



Small plants, large plants: the importance of plant size for the physiological ecology of vascular epiphytes

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Abstract

Recently, a number of publications have reported that many physiological properties of vascular epiphytes are a function of plant size. This short review will summarize what is known to date about this phenomenon, describe the possible mechanism and will discuss the consequences for the present understanding of epiphyte biology. Size-related changes are also known from other plant groups and it is argued that close attention should be paid to the size of the organisms under study in order to understand the performance and survival of a species in the field. In the light of these findings, the results of many earlier studies on epiphyte ecophysiology are now difficult to interpret because essential information on the size of the specimens used is missing.

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

Introduction

A certain degree of plasticity in physiological traits is ubiquitous among plants (Larcher, 1994). Apart from genetic differences among individuals, much of the observed intraspecific variation is due to modifications during ontogeny. For example, depending on light conditions experienced during growth the leaves of a given individual may differ considerably in their photosynthetic response (Boardman, 1977). Similarly, present and past nutrient regime, water supply and temperature are

generally acknowledged as important factors in determining the physiological performance of a plant, and are hence routinely described in detail in every research report. A number of recent studies with vascular epiphytes (Schmidt *et al.*, 2001; Schmidt and Zotz, 2001; Zotz, 1997) have indicated another source of intraspecific variation that many studies in the past have inadvertently missed, i.e. substantial variation related to plant size rather than changing environmental conditions. This short paper will summarize what is known to date about the phenomenon, consider the possible mechanisms and discuss the consequences for the current understanding of epiphyte biology, but also for plant ecophysiology as a whole by briefly reviewing evidence for size-related physiological variation in other plant groups.

Plant size and physiological traits

While the vast majority of physiological studies on vascular epiphytes failed to mention the size of their study organisms (review in Schmidt *et al.*, 2001), Zotz showed recently that important physiological parameters (leaf N, area and mass-based photosynthetic capacity (PC) determined under non-limiting conditions with an oxygen electrode) were a rather tight function of plant size: PC in *Dimerandra emarginata* (Orchidaceae) increased linearly from the smallest to largest individuals by about 100% ($r^2=0.87$) (Zotz, 1997). This study prompted the following questions. (1) Does similar physiological variation also occur in other epiphyte taxa? (2) Do other physiological traits change with size as well? (3) Are these changes relevant for plant functioning under field conditions? (4) Are these changes, which are

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measured on individual organs, also relevant at the level of entire organisms?

A survey of nine additional species, representing the four major taxonomic groups of vascular epiphytes (orchids, bromeliads, aroids, and ferns), answered the first question. Schmidt *et al.* found similar increases in PC in all but one of them (Schmidt *et al.*, 2001). Frequently, the size-related intraspecific variability was even larger than in *D. emarginata*. For example, area-based PC of the C₃-CAM intermediate, *Guzmania monostachya* (Bromeliaceae), increased 5-fold from the smallest to the largest specimen measured (dry mass-based PC increased similarly). This large intraspecific variability led to a considerable overlap of PC values among species so that differences in PC were actually more closely related to plant size than to species. As a consequence, comparing PC of different epiphyte species is rather meaningless unless plant size is defined.

The answer to the second question was also positive. Virtually every physiological and morphological parameter studied to date changed with plant size, often considerably: carbon isotope ratios (Zotz and Ziegler, 1999), maximum rates of instantaneous CO₂ exchange, relative water deficits at stomatal closure, residual transpiration, leaf anatomy and morphology (Schmidt and Zotz, 2001). Size also correlated with some ecophysiological parameters that are not directly related to gas exchange, for example, changes in abscisic acid contents of roots and leaves during prolonged drought stress (Zotz *et al.*, 2001), and nitrogen isotope compositions as an indicator of a shift in nitrogen sources (P Hietz and W Wanek, unpublished results).

Thirdly, a detailed study with the bromeliad, *Vriesea sanguinolenta* (Schmidt and Zotz, 2001) showed that diel leaf carbon gain under field conditions was also size-dependent. This finding was expected in view of the close correlation between PC and the maximum *in situ* rate of CO₂ uptake (A_{\max} , cf. Schmidt *et al.*, 2001) and the well-established correlation between A_{\max} and 24 h carbon gain (Zotz and Winter, 1993). However, the long-term leaf carbon gain of smaller plants is not only affected by lower A_{\max} (under favourable conditions), but also by more frequent reductions in stomatal conductance caused by drought (Schmidt and Zotz, 2001), which adds to the effect of lower PC. The development of a model quantifying the effect of both factors is in progress.

