

## Phenology of a common roadside fig in Sarawak

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The phenology of a dioecious fig (*Ficus fulva*, Reinw. ex Bl.; 25 female, 26 male trees) was studied at Lambir Hills National Park, Sarawak. Dioecious fig phenology provides an excellent opportunity to investigate the influence of climate and sexual specialization on the obligate fig–fig pollinator/ovule parasite interaction. Leaf phenology was strongly correlated between sexes. Trees dropped leaves during drought and initiated new leaf growth after the renewal of rain. Before the production of large crops of syconia, trees shed their leaves and then new leaves and syconia were initiated together. Syconia were produced in synchronous crops with asynchrony between trees maintaining a relatively even production of syconia within the tree group. Syconia abortion on male but not female trees, was negatively correlated with the proportion of trees with male phase syconia. A severe drought in early 1998 significantly disrupted the phenology thereafter. The duration of crop development was approximately twice as long on female trees as on males, and total syconia production was much higher on male trees. Plots of syconia diameter versus dry weight suggest sexual specialization in the investment profile during crop development. Male trees also sometimes produced a small crop of syconia immediately before a large crop, probably to supply wasps for the main crop. Sexes had different growth strategies with male trees growing more as small individuals and slightly delaying reproduction. Diameter at breast height was significantly correlated with total syconia production in male trees but not in females. Syconia production was best predicted by canopy width.

**Key words:** Borneo; climate; dioecy; mutualism; sexual specialization.

### INTRODUCTION

Dioecious figs (*Ficus* spp., Moraceae) are among the most common species in secondary habitats throughout Borneo, often constituting 50% or more of the individual plants in a forest (R. Harrison, unpubl. data, 1999). Approximately half of the estimated 750 species of figs in the world are dioecious, most of which are found in South East Asia (Corner 1965). Their individual dominance and the copious production of fruit on many species mean that figs are an extremely valuable resource for vertebrate seed dispersers (Boon & Corlett 1989; Lambert & Marshall 1991; Tan *et al.* 1998), and thus for forest succession and the reassembly of mature forest (Compton *et al.* 1994; Thornton 1994). Furthermore, the intricate mutu-

alism between figs and their pollinators permits a detailed examination of the constraints and possible benefits of different ecological traits, which may reveal how such an extraordinary diversity of species and individual dominance in secondary habitats could have evolved (Janzen 1979; Compton 1993; Herre 1996; Patel 1996; R. Harrison, unpubl. data, 1999).

All figs have a closed, urn-shaped inflorescence, or syconium, which is lined with tiny uniovulate flowers. The species-specific pollinating fig wasps (Agaonidae, Chalcidoidea, Hymenoptera) enter the syconium through the bracts of the narrow entrance, or ostiole, losing their wings and antennae in the process, then pollinate the flowers and attempt to oviposit. In monoecious figs, ovules that receive a wasp egg then develop a gall on which the larvae feeds, while those without an egg develop into seed in the usual way. Several weeks later, adult wasps emerge and mate within the syconium. The wingless males then cut a tunnel, often through the ostiole, and die. Meanwhile, the females collect pollen from the now mature male flowers, either

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through passive dusting or, in some species, by packing special pollen pockets, and depart in search of receptive syconia. In the case of dioecious figs, female and male roles are segregated in separate trees and female trees only produce seed. The pollinating wasps enter, pollinate and attempt to oviposit but fail because the styles are too long and thin for their ovipositors to reach the ovules. The wasps, therefore, die without reproducing but are unable to avoid female syconia (Patel *et al.* 1995). Male trees bear syconia with modified female flowers (gall flowers), that in most species never produce seed (Galil 1973; but see Kjellberg *et al.* (1987) for an exception in *Ficus carica* L.) or male flowers. The gall flowers have a large ovary and a short style enabling the pollinator's ovipositor to reach the ovary. Male trees, thus, produce only pollen and pollinators (Galil 1973). Previously, dioecious figs have been called 'gynodioecious' in reference to fact that gall flowers are modified female flowers. However, they are functionally dioecious and the latter term is more appropriate.

Adult female pollinators have extremely short life spans (Kjellberg *et al.* 1988; R. Harrison, unpubl. data, 1999), most live less than a day. Hence, they are completely dependent on the availability of receptive male syconia when they emerge, and the maintenance of the pollinator population is dependent on the near continuous presence of receptive syconia, which permits a continuous cycling of pollinators between trees (Bronstein *et al.* 1990; Kameyama *et al.* 1999). Conversely, pollination success is dependent on the production of adult pollinators. Although syconia can wait for a few weeks to be pollinated (Anstett *et al.* 1996), they are eventually aborted if no pollinators are available. A suite of closely related, species-specific, non-pollinating wasps (gallers, gall parasites and parasitoids; West & Herre 1994; Compton & van Noort 1992), most of whom oviposit through the syconia wall using very long ovipositors, are also dependent on the availability of suitable male syconia. The interdependence of the fig–fig pollinator mutualism, its associated non-pollinating wasp community and the separation of the fig's male and female functions on different trees, all contribute to make dioecious figs a model system for investigation.

Plant reproductive activity, such as the production of flowers and fruit, and maintenance activ-

ities, such as leaf renewal or growth, are recurring events in the lives of plants; the timing, frequency and intensity of which vary between species and individuals. Studies of plant phenology examine these activities in relation to abiotic factors, such as habitat or climate, and biotic factors such as the availability of pollinators, or the impact of herbivores and seed predators (van Schaik *et al.* 1993). The populations of these organisms are, in turn, affected by the temporal variation in plant resources, and in several plant species it has been shown that reproductive success is correlated with phenological traits (Augspurger 1981).

The aseasonal lowland Dipterocarp forests of South East Asia are famous for their large-scale community flowering events in which 50% or more of the individuals in a forest may flower after 3 or more years of little or no reproductive activity (Wood 1956; Medway 1972; Ashton *et al.* 1988; Momose *et al.* 1998; Sakai *et al.* in press). In contrast, the need to maintain pollinator populations prevents such long inter-flowering intervals in figs. Hence, fig phenology offers an opportunity to examine the influence of climatic fluctuations and biotic interactions in the short term. Several studies of fig phenology have been conducted on monoecious figs (Milton *et al.* 1982; Bronstein 1988; Damstra *et al.* 1996) and dioecious figs in relatively strong seasonal environments (Hill 1967; Valdeyron & Lloyd 1979; Patel 1996; Spencer *et al.* 1996). However, relatively few studies (Corlett 1987, 1993; R. Harrison, unpubl. data, 1999) have investigated the phenology of figs in aseasonal environments. In tropical regions periodic change in rainfall generally determines seasonality and, hence, plant phenology (Augspurger 1981; van Schaik *et al.* 1993). Despite the constraints of their wasp interactions, figs also tend to show considerable seasonality (Milton *et al.* 1982; Windsor *et al.* 1989; Milton 1991; Damstra *et al.* 1996 for monoecious; Hill 1967; Patel 1996; Spencer *et al.* 1996; Patel 1998 for dioecious). The central part of South East Asia, however, lacks a predictable dry period, although occasional droughts occur, and is essentially aseasonal.

