EFFECTS OF FIRE ON BROMELIADS IN SUBTROPICAL HAMMOCKS OF EVERGLADES NATIONAL PARK, FLORIDA

KEVIN ROBERTSON AND WILLIAM J. PLATT

Department of Botany, Louisiana State University,
Baton Rouge, Louisiana U.S.A. 70803

ABSTRACT. Responses of five species of subcanopy bromeliads (*Tillandsia balbisiana, T. fasciculata, T. setacea, T. utriculata,* and *T. valenzuelana*) to large-scale disruption by naturally-occurring, low-intensity fire were inferred from comparisons of populations in burned and unburned subtropical hardwood hammocks one year after fire on Long Pine Key in Everglades National Park, Florida. In burned hammocks, the soil humus was consumed. Many trees were defoliated and/or killed, which opened the canopy. Comparisons of epiphyte populations in burned and unburned hammocks, which were very similar in pre-fire characteristics, indicate that fire had few direct effects on these species. Nonetheless, by altering the environment, fire changed the basic demography (increased mortality, growth, and flowering) of bromeliad populations. Field study of epiphyte seeds on different species of host trees also indicated that short-term adherence on trunks differed between two species (*T. fasciculata* and *T. utriculata*), and between burned and unburned hammocks. These results indicate that large-scale disturbances of the overstory can result in rapid changes in population dynamics of epiphytes. Such changes can potentially influence long-term composition and dynamics of populations of subcanopy epiphytes.

Efectos de incendio sobre bromelias de los bosques subtropicales de madera dura del Parque Nacional Everglades, Florida.

RESUMEN. Las respuestas de cinco especies de bromelias (*Tillandsia balbisiana, T. fasciculata, T. setacea, T. utriculata,* y *T. venezuelana*) de la canopia inferior del bosque subtropical de madera dura ("hammock") a las perturbaciones de gran escala debidas a incendios de baja intensidad, fueron inferidas a partir de comparaciones entre las poblaciones existentes en áreas quemadas y no quemadas, observadas un año despues de un incendio, en Long Pine Key en el Parque Nacional Everglades, Florida. En las áreas quemadas se consumió el humus del suelo. Muchos árboles fueron desfoliados y/o murieron, lo que determinó la apertura de la canopia. Las comparaciones entre las poblaciones de epífitas de áreas de "hammock" quemadas y no quemadas, muy similares antes del incendio, indican que el fuego tuvo poco efecto directo sobre las especies estudiadas. Sin embargo, a traves del cambio del ambiente, el incendio determinó modificaciones en la demografía (incrementó la mortalidad, crecimiento y floración) de las poblaciones de bromelias. El estudio de campo de la adherencia de semillas de epífitas sobre los troncos de árboles huesped de diferentes especies indicó que, en el corto plazo, la adherencia difiere entre dos especies (*T. fasciculata* y *T. utriculata*) y entre bosques quemados y no quemados. Estos resultados indican que los disturbios de gran escala en la canopia pueden resultar en cambios rápidos en la dinámica poblacional de las epífitas. Tales cambios pueden influir, potencialmente, en la composición y en las dinámica de largo plazo de las poblaciones de epífitas de la canopia inferior.

INTRODUCTION

Studies of the ecology of vascular epiphytes have focused primarily on the harsh nature of the physical environment in the crowns of trees. Epiphyte morphology and physiology have been related to specialization for photosynthesis, absorption of water, and uptake of nutrients in aerial environments that differ in light levels, moisture availability, and mineral nutrients (Benzing, 1990). Epiphytes have been categorized by the relative tolerance of different light levels, desiccation, and by mechanisms for obtaining nutrients (e.g., Pittendrigh, 1948; Benzing & Renfrow, 1971; Griffiths & Smith, 1983; Gentry & Dodson, 1987). Species have been labeled as canopy or subcanopy, based in large part on the degree of tolerance of adverse environmental conditions.

Disturbances are widely recognized as producing important changes in the environments experienced by tropical plants (Brokaw, 1985; Platt & Strong, 1989). Responses of plants to these changes may be as important as tolerance of adverse conditions (Grime, 1977). Responses of epiphytes (particularly those that inhabit closed-canopy forests) to changes in environmental conditions produced by natural disturbances have not been studied. In this study, we explored changes in populations of subcanopy bromeliads in subtropical hardwood hammocks on Long Pine Key in Everglades National Park following a naturally occurring fire. Populations in burned hammocks were censused one year

after the fire and compared to populations in adjacent unburned hammocks.

METHODS

Study Area

This study was conducted on Long Pine Key, a habitat island of about 8,000 ha of oolitic limestone outcroppings in Everglades National Park, Dade County, Florida. Long Pine Key, which has a maximum elevation of 5 m msl, contains extensive pine savannas dominated by *Pinus elliotti* var. *densa* that interdigitate with and are surrounded by short hydroperiod prairies and sawgrass savannas dominated by *Cladium jamaicense* and *Muhlenbergia filipes* (Craighead, 1971; Olmsted *et al.*, 1983; Snyder *et al.*, 1990). Hammocks imbedded within the pine savannas contain an arborescent flora (more than 100 species) that is predominantly tropical and West Indian in origin (Robertson, 1953; Craighead, 1971; Alexander & Crook, 1973; Olmsted *et al.*, 1983). On Long Pine Key, hammocks typically have a closed canopy around 5 m, with scattered trees emergent above the canopy (Olmsted *et al.*, 1980). They are located in areas containing solution holes filled with water. This produces a humid microenvironment, especially during the wet season from June–November (Phillips, 1940). Hammock soils consist of peak deposits of 10–50 cm, depending on elevation and recent fire history (Simpson, 1920; Alexander, 1967; Craighead, 1974; Olmsted *et al.*, 1983). Hammocks on Long Pine Key have been numbered and mapped (Olmsted *et al.*, 1983); that numbering system was used in this study.

Survival, Growth and Flowering Following Fire

In May 1989, a 50,000 ha lighting-initiated fire (the Ingraham Fire) burned part of Long Pine Key. Two hammocks, #8 and #119, were observed in detail during the fire. The fire was confined to the peat layer; flame lengths rarely reached 0.2 m above the substrate. Trees were top-killed and/or completely killed by girdling of trunks or roots (but not by crown fires). Observations during and shortly after the fire indicated that epiphytes were not directly harmed unless they were located on the ground or less than about 1 m above ground.

