

Phenology and the production of seeds and wasps in *Ficus microcarpa* in Guangzhou, China

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Abstract

Ficus microcarpa, a large monoecious fig, is widely cultivated as a street tree in Guangzhou, South China, where only one species of active pollinating wasp, *Eupristina verticillata*, is associated with it. We recorded the flowering phenology, and the production of seeds and wasps, in *F. microcarpa* over a period of 18 months at the South China Botanical Garden. Plants produced 1–4 crops in the year. The production of seeds and wasps varied significantly between seasons, with extremely low production of seeds and wasp offspring in syconia sampled during particularly cool dry months. Most individual trees exhibited intra-tree asynchronous flowering, and typically bore many synconia at different developmental phases. Moreover, within asynchronous crops, earlier ripening syconia were often much larger than normal later ripening figs. These early-ripening syconia were occupied by non-pollinators with very large galls, and fewer seeds were produced. Therefore, it appears that early ripening was not adaptive for *F. microcarpa*. We discuss the implications of these findings for the occurrence of asynchronous flowering in monoecious figs in seasonal environments.

Keywords: *Ficus microcarpa*, non-pollinating fig wasps, phenology, resource allocation

1. Introduction

There are about 750 fig species (*Ficus*, Moraceae) worldwide (Berg, 1989). They can supply food for animals almost all the year owing to their numerical abundance, large crops and asynchronous fruiting within-population. Thus, *Ficus* is often regarded as a keystone genus in tropical rain forests (Shanahan et al., 2001). The fig is defined by an urn-shaped and enclosed inflorescence (the syconium), and depends on highly specific fig wasps for pollination (Weiblen, 2002; but see Machado et al., 2005). The fig wasps in turn depend on the syconia for oviposition sites. Year-round flowering is thus a necessary condition for the mutualism to persist. Typically monoecious figs exhibit flowering synchrony at the individual level and asynchrony at the population level (Bronstein, 1989). However, intra-tree asynchrony is also common in monoecious figs, and occurs in both highly seasonal and aseasonal environments, and both favorable and unfavorable conditions for plant growth (Hill, 1967;

Bajjnath and Ramcharum, 1983, 1988; Corlett, 1984, 1987 Bronstein, 1989; Bronstein and Patel, 1992; Cook and Power, 1996; McPherson, 2005).

Ficus microcarpa L. (section *Conosycea*) is widely distributed throughout the tropics and subtropics. It is indigenous from Sri Lanka, to southern China and Japan, and Australia, and New Caledonia (Wagner et al., 1999). There is only one known species of pollinating wasp, *Eupristina verticillata* (Chen et al., 1999). In addition, *F. microcarpa* is probably associated with 19 non-pollinating fig wasp species comprising three families (Eurytomidae, Ormyridae and Agaonidae) in Taiwan, southeast China (Chen et al., 1999). The average number of female flowers and male flowers per syconium is 233 ± 39.9 and 20 ± 10.1 , respectively. The number of male flowers varies substantially between warm and cool months, but numbers of female flowers hardly vary with the season. This fig is widely distributed throughout the tropics and subtropics, and so the potential exists for adaptation to different environments. Its phenology has been investigated at several localities (Hill, 1967; Corlett, 1984; Bronstein, 1989; McPherson, 2005).

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The results show that asynchronous crops in *F. microcarpa* occur both in relatively seasonal and aseasonal environments. In seasonal conditions, intra-tree flowering asynchrony may allow wasp transfers within-tree and avoid unfavorable conditions for wasp dispersal. However, in aseasonal habitats asynchronous flowering within-tree is also common, and a high proportion of ripe syconia without seeds have been reported in *F. microcarpa* (Corlett et al., 1990).

We conducted our study at the northern edge of *F. microcarpa*'s natural distribution in Guangzhou, south China, where trees can suffer rigorous conditions in winter. The allocation of the female flower resources to seed or wasp production with respect to phenology in a highly seasonal environment has seldom been examined. Our results are discussed with respect to the function of intra-tree asynchronous flowering and the low seed production in *F. microcarpa*.