In dioecious figs, separate individuals perform female and male roles. Hence, seed production has been decoupled from wasp and pollen production, which permits sexual specialization (Lambert 1992; Corlett 1993; Patel 1998). The evolution of

sexual dimorphism in plants with hermaphrodite ancestors helps in understanding the changes associated with the evolution of dioecy and the selective pressures on each sex (Lloyd & Webb 1977; Bawa 1980; Cox 1981). The constraints and possible benefits of a system in which the sexual roles are still coupled, as in the monoecious figs, can then also be better understood (Herre 1996).

In the present study we investigate the influence of sexual specialization and climate, especially rainfall, on the phenology of a common roadside fig, *Ficus fulva* Reinw. ex Bl. (Subgenus *Ficus*, sect. *Ficus*, Corner 1965), in Sarawak, Malaysia.

## METHODS

### Species and study site

*Ficus fulva* is a heliophilic dioecious fig tree that grows to approximately 10 m tall and bears its syconia along smaller branches and on twigs. It is found from lower Thailand through to Sumatra, Java, Borneo, Sulawesi and Timor (Corner 1965). It is pollinated by *Blastophaga compacta* Wiebes (Wiebes 1993) and is also associated with two undescribed, non-pollinating fig wasps, *Apocryptophagus* sp. and *Philotrypesis* sp. (R. Harrison, unpubl. data, 1999). The seed dispersers are small, open space birds, and the yellow-vented bulbul (*Pycnonotus goiavier* Scopoli) is especially prevalent in Lambir Hills National Park (Shanahan 1997), although bats have been known to take *F. fulva* fruit on the Krakatoa Islands (Compton *et al.* 1988). *Ficus fulva* is very common on small ridges along roadsides and among sifting cultivation in Sarawak. In primary forest it is restricted to large landslide gaps (LaFrankie *et al.* 1995).

Lambir Hills National Park (LHNP), Sarawak (4°20'N, 113°50'E, 150–450 m a.s.l.) is an extremely diverse lowland dipterocarp forest. A group of *F. fulva* individuals around the park headquarters area and for approximately 500 m along the road back towards Miri were marked and observed from April 1997 to September 1998. Twenty-four male trees and 23 female trees were initially included, but a further two individuals of each sex found among the other trees were added in June 1997 and one individual of each sex died in early April 1998 from drought stress. Thirteen

immature trees, which did not produce mature crops, and hence their sex could not be determined, were also observed. One male tree and four immature individuals were killed when a section of the road was widened in February 1998. The data on all individuals are included in the analysis. Other *F. fulva* individuals were present along the road in both directions from the area under observation.

Rainfall data for the park for the period 1988–1998 (Fig. 1) were obtained from the Telecom Malaysia tower located in the park, while temperature data for the period 1991–1998 was obtained from Miri Airport which is 20 km from the research site. Annual rainfall varied between 2043 and 3827 mm. Although there is a dry period between January and March in some years, monthly mean rainfall shows a large variation and no clear annual pattern is discernible (Fig. 1a). A plot of 30-day rolling rainfall totals covering the study period, however, clearly indicates how different one period can be from the next and shows a severe drought in early 1998 (Fig. 1b). Meanwhile, plots of mean monthly minimum and maximum temperatures show almost no fluctuation (Fig. 1a). Daily temperature varies between approximately 23 and 32°C.

### Field observations

Phenology censuses were conducted every 10 days from 5 April 1997 until June 1998 and then twice per month until September 1998. At each census the amount of leaf, as a proportion of the crown, and the proportion of new, old and senile leaf were recorded using a 1–4 scale (1, <25%; 2, 25%–<50%; 3, 50%–<75%, 4, >75%). Numbers of syconia were estimated by using a log scale with three subgroupings, thus 1–3, 4–6, 7–9, 10–39, 40–69 and so on. The crop developmental stage was designated as either immature, receptive, pollinated or fruit/male (Galil 1973). Crop stage was assessed by outward appearance through binoculars. This was adequate to assess all stages except receptivity. When a crop was suspected of being receptive, a small number (3–5) of syconia were sampled by climbing the tree and cutting off a twig. However, this was not always possible and the exact timing and duration of receptivity had to be estimated from the occurrence of other phases. The proportion of syconia at each

