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LEAF CHANGE AND FRUIT PRODUCTION IN SIX NEOTROPICAL MORACEAE SPECIES

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SUMMARY

(1) New leaves and fruits of the Moraceae are prominent components in the diets of vertebrate primary consumers on a pantropical basis. In many cases, feeding data suggest that such items from particular genera or species are available in particular habitats for most or all of an annual cycle.

(2) To investigate annual production patterns of new leaves and fruits in Moraceae, a 2-year study was carried out in Panama on individuals of six Moraceae species, *Ficus insipida* and *F. yoponensis* (subgenus *Pharmacosycea*), *F. obtusifolia* and *F. costaricana* (subgenus *Urostigma*), *Cecropia insignis* and *Poulsenia armata*, using bi-weekly inventories of materials in standardized collection plots and data from canopy scans.

(3) Both *Urostigma* species were deciduous but flushed immediately after leaf drop; other species were evergreen. Dead leaves were shed by all species throughout both years. All species produced large crops of new leaves at intervals shorter than 1 year. Although annual leaf production occasionally showed clustering for a particular species, in general, there was considerable intraspecific variability in the timing of new leaf production. Some individuals of three species (*P. armata, C. insignis* and *F. yoponensis*) produced small quantities of new leaves more or less continuously with occasional peaks in new leaf production. Other individuals of these and other species produced large numbers of new leaves more or less episodically.

(4) All species initiated fruit crops at intervals averaging <1 year. In four species, intervals between fruit initiations averaged <26 weeks. Annual fruit production in five species was intraspecifically asynchronous and, within species, individuals tended to alter the time(s) of year of fruit initiation. *C. insignis*, the only dioecious species in the sample, had a single synchronized period of fruit production each year, lasting approximately 6 months. Trees of *F. costaricana* showed fruit in the crown for periods lasting 2, 3 or more consecutive months. Inflorescence production in two larger trees of *P. armata* took place more or less continuously. At the individual level, 87% of the sample trees produced fruit crops at least once per year and many produced more than one.

(5) Overall, phenological activities were more pronounced in the drier half of the year. In spite of this trend, at least some leaf shed, leaf flush and fruit production took place throughout the year in most species. A bimodal trend was noted for some phenological events in some species (e.g. leaf shed and leaf flush in *F. yoponensis*).

(6) As a family, as species and, frequently, as individuals, these Moraceae exhibited phenological traits that would tend to make their new leaves and/or fruits available to primary consumers in this forest for much or all of an annual cycle. Similar patterns of frequent and/or intraspecifically asynchronous new leaf and fruit production

are predicted to be generally characteristic of Moraceae in other tropical forest areas of both the New and Old Worlds. This fruit production pattern is suggested to be an ancient trait of the family, perhaps arising in response to selective pressures related both to outcrossing advantages and improved dispersal of unusually tiny seeds.

(7) The reproductive phenology of *Ficus* species in this study contrasted with that of *C. insignis* and *P. armata* in that individuals of the *Ficus* species were able to produce massive fruit crops at any time of year. This temporal flexibility with respect to the timing of fruit crops appears to relate, at least in part, to the obligate mutualism of fig trees with wasp pollinators.

INTRODUCTION

Plant parts from members of the Moraceae figure prominently in the diets of vertebrate primary consumers on a pantropical basis (McClure 1966; Leighton & Leighton 1983; Terborgh 1983; and many others). In part, the dietary prominence of this family rests on heavy consumption of fruit of the genus *Ficus* by large numbers of tropical frugivores (Janzen 1979; Breitwisch 1983). In some communities, fig fruits are regarded as keystone resources of such importance that, if subtracted from the ecosystem, 'one could expect to see it collapse' (Terborgh 1986). The genus *Ficus* appears to have phenological traits that make its fruits unusually available to tropical frugivores throughout the year. Various *Ficus* species show intraspecific asynchrony in fruit production (Newton & Lomo 1979; Janzen 1979; Milton *et al.* 1982); intervals between fruit crops may also be short with many trees bearing more than one crop per annum (Hill 1967; Newton & Lomo 1979). Both traits contrast with fruit production patterns of many other tropical tree species which often show intraspecific synchrony and a consistent season for annual fruit production and produce, at best, one fruit crop per year (Koelmeyer 1961; Frankie, Baker & Opler 1974; Foster 1982).

Data show, however, that not only *Ficus* fruits but fruits of other genera and species of Moraceae are also important dietary resources for tropical frugivores (Kinzey 1977; Curtin & Chivers 1978; Croat 1978; Cords 1984). For example, some species of *Brosimum* may show two or more episodes of fruit production each year, with some trees initiating two or more fruit crops (Coelho *et al.* 1976; Milton 1980 and personal observations in Panama and Peru). Fruits of *Bosqueia phoberos* and *Morus lactea* are available to Kenyan frugivores for a minimum of 9 and 6 months year^{-1}, respectively (Cords 1984). Such observations suggest that Moraceae other than *Ficus* may also have relatively frequent and/or asynchronous episodes of fruit production. In addition, feeding data on a number of arboreal folivores, particularly monkeys, in tropical forests of both the Old and New Worlds, show that young leaves of many Moraceae are also important dietary resources. In some habitats, new leaves of particular species apparently are consumed by vertebrate primary consumers for most or all of an annual cycle (e.g. howler monkeys, spider monkeys, blue monkeys, two-toed sloths, iguanas; Coelho *et al.* 1976; Montgomery & Sunquist 1978; Milton 1980 and personal observation; Cords 1984). Such observations suggest that many Moraceae species may also show continuous, frequent or asynchronous patterns of new leaf production.

To investigate annual patterns of leaf change and fruit production in Moraceae, a two-year study was carried out on six species of Moraceae in three genera — *Ficus*, *Poulsenia* and *Cecropia* — with the following objectives: (i) to determine annual leaf fall and new leaf production patterns for a number of *Ficus* species to complement data on fruit production in this genus (e.g. Milton *et al.* 1982), (ii) to compare patterns of leaf change and fruit production in *Ficus* species from a single locality, studied over the same period and representing members of both the *Urostigma* (strangler fig) and *Pharmacosycea* (free-standing fig) subgenera and, (iii) to obtain phenological data on two non-*Ficus* Moraceae species in the same habitat for comparison with the *Ficus* data. The overall goal of the study was to use these results as a preliminary test of the hypothesis that Moraceae on a pantropical basis exhibit phenological traits that tend to make their fruits and new leaves available to primary consumers throughout the year.

METHODS

Study site and species

The study was carried out on Barro Colorado Island (BCI), a 1500-ha biological reserve located in Gatun Lake, Republic of Panama (9°09′N, 79°51′W, 137 m a.s.l.), formed in 1914 by damming the Chagras River to create a waterway for the Panama Canal (Dietrich, Windsor & Dunne 1982). Annual rainfall averages 2600 mm, distributed fairly evenly over the 7–8 wet-season months, late April–May until November–mid-December. The wet season is followed by a short transition season from mid-December to early January and then a pronounced dry season from mid-January to April (Fig. 1). During the dry season, mean monthly rainfall is 39 mm (Croat 1978). Barro Colorado is therefore a more seasonal habitat than many tropical areas nearer the equator where annual rainfall tends to be more evenly distributed. Virtually the entire island is covered in moist tropical forest (Holdridge & Budowski 1956). Some sections of the forest are estimated to be as much as 400–500 years old, while others are second-growth, approximately 85–100 years old (Hubbell & Foster 1986).

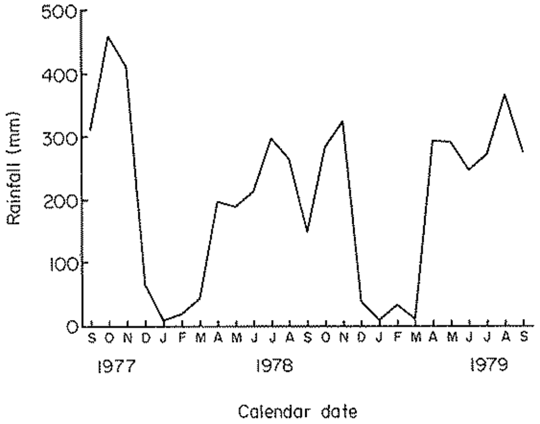


FIG. 1. Rainfall (mm) on Barro Colorado Island, Panama for each month of the phenological study.

Six species were included in the study: *Ficus insipida* Willd., *F. yoponensis* Desv., *F. obtusifolia* H.B.K., *F. costaricana* Liebm., *Poulsenia armata* Miq. and *Cecropia insignis* Liebm. Sample trees came from areas of older second-growth regarded as typical of second-growth Neotropical lowland forest in this geographical region and estimated to be between 85 and 100 years old (Foster & Brokaw 1982). Most trees were found in the central area of the island where much of the terrain is flat; only seven trees, three *Ficus yoponensis* and four *Cecropia insignis*, came from the Lutz Ravine area, the site of an earlier 8-year study of fruit initiation patterns in *F. yoponensis* and *F. insipida* (Milton *et al.* 1982).