2. Material and Methods

Study site

The study was conducted from March 2005 to September 2006 at the South China Botanical Garden (SCBG), Guangzhou, Guangdong Province (23°06' N, 113°18' E). The garden has an altitude ranging from 20 m to 372 m. Over the year, the mean daily maximum temperature ranges from 27.2°C to 38.1°C. Minimum temperatures can, however fall as low as 0°C during December (Fig. 1). The average annual rainfall is 1700 mm, with a relatively strong dry season from December to March (Fig. 1).

Investigation of flowering phenology and the production of seeds and wasps

Ten individual trees of *F. microcarpa* were sampled to investigate flowering phenology. Observations were conducted every one to two weeks. The stage of syconium development and the duration of phases were recorded. The classification of the flower phase was on the basis of that of Galil and Eisikowitch (1968). Fifty-six to seventy-seven ripe figs were collected randomly in two relatively cold months, March and December, and two relatively hot months, June and September, and their contents were counted. The relation between the production of seeds and wasps and climatic variables was analyzed.

Comparison between early-ripe figs and normal-ripe figs

In Guangzhou, China, within-tree asynchronous flowering in *F. microcarpa* occurred almost year round. When most figs reached their receptive or early interfloral phase, a few figs became obviously big and red. Here, we called these figs 'early-ripening figs', whereas the majority of later ripening figs were termed 'normal-ripening figs'. We collected 50 early-ripening and 50 normal-ripening figs and counted their contents.

Data analysis

Data were analyzed using statistical package SPSS 11.0. Bivariate Correlation Analysis was used to see if those climatic parameters have the propensity to affect the relative proportions of each fig stage on trees at different times. The differences, in seed and wasp production, during the months of the year were analyzed by GLM univariate analysis.

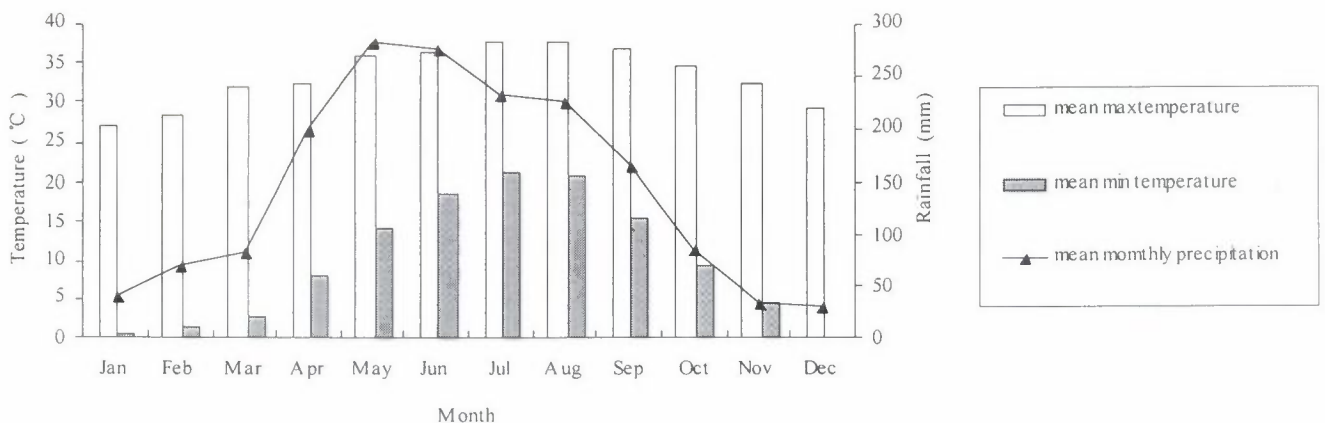


Figure 1. Monthly means of daily maximum and minimum temperature and rainfall over thirty years at the South China Botanical Garden, Guangzhou.