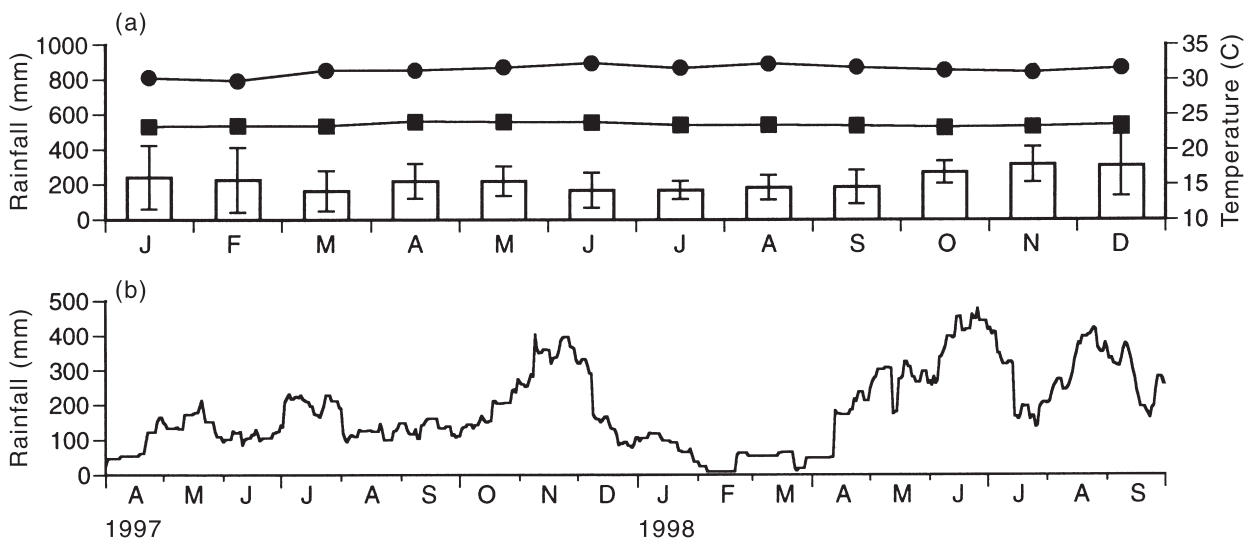


Fig. 1. Climatic data for Lambir Hills National Park, Sarawak. (a) Monthly mean rainfall ( $\pm$ SD) for 1988–1997 as measured at the Telecom Malaysia tower within the park, and monthly mean (●) maximum and (■) minimum temperatures for 1991–1997 as measured at Miri Airport (20 km from the research site). (b) Thirty-day rolling rainfall totals for April 1997–October 1998.

developmental stage was estimated on a 1–4 scale similar to that used for the leaf data.

The diameter at breast height (d.b.h.) was measured on 15 April 1997 (d.b.h.1) and again on 27 June 1998 (d.b.h.2) using a forester's diameter tape. The number of stems measured was also recorded. For trees with more than one stem a combined d.b.h. was calculated from the sum of the basal area of each stem. On 7 August 1998, tree height (using a measuring pole), canopy width (measured by using tape at the widest point) and crown illumination were measured. (Crown illumination was quantified by using the following scale: 5, crown completely exposed; 4, full overhead light (>90%), some or all lateral light blocked; 3, some overhead light (10–90%) or lateral light (<10%); 2.5, high lateral light; 2, medium lateral light; 1.5, low lateral light; 1, no direct light (Clark & Clark 1992)).

Between December 1997 and February 1998, 20 syconia were collected from selected trees at each census, and their diameters and wet weights were measured. Syconia were dried for 5 days in individual envelopes in a constant temperature drying oven and their dry weights were measured at the end of this time. When it was possible, syconia were sampled from the same crop until the crop disappeared from the tree.

## Data analysis

Data were analysed using the SAS program (SAS Institute Inc 1985, Cary, NC, USA; PROC SUMMARY and PROC CORR routines). We calculated the proportions of trees of each sex with new leaf, flushing (>25% of crown consisting of new leaf), senile leaf, bare crown (leaf drop), and syconia at each developmental stage for each census. In aseasonal equatorial climates, leaf exchange often occurs continuously, especially in pioneer species such as *F. fulva*, but with occasional peaks in leaf renewal that are generally referred to as flushing (Reich 1995). Hence, the distinction in the present analysis between the presence of new leaf on an individual, and flushing, defined as when more than 25% of the crown consists of new leaf. An asynchrony index of the syconia on each tree at each census was calculated as follows: 0, one crop stage present; 1, two neighboring crop stages present; 2, immature overlapping with pollinated or fruit/male phases (i.e. two cohorts present on the same tree); 3, receptive overlapping with fruit/male (on the same tree). The latter indicates substantial overlap between cohorts on the same tree and is significant because of the potential for wasps to enter syconia on the same tree in male individuals. The mean crop asynchrony index was then

calculated by census. The proportion of syconia aborted was calculated for each receptive crop as  $(\text{previous crop size} - \text{present crop size}) / \text{previous crop size}$ . A crop was assumed to be receptive if it had receptive syconia on either the previous or present census date. The mean proportion of syconia aborted was then calculated by census. Kendall Rank correlation was used to compare these parameters and the 30-day rolling rainfall totals by census. Delayed correlations of up to 60 days at 10 day intervals were investigated.

In calculating the duration of crop phases, those recorded at only one census, as often occurred for receptive and fruit/male, were assumed to be 5 days. Otherwise, they were assumed to extend from the first date recorded to the last. The pollinated phase generally overlapped completely with the fruit/male phase and often with the receptive phase. The period between crop initiations was calculated from the date of the start of one crop until the start of the next on an individual tree, and the period between crop finishing was calculated likewise between the ends of completed crops. The duration of each phase for each crop was calculated for individuals and then the mean duration for each sex calculated. Crop sizes were calculated only for crops which finished development during the study period.

Total syconia production, mean crop size, number of crops initiated, and the proportion of census dates with new leaf and flushing were calculated for individuals over the entire study period. These were then correlated with d.b.h.2, growth (d.b.h.2 - d.b.h.1), canopy width and canopy illumination index by sex (Pearson correlation). Growth and proportional growth  $((\text{d.b.h.2} - \text{d.b.h.1}) / \text{d.b.h.1})$  were correlated with d.b.h.1 by sex. Growth could not be calculated for trees that died during the study or for trees that lost stems. Proportional factors were arcsin transformed.

