Phenology and reproductive strategy of a common fig in Guangzhou

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ABSTRACTS. *Ficus* spp. (Moraceae) and their pollinator wasps (Chalcidoidae: Agaonidae) have co-evolved a highly mutualistic relationship, and depend completely on each other for reproductive success. Here, we present data on syconia, seed and pollinator production of the dioecious fig *Ficus hirta* Vahly, which were gathered to investigate the phenology and sexual specialization of individual trees. Syconia were produced asynchronously within trees, and there were sufficient degrees of both synchrony and asynchrony among trees to maintain pollinator production throughout the year. Production of receptive syconia and mature male syconia peaked at the same time to facilitate both pollination and pollinator production. The duration of crop development in female trees was longer than that in male trees, and the mean interval between syconia production was also longer in female trees. The mean diameter and total number of female syconia in receptive and ripe phase were lower, but the proportion of female flowers utilized in them was higher than that in male syconia. Syconium production was not correlated with the height of either female or male trees. The number of syconia produced was significantly correlated with the amount of branches on female trees but not on males.

Keywords: Dioecy; *Ficus hirta*; Fig wasps; Mutualism; Sexual specialization.

INTRODUCTION

Globally, there are over 750 species of *Ficus* (Moraceae) (Berg, 2003). Figs are distinguished as a genus by the syconium, a unique enclosed inflorescence which also functions as a pseudocarp. Syconia are considered to be key plant resources in tropical rainforests owing to their heavy and continuous production, providing food for a range of frugivores (especially birds) during periods of fruit scarcity (Janzen, 1979; McKey, 1989). The pollination of figs by highly specific wasps (Hymenoptera: Agaonidae) is arguably the most widely known example of obligate mutualism between plants and their pollinators (Ramirez, 1970; Janzen, 1979; Herre, 1996; Machado et al., 2001). Approximately half of all fig species are monoecious. In these species each inflorescence bears male flowers and female flowers with varying style lengths. When pollen-loaded female wasps enter a syconium, they pollinate the female flowers and oviposit in some of the ovaries. Hence, monoecious figs produce a mixture of pollinators, seeds and pollen in every fruit. In dioecious fig species, the syconium of functionally male trees bear male flowers and modified female flowers with short styles for wasp production, though some species also produce a few viable seeds (Galil, 1973; Valdeyron and Lloyd, 1979; Jousselin and Kjellberg, 2001). Dioecious figs also have true female trees with syconia that do not have male flowers and only very long-styled female flowers. The pollinators cannot lay eggs in these flowers because the styles are too long and thin for their ovipositors (Verkerke, 1987; Weiblen, 2000), so only seeds are produced.

The major developmental phases of the syconia of monoecious figs (Galil and Eisikowitch, 1968) can be applied, with appropriate modifications, to dioecious figs (Patel, 1996; Yu et al., 2003). An immature syconium (A-phase) develops to the receptive phase (B-phase) when it is entered by the first female wasp. During the developing phase (C-phase), each wasp larva feeds on the contents of a single ovary in male trees, and seeds develop in female trees. During the brief wasp-releasing phase (D-phase) in male trees, mature wasp offspring mate within the syconium and then the female pollen-bearing wasps leave the natal syconium to search for another receptive syconium. After the departure of the wasps, the syconia fall to the ground and rot. Female syconia, which do not have wasps, bypass the D-phase and develop further to the mature phase (E-phase). These mature syconia become soft and fleshy, and are attractive to seed dispersers such as birds.

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Adult female wasps have extremely short life spans and most live less than a day (Kjellberg et al., 1988; Harrison et al., 2000). If they are to reproduce, the availability of receptive syconia within their dispersal range is therefore vital. In order to maintain a sufficiently large wasp population to ensure pollination, both monoecious and dioecious figs must provide a continuous source of receptive syconia for emerging wasps (Frank, 1989; Harrison et al., 2000). It is therefore necessary for syconia in B-and D-phases to overlap, either on the same or on different trees within wasp dispersal range. However, in dioecious figs the two sexes specialize in either seed or wasp production, so the situation may be more complex. For example, the D-phase syconia have to coincide temporally with B-phase syconia not only in the female trees but also in the male. The separation of female and male functions between different trees could have led to adaptive changes in some characters of the figs that facilitate pollination and pollinator dispersal, which may have resulted in a greater array of phenological patterns.