Ficus yoponensis and *F. insipida* are members of the subgenus *Pharmacosycea*, free-standing, non-epiphytic trees, which germinate in open areas from seeds in the ground and become large overstorey trees (Croat 1978). *Ficus obtusifolia* and *F. costaricana* are members of the subgenus *Urostigma* or strangling figs. Members of this subgenus typically begin life as epiphytes, germinating from seeds dropped in fissures and forks of canopy trees. The epiphytic fig tree sends roots to the ground, typically encircling its host and occasionally killing it. *Urostigma* figs can reach massive size and become prominent members of the overstorey. Like the *Ficus* species, *Poulsenia armata* is capable of becoming a large member of the overstorey (Croat 1978). In contrast, when fully adult, *Cecropia insignis* is a considerably smaller tree both in girth and crown size, although individuals can reach heights that place them in the canopy (Foster & Brokaw 1982; K. Milton, personal observation). The age, girth and crown size of a tree can influence features of leaf, flower and fruit production (Janzen 1978; Bullock & Bawa 1981; Milton *et al.* 1982). Although the ages of individuals in this study are unknown, an effort was made to insure that, within species, all trees were fully adult individuals of approximately similar size. In some cases, this was not possible. In particular, several *Poulsenia armata* trees were smaller (probably younger) than other trees in the sample. Any implications of size differences are treated in the Results.

All six species are characterized by extremely minute flowers. The four *Ficus* species are monoecious, producing male and female flowers inside closed receptacles known as syconia. Each species is pollinated by an obligately host-specific species of agaonid wasp; no other means of fertilization is available to the tree and wasp larvae can develop only in specialized ovaries inside syconia of that species (Ramirez 1970, 1974; Herre 1989). The complex, co-evolved pollination system of *Ficus* is discussed at length in the literature (e.g. Galil & Eisikowitch 1968; Ramirez 1970; Wiebes 1979; Herre 1989). *Poulsenia armata* is also monoecious but produces separate male and female inflorescences on the same tree. *Cecropia insignis* is dioecious; individual trees produce male or female flowers on slender pendent catkins (Croat 1978). There appears to have been no formal study of pollination in either *C. insignis* or *P. armata*. My observations suggest that both species may be pollinated, at least in part, by insects. It is popularly believed that *Cecropia* species (and, possibly, *P. armata*) are wind-pollinated (Croat 1978), but this assumption appears unsupported. All six species produce fruits eaten by a wide variety of frugivores, most notably birds, bats and monkeys (Bonaccorso 1975; Croat 1978). All six species have extremely small seeds (*Ficus* spp. range = 0·5–5·0 mm in length, Corner 1958), dispersed by a wide range of animals (Croat 1978). Young leaves of all species are eaten by a number of vertebrates on BCI (e.g. howler monkeys, spider monkeys, two-toed and three-toed sloths, iguanas) and mature leaves of at least two species (*Ficus yoponensis* and *F. insipida*) are eaten by howler monkeys and iguanas, respectively (Hladik & Hladik 1969; Montgomery & Sunquist 1978; Milton 1980 and personal observation). Further details on study species are found in Croat (1978).

Sampling

Trees were sampled in two ways: (i) by direct counts of fallen leaves and stipules removed from collection plots beneath each individual and (ii) by examination of tree crowns with binoculars. Plots and trees were examined on the same day at bi-weekly intervals (mean sample interval = 15·3 ± 2·0 days) from 26 September 1977 until 9 September 1979, for a total of forty-eight samples. Details of data collection for each species are described below.

Ficus insipida, F. yoponensis, F. obtusifolia, Poulsenia armata

To determine leaf-fall and new-leaf-production patterns for these four species, two 1-m × 1-m collection plots were laid out under each of ten individuals of *F. insipida* and *F. yoponensis*, each of four individuals of *F. obtusifolia* and (initially) each of ten individuals of *P. armata*. Plots of three *P. armata* were later removed from the sample as they were too difficult to locate; the crowns of these three individuals, however, could easily be seen from a trail and these trees were retained in the fruit scans. Three *P. armata* were subsequently killed in a massive wind storm, leaving a total of four individuals for leaf-shed and stipule data and seven for fruit scans over the total study. Collection of shed leaves and stipules in *P. armata* did not begin until 14 November 1977, giving individuals of this species forty-five rather than forty-eight samples of leafing activity; forty-eight samples were collected for fruit production. Any leaf, stipule or fruit falling into any collection plot or having >50% of its mass inside the plot was counted. Each plot was deliberately placed under a large branch because the purpose was to collect materials falling from the sample tree. In *Ficus* and *Poulsenia* species, new leaves are protected by stipules, two stipules per leaf. Thus the number of stipules falling into plots provides an index of new leaf expansion. During each fortnightly sample, all fallen leaves and stipules were removed from each plot and individually counted. Before collecting data and during the study, decomposition trials were carried out to ensure that leaves and stipules did not decay within 2 weeks.

The sampling route passed by two other large, canopy-level members of the *Urostigma*, one *F. citrifolia* P. Mill. and one *F. trigonata* L. For comparative purposes, two collection plots were also placed under each of these individuals. These plots were emptied and the canopy of each tree scanned for evidence of fruiting activity on regular sampling days, because data could be used to expand the sample of phenological behaviour for the subgenus *Urostigma*.

Collection plots do not provide a reliable index of fruit production. In general, trees drop fruit only when young fruits are aborted or older fruits are rotten. Although animals feeding in trees drop fruits, terrestrial vertebrates monitor fruiting trees and typically consume dropped fruits rapidly (K. Milton, personal observation). Even collection traps placed well above ground level may be affected as mammals such as coatis climb into traps to eat fruit (K. Milton, personal observation). To obtain data on fruit production, the canopy of each individual in the sample was examined with binoculars on regular sample days (the same days on which collection plots were emptied) and the presence of inflorescences, syconia or fruits at any stage of development was recorded. The presence of fruits in collection plots was also noted.

Ficus costaricana

Twice monthly, on regular sample days, the crown of each of the four sample trees was examined with binoculars for the presence of large numbers of new leaves (which are lighter in colour than older foliage) and syconia in any stage of development. The area under each tree was examined for large numbers of recently fallen leaves and aborted or fallen fruits.

Cecropia insignis

Thirteen individuals were included in the study, five females and eight males. Twice monthly, on regular sample days, each tree crown was examined with binoculars. Mature foliage was scored as present or absent; each new leaf was counted and the total number of new leaves tree^{-1} was recorded. As *C. insignis* produces large new leaves which are pink in colour, it is not difficult to count them individually. Inflorescences or fruits in the crown were scored as present or absent.

Analysis of data

Phenological information of three kinds was recorded for each tree for each sample interval: (i) number of shed leaves in collection plots, (ii) number of stipules or new leaves in collection plots, and (iii) presence of fruits on the tree. This information was used to examine the pattern of activity in each category by year for each tree and sample population. To test for non-random temporal patterns, circular statistics were employed (Batschelet 1981). For these analyses, data were divided into two periods, each consisting of twenty-four counts representing one year (two samples month^{-1}). Each year was represented by a circle divided into twenty-four segments, each 15°. Statistics were calculated for each year.

Each phenological event (e.g. the fall of a leaf) is treated as a point on the circumference of the circle, centered within the segment corresponding to the date of collection. When all data for a given tree are considered, a mean vector, extending from the centre of the circle, can be calculated. The angle of the vector, expressed in degrees from 0 to 360°, can be converted into a date which provides an index of timing in that tree with respect to leaf drop, leaf flush or fruit production. The length of the mean vector, r ranges from 0 for data distributed uniformly around the circle to 1 for data that coincide at the same point (Batschelet 1981). Because grouping of data can bias estimates of r, a grouping correction was performed as suggested by Batschelet (1981). It should also be noted that the angle of the mean vector (and the date derived from it) does not necessarily point to the time of peak activity but rather indicates the central tendency. If, for example, a tree had two peaks in leaf flush year^{-1}, the mean angle would fall somewhere between them. Kuiper's test was used to determine whether or not the timing of leaf fall, leaf flush and fruit production for each tree was randomly distributed throughout the year. Kuiper's test is analogous to the Kolmagorov–Smirnov test, but is designed for circular distributions

(Batschelet 1981). The null hypothesis for Kuiper's test is that phenological events are drawn from a uniform random distribution. Kuiper's test rather than Rayleigh's test was used because it is more sensitive to deviations from uniform random distributions caused by bimodal patterns.

