BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

Within-Crown Flowering Synchrony in Strangler Figs, and Its Relationship to Allofusion

Author(s): James D. Thomson, Sara Dent-Acosta, Patricia Escobar-Paramo and John D. Nason

Source: *Biotropica*, Sep., 1997, Vol. 29, No. 3 (Sep., 1997), pp. 291-297

Published by: Association for Tropical Biology and Conservation

Stable URL: https://www.jstor.org/stable/2389144

BIOTROPICA 29(3): 291–297 1997

Within-Crown Flowering Synchrony in Strangler Figs, and Its Relationship to Allofusion[1]

James D. Thomson, Sara Dent-Acosta, Patricia Escobar-Páramo

Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794, U.S.A.

John D. Nason[2]

Department of Botany, University of Georgia, Athens, Georgia 30602, U.S.A.

ABSTRACT

We studied flowering phenology at the level of individual branches within strangler fig trees to determine (1) whether branches bloomed asynchronously within trees and (2) whether asynchrony, if observed, could be ascribed to genetically different branches of mosaic trees (*i.e.*, trees formed by spontaneous grafting of genetically different individuals) undergoing individual flowering cycles that were out of phase with each other. Although asynchrony was fairly common, it most often reflected individual branches failing to bloom during one flowering episode, then coming back to bloom in synchrony at the next episode. We detected fewer mosaic trees than expected, and found only a very weak suggestion that mosaic trees may show less within-tree synchrony than simple trees.

RESUMEN

La fenología de floración de cinco especies de ficus extranguladodres fue estudiada a nivel de ramas individuales dentro de un mismo árbol. El propósito del estudio fue determinar: (1) si las ramas de un mismo árbol producían flores en asincronía, y (2) si la asincronía, de presentarse, podía estar relacionada a la existencia de un mosaico genético en las ramas de un mismo árbol (*e.i.*, árboles formados por la fusión de individuos genéticamente diferentes) donde cada genotipo presenta un ciclo fenológico independiente de los otros genotipos. Aunque los eventos de floración asincrónica fueron comunes, en la mayoría de los casos las ramas que estaban des-sincronizadas en un episodio de floración se unieron al resto de las ramas en el siguiente episodio. El número de árboles "mosaico" encontrados fue mucho menor que lo esperado y sólo se encontró una pequeña evidencia de que estos árboles muestran menos sincronía en floración que los árboles genéticamente uniformes.

Key words: Ficus; *flowering; genetic mosaic; graft; mutualism; Panamá; phenology; pollination; strangler fig.*

STRANGLER FIGS owe their name, their distinctive appearance, and their successful establishment to the spontaneous grafting of the encircling aerial roots that lock a host tree in a lattice of fused wood (Putz & Holbrook 1986). When multiple stranglers of the same species colonize the same host, allofusions may form between them: Thomson *et al.* (1991) found that leaves from different parts of the crowns of large Panamanian stranglers frequently differed in their multilocus electrophoretic genotypes. These authors concluded that multiple seedlings had coalesced into single mosaic trees that appeared unitary because the grafts had long since disappeared under the continuing overgrowth of wood. Such mosaics provoke interesting general questions regarding the extent of physiological integration, the balance between mutualistic versus competitive interactions, and the relatedness of the members. There are also questions specific to figs, one of which is the focus of this paper.

Thomson *et al.* (1991) hypothesized that allofusions could interact with the unique pollination biology of figs in a way that could be relevant to the conservation of small populations. Models of phenology and pollination (Kjellberg & Maurice 1989, Bronstein *et al.* 1990; also see McKey 1989) suggested that figs should require large minimum viable population sizes because populations of the host specific wasps that are required for pollination (Ramirez 1970, 1974; Wiebes 1979) should need a virtually continuous progression of flowering trees throughout the year. Although figs are unusual among flowering plants in that individuals do flower at staggered times, it should still take many trees to maintain wasp populations in one area.

---

[1] Received 21 June 1995; revision accepted 16 January 1996.

[2] Present address: Department of Biological Sciences, University of Iowa, Iowa City, Iowa 52242, U.S.A.

