

## MINERAL NUTRITION OF EPIPHYTES: AN APPRAISAL OF ADAPTIVE FEATURES

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### INTRODUCTION

How do higher plants operate as autotrophs in the crowns of trees, and why are so few major taxa found in any but the more humid forest canopies? Both queries are significant since epiphytism -- a little-studied ecological phenomenon -- is widespread in the tropics and involves elements of more than 60 families of flowering plants, a few gymnosperms and a great many vascular cryptogams (Madison, 1977). Approximately 10% of all angiosperms grow on a host at least occasionally, although usually under more equable conditions than those endured by such extreme epiphytes as bromeliad "air plants" and xeric canopy-dwelling orchids. In the following discussion, I wish to propose a philosophical and methodological framework that could prove useful in studying epiphytism as a life strategy and in attempting to answer questions of the kind posed above.

### PRODUCTIVITY AND REGENERATIVE CAPACITY

*Tillandsia circinnata* Schlecht., a representative air plant and the subject of a number of recent studies on the phenomenon of epiphytism, accumulates biomass very slowly. Its CAM metabolism, designed to promote drought tolerance, limits carbon gain (Benzing & Renfrow, 1971a, 1971b) as do certain oligotrophic features (Benzing, 1978a; Benzing & Davidson, 1979; Benzing & Renfrow, 1980). If *T. circinnata* is typical, the productivity of an individual air plant is severely curtailed by its adaptations to both climatic rigor and mineral deficiency, while the growth of the population as a whole is greatly impeded by substantial, random habitat disturbance and patchiness which cause heavy mortality, particularly of early juveniles (Benzing, 1978b). Because so few offspring reach maturity, extreme epiphytes are probably obliged to be more fecund than are perennials inhabiting comparably stressful, but less patchy and more stable sites (Benzing, 1978a).

Despite the existence of mesophytic epiphytes in at least a fifth of the families of flowering plants, very few of these higher taxa have evolved the regenerative capacity needed to succeed where productivity is limited by so many environmental restraints. For this reason, I have proposed that access to the more stressful reaches of the epiphytic biotope is restricted to those few organisms capable of acquiring sufficient supplies of several key nutrients to generate an appropriately designed and relatively powerful reproductive effort (Benzing, 1978a). Specifically, an epiphyte's ability to live an extreme existence (i.e., free of a perpetually moist, nutritive substratum) is based in large measure on its possession of refined devices for procuring minerals from scarce supplies and, perhaps even more important, on its employment of adaptive patterns of nutrient use. Considerable drought tolerance is indispensable for survival in all but the wettest canopies, but among the many adaptations required for extreme epiphytic life, it is, like the presence of holdfast roots and airborne seeds, of secondary importance in explaining the taxonomic exclusivity of this ecological type.

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## THE NEED FOR QUANTIFICATION

The designations heliophile, xerophyte and oligotroph are relative terms -- expressions of degrees of ecological tolerance and resource requirement along resource continua relating to the availability of light, water and minerals. To merit a particular appellation, an organism's position along the appropriate resource axis must be established with some precision. Therefore, a comparative perspective is essential to any study of stress biology, and the most useful comparisons are quantifiable.

At this time, little can be said about the quantitative aspects of mineral procurement by extreme epiphytes relative to those of other species adapted to more equable (mesotrophic) sites. Equally obscure are the tolerances *T. circinnata* and its kind must exceed to muster sufficient amounts of N, P and K to assure reproductive success. In essence, the question remains: How can the service (designated very broadly here as oligotrophic competence) provided by the absorbing trichome and the highly specialized orchid root, and the many features responsible for determining the way minerals are used by these plants, be expressed to allow comparisons with those of other species?

A particular plant's suitability for life in an infertile environment requiring considerable fecundity is best measured by calculating efficiencies of mineral procurement and by establishing how effectively scarce elements, once acquired, are deployed for vegetative and reproductive purposes. Investigators focusing on oligotrophic procurement and mineral use by any organism should strive to generate three sets of coefficients (one value for each element of interest): (1) a set which describes the proportions of "accessible" nutrients a "successful" organism (one that succeeds in replacing itself) manages to absorb over a lifetime; (2) another set delineating the species' mineral requirement to produce a given amount of biomass; and (3) a set showing what proportions of the element in question are actually invested in reproductive tissue.

## MINERAL PROCUREMENT, COMPETENCE AND DEMAND

The concept of accessible nutrients is especially difficult to circumscribe. Accessible nutrients should include all of a particular element an individual plant manages to absorb, plus an additional quantity that would have been acquired over a lifetime had all of that material (in available form) which ever came within access of its absorbing organs been taken up quantitatively. All of the dissolved K, for instance, that passed over the shoot of a *T. circinnata* specimen and thus was within "reach" of its absorbing trichomes over the plant's entire existence was, by this definition, accessible. That quantity of unabsorbed K must be considered accessible because it resided for a time in the same environmental pool the epiphyte used as a source of the element -- i.e., incorporated K is in all ways identical to unused but accessible K except that the organism managed to absorb the former but not the latter. The plant's success at harvesting accessible K over a particular interval would be a reflection of its mineral procurement competence for that element under the conditions prevailing at that time. Assuming that no other source of K was tapped, should an air plant absorb half of the K that entered the accessible space around its shoot, its index of mineral procurement (MP) for K would be 0.50, using the following equation:

$$\text{MP}_{(K)} \text{ index} = \frac{\text{total of acquired K}}{\text{total accessible K}}$$

Deviation from a quantitative capture (index 1.0) of accessible nutrients is an expression of oligotrophic competence comparable among species regardless of differing sizes, forms or life cycles.