For each phenological trait (leaf fall, leaf flush, fruit production), the mean angle calculated for each individual of a species was cast into a circular distribution with all other mean angles for that species to calculate the mean angle for the sample population. Kuiper's test was used to determine whether or not the timing of each trait was randomly distributed for the entire set of trees. The length of the mean vector for the population, *r*, indicates how tightly the population is clustered in time with respect to that phenological trait in that year.

To determine if mean angles in the first year were correlated with mean angles in the second year, Batschelet's non-parametric test of circular correlation was employed (Batschelet 1981, pp. 184–190). This test is based on ranks and yields a correlation coefficient ranging from 0 to 1.

To estimate intervals between major episodes of leaf shed or leaf flush, for each tree with collection plots, the number of fallen leaves and stipules for each sample interval was summed over the total sample and the mean and standard deviation calculated. The mean ± 1 S.D. was then used as an index of high phenological activity (for convenience referred to in the text as a *peak*) for that tree for that trait, and the sample number (1–48) of each peak was recorded. For trees without collection plots, any sample interval receiving a positive score for high numbers of shed leaves or new leaves, respectively, was treated as a peak. Often there was a series of consecutive peaks in leaf shed or leaf flush for a particular tree. In such cases, for analytical purposes, the sample interval following the first interval in which a run of peaks was noted, was used as the starting point to count weeks until the next peak or run of peaks in that activity for that tree. With this information for each individual of a species, it was then possible to calculate an average leaf shed or flush interval for that species.

The mean interval between fruit crops for each tree was estimated by summing all weeks elapsing between one fruit *initiation* and the next (i.e. initiation = the first sighting of new inflorescences or syconia on a sample tree). Estimates of such intervals therefore include the period during which particular fruit crops were ripening and ripe on trees as well as periods when fruits in any stage were totally absent from the crown.

To examine the temporal order of phenological events within species, for each tree, each leaf-shed peak (or series of leaf-shed peaks) was examined with respect to the temporal location of the leaf-flush peak and fruit initiation closest to it – cut-off for proximity arbitrarily set at three sample intervals (= 6 weeks) preceeding or following a given leaf-shed peak. This same exercise was then repeated for leaf-flush peaks and fruit initiations. For example, if the first leaf-shed peak for tree A occurred in sample interval 15, the sample interval nearest to 15 was located in which a leaf-flush peak or a fruit initiation had been recorded. These could precede, be simultaneous with, or follow interval 15 as long as they were not more than three sample intervals away. The next leaf-shed peak for tree A was then located and the procedure repeated. Data for each tree and sample population could then be examined for any consistent trend in the order of these three phenological events.

RESULTS

Leaf shed

Ficus obtusifolia and *F. costaricana* were deciduous, shedding their leaf crops at approximately 8·6- and 8·1-month intervals, respectively (Table 1). Although deciduous, individuals of both species also shed some dead leaves at other times of year (Fig. 2c,d). The other four species were evergreen. However, throughout each year, dead leaves were shed from individuals of these four species, generally in small quantities but occasionally in large quantities (Fig. 2). No systematic data were collected on leaf shed by individuals of *Cecropia insignis*. Dead leaves were routinely observed under sample trees throughout both years.

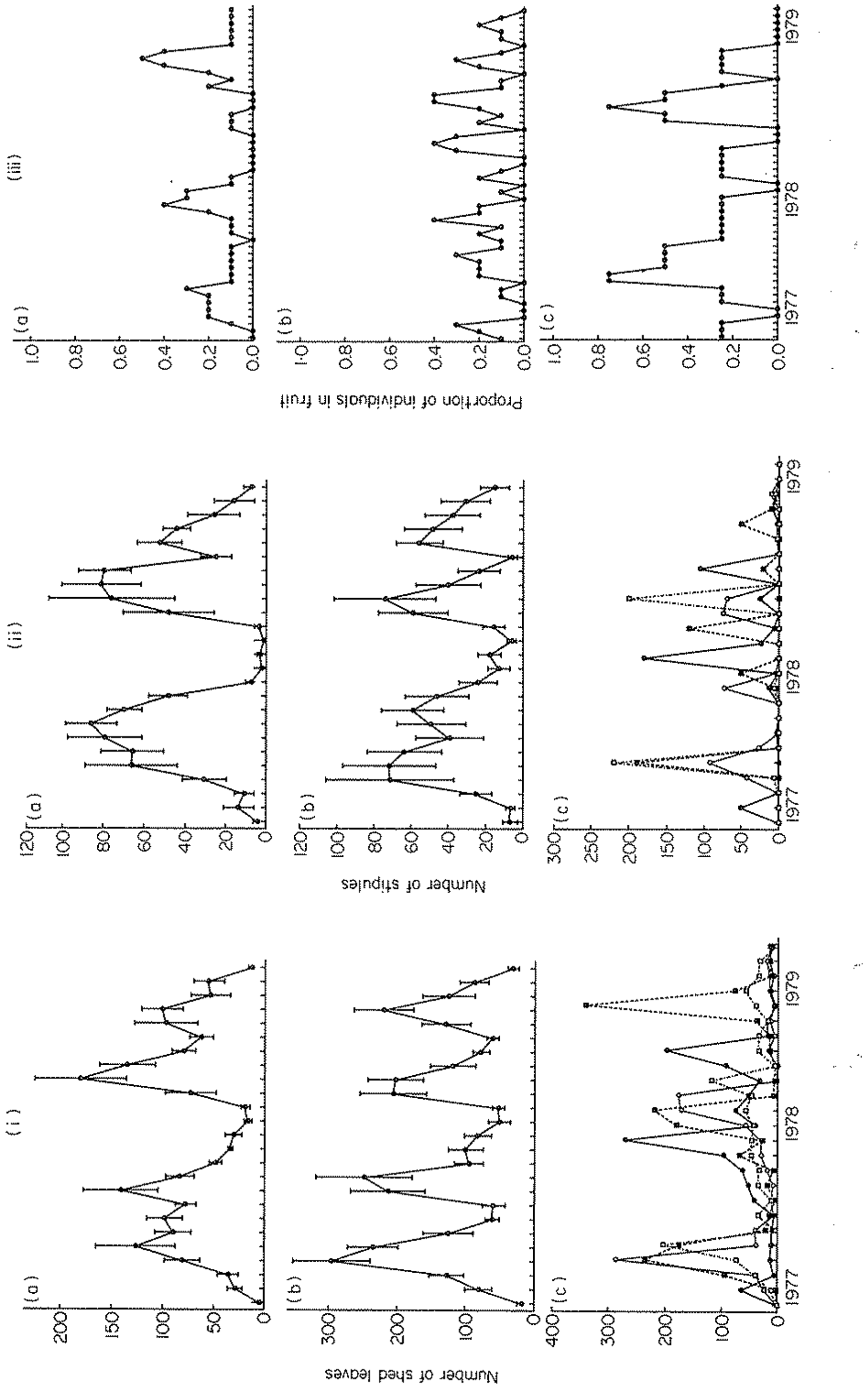
At the individual level, the temporal pattern of leaf shed was significantly non-random for all individuals of *Ficus insipida*, *F. yoponensis* and *F. obtusifolia* in both years (Kuiper's test, $P < 0{\cdot}001$ in all cases). As *F. costaricana* had no collection plots, only periods of heavy leaf fall were recorded. Statistical tests for timing of leaf shed by individual trees could be performed only for one tree in year 1 and two trees in year 2 (Kuiper's test, N.S. in all cases). As noted above, for *Poulsenia armata*, data on leaf shed were available for four trees. These four trees showed non-random patterns of leaf shed in both years (Kuiper's test, $P < 0{\cdot}01$ in all cases).

At the population level, leaf shed in *Ficus insipida* showed significant clustering in both years while no clear pattern was detected in either year for *F. yoponensis* (Table 2). For *F. obtusifolia* and *F. costaricana*, due to small sample size, Kuiper's test could not be used at the population level. In both cases, Hotelling's one-sample test was used (Batschelet 1981). This test is not powerful, and non-significant results do not necessarily indicate that phenologies are random. When mean angles for *F. obtusifolia* were considered, the distribution of mean vectors was consistent with a random distribution in both years (Table 2). Dates corresponding to mean angles were close in both years, although this could occur by chance. For *F. costaricana*, mean vectors of leaf shed were significantly clustered in the first year but not the second; dates indicated by mean angles were not close between years (Table 2). For *Poulsenia armata*, at the population level, the distribution of mean vectors was consistent with a random distribution in both years (Table 2); dates indicated by mean angles were not close between years (Table 2). Two trees of *P. armata* remaining in the sample were considerably larger than the other two. Of the two large trees, one had shed leaves in collection plots in forty-four and the other in forty-three of the forty-five samples. In contrast, the two smaller individuals of *P. armata* each had a large number of samples with no dead leaves in plots (Fig. 2e).

