vided valuable insights and advice in setting up and conducting the field study. We thank Bob Doren and Sue Husari for their encouragement and logistical support. We appreciate comments on the manuscript made by Alan Herndon, Ron Larsen, Bob Doren, Sue Langevin, Martin Quigley, and an anonymous reviewer. The Everglades National Park Research Center provided funding for field work in this study. Kevin Robertson was partially supported for data analysis by a grant from the Howard Hughes Medical Institute to improve undergraduate education at Louisiana State University.

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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 (≈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 (≈>5 years); however, a few of these died. First flowering probably occurred at ≈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.

Materials and Methods

Field work took place from November 1985 to January 1990 in a maritime hardwood hammock at the Harbor Branch Oceanographic Institution adjacent to the Indian River Lagoon in northern St. Lucie County, Florida (27°28′N, 80°20′W). The hammock was once part of a nearly continuous belt of hardwoods that grew along both shores of the lagoon, landward of mangroves. Most of this forest was cleared for citrus and housing developments; only small isolated woodlots now remain. The hammock canopy consists of live oak, swamp laurel oak (*Quercus laurifolia* Michaux), red mulberry (*Morus rubra* L.), and cabbage palm (*Sabal palmetto* (Walt.) Lodd. ex Schultes).

In 1985, *E. tampensis* was common in the hammock. More than 50 plants of flowering size and many more seedlings occurred in a 1–2 ha area. Most grew on older limbs of live oak, from near the canopy top (10 to 15 m high) to within one meter of the ground. A group of *E. tampensis* growing along a 2 m distance of a live oak limb (23 to 28 cm in diameter), 1.5 to 2.5 m above the ground was selected for study. Most of these orchids grew along a horizontal portion of the limb whose upper surface was grown over with resurrection fern (*Polypodium polypodioides* (L.) Watt). Crustose and foliose lichens and mosses also grew on the upper surface of the limb, but were less abundant on the sides. Several small *Tillandsia utriculata* L. also grew on the limb.

All *E. tampensis* plants in the study population were mapped and assigned numbers. Colored, plastic-headed tacks were placed at intervals along the limb as reference points. At intervals of 1 to 4 months, all orchids along the limb were located. Numbers of leaves and pseudobulbs were noted for each plant and measurements of leaf lengths and bulb diameters were taken. New shoots and seasonal reproductive stalks were also noted.

Results

Seasonal Phenology

Over the four-year period, 97 *Encyclia tampensis* plants were found growing along the limb. Size ranged from 1 mm diameter protocorms to flowering plants with up to 30 pseudobulbs from 3 to 20 mm in diameter. Shoot and root growth began in early March, prior to the onset of the rainy season (Figure 1A), and continued into June. In April, mature plants produced one inflorescence from each new pseudobulb. Anthesis occurred in late May or early June and lasted to mid-July. Fruit maturation lasted from July to October. Capsule dehiscence started in November; seed dispersal continued into spring.

Growth Stages

I observed four growth stages. The protocorm was the first stage. Initially they were spherical (Figure 2a), but within a few months each developed a single leaf (Figure 2b). The next stage, the "prebulb seedling", had one or more leaves, but lacked a definite pseudobulb (Figure 2c). This was followed by the "pseudobulb seedling" which had a definite pseudobulb, and finally by the mature plant (Figure 2d). Seedling growth occurred by shoot elongation and by an increase in the number and length of leaves. The number of leaves produced was variable. During dry periods, leaves were shed, so that the number of leaves decreased from one year to the next. The protocorm stage lasted about one year, while the prebulb seedling stage lasted about five years. Finally, after approximately six years, one small pseudobulb formed. Thereafter, one or more new shoots and pseudobulbs were produced yearly. Under good conditions (rainfall throughout the year, absence of leaf predators), successive pseudobulbs became progressively larger until they reached about 25 mm in diameter. Low rainfall can cause leaf fall with the result that pseudobulbs produced in the next year are smaller than previous ones. An inflorescence was first produced on pseudobulbs of about 15 mm in diameter. Based on pseudobulb growth, I predict that flowering first occurs at an age of about 15 years. Under cultivation, the prebulb stage lasts from 0.5 to two years, and first flowering may occur in only five to six years (H. Luther, pers. comm.).