The relevance of these changes, for example, in the rates of net CO₂ uptake for the entire organism, is not necessarily straightforward, because architectural changes during growth may well either decrease or augment the effects of physiological changes (Valladares, 1999). Moreover, similar to other plants (Chapin, 1980), biomass allocation patterns may change with size in epiphytes. For example, in *D. emarginata* the proportion of root biomass to total plant biomass decreases, relative stem biomass

increases, whereas the proportion of leaves remains rather constant as plants grow (Fig. 1). Irrespective of this pattern of biomass allocation, the relative and absolute investment of nitrogen into leaves increases in larger plants. This is clearly inconsistent with the notion that the distribution of nitrogen, or other important 'currencies' of plant growth, can easily be deduced from the distribution of biomass (Reekie and Bazzaz, 1987).

While there are no data yet on whole plant carbon budgets as a function of plant size, aspects of plant water relations have already been investigated. In three

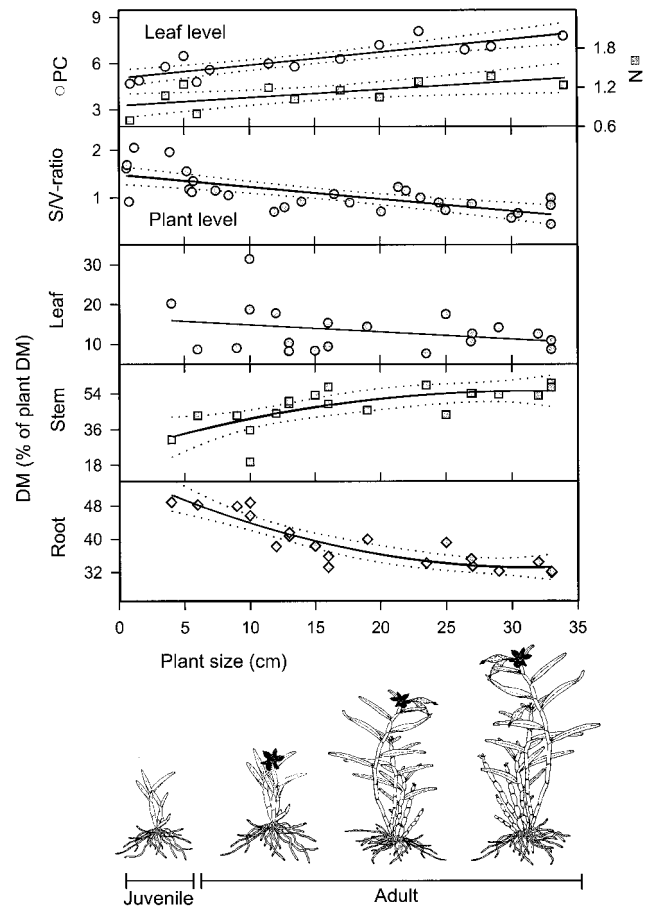


Fig. 1. Size-dependent changes in selected physiological, morphological and allometric parameters on the organ and the plant level in *Dimerandra emarginata*. Trends for leaf area-based photosynthetic capacity (PC, $\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$, open circles, dry mass trend is also significant) and leaf-N (% DM, closed squares) are from Zotz (Zotz, 1997), the ratio of transpiring plant surface (= total leaf area) to plant water content (S/V -ratio, $\text{m}^2 \text{ g}^{-1} \text{ H}_2\text{O} \times 10^{-3}$) is calculated with data from Zotz and Tyree (Zotz and Tyree, 1996). The three lower panels show the relative dry mass (DM) of different compartments (roots, stems and leaves) as a function of plant size (= length of the most recent stem; G Zotz, unpublished data). Relative $\text{DM}_{\text{Stem}} = 12.5 \text{ size} [\text{cm}] / (1 + 0.2 \text{ size} [\text{cm}])$, relative $\text{DM}_{\text{Root}} = 56.1 - 1.4 \text{ size} [\text{cm}] + 0.02 \text{ size} [\text{cm}]^2$. Significant trends ($P < 0.05$) are indicated by a thick line and 95% confidence intervals (dotted lines). The size-dependent change in biomass allocation parallels the decrease in the S/V -ratio of the entire plant. Nitrogen investment into leaves and PC, however, increase as plants grow. All changes are independent of life stage, i.e. juvenile versus reproductive stage.

