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Phenology of *Ficus variegata* in a seasonal wet tropical forest at Cape Tribulation, Australia

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Abstract. We studied the phenology of 198 mature trees of the dioecious fig *Ficus variegata* Blume (Moraceae) in a seasonally wet tropical rain forest at Cape Tribulation, Australia, from March 1988 to February 1993. Leaf production was highly seasonal and correlated with rainfall. Trees were annually deciduous, with a pronounced leaf drop and a pulse of new growth during the August–September drought. At the population level, figs were produced continually throughout the study but there were pronounced annual cycles in fig abundance. Figs were least abundant during the early dry period (June–September) and most abundant from the late dry season (October–November) through the wet season (December–April). The annual peak in reproduction actually reflected two staggered peaks arising from gender differences in fig phenology. In this dioecious species, female and male trees initiated their maximal fig crops at different times and flowering was to some extent synchronized within sexes. Fig production in the female (seed-producing) trees was typically confined to the wet season. Male (wasp-producing) trees were less synchronized than female trees but reached a peak level of fig production in the months prior to the onset of female fig production. Male trees were also more likely to produce figs continually. Asynchrony among male fig crops during the dry season could maintain the pollinator population under adverse conditions through within- and among-tree wasp transfers.

Key words. Australia, Cape Tribulation, dioecy, *Ficus variegata*, figs, flowering asynchrony, phenology, seasonality.

INTRODUCTION

Fig trees have complex reproductive phenologies, resulting in part from the distinctive system of pollination. The pollination of figs, being accomplished only by host-specific wasps of the family Agaonidae, is regarded as one of the few documented cases of an obligatory mutualism between a plant and its pollinator (Bronstein, 1992). The fig (syconium) is an enclosed receptacle containing many flowers and fig wasps, whose larvae depend entirely on developing fig seeds for food. The short-lived, pollen-carrying female wasps emerge from ripe figs, and must locate other receptive figs in which to lay their eggs. This interaction requires that figs in different developmental phases are continually present in a population; otherwise the fig wasp population would become locally extinct. Flowering asynchrony and continual fruiting at the population level, combined with flowering synchrony and sub-annual fruiting at the individual level, is characteristic of figs (Janzen, 1979; Newstrom, Frankie & Baker, 1994). However, many cases of within-tree asynchrony have been documented (Baijnath & Ramcharun, 1983, 1988; Bronstein, 1989; Bronstein & Patel, 1992; Corlett, 1984, 1987, 1993).

Seasonality in fig production has often been noted in phenological studies that report asynchronous flowering and continual fig production at the population-level (Newton & Lomo, 1979; Milton *et al.*, 1982; Baijnath & Ramcharun, 1983; Corlett, 1984, 1987, 1993; Nair & Abdurahiman, 1984; van Shaick, 1986; Kjellberg *et al.*, 1987; Bronstein, 1989; Windsor *et al.*, 1989). The degree of seasonality in fruiting patterns varies geographically, from a slight trend in Panama (Milton *et al.*, 1982) to more extreme cases in Southern France (Kjellberg *et al.*, 1987) and Florida (Bronstein, 1989).

The breeding system of a fig species (either monoecious or dioecious) can also influence reproductive phenology, especially in seasonal habitats. In monoecious species, fig seeds and wasps are produced within the same fig. In dioecious species, however, wasp and seed production is segregated between male and female trees, respectively (Valdeyron & Lloyd, 1979; Berg, 1989; Weiblen, Spencer & Flick, 1995). Many authors have suggested that seasonal climatic variation is less problematic for dioecious figs than for monoecious figs (Valdeyron & Lloyd, 1979; Kjellberg *et al.*, 1987; Bronstein, 1989; Kjellberg & Maurice, 1989; Patel, Hossaert-McKey & McKey, 1993). In dioecious figs, each sex can take advantage of different conditions favouring either seed or wasp production. Female trees flower and fruit during conditions optimal for seed production and dispersal. Male trees produce figs more often than the

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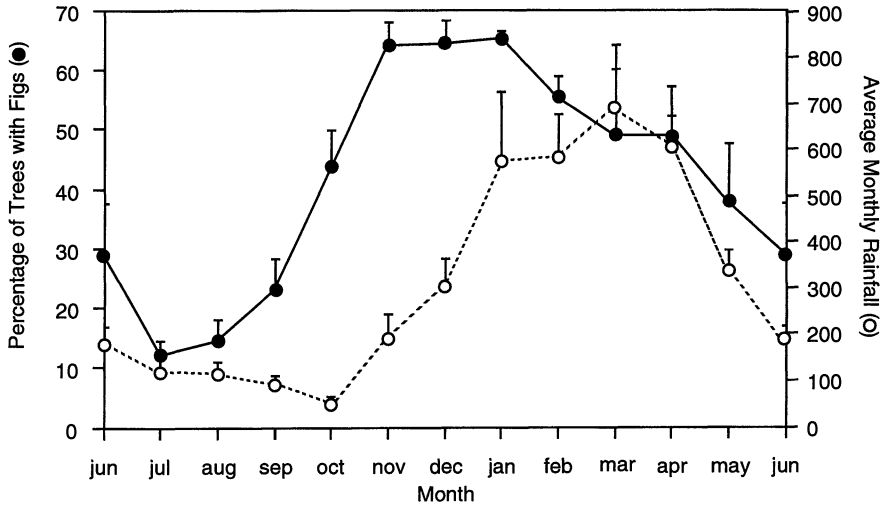

