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Phenology of fruit and leaf production by 'strangler' figs on Barro Colorado Island, Panamá

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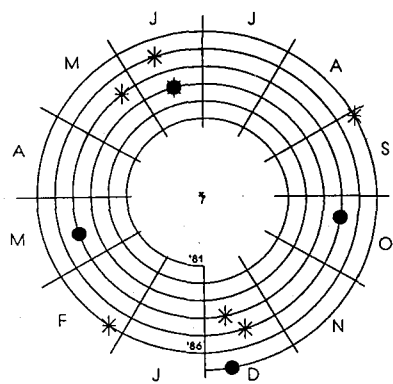
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Summary. Fruit and leaf initiation by 26 trees representing five 'strangler' *Ficus* species in the subgenus *Urostigma* were monitored for 5–8 years in a seasonal lowland forest of central Panamá. Individual trees of each species initiated fruit in synchronized 'crops'. High variation in the number of crops, intervals between crops and dates of crop initiation indicate that these species, like species in the subgenus *Pharmacosycea*, initiate fruit crops the year around. Nevertheless, mean crop initiation dates for four of five species fell within the four-month dry season. Similarly, all species produced new leaf flushes throughout the year, however, mean leaf flush dates of all species fell within the first three months of the dry season.

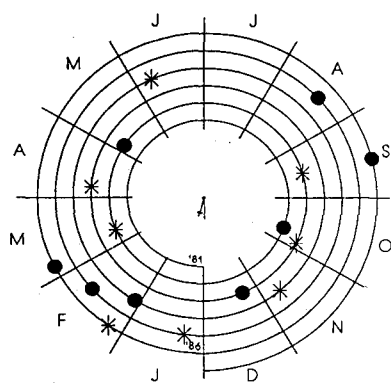
Key words. Fig; *Ficus*; phenology; neotropical; Panamá.

Setting *Ficus* apart from most other dicotyledonous plant genera is an obligatory association with agaonid wasp pollinators^{10,15,24,30}. Most *Ficus* species have only a single reliable wasp pollinator species^{23,25} and pollinator species normally associate with only a single fig species³. Female agaonid wasps arrive, enter the fig ostiole, pollinate many of the stigmatic surfaces within the fig while laying eggs of the next generation of wasps in the ovules, and then die. Wasp larvae prey on roughly one-third to one-half of developing seeds^{5,11,16}, eclose, mate, gather pollen and then disperse to other figs to start the cycle again.

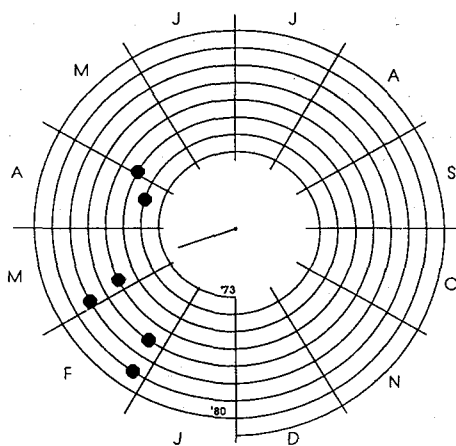
The development of flowers within syconia (the compound reproductive structure or 'fig') is highly synchronized²⁸, and the development of syconia within crowns of individual trees is normally synchronized into recognizable 'crops'^{4,25}. Both Janzen¹⁵ and Bronstein^{3,4} argue that crop synchronization allows individual trees to send a stronger chemical signal and thus be better competitors for pollinating wasps in the neighborhood. Field observations suggest that unlike a great many tropical trees which have tightly synchronized anthesis and fruit production cued by environmental changes such as dry season rainfall^{1,9,13,14,21,22}, the reproduc-