bromeliad species water volumes in tanks were studied to determine their capacity to mitigate prolonged drought (Schmidt and Zotz, 2001; Zotz and Thomas, 1999). Invariably, the largest individuals were most efficient: for example, while the water stored in the smallest tanks of *V. sanguinolenta* was depleted in less than one day during the dry season in Central Panama, the largest individuals could draw on their external water reservoir for more than a week without refill (Schmidt and Zotz, 2001).

The proximate mechanism behind size-related changes in physiological parameters

Clearly, size per se is unlikely to be the immediate cause of the observed intraspecific variation. Considering that size tends to correlate with age, this variation could be caused by developmental changes during ontogeny. Alternatively, the low nutrient availability for most epiphytes (Benzing, 1990) may account for the observed size-dependence: small and presumably young plants may not have had the time to accumulate enough nitrogen and other resources to support higher photosynthetic rates. Finally, differences in plant size may also be associated with changes in surface/volume ratios, which should lead to differential water availability and, as a consequence, to differences in resource allocation.

The first possibility can be rejected. Firstly, growth rates in *D. emarginata* and other epiphytes show considerable variability (Zotz, 1998; and unpublished data), which implies a weak correlation between plant size and age. Furthermore, experimental field studies with *D. emarginata* did not indicate any age effect: over the course of one year PC either increased or decreased depending on water and nutrient availability (G Schmidt and G Zotz, unpublished data).

Distinguishing between the other two possibilities is more difficult, because nutrient uptake is linked to water availability. Remarkably, however, natural or artificial shading of epiphytic orchids in the field led to a decrease in PC in large plants, but an increase in smaller individuals (G Schmidt and G Zotz, unpublished data). This observation accords with the notion that water availability accounts for size-related physiological variation: in smaller plants partial relief from water stress through shading was of overriding importance, while larger specimens showed the expected reduction in PC due to low radiation (Boardman, 1977). In a companion laboratory experiment, the PC of well-watered plants of similar size was found to be invariably higher than the PC of poorly watered individuals, irrespective of nutrient supply (G Schmidt and G Zotz, unpublished data). This means that in the case of low water availability nutrient supply is hardly limiting PC. Indeed, various parameters related to water relations are size-dependent and indicate lower

water availability for small specimens: surface/volume ratios (Schmidt *et al.*, 2001; Zotz, 1997), ABA levels (Zotz *et al.*, 2001), or external water reservoirs (Schmidt and Zotz, 2001; Zotz and Thomas, 1999). In summary, the available information makes nutrient limitation in smaller plants a very unlikely explanation for the observed size-dependent increase in PC.

The interpretation outlined above agrees with Bloom *et al.*'s optimal partitioning theory (Bloom *et al.*, 1985). Lacking access to soil as an external water reservoir, even very brief rainless periods may cause water stress in bark-dwelling epiphytes (Benzing, 1990). Hence, size-related changes in surface/volume ratios (= changes in transpiring surface to plant tissue water) or leaf area/tank volume ratios should have profound consequences for plant water relations and this in turn may influence all other physiological functions. Bloom *et al.* predicted that plants respond to limiting environmental factors by modifying their resource allocation to tissues and processes so as to make all resources equally limiting (Bloom *et al.*, 1985). Thus, investment into the photosynthetic apparatus is curtailed when water shortage prevents the efficient exploitation of additional capacity. Consequently, because nitrogen is in short supply in most plant communities (Chapin, 1980), plants are expected to invest only as much nitrogen in their photosynthetic apparatus as needed, given other limitations. This affects PC because of the close relationship between leaf nitrogen and net photosynthesis (Field and Mooney, 1986). In conclusion, it is suggested that identical environmental conditions impose different levels of stress on smaller and larger conspecifics, which in the long term leads to significant and consistent changes in physiological properties of individual organs.