In the summer of 1990, approximately one year after the fire, six small hammocks were selected for study. Three (#9, 10, and 119) had burned and three (#90, 100, and 113) had not burned during the fire. These hammocks were selected on the basis of the following criteria to minimize pre-fire differences: 1) all hammocks were in close proximity (about 1 km apart at the west end of Long Pine Key); 2) all hammocks had a similar fire history; prior to 1989, all six hammocks were last recorded as burned in 1940 (Olmsted *et al.*, 1983); 3) all hammocks were of similar size, from 80–100 m diameter, and were more or less circular in shape. Burned hammocks 9, 10, and 119 were approximately 0.8 ha, 1.1 ha, and 0.5 ha, respectively, and unburned hammocks 90, 101, and 113 were approximately 0.8 ha, 0.5 ha, and 0.6 ha, respectively.

A transect was established through the center of each hammock and extended to the surrounding pinelands. Quadrats of 5 × 5 m were established at 20 m intervals along the transects. Two out of three each of burned and unburned hammocks contained 5 quadrats; the third hammock of both types contained four quadrats. In each hammock, quadrats 1 and 5 (4) were close to the edge (but still inside the hammock) and 2–4 (3) were in the interior. A total of 700 m² was sampled for this study. Half of this area was in burned hammocks, and half in unburned hammocks.

In each quadrat, the species and the sizes of all trees ≥2 cm dbh (diameter at breast height) were measured and recorded as alive or dead above ground level. In each quadrat, each bromeliad located below 5 m (canopy height) was surveyed and the following data recorded: species, size (measured as length of largest leaf), location (on ground, tree trunk, treefall, branchfall, or vine), and height above ground. If present on a tree, the size (dbh) and species of the host tree was recorded. Each plant was recorded as alive or dead, and notes were taken on bolting, flowering, and ovary/fruit development.

The impact of the Ingraham Fire on survival, growth, and flowering of bromeliads was inferred from differences between plants in burned and unburned hammocks. Five of the ten species of *Tillandsia* recorded for Everglades National Park (Avery & Loope, 1983) were included in this study: (*T. balbisiana* Schult., *T. fasciculata* Sw., *T. setacea* Sw., *T. utriculata* L., and *T. valenzuelana* A. Rich.). Of these five species, *T. setacea* and *T. valenzuelana* have been designated subcanopy species with atmospheric and tank trichomes, respectively (Snyder *et al.*, 1990). *Tillandsia fasciculata* and *T. utriculata* have been described as canopy species with tank- and atmospheric-absorbing trichomes (Pittendrigh, 1948; Griffiths & Smith, 1983). *Tillandsia balbisiana* (which resembles *T. flexuosa* and *T. circinnata* in its morphology) has an incompletely developed tank. *Tillandsia fasciculata, T. utriculata,* and *T. balbisiana* exhibit positive CO_2 fix-

TABLE 1. Density and mean diameter at breast height (dbh) of all trees and of canopy tree species in burned and unburned hammocks.

	Hammock Type							
	Burned				Unburned			
	Density	dbh			Density	dbh		
Species	(trees/ ha)	($\bar{x} \pm$ SE)	Range	N	(trees/ ha)	($\bar{x} \pm$ SE)	Range	N
Bumelia salicifolia	364	8.3 ± 1.0	3.8–17.0	13	448	5.1 ± 0.8	2.0–15.0	16
Bursera simarouba	84	5.3 ± 1.0	2.0–8.0	3	56	8.6 ± 0.2	5.5–6.1	2
Lysiloma bahamense	56	7.5 ± 0.4	7.0–8.0	2	224	8.3 ± 1.8	2.0–18.0	8
Quercus virginiana	336	11.9 ± 1.8	4.5–28.0	12	448	10.9 ± 1.4	2.4–22.0	16
All trees	3,080	6.7 ± 0.5	2–28.0	110	4,172	5.6 ± 0.4	2.0–22.0	149

ation in the dark, which is indicative of CAM (Crassulacean Acid Metabolism) (Medina, 1974).

Seed Adherence

A study of the adherence and initial persistence of seeds on tree trunks was conducted to determine if they were different in burned and unburned hammocks. Four hammocks differing in fire history were used in this study. Two hammocks (#8 and #119) had burned during the Ingraham Fire of late May 1989. The other two hammocks (#4 and #113) were of similar size and were in the same vicinity as the burned hammocks, but had not burned within the past several decades. In each hammock, five live canopy trees each of *Bursera simarouba, Pinus elliotti* var. *densa,* and *Quercus virginiana* were randomly selected. The location of each tree was mapped, and dbh was measured.

Seeds from mature seed pods of *T. fasciculata* and *T. utriculata* were placed in a horizontal row 1.5 m above ground by brushing seeds against the bark. The location of each seed was marked with a plastic map tack color-coded for each species. Ten seeds of *T. utriculata* were placed on each tree on 7 July 1990 and were censused 8, 17, 23, and 41 days after placement. Ten seeds of *T. fasciculata* were set out 15 July 1990 and were censused on 9, 15, and 33 days afterward. During each census, the number of seeds remaining on each tree was recorded.

The number of seeds still attached at each census was used in an analysis of variance. The experimental design involved a hierarchical or split plot design in which individual trees were the experimental units in a randomized complete block design. Census dates were treated as split plots within each cell of the design. Data were tested for homogeneity of variances using an *F*-test involving the largest and smallest variances within the experimental units. Results indicated

no significant differences, so data were not transformed.

RESULTS

Comparison of Burned and Unburned Hammocks

Data from the six hammocks indicated that burned and unburned hammocks contained similar densities of trees at the time of the fire (TABLE 1). The 25 m² quadrats in burned and unburned hammocks contained 7.9 ± 1.7 (SE) and 10.3 ± 1.4 (SE) trees, respectively. These densities were not significantly different ($P > 0.05$; $F_{1,4} = 2.157$), based on analysis of variance using differences in tree density among hammocks as an error term. In addition, densities of trees of the four most abundant overstory species also were similar in the six hammocks at the time of the Ingraham Fire (TABLE 1). *Quercus virginiana* and *Bumelia salicifolia* were most abundant in all six hammocks; *Bursera simarouba* and *Lysiloma bahamense* were common in all six hammocks, but did not occur in all plots.