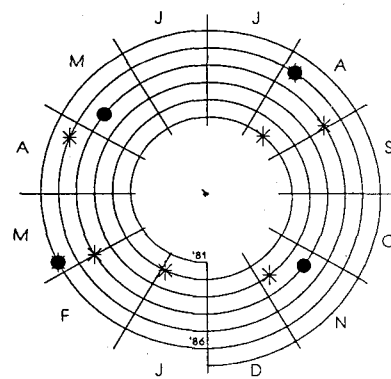
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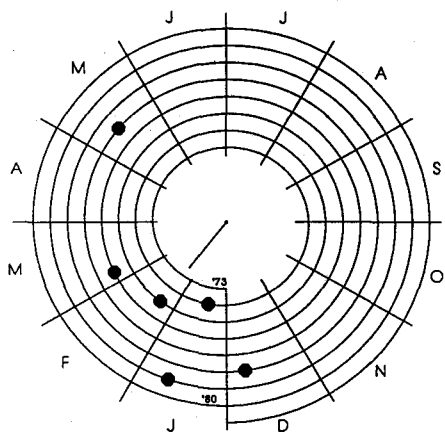
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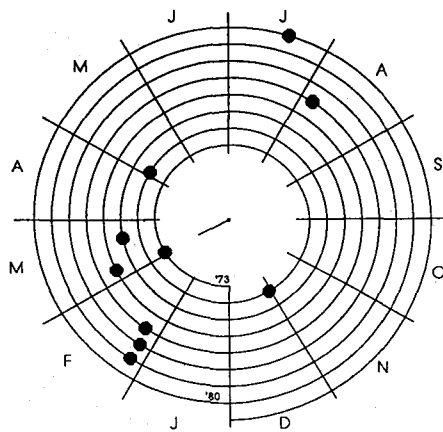
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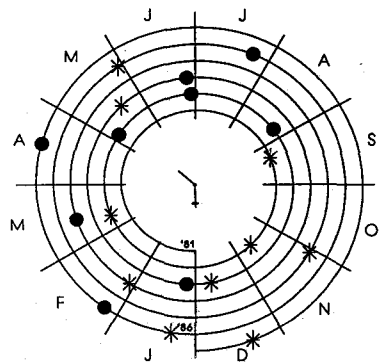
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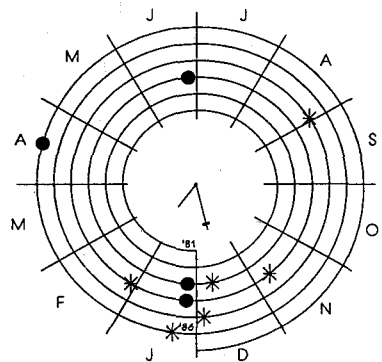
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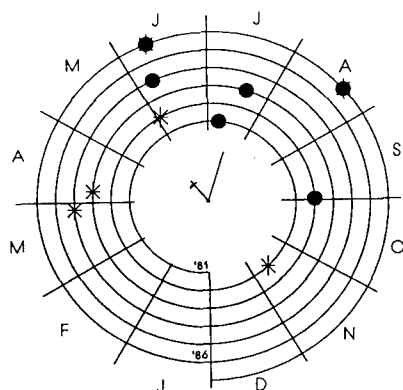
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F.cos. 021

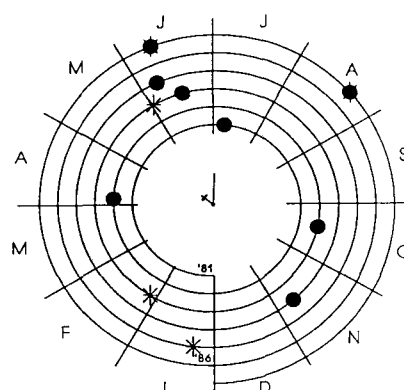


F.cos. 007



C F.pop. 003

Two trees from each 'strangler' figs species illustrating the timing of fruit crop (closed circle) and new leaf flush initiation dates (asterisks). The continuous time axis spirals outward from the beginning to end of observations. The trees chosen had the largest number of fruiting events during the study. The direction of radii from the center of each figure represents