## RESULTS

### Influence of climate and population level phenology

#### *Leaf phenology*

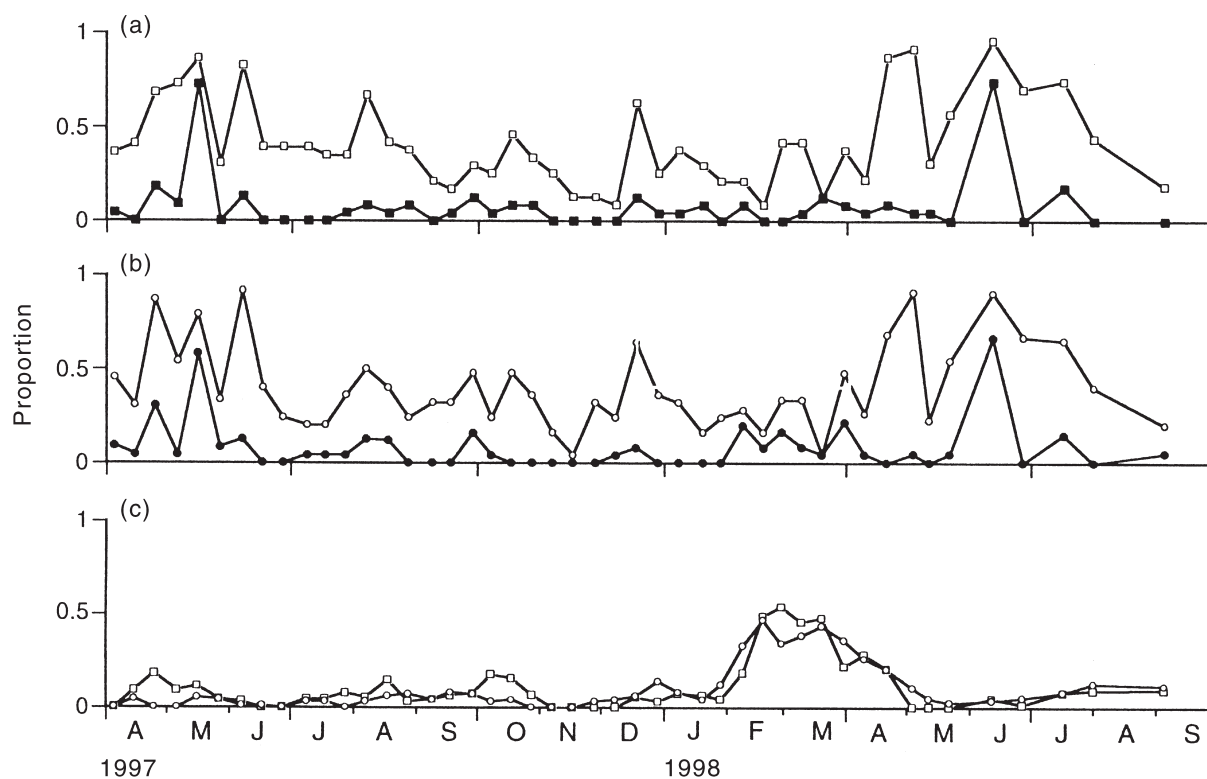
Both sexes of *F. fulva* produced new leaf all year round, although the proportion of trees with

new leaf varied greatly (Fig. 2). The peaks in new leaf and flushing corresponded to periods of new rain after droughts in February–March 1997 and January–April 1998 (Fig. 1b) and reflected leaf renewal after a large amount of leaf drop occurred during the drought period (Fig. 2). There was a highly significant negative correlation of leaf drop with rainfall (Table 1). Leaf renewal, however, was not significantly correlated with rainfall except for a slight negative correlation with flushing on male trees. New leaf, flushing and leaf drop were all significantly correlated between sexes (Table 1). At the end of the study, a heavy caterpillar infestation (R. Harrison, unpubl. obs., 1999) caused another slight increase in leaf drop and possibly affected leaf renewal.

#### *Syconia phenology*

The proportion of female trees with pollinated syconia remained at a relatively constant level of approximately 0.4 until the onset of drought in January 1998 (Fig. 3). By contrast, the proportion of male individuals with pollinated syconia showed a slight cyclic undulation before the drought, indicating that the trees were slightly synchronized at the population level. There were no pollinated syconia on either female or male trees from the end of March to mid-April 1998, indicating a temporary extinction of the pollinator wasps within the observed group, and although pollinators returned thereafter, the proportions of individuals with pollinated syconia never recovered their pre-drought levels. Mean crop asynchrony was generally very low (mean female, 0.12; mean male, 0.12; maximum value, 3), indicating that crops were generally highly synchronous within a tree (Fig. 3). The occasional small peaks, however, showed that cohort overlap sometimes occurred.

Syconia initiation was significantly negatively correlated with rainfall in both sexes (Table 1). This indicates a tendency to initiate crops following dry weather. There was a delay of 30 days on female trees with respect to male trees although syconia initiation was still correlated between sexes (Table 1). Syconia initiation was also highly correlated with flushing. Before the initiation of large crops, trees would shed all their leaves and the bare twigs would then renew leaf and initiate syconia simultaneously.



**Fig. 2.** Proportion of (a) female and (b) male trees with new leaf present and flushing (when >25% of crown consists of new leaf) and (c) the mean proportion of leaf drop (bare crown) on female and male trees at each census. (a), (□) new leaf, (■) flushing; (b), (○) new leaf, (●) flushing; (c), (□) female, (○) male.

**Table 1** Correlations between rainfall, leaf phenology and syconia phenology in *Ficus fulva* at Lambir Hills National Park, Sarawak

	Female		Male	
	Delay (days)	<i>tau</i>	Delay (days)	<i>tau</i>
Climate versus phenology				
Rainfall versus leaf drop	20	-0.445***	0	-0.293**
Rainfall versus new leaf		NS		NS
Rainfall versus flushing		NS	0	-0.212*
Rainfall versus syconia initiation	30	-0.238*	0	-0.313**
Syconia initiation versus new leaf		NS	20	-0.249*
Syconia initiation versus flushing	0	0.444***	0	0.329**
Syconia abortion				
Rainfall versus syconia abortion		NS	20	0.284*
Male phase versus syconia abortion		NS	10	-0.270*
Female versus male				
New leaf versus new leaf		0.642***		
Flushing versus flushing		0.255*		
Leaf drop versus leaf drop		0.420***		
Syconia initiation versus syconia initiation		0.256*		
Syconia abortion versus syconia abortion		0.153		
Female receptive versus male phase		0.166		
Male receptive versus male phase		-0.025		

NS  $P > 0.05$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$  (Kendall Rank Correlation, *tau* compared with a normal distribution). Rainfall, 30-day rolling totals; leaf drop, mean proportion of bare crown; flushing, >25% of crown consists of new leaf.