However, if the genetically different portions of mosaic stranglers tend to flower at different times, the populations of figs required for supporting wasps might be smaller than predicted, at least in terms of the numbers of *trees.*

The literature (reviewed by Janzen 1979, Bronstein 1992) suggests that flowering is usually highly synchronous within trees, a view consistent with more recent studies of Panamanian species (Milton 1991, Milton *et al.* 1982, Windsor *et al.* 1989). Indeed, flowering synchrony in the female phase should be highly advantageous because it should provide a stronger odor cue for attracting pollinators (Van Noort *et al.* 1992, Ware *et al.* 1993, Hossaert-McKey *et al.* 1994). Because flowering times are closely coupled to fruiting times, a second advantage for synchronous flowering might arise through the greater attractiveness of large fruit crops to seed dispersers, particularly bats using odor cues (Herre 1996). However, existing phenological studies have seldom recorded data from subunits within trees.

It is well known that some species characteristically attain asynchrony by producing figs gradually *within* branches, and it has been suggested that such asynchrony may be adaptive for trees in isolation (Ramirez 1970) or near edges of ranges (Bronstein 1989, Bronstein & Patel 1992). For example, in *Ficus aurea* in Florida, trees almost always bear figs at some stage of development, and frequently bear figs at all stages simultaneously (Bronstein & Hossaert-McKey 1995). Such patterns are very unlikely to bear any relationship to mosaic diversity. Also, if continuous fig initiation of this sort occurred in the well-studied Panamanian species, it would surely have been noted (E. A. Herre, pers. comm.). Asynchrony could also occur at the whole-branch level, however, and such asynchrony would be much more likely to escape notice in a typical phenological census. For example, if part of a tree's crown flowered in January and another part in June, this might be recorded simply as "two flowering episodes by one individual", depending on the goals of the study. Given mosaicism, it is possible that a more accurate description would be "two fused individuals undergoing one episode each." Because we occasionally saw trees in Panamá with this sort of heterogeneous crown, we decided to combine a genetic scan of numerous trees for mosaicism with a year of branch-by-branch flowering censuses. The specific goal was to see whether, within trees, genetically different branches were more likely to bloom at different times than were genetically identical branches.

In addition to occurring at various levels of organization, asynchrony—like sin—may arise from omission or commission. Suppose that we observe a tree in which some branches are flowering, some not. One possibility is that the flowering may have been initiated by a tree-wide cue for synchronized flowering, but that some branches were unable to respond to the cue for some branch-specific reason, *e.g.*, low reserves of photosynthate owing to shading. This sort of asynchrony is likely to be transient: such branches, which we call "drop-outs", may bloom in synchrony with the rest of the tree during the next cycle if their resources have been replenished. This is asynchrony by omission: there is only one cycle, and participation in it is incomplete. Alternatively, different branches may flower in response to branch-specific cues that are produced intrinsically and out of phase. The individualistic cycles of such branches constitute asynchrony by commission: there are multiple independent cycles. Clearly, only the latter sort of asynchrony will give mosaic trees a greater ability to maintain wasp populations, and only this sort is relevant to the primary goal of the study. However, the two types are not necessarily easy to distinguish, and observations over several cycles are essential; therefore, we conducted protracted censuses of several Panamanian species.

METHODS

Our work was based at the Smithsonian Tropical Research Institute's field station on Barro Colorado Island (BCI), Panamá. As in the previous study of allofusion (Thomson *et al.* 1991), we chose shoreline trees (on BCI and neighboring islands and peninsulas) that were accessible by boat. Because the crowns of such trees typically descend nearly to the water, fruits could be obtained for dissection to verify their stage of development, rendering our observations more accurate.

