THE LIFE HISTORY PROFILE OF *TILLANDSIA CIRCINNATA* (BROMELIACEAE) AND THE RARITY OF EXTREME EPIPHYTISM AMONG THE ANGIOSPERMS

David H. Benzing *

INTRODUCTION

Families of flowering plants with epiphytic members are numerous, but very few include species capable of exploiting the most stressful (driest and least fertile) portions of the forest biotope. Attempts to explain this disparity have focused on two abiotic restraints that impinge more heavily on extreme than on mesic epiphytes: severe drought and site infertility (Benzing and Renfrow, 1971-a,-b; Benzing, 1973). In this discussion I propose that two additional impediments, in concert with aridity and ombrotrophy, have precluded a broader taxonomic participation in extreme epiphytism. These two factors are habitat disturbance and the patchy nature of the space available to plants practicing this life strategy.

MESIC VS. EXTREME EPIPHYTISM

Extreme epiphytes are plants with great drought endurance and well-developed capacities to scavenge mineral nutrients from dilute sources. Most are succulent to some degree and many, if not all possess CAM metabolism. Oligotrophy is also typical. Given the climatic and nutritional stresses that characterize their habitats — exposed portions of the forest canopy in humid zones and the entire forest profile in arid regions — both qualities are essential. Water and minerals are available to these species only when rain is falling or the supporting vegetation is wet. During dry seasons, weeks or months may pass between opportunities to recharge desiccated tissues and increase internal mineral supplies. Even when available, nutrient solutions are usually dilute. In essence, extreme epiphytes — a category largely composed of certain members of the bromeliad genera *Tillandsia* and *Vriesea* and xeric taxa of Orchidaceae (e.g., certain species of *Encyclia* and *Oncidium*, perhaps some cacti and a few others) — have unusually limited access to moisture and nutrients in both time and space.

In tropical zones where climate and exposure are more accommodating, mesic epiphytes abound. They can survive in these habitats because storms are more frequent and precipitation is held in the canopy for longer periods of time by the layers of detritus and lower plants that cover much of the bark surfaces in moist forests. Some tank bromeliads and other impounding epiphytes are able to operate as mesophytes while growing in relatively arid regions because their growth forms provide for the accumulation of nutritive materials and moisture against absorptive leaf and root surfaces (Benzing, 1970; Benzing and Renfrow, 1974).

Xeric and mesic epiphytism are related ecological strategies located at opposite extremes along a single adaptive continuum. An inverse relationship exists along this continuum between environmental stress and plant vigor. As aridity and infertility increase, rates of plant growth, reproduction and maturation decline. Hence mesic epiphytes have greater regenerative powers than do extreme forms. A similar relationship prevails among mesic and xeric terrestrials and mesotrophic and more oligotrophic, soil-rooted species. All three sequences exemplify the same adaptive response to extreme climatic

*Oberlin College, Oberlin, Ohio 44074, U.S.A.

and nutritional rigor. Low vigor is advantageous in a context of ombrotro-
phy and aridity. Plants with slow growth and weak reproductive efforts re-
quire fewer nutrients and other material resources than do more vigorous
ones.

ECOPHYSIOLOGY OF AN EXTREME EPIPHYTE

At maturity, *Tillandsia circinnata* Schlecht. is a small organism whose
shoot surfaces are densely covered with absorbing foliar trichomes (Benzing
et al., 1976). Roots are short-lived, sclerified and few in number. At maturi-
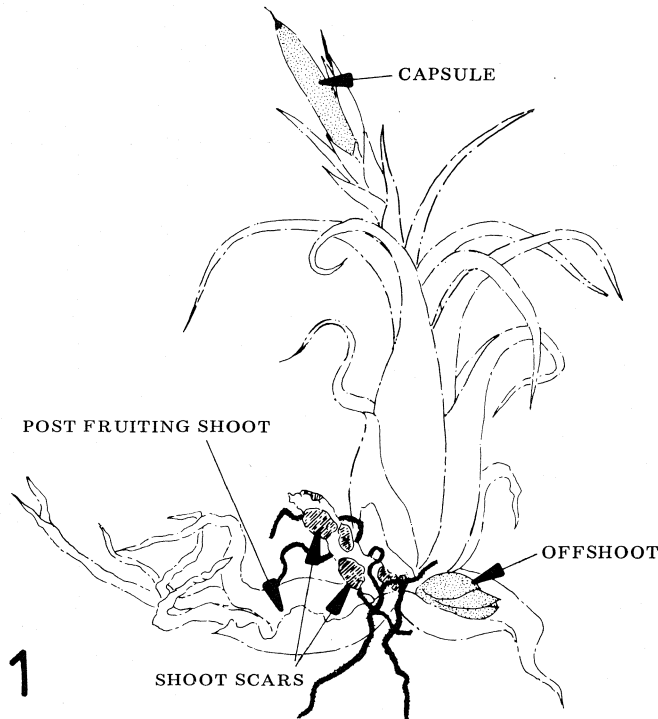ty, the entire root system comprises less than 10% of the plant body (Fig. 1),

