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A NATURAL HISTORY OF STRANGLING BY FICUS CRASSIUSCULA IN COSTA RICAN LOWER MONTANE RAIN FOREST

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ABSTRACT. The life history of *Ficus crassiuscula,* a strangling fig of the subgenus *Pharmacosycea,* differs markedly from that of the better known strangling figs of the subgenus *Urostigma.* Seedlings of *F. crassiuscula* develop into viny saplings, capable of spreading over several m². This growth pattern allows final trunk development to take place at a site other than that of germination. The vininess of very young *F. crassiuscula* also suggests heterochronic pathways for the evolution of the vine growth habit among figs.

Ficus crassiuscula Warburg ex. Standley is an unusual member of the subgenus Pharmacosycea in that it starts life as a viny epiphyte but subsequently establishes an erect trunk and eventually strangles its host to become one of the largest canopy trees in the lower montane rain forests (*sensu* Holdridge 1967) of the Cordillera de Tilaran of Costa Rica (Lawton 1986). In the windward cloud forests of the Monteverde Cloud Forest Reserve *F. crassiuscula* individuals are not distributed randomly among potential host species (Daniels & Lawton 1991). One of the more interesting aspects of the host preference of *F. crassiuscula* is that the critical stage in determining the pattern of host preference involves the morphological transition from a viny epiphyte (hereafter referred to as a viny sapling) to a juvenile stage with an erect trunk (Daniels & Lawton 1991). In previous work we have identified the strangling habit in *F. crassiuscula* (Lawton 1986, 1989), and described host and habitat preferences (Daniels & Lawton 1991) without describing in detail the unusual growth form and life history of this species. This paper will describe more specifically the life history stages of F. *crassiuscula,* and will provide morphometric data on the differences between viny saplings and adult trees.

STUDY SITE

This study was conducted in the lower montane rain forest along the crest of the central Cordillera de Tilaran in the Monteverde Cloud Forest Preserve (10°12′N, 84°41′W) of northern Costa Rica. The Preserve is owned and operated by the Tropical Science Center of San Jose, Costa Rica. The vegetation along the crest of the Cordillera is a complex forest mosaic, the character of which is largely dictated by the patterns of exposure to the northeast trade winds flowing over the mountains (Lawton & Dryer 1980). Dwarfed forest formations (elfin forest) occupying wind-swept ridge crests are interdigitated among stands of taller cloud forest found in protected ravines and on lee slopes. The study site is an 8.8 ha mapped portion of an approximately 10 ha watershed on the southeastern side of the summit of Cerro de las Centinelas at an altitude of about 1500 m. Elfin forest occupies the boundary ridge crests and upper windward slopes, and grades into taller cloud forests in the ravine bottom and along lee slopes. In the taller cloud forest *Ficus crassiuscula* is a prominent member of the upper canopy, and grows to 25 m in height and 1.5–2.0 m in diameter at breast height.

FICUS CRASSIUSCULA LIFE HISTORY STAGES

The general life history of strangling figs in the subgenus *Urostigma,* which includes the common stranglers of both the paleo- and neotropics, is fairly well understood (Richards 1952, Dobzhansky & Murca-Pires 1958, Putz & Holbrook 1986). The seeds of urostigmoid strangling figs are broadly dispersed by bats or birds and usually germinate far from the ground, generally in a humus filled crotch between the trunk and some large branch of the host tree. Here the seedling anchors itself with clasping roots that grow around the trunk and anastomose. The seedling subsequently grows into a stout bush, which then sends roots down to the soil. These descending roots multiply, branch, anastomose, and thicken until the trunk of the host tree is encased in a network

