

Comparative Phenology of Epiphytic and Tree-Phase Strangler Figs in a Venezuelan Palm Savanna¹

Francis E. Putz, Gabriela B. Romano

Department of Botany, University of Florida, Gainesville, Florida 32611, U.S.A.

and

N. Michele Holbrook

Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138, U.S.A.

ABSTRACT

Epiphytic and tree-phase individuals of two hemiepiphytic figs (*Ficus pertusa* and *F. trigonata*) growing in a seasonally dry palm savanna in central Venezuela were compared on the bases of leaf longevity and temporal patterns of leaf production and loss. Epiphytic plants of both species produced new leaves more often and had a greater number of transitions from leaf-bearing to leafless than conspecific trees during the two-year observation period. Leaf production by epiphytic plants but not by trees of either species was positively correlated with rainfall received during the fortnight prior to phenological observation. Epiphytic plants of both species were leafless or nearly so during more of the year and had more separate episodes of becoming deciduous than conspecific trees. Periods of leaf loss generally coincided with dry periods but the negative correlation with rainfall during the previous fortnight was significant only for *F. pertusa* trees. Leaf life spans were shorter on epiphytic than on tree-phase figs. Patterns of leaf production and loss are interpreted to be responses to water deficits suffered by epiphytes, deficits that are at least partially overcome when plants become deeply rooted in the ground.

RESUMEN

Se compararon la longevidad foliar y los patrones temporales de producción y pérdida de hojas en individuos en la fase epífita y arborea de dos higueros estranguladores (*Ficus pertusa* y *F. trigonata*) que habitan la sabana estacional Venezolana. Durante los dos años de observación, los epífitos de ambas especies produjeron hojas nuevas durante más tiempo y perdieron y recobraron sus hojas con más frecuencia que los árboles de la misma especie. En ambas especies, la producción de hojas en epífitos (pero no en árboles) tuvo una correlación positiva con la lluvia caída en la quincena anterior a la observación fenológica. Los epífitos de ambas especies fueron deciduos o casi deciduos durante más tiempo en el año y perdieron las hojas en más oportunidades que los árboles de la misma especie. La pérdida de hojas coincidió, en general, con períodos de sequía, pero la correlación negativa con lluvias en la quincena previa fue significativa sólo para árboles de *F. pertusa*. La vida de las hojas fue más corta en epífitos que en árboles. Los patrones de producción y pérdida de hojas se interpretan como una respuesta al déficit de agua sufrido por los epífitos, el cual es evitado, al menos parcialmente, cuando las plantas enraízan profundamente en el suelo.

Key words: epiphytes; *Ficus*; hemiepiphyte; phenology; strangler fig; water relations.

PECULIARITIES IN GROWTH FORM AND REPRODUCTIVE BIOLOGY have attracted many biologists to the study of strangler figs (e.g., Dobzhansky & Murça-Pires 1954, Janzen 1979). Phenological studies of reproductively mature figs, in particular, abound in the literature (e.g., Kjellberg & Maurice 1989) presumably due to the perceived role of figs as "keystone" species in tropical frugivore communities (Terborgh 1986, but see Susilo 1993). Because strangler figs are hemiepiphytes (i.e., they begin their lives as epiphytes and only later become ter-

restrial, free-standing trees) phenological comparisons of epiphytic- and terrestrial-phase individuals may reveal insights into the consequences of epiphytism. Furthermore, if strangler fig populations are limited by seedling survival, phenological studies that include epiphytic-phase individuals may provide information useful in efforts to maintain figs in fragmented or otherwise disturbed forests (McKey 1989).

Hemiepiphytes provide an excellent "natural experiment" on the effects of water availability on phenology. While atmospheric conditions experienced by individual plants often remain the same, hemiepiphyte access to water is greatly increased when epiphytic-phase plants become rooted in the

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ground (Putz & Holbrook 1986; Holbrook & Putz, in press; Williams-Linera & Lawton, in press). Epiphytic figs at our study site in the Venezuelan llanos (savanna) frequently suffer water deficits but are abundantly supplied with nutrients. Water shortage is indicated by observations that epiphytic-phase leaves have lower stomatal densities and much lower dry season transpiration rates than tree-phase individuals of the same species (Holbrook & Putz, in press). In contrast, foliar tissue and epiphytic soil analyses indicate higher N, P, K, and Mg availability to epiphytic hemiepiphytes than to conspecific tree-phase individuals (Putz & Holbrook 1989).