Studies of phenology in fig plants, such as the time of flowering and fruiting in relation to abiotic factors (e.g. habitat or climatic variables) and biotic factors (e.g. the availability of pollinators, and the impact of herbivores and seed predators) are useful in furthering our understanding of the reproductive basis of the mutualism (van Schaik et al., 1993; Harrison et al., 2000). Because pollinating wasps have such short lifespans the influence of climatic fluctuations and biotic interactions on figs can only be examined over a relatively brief period. Although much attention has been paid to the phenology of monoecious figs (Hill, 1967; Galil, 1973; Milton et al., 1982; Corlett, 1987; Bronstein and McKey, 1989; Herre, 1989; 1993; Weiblen et al., 1995; Patel, 1996; Spencer et al., 1996; Patel and McKey, 1998; 2000; Harrison et al., 2000; Yang et al., 2002; Wang et al., 2005), studies of dioecious figs are few with most being concentrated in the tropics (Galil, 1973; Corlett, 1987; 1993; Weiblen et al., 1995; Patel, 1996; Spencer et al., 1996; Patel and McKey, 1998; 2000; Harrison et al., 2000; Yang et al., 2002).

There are two main phenological types at the level of the individual fig tree: 1) synchronous and 2) asynchronous. The former can be characterized by synchronous receptivity within both male and female trees, and low temporal overlap between the sexes. The latter can be characterized by asynchronous receptivity of both male and female trees, and moderate to high temporal overlap between sexes. In the subtropics, climates are more seasonal and this provides a good opportunity to study the phenological traits of fig trees (Berg, 2003). This is especially so for dioecious species, whose more complex reproductive systems are considered to have evolved as an adaptation to seasonality by some scholars (Kjellberg et al., 1987; Beck and Lord, 1988; Patel and McKey, 1998; Weiblen, 2000; Machado et al., 2001).

The purpose of this paper is to report on a field investigation into sexual specialization and the influence of temperature on the flowering, seed and pollinator production of a common fig species, *Ficus hirta*, in Guangzhou, southern China. Our study consisted of four questions: 1) what are the individual-level phenological traits of *F. hirta*? 2) how does the production of syconia, seeds and pollinators vary during the study phase? 3) what sexual specialization is evident in *F. hirta*; 4) does temperature affect the production of syconia, seeds and pollinators?

MATERIALS AND METHODS

Study site and species

Our study was conducted at the South China Botanical Garden (SCBG, 23°11’ N, 113°11’ E, elevation 20-327 m) in Guangzhou, southern China. The mean annual temperature is 21.8°C. Temperature data for SCBG from July 2002 to July 2003 (Figure 1) were obtained from a climate station which is 2 km from the study site. *Ficus hirta* is a shrub that grows to the height of approximately 3 m and is pollinated by *Blastophaga* (B.) *javana* Mayr. Three species of non-pollinating wasp have been reported in *F. hirta* (Mayr, 1885; Nair et al., 1981), but in SCBG there are mainly two non-pollinating wasps, *Philotrypesis josephi* and *Sycoscapter hirticola* (identified by Prof. Jean-Yves Rasplus and Dr. Zhen Wen-Quan).

Field observations

Phenology censuses of nine male trees and five female trees were conducted every 5-14 days from July 2002 to July 2003 (2-4 times per month). The crops were determined to begin just as a single syconium appeared and to end as all the syconia in an individual disappeared. At each census the number and diameter of syconia in each individual were recorded, and their development was also followed. The diameters were measured at the equator to the nearest 0.1 mm with vernier calipers. The height of each tree and number of its branches were also recorded.