Figure 1. An older, extremely nutrient-stressed *T. circinnata* (about 1/2 natural size)
ripening a minimum-sized seed crop.

a small fraction for a perennial herb. *Tillandsia circinnata* and several hundred
related species have been known for some time as "atmospherics" since they
obtain moisture and mineral nutrients directly from rainfall and canopy
fluids (Schimper, 1888). This organism is locally abundant in Florida south
of Lake Okeechobee and infests a variety of hosts there. Populations also
occur in Mexico, Central America and parts of northern South America. In
Florida, dwarfed *Taxodium ascendens* on shallow, infertile soil is an especial-
ly favored support, but sizable populations are common on *Avicennia germi-
nans*, *Conocarpus erecta*, *Pinus* spp., *Rhizophora mangle*, *Quercus virginiana*
and others.

Distribution within the crowns of hosts seems to be dictated primarily
by exposure. While several other more mesic local bromeliads colonize
shaded sites — perhaps actually preferring them — *T. circinnata* is obliged by its

heliophilic nature to inhabit sparsely foliated trees or just the peripheral branches of denser crowned hosts. Its drought endurance as an adult is not seriously challenged in southern Florida. I have never encountered specimens showing signs of pronounced desiccation even though no rain may have fallen for several weeks. Plants on exposed sites are commonly growth-limited by nutritional stress, but apparently not by insufficient light or water (Benzing and Renfrow, 1971-a; Benzing and Davidson, unpublished MS).

Tillandsia circinnata is an iteroparous perennial with a potentially long life span made possible by the routine production of a series of slow-growing determinate shoots (Fig. 3). Seedlings require at least 5 years to flower; thereafter, the life of the plant continues, perpetuated by a sequence of axillary offshoots. Asexual progeny are usually more vigorous than their seedling parents and reach maturity sooner. Offshoots of vigorous individuals usually flower in 2-3 years. Those generated by nutrient-deficient specimens may require three or more years to mature.

As older adults, vigorous specimens containing the highest concentrations of P and K — and sometimes N and Mg — are comprised of several attached shoots at various stages of maturity. Two or three can flower in a single season, collectively ripening up to 20 capsules enclosing 60-140 seeds each. A very robust plant may eventually support enough shoots of various ages to flower most years. Older, more nutrient-stressed individuals usually consist of a single, very slow-growing, small rosette with an immature axillary offshoot if the specimen is in fruit or has recently produced a seed crop (Fig. 1). Once every 3 or 4 years its sexual efforts will yield one to (occasionally) four capsules, each containing about the same number of seeds as those ripened by better provisioned specimens.

Fruiting intervals in individuals so nutrient-stressed that they can support only one mature shoot at a time appear to be determined in large measure by the interim necessary for the plant to replenish mineral nutrient deficits incurred when the previous crop of seeds was ripened (Benzing and Davidson, unpublished MS). Barring interference by predators or the failure of pollination, the magnitude of the sexual effort of all specimens seems to be governed by the size of the mobile N, P and K pools available to provision a seed crop (ibid.). Offshoots are usually initiated when the parent rosette commences the production of an inflorescence or has its apex aborted by insect or mechanical injury (Fig. 1).