Based on phenological comparisons of plants growing in dry and wet tropical forests (Frankie *et al.* 1974, Opler *et al.* 1980) and comparative studies of gas exchange in epiphytic and terrestrial hemiepiphytes (Ting *et al.* 1987), and evidence in the literature that leaf longevity varies with N concentration and specific leaf area (cm^2/g ; e.g., Chabot & Hicks 1982), we expected epiphytic- and terrestrial-phase individuals to differ phenologically. In particular, we expected the epiphytes to be leafless for longer periods, more restricted in season of leaf production, and to have shorter leaf life spans than tree-phase conspecifics; this paper reports the results of tests of these hypotheses.

STUDY SITE AND METHODS

This study was conducted in a palm savanna 45 km south of Calabozo, Venezuela ($8^{\circ}34'N$, $67^{\circ}35'W$) at an elevation of about 70 m above sea level. Precipitation is markedly seasonal (Fig. 1e) with an annual mean of 1450 mm (Troth 1979). Much of the study area is flooded to a depth of 30–50 cm during the April-to-October rainy season. The vegetation consists primarily of a grass-dominated ground layer overtopped by 100–200 *Copernicia tectorum* (H.B.K.) Mart. palms/ha. Hemiepiphytic (strangler) figs (*Ficus pertusa* L.f. and *F. trigonata* L.) grow on 41 percent of the palms (Putz & Holbrook 1989); both the figs and palms grow to be 6–7 m tall. The figs start their lives as epiphytes but grow to be large, free-standing trees. Duration of the epiphytic phase varies a great deal but averages about 10–20 years; it takes another few years for tree-phase individuals to penetrate the soil down to the permanent water table (pers. obs.).

Phenological comparisons of strangler figs in the epiphytic and tree phases are based on observations made within a 10-ha area at fifteen-day intervals from May 1985 to May 1987. (Missing data for

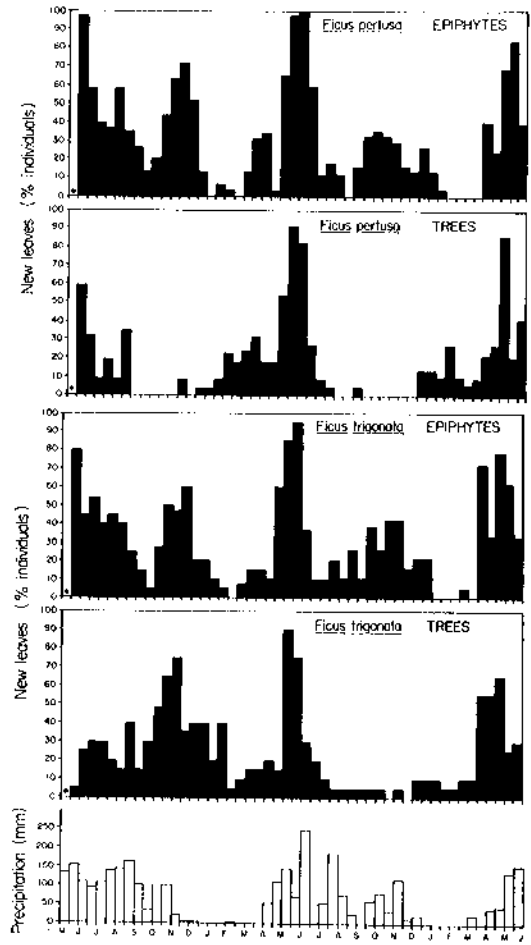


FIGURE 1. The proportion of individuals producing new leaves: *Ficus pertusa* epiphytes ($N = 26$) and trees ($N = 22$); and, *F. trigonata* epiphytes ($N = 18$) and trees ($N = 20$). Bi-monthly precipitation received at the study site beginning one month prior to commencement of phenological observations and continuing through the 1985–1987 study period.

19 November 1985 and 1 March 1986 were approximated by interpolating between the preceding and subsequent observations.) Censused individuals were selected on the basis of accessibility and ease of observation from the ground. Timing of leaf production and loss was monitored on 33 epiphytes and 22 trees of *F. pertusa* and 20 epiphytes and 20 trees of *F. trigonata*. Reproduction was also monitored but the flowering and fruiting stages of reproductive structure (syconia) development were not distinguished.

