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THE POPULATION DYNAMICS OF *TILLANDSIA CIRCINNATA* (BROMELIACEAE): CYPRESS CROWN COLONIES IN SOUTHERN FLORIDA[1]

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Obligate epiphytes are vagrants via reproductive units and move among host islands scattered across hostile seas of treeless space and unaccommodating canopy vegetation. Within acceptable crowns, these plants face a finer-grained patchiness enforced by gaps between adjacent branches and by shade and rain shadows. Surfaces colonized by canopy dwellers are unstable. Quite often the lives of branches or even whole trees are too short to allow a resident epiphyte time to mature or, should adulthood be achieved, to fruit more than a few seasons. Exacerbating the disturbance factor are aridity and site infertility. Both increase a population's vulnerability to environmental perturbations by prolonging juvenility (the interval an organism needs to amass resources for a first reproductive effort) and the "recharge" time subsequently required between successive fruiting seasons. Canopies of most tropical forests experience dry seasons of varying lengths and parallel degrees of oligotrophy (Benzing & Renfrow, 1980). In essence, organisms obligated to anchor on bark surfaces face a particularly formidable combination of density-independent constraints, perhaps a more imposing set than those impacting on most soil-rooting taxa (Benzing, 1978a).

In spite of climatic rigor and the attendant nutritional deprivations, and because of habitat patchiness and disturbance, typical vascular epiphytes require considerable regenerative capacity. Two strategies are involved: an asexual effort designed to encourage short-term success (maximum exploitation of secured microsites); and the production of vagile seeds, a necessity for a more extended (island hopping) persistence (Benzing, 1978a; Benzing & Davidson, 1979; Benzing & Renfrow, 1980). The cost of these activities in terms of certain scarce nutrients is especially high for oligotrophic canopy dwellers (Benzing, 1978a). In fact, of an extreme epiphyte's many adaptive features, those designed to promote N, P and K economy for reproduction should rank high as hallmarks of its ecological type. With this premise in mind, and a wish to better understand epiphytism as a life strategy, I have embarked on a series of studies designed to characterize reproductive phenomena of *Tillandsia circinnata*, a representative epiphytic bromeliad. In this report, the structure of natural colonies on southern Florida dwarfed cypress hosts is described.

STUDY AREA

The study site is situated on the western edge of the Big Cypress Swamp about 5 km due east of Naples, Florida. A sample locality designated as "Naples east" in a previous study (Benzing & Davidson, 1979) is adjacent to this one. Better-drained locations throughout the area support slash pine *(Pinus elliottii)* and saw palmetto *(Serenoa repens)*. Pond cypress *(Taxodium ascendens)* dominates most of the lowland except for localized "bayheads" which feature dense growths of several broadleaf shrubs in addition to cypress. *Taxodium* is dwarfed here, but not to the extreme so often seen farther east where specimens hundreds of years old may be no more than a few meters tall. Epiphytes are abundant. Orchids include *Encyclia tampensis* and *Harrisella porrecta*. By far the most common bromeliad is *Tillandsia circinnata*, but *T. recurvata*, *T. usneoides*, *T. flexuosa*, *T. balbisiana*, *T. utriculata* and *T. fasciculata* also occur in the general area.

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SAMPLING PROCEDURE

Sampling was carried out in late December and early January during the winters of 1978-79, 1979-80 and 1980-81. Study trees were well separated from other sampled supports and totally or largely free of contact with nearest neighbors. Their size and epiphyte load, judged from the ground, seemed representative for the forest locality being worked that year. Each cypress was felled and a census taken of all living *T. circinnata* specimens in its crown colony. Other epiphytes, always a small minority of the total, were disregarded. Each member of a crown population was categorized as juvenile or adult. Immature material was further subdivided into eight size classes (A-