Intuitively, one might expect that oligotrophs capture larger proportions of the scarce mineral resources available to them in infertile habitats than do mesotrophs on their more nutrient-rich sites. This notion is vulnerable to criticism, however, casting some doubt on the suitability of an MP index as a measure of oligotrophic competence. Although much more research on the subject is needed, some data suggests that mesotrophs and oligotrophs in general may have similar abilities to accumulate nutrients when those resources are available at very low concentrations, much as mesophytes and xerophytes are closely equivalent in their powers of moisture absorption from soils (comparing equal root surface areas at a given set of  $\Psi_{\text{root}}$  vs.  $\Psi_{\text{soil}}$ ). Drought-enduring xerophytes cope with aridity in large part by expending what moisture they can acquire very efficiently to gain carbon. They are also more resistant to injury that can accompany the large water deficits required to generate a high  $\Psi$  than are mesotrophs, and can continue to photosynthesize in states of considerable desiccation. Likewise, studies available at present suggest that a number of oligotrophs possess no greater affinities for several macronutrients when provided in dilute supply than do related mesotrophs and, in fact, usually absorb these elements less rapidly when provided access to luxuriant sources (Hackett, 1965; Clarkson, 1967; Bradshaw, 1969; Rorison, 1969; Grime, 1977; Chapin, 1980). Inferior capacities to exploit high quality (relatively concentrated) mineral sources may reflect the oligotroph's modest investments of protein in its carrier systems or the high efflux rates sometimes exhibited by organs equipped to absorb nutrient substances very rapidly (Chapin, 1980). Oligotrophs are adapted to infertile sites by their tolerances to low tissue concentrations of N, P and K that would cause dysfunctions in mesotrophs (Benzing & Davidson, 1979; Benzing & Renfrow, 1980). This capacity, coupled with an oligotroph's inherently slow growth and overall high mineral use efficiency, results in a very low spatial and temporal nutrient demand. Quantified nutrient demand data are therefore likely to be more useful indices of oligotrophic competence than those describing procurement efficiencies.

A mineral demand (MD) coefficient for K would be calculated:

$$\text{MD}_{(K)} = \frac{\text{quantity of K required to produce and maintain a given biomass}}{\text{quantity of given biomass}}$$

#### MINERAL USE EFFICIENCY

The third aspect of oligotrophic competence -- the efficiency of mineral use to generate successful offspring -- can also be expressed as a coefficient. The MUSP<sub>(K)</sub> (mineral use of K for seed production) index would represent the proportion of K directly employed by the individual in the attempt to recruit a successful replacement on a younger patch of habitable space -- i.e., one with a more extended future than the microsite from which it was colonized.

$$\text{MUSP}_{(K)} = \frac{\text{K expended for sexual reproduction}}{\text{total K required}}$$

Once incorporated into the body, an atom of K will experience one of several fates. It can be built into leaf, stem or root tissue to be lost to predators or leaching or ultimately sacrificed in litter. Another fraction can be incorporated into pollen and ovules and some of the latter eventually into seeds, where it will participate directly in the effort to recruit a replacement for the parent. Nutrients committed to petals, bracts and fruit, as well as to vegetative tissues, do contribute to the recruitment process, but not with equal directness. To simplify the analyses, these expenditures should probably be assigned, albeit somewhat arbitrarily, a nonreproductive status.

An expanding body of evidence indicates that a plant's inherent patterns of resource allocation are adaptive (e.g., MacArthur & Wilson, 1967; Grime, 1977). The classic *K*-selected genotype, an evolutionary product of a stable, resource-rich environment, is best programmed to apportion large quantities of its acquired material resources for vegetative purposes in order to assert competitive advantage or defend against predators. An *r*-selected genome is designed to promote an opposing pattern of allocation in order to maximize fecundity and persist on sites where various types of disruptions inflict heavy density-independent mortality. Patterns of mineral investment for one or the other general purpose would be exaggerated in proportion to the severity of the problems of supply, acquisition and demand. If the major restraints on canopy life are indeed as severe as I suggest, then the MUSP value of an extreme epiphyte should be unusually high. Those of the more mesic forms should be somewhat lower, but still higher than many terrestrials. Hence, the employment of *r-K* logic in assessments of the significance of specific patterns of mineral allocation among epiphytes is especially appropriate.

#### CALCULATING AND USING COEFFICIENTS

Even with the best of available technology, the investigator would be hard-pressed to quantify precisely all of the N, for example, lost by a specimen in leachates, litter, or to predators over a life cycle that may have exceeded several decades. Estimates of these losses, as well as inputs and accessible supplies, are possible, however, if a plant's life history profile is known and the magnitude of leaching and predation, mineral content of canopy fluids, and litter and its rate of production, are determined over representative periods of time. Direct measurements of seed production and the nutrient content of reproductive tissue are possible, but juvenile and adult mortality rates, like those pertaining to nutrient supply and exchange, will have to be extrapolated from the results of short-term experiments and field observation.

Coupled with appropriate life table data -- particularly mortality schedules -- coefficients of reproductive use and nutrient demand figures could be especially useful tools for gaining information about epiphytism. For instance, with appropriate numbers, one could calculate how much accessible K or P a population expends per unit time and area to maintain a particular density, or the replacement cost in units of a specific nutrient for each reproducing adult. Ultimately, the epiphytic way of life could be evaluated on a cost-benefit, supply and demand basis with emphasis on those resources most crucial to the successful deployment of that life strategy.

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