (Bradshaw & Hardwick 1989).

Size-related differences in physiological traits will also be a complicating factor, albeit essential, in attempts to develop canopy photosynthesis models from single leaf gas exchange measurements (Beyschlag & Ryel 1999; G. Schmidt & G. Zotz, in prep.). Unless leaf gas exchange characteristics are determined for leaves of smaller and larger plants, calculated canopy gas exchange may be seriously over- or under-estimated.

Finally, future studies should not just pay more attention to plant size as one of many causes of intraspecific variation, but should take a more *integrative* approach to reach a functional analysis of species traits. Rather frequently, it is not adequately acknowledged

that physiological traits are just one of many ways to cope with environmental constraints. I am obviously not the first to call attention to this fact. More than ten years ago, Pearcy *et al.* (1986) discussed the future development of physiological ecology and noted the lack of interactions between this field and other areas of ecology, e.g. population biology. In the light of the finding of consistent, size-related changes in physiological properties of vascular epiphytes, the need for integration of these two fields becomes even more pressing; ecophysiological experiments will greatly benefit from information from population biology (Fig. 2). In particular, in complex ecosystems such as tropical forests, which are characterised by a multitude of biotic interactions, we can only come to a realistic evaluation of physiological adaptations by "putting them into perspective", i.e. using an integrative approach where physiology is studied in conjunction with experiments and observations at the level of morphology, demography and community ecology. This will allow a much deeper appreciation of the relative importance of physiological adaptations for growth and survival of vascular epiphytes and plants in general.

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