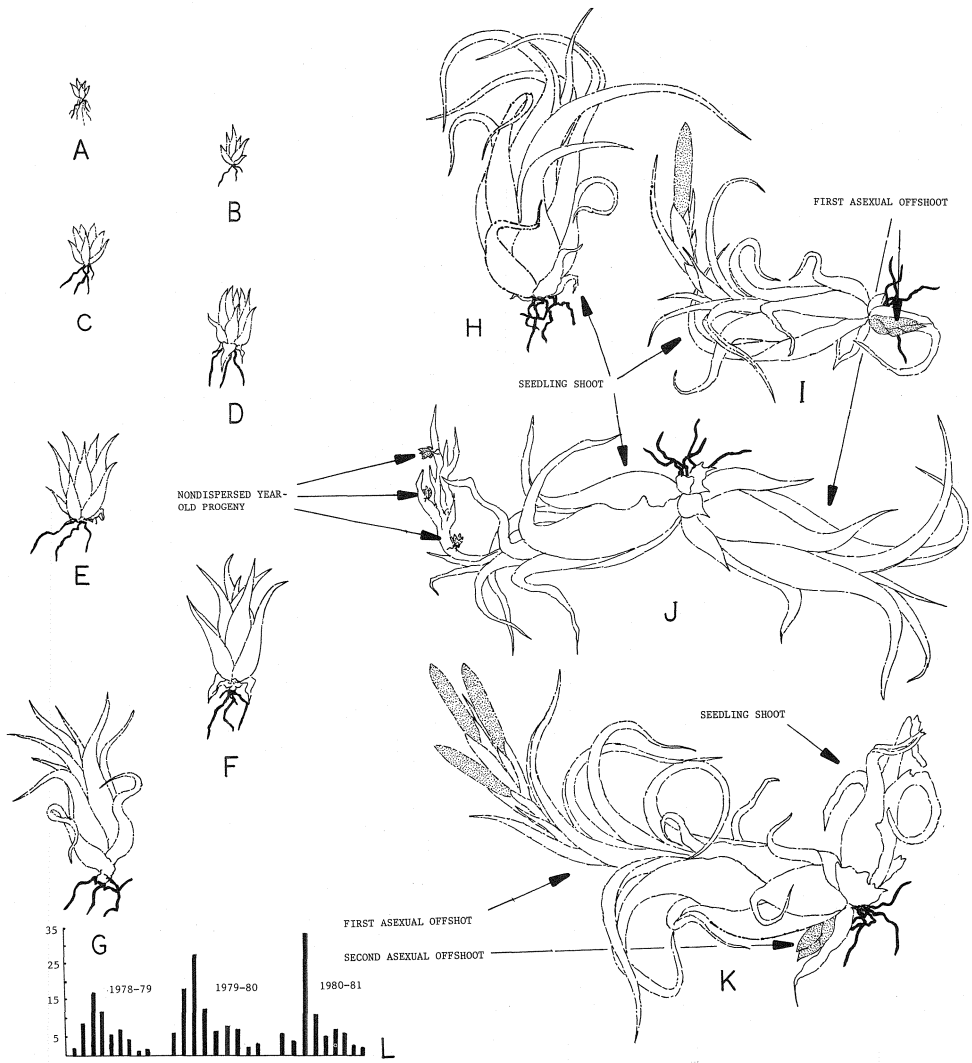

Figure 1. A-H. Age-size categories of juvenile *Tillandsia circinnata*. I. Adult seedling with one capsule and a small first asexual offshoot. J. An asexual adult comprised of a post-fruiting seedling shoot and the first asexual offshoot nearing maturity. K. Asexual adult in fruit generating a second generation asexual offshoot. L. Composite age-size profiles of *T. circinnata* on cypress in 1978-79, 1979-80 and 1980-81. Both seedling adults and asexual adults are pooled in the ninth category.

TABLE 1. Colonies of *Tillandsia circinnata* on *Taxodium ascendens* sampled in winter 1978-79.

Age-size category (mm)	Host number															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Mean ± S.E.
A 0-3	1	0	2	0	0	0	1	2	1	1	13	2	4	2	0	1.9 ± 0.9
B 4-5	21	6	38	16	2	2	1	0	0	0	5	11	18	4	3	8.5 ± 2.8
C 6-10	13	18	8	29	8	9	29	3	3	2	16	31	69	11	10	17.3 ± 4.4
D 11-15	7	22	1	6	4	7	24	43	8	3	11	7	22	13	3	12.1 ± 2.9
E 16-20	7	7	0	11	2	5	16	5	1	4	8	9	9	7	2	6.2 ± 1.1
F 21-30	6	12	1	7	4	15	10	3	3	3	17	8	7	10	2	7.2 ± 1.2
G 31-50	7	8	4	7	6	5	1	3	2	2	11	5	5	4	0	4.7 ± 0.7
H 50+	3	3	3	3	2	2	0	1	1	0	1	0	0	0	0	1.3 ± 0.3
Adults (total)	3	2	1	1	5	2	1	0	0	0	3	4	1	2	1	1.7 ± 0.4
Juveniles (total)	65	76	57	79	28	45	82	60	19	15	82	73	134	51	20	59.1 ± 8.1
Epiphytes (total)	68	78	58	80	33	47	83	60	19	15	85	77	135	53	21	60.8 ± 8.2
Host age (years)	–	89	170	85	113	160	–	250	95	–	106	–	85	100	–	

