Selbyana 5(1): 95-106. 1978.

GERMINATION AND EARLY ESTABLISHMENT OF *TILLANDSIA CIRCINNATA* SCHLECHT. (BROMELIACEAE) ON SOME OF ITS HOSTS AND OTHER SUPPORTS IN SOUTHERN FLORIDA

*David H. Benzing**

INTRODUCTION

Epiphytes cast significant shade and cause limb breakage when they are present in great numbers in the crowns of host trees. These considerations aside, the classical notion persists among most botanists that vascular epiphytes are basically commensals with nonspecific host preferences and little negative impact on their supports. However, accounts have been accumulating at an increasing rate which suggest that some trees may, in fact, be adversely affected in a more systemic manner by their epiphytic associates (Cook, 1926; Went, 1940; Ruinen, 1953; Furman, 1959; Johansson, 1974, 1977; Benzing, Seemann & Renfrow, 1978). The authors of these reports postulate that, under some circumstances, heavily infested hosts may be forced into states of nutritional stress by the activities of their epiphytes. Conventional parasitism, epiparasitism and, most recently (Benzing & Seemann, 1978), stress-inducing degrees of nutritional piracy have been suggested as operative in the supposedly commensalistic epiphyte-host relationship. Attempts to describe the role epiphytes play in tropical forest ecology in a context of parasitism or within that of the biologically distinct but functionally equivalent phenomenon of nutritional piracy are motivated by the increasing realization that many trees harboring orchids or bromeliads experience reduced vigor as their infestations grow heavier.

Whatever effects an epiphyte may have on its support, the epiphyte-host relationship is more intimate than previously realized. It can also be fairly specific. Many bromeliads and orchids do exhibit distinct host preferences, indicating that some woody species are more suitable as supports for these plants than others. Furthermore, certain parts of individual host trees may be more hospitable to specific epiphytes than others. This report describes the methodology and the preliminary findings of a long-term study designed to assess one of the more complex aspects of the epiphyte-host relationship, namely, those factors which influence host selection and the distribution of epiphytes within the crowns of individual trees. The specific subjects of this investigation are the bromeliad *Tillandsia circinnata* Schlecht. and a number of the woody plants in their southern Florida habitats.

MATERIALS AND METHODS

One experiment was completed and two more were initiated during the first phase of this investigation. All three are pilot in scope and are designed to proscribe the magnitude of future efforts that will be necessary to provide more definitive information on the epiphyte-host relationship. Each was carried out using seeds or seedlings obtained from *T. circinnata* specimens which had been collected in the Big Cypress Swamp of southern Florida in 1971-1974 and maintained thereafter in the Oberlin College greenhouse. These plants grow well under artificial culture and routinely flower and ripen seed with the same phenology expressed by their counterparts in Florida. After four weeks of receiving two 2-hour episodes of tapwater mist each day, their seeds regularly germinate at 85-90% on strips of cedar lath.

---

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

Experiment 1. Seeds were collected from the ripe capsules of greenhouse plants in the late February to early March 1977. The numerous coma hairs on individual seeds were twisted together in a manner which permitted each seed to be separated from others and stored by securely affixing its appendages to the inside of a file folder with a small drop of Elmer's Glue-all. Between March 28, and April 1, 1977, these seeds in groups of 4 were glued in like fashion to the bark of various host trees and other plants in 4 localities in the Ding Darling Federal Wildlife Preserve on Sanibel Island off the southwest coast of Florida. One site in a state forest preserve near Copeland, Florida was also employed in this phase of the investigation. (Previous experiments in the greenhouse had demonstrated that seeds attached to bark surfaces with this glue remain securely anchored for at least one year.)

Seed test patterns on each tree consisted of 25 groups of 4 seeds (100 seeds). In most instances, test patterns were located on the main trunk of the support — or on a large limb, if it was a shrub — between 0.5 and 2.0 m above ground level (Figure 1). Where a particular known host was common, a number of patterns were placed on the same number of individuals of that taxon. Within a species, test trees were chosen, when possible, to represent various degrees of light exposure. Fewer specimens of nonhosts were tested since the supply of seeds was limited.

Figure 1. Several groups of four *Tillandsia circinnata* seeds within a test pattern of 100 recently glued to the bark of *Taxodium ascendens* near Copeland, Florida. Each group of seeds is indicated by an arrow.

Figure 2. One-year-old *Tillandsia circinnata* seedlings growing in a test pattern on *Taxodium ascendens* at the Copeland site. Seedlings are about 5 mm long. Large arrows indicate points where the coma hairs are glued to the tree. Smaller arrows indicate the seedlings.