By the conclusion of the study, two species (*Ficus yoponensis* and *Poulsenia armata*) had shown leaf-shed peaks throughout most of the annual cycle (Table 3). The other species showed peaks in 8 or 9 of 12 months. Even when no peaks occurred, there were almost always a few shed leaves in collection plots of individual trees. For example, over the total study, for *F. insipida*, there were only twenty cases in which a tree showed no leaves in plots in a fortnightly sample (4·2% of the total sample of 480); for individuals of *F. yoponensis* there were seven such cases (1·4% of the total sample). Both *F. insipida* and *F. yoponensis* showed a bimodal trend in leaf shed, dropping considerable foliage during the transition period between the wet and dry seasons and again during the transition between the dry and rainy

Table 1. Average interval between each type of phenological event for six Moraceae species on Barro Colorado Island, Panama.

	Number of weeks between peaks in leaf shed (mean ± 1 S.D.)	Number of weeks between peaks in leaf flush (mean ± 1 S.D.)	Number of weeks between fruit initiations (mean ± 1 S.D.)
Ficus insipida (*n* = 10)	24·3 ± 16·4 (*n* = 23)	16·6 ± 16·4 (*n* = 29)	47·0 ± 17·3 (*n* = 11)
Ficus yoponensis (*n* = 10)	24·7 ± 16·4 (*n* = 24)	21·4 ± 16·8 (*n* = 26)	25·4 ± 10·5 (*n* = 19)
Ficus obtusifolia (*n* = 4)	34·4 ± 10·5 (*n* = 5)	30·5 ± 11·6 (*n* = 6)	24·0 ± 12·4 (*n* = 7)
Ficus costaricana (*n* = 4)	32·2 ± 5·2 (*n* = 8)	28·9 ± 9·1 (*n* = 9)	18·9 ± 10·0 (*n* = 14)
Poulsenia armata (*n* = 4: leaf shed, leaf flush; *n* = 7: fruit)	16·4 ± 9·2 (*n* = 17)	14·0 ± 7·9 (*n* = 11)	12·5 ± 4·6· (*n* = 29)
Cecropia insignis (*n* = 13)	no data	13·7 ± 7·9 (*n* = 42)	47·7 ± 2·0 (*n* = 11)


(i)
(a)
200
150
100
50
0
(b)
300
200
100
0
(c)
400
300
200
100
0
Number of shed leaves
(ii)
(a)
120
100
80
60
40
20
0
(b)
120
100
80
60
40
20
0
(c)
300
250
200
150
100
50
0
Number of stipules
(iii)
(a)
1.0
0.8
0.6
0.4
0.2
0.0
(b)
1.0
0.8
0.6
0.4
0.2
0.0
(c)
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of individuals in fruit
1977
1978
1979

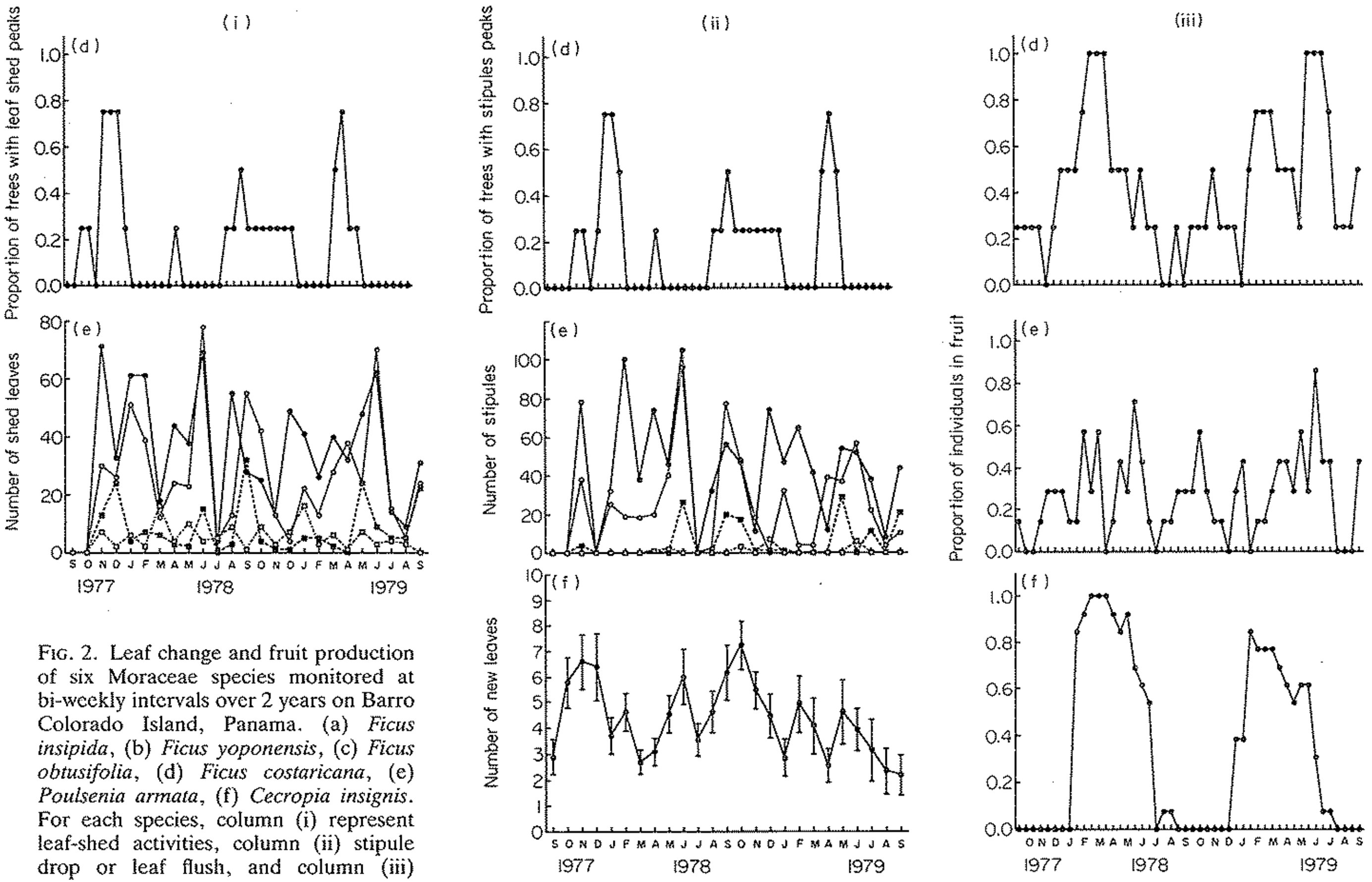


FIG. 2. Leaf change and fruit production of six Moraceae species monitored at bi-weekly intervals over 2 years on Barro Colorado Island, Panama. (a) *Ficus insipida*, (b) *Ficus yoponensis*, (c) *Ficus obtusifolia*, (d) *Ficus costaricana*, (e) *Poulsenia armata*, (f) *Cecropia insignis*. For each species, column (i) represent leaf-shed activities, column (ii) stipule drop or leaf flush, and column (iii) reproductive activities (i.e. inflorescence, syconia or fruit production). For species with ⩾ 10 trees in the sample, monthly means ± 1 S.E. are shown for leaf shed and stipule drop. For species with four trees in the sample, monthly leaf shed and stipule drop are shown for each tree and indicated by a different symbol (○, ●, □, ■). Leaf-shed and leaf-flush peaks for *F. costaricana* are indicated by bi-weekly proportions. No data were collected on leaf shed in *C. insignis*. Reproductive activities for all six species are indicated by bi-weekly proportions.

TABLE 2. Analyses of temporal patterns of phenological events of six Moraceae species on Barro Colorado Island, Panama.