Sizes of trees were similar in burned and unburned hammocks at the time of the fire (TABLE 1). The mean sizes of live trees (all species combined) in the quadrats were not significantly different ($t_{1,22} = 0.96$; $P > 0.05$) in burned [6.7 ± 0.7 (SE) cm dbh] and unburned [5.9 ± 0.7 (SE) cm dbh] hammocks. The ranges of sizes of trees also were similar in the two sets of hammocks. *Quercus virginiana* was the largest tree in both burned and unburned hammocks; scattered large individuals were present in all hammocks and in some of the plots. Trees of *Bumelia salicifolia, Bursera simarouba,* and *Lysiloma bahamense,* smaller than those of *Q. virginiana* in all hammocks, were similar in size in burned and unburned hammocks (TABLE 1).

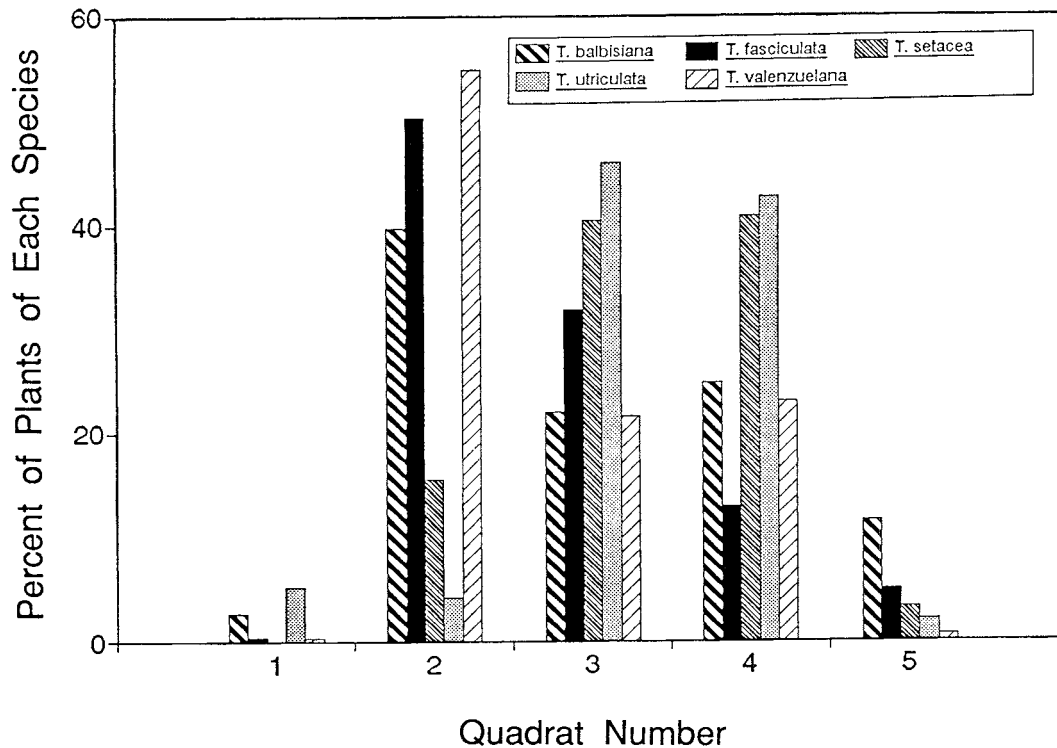The fire altered the vegetation structure in the three burned hammocks. All quadrats in the un-

FIGURE 1. The percentage of each species of bromeliad that occurred in the different quadrats in each hammock. Quadrats 1 and 5 are located at the periphery of hammocks; quadrats 2–4 are located in the interior of hammocks.

burned hammocks contained 100% crown cover, while all quadrats in the burned hammocks contained less than 25% crown cover. Dead trees comprised more than twice as many of the trees in the quadrats in burned (78%) as in unburned (34%) hammocks. In addition, mean sizes of dead trees in burned hammocks [6.7 ± 0.7 (SE) cm dbh] were significantly larger [$t_{1,23}$ = 3.08; P < 0.005] than the mean sizes of dead trees in unburned hammocks [4.6 ± 0.4 (SE) cm dbh]. Many dead trees in burned hammocks were only top-killed, and by one year after the fire, resprouting had occurred from the trunks, bases, or roots. In addition, two species (*Trema micranthum* and *Carica papaya*) had sprouted from dormant seeds and were present in most quadrats in burned hammocks as shrubs 1–2 m tall. Neither sprouting nor germination of *Trema* and *Carica* occurred in any of the quadrats in unburned hammocks, which were characterized by sparse vegetation near ground level.

Distribution of Bromeliads in Hammocks

All five species of bromeliads occurred in at least two out of the three hammocks in each burn

category (TABLE 2). All species tended to occur primarily in the interior of hammocks: peripheral quadrats (#1 and #5) contained many fewer epiphytes than did interior quadrats (FIGURE 1).

Species tended to be patchily distributed in the interior of hammocks, with no apparent species-specific distribution. Three species, *T. balbisiana*, *T. fasciculata*, and *T. setacea*, were common and occurred in six to eight of the fourteen quadrats in both burned and unburned hammocks. The other two species, *T. utriculata* and *T. valenzuelana*, were less common; each occurred in only three quadrats in unburned hammocks (TABLE 2). The three most abundant species were located primarily at heights well below the canopy. The density of *T. balbisiana*, *T. fasciculata*, and *T. setacea* decreased as the height above the ground increased (FIGURE 2). *Tillandsia valenzuelana*, which occurred primarily in burned hammocks, also tended to be located at heights below the subcanopy; 59% of the plants were located in the 0–1.0 m height category. Only *T. utriculata* tended to be more abundant in the canopy; there were large numbers of this species above 5 m in some quadrats.