To investigate the development of syconia, especially

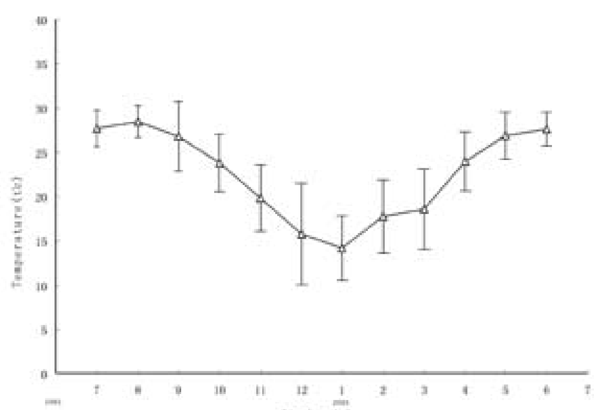

Figure 1. Annual variation of temperature (°C) obtained from the climate station where is 2 km from South China Botanical Garden (SCBG), South of China. (△) Represents monthly mean temperature.

B- and D-phases, syconia on individuals near the sample trees were dissected and their positions on the tree were noted in September in 2003.

The number of seeds and pollinators per syconium provide indicators of female and male function, and may be affected by the temperature. Between July 2002 and June 2003, 10-20 C-phase female and D-phase syconia were collected randomly from SCBG in each month. The key syconia parameters, such as the number of flowers, seeds and pollinators were counted under a dissecting microscope (SE-CTV, Olympus, Japan).

Data analysis

Total syconia production was calculated for individuals over the entire study period. Number of syconia produced in each individual was classified by plotting log-transformed frequency distributions in classes of 1-10, 11-20, 21-30 and >30. Mean durations of crops at individual and population-level were calculated. Mean durations of inter-crop interval at individual and population-level were also calculated. Monthly mean number syconia initiated, B-phase syconia, D-phase syconia, seeds and pollinators in syconia were calculated from all the censuses of this month. Mean diameters of syconia at each developmental stage were calculated from all the censuses. Frequency distributions of diameters were plotted in 5.5 mm intervals (0-5.4 mm, 5.5-10.4 mm, 10.5-15.4 mm, 15.5-20.4 mm and 20.5-25.4 mm).

All tests were carried out at $P \leq 0.05$ significance level using SPSS (version 11.0). The differences in syconia initiation, production of B- and D-phase syconia, production of pollinators and seeds were tested by One-way ANOVA among different months in our study period. Means of the significant ANOVA effects were compared using Tukey *post hoc* comparisons. Differences in mean duration of crops, mean duration of inter-crop interval (bearing no syconia), and the mean height of male and female trees were tested by Student's *t*-test. Correlation analysis was performed for temperature versus syconia initiation, B- and D- phase syconia production, seeds and pollinators production; female versus male syconia initiation and B-phase syconia production; D-phase versus B-phase syconia production; pollinator production versus short-styled female flowers; and height and branches versus syconia production.

RESULTS

Reproductive phenology

Syconia at different developmental stages appeared both synchronously and asynchronously on a single plant and between sample trees. They were produced in all seasons of the year. At each census, most syconia were in A- or C-phase. The duration of these phases was longer than the others phases, but there were wide variations in the development of syconia. Occurrence of both B- and D-phase syconia on the same tree was common (Table 1). The numbers of syconia found on a single plant generally ranged from several to 30, and never exceeded 100 (Figure 2). Female trees were devoid of syconia for 26.2% of the time, on average, whereas for male trees for only 5.6% of the time and two male trees bore more than five syconia every time they were observed.