Consequences for ecophysiological studies with epiphytes

In view of the findings described above, the results of many ecophysiological studies of the past are now difficult to interpret. It will be essential in future work to select specimens of 'appropriate' size, which depends of course on the particular research question. This selection requires at least some demographic background information, prompting Schmidt *et al.* to call this the 'demographic' approach to physiological ecology (Schmidt *et al.*, 2001). For example, if the physiological basis of spatial distributions is to be understood, it is not permissible to study large individuals and then to deduce similar features for smaller conspecifics. Clearly, the outcome of interspecific comparisons may depend upon the size of the study organisms (Zotz and Andrade, 1998). Another example may demonstrate that the lack of attention to plant size can easily produce misleading

conclusions: in many bromeliads, for example, *Tillandsia depeana* (Adams and Martin, 1986a, b), there is a conspicuous ontogenetic shift from atmospheric juveniles to tank forms. However, these researchers studied the physiological changes associated with this transition by comparing 'juveniles' and 'adults' of unspecified size. This could be problematic, because it was shown in a recent study with the similarly heteroblastic *Vriesea sanguinolenta* that the outcome of such a comparison strongly depends on the chosen size of individuals in the tank phase (Schmidt and Zotz, 2001). Many of the anatomical and physiological differences between atmospheric and tank form may be incorrectly attributed to the change of life forms, instead of size-related changes within the tank life stage. Also recently, the nitrogen nutrition of a few heteroblastic *Tillandsia* species was studied using stable isotopes (P Hietz and W Wanek, unpublished data). They expected and found substantial differences in the nitrogen isotope composition between atmospheric juveniles and tank forms. Surprisingly, however, a sudden change in $\delta^{15}\text{N}$ -values was found at a larger size than the morphological change. They concluded that intermediate forms and small tanks obtain about the same proportion of nitrogen from rainwater as atmospheric plants. Similar to the efficiency in bridging rainless periods increasing with size (Zotz and Thomas, 1999), there seems to be an increasing efficiency in procuring nutrients from the tank. Taken together, a morphological step change does not necessarily parallel similar physiological changes. Hence, adequate attention to changes only due to size is essential if the implications of the phase change from atmospheric to tank forms in the Bromeliaceae are to be understood.

Size-related variation of physiological parameters in other plant groups

Size-dependent changes in the physiological properties of individual organs may be more likely in epiphytes, which frequently occur at arid, 'soil-less' growing sites, but similar observations have been made in several other plant groups. To prevent the impression that size-dependence is found only in this rather unusual group of plants, evidence is briefly discussed from three other plant groups, which are functionally, ecologically and taxonomically distinct: trees, alpine rosette plants and bryophytes.

Intraspecific, size-related differences in tree growth were noted long ago, although the physiological mechanisms are only now coming to light. Most available evidence suggests that the primary cause is the increased hydraulic resistance in tall trees, whose numerous branch nodes and longer hydraulic pathways pose higher frictional resistance (Mencuccini and Grace, 1996; Ryan and Yoder, 1997). Therefore, even if leaf nitrogen

concentrations are the same, leaves of taller trees have lower rates of photosynthesis because reduced stomatal conductance is obliged by lower leaf specific hydraulic conductance (Yoder *et al.*, 1994). In part, plants compensate by investing proportionally more in the production of conductive sapwood and fine roots, but at the expense of leaf area and thus of photosynthesis and growth (Magnani *et al.*, 2000).

Even more than in epiphytes, one has to be careful to distinguish the effect of environmental changes during growth from physiological changes more directly related to plant size. Seedlings in the field generally have lower rates of photosynthesis because they are adapted to the shade and their root system does not access deeper soil layers (Bond, 2000). However, by comparing seedlings on the forest floor with mature trees and with seedlings grown under a simulated mature tree environment, Cavender-Bares and Bazzaz showed that about 50% of the difference in A_{max} was related to the environment and the remainder to an ontogenetic component (Cavender-Bares and Bazzaz, 2000). They did not speculate on the mechanism behind this 'ontogenetic effect', but because the seedlings of late-successional trees normally grow in the shade, they may be genetically determined not to obtain high photosynthetic capacities.