	Number (mean ± 1 S.E.)	r for individual trees (mean ± 1 S.E.)	Mean angle for population		r for mean angle of population	P^*
			Degrees	Date		
Ficus insipida ($n = 10$)						
Shed leaves						
Year 1	877 ± 119	0·38 ± 0·04	194·2	23 Mar	0·74	< 0·02
Year 2	896 ± 156	0·39 ± 0·05	187·0	20 Mar	0·76	< 0·002
Stipules						
Year 1	486 ± 64	0·59 ± 0·05	191·3	21 Mar	0·90	< 0·001
Year 2	460 ± 87	0·53 ± 0·06	178·0	13 Mar	0·91	< 0·001
Samples with syconia						
Year 1	3·7 ± 0·4	0·77 ± 0·09	352·8	6 Sep	0·28	N.S.(> 0·5)
Year 2	2·7 ± 0·3	0·98 ± 0·01	238·3	15 May	0·66	< 0·05
Ficus yoponensis ($n = 10$)						
Shed leaves						
Year 1	1694 ± 191	0·29 ± 0·04	148·0	9 Feb	0·31	N.S.(> 0·5)
Year 2	1413 ± 192	0·28 ± 0·04	193·5	25 Mar	0·29	N.S.(> 0·5)
Stipules						
Year 1	487 ± 124	0·43 ± 0·06	160·2	21 Feb	0·66	< 0·05
Year 2	419 ± 113	0·37 ± 0·08	158·7	23 Feb	0·37	N.S.(> 0·2)
Samples with syconia						
Year 1	2·8 ± 0·5	0·64 ± 0·12	212·7	12 Apr	0·18	N.S.(> 0·5)
Year 2	3·7 ± 0·8	0·53 ± 0·11	154·3	19 Feb	0·45	N.S.(> 0·2)
Ficus obtusifolia ($n = 4$)						
Shed leaves						
Year 1	630 ± 54	0·51 ± 0·07	70·6	26 Nov	0·60	N.S.(> 0·5)
Year 2	597 ± 87	0·43 ± 0·12	46·4	1 Nov	0·47	N.S.(> 0·5)
Stipules						
Year 1	245 ± 7	0·68 ± 0·13	106·4	31 Dec	0·57	N.S.(> 0·5)
Year 2	181 ± 14	0·69 ± 0·13	79·7	5 Dec	0·67	N.S.(> 0·5)

Samples with syconia						
Year 1	7 ± 1·47	0·69 ± 0·14	161·1	23 Feb	0·35	N.S.(> 0·5)
Year 2	5 ± 1·68	0·75 ± 0·20	157·2	21 Feb	0·56	N.S.(> 0·5)
Ficus costaricana ($n = 4$)						
Leaf shed peaks						
Year 1	3·7 ± 0·58	0·71 ± 0·16	74·5	30 Nov	0·88	< 0·05
Year 2	4·8 ± 1·70	0·54 ± 0·16	118·1	12 Jan	0·24	N.S.(> 0·5)
Leaf flush peaks						
Year 1	3·3 ± 0·48	0·72 ± 0·15	123·7	16 Jan	0·96	< 0·025
Year 2	4·3 ± 0·85	0·43 ± 0·05	129·7	23 Jan	0·65	N.S.(> 0·5)
Samples with syconia						
Year 1	9·5 ± 1·4	0·53 ± 0·15	168·1	1 Mar	0·98	N.S.(> 0·5)
Year 2	11·5 ± 1·4	0·36 ± 0·08	223·5	29 Apr	0·38	N.S.(> 0·5)
Poulsenia armata						
Shed leaves ($n = 4$)						
Year 1	235 ± 98	0·16 ± 0·05	116·6	10 Jan	0·55	N.S.(> 0·5)
Year 2	226 ± 82	0·25 ± 0·07	255·7	1 Jun	0·26	N.S.(> 0·5)
Stipules ($n = 4$)						
Year 1	221 ± 127	0·52 ± 0·21	225·1	28 Apr	0·79	N.S.(> 0·5)
Year 2	306 ± 104	0·25 ± 0·13	330·7	13 Aug	0·33	N.S.(> 0·5)
Samples with inflorescences or fruits ($n = 7$)						
Year 1	5·9 ± 0·55	0·33 ± 0·07	169·5	5 Mar	0·61	< 0·025
Year 2	6·9 ± 1·14	0·30 ± 0·06	261·9	7 Jun	0·47	N.S.(> 0·5)
Cecropia insignis ($n = 13$)						
New leaves						
Year 1	51·8 ± 6·0	0·18 ± 0·03	4·7	15 Sep	0·68	< 0·005
Year 2	51·0 ± 7·0	0·27 ± 0·03	48·6	3 Nov	0·63	< 0·005
Samples with inflorescences or fruits						
Year 1	9·5 ± 0·56	0·73 ± 0·02	195·4	24 Mar	0·99	< 0·001
Year 2	7·5 ± 1·20	0·75 ± 0·03	177·2	13 Mar	0·94	< 0·001

* Kuiper's test was used for *Ficus insipida*, *F. yoponensis* and *Cecropia insignis*, Hotelling's test for the other three species.

Table 3. The total number of peaks month^{-1} for leaf shed and leaf flush and positive scores for fruit production over a 2-year period for six Moraceae species on Barro Colorado Island, Panama.

	Month												
	J	F	M	A	M	J	J	A	S	O	N	D	Total
Ficus insipida ($n = 10$)													
Number of peaks, leaf shed	15	11	7	4	15	10	2	0	1	0	0	6	71
Number of peaks, leaf flush	10	10	16	17	13	7	1	0	0	0	0	2	76
Number of positive scores for fruit	6	2	3	4	11	8	9	7	3	1	4	5	63
Ficus yoponensis ($n = 10$)													
Number of peaks, leaf shed	14	3	0	1	11	12	4	2	1	1	2	15	66
Number of peaks, leaf flush	13	5	4	6	15	7	2	0	2	2	3	10	69
Number of positive scores for fruit	3	10	10	2	8	5	2	5	4	5	7	5	66
Ficus obtusifolia ($n = 4$)													
Number of peaks, leaf shed	1	1	1	0	0	1	0	1	1	1	2	3	12
Number of peaks, leaf flush	5	2	0	0	0	0	0	1	0	1	2	1	12
Number of positive scores for fruit	7	10	7	5	4	3	2	0	3	4	1	2	48
Ficus costaricana ($n = 4$)													
Number of peaks, leaf shed	1	0	1	3	0	0	0	2	3	2	3	7	22
Number of peaks, leaf flush	6	2	0	5	2	0	0	1	1	2	1	3	23
Number of positive scores for fruit	6	13	13	8	8	11	5	3	4	4	4	5	84
Poulsenia armata ($n = 4$: leaf shed, leaf flush; $n = 7$: fruit production)													
Number of peaks, leaf shed	5	2	1	1	4	4	0	1	3	2	2	2	27
Number of peaks, leaf flush	1	2	0	2	1	6	0	0	3	2	2	1	20
Number of positive scores for fruit	6	11	11	13	15	15	7	3	9	6	8	8	112
Cecropia insignis ($n = 13$)													
Number of peaks, leaf flush	6	12	7	2	12	18	5	11	10	18	20	15	136
Number of positive scores for fruit	27	45	45	38	37	20	2	1	0	0	0	5	220

seasons (Fig. 2a,b). The two *Urostigma* species averaged longer between leaf shed peaks than the two *Pharmacosycea*. In contrast, *Poulsenia armata* had the shortest average leaf-shed interval of the six species (Table 1).

Stipule fall and leaf flush

Stipule fall, which, as noted, is an index of new leaf expansion, was significantly non-random for all individuals of *Ficus insipida* and *F. yoponensis* in both years (Kuiper's test, $P<0{\cdot}001$ in all cases). At the population level, stipule drop in *F. insipida* was significantly clustered in both years and mean angles pointed to almost identical dates; scores for r were high and similar in both years. For *F. yoponensis*, at the population level, mean angles of stipule drop were significantly clustered in the first year but not the second; in both years, mean angles pointed to almost identical dates (Table 2).

Stipule fall was non-random for all trees of *Ficus obtusifolia* in both years (Kuiper's test, $P<0{\cdot}001$ in all cases). At the population level, however, the distribution of mean vectors was consistent with a random distribution (Table 2). Over the 2-year sample, some stipule fall was recorded for *F. obtusifolia* in all months of the year (Fig. 2c) although peaks occurred in only 6 months (Table 3). In this species, individual trees do not produce new leaves continuously but rather produce a few new leaves occasionally and large new leaf crops at 7–8-month intervals (Table 1). For *F. costaricana*, at the individual level, statistical tests could be performed for only two trees in year 2 (Kuiper's test, N.S. in both cases). At the population level, mean vectors of leaf flush were significantly clustered in the first year but not the second (Table 2). Dates corresponding to mean angles were similar between years for both *F. obtusifolia* and *F. costaricana*

Data for statistical testing in *Poulsenia armata* were available for three trees over the total sample, because data for the fourth individual (one of the smaller trees) were too few for analysis. All three trees showed significantly non-random patterns of stipule drop in both years (Kuiper's test, $P<0{\cdot}001$ in all cases). At the population level, the distribution of mean vectors was consistent with a random distribution in both years; dates indicated by mean angles were very different between years (Table 2). As was found for leaf shed, the two larger trees of *P. armata* were far more productive in stipule drop throughout the year than the two smaller trees. Out of ninety samples (forty-five for each large tree), there were only eighteen (20% of the total) in which no stipules were found in collection plots of these large trees and these eighteen samples (twelve cases for one tree and six for the other) were scattered throughout the year, though often simultaneous for both trees. It therefore seems reasonable to describe *P. armata*, at least in terms of larger trees, as a continuous flusher (Fig. 2e).