FIG. 1. The mean monthly rainfall (mm) and mean monthly percentage of fig-bearing trees in a population of 198 reproductive individuals of *F. variegata*. Rainfall averages are from 1980–92 data for Cape Tribulation. Bars indicate standard errors.

females, maintaining the local pollinator population under adverse conditions while donating pollen to female figs under optimal conditions. Currently, there is much speculation but few data to support a hypothesis that the evolutionary transition from monoecy to dioecy represents an adaptation to seasonal environments (Corlett, 1987, 1993; Kjellberg *et al.*, 1987; Berg, 1989).

Among more than 300 species of dioecious figs worldwide (Berg, 1989), few have been studied in detail (see appendix in Bronstein, 1989). The fruiting phenologies of several dioecious species are correlated with seasonal conditions, such as: the edible fig *F. carica*, in France (Kjellberg *et al.*, 1987), *F. fistulosa* in Hong Kong (Corlett, 1987) and *F. grossularioides* in Singapore (Corlett, 1993). These studies also show some degree of sexual differentiation in phenological patterns, but there is a need for more data describing the phenological responses of dioecious figs to seasonal variability. With this objective in mind, we examined the phenology of a dioecious fig population in a seasonally wet tropical environment. We selected *F. variegata* because of its abundance at the study site, and because a parallel study suggested that this species might be a vital food resource for the local tube-nosed bat, *Nyctimene robinsoni* (unpub. data, H. Spencer).

STUDY SITE

The study area, Cape Tribulation, is situated in the far north east of Queensland, Australia on the Coral Sea coast (16°05′ S, 145°27′ E). Cape Tribulation is backed by a coastal range, rising to 1000 metres, enclosing a shallow east-facing basin which contains the study site. The basin floor is comprised of unconsolidated rock and sediments, with the result that many streams are ephemeral and flow underground during the dry season. The local climate is seasonally wet and tropical, with an average rainfall of 4000 mm per year, falling mostly in the period from December to May (Figs 1 and 2a). May to November is the dry period, with as little as 100 mm rainfall per month. Temperatures range from a minimum of 10°C in the dry season to a maximum of 40°C in the wet season, with high humidity throughout the year.

The humid and seasonally wet climate supports lush vegetation classified by Tracey (1982) as lowland complex mesophyll vine forest. The region is among the most floristically diverse in Australia, with over 125 species of trees per ha (A. Small, unpub. data). Figs are abundant, both as hemi-epiphytic stranglers and as free-standing trees. Of the twelve *Ficus* species reported for Cape Tribulation (Jessup & Guymer, 1985), *F. variegata* and *F. congesta* are the most common dioecious species.

BIOLOGY OF *FICUS VARIEGATA*

F. variegata is a pioneer tree mostly occurring along watercourses, although some individuals are found in relatively open forest as isolated trees (Corner, 1933). The older trees are usually buttressed, particularly on river banks, where the more elaborate buttresses reach up to 4 m above the ground. In undisturbed rain forest, canopy trees can attain trunk diameters of up to 1 m at breast height. Mature trees are cauliflorous, bearing a profusion of figs on the trunk and major branches.

Mature fruit are about 30–40 mm in diameter and are borne on pedicels 15–25 mm in length which arise from clusters of woody spurs. Fig-bearing spurs increase in length and branching complexity with age. Spurs range from a few mm long, with one or two figs, to over 150 mm with multiple branches bearing more than thirty figs each. The positioning of the fig-bearing spurs within trees is highly variable. Some trees produce figs predominantly along the trunk, and others produce figs along the branches. Crop size is also highly variable among individuals, ranging from trees with fewer than ten spurs, to trees with profuse spurs capable of carrying hundreds of figs per metre of branch length.