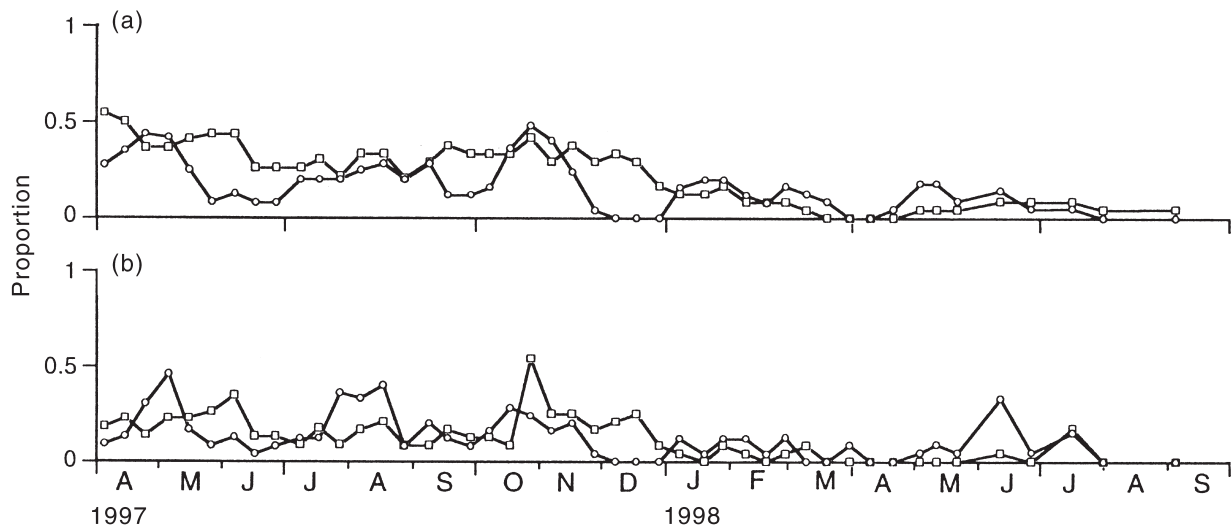


Fig. 3. Proportion of (a) female and male trees with pollinated syconia and (b) the mean crop asynchrony index at each census. The proportion of pollinated syconia is the best indicator of syconia production among the observed trees because it includes all stages of wasp larvae or seed development on the trees. The mean crop asynchrony index has a maximum value of three and reflects the degree of stage / cohort overlap on an individual ( $\square$ ), female; ( $\circ$ ), male.

The proportion of trees of either sex with receptive syconia was generally low (Fig. 4), reflecting the normally short duration of this phase, but generally there were some receptive individuals present, and there was a large degree of overlap between the sexes. There were always male-phase syconia present until just prior to the drought in 1998, indicating a continuous production of pollinating wasps within the observed group of trees. Likewise, the production of fruit on female trees was almost continuous up until the drought and the pollinator extinction. Following the drought, a sudden production of syconia crops produced a peak in receptive trees but, although some syconia were pollinated, wasp and fruit production did not recover to the pre-drought levels (Fig. 4). The proportion of trees with male phase syconia and with receptive syconia on either male or female trees were not significantly correlated (Table 1), indicating that there was no coordination between these phases at the population level. There was a significant negative correlation between the proportion of trees with male phase syconia and syconia abortion on male trees but not on female trees (Table 1). The significant correlation with rainfall on male trees possibly reflects the high levels of abortion through lack of pollinators and high rainfall following the drought in 1998.

### Sexual specialization

#### *Parameter means compared between sexes*

Table 2 compares the phenology of female and male trees. The number of crops initiated on female trees was slightly higher but the proportion of these which finished was considerably lower than on male trees. The duration of the immature phase was similar on male and female trees, but all other phases were longer on female trees. The extension of receptivity on female trees probably reflects delayed pollination, but as mentioned above, recording this phase accurately was difficult. Thereafter, syconia took approximately twice as long to develop on female trees than on male trees. There is an interesting difference between female and male trees in the plot of syconia diameter versus dry weight (Fig. 5). On female trees, dry weight increased linearly with syconia diameter while on male trees it appears to increase exponentially, especially when the courses of individual crops are followed. The crowding of many points on the female plot reflects the slower maturation of syconia.

The mean period between crop initiations, or crop finishings, however, was only marginally longer on female trees, indicating that these had shorter intervals between successive crops when

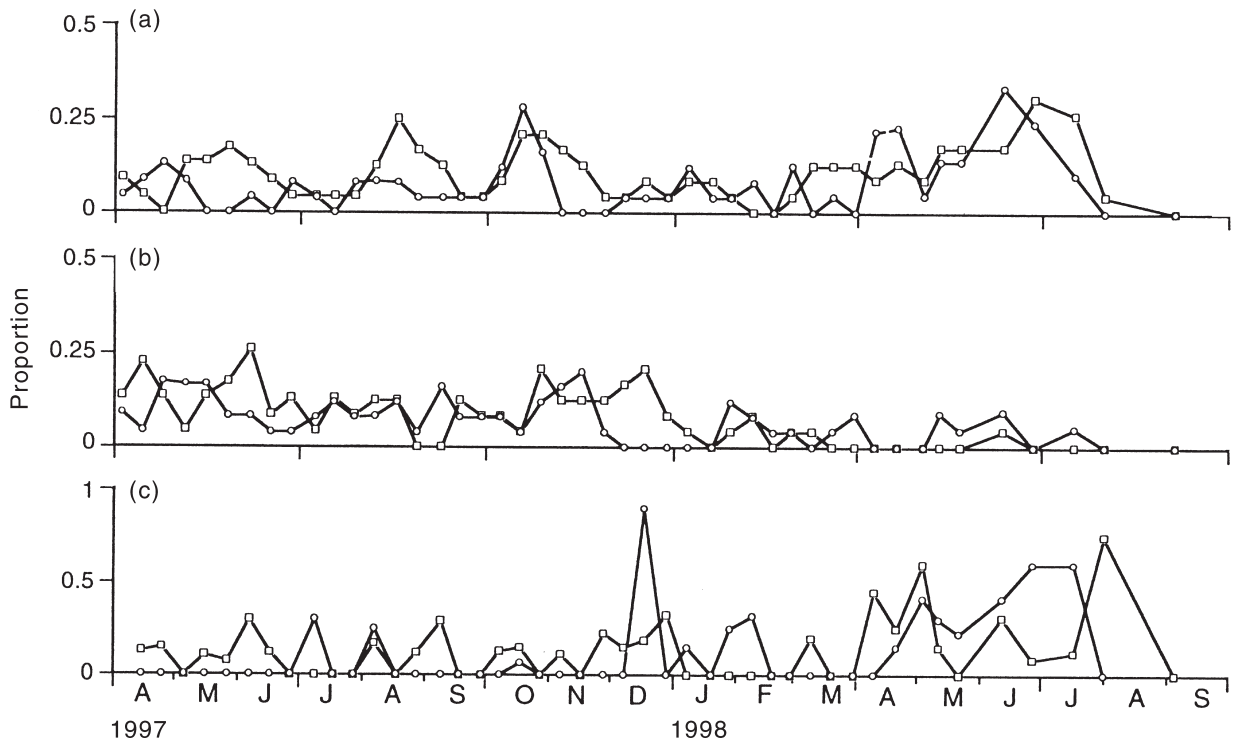


Fig. 4. Proportion of (□) female and (○) male trees with (a) receptive syconia, (b) fruit/male phase syconia and (c) the proportion of syconia aborted at each census.