Examinations of ripe seed crops and parent vegetative bodies indicate that the sexual product contains minerals in various proportions of the specimen's total nutrient content (Table 1). Nitrogen is expended most lavishly

Table 1. Mean dry weight percentages ± S. D. (sample standard deviation) of 11 elements in ripe seed crops of *T. circinnata.*[*]

N	P	K	Ca	Mg	Mn
29.1±7.1	25.9±6.6	16.9±7.7	3.3±1.2	12.0±5.0	12.5±7.3

Fe	B	Cu	Zn	Mo
4.0±1.6	9.5±3.0	11.7±4.0	7.7±3.2	10.1±3.0

[*]These data were gathered as part of a study of the reproductive biology of this epiphyte in South Florida (Benzing and Davidson, unpublished MS).

in seed tissue where it occurs at 2.5-3 times the concentration prevailing in the parent vegetative body. Up to 40% of a specimen's total N pool at the

time of capsule dehiscence can be invested in the enriched seed crop. Potassium and P are also expended quite liberally. Calcium and Fe are much more conservatively provisioned in seed tissue with 95% or more of the total pool remaining in parental organs after capsules have ripened. Fruit maturation also places relatively high demands on stores of several metallic micronutrients.

Seeds are equipped with an extensive series of coma hairs that represent outgrowths of the testa. The average dry weight of a seed is approximately 0.7 mg. About 60% of this mass is contributed by the coma. Offshoots are borne on short stems so that the recruitment of new microsites on other hosts, adjacent branches or surfaces on the same axis more than a few cm removed from a parent can be accomplished by seed only.

Tillandsia circinnata seems to have few predators. Insect damage, when it does occur, is seldom lethal. The small seeds, once dispersed, seem to be free of heavy predation (Benzing, 1978). Cold weather is a more destructive agent and occasionally causes heavy localized kills in some areas of southern Florida. Considerable mortality is regularly associated with limb breakage. Dead and moribund specimens are fairly commonly encountered attached to fallen twigs and small branches on all sites where *T. circinnata* occurs in large numbers. Direct contact with moist soil cannot be tolerated and the epiphyte soon dies.

LIFE HISTORY ANALYSES

Increasingly, life history characteristics of both plants and animals are being ascribed adaptive significance and given labels according to the precepts of theories originally developed by demographers and subsequently modified by evolutionary biologists. Properly used, these paradigms serve as useful tools in the assessment of ecological strategies and as aids in the search for the environmental restraints that determine the occurrence and distribution of organisms in nature. I refer to the concepts of r- and K-selection (Cole, 1954; MacArthur and Wilson, 1967) and the more recent expansion of these ideas as they relate to plants (Grime, 1977).
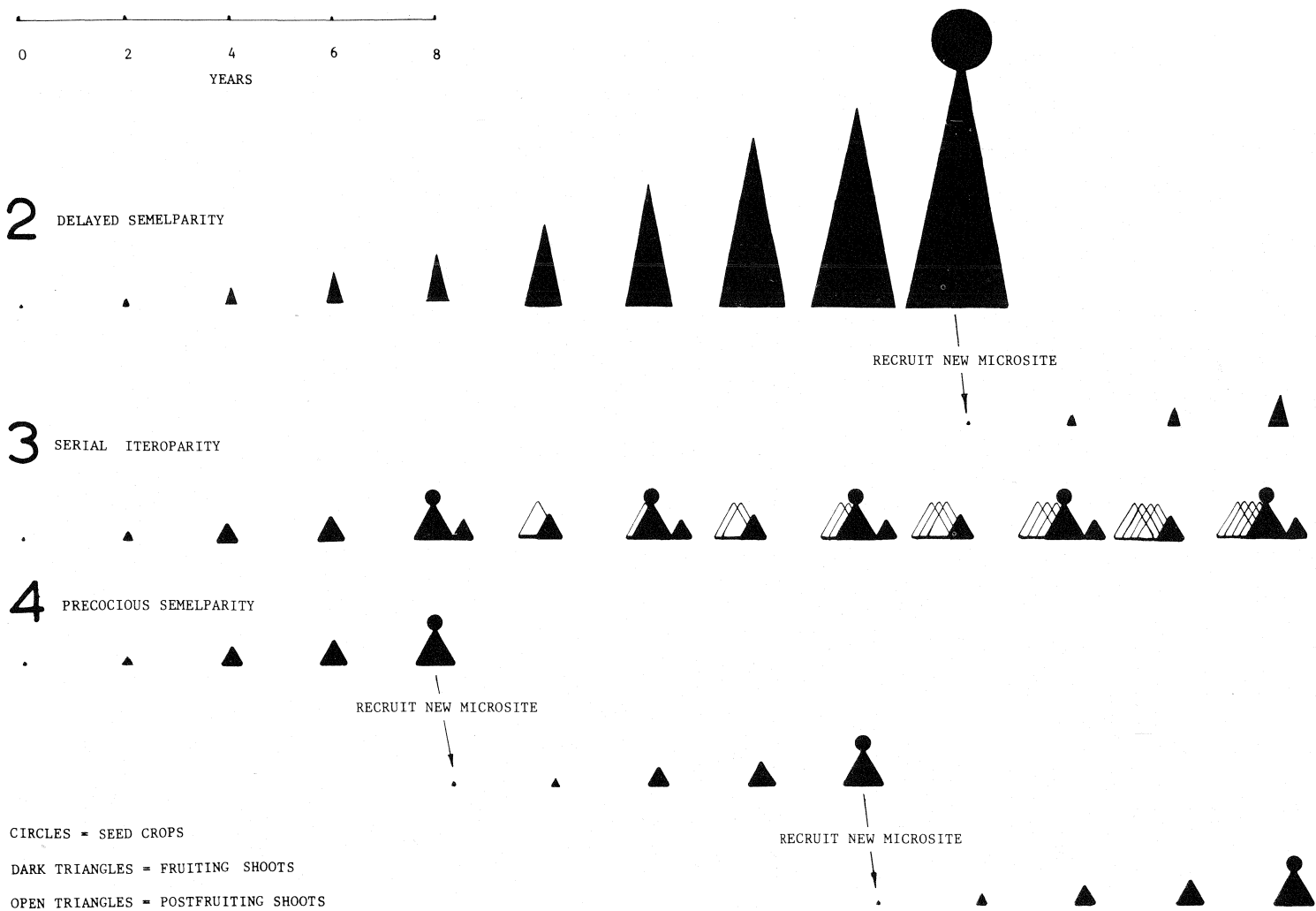
Organisms which apparently evolved under selection pressures (most often attributable to abiotic forces) that enforced high density-independent mortality are designated as r-strategists by r-K logic. Organisms conforming to this definition inhabit sites where Darwinian fitness is enhanced by reproductive patterns that maximize r, the intrinsic rate at which a population can grow. K-selected strategists fall at the other end of the same selective continuum, based on competition and resource availability. K-strategists typically occur where one or more major resources is limited because their populations commonly exist at or near carrying capacity (K). Rates of recruitment are low compared to those of r types whose numbers in any one locality are often expanding.