F. variegata is morphologically gynodioecious and functionally dioecious, with populations comprised of female individuals and hermaphrodites (Weiblen, Spencer

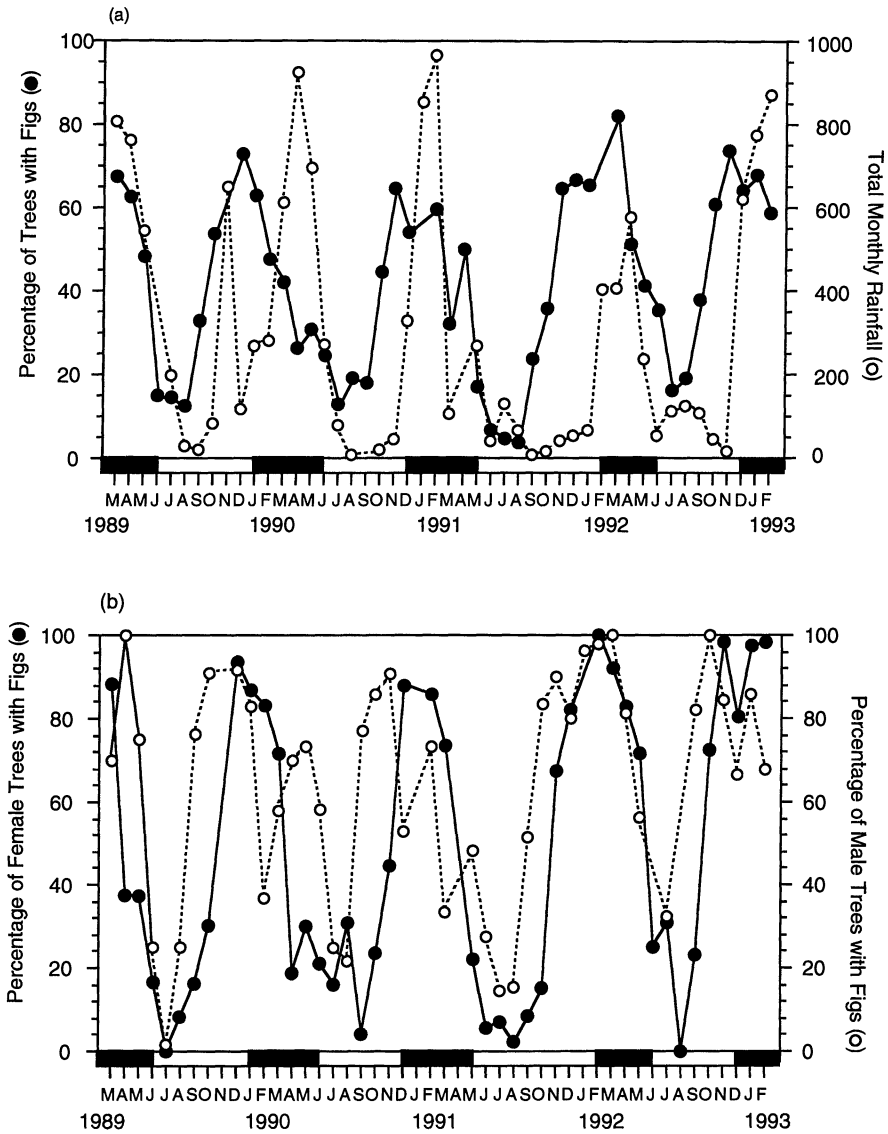

FIG. 2. (a) Monthly rainfall and population-level fruiting phenology of *F. variegata*. The percentage of fig-bearing trees in the population and total rainfall (mm) are reported for each month from March 1989 to February 1993. At the bottom of the figure, black bars approximate the annual wet seasons and white bars indicate the interval between rainy episodes. (b) Seasonal patterns of female and male fig production at Cape Tribulation. Percentages of fig-bearing trees are based on thirty male and fifty-five female trees.

& Flick, 1995). For reasons outlined in Weiblen, Spencer & Flick (1995), we refer to the two sexes of trees as female and male. Female fruit have a sweet odour which is absent in male fruit. Female fruit colour varies from green to red, and does not to appear to be correlated with fruit maturity.

As with other figs, *F. variegata* is pollinated by a host-specific agaonid wasp (Wiebes, 1994). *Ceratosolen appendiculatus* Mayr enters the fig (syconium) at the appropriate time of female flower receptivity, by pushing through the closed ostiolar bracts and into the syconium cavity. Once inside, the wasp pollinates the stigmatic surfaces of the fig florets with pollen collected from her natal syconium. In the figs of male trees, the styles are short and the wasp lays eggs in the vicinity of fig ovules by inserting her ovipositor into the style. In the figs of female trees, the styles are long and the wasp is unable to reach the ovules, but she still pollinates a fraction of the fig florets. Female wasps (foundresses) presumably die within the fig cavity. Wasps entering female figs do not leave offspring but they do pollinate the florets that produce seed. In contrast, male figs produce no seeds; instead they host the pollinator offspring and donate pollen to female figs (Weiblen, Spencer & Flick, 1995).