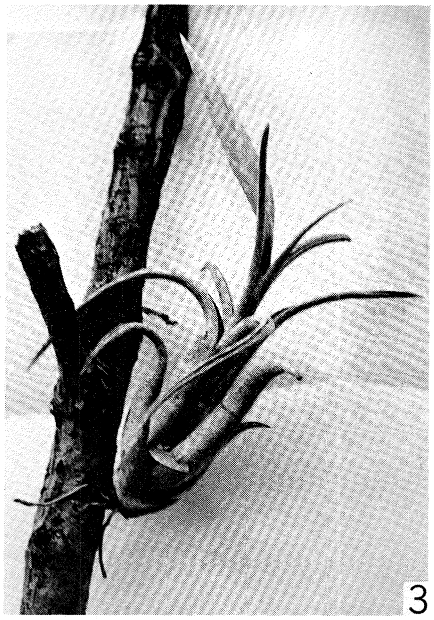

3

Figure 3. Adult *Tillandsia circinnata* about to flower.

Six hundred seeds were placed on adult *Forestiera segregata* (Jacq.) Krug & Urban and *Bursera simaruba* (L.) Sarg. specimens in a coastal strand shrub community on Sanibel dominated by these two hosts, as well as by *Myrsine guianensis* (Aubl.) Kuntze. On this site, *Tillandsia balbisiana* Schultes, *T. circinnata*, *T. flexuosa* Sw., *T. recurvata* L. and *T. usneoides* L. occur sparingly, while *T. utriculata* L. is abundant. Here, *T. circinnata* grows on *Forestiera* and *Myrsine* but not on *Bursera.*

Thirteen hundred seeds were placed on *Quercus virginiana* Mill. var. *geminata* Sarg., *Bursera simaruba, Forestiera segregata* and *Myrsine guianensis* in an upland hardwood forest dominated by these 4 species as well as by *Psidium guajava* L. and several palms. All of the bromeliads in the first site were present here also, with *T. circinnata* growing on all tested supports except *Bursera.*

Thirteen patterns were established on *Avicennia germinans* (L.), *Ficus aurea* Nutt. *Rhizophora mangle* L. and *Conocarpus erecta* L. in a mixed mangrove swamp forest fringing the mainland side of the island. Bromeliads are not abundant here although occasional specimens of *T. utriculata, T. balbisiana* and *T. circinnata* are encountered on *Avicennia, Conocarpus* and *Rhizophora.*

The fourth site on Sanibel is a mangrove forest and nearby Indian shell mound along Tarpon Road on the mainland side of the island. Two thousand seeds were affixed to *Avicennia, Bursera, Conocarpus, Ficus* and *Rhizophora. Tillandsia balbisiana* and *T. recurvata* occur here on all supports tested except *Bursera* and *Ficus. Tillandsia utriculata* is found on all these except *Ficus.* Only one adult specimen of *T. circinnata* was encountered in the area and it was growing on the trunk of a mature *Conocarpus.*

The Copeland site consists of a stand of mature *Taxodium ascendens* Brogn. located along the margin of a small bayhead broadleaf forest about 0.5 km north of the ranger station. These cypress trees host *T. balbisiana, T. circinnata* and *T. fasciculata* Sw. Nine specimens were used as supports for test patterns.

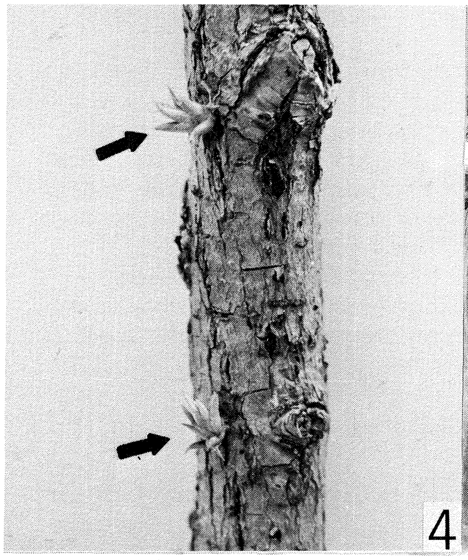
Seed success in all these sites was recorded one year later in late March 1978.