In July 1993 we located strangler figs of five species: *Ficus citrifolia* (N = 12), *F. obtusifolia* (N = 11), *F. popenoei* (N = 6), *F. nymphiifolia* (N = 12), and "*F.* near *trigonata*" (N = 8; for nomenclature, see Herre (1989)]. We used sketches and Polaroid photographs to characterize the branch structure of the trees, then collected a leaf or leaves from each branch. In some cases, we could only reach a single branch with our 4 m pole pruner. We kept these trees in the study; if subsequent observations revealed asynchronous flowering in these trees, we planned to obtain leaves from the inaccessible high branches by other methods. The

TABLE 1. *Criteria used to characterize the reproductive status of individual branches. Not all branches passed through all these phases: some crops of syconia aborted and abscised during the bud phase, others during interphase.*

Reproductive phase	Defining characteristics
None	No buds visible
Bud	Buds large enough to identify reliably (*ca.* 3 mm diam.)
Prefemale	Buds are full-sized, flowers are open with receptive stigmas that look white and fresh; wasps absent
Female	Foundress wasp(s) moving about in syconia
Interphase	Seeds and offspring wasps developing in syconia; foundress(es) dead; stigmas brownish, senescent
Male	Exit tunnel opened, female wasps leaving or very recently gone; male wasps alive; anthers open, white pollen visible
Postmale	Male wasps dead, syconia ripening
Dispersal	Figs falling and being removed by animals

leaves were returned to BCI within hours, cut into small pieces, and freeze-dried. At the University of Georgia, Nason determined the multilocus allozyme genotype of each leaf, using the methods of Nason *et al.* (1996). Ten polymorphic loci were scored for each species: AAT1, AAT2, DIA1, FE2, IDH, LAP1, MDH1, PGI2, TPI1, and TPI2. Based on the high levels of diversity at these loci, failure to detect true genetic differences between branches in a mosaic tree should be only about 3 percent in *F. popenoei* and less than 0.6 percent in the other species (J. Nason, pers. obs.).

Beginning on 25 July 1993, we began a program of censuses. The census intervals were irregular, both by design and necessity: we tried to ensure that each tree was visited at least every two weeks, and more often (every 5–7 d) as it flowered. Aside from a gap from 9 to 26 December 1993, this routine was maintained for the 49 trees until 2 July 1994. Eight of these trees had only a single branch genotyped. Given the observed duration of the cycles of flower and fruit production, it is unlikely that any reproductive events were missed.

At each census visit, we searched for reproductive structures and classified each branch into a developmental category, as defined in Table 1. Where branches could be reached with a 4 m pruning pole, we took a sample of 5–10 developing syconia and dissected them to verify their internal state of development. Branches that were out of reach were examined by binoculars and the state of the figs estimated based on the information gained from dissections of other figs of the same species.

RESULTS

Mosaicism.—The genetic survey turned up considerably fewer allofused trees than we expected, based on the previous results of Thomson *et al.* (1991). The previous samples were from trees in the same areas, chosen with similar criteria; indeed, a number of trees were probably assayed in both studies. Also, we used the same criterion–a single allozyme difference–to determine mosaicism. Extrapolating from the 1991 study, where 13 of 14 trees appeared to be mosaics, we would have expected to find roughly 39 mosaic trees in our sample of 41 trees for which we sampled multiple branches. Instead we found seven, with no mosaics at all in *Ficus popenoei* and *F.* near *trigonata.* Although we cannot make a precise evaluation, owing to variation in the species sampled and the distribution of branches sampled per tree, we doubt that the *ca* six-fold difference between the two surveys can be attributed to mere chance. The distributions of alleles reported by Thomson *et al.* (1991) were derived by scoring as many loci as possible, to the extent of including some enzymes for which patterns of expression and inheritance had not been established. These less reliable enzymes apparently contributed a large number of the apparent differences reported in that study. The newer survey used much stricter criteria for deciding which enzymes to score. We scored only those that were regularly expressed and for which Mendelian inheritance in progeny arrays had been confirmed. The lower frequency of mosaics observed here is not due to a decrease in the genetic information available, because 97 percent or more genetic differences should have been detectable based on the loci used (J. Nason, pers. obs.). We regard the new data as much more reliable, and believe that Thomson *et al.* (1991) erred in classifying so many of their trees as mosaics. Mosaicism definitely occurs, however, and in *F. obtusifolia* it occurs in almost 50 percent of the trees examined. Still, the lower frequency of mosaicism gives us unexpectedly low statistical power for our comparison of flowering synchrony in mosaic versus non-mosaic trees.