SAMPLING PROCEDURE

At Cape Tribulation, 218 mature trees of *F. variegata* were located and numbered within the study site, which covered approximately 140 ha. The leafing, flowering and fruiting status of each tree was assessed using a six-point scoring

TABLE 1. Indices for leaf maturity, fig abundance and fig maturity for *F. variegata* were estimated independently. Fig abundance was estimated as a percentage of the total crop capacity for each individual tree. Fig diameter served as an indicator for fig maturity stage, since the size of figs is roughly correlated with the developmental phases (A–E; Galil & Eisikowitch, 1968).

Value	Leaf maturity index	Fig abundance index	Fig diameter index	Fig maturity (developmental phase)
0	No leaves	No figs	No figs	
1	Buds	0–5%	1–3 mm	Pre-receptive phase: early floral development; ostiole closed (A)
2	New leaves	5–10%	4–10 mm	Female phase: female flower receptivity; wasps penetrate ostiole, pollinate, and oviposit (B)
3	Mature leaves	10–20%	11–30 mm	Interfloral phase: fig seeds and wasp larvae develop (C)
4	Mixed mature & senescent leaves	20–40%	>30 mm	Male phase: pollen-carrying, fertilized female wasps emerge from male figs; female figs become fleshy (D)
5	Senescent leaves	40–100%	Fallen figs	Post-floral: female figs dispersed; male figs drop from trees (E)

procedure (Table 1). Given the presence of asynchronous crops on many trees, we recorded the stage of maturity for the most abundant age class of fig on the tree but also recorded any other stages of fig maturity.

Fig abundance is difficult to estimate in a cauliflorous tree, given the dense packing of fruits on the highly branched spurs. We used a percentile scale, based on the maximum crop size that a particular tree was likely to support. We assessed the abundance of figs in relation to the density of fig-bearing spurs within the tree, and estimated abundance as a percentage of the total crop capacity for that tree. Percentages were then assigned a rank between 0 and 5 (Table 1). For example, if every spur on a tree bore figs then the tree was considered to be producing at 100% of its capacity, and was ranked '5' for fig abundance.

The presence of asynchronous fig crops within individual trees was recorded by a yes (1) or no (0) response. For example, an asynchronous crop might consist of figs in maturity stages 2 and 5 within the same tree (see Table 1). As a crude estimate of tree size and age, we also measured the diameter at breast height (d.b.h.) of each tree. Measurements were made at 1.5 m from ground level wherever possible; however, it was necessary in some cases to measure d.b.h. above the buttresses. Trees with a d.b.h. greater than 25 cm were included in our census. The sexes of eighty-five of 198 fruiting trees in the study (43%) were determined by examining ripe and fallen figs. We identified a total of thirty males and fifty-five females.

Over the four-year study, from March 1989 to February 1993, trees were assessed at approximately 1-month intervals. The number of trees in the census was increased as the study progressed, from 148 trees in 1989, until a total of 218 trees was reached in April 1991. During the census period, a few trees were lost through storm damage or fungal disease. Fifteen trees that showed no evidence of fig production during the census were excluded from our analysis.

FIG PHENOLOGY AT THE POPULATION LEVEL

Fig. 1 shows the mean monthly rainfall and the mean monthly percentage of fig-bearing trees for 198 individuals averaged over a 4-year period. Although there was considerable variation in fruiting among years, an obvious seasonal fruiting pattern for the population was indicated by the percentage of trees that carried figs each month (Fig. 2a). The onset of fig production at the population level preceded the onset of the rainy season by about 2 months, but the peak period of population-level fig production coincided with the wet season in each year.

SEXUAL DIFFERENCES IN REPRODUCTIVE PHENOLOGY

The timing of peak fig production at the population level differed between male trees and female trees (Fig. 2b). Most male trees initiated fig production about 2 months before the peak in fig production for female trees. The bimodal pattern of fig initiation in *F. variegata* was consistent across all 4 years of the study, and is suggestive of within-sex flowering synchrony. The population of male trees appeared to initiate fig production about 2 months prior to the onset of the wet season, while the peak in the percentage of fig-bearing female trees coincides with periods of peak rainfall. In each year except 1989, there were few or no fig-bearing female trees during the dry months of July and August, while a small fraction of the male trees bore figs in different stages of development.

Sexual differentiation in phenological patterns is further illustrated by the variable behaviour of some individual trees (Fig. 3). Male tree no. 22 produced figs almost continually, often at 100% of its capacity in spite of dry-season conditions. Male tree no. 196 produced figs sporadically, but peaks in fig abundance during each late dry season are suggestive of annual regularity in fig production. Female tree no. 23 produced figs sub-annually, but almost without exception, during rainy episodes. The pattern for female tree no. 201 also suggests an annual cycle of fig production during the wet season.