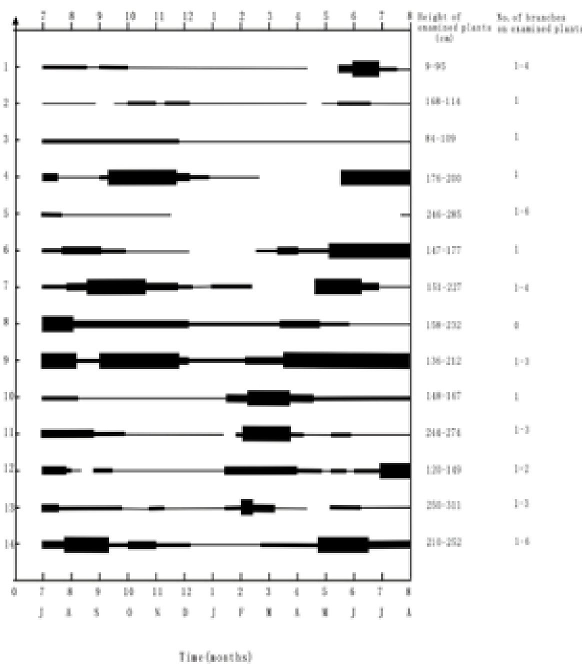

Figure 2. Reproductive phenology of 5 female and 9 male individuals of *Ficus hirta* in SCBG, South of China. Each bar represents a period in which syconia were present on the plant. (—1-10; ▬11-12; ▬21-30; ▬ >30) Four bar thicknesses represent number of syconia in individual in our study period.

Table 1. Syconia developments of *Ficus hirta* in South China Botanical Garden (SCBG), Guangzhou, South of China observed in Sept. 2003. A, B, C, D and E represent syconia in the A-, B-, C-, D- and E-phases, respectively; n represent number of individuals sampled in SCBG.

Types of syconium developments in individuals in SCBG												
	Female (n=15)						Male (n=17)					
Type of syconia developments in individual	A	AB	ABC	ABCE	AC	ACE	A	ABC	ABCD	AC	ACE	C
% Of individuals of the type in total individual observed	6.7	6.7	6.7	6.7	40	33.3	11.8	17.6	47.1	5.9	11.8	5.9

Production of syconia, seeds and pollinators

There were significant differences in syconia initiation among different months in both sexes (Figure 3; P<0.01). The female trees initiated more syconia in May, and male trees in February and May. Annual variations in the number of B- and D-phase syconia are shown in Figure 4 and have significant differences (P<0.01) among different months except D-phase syconia (P>0.05). They were generally low reflecting the normally short duration of these two phases. However, they present a large degree of overlap that could maintain continuous productions of seeds and pollinators. Productions of three types of syconia in May-June were all significantly different from that in most of the other months (P<0.05), indicating that all three types of syconia were peaking in this period. Moreover, they were significantly correlated with each other in this period (P<0.01).

Significant differences are in annual production of pollinators and seeds (P<0.01). Pollinator production was significantly higher in May (P<0.05) and has no correlation with number of short-styled female flowers (P>0.05). Seed production was significantly higher in January and June (P<0.05), and correlated with pollinator production in June (P<0.01).

Sexual specialization

Male trees were significantly taller than females. The height of the individuals had no correlation to syconia production, but the number of branches was significantly correlated with female syconia production (P<0.05). The mean duration of crops on male trees was shorter than that of on the females (P<0.05). The mean duration of the time between crops was shorter for male trees compared to the females (P<0.05). The mean diameter and total number of syconia in B- and D-phase were both higher on male trees than those in B- and E-phase syconia on female trees (Table 2).

In male syconia, the mean number of female flowers utilized by pollinators was 21±9%, and the mean number utilized by symbiotic wasps (including pollinators and non-pollinating wasps) was 37±7%, indicating that less than half of the short-styled female flowers were used by symbiotic wasps. In female syconia, the mean number of pollinated female flowers was 50±13%, nearly half of the total. So the number of female flowers utilized in female syconia was 30% higher than that in males. In D-phase syconia a few seeds could be found, whereas in E-phase syconia offspring of pollinators were never found.