F.pop. 019

the mean day of year while the length of each radius represents the concentration of the data points around the mean direction. Hatched radii refer to the distribution of leaf flushing dates; unhatched radii refer to the distribution of fruit crop initiation dates.

tive schedules of tropical figs are highly unsynchronized^{7, 12, 15, 19, 25}. *Ficus* asynchrony has been explained in terms of the basic interests of individual trees¹⁵. The sole source of short-lived, host-specific, wasp pollinators is the ripening fruit crop of conspecifics. Thus, trees fruiting just after or just before neighboring conspecifics should benefit from greater numbers of pollinators or increased pollen transfer than trees synchronized with nearby conspecifics. A fig tree can avoid reproducing in synchrony with conspecifics by initiating fruiting at some random period of time after a minimum quantity of reserves have been accumulated. Alternatively, if a tree could sense the ripening fruit crop of a neighbor or neighbors, it should then initiate a crop of its own to take advantage of the pollinators that will soon be looking for receptive figs. Other factors (temperature, light, water, seed dispersers, seed predators) should also affect the optimal timing and reproductive output of figs. Dry and wet seasons are common in most tropical regions and we might expect figs to respond phenologically to these changing conditions.

New world *Ficus* fall into one of two subgenera which are morphologically distinct. The subgenus *Pharmacosycea* (section *Pharmacosycea*), are 'free-standing' species common in large openings and young forest, bear figs solitarily in axils with three or three-lobed basal bracts, have dehiscent pollen and are pollinated by *Tetrapus* wasps lacking corbiculae. The subgenus *Urostigma* (section *Americana*), primarily 'strangler' species typical of older forest, bear fruit paired in axils with two or two-lobed basal bracts, have indehiscent pollen and are pollinated by *Blastophaga* (subg. *Pegoscapus*) wasps possessing both coxal and sternal corbiculae^{6, 27}.

Neotropical fig phenology was first documented by Morrison²⁰ who recorded the dates immature and ripe fruit were present in the canopies of 71 *Ficus yoponensis* and

45 *F. insipida* trees on Barro Colorado Island, Panamá. Individuals of both fig species had differing intercrop intervals with smaller individuals fruiting at longer intervals¹⁹. Although crops were initiated around the year, neither species initiated crops in a completely uniform manner. Both species had a bimodal distribution of crop initiation dates, one mode located near the onset of the wet season and the other near the onset of the dry season. Changes in topography did not correlate with the length of intervals between successive crops.

This paper examines the phenology of fruit and leaf initiation by *Ficus* species in the subgenus *Urostigma*. The data suggest that reproductive asynchrony within populations is also a characteristic of species in this subgenus, that there are discernible seasonal peaks in reproductive activity and that these peaks appear to fall into different seasons. The timing of new leaf flushes is similarly distributed, however, there is no evidence that leaf and fruit production are sequentially related.

Methods

The trees examined in this paper grow in the semi-deciduous lowland forest on Barro Colorado Island, Panamá¹⁸. Climate is determined largely by the distribution of 2600 mm average annual rainfall, 90% falling during the wet season (May to December), 10% during the four months of the dry season³¹. Data from two studies were pooled during our analysis. The first study included two *Ficus obtusifolia* H.B.K. (Nos 64 and 86) and one *F. trigonata* L. (No. 219) observed between February 1973 and December 1980 (200 censuses) in the Lutz catchment. Although Janzen¹⁵ commented that there were other trees on Morrison's original census, these trees were terminated within the first year, most before they had initiated fruit. Observers (D. Morrison and

M. Estribi) noted the presence and approximate size category of syconia in the canopy of each tree on the census. Trees were surveyed weekly during the first year and biweekly thereafter.