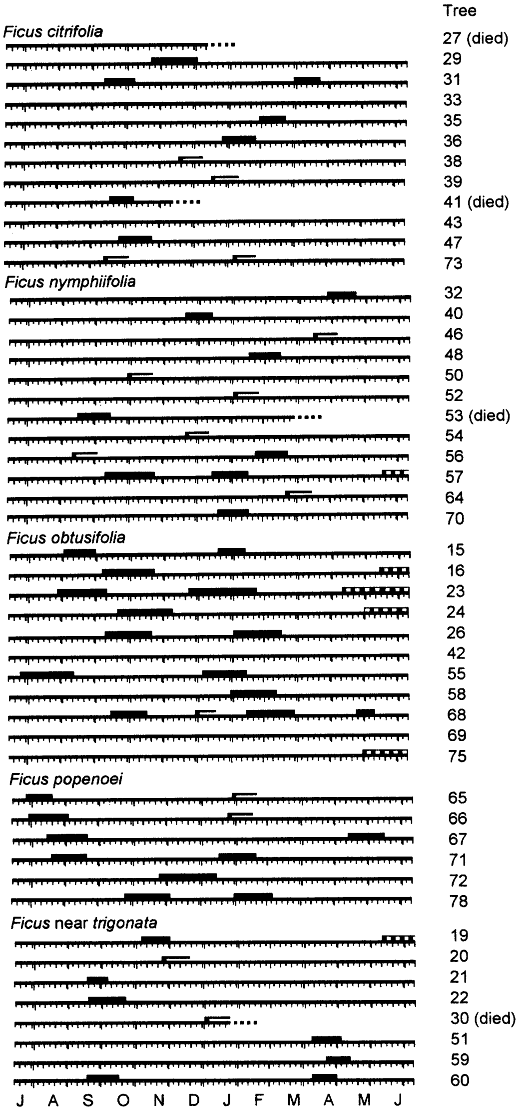

FIGURE 1. Flowering phenology of five species of strangler fig in the vicinity of Barro Colorado Island, Panamá, monitored from 25 July 1993–2 July 1994. A heavy bar indicates a flowering episode, lasting from the onset of female phase until male phase (see Table 1 for definitions). A half-filled bar indicates the initiation of female phase but abortion before the male phase. In this analysis, we have not attempted to distinguish true, maternally-caused abortion from fruit failure due to insufficient pollination. Checkerboard patterns indicate flowering episodes that were still in progress when the study ended.

SYNCHRONY.—The census data (Fig. 1, Table 2) support the traditional picture of fig flowering phenology: episodes of mass flowering are highly synchronized within trees and asynchronous among trees. We did not observe asynchronous flowering within branches, which greatly simplified the assignment of developmental categories. In all five species, instances of among-branch asynchrony were almost entirely "asynchrony by omission", with one or more branches dropping out for one flowering cycle, but coming back to flower synchronously in the next cycle. Only a few possible cases of "asynchrony by commission" were observed, and none of them is definitive. In *F.* near *trigonata* 20 (non-mosaic), we saw only one flowering cycle, so the asynchrony there might have been of either type. In *F.* near *trigonata* 30 and *obtusifolia* 68, both of which were non-mosaic trees, potential interbranch asynchrony was followed by the death of the tree (in tree 30) or the death of the branch (tree 68). This suggests that the breakdown may have been a pathological response to disease or breakage; in any event, there was no way to confirm that these asynchronies were not simple dropout cases. (S. G. Compton (pers. comm.) has stimulated fruiting on individual branches of *Ficus burt-davyi* by half-breaking the branches).

Of the seven mosaics, only two showed possible "asynchrony by commission." *Ficus obtusifolia* 42 and 69 both failed to develop any mature figs, even to the female stage, but in both cases the different branches initiated buds at different times. These buds were either dormant or abortive, remaining on the trees for weeks to months, but never completing their development. In the other cases, flowering was either uniformly synchronous or synchronous with transient dropouts.