While increased stem water storage appears to provide little advantage for larger trees (compare, for example, Waring and Running, 1978), size-related changes in stem capacitance are of utmost importance for Andean giant rosette plants. In *Espeletia* species water stored in the large piths is crucial for maintaining transpiration when water uptake is restricted by frozen soil or cold roots. Because the number of live leaves changes little as stems become taller, the amount of pith water available per unit leaf area increases substantially. Large plants therefore have higher growth rates, lower mortality and higher leaf water potentials (Goldstein *et al.*, 1984, 1985). Taller plants are thus more resistant to drought stress, which explains the apparent paradox that the maximum size of these plants increases with altitude (Smith, 1980).

Desiccation-tolerant organisms, for example, most liverworts, mosses or lichens, should also show size dependency in their physiological performance. Water storage is determined by plant volume, while water loss is a function of the surface area. Because the length of the wet state prolongs the time for carbon gain and growth (Proctor, 1972), size-related differences in surface/volume ratios should lead directly to differences in long-term net CO_2 gain as long as there is no variance in rates of net CO_2 uptake. A recent study (Zotz *et al.*, 2000) showed that the situation may actually be more complicated: both the maximum rates of net CO_2 uptake and respiration were negatively correlated with cushion size in the moss, *Grimmia pulvinata*. Simulation of *in situ* gas exchange suggested a complex relationship between size and carbon

gain, which led the authors to conclude that the outcome of a comparative, ecophysiological study may strongly depend upon the chosen plant size.

In summary, the size-related changes in physiological properties in the three plant groups mentioned in this section are primarily caused by size-dependent differences in the availability of water. This resembles the situation in vascular epiphytes, but the particular mechanisms in epiphytes, trees, giant rosette plants, and poikilohydric plants differ substantially.

Conclusions and recommendations for future studies

Although to date differential water availability seems the best explanation behind size-related physiological changes, further experiments are necessary to clarify the proximate mechanism unequivocally. Our explanation allows clear hypotheses for such experiments. For example, no size-dependency is expected at experimentally high water availability. Conversely, ample nutrient supply combined with low water availability should result in differences between small and large conspecifics. Irrespective of the mechanism, however, the mere observation of size-related variation calls for attention to plant size in future ecophysiological studies. One obvious request is to report plant size in all studies on epiphyte ecophysiology, and, to be safe, for any plant. On the other hand, it is not known if plant size is always as important as in the examples shown. In some cases, the significant effect that was being sought was not found and it is also conceivable that others did not find such size effects either, because they are less common than this review suggests: negative results are obviously less likely to be reported in the literature.

Accepting the proposed mechanism behind size-related changes, namely the availability of externally or internally stored water, little effect of size would be predicted in those epiphytes that do not rely heavily on stored water because they are rooting in thick layers of canopy soil, for example, in cloud forests. Furthermore, if surface/volume ratios do not change during ontogeny, as in many plants with predominantly clonal growth (e.g. in ferns with individual fronds growing on a creeping rhizome) water availability should not depend on size, and size-related changes in physiological parameters are not expected.

Considering the importance of size-related water-storage capacity in epiphytes, very similar size effects were expected in desert succulents, which also rely heavily on stored water. Nobel emphasized the importance of stem capacitance for these plants (Nobel, 1988). Low capacitance explains the high mortality in juveniles, but detailed studies on size-related changes of the ecophysiology of these plants at the level of organs are lacking.

Most physiological research is done on plants organs, not on entire individuals. Although the effect of environmental variables on plant functioning is acknowledged in virtually every publication, the fact that the rest of the *plant* is always an important part of the environment of an individual *organ* is frequently not taken into consideration. In vascular epiphytes, as in many other plant groups, a problem of scale has to be faced: the same *external* environment imposes different levels of stress on smaller versus larger individuals of a given species. This difference leads to both long-term (e.g. PC, leaf anatomy) and short-term differences (e.g. stomatal functioning) in the physiology of organs such as leaves. Strictly speaking, size-related variation in physiological traits in vascular epiphytes is not a newly discovered form of intraspecific variation, rather it is the consequence of functional adjustment of a plant to past and present environmental constraints. Thus, studying the ecophysiological consequences of differences in plant size at the level of individual organs is likely to provide much insight into the physiological integration of whole organisms and their plastic response to stress.

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