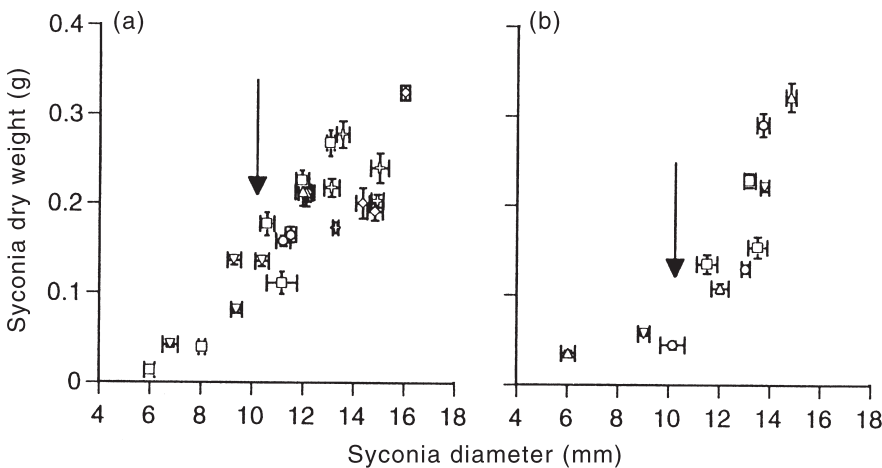


Fig. 5. A plot of syconia diameter versus syconia dry weight for (a) female and (b) male trees (data points with SE bars). (□) Indicates single unconnected samplings. Each of the other symbols (○, ▽, ◇, △, +) represent samples taken from the same crop at 10-day intervals. The arrows indicate the approximate size of the syconia at receptivity.

the tree was not bearing any syconia. However, a frequency distribution plot of the period between crop initiations shows an interesting difference between the sexes (Fig. 6). The graph is strongly left-skewed in females but has a bimodal distribution in males. The short periods between crop initiations on female trees are caused when the previous crop fails to develop and hence the tree produces the next one quickly afterwards. How-

ever, male trees often initiated a small crop of 20–50 syconia just before a large crop, and there was then a long interval until the next pair of crops, thus producing a bimodal distribution.

The mean crop size and total number of syconia were both much higher on male trees than on female trees (Table 2).

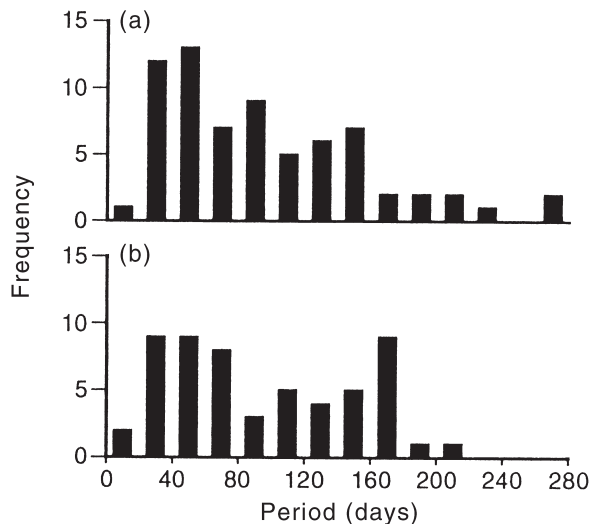
Of the tree characteristics measured, female and male trees differed little except in stem mortality,



**Table 2** Comparison of sexes for *Ficus fulva* in Lambir Hills National Park, Sarawak

	No. trees	No. crops initiated	No. crops finished	Immature	Phases (days)			Fruit/Male
					Receptive	Pollinated		
Female	25	80	46	12.4±0.79	9.68±1.21	55.2±3.21	10.4±1.25	
Male	26	72	53	11.4±0.59	5.95±0.36	29.9±1.76	7.0±0.62	
		Period between crop initiations (days)	No. crops finished ( <i>n</i> )	Period between crop finishings (days)		Crop size	Total no. syconia (18 months)	
Female	25	105.4±7.44	69	118.1±14.33	19	309.7±82.14	13 935	
Male	26	102.9±7.47	56	113.6±10.01	26	727.3±138.64	39 273	
		Diameter at breast height* (mm)	No. stems*	Stem mortality rate	Diameter growth* (mm)	Canopy width (m)*	Canopy illumination index*	
Female	25	100.9±35.96	1.3±0.76	0.16	17.2±11.11	5.0±1.83	4.7±0.52	
Male	26	108.7±44.55	1.7±0.90	0.25	25.1±28.59	5.1±1.94	4.7±0.55	
Immature	13	43.1±37.89	1.0±0.00	0	14.3±22.28	2.7±1.21	4.2±0.60	

Data are mean ±SE unless indicated otherwise. \*Data are mean ±SD.



**Fig. 6.** Frequency distribution of the period between crop initiations on (a) female and (b) male trees. Each datum is generated from the duration in days between date of the start of one crop to the date of the start of the following crop on an individual tree.

which was higher in male trees. One male stem and four immature stems died because of the road widening. Growth appears to have been higher in

male trees but the very large variation obscures this result. Growth and proportional growth were significantly negatively correlated to d.b.h.1 in male trees (Pearson's *r*: growth,  $-0.452$ ; proportional growth  $-0.488$ ;  $P < 0.05$ ,  $n = 21$ ), but not in female trees (*r*: growth,  $-0.167$ ; proportional growth,  $-0.069$ ;  $P > 0.05$ ,  $n = 21$ ), indicating that while larger male trees grew more slowly than smaller ones, growth in female trees did not decrease with increasing size. As expected, immature individuals were much smaller but growth was not any higher except that of one individual which grew from 63 to 131 mm, or more than doubled in stem diameter in the 14 months between measurements.

The mean size of the three smallest and largest individuals was different in female and male trees (female: mean minimum, 37 mm; mean maximum, 148 mm; male mean minimum, 46 mm; mean maximum, 174 mm). Female trees were smaller at both minimum and maximum ends of the range which suggests that female trees start reproducing at a smaller stem diameter and reach a smaller maximum stem diameter than male trees. However, a larger sample of trees would need to be measured to confirm this.