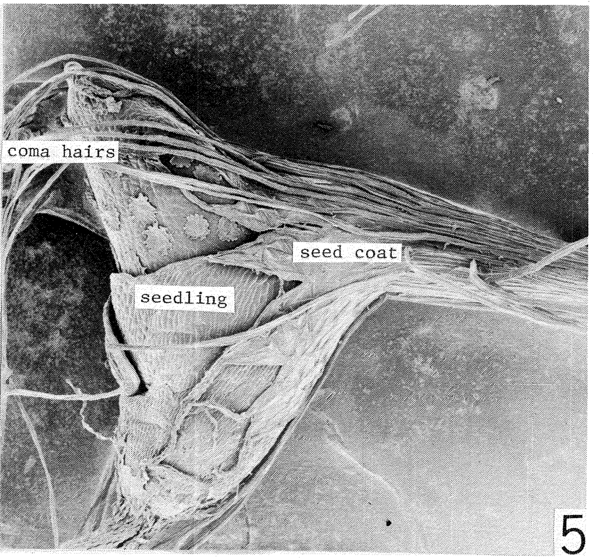
Experiment 2. Seedlings from seeds of cultivated specimens grown upon strips of cedar lath on a greenhouse misting bench for 3 or 9 months were employed in a second experiment. These were individually anchored by their coma hairs to most of the same trees that were later used for the seed germination study in the upland oak site and the two mangrove forests on Sanibel Island. Two or three vertical rows of 10 seedlings each were placed on each support within 0.5 m of the points where seed test patterns were to be located the following spring. Within a vertical series, each seedling was spaced 10-20 cm from its nearest neighbors. Four hundred and seventy 3-month-old seedlings were set out in the upland live oak community and one of the two mangrove forest sites in July 1976. An additional 430 nine-month-old seedlings were placed in the mangrove-Indian mound community in early January 1977. Survivorship was recorded 5 or 6 times at intervals of 2.5-6 months.

Experiment 3. Freshly cut limbs, 7-15 cm thick, of two common hosts (*Taxodium ascendens* and *Conocarpus erecta*), one occasional support (*Rhizophora mangle*) and one nonhost for *T. circinnata* (*Bursera simaruba*) were placed under a series of misting nozzles on a greenhouse bench exposed to full sun in July 1977. Timers controlling single nozzles were set to provide 2-hour episodes of tapwater mist once at mid-afternoon every 1, 2, 4 or 6 days. No additional moisture was provided. As in the first experiment, test patterns of 100 seeds were placed on a limb of each tree under each misting regimen. The experiment continued for 14 weeks until a malfunction in the misting apparatus forced termination.

THE RESULTS AND THEIR INTERPRETATION

One year after they were attached to various trees in 4 habitats on Sanibel Island and in a single location on the mainland, only 185 of 6000 seeds were represented by surviving seedlings (Table 1; Figure 2). Seed success was limited to 6 of 51 tests patterns on as many trees on Sanibel and to 8 of 9 groups of seeds on that number of cypress hosts at the Copeland site. At least one successful germination took place in all Sanibel sites except the mixed mangrove forest; the average number of successful seeds among individual test patterns where at least one seed germinated was 12.5 (Table 1). In


4



5

Figure 4. A scanning electron micrograph of a six-week-old *Tillandsia balbisiana* seedling minus some of its associated coma hairs × 85.

Figure 5. Two-year-old *Tillandsia circinnata* seedings. Seedlings are about 10 mm long.

the mainland cypress stand, the average was 12.2. At least one seed succeeded on all supports tested except *Bursera*, *Ficus*, *Quercus* and *Rhizophora*.

TABLE I

The fate of *Tillandsia circinnata* seeds after one year of attachment to the bark of various supports on Sanibel Island and near Copeland, Florida.

Habitat	Support	No. Patterns exposed	No. Patterns shaded	No. Seeds tested	No. Seedlings produced
Sanibel upland live oak forest	*Quercus virginiana*	0	5	500	0
	Forestiera segregata	0	3	300	0
	Bursera simaruba	0	1	100	0
	Myrsine guianensis	2	2	400	6 (on 2 exposed trunks)
Sanibel mixed mangrove forest	*Avicennia germinans*	0	3	300	0
	Conocarpus erecta	0	4	400	0
	Ficus aurea	0	1	100	0
	Rhizophora mangle	0	5	500	0
Sanibel mixed mangrove-shell mound community	*Avicennia germinans*	4	2	600	57 (on 2 exposed trunks)
	Bursera simaruba	2	1	300	0
	Conocarpus erecta	3	2	500	11 (on 1 exposed trunk)
	Ficus aurea	0	1	100	0
	Rhizophora mangle	0	5	500	0
Sanibel coastal strand shrub community	*Bursera simaruba*	1	0	100	0
	Forestiera segregata	4	0	400	1
Copeland open cypress forest	*Taxodium ascendens*	9	0	900	110 (on 8 trunks)

Given the demonstrated potential for high rates of germination under greenhouse culture, seed performance in the field was unexpectedly poor. Neither bark instability nor the dislodgment of the seeds by any other means affected their fate on any support tested. All but a few remained in place one year later. In all instances, coma hairs and attached seeds were matted but still visible on adjacent bark surfaces, evidence that water had passed over all 60 test patterns at least once during the year. Many unsuccessful patterns had been moistened often enough to permit colonies of green algae to become established in the hairs. Thus none were in complete rain shadows and many were sufficiently exposed to be subjected to frequent wettings.