Recruitment and Mortality of Protocorms

During this study, 36 seedlings became established on the oak limb. Protocorms were first seen in June, but the majority appeared in August and September (Figure 1B). Most of the protocorms were growing on the sides of the limb rather than on the top; no colonization occurred on the underside. Protocorms were found both in exposed areas of the bark (Figure 2a) and in crevices (Figure 2b).

The number of protocorms was highly variable from year to year (Figure 3). Protocorms were mostly short-lived (mean life span was 4.4 ± 0.8 months) (Figure 4). None lived more than 17 months. Seedling mortality was lowest during the summer wet season (May–October) and increased to a maximum during the winter dry season (November–February) (Figure 1C).

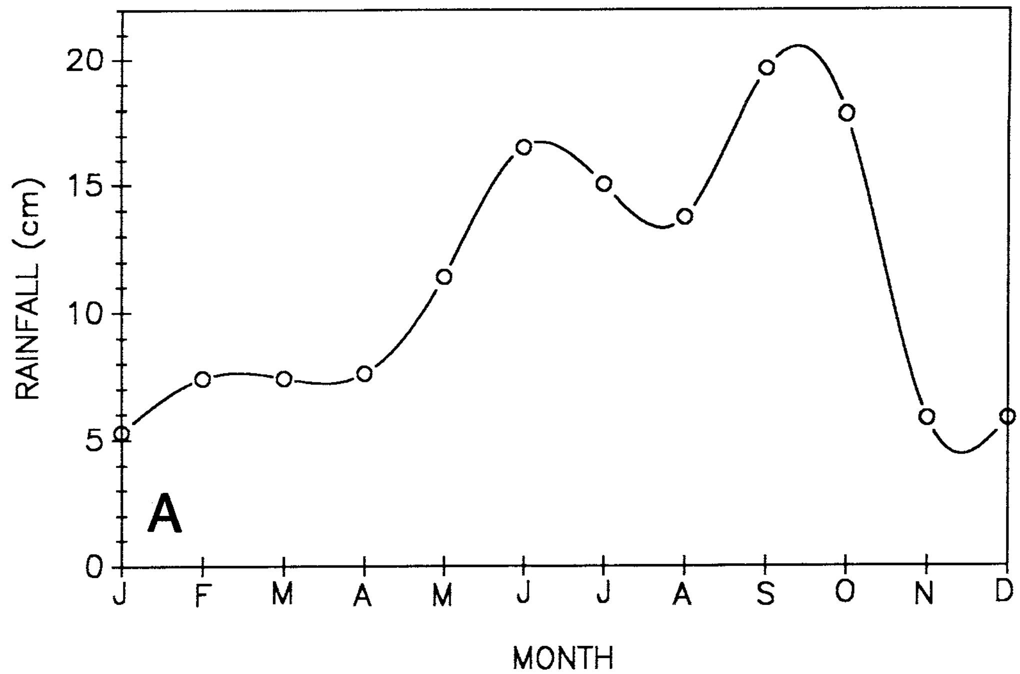

FIGURE 1. A. Mean monthly rainfall at Fort Pierce, Florida (data from NOAA, National Climatic Data Center). B. Percent of total recruitment of *Encyclia tampensis* protocorms, based on four years of observations ($N = 36$). C. Percent of total mortality of *Encyclia tampensis* protocorms, based on four years of observations ($N = 39$).

Mortality of Seedlings and Mature Plants

Prebulb seedlings had higher survivorship than protocorms. Of 42 prebulb seedlings, the average observed longevity was 21.5 ± 2.2 months (age of these seedlings was greater by one to four years, since they were already seedlings when the study was initiated). Seasonality of seedling mortality differed somewhat from that of protocorms, with 51% of the total mortality occurring from January to May, 14% from May to September, and 35% from October through December. Only two of the 11 pseudobulb seedlings died during the study. None of the three mature plants died during the study (however, two mature and five immature plants were removed by vandals).

Effects of December 1989 Freeze

Freezing temperatures occasionally occur throughout mainland Florida. Between November 1985 and December 1989, however, temperatures were insufficiently low to produce mortality. In December 1989, an intense arctic cold front moved through Florida. In a nearby maritime hammock (6 km north of the study area), temperatures fell below 0°C at 1600 hr on 23 December. Minimum values reached −5°C at 2400 hr and stayed below freezing until about 0600 hr on 24 December (measured at 1 m height below a live oak canopy; P. Lounibos, unpubl. data). Freezing conditions lasted for 14 hr. After warming to 6°C, temperatures again dropped to zero at 1700 hr on 24 December and stayed below freezing for 10 hr.