We compared measures of fig abundance, asynchrony and d.b.h. between thirty male and fifty-five female trees using the pooled monthly data from 4 years of the census (Table 2). Mann–Whitney *U*-tests compared the index of fig abundance, the proportion of asynchronous crops and d.b.h. between the sexes. While male and female trees

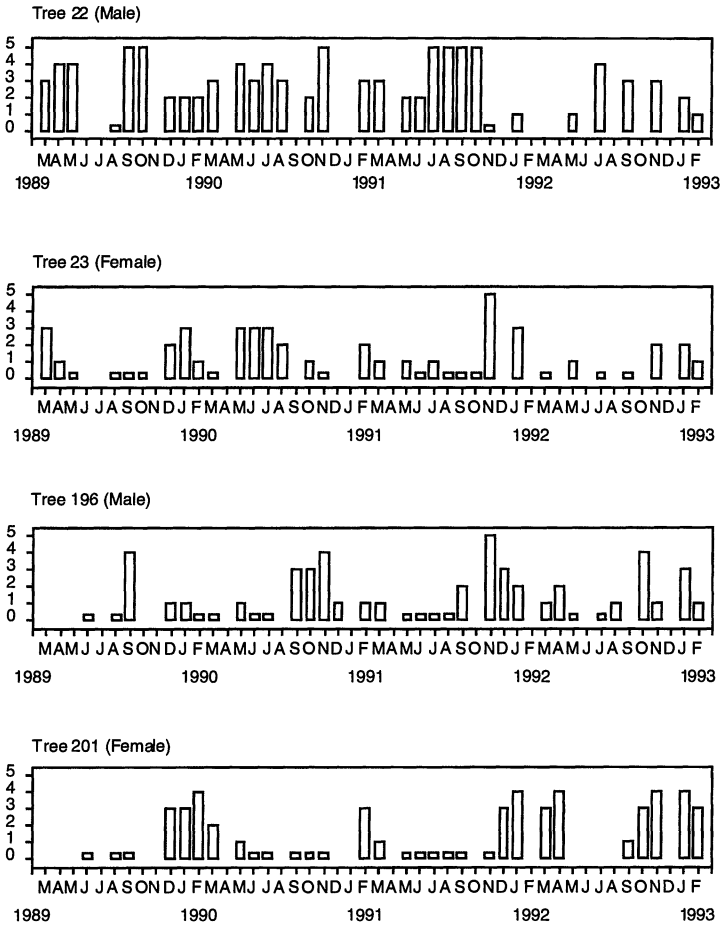

FIG. 3. Patterns of fig abundance in two male and two female trees of *F. variegata* at Cape Tribulation. Values for fig abundance (see Table 1) reflect the frequency and amplitude of flowering and fruiting from 1989 to 1993. The smallest bars indicate the intervals between fig crops and gaps in the temporal sequence indicate missing data. We could not determine the exact phases of flowering and fruiting for individual trees, due to pronounced developmental asynchrony of fig crops within trees (Newstrom *et al.*, 1994).

TABLE 2. Fig abundance, the proportion of trees bearing asynchronous fig crops and diameter at breast height (d.b.h.) in thirty male and fifty-four female trees of *F. variegata* at Cape Tribulation. Pooled data for the index of fig abundance, the proportion of trees bearing asynchronous fig crops in any particular month and d.b.h. were compared using Mann–Whitney *U*-tests.

	Male trees			Female trees			Test statistic	
	$\bar{X}$	(SD)	*N*	$\bar{X}$	(SD)	*N*	*U* or *F*	*P* value
Fig abundance	1.39	(1.52)	804	1.14	(1.40)	1480	4.42	<0.001
Asynchrony	0.36	(0.48)	494	0.24	(0.47)	743	4.67	<0.001
d.b.h. (cm)	56.1	(21.3)	30	49.1	(23.7)	55	1.70	NS

NS = P>0.05.

did not differ significantly in girth, male trees produced significantly larger fig crops on average, according to our measure of fig abundance as a percentage of the total fruiting capacity for a given tree. We also found that a higher proportion of male trees carried asynchronous crops than female trees.