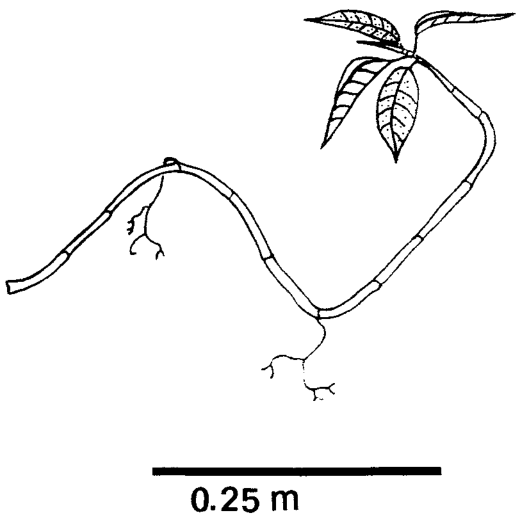

FIGURE 1. Young *Ficus crassiuscula* viny sapling showing rooting at the nodes and juvenile foliage.

of strong roots; meanwhile the crown of the fig grows large, usually shading that of the host. Below ground the fig probably competes with the host for water and nutrients. After a time the host tree usually dies and rots away, leaving the fig as a wholly independent tree, with a hollow, lattice-work trunk of root origin, in the host's place.

The life history of *Ficus crassiuscula* differs notably from that of the urostigmoid stranglers, and for our purposes can conveniently be divided into four distinct stages: (1) a seed, or initial dispersal stage, (2) a subsequent viny sapling stage, (3) a transitional juvenile stage when an erect trunk develops, and (4) a reproductively mature, adult canopy tree stage.

We know relatively little about seed dispersal in *F. crassiuscula.* The syconia (hereafter "figs") are quite large, ca. 5 cm in diameter. While unripe, these release a great deal of very sticky latex if damaged. When fully ripe, no latex is released on damage, and the figs are soft, pink inside, and quite palatable to people. We have observed fruits eaten by frugivorous and omnivorous mammals, including white-faced and howler monkeys, squirrels, and coatis; and birds, including parrots, emerald toucanets, and clay-colored and mountain robins. Many figs fall to the forest floor and are there eaten by agouti, paca, brocket deer, collared peccary, and Baird's tapir. We do not know if bats, major dispersers of *Ficus* spp. (see the reviews of Janzen 1979, Marshall 1985, Fleming 1988), eat the figs of *Ficus crassiuscula,* but suspect that they do.

Little is known abut the germination requirements of *F. crassiuscula,* but the distribution of

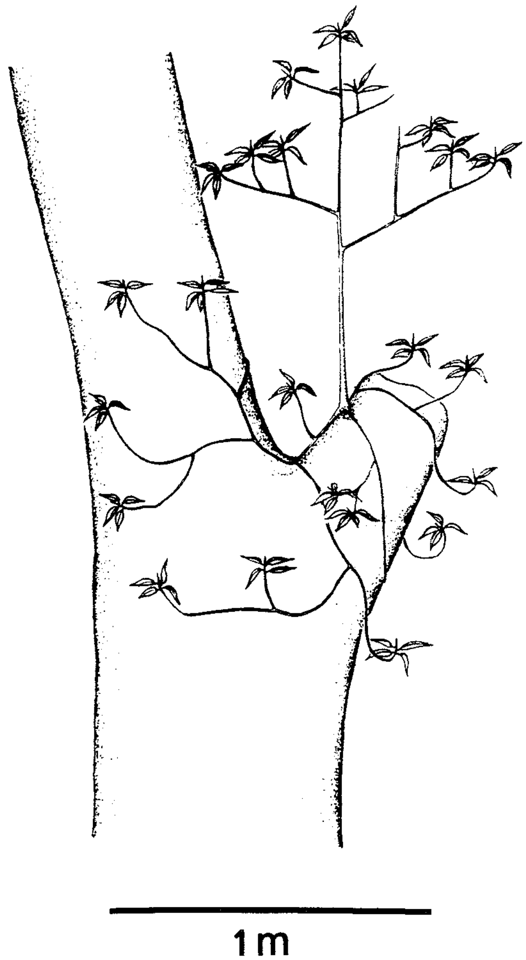

FIGURE 2. Young transitional juvenile stage *Ficus crassiuscula* on a major crotch of *Guarea tuisana.* A freestanding vertical leader has been established, but much of the viny sapling stage persists.

viny saplings suggests that germination and early seedling establishment are not detectably influenced by species identity of potential hosts (Daniels & Lawton 1991).