The only ecological parameter that is fairly uniform among the test patterns exhibiting some degree of success was exposure. A location on a tree or shrub positioned well enough removed from nearby vegetation or within a crown sparse enough to allow direct sunlight to fall on the test pattern for several hours each day was determined to be "exposed" (Table 1). A "shaded" pattern was deemed to be one situated on a tree with a dense crown or one so overgrown by neighboring vegetation that no direct light fell on the seeds during most of the day. Crude estimates of overall habitat and individual site exposures must suffice for the moment, since instantaneous readings with a conventional two-dimensional light sensor are of little value for measuring the amount of photosythetically active radiation available for a plant at a point located in a forest or deep within an individual tree crown. Although some shade was cast on all 60 test sites, no seed located on a very dark microsite produced a one-year-old seedling (Table 1). Exposure itself was not decisive, however. For example, only one of 600 seeds produced a one-year-old seedling in the most exposed community of the five surveyed, the island strand shrub stand. Furthermore, most of these seeds failed on *Forestiera*, a shrub which even supports a few *T. circinnata* adults on the specimens employed as test supports.

Seedlings anchored to a majority of the same trees used in three of the four sites for germination tests on Sanibel fared much better than the adjacent groups of seeds (Figure 6, 7). Of the 470 three-month-old seedlings set out, 145 were viable on 23 of 24 trees 21 months later. Among the group of 430 nine-month-old seedlings, 109 were growing on 13 of 20 trees 16 months later. Growth was uneven among and within the test groups of 10 seedlings but a nondestructive analysis of their vigor was not practical since the most robust individuals were only 10-12 mm long exluding the roots (Figure 4). Dead seedlings were occasionally encountered, but much more often all evidence of their former presence (except for the tiny spot of glue) had disappeared by the time an inspection was made. Either detachment by hair breakage or predation was the probable fate of the missing young epiphytes.

Mortality was total on *Ficus aurea* by the time the first observations of the second group of seedlings were carried out in March 1977, but only 20 specimens had been placed on this species. Although not total, the mortality of both three- and nine-month-old seedlings on other supports was greatest during the first one or two inspection intervals. Mortality continued thereafter, but generally at a decreasing rate, i.e., the probability that an individual seedling would survive to the next inspection went up as the experiment progressed.

Percent survivorship among all 900 seedlings tested in March 1978 was highest on *Quercus* (61.0), considerably lower for *Conocarpus* (39.5) and *Myrsine* (36.7), and poorer yet on *Forestiera* (26.0), *Rhizophora* (16.5) and *Avicennia* (12.5). Overall seedling survivorship varied among the three seedling test sites on Sanibel, being highest on locations featuring the most exposed limbs and trunks — though many test plants grew as vigorously on the heavily shaded limbs and trunks as well.

Overall survivorship at 44.6% was greatest in the upland oak forest (Figure 6). Here all test trees harbored at least one survivor after 21 months. Only 6 seeds produced one-year-old seedlings at this location (Table 1).

At the Tarpon Road shell mound mangrove habitat overall seedling survival was 23.7% (Figure 2). Survivorships after 16 months were: *Conocarpus*, 35.0%; *Avicennia*, 16.7%; *Rhizophora*, 14.6%; *Ficus*, 0%. Of a total of 13 individual trees assayed at this location, seedlings survived on only 6. Survivorship was greatest on one *Conocarpus* (22 of 30 seedlings) and a single *Avicennia* specimen (17 of 30 seedlings). These were the same two trees where the bulk of the successful seeds on Sanibel were located. Of the 75 seeds that had produced one year-old seedlings on the island, all but 18 were on this pair of adjacent well-exposed hosts one year later (Table 1).

Seedling mortality was greatest at the mangrove forest site (Figure 6). There, only 16.6% of all seedlings were still alive in March 1978. Success on *Rhizophora*, *Conocarpus* and *Avicennia* was 24.4%, 20.0% and 0% respectively. Survivors were nevertheless well distributed, as living seedlings remained on 11 of 12 trees tested. No seeds succeeded on any of these trees.