To estimate leaf life spans, newly emerged leaves were marked on 2–3 branches 2–4 m from the

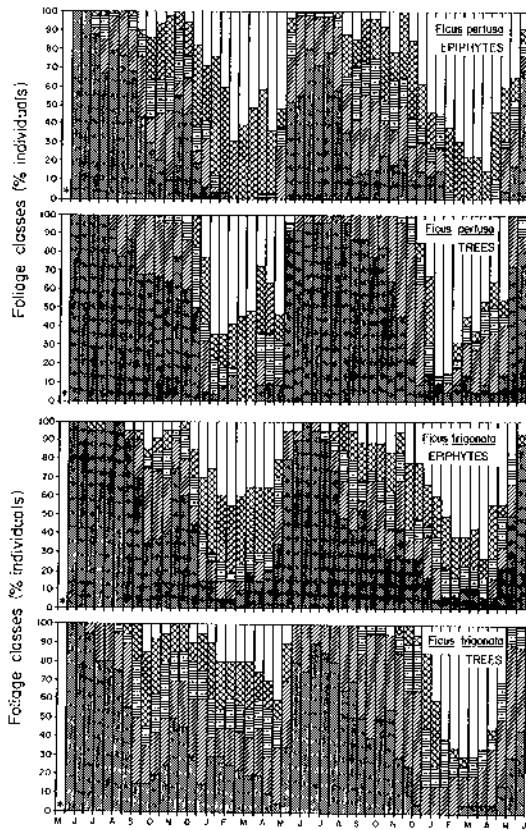


FIGURE 2a-d. Proportion of individuals with different classes of leaf cover: stippled = full leaf (>90%); diagonal lines 70-90%; horizontal lines = 40-70%; cross-hatched = 20-40%; and open = deciduous (<20% see Fig. 1 legend or text for sample sizes).

ground on each of 9 epiphytes (median = 50 leaves/individual) and 10 trees (median = 26 leaves/individual) of *F. pertusa* and 9 epiphytes (median = 14 leaves/individual) and 8 trees (median = 34 leaves/individual) of *F. trigonata*. The marked leaves were exposed to full sun at least part of the day and were monitored at 15-day intervals from emergence until abscission. Newly expanded leaves were marked throughout the first year of observation. Within-species comparisons of leaf life spans on epiphytes and trees are based on the number of census periods between expansion and abscission for half of the marked leaves on each individual (L_{50}).

RESULTS

Mortality rates of the monitored figs were higher for epiphytes than for trees. While there was no mortality of trees in either species during the 25-month observation period, 7 of 33 epiphytic *F. pertusa* and 2 of 20 epiphytic *F. trigonata* died. Cause of death could not be determined in most cases, but several epiphytes were dislodged when leaf bases of the host palms were shed.

Epiphytic plants tended to produce leaves during more of the year but had shorter episodes of leaf production than conspecific trees (Table 1). Leaf production by epiphytes and trees of both fig species was concentrated during, but not restricted to, wet periods (Fig. 1). The proportion of individuals producing new leaves was positively correlated ($P < 0.05$) with rainfall received during the preceding fifteen days in epiphytes of both *F. pertusa* and *F. trigonata* ($r_s = 0.58$ and 0.45 , respectively) but not

TABLE 1. Leaf phenology of epiphytic and tree phase individuals of *Ficus pertusa* and *F. trigonata* during a two-year period in central Venezuela (means and SE). Within species-comparisons based on Student's *t*-tests; variances were pooled when unequal (* $P < 0.05$; ** $P < 0.01$). The interval was 15d and the data presented cover the entire observation period (49 censuses).

	<i>Ficus pertusa</i>		<i>Ficus trigonata</i>	
	Epiphytes (<i>N</i> = 28)	Trees (<i>N</i> = 22)	Epiphytes (<i>N</i> = 18)	Trees (<i>N</i> = 20)
Census periods with new leaves	15.0 (0.86)	** 7.5 (0.44)	14.6 (1.29)	12.5 (1.06)
Number of discrete episodes of leaf production	6.7 (0.28)	** 4.3 (0.22)	8.1 (0.67)	** 5.6 (0.45)
Census periods when completely deciduous	12.0 (1.14)	* 8.6 (0.97)	7.9 (1.46)	6.7 (1.00)
Census periods with <25% leaf cover	21.3 (1.03)	** 12.2 (1.01)	14.8 (1.54)	* 11.0 (1.09)
Number of discrete episodes with <25% leaf cover	4.8 (1.40)	** 3.4 (1.14)	3.6 (1.65)	* 22.7 (0.73)