DISCUSSION

Determining the nature of intra-crown asynchrony requires long observation. Eleven of our 41 multi-branched trees showed asynchrony by omission, having at least one flowering episode in which at least one branch failed to bloom with the others. Had these trees only been observed during that one flowering period, they would have appeared consistent with the hypothesis that different branches were flowering on different cycles. Indeed, our observation of trees in just such a condition was one of our justifications for the present study. Only by observing multiple cycles could we ascertain that these cases represented transient dropouts rather than the out-of-phase cycling of two reproductively independent entities.

That dropouts are common exceptions to the general rule of synchrony within trees suggests the hypothesis that flowering is controlled by a tree-wide stimulus, probably hormonal, and that some

TABLE 2. *Summary of branch characteristics and flowering histories of 49 Panamanian fig trees from 25 July 1993–2 July 1994. Tree numbers are arbitrary identifiers used in a larger study by J. Nason. Boldface type highlights the seven mosaic trees detected, and the fraction of trees that are mosaic is shown after the species name. Large branches within a crown are labeled A, B, C, etc. Under "asynchrony history," the term "synchrony" used alone indicates that all branches flowered simultaneously during each flowering episode recorded. When combined with other descriptions and set off by semi-colons, "synchrony" refers to a single synchronous flowering episode preceded or followed by others that were not synchronous. The behavior of different branches is described: a branch "drops out" when it fails to reach the prefemale stage during a flowering episode. There were no definite cases of within-crown reproductive asynchrony associated with mosaicism.*

Species	Tree	Genotypes	Asynchrony history
Ficus citrifolia	27	1/1	single branch
(1 mosiac/8 possible)	**29**	2/2	A initiated female phase lone, aborted; later, synchrony
	31	1/3	synchrony
	33	1/2	ambiguous; single flowering episode poorly observed
	35	1/5	synchrony
	36	1/1	single branch
	38	1/1	single branch
	39	1/2	synchrony
	41	1/1	single branch; tree died
	43	1/3	did not flower
	47	1/3	synchrony
	73	1/3	synchrony, then one branch died
Ficus nymphiifolia	32	1/1	single branch
(1 mosaic/10 possible)	40	1/3	synchrony
	46	1/3	synchrony
	48	1/4	A & B made abortive buds without C; then C made abortive buds without A & B; then synchrony
	50	1/1	single branch
	52	1/2	A made abortive buds without B; then synchrony
	53	1/2	synchrony, then tree died
	54	1/2	synchrony
	56	1/2	A dropped out; then synchrony
	57	1/6	synchrony; then 3 branches dropped out; then synchrony
	64	2/4	synchrony
	70	1/4	synchrony
Ficus obtusifolia	15	1/4	B dropped out; then synchrony
(5 mosaics/11 possible)	**16**	2/4	synchrony
	23	2/2	A dropped out; then synchrony
	24	1/3	synchrony; then C dropped out; then synchrony
	26	1/2	synchrony
	42	2/3	A, then C, then B (the unique branch) initiated abortive buds; B and C small and in shade
	55	2/3	B and C dropped out; then synchrony
	58	1/2	B died, then A flowered
	68	1/4	C and D dropped out; then C initiated buds alone; then C and D died
	69	2/2	B only initiated abortive buds, lost them, then repeated this; A small and in shade
	75	1/3	synchrony
Ficus popenoei	65	1/6	B dropped out; then synchrony; B in shade
(0 mosaics/4 possible)	66	1/1	single branch
	67	1/1	single branch
	71	1/7	synchrony
	72	1/3	synchrony
	78	1/5	synchrony
Ficus near *trigonata*	19	1/4	synchrony
(0 mosaics/8 possible)	20	1/3	synchrony
	21	1/3	A initiated abortive buds alone; no other episodes
	22	1/3	synchrony
	30	1/3	synchrony; then B expanded abortive buds while A and C retained non-developing buds; tree died
	51	1/3	synchrony
	59	1/2	synchrony
	60	1/4	synchrony

branches fail to respond because of low reserves of resources. In several cases, asynchronous branches were small and shaded (Table 2). Herre (1996) speculated that the trunk-based control works by usually inhibiting flowering. This accords with the observation that broken branches are more likely to flower out of synchrony. The observation that genetically different branches in mosaic trees can also be tightly synchronized suggests that, in the absence of damage, the putative hormonal signal can be transmitted through grafted connections. Given that massive simultaneous flowering is likely to be highly advantageous for the olfactory attraction of pollinators and dispersers, it is not surprising that flowering should be under strong, systemic control. It appears from our study that this control is usually strong enough to override individualistic flowering tendencies that might otherwise tend to characterize different genotypes.