H) in order the establish an approximate age profile for juveniles on each host (Figure 1). First-year seedlings (category A -- products of seed shed the previous spring) are recognizable by their size, light green color and persistent seed coma hairs. Older individuals are not so reliably identified by specific age (see discussion). In 1979-80 and 1980-81, adults were divided into those fruiting for the first time (seedling adults) and those which had ripened seed at least once before and consisted of one or more spent rosettes and their offshoots (asexual adults). Some of the latter were fruiting. Since post-fruiting material eventually falls away, one cannot determine how many seasons an older asexual specimen has borne capsules. A detailed description of the life history of *T. circinnata* is available elsewhere (Benzing & Davidson, 1979).

In those cases where the trunk was solid, a section of wood taken at about breast height was dated. Growth rings were usually distinguishable, but in a few cases involving very old or slow-growing individuals, some annual xylem increments may have been combined, and these individuals were dated somewhat conservatively.

RESULTS AND DISCUSSION

Plants secured to fallen twigs and detached bark fragments were lying beneath many supports. Unable to tolerate continuous contact with moist soil, these individuals die within a few months. Occasional (1-4) dead or moribund epiphytes -- apparent victims of drought, frost or disease -- were encountered on most trees. Both juveniles and adults were among these casualties, but more specific age-size determinations of dead plants could not be made. Evidence of predation (leaf damage) among living specimens was negligible.

Variance within age-size classes was too great (Tables 1-3) to allow statistical analyses of relationships among individual crown colonies or collection years. Nevertheless, some useful observations and deductions can be gleaned from the data. Juveniles far exceeded adults on all 35 hosts sampled. Average numbers of individuals within crowns varied from year to year, quite likely reflecting what appeared to be local differences in epiphyte desity within the sampled area. Proportional representations among age-size classes, however, remained fairly similar in all of the three winter seasons (Figure 1-L). Categories A (first-year seedlings) and H (subadults) each usually contained many fewer individuals than any other juvenile age-size group. When numerous (at least 10 per host), most one-year-olds were clustered within about a meter of an adult which had fruited the previous season.

The presence of one or more fruiting specimens on a host in one season did not guarantee the occurrence of one-year-old seedlings there the next, nor were cypress crowns consistently denied new recruits in barren years (Tables 1-3). During the 1979-80 and 1980-81 seasons, 99 of 116 new seed products on 20 trees could have originated from one or more maternal parents anchored in the same crowns. Those 17 other seedlings were "island jumpers" (i.e., fugitives), having arrived on their hosts from other supports. Two crowns harboring fruiting material either in 1978 or 1979 recruited no progeny from those parents, while other supports with the same history bore 1-36 one-year-old seedlings the following season. Crowns that hosted no seed sources the year before supported 0-5 first-year seedlings when sampled. Seed source size no doubt varied among fruitful crowns and had a great influence on these recruitment patterns. Unfortunately, capsules fall away from spent inflorescences too quickly after dehiscence to permit winter

TABLE 2. Colonies of *Tillandsia circinnata* on *Taxodium ascendens* sampled in winter 1979-80.

Age-size category (mm)	Host number 1	2	3	4	5	6	7	8	9	10	Mean ± S.E.
A 0-3	3	4*	2	0*	0	36*	1	5	5	0	5.6 ± 3.4
B 4-5	16	32	5	18	2	3	18	7	8	72	18.1 ± 6.7
C 6-10	29	25	10	43	21	36	15	35	21	43	27.8 ± 3.6
D 11-15	10	14	4	12	8	3	12	21	34	13	13.1 ± 2.8
E 16-20	7	3	5	4	3	2	5	7	22	7	6.5 ± 1.8
F 21-30	7	3	5	7	9	6	9	10	18	8	8.2 ± 1.3
G 31-50	9	3	7	7	5	7	4	13	15	3	7.3 ± 1.3
H 50+	1	3	1	4	0	4	4	2	0	0	2.1 ± 0.4
Nonfruiting adults	1	3	0	1	0	4	4	2	0	0	1.5 ± 0.5
Fruiting adults**	2	2	2	1	1	0	0	4	2	1	1.5 ± 0.4
Total juveniles	82	87	39	92	48	94	66	102	125	149	83.4 ± 12.6
Total adults	3	5	2	2	1	4	4	6	2	1	3.0 ± 0.5
Total epiphytes	85	92	41	97	49	98	70	108	127	150	91.7 ± 10.5
Host age (years)	–	75	49	117	–	67	131	65	140	160	