To persist over the long term, individual r-strategists must invest much of their resources in the reproductive effort while K-selected forms favor allocations promoting the growth and long-term maintenance of the estab-

Figure 2. Schematic representation of delayed semelparity.

Figure 3. Schematic representation of iteroparity as expressed by *T. circinnata*.

Figure 4. Schematic representation of the pattern of semelparity *T. circinnata* would express if it fruited each time sufficient nutrient resources were accumulated to provision a minimum-sized seed crop.

0   2   4   6   8

YEARS

2 DELAYED SEMELPARITY

RECRUIT NEW MICROSITE

3 SERIAL ITEROPARITY

4 PRECOCIOUS SEMELPARITY

RECRUIT NEW MICROSITE

CIRCLES = SEED CROPS

DARK TRIANGLES = FRUITING SHOOTS

OPEN TRIANGLES = POSTFRUITING SHOOTS

RECRUIT NEW MICROSITE

lished individual rather than the rapid expansion of its population. Semel-
parity or iteroparity with a short prereproductive phase and large litters is
expected of r-strategists. Iteroparity involving numerous modest reproduc-
tive efforts relative to resources available to the organism, delayed maturity
and a potentially long adult life are among those life history traits predict-
able in K-strategists.

Several workers have demonstrated that r-K selection theory, as initially
conceived, focuses too narrowly on the relationship between r and the ques-
tion of whether biotic or abiotic factors are the major causes of mortality
(e.g., Menge, 1974; Wilbur et al., 1974; Wilbur, 1976). Autecological analy-
ses of several plant and animal species have revealed that additional (or more
specific) environmental parameters determine the appropriateness of a parti-
cular r value in a particular natural setting. Predation, habitat stability and
predictability of adult and juvenile mortality schedules (e.g., Holgate, 1967;
Murphy, 1968; Schaffer, 1974, among others) are now known to be selective
forces that may affect the evolutionary canalization of r.

Grime's (1977) broadened concept of R- (ruderal), S- (stress) and C-
(competition) selected strategies formally accommodates the notion that
physical (climatic and edaphic) restraints are major forces in the evolution of
life history profiles. This premise is especially applicable to atmospheric epi-
phytes, but Grime's framework, even though expanded to include three pri-
mary selection regimens, still lacks sufficient resolution to point the way to
an identification of all the extrinsic forces responsible for the evolution of a
specific reproductive strategy and general growth profile.