All orchids in the study population were killed. Examination of other visible *E. tampensis* plants in the hammock ($N = 52$) revealed that most were killed; only two live pseudobulbs on two plants were still green. As of February 1991, no living *E. tampensis* plants were seen in the hammock. At Highlands Hammock State Park near Sebring, Florida (27°30′N, 81°30′W), *E. tampensis* mortality was nearly 100% among seedlings, and was about 70% in mature plants. Most of the surviving plants were found within 1 m of the ground and had only a few live pseudobulbs. No *E. tampensis* recruitment or flowering was detected at other central Florida sites during 1990.

DISCUSSION

High protocorm mortality was probably due to drought-related water stress. Owing to their

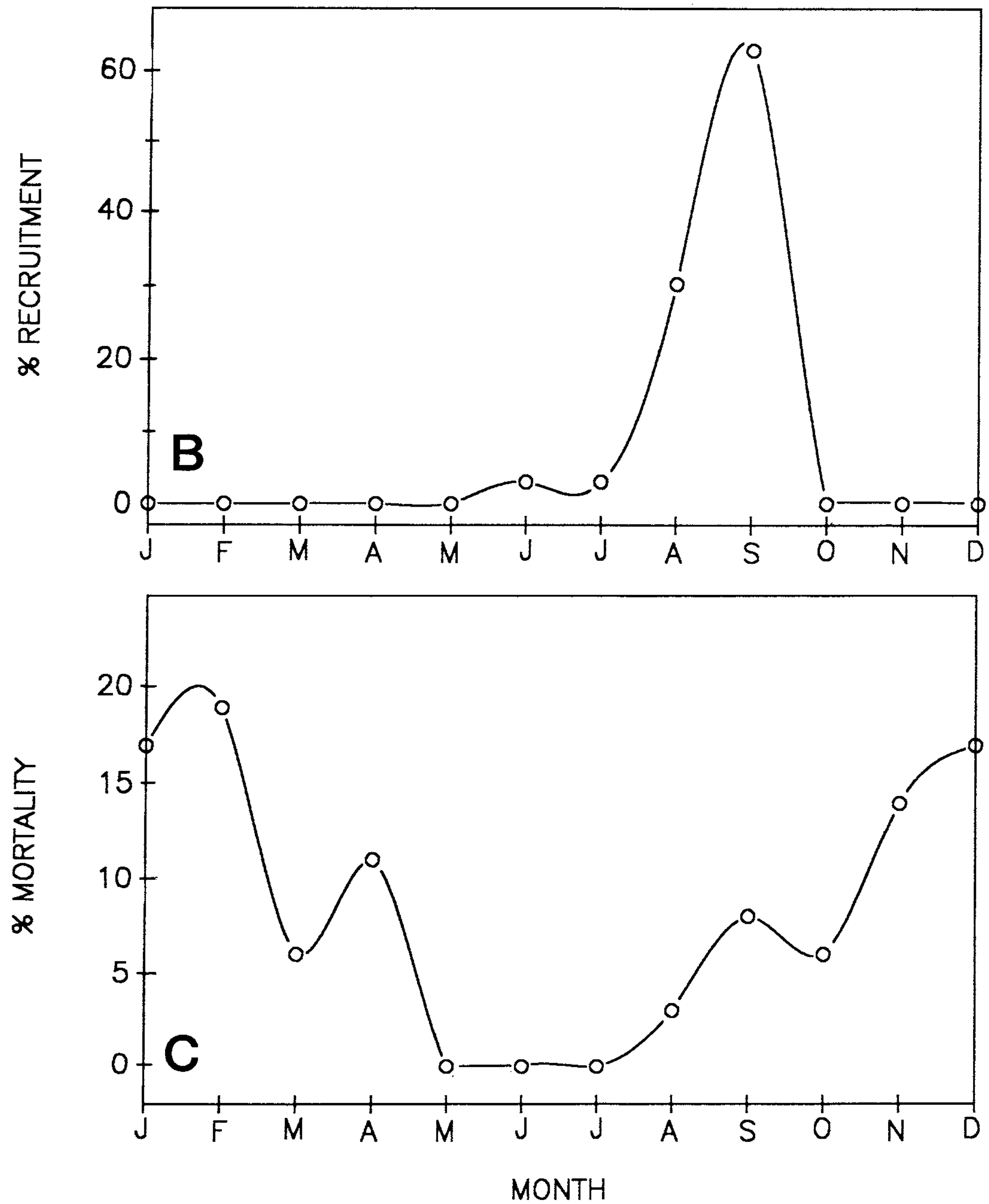

FIGURE 1. Continued.

small size, protocorms have a relatively large surface-to-volume ratio, making them vulnerable to desiccation. Their spherical shape may be an adaptation to reduce water loss. The reduced mortality of prebulb seedlings was perhaps a result of a more favorable surface-to-volume ratio, which allowed water to be conserved longer.