Size of host did not appear important in de-

termining bromeliad distribution. Shrubs such as *Myrica cerifera, Ardisia escallonoides* and *Psychotria nervosa,* as well as small trees less than 1 cm in dbh (e.g., *Bumelia salicifolia*), were common hosts of epiphytes. For each species, more than half of the individuals (*T. balbisiana*: 54%, *T. fasciculata*: 68%, *T. setacea*: 76%, *T. utriculata*: 54%, *T. valenzuelana*: 63%) occurred on trees between 2 and 9 cm in diameter at breast height (1.5 m). Since 60% of trees in the transects were in this size range, the proportions of small and large trees with epiphytes were close to the observed frequencies of these trees in the hammocks.

Survival, Growth, and Flowering Following Fire

The proportions of live bromeliads in the quadrats were lower in burned than unburned hammocks (TABLE 2); 20.3% of the bromeliads were dead in the burned hammocks, but only 2.3% were dead in the unburned hammocks. The percentages of dead plants in burned hammocks differed among species, ranging from less than 10% for *T. fasciculata* and *T. utriculata* to over 50% for *T. valenzuelana.* The higher percentages of dead plants in burned hammocks appears to have resulted directly from fire and/or indirectly from cold damage following the fire. Although dead plants in general did not appear to have been burned, there may have been some direct effects of fire on plants located on the ground or very low on tree trunks. The dead plants were not randomly distributed with respect to height above the ground. In burned hammocks, the percentages of dead plants of some species (e.g., *T. setacea, T. valenzuelana*) increased as the elevation above the ground decreased (FIGURE 3). For *T. valenzuelana,* the majority of dead plants of this species below 1 m was charred. Mortality of this species was probably high because its vertical distribution was strongly skewed towards hammock floors.

For *T. balbisiana, T. fasciculata,* and *T. setacea,* there was a decrease in the percentage of plants in the 0–1.0 m height categories in burned relative to unburned hammocks (FIGURE 2). Since percentages of plants in this category included those that had fallen to the ground, the decrease may have resulted from the consumption of such plants by fire. This biased the fire-related mortality, because more plants were killed by the fire than were recorded one year after fire.

Bromeliad mortality could have also resulted indirectly from the fire. A severe freeze occurred 24–25 December 1989. At the research center of Everglades National Park, located about 2 km east of the burned hammocks, the temperature

TABLE 2. Characteristics of subcanopy populations of five species of *Tillandsia* in burned (B) and unburned (U) hammocks on Long Pine Key in Everglades National Park. Numbers of plants are those that occurred below 5 m in 25 m² quadrats in 3 hammocks (a total area of 350 m²). The number of hammocks and quadrats in which a given species occurred are based on maxima of 3 and 14, respectively. Maximum leaf sizes (lengths of longest leaves) are presented as means ± standard errors. All data were collected in 1990, one year following fire in the burned hammocks.

| Species	*T. balbisiana*		*T. fasciculata*		*T. setacea*		*T. utriculata*		*T. valenzuelana*	
Hammock type	B	U	B	U	B	U	B	U	B	U
Total number of plants	42	119	155	100	762	681	85	12	320	9
Number of hammocks in which plants occurred	3	3	3	2	3	3	3	2	3	2
Number of quadrats in which plant occurred	7	8	8	6	7	8	10	3	10	3
Percent of plants alive in 1990	71.4	95.0	91.6	100.0	89.4	97.5	91.8	91.7	48.8	100.0
Maximum leaf size (mean ± SE)	26.0 ± 2.34	20.8 ± 2.06	11.8 ± 1.08	8.3 ± 0.75	18.7 ± 0.30	6.0 ± 0.26	31.6 ± 2.23	35.1 ± 6.59	20.2 ± 0.69	20.3 ± 6.00
Percent bolting in 1990	29.3	1.8	6.5	0.0	55.9	9.6	9.8	0.0	10.1	0.0
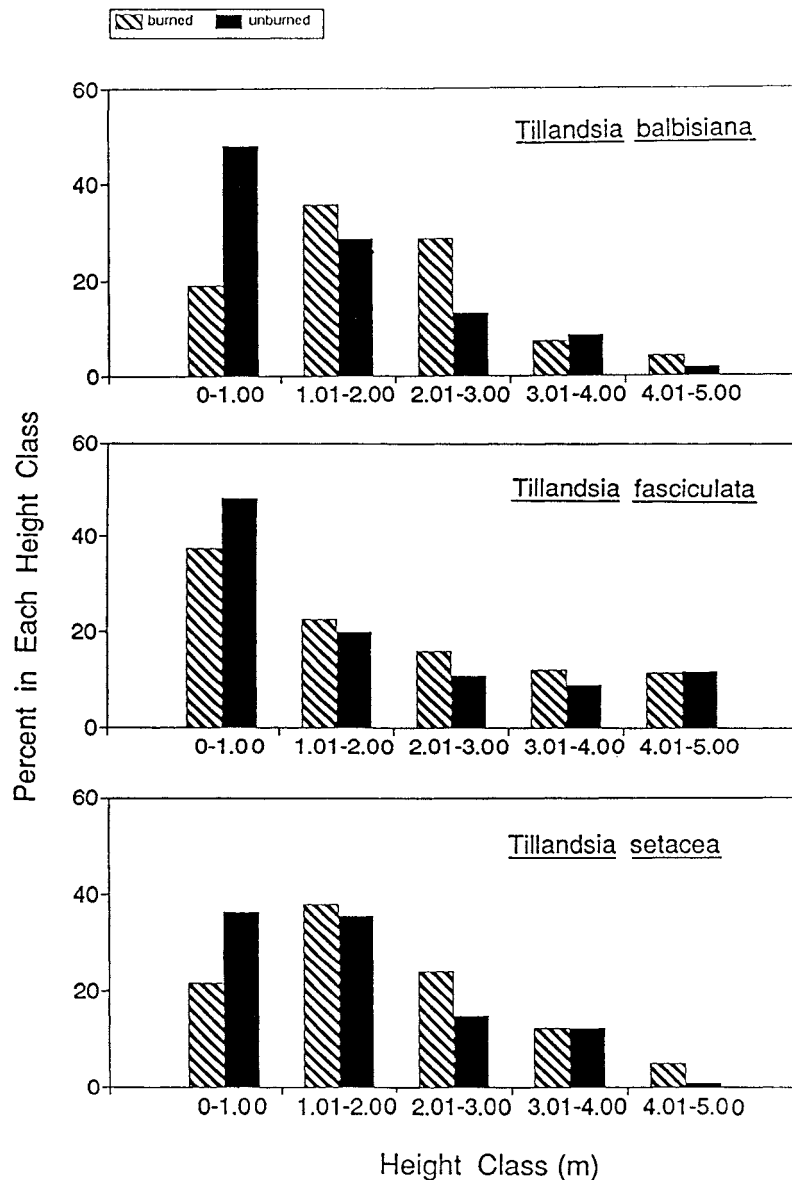
FIGURE 2. The percentage of populations of each of three species of *Tillandsia* that occurred in one meter height classes in burned (diagonal hatching) and unburned (solid) hammocks.