Tillandsia circinnata seeds placed on the cut limbs of *Taxodium* under the wettest misting regimens germinated at percentages below some of the test trees located in the field. When misting was frequent, germination on the

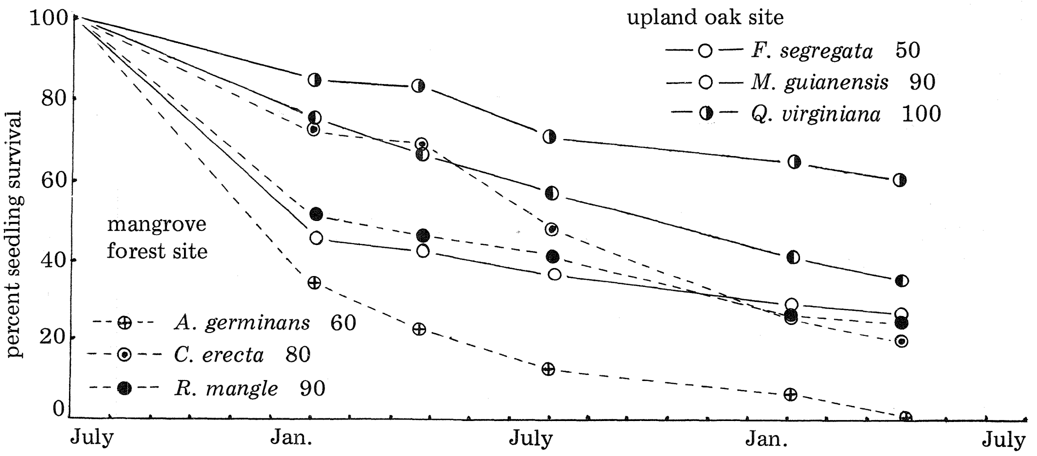


Figure 6. The survivorship of 3-month-old seeds placed on supports in two habitats on Sanibel Island. The number of seedlings placed on a particular kind of support is indicated after the name of that support.

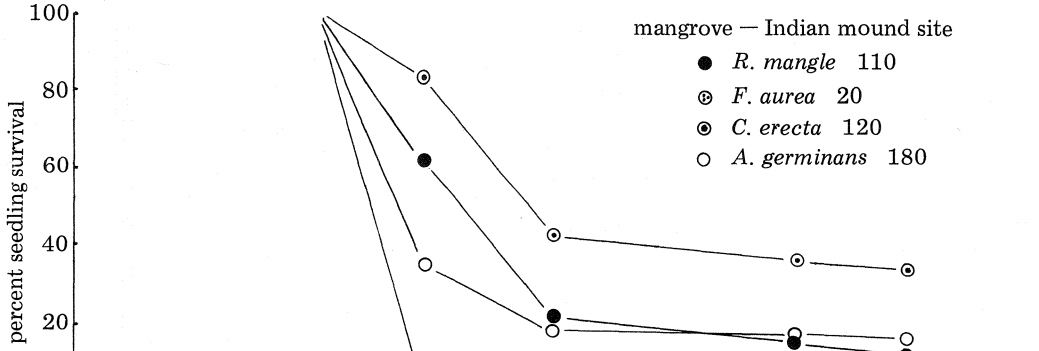


Figure 7. The survivorship of 9-month-old seedlings placed on supports in one habitat on Sanibel Island. The number of seedlings placed on a particular kind of support is indicated after the name of that support.

other three supports was much higher in the greenhouse than in the field. From 6-35% of the seeds placed on each cut limb section of all four supports had produced seedlings 14 weeks later (Table 2). Except for *Rhizophora*, where seed success was fairly uniform under all treatments, germination and survival on the other three supports were greatest under the three wettest culture regimens. Under the driest conditions, germination was best accommodated by *Rhizophora*.

TABLE II

Percent germination of *Tillandsia circinnata* seeds after 14 weeks under various misting regimens while attached to cut limbs of four supports.