* Tree bore one or more fruiting epiphytes the year previous to census.
** Includes both seedling adults and asexual adults in fruit.

counts to be made 8-10 months later.

Class B juveniles (mostly second-season young, but certainly some slow-growing third-year seedlings too), like representatives of class A, tended to be few and aggregated on a small minority of hosts, but I could not reliably determine which of these were the issue of same-crown mothers (i.e., autogenetic in origin). Clustering had diminished considerably by the time specimens qualified for inclusion in category C. Here larger numbers and more even dispersions of samples within hosting crowns probably reflected a coalescence of several cohorts caused by unequal rates of seedling growth. Differences in leaf shapes and thickness, also a moderately reliable index of this epiphyte's age (Benzing, 1978b), suggest that category C encompasses members of at least three cohorts and probably weaker-growing elements of se-

veral more. Reduced sample numbers and further reductions in clustering through categories D-H probably reflect increased rates of growth (log phase) through later juvenile stages and a steady attrition of established plants. Category C's consistent numerical superiority could, of course, reflect one or more unusually heavy recruitments sometime between 1970-75. This second interpretation seems less likely, however, since large crops of first year seedlings have never been in evidence at the sample site over the past 10 years, nor have I ever noted seasonal variations in epiphyte fruitfulness during numerous visits to that region.

Each of the 20 supports examined in 1979-80 and 1980-81 to determine the reproductive status of their resident adult bromeliads harbored an

TABLE 3. Colonies of *Tillandsia circinnata* on *Taxodium ascendens* sampled in winter 1980-81.

Age-size category (mm)	Host number										
	1	2	3	4	5	6	7	8	9	10	Mean ± S.E.
A 0-3	2*	1*	24*	28*	1	4*	0*	0	0	0	6.0 ± 3.4
B 4-5	3	3	3	15	0	12	3	3	0	1	4.3 ± 1.6
C 6-10	46	40	58	25	75	34	12	46	12	1	34.9 ± 7.2
D 11-15	5	21	12	6	24	11	13	16	2	1	11.1 ± 2.5
E 16-20	5	8	3	9	7	2	9	3	5	0	5.1 ± 1.0
F 21-30	6	16	6	2	10	5	8	12	4	2	7.1 ± 1.4
G 31-50	5	11	0	6	5	6	14	6	7	1	6.1 ± 1.3
H 50+	6	1	2	3	3	3	4	3	2	0	2.7 ± 0.5
Nonfruiting adults	1	2	1	3	2	2	1	1	0	1	1.4 ± 0.3
Fruiting adults**	2	1	0	3	1	0	0	3	1	0	1.1 ± 0.4
Total juveniles	78	101	108	94	125	77	63	89	32	6	77.3 ± 11.3
Total adults	3	3	1	6	3	2	1	4	1	1	2.5 ± 0.5
Total epiphytes	81	104	109	100	128	79	64	93	33	7	79.8 ± 11.6
Host age (years)	155	92	–	125	173	129	200+	70	38	35	

* Tree bore one or more fruiting epiphytes the year previous to census.
** Includes both seedling adults and asexual adults in fruit.

average of 2.8 mature individuals including 1.3 in fruit (Tables 2, 3). Fourteen of the 26 specimens bearing capsules were reproducing for the first time. The remaining 12 supported capsules on one or more asexual offshoots, indicating that their present crop had been preceded by at least one other. Apparently, mortality rates of *T. circinnata* remain substantial through the later portions of its life cycle. Were this not so, many fewer fruiting seedlings would have been counted among the adults. In 1980-81, trees bore 11 fruiting individuals ripening a total of 15 capsules or about 1,500 seeds (based on previous calculations -- Benzing & Davidson, 1979). Should these figures be representative and each crown produce about 150 seeds annually, one conclusion is unavoidable -- few of this epiphyte's propagules survive even a first season. Postgermination survivorship seems to conform most closely to a Deevey-Type II life table curve, probably in large part because disturbance is a major cause of death subsequent to establishment. *Tillandsia* seeds appear to impact and adhere to cypress bark without regard to its age. Except where a bromeliad's weight promotes early detachment, its degree of maturity will have no influence on when a supporting twig or bark fragment falls to the ground.