Until all the environmental restraints impinging on any organism are re-
cognized and the costs and tradeoffs obliged by the adaptations required to
counter these stresses are known, pronouncements on the adaptive advan-
tages of many life history traits and the environmental parameters that
helped mold them through selection will remain speculative. Nevertheless,
biologists should not shy away from the task of circumscribing and evalu-
ating ecological strategies since it is by this route that a fuller understanding
of plant ecology will evolve. I adhere to this notion and use Grime's (1977)
more flexible series of paradigms as a point of departure for an analysis of
T. circinnata and, more generally, the life strategy previously described as
extreme epiphytism.

Grimes, in his discussion of the "primary" strategies of plants, states
that, of the four possible combinations of high or low habitat stress and
much or little disturbance, plants can adapt to only three. Highly stressed,
unstable environments supposedly fail to support vegetation because plants
grow too slowly under severe aridity, low temperature or infertility or any
combination of the three to regenerate between closely spaced perturba-
tions. At some point this must certainly be true. I propose that *T. circinnata*,
as an extreme epiphyte, is operating just short of these limits more than are
most other life forms.

Neither disturbance nor climatic stress — plus one of its outcomes,
site infertility — alone can account for the exclusive membership in the
category of extreme epiphytes. Dozens of families include weedy forms high-
ly suited to ephemeral habitats, or desert dwellers capable of tolerating ex-
treme climatic stress, yet harbor no species with habitat preferences and
associated tolerances equal to those possessed by hundreds of atmospheric
bromeliads and equally xeric, epiphytic orchids. If they did, several times the
current numbers of major taxa would in all likelihood be included among the

extreme epiphytes. Judging by their occurrence in many families, buoyant seeds and aerial, drought-tolerant holdfast roots — additional requirements for life in the canopy — are relatively easily evolved and represent no more than minor barriers along the path to epiphytism, whether in its mesic or extreme expression. In the final analysis, it is the combination of stress and disturbance and, as we will see in the following paragraphs, the patchiness of the habitat — not any one of these three nor any additional obstacle — that makes the driest, most exposed portions of the forest canopy so formidable and difficult for plant life to penetrate.

ENVIRONMENTAL RESTRAINTS AFFECTING *T. CIRCINNATA*

Selective pressures related to resource availability, as well as those that enforce juvenile and adult mortality schedules, certainly have canalized the life history profile of *T. circinnata* (Table 2). In this case, owing to the un-

Table 2. Major life history characteristics of *T. circinnata* and the selective forces most likely responsible for their evolution. Included are the assignments each adaptation would receive within the r-K selection strategy scheme.

ADAPTATION	PRIMARY SELECTIVE FORCE INVOLVED	R-SELECTED	K-SELECTED
Iteroparity	High and unpredictable juvenile mortality leading to the need for multiple use of each successfully recruited microsite		+
Regular asexual reproduction	High and unpredictable juvenile mortality, leading to the need for multiple use of each successfully recruited microsite		+
Small seeds	High juvenile mortality leading to the need for high fecundity	+	
Highly dispersible seeds	Patchiness of habitable space	+ (fugitive spp.)	
Large portions of nutrient reserves expended in each seed crop	High juvenile mortality leading to the need for high fecundity	+	
Low vegetative vigor	High physical stress related to aridity and ombrotrophy		+?
Long juvenile phase	High physical stress related to aridity and ombrotrophy		+
Long life	Unpredictability of juvenile mortality, leading to the need for multiple use of each successfully recruited microsite		+
Small size at maturity	High physical stress related to aridity and ombrotrophy	+	
High shoot to root ratio	High physical stress related to ombrotrophy. High juvenile mortality, leading to the need for high fecundity.	+	

usual character of the epiphytic biotope, the results, when considered in the context of r-K selection theory, seem inconsistent, if not paradoxical. Stressful habitats supporting plant life, specifically those of high aridity, insolation and temperature — and probably many of low fertility — are typically stable. Plants encountered there are notable for stress tolerance, but not for their competitive ability or high fecundity. This is reasonable since neither of the latter characters is particularly adaptive in deserts or on dry cliffsides and other localities where the substratum is stable, vegetation is sparse and productivity is held to a low level by climatic or edaphic stress. A barrel cactus

may grow very slowly for hundreds of years with little chance of being over-
grown, uprooted or otherwise displaced by physical factors. *Tillandsia circin-
nata* and other extreme epiphytes occupy a more precarious spatial niche. To
succeed there they must meet a broader array of restraints with a corre-
spondingly more extensive set of adaptations. Some of these adaptations are
inherently antagonistic.