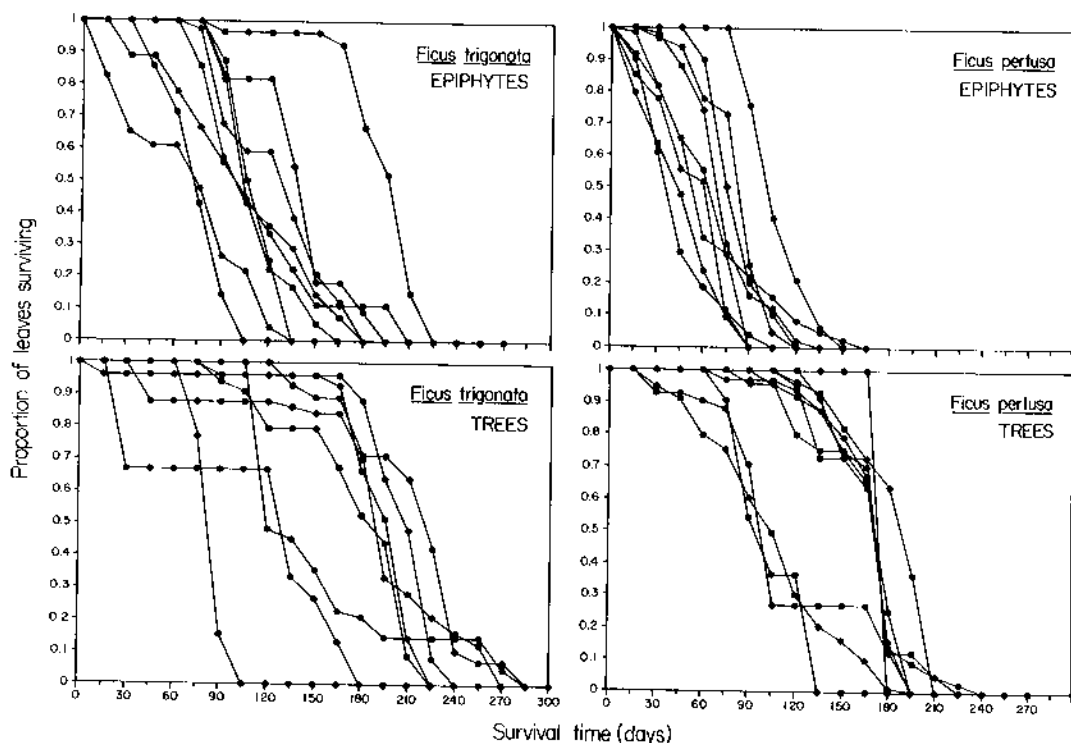


FIGURE 3. Leaf survivorship curves for epiphyte and tree-phase individuals of *F. pertusa* ($N = 9$ and 10 , respectively) and *F. trigonata* epiphytes and trees ($N = 9$ and 8 , respectively).

in trees of either species ($r_s = 0.20$ and -0.15 , respectively).

Epiphytic-phase individuals of both species tended to be leafless or nearly so for longer periods than tree-phase individuals (Fig. 2) and had more discrete episodes of leaf loss than conspecific trees (Table 1). More plants in both phases were leafless or nearly so during dry seasons, but occasionally shed all their leaves when it was very wet. Correlations between the proportion of individuals going leafless and rainfall during the preceding fifteen days were significantly negative for *F. trigonata* epiphytes ($r_s = -0.47$, $P < 0.05$) and *F. pertusa* trees ($r_s = -0.56$, $P < 0.01$) but not for *F. trigonata* trees or *F. pertusa* epiphytes ($r_s = -0.33$ and -0.22 , respectively). We also observed on several occasions complete defoliation of several *F. trigonata* trees by larvae of an unidentified Lepidoptera among individuals not included in the phenological study. Howler monkeys (*Alouatta seniculus*) were observed removing leaves and eating the petioles of epiphytes and trees of both species.