fell below 0°C at 2300 hr and remained below freezing for 10 hours, reaching a minimum of −3°C. These measurements, taken in the open, probably are close to those experienced in burned hammocks. The settling of cold air might have killed plants closer to the ground (especially sensitive species). There may have been a relationship between mortality and distribution; mortality was lowest for those species (*T. fasciculata, T. utriculata*) with distributions that reach lati-

tudes above 26°N along the Florida peninsula (A. Herndon, pers. comm.).

The sizes of plants varied between burned and unburned hammocks. The mean maximum leaf length was greater for plants in burned than unburned hammocks for three species: *T. balbisiana, T. fasciculata,* and *T. setacea* (TABLE 2). These lengths were compared using a two-sample *t*-test (Sokal & Rohlf, 1969). The maximum leaf sizes of *T. setacea* and *T. fasciculata* were sig-
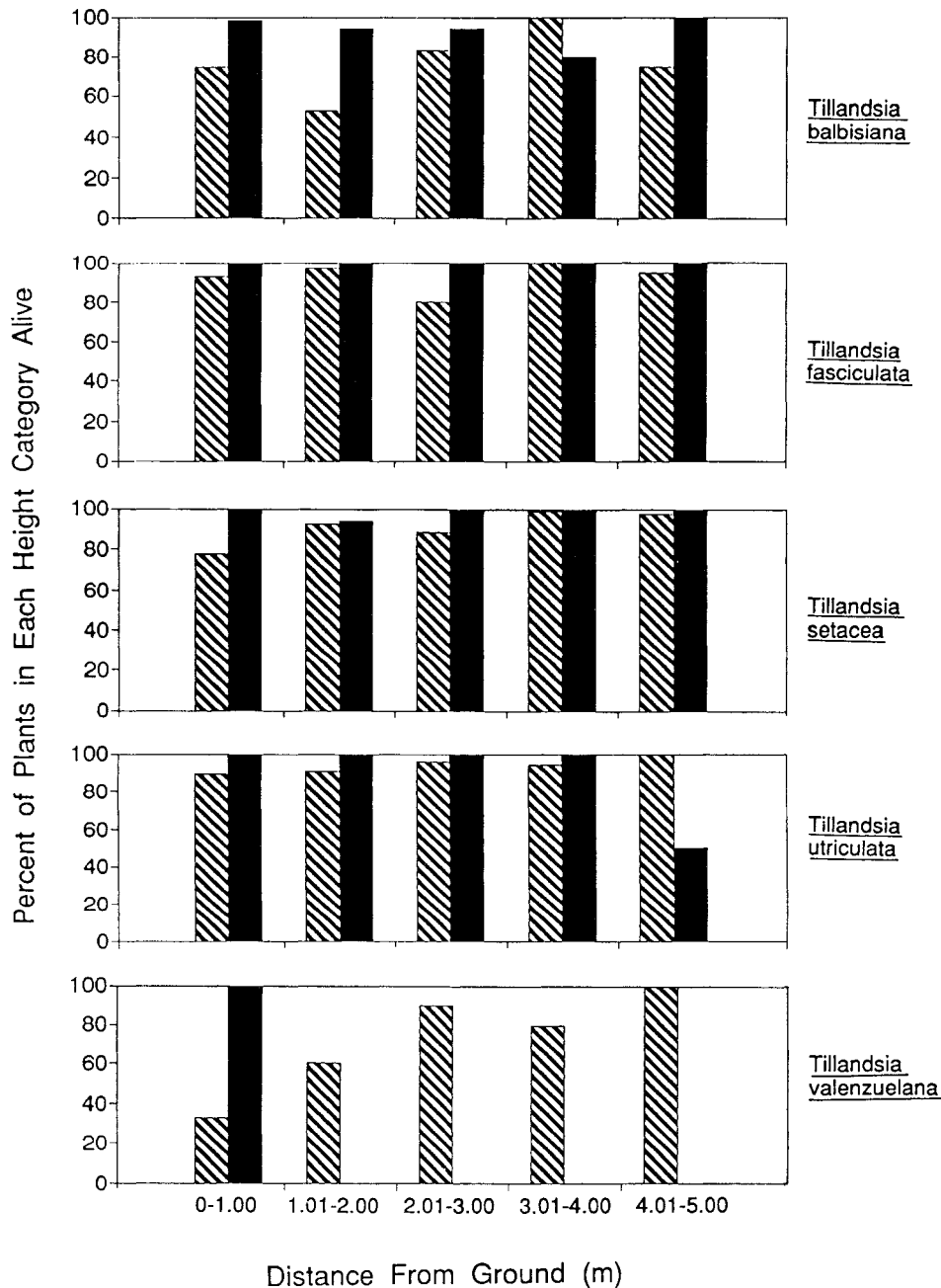
FIGURE 3.   Percentage of live subcanopy bromeliads of a given species in different height classes in 1990 in hammocks burned (diagonal hatching) and not burned (solid) during the Ingraham Fire of 1989.

nificantly larger in burned than unburned hammocks ($t_{1,4441}$ = 31.7; P < 0.0001 and $t_{1,253}$ = 2.36; P < 0.01, respectively). The maximum leaf size of *T. balbisiana* was marginally significantly larger in burned than unburned hammocks ($t_{1,159}$ = 1.39; 0.10 > P > 0.05).