3. Results

Phenology of *F. microcarpa*

In Guangzhou, *F. microcarpa* had one to four crops per year, with the most usual number being three or four. The duration of each crop was usually one to two months. However, this time was extended in the relatively cold season from October to January and in the rainy season from April to July. Some trees retained fruit for the entire year as a result of flowering asynchrony. There was a significantly higher proportion of each fig stage on sampled trees in the favorable season from August to September and in the rigorous season from the end of November to the end of March (Fig. 2). The overlap of crops was also more frequent in these two periods. Moreover, the proportion of A, B and C fig stages was significantly related to low temperature (Table 1), indicating that these stages of fig development were prolonged in the cool winter.

Production of seeds and wasps in different months

There was a significant difference of production of seeds and wasps between months (Table 2). Production was significantly higher in September which is wet and hot than in the dry cooler months (Table 2). There was no significant difference in seed production between winter months, but the production of wasps was higher in December than that in March (Table 2). In general, seed production was low (mean=15.6) with about 50% of aborted female flowers (Table 3) compared with endemic fig species. For example, the mean number of seeds per syconium for *F. virens* and *F. altissima*, was respectively 141.0 and 285.7 (Yao et al., 2005).

Characteristics of early-ripening figs

In early ripening figs, female flowers with very large ovaries could be seen (Table 3), and seed production was low (<10%). However, the number of female flowers in early-ripening figs was not significantly different from that in normal-ripening figs (Table 3). There was no significant difference in wasp production between in the two kinds of figs (Table 3). It is interesting that the larger galls with short styles, produced in early-ripening figs, contained non-pollinators, mainly existing in inner ovary layers (near the fig cavity). Figs without seeds occurred occasionally in some early-ripening figs (11%) and had even larger diameters (12.00 ± 0.56 mm) and gall ovaries (length/width: 1.76/1.61 mm) than other early-ripening figs.

Table 1. Correlation between climatic parameters and the relative proportions of each stage on trees at different times.

Crops	Average monthly rainfall	Average max. temperature	Average min. temperature
A phase	0.179	-0.596*	-0.558*
B phase	0.270	-0.522*	-0.458*
C phase	0.253	-0.488*	-0.433*
D phase	-0.071	-0.249	-0.053
E phase	0.003	-0.373	-0.206

An asterisk (*) denotes mean differences is significant at 0.05 level.

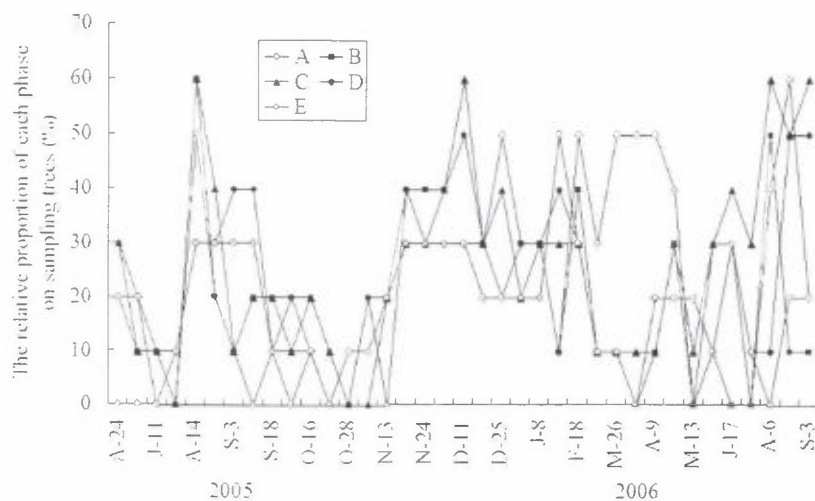


Figure 2. The flowering phenology of ten individuals of *F. microcarpa* over 18 mo at SCBG.

Table 2. The mean number of seeds and wasps produced per syconium in different months (\pm SD).