Habitat instability and patchiness and physical stress all induce high
density-independent mortality in populations of *T. circinnata*, but the three
conditions do not have equal impact on the same life stages (Table 2). Thus
they can be expected to exert distinct selective pressures on reproductive
performance and other life history characteristics (Stearns, 1976). Juvenile
attrition is largely attributable in this instance to physical stress — probably
most importantly aridity — and the scattered locations of suitable substrate
(properly exposed bark surfaces). Seeds and young seedlings of this epiphyte
attached to the bark of trees in southern Florida and observed over two
years suggest that even among those propagules that do manage to impact
and lodge on acceptable hosts, a very small percentage reaches adulthood
(Benzing, 1978). No doubt few seeds of the total produced are intercepted
by a suitable tree crown. (Incidentally, many mesic epiphytes produce larger
seeds in fleshy fruits — e.g., Cactaceae, Araceae, Bromelioideae of Bromelia-
ceae and Ericaceae. These species benefit from a more directed seed dispersal
— by animals — and a larger nutritional reserve per seedling than are avail-
able to atmospherics or orchids).

Adult mortality is also quite heavy for a slow-growing species; in this
case, in large measure because bark is not a particularly stable substratum.
Space exploitable by *T. circinnata* and its ecological counterparts is not only
broken up into scattered patches but the individual anchorage points are
ephemeral. Although no empirical data are as yet available to support this
contention, a particular bark surface large enough to support a shade-tolerant
T. circinnata specimen seems unlikely to remain serviceable for more than
2-3 decades. By that time the average anchorage point will have become
darkened by host crown expansion or the epiphyte once located there will
have fallen to the ground when a limb or twig involved in its support self-
pruned or a bark fragment exfoliated. Host death, fires and other natural
catastrophies bring about larger-scale disruptions of habitable space. Distur-
bances of both magnitudes are especially restrictive to a species already en-
cumbered with low vigor obliged by other — in this case unrelated — physical
restraints.

POTENTIAL AND REAL RESPONSES TO HIGH MORTALITY

If *T. circinnata*, for whatever reason, is close to that limit imposed by
the combined effects of high stress, frequent habitat disturbance and patchi-
ness — i.e., its regenerative potential is strained to near the limit — then r
should be high and demonstrably expensive in terms of the amounts of
growth-limiting resources individuals must expend on replacement, specifi-
cally for sexual replacement. Resources that seem to most severely depress
the vegetative vigor and sexual efforts of *T. circinnata* below those maxima
allowed by its genome are N, P and K (Benzing and Renfrow, 1971-a; Ben-
zing and Davidson, unpublished MS). Patterns of allocation of these three
macronutrients do provide circumstantial evidence that mortality rates rela-
tive to resources available are indeed high (Table 1). Whether these unusually

large expenditures for the sexual effort are, in larger part, responses to adult or juvenile mortality schedules is not apparent at this point.

What is clear are the adaptations designed to maximize each sexual effort without sacrificing the ability of the individual to produce successive seed crops. Specimens of *T. circinnata* in the most nutrient-stressed forests reproduce as soon as they accumulate sufficient mineral resources and the leaf area these minerals can support to generate one small offshoot and to ripen one or a few capsules containing small, highly dispersible seeds — i.e., a minimum-sized seed crop (Benzing and Davidson, unpublished MS). This requires no less than 5 and may involve 10 years' time (Fig. 3). Seed crops are generated by the same parent thereafter whenever nutrient resources are replenished, again a slow process measured in years. Proportions of total N, P and K reserves expended in individual seed crops each sexual generation commonly reach 25-40% if pollination success promotes (Table 1) — as it often does — a high or complete fruit set (*T. circinnata* is self-fertile). These expenditures more closely parallel patterns of N, P and K use by r-selected, semelparous annuals and old field perennials native to the Great Lakes region of the United States than long-lived, K-selected, understory perennial herbs found under mature stands of eastern American deciduous forests (unpublished data).