Following germination *Ficus crassiuscula* forms a delicate stem (approximately 0.3 cm in diameter) with 3–5 small leaves at the apex that are distinctly juvenile in character (FIGURE 1). To compare juvenile and adult foliage and branches we gathered samples haphazardly from viny saplings within reach (near the ground or only a short climb above it), and from a freshly fallen adult. Several fully expanded, but not senescent, leaves from each twig were measured. In comparison to the leaves of adult *F. crassiuscula,* the juvenile leaves are both shorter and narrower (juvenile mean leaf length = 9.51 cm, SE = 0.23 cm, mean leaf width = 2.85 cm, SE = 0.09 cm, N = 37; adult mean leaf length = 11.65 cm, SE = 0.31 cm, mean leaf width = 5.18 cm, SE = 0.11, N = 25; $P < 0.001$ for both t-test comparisons). Juvenile leaves also have pronounced drip tips, and conspicuous widely scattered hairs on the adaxial leaf surface, features absent from the leaves of adults. The juvenile leaf form persists through the viny sapling growth phase described below.

The initial stem elongates and branches sparsely to form a sprawling viny tangle, that consists of many (2–20 or more) branching primary stems generally less than 0.5 cm in diameter (FIGURES 1, 2 in part). We call these viny saplings; they have no apically dominant leader. The branching pattern and stem taper of these viny saplings differ from those of adult *F. crassiuscula.* The mean stem length between branchings was 46.4 cm (SE = 4.88 cm, N = 3) in an extensively sprawling viny sapling, but 26.9 cm (SE = 1.53 cm, N = 3) in canopy branches taken from a large adult. The mean taper, the change in stem diameter over a length of stem, was 0.58 cm/m in the viny sapling (SE = 0.017 cm/m, N = 3), but 1.18 cm/m (SE = 0.012 cm/m, N = 3) in the self-supporting twigs and primary branches from the adult. The stems of viny saplings grow over and through existing vegetation and are at least partially appressed to the epiphytic mat of bryophytes and soil-like organic debris which covers nearly all exposed tree surfaces in this forest (Nadkarni 1981). The stems root freely where nodes contact the substrate. These nodal roots do not thicken or anastomose, and they are generally 1–3 mm thick and 1–10 cm long. They are similar in these respects to those roots found in the Asian climbing figs of the subgenus Ficus (e.g., *F. hederacea* Roxb. and *F. pumila* L.) (Hill 1967, Corner 1976). Individual viny saplings may cover several square meters and may propagate vegetatively through fragmentation. We have observed viny saplings which sprawled from one host to another.

Apparently any stem of a viny sapling may undergo the transition to an erect trunk with secondary growth, but usually only one, generally in a well lit location, will begin to thicken and grow erectly. At this stage the plant becomes more tree-like in appearance, and begins to send down the host trunk a single large root about as thick as the erect trunk of the fig (FIGURES 2, 3). This main root generally grows flattened against the trunk of the host, and coils gently down the host trunk, but does not develop into a clasping anastomosing net of many roots as do the roots of the urostigmoid stranglers. Where this main root contacts the ground, it thickens and often branches 1–2 m above the soil. These root branches grow obliquely away from the main root while remaining appressed to the trunk of the host. Meanwhile, the crown grows larger and comes to exhibit the branching patterns and leaf morphology characteristic of adult *Ficus crassiuscula.*