Size-specific mortality rates are similar to those reported by Benzing (1978, 1981, 1990), who studied survivorship in *Tillandsia paucifolia* Baker in south Florida. By following survivorship, he determined how cohort success varied yearly. Mortality was variable from one year to the next, and was especially high in seedlings <2 years of

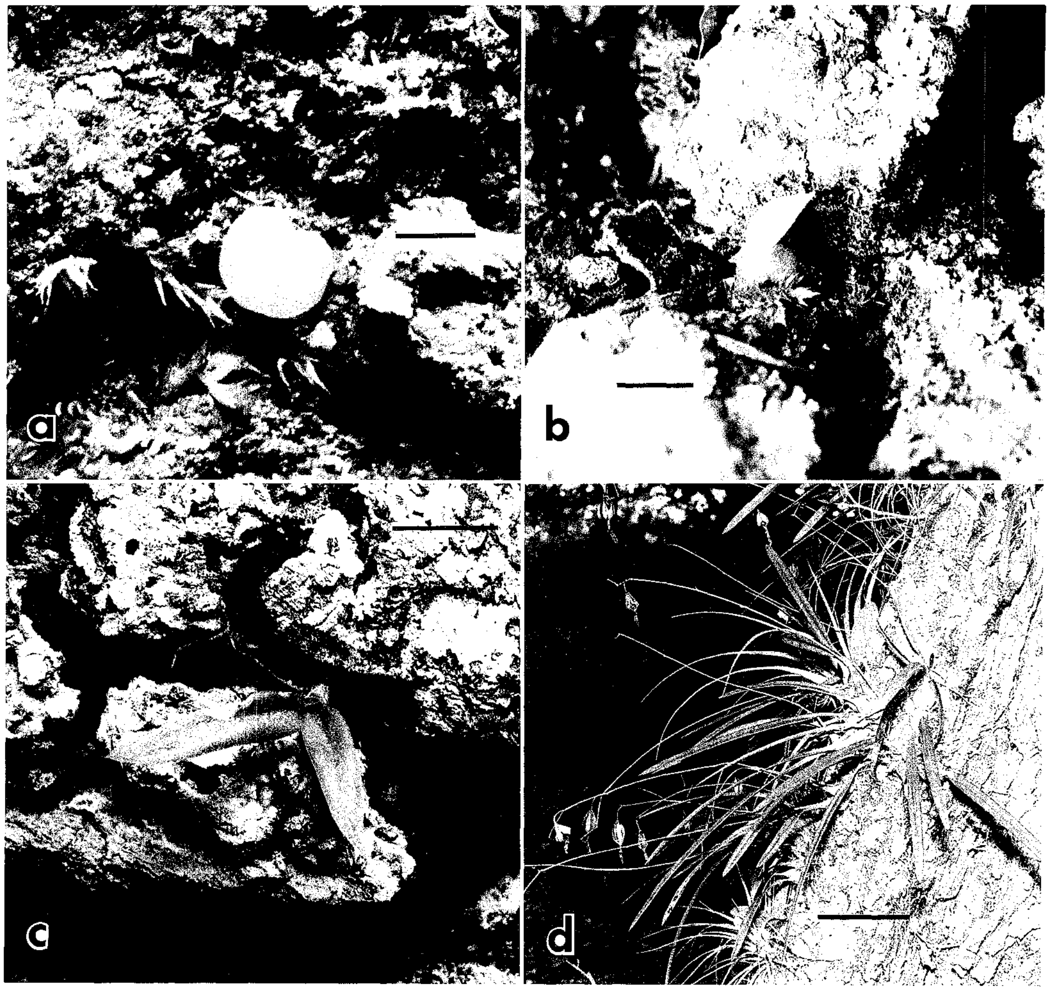

FIGURE 2. Life-history stages of *Encyclia tampensis* (all plants on live oak). a. Early protocorm. Scale bar = 1 mm. Note exposed position on bark. b. Late protocorm with developing leaf. Scale bar = 3 mm. Note position in bark crevice. c. Prebulb seedling with two leaves. Scale bar = 1 cm. d. Mature *Encyclia tampensis* plants with capsules. Scale bar = 10 cm.

age; it steadily decreased thereafter. These results suggest that rainfall patterns play a critical role in epiphyte survival.