LEAF PHENOLOGY

In the seasonally wet tropical environment at Cape Tribulation, *F. variegata* was deciduous (Fig. 4). Leaf drop was highly seasonal, occurring chiefly during the dry season of late August and early September. This period was

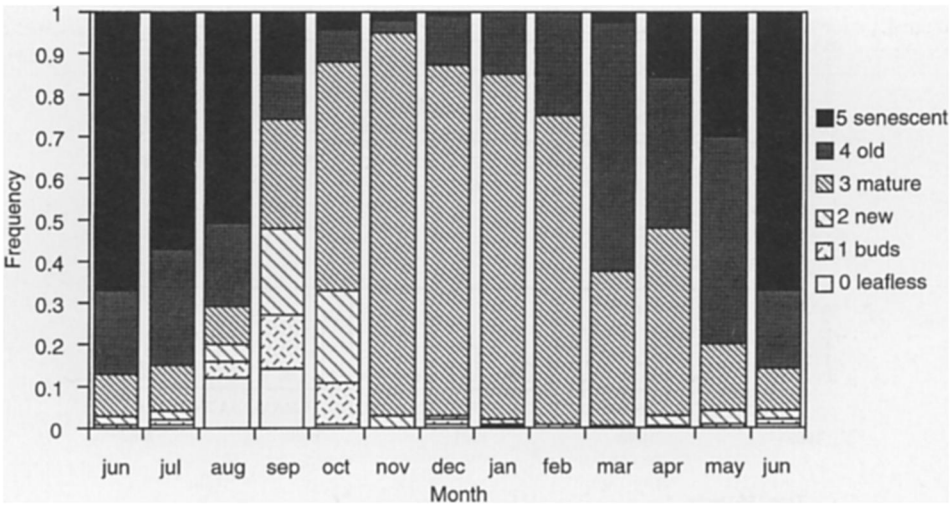

FIG. 4. Seasonal leaf production in *F. variegata* at Cape Tribulation. We plotted the frequency distributions of leaf maturity stages by pooling the data for 198 trees monitored for 4 years.

TABLE 3. Kendall rank correlations between rainfall, leaf maturity, fig maturity, fig abundance and d.b.h. for eighty-five mature trees of *F. variegata* monitored at Cape Tribulation from 1989 to 1993. Calculation of τ followed Kendall & Gibbons (1990). Each significance test involves a separate risk of a type I error.

		Female trees		Male trees	
x	*y*	τ	*P* value	τ	*P* value
Leaf maturity	Monthly rainfall	0.059	<0.001	0.050	<0.05
Fig abundance	Monthly rainfall	0.160	<0.001	−0.052	<0.05
Fig maturity	Monthly rainfall	0.117	<0.001	0.119	<0.001
Leaf maturity	Fig abundance	−0.175	<0.001	−0.278	<0.001
Fig maturity	Fig abundance	−0.017	NS	−0.053	NS
Fig maturity	Leaf maturity	0.153	<0.001	0.147	<0.001
Fig abundance	d.b.h.	0.094	<0.001	0.065	<0.01

NS = P>0.05.

followed by a flush of new leaves and the peak in fig abundance. Emergence of new growth occurred during October. New leaves dominated the fig canopy from November to March, prior to and during the wet season. The frequency of trees with senescent leaves in the population increased with the onset of the dry season in May. Leaf drop coincided with the period of lowest rainfall, but not necessarily of lowest soil water availability, which is likely to occur during the late dry season, from October to November. The period of leaf abscission to bud-burst was relatively short, usually about 7–10 days, and the period during which fig leaves attained mature status was approximately 30 days. We under-sampled the number of trees in early stages of leaf development because our monthly census often missed the developmental stages of shorter duration.

RELATIONSHIPS AMONG PHENOLOGICAL TRAITS

For the statistical analysis of relationships among categorical variables we used Kendall rank correlations (Table 3). Although time series analysis could examine the temporal scales of correlation over 4 years (and evaluate the likelihood of temporal autocorrelation), we used a more simplistic approach. Correlations were calculated separately for male and female sub-populations, due to the phenological difference between the sexes. The stage of leaf maturity was significantly positively correlated with rainfall across months, although the relationship was less strong for male trees, which tended to retain more leaves during the dry season. Fig abundance on female trees was significantly positively associated with rainfall, but for male trees fig abundance showed a significant negative relationship with rainfall. This is consistent with our observations that: (1) male trees retain more figs during the dry months than females, and (2) the male sub-population initiates its annual fig crop prior to the onset of the rainy season. Developmental phase (fig maturity), however, was positively correlated with rainfall for both the male and female sub-populations. We believe that this correlation reflects the ripening of male figs during the early wet months (December–January), and the ripening of female figs during the later wet months (February–March). Leaf maturity was negatively correlated with fig abundance in both sexes, which could be explained

TABLE 4. Kendall partial τ for rank correlations from Table 3. Partial τ measures the agreement between two variables (x,y) independently of the influence of a third variable (z).