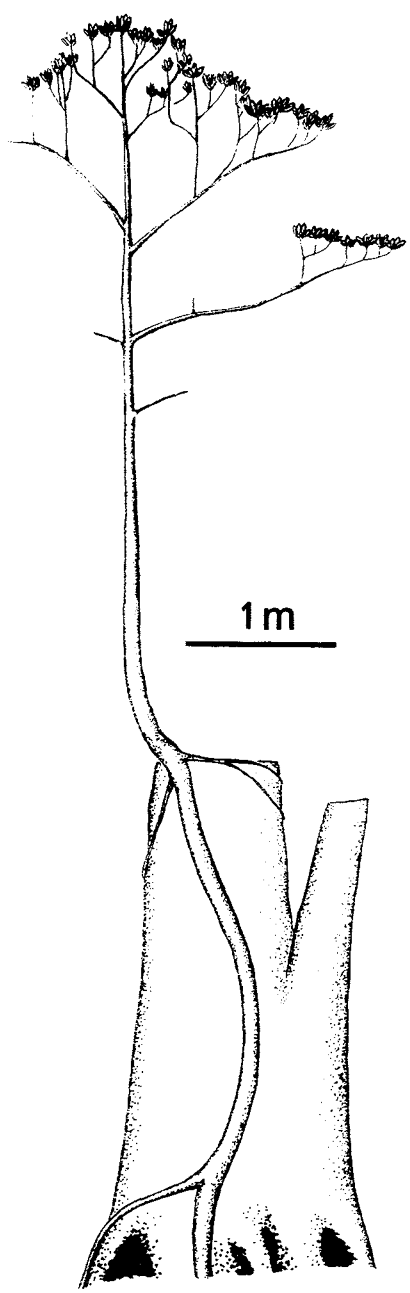

FIGURE 3. Young adult *Ficus crassiuscula* established atop an *Ocotea* sp. stump.

As *F. crassiuscula* grow larger, they produce a

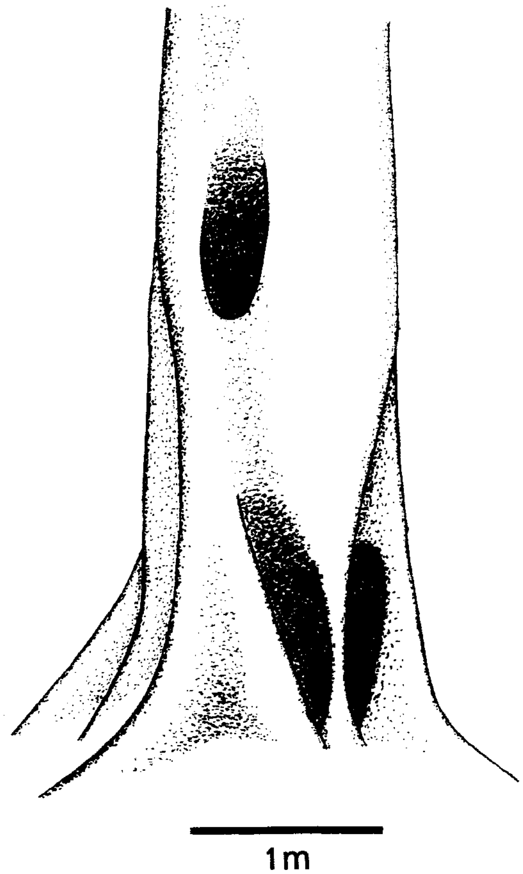

FIGURE 4. Lower trunk of large mature *Ficus crassiuscula* showing the typical convolutions resulting from the strangling root growth and amalgamation.

broadly spreading crown and continue to envelop the host trunk with roots. The envelopment of the host trunk generally proceeds as the main root, and perhaps one or two other large roots, undergo accelerated radial growth parallel to the surface of the host trunk. This results in *F. crassiuscula* roots with a strongly flattened appearance, that gradually coalesce, and envelop the host from the ground up. This contrasts strongly with the urostigmoid stranglers, that envelop the host trunk in a reticulum of anastomosing roots. Envelopment by *F. crassiuscula* continues until the fig tree has completely encased all or a large portion of the trunk of the host below the point of establishment. The host then usually dies and rots away, leaving the fig tree free-standing in its place. Although the trunks of successful urostigmoid stranglers often have a large central cavity originally occupied by the host trunk, such central cavities are much less prominent in mature *F. crassiuscula,* and are commonly completely occluded by secondary growth of the massive trunk roots.