As new leaves of *Cecropia insignis* may retain their pink colour for more than two weeks, the possibility exists that a new leaf counted in one sample may also have been counted in a later sample. For this reason, results of circular statistics should be viewed cautiously. Results indicate that only around half of the individuals of *C. insignis* showed a non-random pattern of new leaf production (five cases in the first year, Kuiper's test, $P<0{\cdot}02$ in all cases; seven cases in the second year, Kuiper's test, $P<0{\cdot}01$ in all cases). At the population level, however, leaf flush showed significant clustering in both years and dates indicated by mean angles were very close (Table 2). Although the population shows clumping, *C. insignis* produces some new leaves continuously and all individuals in the sample tended to show new leaves in the crown throughout the year, both years (Fig. 2f).

With the exception of *Cecropia insignis*, and to a lesser extent *Ficus obtusifolia*, species tended to show more evidence of new leaf production during the early rather than later 6 months of the year (Table 3). In both years, during the mid-to-late rainy season, August until November, *Ficus insipida* showed no peaks in stipule drop; similarly, *F. yoponensis* and *Poulsenia armata* showed no peaks in stipule drop in August of either year, and leaf flush for *F. costaricana* was also low during this period (Table 3).

Although all species produced considerable new foliage during the drier portion of the year, months of greatest flush production, as indicated by the number of peaks, were not the same for all species, Stipule drop in *F. yoponensis* showed a bimodal trend in both years (Fig. 2b); January and May had the greatest number of peaks (Table 3). A tendency toward a bimodal trend was also observed in *F. insipida*, more obvious in the second year (Fig. 2a); March and April had the greatest number of peaks (Table 3). For *F. obtusifolia* and *F. costaricana*, January had the greatest number of peaks while June showed the highest number for *Poulsenia armata*. (Table 3). In contrast to these five species, *Cecropia insignis* showed the greatest number of new leaf peaks in November, the last month of the rainy season; October and June were also months of high new leaf production in this species (Table 3). Almost half of the flush peaks recorded for *F. obtusifolia* also occured during the mid-to-late rainy season (Table 3).

On occasion, one or more individuals of *F. insipida* and/or *F. yoponensis* lacked stipules in collection plots for one or more consecutive samples. In combined data, there were 128 such cases for *F. insipida* (27% of the total sample of 480), while for *F. yoponensis* there were ninety (19% of the total). Likewise, one or more individuals of the other four species also had sample intervals when no stipules were present in plots (*F. obtusifolia* and *Poulsenia armata*) or no new leaves were visible in the crown (*F. costaricana* and *Cecropia insignis*). Periods of low or no new leaf production could be prolonged for trees of the *Urostigma*. On occasion, however, although an individual might not have stipules in plots, stipules were present beneath the tree outside plots, indicating that some new leaf expansion was occurring even though the score for the tree in that sample interval was zero. At the population level, five species showed some evidence of new leaf production in every sample month, both years (Fig. 2). No comment can be made for *F. costaricana* as only flush peaks were recorded.

Fruit production

All *Ficus* species exhibited intraspecific asynchrony in fruit production, initiating and ripening fruit crops throughout the year (Fig. 2). For *F. insipida* and *F. yoponensis*, sample sizes for individual trees were too small in most cases for statistical testing. At the population level, mean angles of *F. insipida* were significantly clustered in the first year but not the second; scores for r were very different between years as were dates corresponding to mean angles (Table 2). At the population level, for *F. yoponensis* there was no evidence of non-random distribution of mean angles in either year, although dates corresponding to mean angles were fairly close; scores for r tended to be low in both years, indicating considerable scatter around the mean. In combined data, intervals between fruit initiations averaged slightly less than 1 year for *F. insipida* and slightly more than a half-year for *F. yoponensis* (Table 1).

Because of small sample size, only three trees could be analysed for fruit production patterns in *Ficus obtusifolia*. Two of three trees in the first year showed a non-random pattern (Kuiper's test, $P<0{\cdot}005$) as did one tree in the second year (Kuiper's test, $P<0{\cdot}005$). At the population level, for *F. obtusifolia*, there was no evidence of non-random distribution of mean vectors in either year (Table 2). For *F. costaricana*, there were sufficient data on fruit production to analyse temporal patterns for all four trees in both years. Timing of fruit production was significantly non-random for two trees in the first year (Kuiper's test, $P<0{\cdot}05$ in both cases) but for no trees in the second year (Kuiper's test, N.S. in all cases). At the population level, for *F. costaricana*, there was no evidence in either year for non-random distribution of mean vectors (Table 2). Dates corresponding to mean vectors were almost identical between years for *F. obtusifolia* and were similar for *F. costaricana* (Table 2).

For *Poulsenia armata*, fruit production data for statistical testing were available for six of seven trees in year 1 and five of seven trees in year 2. Fruit production appeared random for all individuals in both years (Kuiper's test, N.S. in all cases). At the level of the population, there was no evidence for non-random distribution of mean vectors in either year and dates indicated by mean angles were not close (Table 2). During the study, there were only two months (October 1977 and August 1979) in which inflorescences or fruits in some stage of development were absent from all plots of *P. armata* (Fig. 2e). Fruit production appeared episodic in that inflorescences or fruits generally were noted in the crown of each individual from three to seven different times each year. The larger trees might even be described as more-or-less continuous in their pattern of inflorescence production. In both years, inflorescence and fruit production was most obvious in the population between February and June, although, in general, the number of individuals producing inflorescences or fruits at any one time was highly variable (Fig. 2e). On occasions, both male and female inflorescences were seen in the crown or beneath a particular individual of *P. armata* at the same time, suggesting the possibility of both self- and outcrossing.

Cecropia insignis was the only dioecious species in the sample. Almost without exception, individuals showed significantly non-random patterns of fruit production in both years (Kuiper's test, $P<0{\cdot}02$ in all cases). At the population level, mean angles of fruit production were significantly clustered in both years (Table 2). Dates indicated by mean angles were almost identical between years and r scores were extremely high (Table 2). In both years, all trees were completely bare of inflorescences or fruits during the mid-to-late rainy season, September until November and most of December as well (Fig. 2f).

Between-year correlations

Only one significant result was obtained for between-year correlations for any species in any phenological category. In this one case, leaf shed in *Ficus insipida*, the rank order of mean angles for trees of *Ficus insipida* showed a significant correlation between years ($r=0{\cdot}924$, $P<0{\cdot}001$). Thus, for example, trees that tended to shed leaves later in the first year shed them later in the second year as well.

Temporal order of phenological events

The temporal order of phenological events was clear for *Ficus obtusifolia*, *F. costaricana* and *Cecropia insignis*. In *F. obtusifolia*, trees first showed a period of intense leaf shed lasting 4–6 weeks. Simultaneous (within the same 2-week sample period) with the final peak in leaf shed, a flush crop was expanded. A new fruit crop was generally observed on the tree in the same interval as the initial leaf-flush peak or within the next two sample intervals (seven of nine cases for four trees). In *F. costaricana*, trees first shed leaves, then, simultaneously or within the next fortnight, flushed new leaves. Fruit crops were typically initiated simultaneously with leaf-flush peaks or within 2 weeks thereafter. A very similar temporal pattern was also noted for the single individuals of *F. citrifolia* and *F. trigonata* observed over the 2-year sample. Both trees were deciduous; both dropped the final portion of their leaf crop and then expanded a flush crop and both tended to initiate fruit crops shortly after flushing (*F. citrifolia*, three of four fruit crops; in *F. trigonata*, the first fruit crop occurred too early in the study for the leafing phenology preceding it to be documented; the second fruit crop was initiated immediately after leaf shed and flush expansion). Contrary to findings of Windsor *et al.* (1989), who speculated that the timing of flush and fruit production in *Urostigma* were not sequentially related, results presented here suggest a strong and consistent relationship between the timing and order of these events in members of *Urostigma*.

Cecropia insignis also showed a clear pattern of phenological events. Trees first produce a number of new leaves in the late rainy season, i.e. October, November and early December (Fig. 2f). This is followed by production of inflorescences and fruits, which reaches its maximum during the dry season, particularly February and March. Trees put out large numbers of new leaves again in the early portion of the rainy season, May–June, after fruit production has begun to decline. At all times of year, however, at least some new leaves were produced by most trees.