			Female trees		Male trees	
x	y	z	τ	P value	τ	P value
Rainfall	Fig abundance	d.b.h.	0.160	<0.001	−0.062	<0.01
Rainfall	Fig maturity	d.b.h.	0.117	<0.001	0.046	NS
Rainfall	Leaf maturity	d.b.h.	0.059	<0.001	0.052	<0.05
Fig abundance	Fig maturity	Rainfall	−0.036	NS	−0.047	NS
Fig abundance	Leaf maturity	Rainfall	−0.187	<0.001	−0.276	<0.001
Fig maturity	Leaf maturity	Rainfall	0.147	<0.001	0.142	<0.001
Rainfall	Fig maturity	Fig abundance	0.121	<0.001	0.116	<0.001
Rainfall	Leaf maturity	Fig abundance	0.089	<0.001	0.037	NS
Fig maturity	Leaf maturity	Fig abundance	0.152	<0.001	0.138	<0.001
Rainfall	Fig abundance	Fig maturity	0.163	<0.001	−0.046	0.05
Rainfall	Leaf maturity	Fig maturity	0.042	<0.05	0.033	NS
Fig abundance	Leaf maturity	Fig maturity	−0.174	<0.001	−0.273	<0.001
Rainfall	Fig abundance	Leaf maturity	0.173	<0.001	−0.040	NS
Rainfall	Fig maturity	Leaf maturity	0.109	<0.001	0.113	<0.001
Fig abundance	Fig maturity	Leaf maturity	0.010	NS	−0.013	NS

NS = P>0.05.

by the fact that figs are most abundant on individual trees during the earlier developmental stages, before the leaves have attained mature status. Fig abundance and developmental phase were negatively, but not significantly, correlated possibly due to the fact that fig crops decrease in size as they reach maturity. The reduction in crop size appears to result from abscission of non-pollinated figs, or from the premature removal of figs by frugivorous bats and birds. Fig abundance and tree size (as estimated by d.b.h.), were positively correlated, suggesting that larger trees tended to bear larger fig crops. We also established the rather obvious relationship between fig and leaf maturity, namely that trees with older leaves tended to carry older figs.

As with all multivariate data, there exists the possibility that correlations between two variables result from correlations with an additional variable. We computed Kendall's partial rank coefficient (τ) to test for pairwise associations between variables after removing the effects of a third variable (Table 4).

Calculations of partial τ followed Kendall & Gibbons (1990), and sample size was sufficiently large that partial τ could be compared against the normal distribution (Maghsoodloo & Pallos, 1981). Correlations of tree-related variables with rainfall in Table 3 persisted when d.b.h. was held constant, except in the case of rainfall and fig maturity in male trees (Table 4). In every case, the significance of associations among the tree-related variables (fig abundance, fig maturity, and leaf maturity) were unaffected by accounting for rainfall (Table 4). However, the positive correlation between leaf maturity in male trees and monthly rainfall was not significant after removing the effect of fig abundance. Also, the negative association between fig abundance in male trees and rainfall lost significance after controlling for the effect of leaf maturity. In both sexes, correlations of monthly rainfall with fig abundance and leaf maturity were weakened after the effect of fig maturity was removed. In all other cases, the correlations reported in Table 4 were of the same direction and level of significance as in Table 3.

DISCUSSION

Phenological data have a reputation for being notoriously difficult to analyse, and our data are no exception. We rely on the terminology of Newstrom *et al.* (1994) to highlight several limitations of our phenological census. Syconium development from flower receptivity to fruit maturity took about 6–7 weeks, and for this reason our monthly census did not follow individual cycles of fig production through all stages of development. Furthermore, it was impossible to follow individual fig crops from the initiation stage to maturity, due to asynchronous flowering and fruiting patterns within many trees. Another difficulty was that not all trees were surveyed in each month of the study. Despite our best efforts to obtain complete census data, observers did not always successfully locate and survey all trees in the population. Also, we did not determine the sex of every tree in the population, thereby reducing our power to detect sexual differentiation of phenological patterns. In spite of the irregularities in our census, population-level phenological patterns were evident. In all, our data represent 5166 tree census events for 198 individuals that produced figs during the study.

The *F. variegata* population at Cape Tribulation produces figs continually, although there are pronounced annual peaks in amplitude that are strongly correlated with rainfall. Trees were deciduous, and vegetative phenology in female trees was also highly correlated with rainfall. Patterns of fig and leaf production in *F. variegata* are consistent with three general patterns reported in the literature for figs in seasonal environments. First, leaf drop often occurs during dry periods and leaves often emerge during the transition from dry to wet conditions (van Shaick, 1986; Windsor *et al.*, 1989; Milton, 1991). Secondly, increased fig production

often follows rainfall (Newton & Lomo, 1979; Baijnath & Ramcharun, 1983; van Shaick, 1986). Thirdly, fig production appears to follow leaf development (Milton, 1991). However, this temporal sequence is not universal among figs. Correlations between vegetative and reproductive phenologies occurred in some figs, including *F. aurea* (Bronstein & Patel, 1992) and *F. yoponensis* (Milton *et al.*, 1982), but not in *F. capensis* (Baijnath & Ramcharun, 1983) or the Panamanian strangler figs of Windsor *et al.* (1989).