Except in habitats where fog commonly occurs, epiphytes are primarily dependent on rainfall for moisture supply. It is thus not surprising that epiphyte growth and survival should be correlated with rainfall (Benzing, 1990). At Fort Pierce, mean annual rainfall is 134 cm, with 62% occurring from June to November (NOAA, 1986, 1987, 1988, 1989) (FIGURE 1A). In 1986, rainfall was 19 cm above normal; in 1987, 1988, and 1989, it was 20, 50, and 41 cm below normal, respectively. In 1986, 24 protocorms were found on the study limb. In the following three years, a total of only 12 protocorms was found. The drought conditions from 1987 to 1989 may have reduced recruitment by adversely affecting seed production, germination, and/or protocorm survival. Seasonal mortality of seedlings also appeared to be a result of drought during that period.

Occasional freezes have a significant impact on epiphytes. Mortality was not confined to orchids, as bromeliads were also affected by the December 1989 freeze. Approximately 90% of the large *Tillandsia setacea* Swartz population were killed. Additionally, all of the small *T. flexuosa* Swartz population ($N = 10$) located in nearby mangroves died. Also, most of the small *T. utriculata* died, but few of the larger plants succumbed. In the open, some mortality of *T. re-*

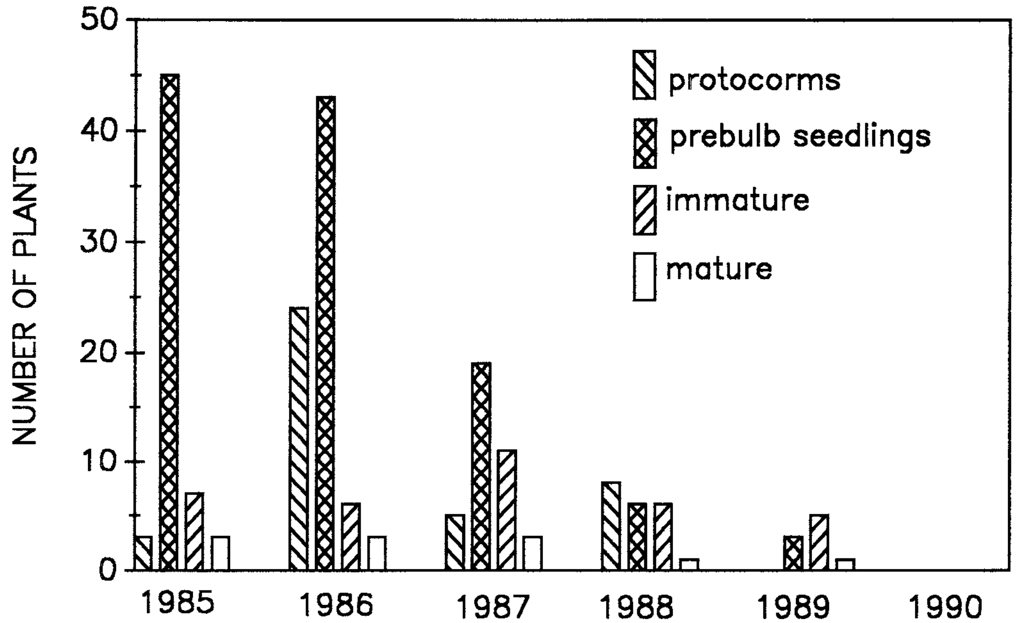

FIGURE 3. Number of *Encyclia tampensis* plants at each stage from 1985–1990. See text for explanation of life-history stages.