The order of phenological events is less clear for the other three species. Data suggest that in *Poulsenia armata*, leaf-shed peaks are followed by leaf-flush peaks and then by fruit initiations, but it is difficult to discern a clear pattern as individuals tended to be so active (Fig. 2e). For *Ficus insipida* and *F. yoponensis*, phenological events did not appear to follow any clear pattern. In both species, for example, fruit initiations could occur simultaneously with leaf drop and leaf flush, or the three events could take place in any order or permutation (twenty-one fruit initiations examined for *F. insipida* and twenty-two for *F. yoponensis*). *Ficus insipida* also had three totally isolated fruiting events, i.e. episodes of fruit production not in close proximity to either a leaf shed or a leaf flush peak ('proximity' as defined in Methods), while *F. yoponensis* had five. Overall, leaf shed and leaf flush in *F. insipida* showed a high degree of temporal association within and between years and tended to be concentrated into the period between January and May. Fruit production in this species, however, was less tightly synchronized. At the individual level, trees of both species showed a tendency to carry out all three phenological events within the same general period; i.e. if a tree showed a flush peak (or a leaf-shed peak or a fruit initiation), it was likely that the other two phenological events for that tree would also occur at some closer rather than further time. At the individual level, > 50% of the leaf-shed and leaf-flush peaks in *F. yoponensis* occurred simultaneously (sixty-six leaf-shed and sixty-nine leaf-flush peaks examined). Similar to *F. insipida*, the timing of fruit initiation and production in *F. yoponensis* seemed to be the most variable of the three phenological traits. Likewise, in *F. yoponensis* phenological events were more likely to take place during the dry and transition seasons each year, although each could also occur at any time.

DISCUSSION

As noted by Janzen (1978), well-documented examples of annually fruiting species of tropical trees are surprisingly rare. The six Moraceae species in this study all bore fruit crops at least once a year and all had fruiting intervals averaging <52 weeks. In four species, fruiting intervals averaged 26 weeks or less. Two species, *Cecropia insignis* and *Ficus costaricana*, showed fruit in the crown for long periods each year and larger trees of *Poulsenia armata* initiated inflorescences more or less continuously. In addition, with the exception of *Cecropia insignis*, all species showed intraspecific asynchrony in fruit production and, within species, most individuals altered the time(s) of year at which fruit crops were initiated. With six exceptions (12·8% of the total trees in the sample), all trees in the study produced a minimum of at least one fruit crop year^{-1} in both years and many produced more. Four of the six individuals producing only a single fruit crop over the 2-year study had large numbers of vines in the canopy. The effect of these vines on productivity of the host tree was only realized at the conclusion of the study when inter-individual productivity was compared. These observations suggest that extensive vines in the canopy of a tree may have a markedly negative effect on host productivity with respect to both fruit crops and new foliage.

In general, at the population level, new leaf production appeared to be more or less continuous for all species. Even in months when no peaks were recorded for a particular species, one or more trees of each species generally showed some evidence of new leaf production. In a few cases, analyses showed significant clustering of leaf flush activity by a particular species (e.g. *Ficus insipida* and *Cecropia insignis*). Even when the timing of maximum leaf production was clustered, smaller quantities of new foliage were also produced by these species at other times of year. This was particularly obvious in *C. insignis*, where most individuals showed new leaves in the crown throughout both years. For some individuals of *F. insipida*, *F. yoponensis* and *Poulsenia armata*, it was unusual not to recover at least some stipules from collection plots in all months of the study, suggesting that for these individuals new leaf production was more or less continuous. The two species of *Urostigma* were less active than other species in terms of new leaf production and tended to produce quantities of new leaves only when old leaf crops were dropped.

All mean intervals calculated in Table 1 are <52 weeks. Further, with the exception of leaf shed in *Ficus insipida*, intraspecifically, trees tended to shift their order in terms of the timing of phenological events across years. These two findings suggest that most trees in the study were constantly altering the time(s) of year at which they carried out phenological activities. The central tendency for the population of each species for a particular trait often fell in the same time period in both years, however. Overall, there was a total of thirty-four mean angle scores for populations in the study, six for each species except *Cecropia insignis*, which lacked scores for leaf drop (Table 2). If the year is divided in half, twenty-six of the thirty-four scores (76·5%) fall in the first 6 months of the year, January–June. Examination of leaf activity peaks and positive fruit scores recorded in Table 3 similarly show that 70% occurred between January and June. Thus, it seems safe to say that for these Moraceae species in this locality, there is a tendency to concentrate phenological activity into the drier portion of the year (see also Windsor *et al.* 1989; Milton *et al.* 1982). In spite of this seasonal trend, however, some leaf shed, leaf flush and fruit initiation and production take place in most species throughout the annual cycle.

Implications for primary consumers

Implications of phenological patterns of these Moraceae for primary consumers are clear. Primary consumers which exploit these species should have a relatively continuous supply of fruits and new leaves throughout the year if there are enough trees in the habitat to provide a dietary foundation. Although the transition periods and dry season consistently offer higher abundances of both new leaves and fruits, at least some new leaves and fruits can be expected from most species throughout the year. Nor is it necessary for animals to focus only on dietary items from the genus *Ficus*. Larger trees of *Poulsenia armata* produced new leaves, inflorescences and fruits throughout the year (although, in contrast to *Ficus* species, *P. armata* was never noted to produce a large crop of ripe fruits on any tree), while individuals of *Cecropia insignis* produced new leaves throughout the year and held inflorescences or fruits (both of which are edible) on trees each year for 8–9 months. Opportunistic observation of another Moraceae species in this forest, *Brosimum alicastrum* (Pitt) C. C. Berg, indicates that some trees initiate two flush and two fruit crops year^{-1} [Milton (1980) and personal observation; see also Coelho *et al.* (1976) for discussion of phenological patterns of *B. alicastrum* in Guatemala]. Croat (1978) notes that two other Moraceae occurring on BCI, *Olmedia aspera* and *Castilla elastica*, are reported to have year-round flowering and another, *Perebea xanthochyma*, may flower each year for periods of up to 9 months (Croat 1978). Bawa (1983) points out that in Costa Rica, *Trophis involucrata* (a wind-pollinated, dioecious, understorey Moraceae), produces flowers in January and February and that some 15% of the population flowers again in July–August. These and other similar observations (e.g. Cords 1984) suggest that many species of Moraceae may show frequent fruit (and new leaf) production. If future research confirms this prediction for the majority of tropical Moraceae, such patterns would help to explain the general prominence of fruits and foliage of Moraceae, both *Ficus* and non-*Ficus* species, in the diets of primary consumers on a pantropical basis. Nutritional and other chemical factors are obviously of importance in diet selection, but to be considered as an item of diet at all, a new leaf or fruit must first be available.

Proximate factors

Few comments can be made on proximate factors which may influence these phenological patterns. Water-related factors, photoperiod and temperature variation are frequently suggested to influence the timing of phenological events in tropical trees (Ng 1977; Whitmore 1985; Ashton, Givnish & Appanah 1988; Newstrom *et al.* 1991). For example, van Schaik (1986) has suggested that in the seasonally dry tropics, water-related factors may be a primary influence on phenological patterns, while in the humid tropics, degree of insolation may exert a strong influence.

Borchert (1983) has suggested that flower initiation in tropical trees may be mainly under endogenous control and affected by environmental factors only indirectly through their effects on seasonal vegetative development. For example, physiological factors related to seasonal changes in tree water status may trigger the first phenological event, generally leaf shed, and the timing of this event may, through interrelated physiological mechanisms, influence the timing of other phenological events such as flower initiation and anthesis (Borchert 1983).

Overall, the seasonal pattern of leaf changes and flowering activities in these Neotropical Moraceae seems similar to that of a number of other tropical tree species in both the Old and New Worlds. For example, the seasonal pattern of leaf flush and flower production described by Medway (1972) for many evergreen rainforest species in the Ulu Gombak valley in Malaya is similar to that described here. However, the principal fruiting season for the Ulu Gombak community, including the peak in ripe fruit availability, falls during the more rainy portion of the year — a period of relatively low fruit production by most Moraceae in this study. Constraints related to syconia–wasp development may prohibit any prolonged temporal displacement between flowering and fruit maturation in individuals of the *Ficus* species in this study. Thus, if some factor(s) favours flower production by *Ficus* species during the drier portion of the year on BCI, fruit maturation presumably must also occur at that time. In contrast to the *Ficus* species on BCI, in Ketambe, Sumatra, where mean annual rainfall is considerably higher and even the drier months receive >150 mm of rain, strangler figs show fruiting peaks in April and October, which are both wet-season months with high rainfall (van Schaik 1986). Discussion of proximate factors related to phenological patterns in Moraceae is further complicated by the fact that individuals of species in this study did not necessarily carry out phenological activities only during the drier portion of the year; rather, trees could apparently shed old leaves, produce flush, or initiate inflorescences or syconia in any month (one notable exception being inflorescence and fruit production by *Cecropia insignis*). This suggests that trees of these Moraceae fall largely into the 'day-neutral' category, i.e. they can flower or initiate syconia irrespective of environmental conditions once they have attained a certain minimal size and the ill-defined state of "ripeness to flower"' (Borchert 1983; see also Koelmeyer 1961; Milton *et al.* 1982). Ripeness to flower is presumed to relate to individual resource accumulation (e.g. Milton *et al.* 1982).