Size frequency distributions of plants varied between burned and unburned hammocks (FIGURE 4). In the burned hammocks, there were markedly fewer plants of *T. setacea* and *T. balbisiana* in the smallest size category(ies) and higher percentages in larger categories. A similar
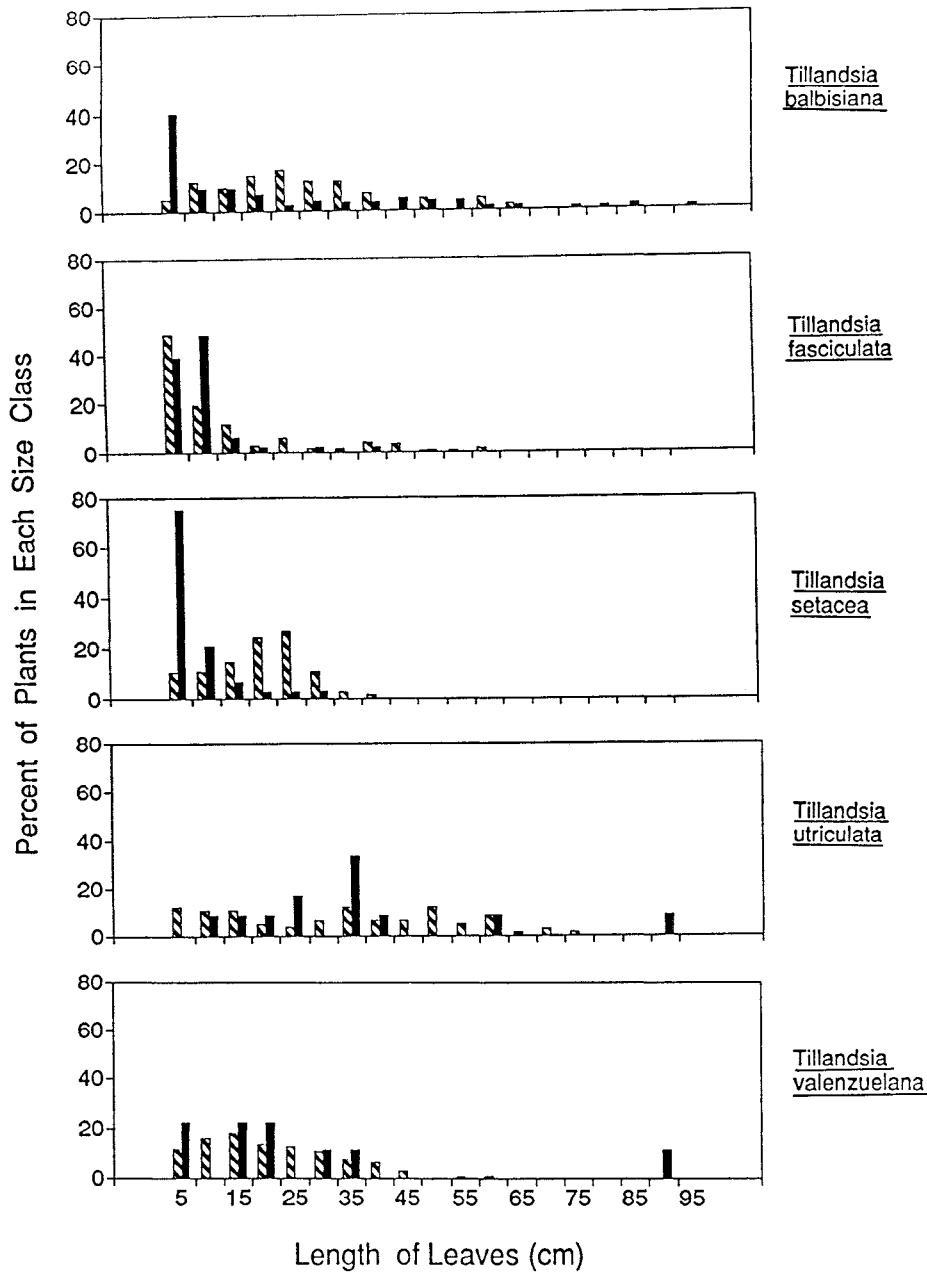
FIGURE 4. Percentage of subcanopy bromeliads in different size categories (based on lengths of longest leaves) in hammocks burned (diagonal hatching) and not burned (solid) during the Ingraham Fire of 1989.

pattern characterized *T. fasciculata*, while insufficient data were obtained on *T. utriculata* and *T. valenzuelana* to make comparisons of sizes in burned and unburned hammocks.

A larger proportion of the plants bolted in burned than unburned hammocks (TABLE 2). Over half the *T. setacea* and almost 30% of the *T. balbisiana* bolted in burned hammocks, while less than 10% of the former and less than 2% of the latter species bolted in unburned hammocks. For the other three species, 6–10% of the plants bolted in burned hammocks, while no individuals of these species bolted in unburned hammocks. A similar proportion of the epiphytes that bolted died in burned (16%) and unburned (21%) hammocks.
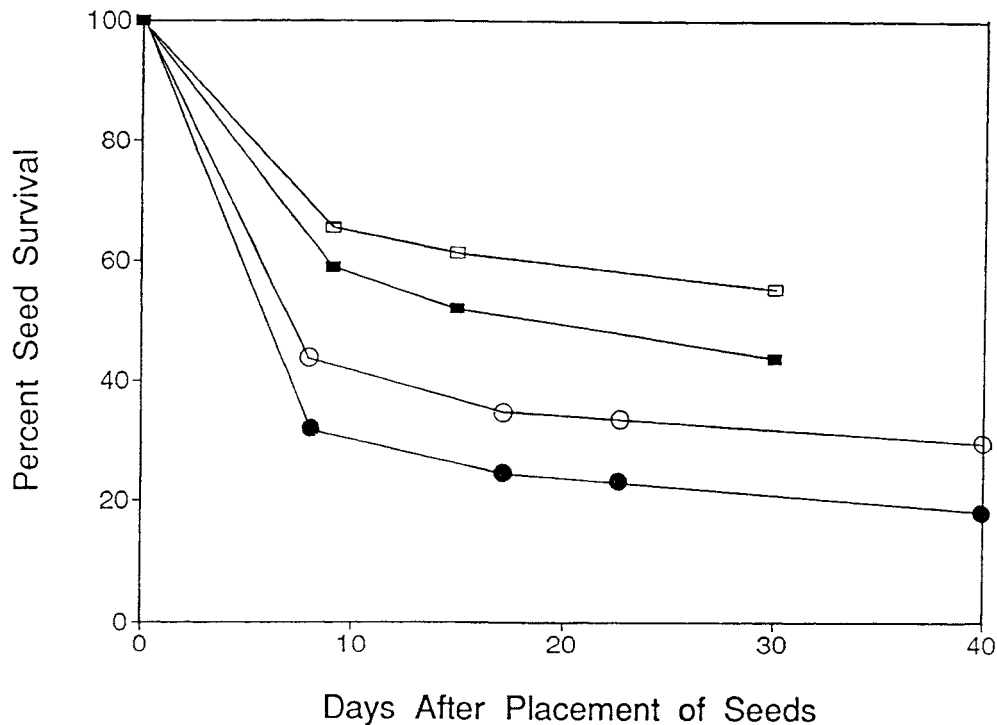
FIGURE 5.   Percent survival of seeds of *Tillandsia fasciculata* (squares) and *Tillandsia utriculata* (circles) in experimental cohorts placed on trunks of trees in burned (closed symbols) and unburned (open symbols) hammocks in Everglades National Park.