Discussion

Ficus crassiuscula adds several dimensions to our appreciation of the complexities of tropical tree regeneration. First, the viny sapling stage of the life cycle, in which a seedling develops into a sprawling vine covering several square meters, offers clear advantages in that it allows for the morphological transition into an adult with an erect trunk at a site other than that of germination. Second, the viny sapling stage of *Ficus crassiuscula* appears to illustrate a possible evolutionary transition between trees and vines. And finally, the establishment biology and growth patterns of plants like *Ficus crassiuscula* reinforces the contention of Grubb (1977) that specialization in the regeneration niche is an important contributor to diversity in both temperate and tropical habitats.

In most trees and shrubs germination fixes an individual in space. While dormancy mechanisms may help ensure that germination occurs under conditions favorable for seedling establishment, and presumably growth to maturity, they cannot guarantee that conditions just a short distance away might not be still better suited for the plant. There seem to be several solutions to this problem. Specialized dispersal may help. Two-phase seed dispersal, in which myrmechory follows vertebrate endozoochory, is known in several *Ficus* species (Roberts & Heithaus 1986, Davidson & Epstein 1989, Kaufman *et al.* 1991). These systems have the potential advantages of broad dispersal in the initial phase, followed by the secondary removal of seeds to sites more suitable to germination. While two-phase dispersal may provide fine tuning in the dissemination of seeds to safe-sites for germination, clonal growth like that of *Ficus crassiuscula* viny saplings may also provide strategically similar, if tactically different, options for determining the site of final establishment. Clonal growth, unlike two-phase seed dispersal, leaves the options of where to grow to the plant concerned (Salzman 1985, Bazzaz 1991).

The importance and utility of this option in *F. crassiuscula* (considering that adults grew from viny saplings and assuming that the distribution of viny saplings is the same as it was in the past) is demonstrated by the distributions of viny saplings and subsequent life history stages (Daniels & Lawton 1991). These differ both among host species, and among locations within host species. Relative to viny saplings, adults are more likely to be established in trunk crotches than in other locations. In addition, viny saplings of *F. crassiuscula* exhibit no host species preferences, yet host preference is clearly evident at later life history stages. This implies that some sites and hosts are more suitable for growth to maturity than others. Whether this is the result of disproportionate mortality in certain locations within hosts or between different host species is unclear, but it is obvious that the ability to grow to better sites will be advantageous in this setting.

The similarities between some Asian climbing figs and *F. crassiuscula* viny saplings is interesting in light of Corner's (1976) suggestion that the Asian climbing figs arose through the neotenic retention of the juvenile viny or leptocaulous character found in ser. Superbae, ser. Drupaceae, ser. Subvalidae, and other series of subgenus *Ficus*. Corner notes that these climbing figs begin epiphytically, as do stranglers, except that they are generally rooted closer to the ground. Similarly, the majority (58%) of the viny saplings of *F. crassiuscula* are initially established within 4 m of the ground (Daniels and Lawton 1991). We also note that reiteration at wound sites on the trunks of adult *F. crassiuscula* produces young stems with the viny sapling form. All this suggests that there is an opportunity for the evolution of neotropical viny figs from forms like *F. crassiuscula.*

The advantages of hemiepiphytism and strangling are manifold, and have been discussed elsewhere (Richards 1952, Dohbzansky & Murca-Pires 1958, Whitmore 1975, Putz & Holbrook 1986). Furthermore, strangling has long been recognized as a highly specialized regeneration strategy (Schimper 1903, Richards 1952). As Bazzaz (1991) points out though, notions about habitat selection are rarely applied to plants, "perhaps because the majority of them are immobile." The case of *Ficus crassiuscula* demonstrates that such behaviors may be important in shaping the patterns of individual distribution of individual species populations, and as such, important determinants of community structure.

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