The only possible exceptions to the overriding influence of systemic control are the two mosaic *Ficus obtusifolia,* 42 and 69, where different branches alternated in their production of buds that never developed. The interpretation of this observation depends on whether these buds are better considered dormant or abortive. If they indeed are abortive buds whose normal development has been interrupted, might both the asynchrony and the abortion be symptoms of a more balanced struggle for hormonal dominance by two genetic individuals sharing a soma? Evolutionary theory would certainly suggest the potential for conflicts of interest in such a situation. Repeated production of such buds was rare in non-mosaic trees; however, there are too few mosaic trees to even consider a statistical test. On the other hand, these buds may not have been abortive but only dormant. Bronstein and Hossaert-McKey (1995) suggested an adaptive role for holding such buds in reserve to hasten the recovery of the fig-wasp mutualism following catastrophes such as hurricanes.

Overall, this study lends no support for the idea that staggered blooming of mosaic figs will be an important factor in maintaining populations of pollinating wasps. First, mosaicism does not occur very often; second, when it does, it does not necessarily produce asynchrony. Indeed, we have only a suggestion that it ever produces asynchrony, and in the two most likely cases there was no successful reproduction at all. Based on the slim evidence available from this study, mosaic trees seem more likely to produce reproductive stalemates–*i.e.*, cohorts of abortive buds– than extra flowering cycles. Furthermore, recent studies (Compton *et al.* 1994, Bronstein & Hossaert-McKey 1995, Nason *et al.* 1996; reviewed by Herre 1996) have challenged the traditional picture of fig wasps as frail creatures that encounter great difficulty getting from one tree to another. Certainly the Panamanian wasps routinely move kilometers, crossing substantial expanses of water (Herre 1996). In Florida, wasps quickly repopulate areas in which they have been extirpated by hurricanes (Bronstein & Hossaert-McKey 1995). Although wasp biology remains poorly understood, new studies make it clear that these insects can be more effectual than was assumed in some older models (Kjellberg *et al.* 1987, Kjellberg & Maurice 1989, Bronstein *et al.* 1990). Therefore, the advantage of among-branch asynchrony postulated by Thomson *et al.* (1991)—that of maintaining wasps—may not be very important after all.

It is important to note that we looked for blooming asynchrony in a group of well-studied species that have been thought to be essentially synchronous. Our more detailed work simply reinforces that point, but it would be risky to extrapolate beyond these species. Conceivably, mosaicism might be more correlated with asynchrony in other taxa. For example, if trunk-based inhibition of flowering is weaker in some species, genetic differences among fused branches might be more freely expressed.

As suggested before (Thomson *et al.* 1991), further work on the costs and benefits conferred on fusing figs may be worthwhile, and the present study suggests that hormonal interactions might particularly repay study. Unfortunately, we must also point out that it will be harder than we thought to find suitable fused individuals for such studies. An electrophoretic survey of two Australian "rock stranglers", *Ficus leucotricha* and *F.* rubiginosa, whose low stature would greatly ease access to their crowns, failed to find allofusions (J. Nason & J. Thomson, pers. obs.). Of the Panamanian species examined here, only in *F. obtusifolia* does allofusion seem to be common enough to be considered part of the species' normal biology. In the other taxa, its rarity makes it best considered as the sort of accident that would be expected occasionally in a species with a high propensity for root grafts.

ACKNOWLEDGMENTS

We particularly thank J. L. Bronstein, S. G. Compton, E. A. Herre, J. L. Hamrick, E. Leigh, J. L. Stone, and the staff of STRI. Research supported by a grant from the National Geographic Society to JDT. This is contribution number 988 in Ecology and Evolution from the State University of New York at Stony Brook.