Leaf life spans were generally longer on trees than on epiphytes of the same species (Fig. 3). Mean

leaf lifespan (L_{50}) on 8 censused *F. trigonata* trees was 158.0 days (SE = 17.69); whereas, the mean for *F. trigonata* epiphytes ($N = 9$) was only 93.8 days (SE = 8.14; $t = 3.4$, $P < 0.01$). Mean leaf spans on *F. pertusa* trees ($L_{50} = 144.4$ days, SE = 11.84, $N = 10$) were much longer than on epiphytes ($L_{50} = 58.7$ days, SE = 6.80, $N = 9$; $t = 6.1$, $P < 0.01$).

With the exception of the late 1985 rainy season, reproductive individuals were observed throughout the year (Fig. 4). Reproduction among *F. pertusa* trees was more frequent and temporally more evenly distributed than observed in *F. trigonata*. Frequency of reproduction was not correlated with trunk diameter in either species but epiphytes of neither species reproduced. Reproductive episodes were occasionally curtailed and did not result in seed production because birds and howler monkeys removed the immature syconia.

DISCUSSION

Differences between epiphytic and terrestrial strangler figs in leaf phenology support the idea that

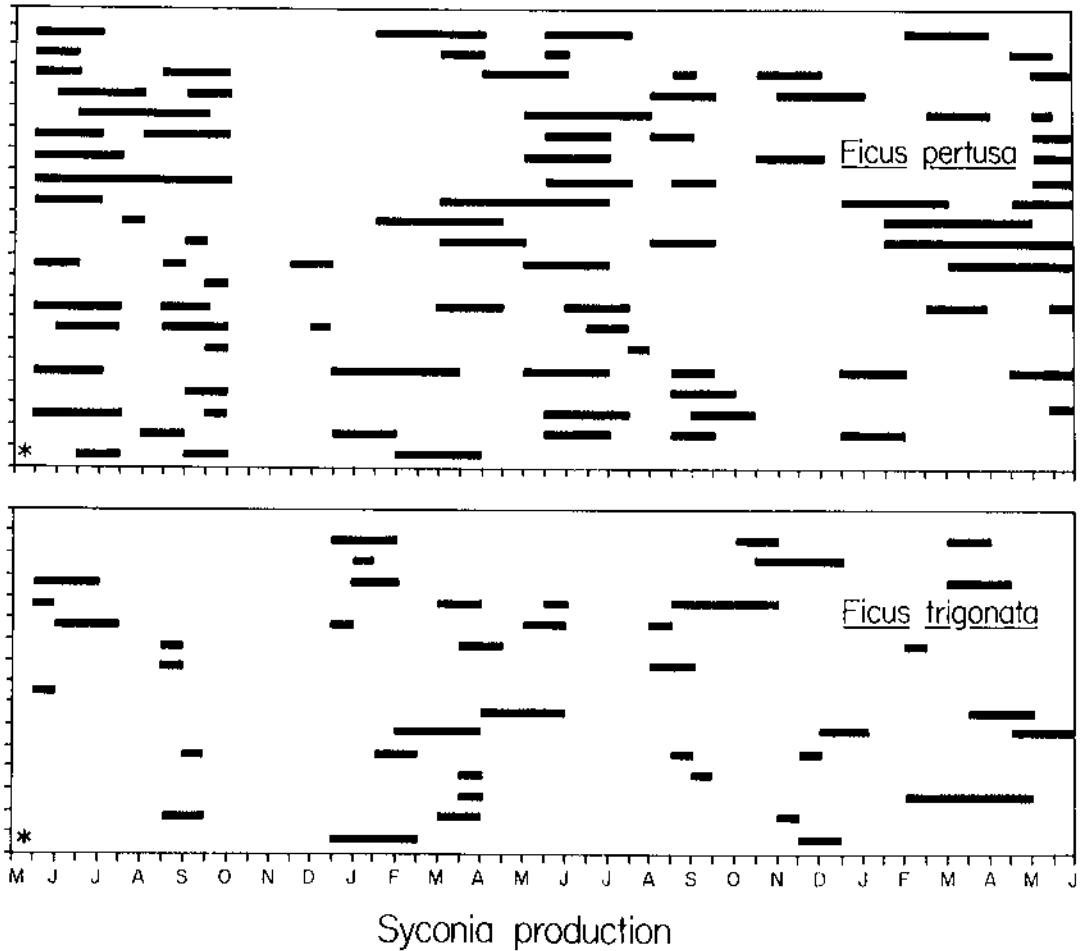


FIGURE 4. Syconia (flower and fruit) production by *Ficus pertusa* and *F. trigonata* trees that reproduced at least once during the 25-month observation period. Each horizontal line across the figure represents one individual.