In *F. variegata*, the reproductive phenologies of male and female trees were different. This has been noted for other dioecious figs (Valdeyron & Lloyd, 1979; Berg, 1989), including: *F. carica* in France (Kjellberg *et al.*, 1987), *F. exasperata* in India (Nair & Abdurahiman, 1984) and *F. fistulosa* and *F. grossularioides* in Singapore (Corlett, 1987, 1993). We argue below that population-level differences in the flowering and fruiting patterns of male and female trees makes adaptive sense in seasonal environments such as Cape Tribulation.

SEASONALITY AND DIOECIOUS FIGS

The dioecious figs are centered in the Paleotropics, where they often occur in habitats such as seasonally wet forests, along riverbanks and in periodically submerged areas (Berg, 1989). Kjellberg & Maurice (1989) proposed that dioecious figs respond differently to seasonal variability than monoecious figs, due to the separation of seed and wasp production between trees. In dioecious *Ficus*, each gender specializes in making either seeds or wasps, but wasp production translates directly into male reproductive function since wasps are the pollen vectors. Kjellberg & Maurice (1989) predicted that female figs would be produced during the wet season, presumably under the most favourable conditions for seed production, germination and establishment. On the other hand, male trees maintain a local wasp population by producing figs during adverse conditions. A peak in male fig production preceding the wet season can increase the pollinator population, releasing pollen-carrying wasps at a time when the majority of female figs are receptive to pollinators. This pattern benefits male individuals (not simply the population as a whole) by increasing their reproductive success through the donation of pollen to females.

The population-level phenology of *F. variegata* is similar to the phenological pattern for dioecious figs proposed by Kjellberg & Maurice (1989), and parallels the patterns of *F. carica* (Kjellberg *et al.*, 1987) and *F. exasperata* (Nair & Abdurahiman, 1984). A female tree produces one to several fig crops during the optimal season for seed production, while some male trees bear figs continually. Continual male fig production at the population level is a consequence of flowering asychrony at the individual level. In addition to enhancing the fitness of male individuals, crop asynchrony can maintain a local wasp population during the less favourable dry season. We predict that the annual peak in male fig ripening (and wasp-release) should be synchronous with the annual peak in female fig receptivity.

Newstrom *et al.* (1994) noted in general that phenological patterns in dioecious species may be sexually dimorphic. For example, in *Compsoneura sprucei* (Myristicaceae) and *Guarea rhopalocarpa* (Meliaceae), dioecious understorey trees in Costa Rica, male trees have sub-annual flowering patterns and females have annual flowering patterns (Bullock, 1982; Bullock, Beach & Bawa, 1983). The tendency for males to produce more crops per year than females occurs in *F. exasperata*, which produces six crops of wasps and one to two crops of seed figs per year (Nair & Abdurahiman, 1984). In *F. variegata*, male trees seem to produce fig crops more frequently than females (Fig. 3). Also, male *F. variegata* trees produce a greater proportion of asynchronous crops than females (Table 2). This pattern differs from that of dioecious *F. grossularioides* in Singapore, characterized by male within-tree synchrony and female within-tree asynchrony (Corlett, 1993). The climatic difference between seasonal Cape Tribulation and aseasonal Singapore could account for the different phenological responses, since Singapore lacks predictable cues for synchrony (Corlett, 1993). In fact, tropical phenological patterns can vary widely over the geographic range of a species (Newstrom *et al.*, 1994). It would therefore be instructive to compare the phenological patterns of *F. variegata* in seasonal and aseasonal parts of its range. Hill (1967) reported that *F. variegata* in seasonal Hong Kong was deciduous, and that fig crops were synchronous within male trees. However, Hill (1967) did not distinguish patterns at the population level from individual patterns, which are different for *F. variegata* at Cape Tribulation.

Male trees were more likely to bear asynchronous fig crops than females, but we do not know exactly which development phases overlapped within trees, and whether these would be ecologically important. Bronstein *et al.* (1990) stated the need for detailed phenological data because the ecological consequences of asynchrony depend on duration and interval between reproductive episodes. The consequences of within-tree flowering asynchrony for pollination and dispersal in dioecious species depends on gender as well as on the timing and frequency of sexual phase overlap.

In dioecious species, within-tree asynchrony in male figs has the advantage of promoting male fitness through increased pollen donation without the negative effect of self pollination (Milton, 1991). Also, female trees can flower asynchronously without the cost of self pollination resulting from within-tree wasp transfers (Patel *et al.*, 1993). Staggered female fig crops could enhance the chances of frugivorous seed dispersal and increase the probability of seedling establishment in temporally patchy microsites, such as light gaps (Milton, 1991; Corlett, 1993). More detailed studies are needed to closely examine the degree of sexual phase overlap in dioecious fig populations and its ecological consequences.

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