Seed Adherence

Persistence of seeds of both *T. utriculata* and *T. fasciculata* decreased most rapidly during the initial time period after they were placed on trees (FIGURE 5). Analysis of variance indicated that significant differences in numbers of seeds occurred only during the first time interval ($P < 0.001$ for both species); subsequently, there were no significant differences in persistence for seeds of either species in burned or unburned hammocks or on trees of different species ($P > 0.05$ for all comparisons).

Persistence was greater for seeds of *T. fasciculata* than for seeds of *T. utriculata*. Although significant at all time intervals ($P < 0.001$), the differences resulted from considerably lower persistence of *T. utriculata* during the initial week that seeds were present on the trees (FIGURE 5). Subsequently, persistence of seeds of both species was high. Thus, although seeds of *T. utriculata* were placed out in the field a week earlier than those of *T. fasciculata* (pods of the former dehisce earlier during the growing season), the differences in the lengths of time that seeds were present in the field did not cause the observed differences in persistence of seeds.

Persistence of seeds of both species was slight-ly, but significantly ($P < 0.05$) higher in unburned than burned hammocks (FIGURE 5). The observed differences between burned and unburned hammocks resulted from differences in persistence prior to the second census. The species of host tree did not influence persistence of seeds. There were no significant differences among the other three species (*Quercus virginiana, Pinus elliotti,* and *Bursera simarouba*) in persistence of seeds ($P > 0.05$). Two- and three-way interactions among treatments were also not significant.

DISCUSSION

Among the most pronounced differences in the demography of epiphytes in burned and unburned Everglades hammocks were increases in mortality, flowering, and size of plants in burned hammocks. Because the hammocks selected for study were located in close proximity and were similar in size, fire history, and tree species composition and size, the observed differences in epiphyte demography were inferred to have resulted from fire and/or changes in environmental conditions occurring after fire. Although the Ingraham Fire damaged some epiphytes, mortality resulting from fire was restricted to plants closest

to or on the ground. While these plants might have flowered (if not killed), their seeds would not likely have colonized other tree trunks. Thus, direct mortality from fire probably had minimal impact on the post-disturbance population dynamics of epiphytes in the Everglades hammocks.

Changes in the Everglades hammock environment following fire may have altered epiphyte population dynamics. The loss of canopy cover and organic humus on the hammock floor exposed the epiphytes in burned hammocks to more extreme environmental conditions—drier and colder (during the freeze of December 1989)—than those in unburned hammocks. Differential reductions in population sizes of bromeliads (by events such as a freeze) could potentially have an impact on the relative abundances of bromeliad species in hammocks recovering from fire as a result of reduced flowering and seed dispersal.

Increased flowering of bromeliads in burned hammocks occurred in both the canopy and in the subcanopy. Increased light levels following removal of the canopy may have triggered bolting. Alternatively, increased flowering may be a result of fire. Abeles (1973) summarized the effects of ethylene (or ethylene analogs) produced during the combustion of organic materials as stimulatory to flowering in the Bromeliaceae. Long exposure to low concentrations of ethylene have been shown to have a considerable stimulating effect on flowering; such conditions may well have occurred in the Everglades hammocks, many of which burned for several days and were full of smoke (especially at night). Ethylene levels may also be increased by cold damage (Abeles 1973; Field 1985). Increased flowering in burned hammocks might also have resulted from cold damage during the December 1989 freeze.

As suggested by our study and those of Benzing (1978, 1981), colonization of bark surfaces is not a random process. First, there appear to be differences among epiphyte species in the adherence of seeds to the bark of trees. In our study, *T. fasciculata* seeds were more likely to adhere to tree trunks than were *T. utriculata* seeds; presumably these differences reflect differences in coma morphology. Second, although dispersal is undoubtedly enhanced by the opening of the forest by fire, it is likely to be a local phenomenon, with seeds having the greatest likelihoods of immigrating onto nearby trees and at lower heights than onto parent plants (Benzing, 1990). Third, if seeds do land on hosts, there is a strong likelihood that the seeds may be transported down the trunks by heavy rainfall, skewing the distributions of new recruits towards the forest floor. Fourth, although seeds readily become attached to some potential hosts (e.g., *Pinus elliotti, Bur-*

sera simarouba) frequent sloughing of the bark may greatly lower the chances of survival on those hosts (Benzing, 1981, 1990).

Reproduction, dispersal, and colonization, as well as rapid growth, occur in the intervals between fires. The growth rates suggested by size differences between epiphyte populations in burned and unburned hammocks indicate that at least some species may be capable of rapid growth under high light conditions that occur following disturbances. Humidity may also remain fairly high in the interior of opened hammocks, especially for subcanopy plants, because of the dense ground cover of plants that have resprouted or that have initiated growth shortly after the fire. Thus, survival and growth of juveniles in high light environments of burned hammocks may be higher than hammock edges or in more exposed habitats such as cypress swamps (Benzing, 1978, 1981, 1990).