In spite of the many restraints that routinely promote nutritional stress in this epiphyte, it nonetheless has one major advantage shared by few other plants — little nutrient material need be expended for roots. Carbon gain, and moisture and salt procurement are accomplished by the trichome-equipped shoot. Mineral resources are largely available for expenditure on stem, leaf and, most importantly, on reproductive tissue. Small size at maturity, another oligotrophic adaptation, permits the organism to reproduce after investing a rather modest amount of material in nonreproductive tissue. The economy effected by these two factors may be of paramount importance to an oligotroph, especially one with a requirement for high fecundity.

Compared to plants with short life cycles (typical r-strategists), the regenerative capacity of *T. circinnata* is low in absolute terms but impressively high relative to available mineral resources. Two other patterns of reproduction would be possible without deviating from the family-wide habit of producing determinate shoots. One of these could potentially further enhance r. Were *T. circinnata* to expend all of its accumulated resources in a single seed crop after just 5 years or so when it normally flowers for the first time — that is, become monocarpic — r could theoretically be increased to the maximum allowed by the remaining environmental and intrinsic restraints limiting the fecundity of the species (Fig. 4). If all other factors are disregarded, the most effective way to increase r in any species is to shorten its juvenile stage and expend all resources that can be mobilized in one sexual effort (Lewontin, 1965). Should the species be semelparous but put off reproduction for additional years until greater resources are amassed, a much larger seed crop would be possible (Fig. 2). In the latter instance, the attrition of older juveniles caused by site destruction and other factors might be unacceptably heavy, rendering this strategy untenable. The retention of the nearly family-wide polycarpic habit rather than the adoption of either short- or long-term semelparity is probably consistent with the selective pressure reflected by its juvenile mortality schedule.

Since the frequency of rainfall, not necessarily its amount, is very important to the establishment of this epiphyte's seedlings (Benzing, 1978),

chances are good that juvenile mortality is unpredictable and varies considerably from year to year. By retaining enough resources at the cost of a larger seed crop to support an offshoot each time an individual ripens fruit, a successfully occupied microsite can be utilized as a source of repeated, though smaller, seed crops over many seasons — potentially for as long as that anchorage point remains serviceable. If *T. circinnata* were semelparous in any fashion, each recruited microsite could be used just once as a seed source. The significance of a successfully recruited microsite and of the spent parent, including the hard-won nutrients contained in its litter, to the population as a whole would vanish once that single reproductive effort was completed.

On balance, the advantage of a somewhat greater fecundity or fewer but larger individual reproductive efforts is probably outweighed by the benefits that come with repeated, smaller seed crops. Iteroparity is thought to be the most appropriate mode of reproduction for organisms native to habitats where stresses of either biotic or abiotic origin fluctuate such that some years favor greater juvenile success than others (Murphy, 1968; Schaffer, 1974; Stearns, 1976). Gadgil and Bossert (1970) and Charnov and Schaffer (1973) have developed predictive models suggesting that organisms subjected to high juvenile vs. adult mortality should be advantaged by long rather than short life cycles. Quite likely, except for occasional severe tropical storms and perhaps fire, season to season adult mortality is much lower than that of juveniles and is more predictable and steady.

THE WIDER OCCURRENCE OF MESIC EPIPHYTISM

Attempts to explain why extreme epiphytism involves so few major taxa have so far centered on the biology of *T. circinnata.* Equally important to this discussion is an explanation of why mesic epiphytes are so much more taxonomically diverse. Again I turn to Bromeliaceae for a possible explanation.

In addition to their greater regenerative powers, many mesic bromeliads (a group of about 20 genera from two subfamilies) can tolerate more shade than their xerophytic relatives (Benzing and Renfrow, 1971-c). Apparently low shoot surface to volume ratios, high leaf reflectance, CAM and associated features required to promote drought endurance in this family take their toll on photosynthetic performance. In any case, both greater vigor and shade tolerance better equip mesic forms to successfully exploit relatively robust hosts (plants that generally have a high leaf area index) where microsites may have an even shorter life in real time than those on nutrient-stressed supports or others which, for various reasons, have more transparent crowns (Benzing and Seemann, 1978). Patch life is effectively longer for nonsucculent tank forms in highly productive forest communities not only because they grow faster but also because, as shade-tolerant organisms, survival is possible for some time while an anchorage site is being overshadowed by an expanding canopy.