Ultimate factors

Well before this study, an intraspecifically asynchronous pattern of fruit production had been documented for a number of *Ficus* species in tropical areas of both the Old and New Worlds (e.g. Hill 1967; Medway 1972; Newton & Lomo 1979). Typically, this fruiting pattern has been described as essential to ensure the continued survival of the obligate wasp pollinators (e.g. Ramirez 1970, 1974; Rathcke & Lacey 1985; Kjelberg & Maurice 1989). If this were the only factor influencing intraspecific asynchrony, fruit production might be expected to occur more or less evenly throughout the year. On BCI, however, various *Ficus* species show what appear to be consistent annual peaks and valleys in fruit production. Some direct benefits beyond 'providing a haven for the pollinator' are predicted to accrue to individuals fruiting when most other members of their population do not. Otherwise, it would appear that each year some trees place themselves at an apparent selective disadvantage by initiating syconia when most other members of their population do not, ostensibly to keep pollinators alive for other individuals to use during more favoured times of year for fruit production. Obviously the present-day pattern of floral development in *Ficus* syconia, in which male flowers mature some weeks after female flowers, favours some lack of synchrony between conspecifics, because trees in perfect synchrony would have no recipients for pollen. Potential pollen-transfer, however, seems insufficient to explain syconia initiation by fig trees during population-wide low points in fruit production. Furthermore, various other tropical tree species, both Moraceae and non-Moraceae, also show intraspecific asynchrony in flower production (Putz 1979; Whitmore 1985; Fleming *et al.* 1985; Newstrom *et al.* 1991). Although in some cases, this pattern may well relate to pollination advantages, other factors can also be suggested to account for it. For example, seed dispersal might be enhanced by a pattern of individual fruiting that puts fruit crops into the forest-wide fruit pool at different points over consecutive annual cycles rather than in one fixed period each year; such a pattern could also help to confound seed (or wasp) predators (Janzen 1967). For the Moraceae, however, and for *Ficus* species in particular, one very important factor would appear to be strong selective pressures related to the efficient distribution of unusually tiny seeds which presumably require large light gaps for successful establishment.

In the Barro Colorado forest, large light gaps are less abundant than small light gaps (Hubbell & Foster 1986). Therefore, the distance a shade-tolerant species must disperse its seeds to encounter a suitable germination site is considerably less than for light-demanding species. Hubbell & Foster (1986) have calculated that a shade-tolerant species with 200 adults and a minimum critical gap size of 25 m^2 would encounter twenty gaps within 100 m; on the other hand, seeds of light-demanding species, which minimally require 100-m^2 gaps, would have to travel over 300 m to encounter twenty gaps. Schupp *et al.* (1989) point out the disproportionate importance of landing in a recent gap for small seeds. Martínez-Ramos, Alvarez-Buylla & Sarukhán (1989) note that seedlings of *Cecropia obtusifolia* in Mexico survive only in gaps with areas $> 100\,m^2$. Individuals of plant species with very small seeds appear to be under unusually strong pressure to produce quantities of seeds each year to compensate for their lowered probability of establishment per unit distance. It is this pressure which appears to offer the single most satisfactory explanation for the frequent and/or intraspecifically asynchronous pattern of fruit production found in many present-day Moraceae, a family noted for small seeds and various highly successful colonizing genera. Because light gaps appear largely by chance, all else being equal, the more seeds (and pollen) a given individual can produce and disperse in its lifetime, the greater the probability of successful establishment (Milton *et al.* 1982).

Although *Urostigma*, as stranglers, avoid the necessity for large terrestrial light gaps, their seeds, unlike those of the *Pharmacosycea*, have achenes covered by a thick, viscid coat which apparently must be removed by Gram-positive rod bacteria before germination will occur (Ramirez 1976). Seedling establishment in the canopy by members of the *Urostigma* appears to require successful placement of seeds in fissures and tree forks containing soils or organic matter with such bacteria, as well as considerable exposure to sunlight and some moisture (Ramirez 1976). Frequent fruit production in *Urostigma* should improve an individual's chances for meeting this set of conditions with some seeds.

I hypothesize that a pattern of frequent flower and fruit production is an ancient trait of both Moraceae in general and the pre-*Ficus* ancestor in particular and a trait which originally had little or nothing to do with wasp pollinators. Some support for this view is found in Wiebes (1979), who speculates that the pre-agaonid ancestor of the pollinating wasps may have been gall-producing parasites of the pre-*Ficus* flower and suggests that evolution of the fig syconium may relate more to seed dispersal than pollination of flowers. Ramirez (1976) likewise suggests that fig wasps may descend from pollen-eating gall-makers on pre-*Ficus* plants, and Borchert (1983) suggests that any temporal correlation between flowering and insect activity in the tropics may result from adaptation of insect life cycles to seasonal tree development. Various extant Moraceae, even understorey species, are anemophilous (Bawa & Crisp 1980), and wind- rather than insect-pollination is hypothesized to be the ancestral condition for the family (Ramirez 1980). Present-day pollinators of *Ficus* may initially have been pollen-eating opportunists that, over evolutionary time, adapted to and fine-tuned a pre-existing fruiting pattern (and floral morphology) initially selected for to enhance seed dispersal and germination prospects in a small-seeded, anemophilous tropical colonizer.

A comparison of the reproductive phenology of other Moraceae with that of *Ficus* offers insight into other possible reproductive advantages conferred by the *Ficus*–fig-wasp symbiosis. Unlike these *Ficus* species, which (like all members of the *Pharmacosycea* and *Urostigma*) are monoecious, most Neotropical Moraceae are dioecious (Berg 1972, 1989; Burger 1977; Croat 1978). Dioecy is common in the tropics and some evidence suggests that it is favoured under conditions of environmental heterogeneity [Iglesias & Bell (1989); see Thomson & Brunet (1990) for a review of hypotheses related to the evolution of dioecy and Verkerke (1989) and Bronstein (1989) for discussion of gynodioecy in the genus *Ficus*]. Although structurally monoecious, through the intermediary of the wasp pollinator, trees of these *Ficus* species are functionally dioecious. Delayed maturation of male flowers in the fig syconium and the wasp life cycle are such that pollen from syconia of one fig tree is taken away by female wasps to receptive syconia of conspecifics elsewhere, ensuring outcrossing. However, although functionally dioecious, unlike the individuals of *Cecropia insignis* in this study, which are morphologically dioecious, these fig trees are not constrained to flower at only one (or, as is the case for some other dioecious species, a few) temporally fixed period(s) each year to assure pollination; nor are these fig trees limited to producing small quantities of flowers at multiple irregular intervals or more or less continuously, the condition noted for individuals of *Poulsenia armata* in this study and found also in some dioecious species (e.g. Newstrom *et al.* 1991). Rather, these fig trees can initiate syconia at any time of year and produce massive fruit crops. The short life-span of individual wasps appears to place them under strong pressure to find host trees regardless of time of year. As pollination is never guaranteed, through chance events even trees fruiting during peaks in population-wide syconia production may fail to receive pollinators; conversely, trees fruiting during population-wide low points may obtain pollinators and perhaps reap other important benefits as well (e.g. escape from seed predators, access to large numbers of seed dispersal agents and so on). The ability consistently to alter the time of year of fruit production may therefore be the best lifetime pattern for an individual fig tree, because different reproductive benefits presumably accrue to individual trees at somewhat different times each year (Milton *et al.* 1982). Furthermore, evidence suggests that under certain environmental conditions, individuals of some *Ficus* species can produce syconia in different stages and, apparently, self-pollinate (Janzen 1979; Bronstein 1989; McKey 1989). Single branches with syconia present were occasionally observed on some individuals of both *F. yoponensis* and *F. obtusifolia* during this study although the function served by this behaviour is unknown. In effect, through their obligate mutualism with wasp pollinators, these *Ficus* species appear to have liberated themselves, at least to some degree, from many constraints postulated to structure reproductive phenology for a number of other tropical tree species, constraints not only related to pollination but also to seed dispersal and perhaps to the avoidance of parasites and seed (and wasp) predators as well (see, for example, Janzen 1967; Milton *et al.* 1982; Frank 1989).

The genus *Ficus* is noted for its numerical abundance (> 900 species) and its remarkable ability for colonization and the development of endemic species and different life forms (Corner 1958; Janzen 1979). In this latter respect, obligate pollinators presumably confer a selective advantage (Ramirez 1976). Obligate pollinators should also permit individuals of particular *Ficus* species to move into new areas without having to compete for or adjust to local pollinators (Milton *et al.* 1982). The unusual success of *Ficus* as a genus indicates that pollinators manage to track colonizing individuals successfully. Corner (1958), for example, discusses the spread of introduced fig wasps throughout the islands of Hawaii in only a few years and Hill (1967) speculates that in the 10–20 years it takes most fig trees to reach reproductive maturity, wasp pollinators would eventually reach most naturally dispersed plants. If, for whatever reason, local extinction of wasp pollinators should occasionally occur, these observations also suggest that such areas would be rapidly repopulated by appropriate wasps from neighbouring communities.

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