The second data set is derived from a biweekly study of the leafing and fruiting phenology of forest trees on the Barro Colorado Island plateau initiated by the Smithsonian Institution's Environmental Sciences Program in 1981. Initially, 23 of these trees were 'strangler' figs, species typical of 'old forest': *F. popenoei* Standl. (5 individuals), *F. obtusifolia* (7 individuals), *F. costaricana* (Liebm.) Miq. (4 individuals), *F. dugandii* Standl. (2 individuals) and *F. trigonata* (5 individuals). Each census (by B. de Leon) consisted of noting the fullness of the canopy, the presence of a heavy new leaf crop in the canopy and the presence of immature and mature fruit using a subjective scale where '1' signified a full response, '2' an intermediate response, '3' a small or questionable response and '0' no response.

Analysis of data collected from 1981 through the end of 1986 proceeded in the following manner: 1) the 4-point observer code was reduced to a 2-point code by accepting a '1' or '2' as indicating presence, any other score as absence, 2) the first in a series of dates was accepted as the date of either fruit crop or leaf flush initiation and other scores in that run were converted to '0', 3) the day of year (0–365) was converted to degree (0–360), 4) the direction and length of the mean vector were calculated²⁹ and 5) average date was obtained by back calculating from the mean angle. The null hypothesis that crop initiation or leaf flushing dates were distributed uniformly (= randomly) throughout the year was tested with the Rayleigh test³² for all trees with a minimum of two phenological events occurring during the study. The same hypothesis was evaluated for species (rather than trees) by applying the Rayleigh test to tree means placed on a unit circle. All statistical tests were two-tailed with an acceptance level (alpha) of 0.05.

Life history characteristics of the five 'strangler' figs are reviewed by Croat⁶. Briefly, the fruit of *F. costaricana* are small (12–14 mm), red and bird-dispersed while the other species, are large (15–35 mm), green and bat-dispersed fruit. *Ficus popenoei* is the smallest tree reaching 17–25 m in height at maturity while the other species commonly reach 30–40 m in height. All but *F. dugandii* are thought to commonly strangle their host trees. Although birds do disperse the green fruit of *F. trigonata*, bats have been considered the more reliable dispersal agent².

Results

New leaf flushes

Leaf flush data were gathered during the second study, 1981–1986. The number of times trees were observed producing a major flush of new leaves varied greatly among individuals and species (fig.). For example, 10 leaf flush events were recorded for *F. costaricana* 'F021' in six

years while only three events were recorded for 'F009' in the same time period. The average number of leaf flush events per year varied from a high of 1.25 in *F. dugandii* (n = 2) to a low of 0.65 in *F. obtusifolia* (n = 7). The hypothesis that individual trees initiate new leaf flushes randomly over time was rejected for only one of 22 trees ('F007'–*F. costaricana*) (table).

Leaf flushing tendencies at the species level were examined by collecting the unweighted, mean, phenological vectors for each tree and then testing that distribution for uniformity. Uniform leaf flushing was rejected for *F. costaricana*, the only species which had a significant seasonal tendency (late Dec). Although uniformly distributed leaf flushing dates could not be rejected for the other four species, the mean vectors for each fell within dry season months (late Dec–early May). For this reason, the nonuniform distribution of species means was highly significant, indicating consistent tendency to initiate slightly more new leaf crops in the early dry season (mean of species means, mid February).

None of the trees observed in this study entered a prolonged period of deciduousness. Typically, trees leafless on one census were flushing new leaves on the next census. Because the deciduous period appears to have been less than or equal to the time between censuses we cannot claim to have recorded all such events. There were nine records of leaflessness by four *F. obtusifolia* trees, five records by two *F. popenoei*, four records for the five *F. trigonata*, and no records of leaflessness by the four *F. costaricana* or the two *F. dugandii* in six years. Six of the nine *F. obtusifolia* records and all six of the *F. popenoei* records occurred during dry season months.