Support	Misting regimen			
	one/day	one/2 days	one/4 days	one/6 days
Bursera simaruba	32	35	25	7
Conocarpus erecta	33	17	21	6
Rhizophora mangle	22	24	26	20
Taxodium ascendens	23	21	18	9

Although these results underscore the remarkable capacity of *T. circinnata* to germinate under extremely arid conditions, the figures given above would be somewhat misleading without qualification. While some germinations could still take place under the driest conditions provided, seedling growth was much depressed by severe drought. On all four supports, seedlings watered once every sixth day had achieved only 10-20% of the size of those grown under the two wettest regimens. Those watered every fourth day were somewhat larger but still had accomplished less than half the growth of those misted each or every other day. Seedlings surviving under a particular misting regime were of approximately uniform size on all four kinds of supports. More precise estimates of the vigor of the sample groups were precluded by the close association between the delicate early life stages of *T. circinnata* and its coma hairs and seed coat. Dissection of a 1-2 mm seedling intact from these seed parts for weight determination is simply not practical. An electron micrograph of a similar-sized seedling of *T. balbisiana* minus most of its coma hairs illustrates the problems that would attend any attempt to assess precisely the vigor of very young *Tillandsia* seedlings (Figure 5). In any case, the final size of surviving seedlings on detached limb segments was primarily influenced by the availability of moisture. The type of substratum involved had no obvious effect on vigor.

THEORETICAL CONSIDERATIONS

As inhabitants of unusually stressful environments, vascular epiphytes routinely experience severe exogenous constraints on germination and growth. Life for *T. circinnata*, a high light-demanding xerophytic bromeliad, is tenuous from the start. Like other epiphytes, its life cycle begins with a seed precariously lodged in the crown of a tree against the force of gravity. From germination to death, all parts of the plant are subjected to local ecoclimatic events on their away-from-the-bark exposure and, in addition, on all sides to biological happenings originating from the host. Bark, unlike soil, is only weakly buffered against the drying, heating and cooling effects of the surrounding air mass. Periodic and sometimes prolonged drought and rapid fluctuations in temperature are characteristic in most forest canopies. Mineral nutrients are scarce and available for absorption only when the shoot is wet during and briefly following episodes of rainfall (Benzing, 1973; Benzing & Renfrow, 1974). Allelopathy, perhaps in extreme form, may operate in the forest canopy. Frei and Dodson (1972) have demonstrated that some trees generate phenolic substances in their bark that can inhibit germination on their surfaces of seed of the orchid *Encyclia tampensis* (Lindl.) Small. Epiphytes are potentially more vulnerable to allelopathy than are terrestrial species. Compared to terrestrial sites, dilution, physical absorption and microbial degradation will be less effective in attenuating possible injury from organic chemicals secreted by a host. Epiphytes are periodically bathed in stemflow and throughfall which could easily contain soluble toxins picked up just minutes before from a potential allelopath.

Vascular epiphytes from the drier portions of the epiphytic biotope number among the most stress-tolerant of all higher plants. To survive in their preferred sites, extreme epiphytes rely on an efficient water economy, well-developed holdfast devices and a capacity to scavenge mineral nutrients from very dilute sources. To colonize one host canopy from another, they effectively employ air currents or birds as seed-dispersal agents.

As effective as these plants are in dealing with several kinds of environmental stress, their success is not without limits. While numerous species of trees in many kinds of forests are regularly infested with vascular epiphytes, many others in these and other communities harbor none at all. Since shading, limb breakage, nutritional piracy and possibly parasitism all can adversely affect heavily infested hosts, one can safely assume that selective pressures favoring the development of defenses against heavy epiphyte infestation have existed as long as the epiphytes themselves. These selective forces have probably led to adaptive responses in some cases. Trees that seldom or never harbor epiphytes may, in fact, be benefitting from adaptations (such as allelopathy or others) specifically designed to render their crowns inhospitable to one or more epiphytic species. Of the conceivable possibilities for effective intervention, those designed to interfere with the early stages of an epiphyte's life cycle are most likely to be decisive and easily developed.

Bark stability and texture are primary determinants of host suitability. High rates of exfoliation no doubt preclude the establishment of epiphytes on some woody species even though all other requirements for effective exploitation by these plants may be present. At the other extreme, trees with smooth surfaces, however stable, may fail to serve as hosts simply because the delicate coma hairs on the seeds of *T. circinnata* and its kind encounter too few irregularities to permit attachment. Prolonged anchorage by seed appendages is necessary since this bromeliad and its close relatives remain rootless until the seedling is 4-6 months old. Lacking appendages, the seeds of many other epiphytes are even more dependent on bark irregularities for interception and preliminary attachment to their hosts. The question of whether the high rates of exfoliation or smooth bark textures exist in certain tropical trees expressly for the purpose of shedding epiphytes is currently untestable. Surely the existence of an unstable or smooth bark on many temperate trees growing well beyond the range of any vascular epiphyte points to another raison d'être. Perhaps particular bark patterns featured by temperate and tropical trees alike serve primary purposes which are unrelated to defense.