LITERATURE CITED

Bronstein, J. L. 1989. A mutualism at the edge of its range. Experientia 45:605–611.

———. 1992. Seed predators as mutualists: ecology and evolution of the fig/pollinator interaction. *In* E. Bernays (Ed.). Insect-plant interactions, Volume IV, pp. 1–44. CRC Press, Boca Raton, Florida.

———, P. Gouyon, C. Gliddon, F. Kjellberg, and G. Michaloud. 1990. The ecological consequences of flowering asynchrony in monoecious figs: a simulation study. Ecology 71: 2145–2156.

———, and M. Hossaert-McKey. 1995. Hurricane Andrew and a Florida fig pollination mutualism: resilience of an obligate interaction. Biotropica 27: 373–381.

———, and A. Patel. 1992. Causes and consequences of within-tree patterns in the Florida strangling fig, *Ficus aurea* (Moraceae) Am. J. Bot. 79: 41–48.

Compton, S. G., S. J. Ross, and I. W. B. Thornton. 1994. Pollinator limitation of fig tree reproduction on the island of Anak Krakatau (Indonesia). Biotropica 26:180–186.

Herre, E. A. 1989. Coevolution of reproductive characteristics in twelve species of new world figs and their pollinator wasps. Experientia 45: 637–647.

———. 1996. An overview of studies on a community of Panamanian figs. J. Biogeogr. 23: 593-607.

Hossaert-McKey, M., M. Gibernau, and J. E. Frey. 1994. Chemosensory attraction of fig wasps to substances produced by receptive figs. Ent. Exp. Appl. 70: 185.191.

Janzen, D. H. 1979. How to be a fig. Ann. Rev. Ecol. Syst. 10: 13–51.

Kjellberg, F., P.-H. Gouyon, M. Ibrahim, and G. Valdeyron. 1987. The stability of the symbiosis between dioecious figs and their pollinators: a study of *Ficus carica* L. and *Blastophaga psenes* L. Evolution 41: 693–704.

———, and S. Maurice. 1989. Seasonality in the reproductive phenology of Ficus: its evolution and consequences. Experientia 45:653–660.

McKey, D. 1989. Population biology of figs: applications for conservation. Experientia 45: 661–673.

Milton, K. 1991. Leaf change and fruit production in six neotropical Moraceae species. J. Ecol. 79: 1–26.

———, D. M. Windsor, D. W. Morrison, and M. A. Estribi. 1982. Fruiting phenologies of two neotropical *Ficus* species. Ecology 63: 752–762.

Nason, J. D., E. A. Herre, and J. L. Hamrick. 1996. Paternity analysis of the breeding structure of strangler fig populations: Evidence for substantial long-distance wasp dispersal. J. Biogeogr. 23: 501-512.

Putz, F. E., and M. Holbrook. 1986. Notes on the natural history of hemiepiphytes. Selbyana 9: 61–69.

Ramirez, W. 1970. Host specificity of fig wasps (Agaonidae). Evolution 24: 680–691.

———. 1974. Coevolution of Agaonidae. Ann. Missouri Bot. Gard. 61:770–780.

Thomson, J. D., E. A. Herre, J. L. Hamrick, and J. L. Stone. 1991. Genetic mosaics in strangler fig trees: implications for tropical conservation. Science 254: 1214–1216.

Van Noort, S., A. B. Ware, and S. G. Compton. 1992. Pollinator-specific volatile attractants released from the figs of *Ficus burtt-davyi.* Sud-Afrikaanse Tydskrif vir Wetensap. 85: 323–324.

Ware, A. B., T. K. Perry, S. G. Compton, and S. Van Noort. 1993. Fig volatiles: their role in attracting pollinators and maintaining pollinator specificity. Plant Syst. Evol. 186: 147–156.

Wiebes, J. T. 1979. Co-evolution of figs and their insect pollinators. Ann. Rev. Ecol. Syst. 10: 1–12.

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, Panama. Experientia 45: 647–653.