epiphytic individuals suffer water deficits more frequently than do tree-phase individuals. As hypothesized, epiphytic-phase plants less frequently expanded leaves during dry periods, more frequently went deciduous, and had shorter-lived leaves than conspecific trees. Given the length and severity of the dry period at the study site and the fact that epiphytes have access only to water collected in the crown of the host whereas trees have roots down to the water table (Putz & Holbrook 1989), it is surprising that the differences are not more marked. The majority of tree species in the study area are leafless during much of the dry season (Troch 1979). Thus, the existence of epiphytic-phase strangler figs that expand or even maintain leaves during the dry season was not expected.

Physiological measurements of *F. pertusa* and *F. trigonata* indicate that leaf turgor pressures above zero throughout the day, even during the dry season (Holbrook & Putz, in press). Indeed, wilted leaves of either epiphytic or tree-phase plants were not observed. Due to the effect of the high evaporative demand during the dry season on the relatively exposed epiphytic substrate as well as on leaves, turgor maintenance is apparently achieved by strong stomatal control in epiphytic plants, whereas the trees extract water from deep in the soil (Holbrook & Putz, in press). During the dry season, stomatal opening in epiphytic plants occurred only for a brief period in the morning, with stomatal conductances much lower than in conspecific trees; stomates on tree-phase figs remained open throughout the day.

Epiphytic plants are also better able than tree-phase individuals to retard water loss through leaf surfaces once the stomata are closed (Holbrook & Putz, in press).

The observation that epiphytic plants retain leaves during dry seasons suggests that they are able to maintain a positive carbon balance. Considering that during the dry season stomata on epiphytic plants open each day for only a brief period, the epiphytes are expected to have characteristics that enhance net carbon gain such as a high intrinsic capacity for CO₂ fixation and low leaf construction/maintenance costs. Although we do not have any field measurements of CO₂ uptake in these species, there are marked differences in leaf structure between conspecific epiphytes and trees. Specific leaf area (cm² leaf surface area/g dry leaf mass) of epiphytic plants is 2.4 to 2.8 times greater than in conspecific trees (Putz & Holbrook 1989); this should contribute to the overall carbon budget by reducing the cost of producing leaf surfaces. Shorter leaf life spans are also consistent with the reduced investment in leaf structure in epiphytic individuals (e.g., Chabot & Hicks 1982, Reich 1993) and with their higher N concentration (on a dry mass basis). Nitrogen concentration is often considered to be indicative of maintenance respiration (Field & Mooney 1986) and is negatively correlated with leaf life spans in many multi-species studies (e.g., Reich 1993). The small magnitude of the differences in leaf phenologies reported in this study was unexpected and may in part be explained by the observation that the two growth forms have similar leaf nitrogen contents per unit surface area (Putz & Holbrook 1989).

Epiphytic phase individuals displayed more phenological plasticity than did co-occurring conspecific trees. Episodes of leaf production and loss occurred more frequently and were temporally more tightly linked with rainfall events in epiphytes than in trees. The apparent responsiveness of epiphytic plants to short-term environmental changes may be due to their growth habit as well as their relatively small size. Palm leaves funnel water towards the trunk and consequently even modest rainfall events

are probably sufficient to saturate epiphyte rhizospheres. This same substrate, however, is relatively exposed to the atmosphere and dries quickly. Substantial drying may take place even between rains during the wet season as well as during the prolonged dry season. The swollen, rather fleshy stem bases of epiphytic strangler figs may allow water scavenged from the epiphytic humus to be stored, and then slowly lost through the stomata (Holbrook & Putz, in press).

Reproduction of *F. pertusa* and *F. trigonata* apparently commences only after individuals are well-rooted in the ground; epiphytes were never observed with syconia. Flowering was not associated with any particular leaf phenophase; young syconia were observed on deciduous trees, trees with young leaves, and trees with mature leaves. Like other tropical figs that have been studied (e.g., Windsor *et al.* 1989), *F. pertusa* and *F. trigonata* are fairly aseasonal in reproduction presumably because the wasps upon which they depend for pollination do not survive long outside syconia (Galil 1977, Kjellberg *et al.* 1988).