Most xeric epiphytes have high light demands. Trees with dense canopies may intercept too much sun or rainfall to permit even the most shade-tolerant or drought-resistant epiphyte to become established in their crowns. Most bromeliads require light for germination as well (Smith & Downs, 1974). Trees cast shade which, because of differential absorption by the leaves, can be proportionally enriched in photomorphogenetically active 700-750 μm radiation. Many seeds with light-dependent germination remain dormant when irradiated with energies of this quality (Mayer & Poljakoff-Mayber, 1975). Responses to light quantity and quality can be exclusive. Sufficient photosynthetically active radiation may pass through a canopy to support a positive carbon balance in a particular plant positioned within or below the crown, but its quality may nevertheless inhibit the germination of that species at the same site. Even the most suitable hosts seem to feature inhospitable zones where sun or rain shadows, or possibly the levels of near infrared radiation, are too heavy to allow certain epiphytes to germinate or grow. Whether specific woody species have evolved particular patterns of selective absorbancy primarily to provide advantage in their interactions with parasites, epiphytes or competitors has not been clearly demonstrated up to this time.

"Leakiness" of another sort may be an important determinant of host suitability. True epiphytes without impoundments or connections of any kind to the vascular systems of their hosts are heavily dependent on nutrients contained in stemflow and throughfall. Trees susceptible to mineral loss by leaching will enrich the water passing through their canopies to a greater degree than those that bind their foliar nutrients more tightly. By "tightening" its salt retention mechanisms, a tree would become less hospitable to epiphytes heavily dependent on leachates as nutrient sources. Schlesinger & Marks (1977) have demonstrated that the foliage of *Taxodium distichum* (L.) Richard supporting *T. usneoides* in the southeastern United States can be leached more readily than comparable material from nonhost *Cinnamomum camphora* (L.) Nees & Eberm.

While the inherent capacity of a tree to retain foliar nutrients against leaching may be an important parameter of host suitability over the long term, *T. circinnata* and many similar epiphytes grow so slowly that the mineral nutrients provisioned in their seeds may require little supplementation during the first 6 months or year of the plant's life. However, once these reserves have been expended by the seedling, the quality of the exogenous sources of mineral salts becomes all-important in determining the vigor of the specimen and the magnitude of its reproductive efforts (Benzing & Renfrow, 1971).

CONCLUSIONS

Field observations and the results presented here suggest that *Taxodium ascendens* is superior to all other plants examined as a host for *T. circinnata* in southern Florida. Judging by the numerous specimens encountered on its trunk and major and minor branches in the Big Cypress Swamp, much of the surface of this tree is hospitable to *T. circinnata* and many other epiphytes. Many of the reasons for these dense infestations are apparent. Cypress crowns are leafless from November to March when insolation is lowest. When fully leafed out, their canopies are still relatively transparent. *Taxodium* bark is irregular in texture but apparently stable. Old bark is lichen-covered and very absorbent. Drops of moisture placed on dry bark fragments are immediately absorbed in sponge-like fashion. Seeds positioned against its bark will remain moist longer after a rainstorm than those lodged against less absorbent surfaces. Of course, the superior success of *T. circinnata* seeds on *Taxodium* at Copeland witnessed last year may have been independent of the substratum and primarily attributable to better growing conditions on the mainland during the 1977-78 season relative to those on Sanibel.

Too few seeds germinated on Sanibel to make judgements about the suitability of the other supports as hosts for *T. circinnata. Ficus aurea* does not harbor bromeliads in southern Florida and the few seedlings placed on it died quickly. *Bursera* was not tested for seedling performance but it does occasionally support heavy infestations of *T. utriculata* in Florida, mostly on smaller branches in the crown. The extensive root system of this largest of Florida bromeliads may be able to encircle completely a narrow supporting axis before the seedling is sloughed off with a bark fragment. On the trunk and main limbs, bark fragments exfoliate rapidly but not fast enough to slough off *T. circinnata* seeds in one year. *Ficus*, much more so than *Bursera*, has a dense evergreen canopy and a very smooth stable bark. Considering the failure of all seeds and seedlings placed on the trunk of this tree, the possibility of allelopathy as an additional barrier to its exploitation by *T. circinnata* and other epiphytes cannot be discounted. The germination and early survival of *T. circinnata* seeds on cut limbs of *Bursera* in the greenhouse cannot be cited as proof that this tree is not allelopathic. Toxins may originate from the leaves or, if secreted by the bark, may quickly disappear when the limb is detached.