During the transient period of high light conditions, species that are normally characterized as canopy CAM species with tank and atmospheric trichomes (i.e., *T. utriculata, T. fasciculata*; Pittendrigh, 1948; Griffiths & Smith, 1983), as well as other known CAM species (*T. balbisiana*; Medina, 1974), may colonize and grow at low heights along trunks of suitable hosts in the Everglades hammocks. These species appear to be capable of surviving intervening periods with lower light levels and then responding again when the forest overstory is reopened. As a result, differences in vertical height distributions of different species of epiphytes may be less apparent in Everglades hammocks than in other forests which are less likely to experience periodic disruptions of the canopy.

Our study of the effects of the Ingraham Fire on epiphyte populations in Everglades hammocks suggests that periodic openings of hammocks are punctuations that interrupt longer intervening phases of greater stasis. We suggest that the ephemeral periods of opening by disturbance are likely to be times of rapid turnover that result from changes in mortality, reproduction, dispersal, and growth. As a consequence, the composition and dynamics of subcanopy epiphyte populations can change. Hence, observed patterns in the distribution and abundance of epiphytes may reflect the nature and pattern of disturbances (and responses of populations to environmental conditions following disturbances), more than the conditions experienced in intervening years.

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POPULATION DYNAMICS OF
ENCYCLIA TAMPENSIS IN FLORIDA

RONALD J. LARSON

Harbor Branch Institute, Fort Pierce, Florida 34946 U.S.A.
Present address: U.S. Fish & Wildlife Service, 801 Gloucester St., Rm. 334,
Brunswick, Georgia 31520 U.S.A.

ABSTRACT. A population of *Encyclia tampensis* was studied in a hammock near Fort Pierce, Florida, U.S.A. between November 1985 and January 1990. Nearly 100 orchids were recorded from a single live oak (*Quercus virginiana*) limb 2 m in length. Orchids ranged in size from 1 mm diameter protocorms to flowering plants with up to 30 pseudobulbs (3–20 mm in diameter). Recruitment occurred in three of the four years, resulting in a total of 36 protocorms. Most protocorms were short-lived (4.4 ± 0.8 months); however, four lived more than one year and the oldest lived for 17 months. "Protocorms" first appeared in early summer and died in fall and winter, apparently from desiccation. Older "prebulb" seedlings ($\approx$2–5 years old) were the most numerous growth stage and lived longer than protocorms, with the majority surviving >2 years (mean observed longevity = 21.5 ± 2.2 months). The longest-lived prebulb plant lived >48 months. Mortality was lowest for plants with pseudobulbs ($\approx$ >5 years); however, a few of these died. First flowering probably occurred at $\approx$15 years of age. In December 1989, a severe cold front passed through Florida; temperatures reached $-5°C$, killing all the orchids. At other central Florida sites, mortality of *E. tampensis* was high (>80%). *Tillandsia* spp., bromeliads (e.g., *T. bartrami, T. fasciculata, T. flexuosa*, and *T. setacea*) suffered variable mortality. *Tillandsia recurvata* showed some mortality at exposed sites, but *T. usneoides* was unaffected. These observations suggest that meteorological factors (e.g., rainfall and low temperatures) can significantly affect epiphytes in Florida and must be considered in the context of conservation.

Dinámica de poblaciones de orquídea *Encyclia tampensis* en el Estado de la Florida (Estados Unidos).

RESUMEN. *Encyclia tampensis* fue estudiada en bosque costero "hammock" cerca de Fort Pierce, Florida, por mas de un período de cuatro años (Nov. 1985 a Dec. 1989). Más de 80 orquídeas fueron localizas en los cedros "live oak" (*Quercus virginiana*) en ramas de 2 m de largo. Las orquídeas variaban de tamaño, desde protocormos de 1 mm de diámetro, hasta plantas en floración con 30 pseudobulbos (3–20 mm en diametro). La colección de se hizo sólo en tres de los cuatro años del estudio, recolectádose 32 protocormos. La mayoría de éstos sobrevivieron sólo cuatro meses ($\bar{x}$ = 4.2, SE ± 1.0 meses); sin embargo, cuatro protocormos vivieron mas de un año, el de mayor duración vivió 17 meses. La mayoría de protocormos aparecieron en el verano pero morían en el otoño o el invierno, aparéntemente por desecación. Por otra parte las formas mas maduras de 'prebulbos' (=2–5 años de edad) fueron mas numerosos y vivieron más, llegando unos hasta sobrevivió 2 años (X = 22.5, SE ± 2.0 meses). El prebulbo que mas sobrevivió alcanzó 46+ meses. La mortalidad fué baja en las plantas con bulbos (=>5 años), aunque algunas plantas pequeñas murieron. La primera floración probablemente ocurrió entre los 10–15 años. En Diciembre de 1989, un viento severo frío pasó por Florida; las temperaturas alcanzadas fueron de $-5°C$, aniquilando todas las orquídeas. En otros sitios de la parte central de la Florida, *Epidendrum conopeum* y *Harrisella filiformis*, aparentemente no fueron afectadas; bromelias como *Tillandsia* spp. (*T. fasciculata, T. flexuosa*, y *T. setacea*) mostraron una mortalidad variable.

INTRODUCTION

Florida has approximately 70 species of vascular epiphytes, more than any other state in the United States (Long & Lakela, 1976; Wunderlin, 1986). One of Florida's most common epiphytic orchids is *Encyclia tampensis* (Lindley) Small, the butterfly orchid. It is an evergreen species found throughout south and central Florida, primarily in hammocks and swamps (Luer, 1972). Many species of phorophytes are colonized (e.g., *Juniperus virginiana* L., *Nyssa sylvatica* Marshall, *Quercus* spp., *Salix* spp. *Taxodium* spp.), but *E. tampensis* is most abundant on live oak (*Quercus virginiana* Miller).

Encyclia tampensis is considered threatened by the state (Wood, 1990) because of habitat destruction, illegal collecting, and other causes. This orchid also occurs in the Bahama Islands, but its population levels there are unknown. Conservation of this and other threatened epiphyte species requires knowledge of demography, factors that affect survival, and habitat requirements, data which are mostly lacking. In 1985, I studied the recruitment and survival of a population of *E. tampensis* in central Florida. A severe freeze occurred in December 1989 and its effects on epiphytes were also documented.