**Table 3** Individual level analysis of syconia and leaf production in *Ficus fulva* at Lambir Hills National Park

	d.b.h	Growth	Canopy width	CI
Female				
Total syconia production	0.347	-0.010	0.564**	0.037
Mean crop size	0.191	-0.100	0.451*	0.044
No. crops finished	0.450*	0.307	0.390	0.219
New leaf	0.510*	0.624**	0.471*	0.044
Flushing	0.128	-0.128	0.073	0.204
Male				
Total syconia production	0.484*	-0.130	0.596**	-0.051
Mean crop size	0.373	-0.164	0.503**	-0.096
No. crops finished	0.132	-0.111	0.127	0.086
New leaf	0.485*	0.050	0.332	-0.114
Flushing	0.044	-0.184	-0.002	-0.083

Diameter at breast height (d.b.h), diameter growth, canopy width and canopy illumination index (CI) were correlated with total number of syconia produced, mean crop size and number of crops finished, and with the proportion of census dates an individual had new leaf present and was flushing (>25% of crown). Pearson correlation coefficients; ns, \* $P < 0.05$ ; \*\* $P < 0.01$ . Females,  $n = 25$ ; males,  $n = 26$ .

#### *Individual tree characteristics and phenology compared by sex*

An analysis of the correlation between tree characteristics and phenology generally produced a good agreement between sexes (Table 3). The d.b.h. was significantly correlated with total syconia production in male trees but not in female trees. However, canopy width rather than d.b.h. was the best predictor of mean crop size and total syconia production in both sexes. The strong correlation between total syconia production and canopy width is not surprising given that the latter is indicative of both the area of canopy available to intercept sunlight for photosynthesis and also of the number of twigs on which syconia can develop. The proportion of census dates with new leaf present was significantly correlated with d.b.h., growth and canopy width in females but only with d.b.h. in males.

## DISCUSSION

### Influence of climate and population level phenology

#### *Leaf phenology*

Although some new leaf was present at all times, the pattern of leaf phenology was strongly influ-

enced by drought and the initiation of large crops of syconia. Drought caused a significant increase in leaf drop which was then followed by new leaf production with the renewal of rain. The severe drought in early 1998 clearly caused substantial water stress, inducing the death of two individuals, and by dropping leaf, the trees attempted to alleviate water loss. Following the drought, although new leaf was produced, the trees under observation did not appear to recover well. Syconia production did not return to its pre-drought levels and the very heavy caterpillar infestation observed at the end of the study period probably indicated that the trees were ailing. Rates of herbivore attack are usually very low in figs (R. Harrison, unpubl. obs., 1999), because they are protected by copious production of latex. However, latex production is expensive (Farrell *et al.* 1991); hence when plants are stressed, they may not be able to allocate sufficient resources to its production. In *Ficus variegata* Bl. in northern Australia leaf production was strongly correlated to rainfall seasonality (Spencer *et al.* 1996), and in another study at Lambir Hills National Park (R. Harrison, unpubl. data, 1999), leaf renewal showed a strong negative correlation with drought. The correlation of leaf flushing and syconia initiation almost certainly reflects a physiologically based constraint on species such as *F. fulva*, which produce

their syconia at the tips of the twigs. At least one other species found in LHNP, *Ficus aurata* Miq. which is found in similar habitats to *F. fulva* and also produces syconia at the twig tips, also had correlated leaf flushing and syconia initiation (R. Harrison, unpubl. data, 1999), but in other cauliflorous species the two events were unrelated (R. Harrison, unpubl. data, 1999).

#### *Syconia production*

*Ficus fulva* produced highly synchronous crops within trees, but within the group inter-trees, asynchrony maintained almost continuous production of both male phase syconia (pollinator production) and fruit until the severe drought in early 1998. The cyclic undulation in the proportion of trees with pollinated syconia on male trees indicates a slight synchrony between trees but it was not sufficient to cause breaks in pollinator production within the group. Crop initiation was negatively correlated with rainfall, which reflects the large numbers of crops started during and immediately following the drought. However, the proportion of pollinated syconia was not significantly correlated with rainfall, which is in contrast to other studies of dioecious fig phenology, where syconia production showed a strong correlation with rainfall seasonality (Hill 1967; Patel 1996; Spencer *et al.* 1996), and with drought at LHNP (R. Harrison, unpubl. data, 1999).

Within the group, inter-tree asynchrony also produced a broad overlap between syconia receptivity on female and male trees and pollinator production. Overlap in receptivity on female and male trees allows wasps to select male syconia, where they can reproduce, over female syconia, where they cannot. The longer duration of receptivity recorded on female trees may reflect some partial preference (Patel *et al.* 1995) for male syconia. However, considerable caution is warranted given the difficulties in accurately assessing the duration of the receptive phase, as explained above, and the possibility of other causes, such as the potential for male trees to provide their own pollinators. Wasp preference can only be assessed properly by using wasp choice experiments.

There was an overall lack of group level coordination between trees with male phase syconia and receptive phase syconia on female trees, but the correlation between syconia initiation and rainfall was

delayed 30 days on female trees relative to male trees. Previously, a delay in peak initiation of syconia on female relative to male trees in strongly seasonal environments has been interpreted as an adaptation that allows the male figs to pollinate female syconia, ensuring male reproductive success and female pollination success (Patel 1996; Spencer *et al.* 1996). The initiation of syconia in *F. fulva* after the drought may thus be similar to the behaviour of dioecious figs in strongly seasonal environments. However, adult wasp life spans are very short, so unless pollinator production actually overlaps with receptivity on female trees, there is no advantage to this arrangement, and caution should be exercised when assuming an adaptive interpretation.

The almost continuous production of wasps within the group may have important implications for the population size of genetically interacting *F. fulva* trees. Although wasps may be able to disperse long distances, as has been demonstrated in some monoecious figs in Panama (Nason *et al.* 1996), the continuous proximity of trees releasing pollinators suggests that these may swamp more distant sources, as was observed occasionally in the Panamanian figs. The negative correlation between syconia abortion on male trees and the proportion of trees with male phase syconia within the group also suggests that local wasp sources may be important. Syconia abortion can be caused by resource limitation, pollen limitation or possibly disease, although evidence of the latter was never found. However, separating these components is difficult because unpollinated and pollinated syconia are often aborted from a crop at the same time, and very few aborted syconia were found in the field until the time of the drought. The low rates of abortion until December 1997 likely reflect mostly resource limitation, while the later peaks in abortion are likely to reflect pollen limitation. In this instance, whether pollen limitation was caused by local pollinator shortages and limited wasp dispersal or a regional pollinator paucity cannot be separated, but clearly, a genetic study of *F. fulva* and other dioecious figs in LHNP similar to the one carried out on Panamanian figs would be very interesting.