Fruit production

Generally, the timing of fruit crop initiation was more variable than that of new leaves (table). The number of fruit crops initiated by individual *F. costaricana* varied from one to nine, *F. obtusifolia* from zero to ten, *F. popenoei* from one to eight and *F. trigonata* from zero to six. Five of nine *F. obtusifolia* did not initiate a single fruit crop during six years – all large trees with expansive crowns. However, the distributions of crop initiation dates were nonuniform for four of 18 trees fruiting at least twice during the period of observation (one *F. obtusifolia*, one *F. popenoei* and two *F. trigonata* trees) (table).

At the species level, a uniform distribution of crop initiation dates was rejected for only *F. obtusifolia*. *Ficus costaricana* may also initiate fruit crops nonuniformly, however, our confidence in this is slightly lower (p = 0.06). The average fruit crop initiation dates fall in the mid to late dry season (late February through late March) for all species except *F. popenoei* (early July). By inspecting the figure, it is clear that in each species new leaf flushes do not occur predictably either before or after the production of a fruit crop. Thus it seems that the

New leaf flush and crop production schedules of five 'strangler' fig species on Barro Colorado Island (yrs = number of years of observations, n = number of phenological events during this period, r = length of the mean vector, s = angular deviation, dy = mean date, p = probability that phenological events are distributed uniformly about the year).

	Tree	yrs	Leaf flush				p	Fruit crop				p
			n	r	s	dy		n	r	s	dy	
<i>Ficus costaricana</i>	F021	6	10	0.36	82	2	-	9	0.35	83	138	-
	F009	6	3	0.81	37	344	-	2	0.57	61	53	-
	F015	6	5	0.66	52	352	-	1	1.00	0	108	-
	F007	6	6	0.71	48	355	0.05	4	0.34	84	60	-
	Mean		4	0.99	8	354	0.02	4	0.82	88	89	0.06
<i>Ficus dugandii</i>	F018	6	8	0.29	90	16	-	8	0.24	97	2	-
	E871	6	7	0.09	127	133	-	4	0.13	115	13	-
	Mean		2	0.54	55	74	-	2	0.99	5	8	-
<i>Ficus obtusifolia</i>	F012	6	4	0.22	100	12	-	0	-	-	-	-
	F002	6	3	0.34	84	36	-	3	0.33	85	97	-
	F006	6	5	0.07	134	66	-	0	-	-	-	-
	LabW	6	1	1.00	0	348	-	0	-	-	-	-
	F014	6	2	0.28	91	217	-	0	-	-	-	-
	F008	6	5	0.61	57	58	-	0	-	-	-	-
	F005	6	7	0.46	72	333	-	5	0.09	127	100	-
	Ob64	8						6	0.73	46	39	0.05
	Ob86	8						10	0.45	72	63	-
	Mean		7	0.56	54	17	-	4	0.91	24	76	0.05
<i>Ficus popenoei</i>	F010	6	3	0.64	54	232	-	3	0.43	74	25	-
	F020	6	6	0.36	82	94	-	1	1.00	0	164	-
	F019	6	5	0.18	106	135	-	8	0.43	74	193	-
	F739	6	3	0.38	79	39	-	3	0.59	59	226	-
	F003	6	6	0.37	81	38	-	6	0.78	41	204	0.02
	Mean		5	0.44	61	86	-	5	0.55	54	193	-
<i>Ficus trigonata</i>	F004	6	6	0.44	73	131	-	3	0.98	12	105	0.05
	F017	6	2	0.69	49	108	-	2	0.92	24	337	-
	F013	6	6	0.19	104	62	-	6	0.33	85	89	-
	F731	6	8	0.06	136	59	-	4	0.12	119	141	-
	F016	6	5	0.40	77	334	-	0	-	-	-	-
	219	0						6	0.84	34	72	< .01
	Mean		5	0.62	50	73	-	5	0.62	50	86	-
Mean of means			5	0.85	32	45	0.01	5	0.63	55	68	-

production of new leaf flushes and fruit crops are on largely independent schedules.