As species with higher regenerative powers and lower light requirements, reproducing populations of tank bromeliads may be able to persist in forests largely inaccessible to atmospherics because patch life there is too short to allow the latter to perform at replacement levels. Numerous families appear to contain epiphytic forms with growth requirements including light demands and inherent rates of vigor similar to those of shade-tolerant bromeliads. Only Bromeliaceae, Orchidaceae and perhaps a very few others have

evolved genomes featuring the combinations of stress tolerance and regenerative capacity required to cross the adaptive continuum and exploit those portions of the forest canopy occupied by *T. circinnata* and its kind.

LABELING THE STRATEGY

Still remaining is the task of assigning the specialized life style of epiphytism to a specific primary ecological strategy. Judging from the data that studies and observations of *T. circinnata* have produced, at least this extreme epiphyte faces an unusual combination of environmental restraints. These oblige the organism to rely on a constellation of structural and functional features that seem to blend those of both the classic r- and K-strategists (Table 2). Characteristics that mimic K-selected traits, but are in fact mandated by aridity and oligotrophy, are obvious — one of those that accurately reflects an r-strategy, namely its pattern of nutrient allocation, is not (Table 2).

Tillandsia circinnata could, with substantial justification, be labeled an r-strategist — albeit in slow motion — and as a fugitive species at that. In no way can this epiphyte be considered a K-strategist. Seldom, if ever, do populations anywhere approach K, i.e., cover most of the suitable bark surfaces or intercept most of the light, moisture or nutrients available to it. In fact, only a small fraction of the anchorage sites and other resources accessible to the species in the space that could be occupied by its members before intraspecific or interspecific competition with other epiphytes ensued is ever exploited at any one time.

Central to my proposed explanation for the rarity of extreme epiphytism in the angiosperm complex is the notion that the arid portion of the forest canopy biotope is an unusually rigorous SD- (stress disturbance) selecting habitat — that is, a physically stressful, unstable one relatively free of competition. Whether *T. circinnata* and its ecological counterparts should be designated SD-selected strategists depends, in large part, on one's definition of habitat stability and disturbance.

Particular events in nature may or may not qualify as disturbances depending on the biological references involved. Likewise, the lengths of the intervals between the occurrences of individual events in a series of truly disruptive ones will determine whether a particular space is stable or not. All habitats are at least occasionally disturbed to an extent that all of their resident species experience major population dislocations as a result. Yet most types of sites are considered relatively stable by biologists. Close-interval environmental disturbance — i.e., habitat instability — is organism-defined in the sense that, if significant to a particular species as a selective force in its evolution, that organism will exhibit major adaptations or, more likely, suites of adaptive features primarily designed to reduce the impact of that specific destabilizing force. So far, available data indicate that *T. circinnata* is defining its habitats as unstable (disturbed) as well as patchy and stressful.

My argument that the life history profile of *T. circinnata* is indicative of a genome designed to cope with an unusually difficult combination of stress, patchiness and disturbance is circular in two distinct respects. Circularity is inherent to the concept that the environment is organism-defined, although few, if any, ecologists would reject this notion completely. More vulnerable to criticism is my claim that the rarity of evolutionary breakthroughs leading to the exploitation of the driest, least fertile and exploited portions of the

forest canopy can be taken as evidence that an unusually formidable combination of environmental restraints operates there. As difficult as they may be to prove, these related hypotheses can be tested in a meaningful way by carrying out empirical studies designed to: (1) further assess how effectively the fecundities of various extreme epiphytes are maximized in the face of severe nutrient stress and (2) determine how long habitable patches remain serviceable in the canopy and to what extent this factor, spatial patchiness — and stress in general — affect the juvenile and adult mortality schedules of these epiphytic plants.

SUMMARY

Tillandsia circinnata, an extreme epiphyte assumed to be typical in life history profile for its ecological type, possesses an unexpectedly high fecundity and mineral expenditure for seed tissue for an organism adapted to such stressful habitats. Considering the broad extent and emptiness of their forest canopy biotope, the occurrence of extreme epiphytes in so few families suggests that the potential for the success of angiosperms in the drier portions of the forest canopy is marginal and is tenable for only a very few specialized genotypes. This is so probably because life, as embodied in the Anthophyta, is, in spite of its overall flexibility, still hard-pressed to deliver the regenerative power necessary to cope with the additional obstacles presented by the patchy, ephemeral living space in the arid forest canopy. Extreme epiphytes would probably be much more diverse and common if their spatial niches were more fertile and humid, or stable, or contiguous rather than patchy.

ACKNOWLEDGMENT

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