	December	March	June	September
Seed	5.15 \pm 6.37	4.09 \pm 6.68	10.63 \pm 8.16	28.77 \pm 19.28**
Wasp	40.13 \pm 22.57*	28.24 \pm 18.94*	59.95 \pm 26.16*	86.20 \pm 24.46**

Note: *and ** indicates significant difference at 0.05 level and 0.001 level, respectively.

Table 3. Comparison of syconium characteristics between the early-ripening and normal-ripening figs in *F. microcarpa*. Fig diameter (mm) which was measured at male phase and 50 syconia from two trees were sampled, the number of female flowers and male flowers per syconium, the proportion of female flower resources allocated by seeds, wasps (including pollinators and non-pollinators) and aborted flowers (%). All data were showed by (mean \pm SD).

	Fig diameter	Female flowers	Male flowers	Seeds (%)	Wasps (%)	Aborted female flowers (%)
Normal-ripening fig	10.37 \pm 0.55	233.62 \pm 32.56	18.69 \pm 6.65	16.58	36.22	46.20
Early-ripening fig	11.48 \pm 0.79	229.63 \pm 30.43	16.04 \pm 8.04	7.76**	31.74	60.50

Note: **Significant difference at 0.001 levels.

4. Discussion

Phenology of F. microcarpa

Ficus microcarpa showed both intra-tree and inter-tree asynchronous flowering in the seasonal environment at Guangzhou, producing one to four crops in a year. There was a nearly continuous production of fruits throughout the year. Maximum asynchrony was produced in relatively dry and cold seasons from November to March that were rigorous for wasp dispersal (Fig. 2). Furthermore during this time, syconia of B and D stages were present on the same tree, which suggests the likelihood that self-fertilization had occurred. Asynchrony may permit pollinators to transit in native trees and avoid the rigorous winter conditions. This flowering pattern may have important implications for the maintenance of the pollinator population. However, there was a significantly higher proportion of each stage on sampled trees in the favorable season from August to September (Fig. 2). There was also a significant correlation between the primary syconial development stages (A, B and C phase) and Temperature, with crop overlap frequently occurring during cool conditions. Intra-tree asynchronous flowering in *F. microcarpa*, has also been observed at other sites, including Singapore, which has an aseasonal climate (Corlett, 1984; Bronstein, 1989; Hill, 1967; McPherson, 2005). It is therefore unlikely that asynchronous flowering is a specific adaptation to a seasonal climate. Finally, in Taiwan, *F. microcarpa* bears variable numbers of crops; most trees having 1–2, but some trees producing up to 8 crops (Chen et al., 2004).

The production of seeds and wasps

The production of seeds and wasps of *F. microcarpa* was related to the season. Compared with seed production, wasp production was highly variable (Table 2). In the relatively warm and wet month of September, the production of both seeds and wasps in *F. microcarpa* was high (Table 2). This is consistent with the previous observation that more male-phase syconia are produced in warmer weather (McPherson, 2005). The duration of crops, especially the interfloral phase, was often prolonged in the relatively cold and dry months. This is to be expected if seed and wasp development are temperature dependent (Bronstein, 1989).

In our study, we also found an overlap between receptive and wasp emerging phases on the same tree. Seed production was also far less than wasp production in both normal-ripening and early-ripening figs (Table 3). *F. microcarpa* trees have an extremely low frequency in rain forests so that high levels of wasp production, relative to seed production, may compensate for low survival rate in wasps dispersing between trees (Harrison and Rasplus, 2006). In Singapore, more than one third of ripe figs had no seeds, and no pollinator production. Furthermore, non-pollinators only occurred in few syconia (Corlett et al., 1990). In Hong Kong, the average number of seeds per syconium in Hong Kong was only 12 (Corlett, 2006). Thus we may conclude that low seed and wasp production per syconium may be ubiquitous (or at least common) in *F. microcarpa*. This fig forms a very large tree, capable of producing over one million syconia in a single crop. It can also be long lived because of its banyan growth-form which

enables it to persist beyond the longevity of individual stems or stilt-roots. Thus, *F. microcarpa* trees may therefore be able to sustain a low seed and wasp production per syconium, through a very high total lifetime output of syconia.

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