Discussion

Individuals of each of five species of *Urostigma* figs exhibited great variability within and among years in the dates they initiated fruit crops. Had larger numbers of trees in each species been observed there is little doubt that some trees in each species would have been found initiating fruit in all months of the year. Thus, year-around fruit crop initiation has appeared in all species of neotropical subgenera of *Ficus* thus far examined, a reproductive pattern which Ramirez²⁵ predicted all *Ficus* species should share because of their common dependence on short-lived, host-specific pollinators.

Further, our observations indicate that a modest seasonal tendency is superimposed on the nearly random fruiting schedules of *Urostigma* fig species. Four of the five *Urostigma* species examined in this study initiated fruit crops more commonly during the mid to late dry season.

The crops initiated by *Ficus popenoei* fell more commonly during the early to mid wet season. While small sample sizes hindered our ability to compare seasonal tendencies among species, our observations do suggest that *Urostigma* figs are similar to *Pharmacosycea* species in that they exhibit mild seasonal peaks and a pattern of year-around crop initiation. The timing of these peaks, however, appears to differ. While four of five *Urostigma* species had a single peak falling within the dry season, the two free-standing figs, *F. yoponensis* and *F. insipida*, each had two fruiting peaks, one at the onset of the dry season (Dec–Jan) and the lesser one at the onset of the wet season (May–June)¹⁹.

While the adaptive significance of starting crops throughout the year can be logically related to individual pollination success¹⁵, it is far less clear why weak seasonal peaks exist. It has been suggested that a peak superimposed upon year-around fruiting represents the outcome of opposing selection pressures by pollinators and seed dispersal agents¹⁹. Figs are relatively cheap, carbohydrate-rich fruit which ought to be more attractive to dis-

persers when more nutritious fruit are less available. On BCI there are two distinct periods of fruit availability generated largely by canopy trees. The time of greatest forest-wide fruit availability occurs in Apr–May followed by a lesser peak in Sep–Oct⁸. In the cases of *F. yoponensis* and *F. insipida*, their major fruiting peaks fall between the two periods of maximum fruit abundance in the forest and thus are consistent with a seed dispersal hypothesis. However, the lesser peak that each of these species also has coincides with the May–June peak in forest fruit abundance and appears inconsistent with the same hypothesis. Some *Urostigma* fig species, by initiating fruit crops during the dry season, may place their seeds between the two peaks in forest fruit availability while others will fall in the early part of the Apr–May peak⁸. The small red fruit of *F. costaricana* are generally thought to be bird dispersed⁷. *Ficus popenoei*, by fruiting in Jun–Aug, may fit into the other period of fruit scarcity and thereby also be minimizing interspecific competition for mammalian dispersal agents.

Because the forest environment on Barro Colorado Island is not unlike that of much of tropical South America and a good portion of Central America in experiencing 2–3 m rainfall per year with a distinct dry season^{18,31} we expect the phenological patterns of *Ficus* species observed in Panamá will be fairly widespread. Exceptions might occur at higher elevations, however, the climate in these areas may be less seasonal than adjoining lowland areas. Bronstein^{4,5} noted that *Ficus pertusa* L.f. initiated fruit crops throughout the year at 1000 m elevation in Costa Rica. Phenologies of *Ficus* species in extremely seasonal tropical habitats such as the lowlands of Guanacaste Province, Costa Rica, or the llanos of Venezuela, have not been well documented. If the dry season in these habitats is sufficiently prolonged that fruit production decreases and the ability of wasps to find other trees in fruit decreases, phenologies may differ from those on BCI. Trees which decreased within-crown synchrony while continuing to produce fruit during the dry season might have a reproductive edge over trees that shut down entirely in that they alone would be the pollen source for seed produced during the first wet season crops.

Little is known about how New World *Ficus* phenology varies with latitude. Ramirez²⁴ suggested that phenologies may differ on small oceanic islands and near the limits of species ranges. He reported asynchronous fruit initiation within crowns of *F. aurea* in Florida and on the Caribbean island of San Andres. Unfortunately, there was no comment on how synchronous this species was in other parts of its range. Within-crown fruiting synchrony has not been carefully studied in any of Barro Colorado Island *Ficus*. Casually, we have noted variation within and among species so that work on within-crown synchrony is practicable.