In spite of the incomplete nature of these preliminary data, several tentative statements about the population dynamics of *T. circinnata* can be made. Results for the 1977-78 year indicate that its germination requirements are more exacting than those needed for subsequent seedling growth. Relatively few seeds shed by this species, perhaps less than 10-15%, germinate and survive the first year of life even when anchored on the surfaces of its most suitable hosts. Considering that few of the seeds will lodge on trees of any type, the probability that the individual propagule will succeed in generating a reproductive adult is remote. Compounding the difficulties of recruiting adults is a pattern of very slow maturation — reproductive size is attained only after 5-8 years (Figure 3). Once the seedling has flowered, asexual offshoots, produced each time a monocarpic parent shoot flowers, require an additional two or more years to reach sexual maturity. A shoot in its single sexual effort produces an average of 2-3 capsules, each containing an average of about 80 seeds (unpublished information). Given its sluggish growth, parsimonious and infrequent seed production, and low seed and early seedling stage success, the recruitment of mature individuals in southern Florida must be very slow indeed. Stabilized populations apparently maintain themselves primarily by asexual propagation and the life of the matured seedling may be perpetuated through many generations of offshoots. Following catastrophic perturbations of their habitats, re-establishment of dense populations of adults must require several decades. To persist in natural preserves, particularly in small ones with no nearby seed sources, this epiphyte, more than species with greater regenerative powers, will have to be carefully protected against collectors and natural disturbances.

Perhaps most importantly, these preliminary findings underscore the need for large numbers of samples if statistically significant results are to be obtained for life table or host preference studies of this and probably most other epiphytes. To that end, in late March 1978, an additional 16,000 seeds were placed in test patterns of 48 on a much larger number of woody plants. Future analyses will also include integrated measurements of salt retention, canopy transparency and various physical and chemical characteristics of these and additional woody species. After several years of seed performance are recorded, local weather data will be examined to determine the effects of various ecoclimatic factors on the establishment of this epiphyte on its hosts in southern Florida.

ACKNOWLEDGMENT

Funds from the National Science Foundation granted to the author were used to support this effort.

LITERATURE CITED

Benzing, D. H. 1973. The monocotyledons: their evolution and comparative biology. I. Mineral nutrition and related phenomena in Bromeliaceae and Orchidaceae. Quart. Rev. of Biol. 48 (2): 277-290.

Benzing, D. H. & A. Renfrow 1971. The biology of the atmospheric bromeliad *Tillandsia circinnata* Schlecht. I. The nutrient status of populations in South Florida. Amer. J. Bot. 58 (9): 867-873.

________________ 1974. The mineral nutrition of Bromeliaceae. Bot. Gaz. (Crawfordsville) 135: 281-288.

Benzing, D. H. & J. Seemann 1978. Nutritional piracy and host decline: a new perspective on the epiphyte-host relationship. Selbyana 2(2-3): 133-148.

Benzing, D. H., J. Seemann & A. Renfrow 1978. The foliar epidermis in Tillandsioideae (Bromeliaceae) and its role in habitat selection. Amer. J. Bot. 65 (3): 359-365.

Cook, M. T. 1926. Epiphytic orchids, a serious pest on citrus trees. J. Dept. Agric. Puerto Rico 10 (2): 5-9.

Frei, Sister John Karen & C. H. Dodson 1972. The chemical effect of certain bark substrates on the germination and early growth of epiphytic orchids. Bull. Torrey Bot. Club 99 (6): 301-307.

Furman, T. E. 1959. Structural connections between epiphytes and host plants. Proc. 9th Int. Bot. Cong. 2: 127, Toronto.

Johansson, D. 1974. Ecology of vascular epiphytes in West African rain forest. Acta Phytogeogr. Suecica 59. Uppsala.

________ 1977. Epiphytic orchids as parasites of their host trees. Amer. Orchid Soc. Bull. 46(8): 703-707.

Mayer, A. M. & A. Poljakoff-Mayber 1975. Germination of Seeds. Pergamon Press, New York.

Ruinen, J. 1953. A second view on epiphytism. Annales Bogoriensis 1 (2): 101-157.

Schlesinger, W. H. & P. L. Marks 1977. Mineral cycling and the niche of Spanish moss, *Tillandsia usneoides* L. Amer. J. Bot. 64 (10): 1254-1262.

Smith, L. B. & R. J. Downs 1974. Pitcairnioideae (Bromeliaceae). Hafner Press, New York.

Went, F. W. 1940. Soziologie der Epiphyten eines tropischen Urwaldes. Ann. Gard. Bot. Buitenzorg 50: 1-98.