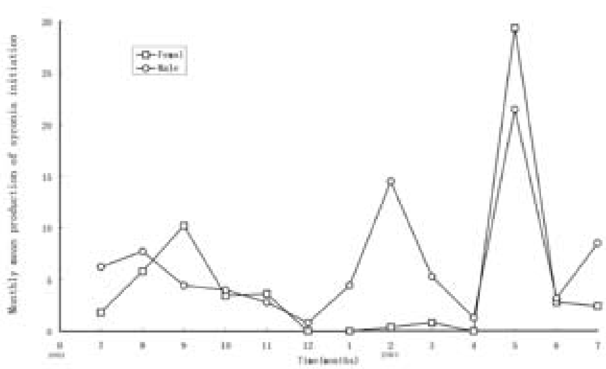

Figure 3. Annual variations of initiated syconia in individual in SCBG, South of China. (□) Represents monthly mean production of female syconia initiation; (○) Represents monthly mean production of male syconia initiation.

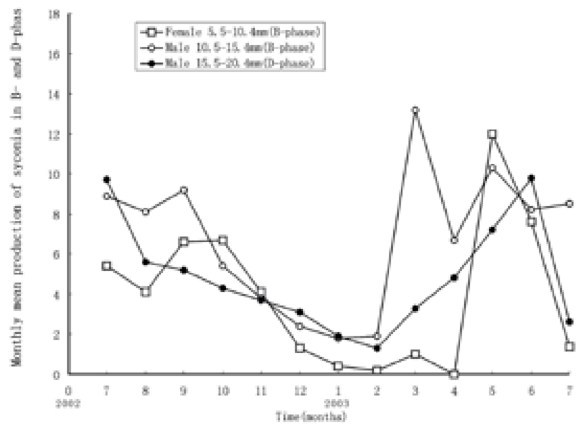

Figure 4. Annual variations of syconia in B- and D-phase in didividual in SCBG, South of China. (□) Represents monthly mean production of female syconia in B-phase (5.5-10.4 mm); (○) Represents monthly mean production of male syconia in B-phase (10.5-15.4 mm); (●) Represents monthly mean production of male syconia in D-phase (15.5-20.4 mm).

The effects of temperature on the production of syconia, seeds and pollinators

Correlations between temperature and production of syconia, seeds and pollinators were only significant in some months. Temperature was not correlated with female syconium initiation (P>0.05), but was correlated with male syconium initiation in August and January (P<0.05), which were the hottest and coldest months, respectively. Temperature was correlated with production of female B-phase syconia in March and December (P<0.01), with male B-phase syconia in July and August (P<0.05), and with male D-phase syconia in August (P<0.05). Pollinator production has no correlation with temperature, but seed production was correlated with increase in temperature in January (P<0.05). Of course these results are only preliminary, more accurate conclusions on temperature effect warrant further examination, and more data should be included.

DISCUSSION

Reproductive strategy

Female pollinators of *F. hirta* can survive in the laboratory for 24-48 hours at most (personal observation), so it is essential for them to find receptive syconia as soon

Table 2. Sexual specialization of *Ficus hirta* in South China Botanical Garden (SCBG), Guangzhou, South of China*.

Sex	Mean duration of bearing no syconia (days)	Mean duration of crops (days)	Mean diameter of syconia in different phases (mm)			Total syconia initiated in individual (13 months)
			B-phase	D-phase	E-phase	
Female (n=5)	95.5±85.9	61±21.4	8.5±2.2		13.2±2.6	60.6±42.8
Male (n=9)	20.3±23.2	49.3±15.9	12.1±1.9	17.1±2.8		81.6±17.5

Total syconia of selection	Mean % of seeds, pollinator wasps and all symbiltic wasps in female flowers in syconia		
(female: n=112; male=105)	Seed	Pollinator wasp	All symbiotic wasp
	50±13	21±9	37±7

	Height of the sampled individuals (cm)			Number of branches in individual	
	The first measurement	The last measurement	Range of increasing	Range	Mean
Female (n=5)	133.8±75	166.6±76	32.8±9.5	1-6	2.6±2.3
Male (n=9)	173.8±48.1	222.3±52.6	48.6±23.1	0-6	2.6±1.8

*Data presented as mean ± SD.

as possible. Within the sampled trees, the combination of inter-tree asynchrony and varying degrees of intra-tree synchrony and asynchrony resulted in a broad overlap between D- and B-phase syconia, allowing pollinators to potentially find receptive syconia relatively easily. In addition, B-phase syconia in both sexes and D-phase syconia all peaked at same time and were significantly correlated with each other which may facilitate both pollination and pollinator production. Thus, asynchrony between and within trees seems to optimize the chance for pollinators to find a receptive tree.