Several additional tentative deductions about the reproductive biology of *T. circinnata* can be drawn from these observations. If the 1978-81 seasons were typical, its reproductive activity in the sampled forest is characterized by uneven and rather modest overall recruitment successes involving few survivors relative to the size of the parenting colonies. Almost certainly, however, this epiphyte recruits new genets more regularly than many plants inhabiting xeric environments -- e.g., some other epiphytes (McWilliams, 1974) and desert terrestrials, at least a few of which parent seedlings less than one year in 10 (Turner *et al.*, 1969; Jordan & Nobel, 1979). Although cypress crowns in southern Florida are also quite arid, daily convectional summer rainstorms provide sufficient moisture for establishment of an air plant (Benzing, 1978b). Seeds of *T. circinnata* germinate if moistened as little as a few hours every few days; in fact, prolonged contact with a moist substratum is lethal to its seedlings.

Tillandsia circinnata matures very slowly in southern Florida, requiring at least 8-10 years to disperse a first crop of seeds. Whatever disadvantage this characteristic may pose elsewhere, mature populations here (as judged by the symmetry of their age-size distributions) may develop on a dwarfed cypress early enough to use that host as a point of departure to colonize other "islands" over intervals that must, in extreme cases, measure hundreds of years. Absence of correlations among numbers of juveniles, adults and total epiphytes in crowns and ages of those supports (r values in all cases lacked significance at the 0.05 level) further suggest that colony size and age composition stabilize on these slow-growing, long-lived trees in a surprisingly short time. The expansion and maintenance of *T. circinnata* crown colonies, once initiated from previously colonized supports, seems to be heavily dependent on autogenetic accretion, although allogenetic recruitment continues thereafter. Contagious recruitment has also been reported for other wind-dispersed epiphytes (Madison, 1979).

Contrary to the findings here, one might expect colony size to expand steadily over much of the life of a host as epiphytic growth tracks expansion of the tree crown. This may, in fact, often be the case, but dwarfed cypress crowns probably reach maximum dimensions early in life -- perhaps earlier than many other trees with equal longevity, even *Taxodium* on more equable sites. Whether heavily infested crowns of the oldest trees at the sample site are saturated with epiphytes is unclear. Conceivably, only a small portion of what

appears to be uniform bark surface in a dwarfed cypress crown is suitable for *T. circinnata* colonization. Perhaps disturbance of the type described elsewhere (Benzing, 1981) or some unidentified density-dependent constraint holds colony size well below what seems to be a crown's carrying capacity.

Low diversity, high density, dwarfed cypress forests such as this one are well suited for epiphyte success, a fact borne out by the abundance of resident canopy-dwelling bromeliads and orchids. Several factors probably account for this amenability aside from the extended longevity of cypress when compared to many other trees and the rough texture and relatively low turnover rate of its bark surfaces. *Taxodium* crowns are unusually transparent, even when bearing mature foliage. Thus irradiation and air turbulence within the canopy are maximized -- two factors of undeniable importance to heliophilic, wind-dispersed epiphytes such as *T. circinnata*. Equally important may be the spacing of accessible host islands. Cypress crowns at the study site often touch or are separated by just a few meters. Such close juxtapositions surely encourage the observed early colonization of emerging hosts and probably assure steady allogenetic inputs as their crown colonies mature. Colonies of epiphytes with similar fecundity, and pollen and seed vagility, residing in more species-rich (i.e., patchy) forests, should be more inbred and their regenerative capacity taxed to greater degrees. At what point spacing reaches an intolerable interval must vary with the species and with various characteristics of the supporting canopy such as its transparency, floristic composition and stability. Whatever the study subject's tolerances vis-à-vis cypress, the margin for success appears to be ample at the sample site.

Much more data of the type collected in 1980-81 for this and other less amenable sites must be processed in order to establish the limits of this bromeliad's regenerative power and to explain its absence from some southern Florida forests with cypress components. Should this be accomplished, the efficacy of one epiphyte's peculiar patterns of resource allocation and reproduction can be more fully appreciated.

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