#### **Sexual specialization**

The present study of the reproductive phenology of *F. fulva* demonstrated considerable sexual

specialization. The crop development period was approximately twice as long on female trees. Other studies of dioecious fig phenology have also tended to demonstrate a longer development time of syconia on female trees than on male trees (Hill 1967; Corlett 1987, 1993; Chou & Yeh 1995; Patel 1998). In the present study, a longer receptive phase on female trees most likely reflects pollinator shortage, rather than any advantage arising from extending the receptive phase, especially as wasp production in the group was almost continuous. This may well reflect the ability of male trees to supply their own pollinating wasps. Patel (1998) suggested that the longer development time of syconia on female trees was due to the greater number of ovaries and fleshier syconia on female trees, which would require a greater investment of resources. However, in *F. fulva*, crop periodicity was similar, hence the number of crops produced per unit time was almost the same on female and male trees. On male trees, physiological development of the wasp larvae may be inflexible (Galil 1977) thus preventing a more gradual investment by the fig, or it could be a predator avoidance strategy that reduces the time window available for non-pollinating wasps to oviposit on the figs. Non-pollinating wasps have longer adult life spans than the pollinators (R. Harrison, unpubl. data, 1999) and because they oviposit from outside the fig, they are able to move from one syconium to the next. Alternatively, longer development periods on female trees may reflect selection in order to sample a wider range of seed dispersal environments (Patel 1998), given the greater variation in syconia development and hence a longer fruit phase. However, one could also expect selection in male trees to sample a wider range of pollination environments. Crop development on monoecious figs is generally short (3–8 weeks; Patel 1998; R. Harrison, unpubl. data, 1999), more similar to the development time of male trees, suggesting that it is the syconia development on female trees that has become extended (Patel 1998). This would also suggest that in monoecious figs, female reproductive fitness may be compromised by the duration of wasp larval development.

Female and male trees also differed in their syconia investment profiles. In female trees, syconia dry weight increased linearly with syconia diameter, which suggests that investment in

syconia is independent of crop phase. On male trees, initial investment was low up until approximately the time of receptivity and thereafter increased rapidly. It therefore appears that males are minimizing investment until pollination has occurred. This strategy may reflect the much larger crop sizes on male trees, which could lead to a heavy loss of resources from abortion if pollinator shortages occur.

The large number of crops with short periods and the lower proportion of crops which finished on female trees reflects the large number of crops which were initiated but failed to develop at the time of the drought. This exception, female trees produced crops of similar size with even periodicity. The tendency for male trees to initiate a small crop immediately prior to a large one, producing a bimodality in crop periodicity, is interesting. The obvious suggestion is that the trees are kick-starting the main crop by investing in the small crop to produce the pollinators for the main crop. In monoecious figs, self-pollination carries a double cost of inbreeding depression and reduced pollen flow, but in dioecious figs, only the latter applies. Hence, it is quite possible to envisage how investing in a small number of syconia to guarantee pollination of the main crop may be advantageous. The male phases of the small crops often overlapped with receptivity in the larger crop, but there were also occasions when the phases did not appear to overlap. Interestingly, the smaller crops were generally produced on the main branches, back from the tips, similar to the situation described in *Ficus carica* L. (Valdeyron & Lloyd 1979), and possibly reflecting the need to decouple syconia production from leaf renewal that would occur with the main crop.

Figs are iteroparous plants; *F. fulva* produces an average of three crops per year and individuals are reproductive for at least 5 years (R. Harrison, unpubl. obs., 1999). Given the degree of sexual specialization in syconia phenology, we might expect to find sexual specialization in their life history strategies. The smaller mean minimum diameters in female trees, and the fact that female trees did not show any significant growth/diameter relationship, suggest that female trees start reproducing at a smaller diameter and then continue growing at a constant rate. However, male trees appear to delay starting reproduction until

they reach a larger diameter, and grow quickly as small trees, but increasingly slowly as they reach a large size. This difference in growth strategy between the sexes has two possible explanations. If mortality is size independent in female trees but higher in smaller individuals for male trees, then higher investment in growth until a larger size is reached would be selected in males. The data here were insufficient to test this hypothesis, although most stem mortality was in smaller stems in both sexes. If however, a larger crop size were advantageous for male trees, then again investment in growth until a larger size is reached would be selected (Charnov 1982), and given the much larger mean crop size on male trees, this seems likely. The lack of a good correlation between d.b.h. and mean crop size is misleading because of the tendency for male trees to produce small crops before the main crop. There was significant correlation between total syconia production and d.b.h. in male trees. In female trees, however, total syconia production was independent of d.b.h., which is predicted if there is selection for a continuous rate of investment in reproduction and growth. Size-related sexual specialization is reported in *Arisaema* (e.g. Kinoshita 1986), which actually change from small male to large female plants, and a closer correlation between plant size and reproductive allocation in males than in females has been demonstrated in other dioecious plants (e.g. Nicotra 1999).

It is perhaps surprising that in *F. fulva*, sexual specialization in leaf phenology, or other tree characteristics and their relationship to syconia production were not found. A difference in, for example, canopy illumination index might have indicated different habitat preferences in female and male trees. The short duration of the present study, however, may have prevented their elucidation. This could be an interesting line of enquiry for future studies.

## Conclusions

Synchrony of crops within trees but asynchrony between trees, and relatively high frequencies of crop production acted to maintain an almost continuous production of pollinator wasps and fruit within a small number of trees. However, the severe drought in early 1998, a rare extreme in a

normally aseasonal climate, had a very significant influence on the phenology of *F. fulva*, causing leaf drop and disrupting syconia production.

*Ficus fulva* demonstrated considerable sexual specialization in reproductive phenology and growth, but not in leaf phenology or other tree characteristics. Six aspects of sexual specialization can be recognized: (i) timing/frequency of syconia initiation; (ii) crop size; (iii) crop development time; (iv) syconia investment profile; (v) the ability of male trees to supply their own pollinators; and (vi) a sex-dependent growth strategy. Each of these suggests a possible route for the evolution of dioecy from monoecy, which has occurred at least twice and possibly three times in figs (Berg 1989) and also suggests a compromise between the sexual roles in the monoecious system. Yet 50% of the fig species worldwide, and 30% at the study site of the present investigation are monoecious. What are the advantages of the monoecious system?

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