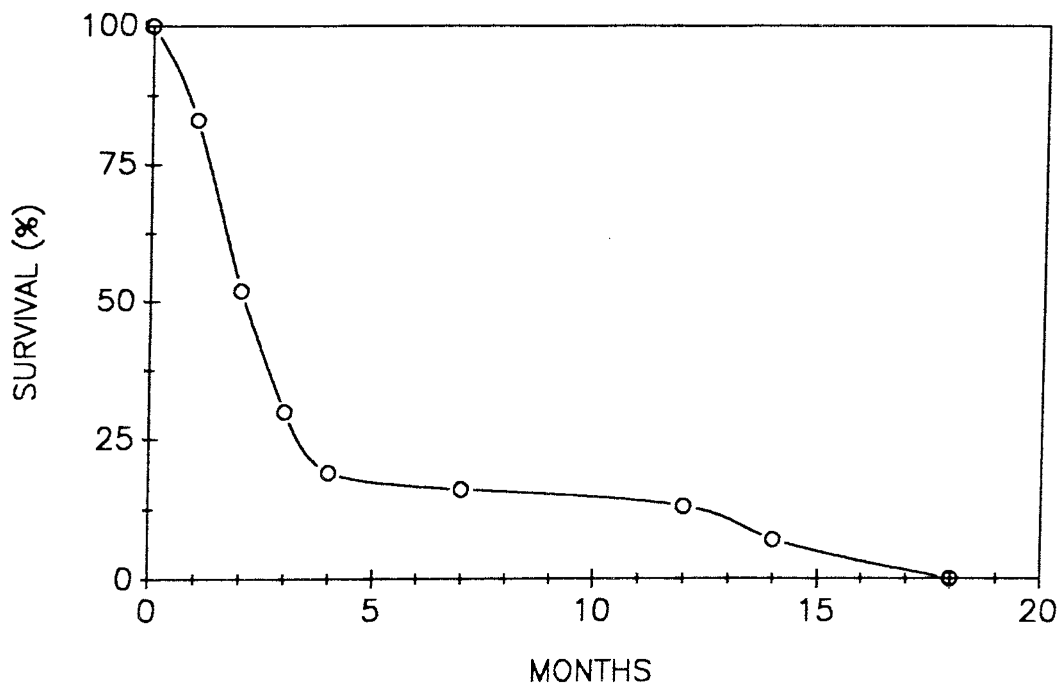

FIGURE 4. Survival of *Encyclia tampensis* protocorms through time ($N = 39$).

curvata L. was noted. *Tillandsia usneoides* (L.) Linnaeus showed no mortality.

Similar bromeliad mortality was observed at other sites in central Florida (e.g., Alexander Springs, Ocala National Forest; Highlands Hammock; Lake Woodruff National Wildlife Refuge; Paynes Prairie State Preserve; and Tosohatchee State Preserve). Most notable was the high mortality of *T. setacea* and *T. bartrami* Elliot. These two species are dominant mesic/hydric forest bromeliads in south and south-central, and north-central and north Florida, respectively. These species often colonize winter-deciduous red maples (*Acer rubrum* L.) and swamp blackgum (*Nyssa biflora* Walt.) where they grow high into the canopy. In 1990, I noted some *T. setacea* seedlings at Fort Pierce and Highlands Hammock, suggesting that some seeds survived the low temperatures. In general, there was a direct relationship between cold hardiness and range, with *T. recurvata* and *T. usnoides,* the two bromeliads with the broadest latitudinal ranges, showing the greatest resistance to low temperatures.

The December 1989 freeze was harsh on epiphyte populations in central Florida, but lower temperatures have been reported. Significant freezes also occurred in January 1940, December 1957, and January 1981 (Stowers & LeVasseur, 1983). In January 1981, temperatures reached −13°C in west-central Florida. In December 1989, temperatures reached −9°C in central Florida (NOAA, 1989). Comparison of minimum temperature data with the distribution *E. tampensis* would prove interesting. The northern limit of this orchid is in Flagler, Putnam, and Levy Counties in Florida (R. Wunderlin, pers. comm.). Severe recent freezes may have shifted the range of this orchid farther south.

Although Florida has a significant number of vascular epiphytes, many of these are represented by small and easily extirpated populations. Results of this study suggest that drought and low temperatures may significantly affect their survival. Conservation efforts should include studies on the effects of physical factors on recruitment and survival. Such studies must be of sufficient duration to account for annual and multi-year variations in weather.

Acknowledgments

I thank R. Wunderlin for providing *Encyclia tampensis* distribution data and P. Lounibos for furnishing temperature data. D. Benzing, H. Luther, and K. Larson, and an anonymous reviewer made helpful comments. T. Smoyer printed the photographs.

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