When male and female trees are receptive simultaneously, there should theoretically be strong selection for pollinators to avoid female syconia, in which they have zero fitness, and to enter only male syconia, in which they can reproduce (Patel, 1996). However, in contrast to this expectation, both seeds and pollinators were produced simultaneously. It is essential for pollinators to find receptive syconia quickly due to their short life-spans and high mortality rates, so the most likely reason is that pollinators may simply try to enter the first receptive syconium they meet (Patel et al., 1995; Moore et al., 2003), though other causes, such as pollinators cannot discriminate between male and female trees (Grafen and Godfray, 1991) or syconia could emit volatile chemicals that attract their specific wasps (Hossaert-McKey et al., 1994; Ware and Compton, 1994), maybe existed too.

Sexual specialization

In this study, considerable sexual specialization was found. The crop development period for female trees was significantly longer than the corresponding period for male trees, as found for other dioecious figs (Hill, 1967; Corlett, 1987; 1993; Patel and McKey, 1998; 2000; Harrison et al., 2000). Mean duration of inter-crop interval was significantly longer in female trees than that in male trees. This shows that the degree of synchrony was highest among female trees. In *F. hirta*, more syconia were produced in male trees than in female trees, but mean production of pollinators was lower than that of seeds in a single syconium.

Male syconia were larger than female syconia. In female syconia, flowers have longer styles, but the lengths of flowers are much shorter than the radius of syconium cavity (personal observation), so the smaller diameter of female syconia could not affect the action of pollinator in them. The proportions of female flowers utilized for seed production and pollinator production in individual syconia could be 97.7% and 85.9% at most, respectively, but the average proportion of female flowers utilized in both sexes were much lower than them (50±13% in female syconia and 21±9% in male syconia) which maybe limited by resource limitation or dispersal selection.

Phenological characters of *F. hirta* at other sites

Although few details have been published about the syconia and flowering phenology of *F. hirta*, in Hong Kong (Hill, 1967) they appear to be similar to those trees in our study. This may reflect the climatic similarities between the two regions. Li et al. (2003), however, found in a study of *F. hirta* in the more seasonal Chinese province of Fujan, that syconia were more synchronous among trees. Li and colleagues also found that crops of female and male trees were initiated alternately, with one population-level crop per year in female trees and two in males. Other studies of dioecious fig phenology have also found that crops tend to be smaller, with a greater degree of population synchrony in more seasonal environments

(Valdeyron and Lloyd, 1979; Corlett, 1987; Patel, 1996). Whether or not these findings apply to all dioecious figs warrant further examination.

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廣州常見一種榕樹的生殖策略和氣象學之關係

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桑科（Moraceae）榕屬（*Ficus* Linn.）植物與傳粉昆蟲（Chalcidoidae: Agaonidae）形成了專一性很強的互利共生體系。本論文研究了廣州華南植物園雌雄異株植物粗葉榕（*Ficus hirta* Vahl.）花序，種子和傳粉者的物候資料及雌雄植株之間的性別特化。研究結果表明：粗葉榕的花序在一年四季均可產生，株內花序非同步，株間花序同步和非同步共存，在適宜期大量產生接收花序和供給花序（提供傳粉者）並彼此相關，來促進傳粉和傳粉者的生成。雌株上每季花序持續時間長於雄株，沒有花序生成的時間也長於雄株。雌株上接收期花序和成熟期花序的直徑和產量都小於雄株，但雌株花序的雌花利用率即種子產量顯著高於雄株花序。花序產量與株高無關，但雌株的花序產量與植株上的分支數顯著相關。

關鍵詞：雌雄異株；粗葉榕；榕小蜂；互利共生；性別特化。