Trees monitored for leaf change and reproduction showed clear within-crown phenological synchrony, but two large *F. trigonata* trees not included in this study displayed marked phenological asynchrony. The shapes of the trunks of these trees suggest that they each represent two individuals that fused together. This observation provides further support for the idea that individual strangler fig trees can be composed of several distinct individuals (Thomson *et al.* 1991). The rarity with which we observed within crown phenological asynchrony, however, suggests that either fig fusion is rare or that fused individuals become physiologically integrated and phenologically coordinated.

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LITERATURE CITED

- CHABOT, B. F., AND D. J. HICKS. 1982. The ecology of leaf life spans. *Annu. Rev. Ecol. Syst.* 13: 229-259.
- DOBZHANSKY, T., AND B. J. MURÇA-PIRES. 1954. Strangler trees. *Sci. Am.* 190: 78-80.
- FIELD, C., AND H. A. MOONEY. 1986. The photosynthesis-nitrogen relationship in wild plants. In T. Givnish (Ed.), *On the economy of plant form and function*. Cambridge Univ. Press, Cambridge, England.

- FRANKIE, G. W., H. G. BAKER, AND P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62: 881-919.
- GAUL, J. 1977. Fig biology. *Endeavor* 1: 52-56.
- HOLBROOK, N. M., AND F. E. PUTZ. In press. Physiology of tropical vine and hemiepiphytes: plants that climb up and plants that climb down. In S. Mulkey and K. Winter (Eds.), *Tropical plant ecophysiology*. Chapman and Hall, New York, New York.
- JANZEN, D. H. 1979. How to be a fig. *Annu. Rev. Ecol. Syst.* 10: 13-51.
- KJELLBERG, F., AND S. MAURICE. 1989. Seasonality in reproductive phenology of *Ficus*: its evolution and consequences. *Experientia* 45: 653-673.
- , B. DOUMESCHE, AND J. L. BRONSTEIN. 1988. Longevity of a fig wasp (*Blastophaga psenes*). *Proc. K. Ned. Akad. Wet. Ser. C Biol. Med. Sci.* 91: 117-122.
- McKEY, D. 1989. Population biology of figs: applications for conservation. *Experientia* 45: 661-673.
- OPLER, P. A., G. W. FRANKIE, AND H. G. BAKER. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 68: 167-188.
- PUTZ, F. E., AND N. M. HOLBROOK. 1986. Notes on the natural history of hemiepiphytes. *Selbyana* 9: 61-69.
- , AND ———. 1989. Strangler fig rooting habits and nutrient relations in the llanos of Venezuela. *Am. J. Bot.* 76: 781-788.
- REICH, P. B. 1993. Reconciling apparent discrepancies among studies relating life span, structure and function of leaves in contrasting plant forms and climates: 'the blind man and the elephant retold.' *Funct. Ecol.* 7: 721-725.
- SUSILO, A. 1993. Frugivores, remnant trees, figs and regeneration of burned forest in Kutai National Park. East Kalimantan, Indonesia. M.S. Thesis, Univ. Florida, Gainesville, Florida.
- TERBORGH, J. 1986. Keystone plant resources in tropical forests. In M. E. Soule (Ed.), *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- THOMSON, J. D., E. A. HERRE, J. L. HAMRICK, AND J. L. STONE. 1991. Genetic mosaics in strangler figs: implications for tropical conservation. *Science* 254: 1214-1216.
- TING, I. P., J. HANN, N. M. HOLBROOK, F. E. PUTZ, S. L. DA STERNBERG, D. PRICE, AND G. GOLDSTEIN. 1987. Photosynthesis in hemiepiphytic species of *Clusia* and *Ficus*. *Oecologia* 74: 339-346.
- TROTH, R. G. 1979. Vegetational types on a ranch in the central llanos of Venezuela. In F. Eisenberg (Ed.), *Vertebrate ecology in the northern Neotropics*, pp. 17-30. Smithsonian Institution Press, Washington, D.C.
- WILLIAMS-LINERA, G., AND R. O. LAWTON. In press. The ecology of hemiepiphytes in the forest canopies. In M. D. Lowman and N. Nadkarni (Eds.), *Forest canopies*. Academic Press, Orlando, Florida.
- WINDSOR, D. M., D. W. MORRISON, M. A. ESTRIBI, AND B. DE LEON. 1989. Phenology of fruit and leaf production by 'strangler' figs on Barro Colorado Island, Panamá. *Experientia* 45: 647-653.