Obligate association with a short-lived wasp pollinator may have effects on reproductive phenology which can only be appreciated by comparison with other tropical

Moraceae which rely on different pollinating agents. Unfortunately, little is known of the phenology or pollinators of other Moraceae. The comments by Croat⁶ based largely on herbarium material suggest that flowering seasons of most Moraceae on BCI are quite broad. Year-around flowering is mentioned for two species, *Castilla elastica* Sesse and *Poulsenia armata* (Miq.) Standl. and broad flowering seasons are noted for species of *Coussapoa*, *Dorstenia*, *Maquira* and *Sorocea*. Thus, reproductive variability in *Ficus* may only represent an extreme condition within a phylogenetic group already possessing great phenological variability. The evolution of the blastophagous habit, as hypothesized by Ramirez²⁶, might even have been facilitated in the ancestral 'pre-*Ficus*' species by this variability. Knowledge of the pollinators, seed predators and phenologies of other Moraceae could cast additional light on how and why blastophagy evolved.

Finally, the unusual nature and reproductive schedules of neotropical figs may be important in reforesting areas of degraded pasture land in the tropics. Figs almost always bear a dense canopy of green leaves, flushing new leaves, as we have seen, at irregular intervals. Fruit attractive to birds and mammals are produced in distinct crops throughout the year. During years of lower than average fruiting by other trees on Barro Colorado Island, it is the regular fruiting of *Ficus* species that appears to sustain populations of mammals and birds during a 2–3-month period of famine in the late wet season⁸. Fig trees, especially species of stranglers, can be planted as living fence posts (or forests) merely by opening a hole in the soil during the wet season and inserting a recently cut branch. Several species survive well and support enormous spreading crowns in the pastures and savannas in the lowlands of Pacific northwestern Costa Rica. Much of the degraded lands of central Panama support substantial but dispersed stands of *Byrsonima crassifolia* (L.) H.B.K. (Malthaceae), *Curatella* sp. (Dilleniaceae) and *Xylopia* sp. (Annonaceae), undoubtedly shaping the faunal assemblage that persists in these areas. Planting *Ficus* species for shade, moisture recycling and wildlife could be a useful first step in renewing these lands.

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Seasonality in the reproductive phenology of *Ficus*: Its evolution and consequences

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Summary. *Ficus* can only reproduce if they are pollinated by mutualistic wasps that breed within the figs. Pollen-loaded wasps enter the figs when the female flowers are receptive. Several weeks later, their offspring load pollen within the fig and then emerge. As individual trees typically produce crops of synchronous figs at long intervals, the short-lived wasps have to move to another, receptive, tree. The wasp population can only survive, and hence the fig population reproduce, if there are trees fruiting all over the year. When only few trees are present within a population gaps in the flowering sequence may lead to the extinction of the local pollinator population. Two models are presented. One investigates the number of trees necessary in order to sustain a local pollinator population when the tree population has a seasonal pattern of fruiting. The second model investigates how such a seasonal pattern may evolve within a fig population as a result of individual selection on the trees. It is shown that pollinator populations are fragilized under seasonal conditions. Hence, the breeding system of *Ficus* limits their expansion into highly seasonal habitats. Seasonal habitats may also lead to seasonal adjustment of male versus female investments and to the evolution of dioecy.

Key words. *Ficus*; reproductive phenology; sex allocation.

Introduction

The relationship between *Ficus* and their pollinators constitute one of the best studied cases of obligate species-specific mutualistic pollination. *Ficus* have to be pollinated by tiny wasps that only breed within the enclosed

inflorescence or fig. With few exceptions, each of the some 700 *Ficus* species has its own species of pollinator. Mated female wasps enter the figs when female flowers, up to several hundreds enclosed within each fig, are re-