Adaptive significance of asynchronous syconia production in a dioecious fig

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Abstract

Ficus trees can only reproduce if they are pollinated by highly specific wasps, which lay their eggs in some of the flowers. The wasp population can therefore only survive if there are some fig trees flowering at all times of the year. In highly seasonal habitats, when only a few trees occur at a site, gaps in fruiting may lead to the extinction of the local pollinator population. This paper demonstrates that in a dioecious fig tree, *Ficus hirta*, the fig wasp population can be maintained successfully within an individual plant, through the strong intra-tree asynchrony in flowering. By experimentally bagging trees, we showed that the pollinating wasps (*Blastophaga javana hilli*) could live for two generations, and the non-pollinating wasps (*Sycoscapter* sp.) for up to three generations in a closed intra-tree system. However, there was a sharp decline in wasp abundance, as indicated by declining sex ratios (0.31 ± 0.05 to 0.28 ± 0.098, mean±SD, not significantly) and the flower occupancy (11.31 ± 1.49 to 1.78 ± 0.59 by the 3rd generation, mean±SD, significantly) before their ultimate extinction, indicating that the wasp populations were not sustainable. This phenological strategy may enable dioecious figs, which are not constrained by the cost of selfing, to occupy a wider breadth of niches in both tropical and seasonal habitats.

Keywords:　*Ficus hirta*, propagative pattern, intra-tree system, coevolution

1. Introduction

Fig trees (*Ficus* spp., Moraceae) are pollinated by highly specific fig wasps (Hymenoptera: Agaonidae) and have long been held as a prime example of coevolution (Galil, 1968; Janzen, 1979; Kjellberg et al., 2001; Jousselin et al., 2003; Rønsted et al., 2005). An enclosed fig inflorescence (syconium) contains many flowers and (or) fig wasp larvae that depend entirely on galled ovules for food. Wasps are short-lived (Compton et al., 1994). They must locate a receptive fig quickly to lay their eggs when as adults they emerge from the ripe figs. This requires that syconia in different developmental phases are always present in the fig population. This is possible because of flowering asynchrony and thus year-round fruiting at the population level (Janzen, 1979; Kjellberg, 1989).

Many fig species show flowering synchrony at the individual level with asynchrony maintained between individuals, but the intra-tree asynchrony also has been reported in several species (Bronstein and Mckey, 1989; Bronstein, 1992; Hossaert-Mckey and Bronstein, 2001; Bronstein and Patel, 1992; Cook and Power, 1996; Harrison and Yamamura, 2003).

Many scientists have suggested that dioecious fig species, which have male individuals that produce just wasps and pollen and female individuals that produce only seeds, might reproduce better under seasonal conditions than monoecious figs (Berg, 1984; Patel et al., 1993). The major difference between seasonal and aseasonal environments for figs should be the suitability of different times of year for flowering, seed production, seed dispersal and germination. During poor periods in strongly seasonal regions, fig wasp survival and flight ability may be strongly limited, and hence fig trees should initiate flowering much more rarely.

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If the trees of a given fig population all fail to flower for a period longer than the life cycle of their pollinators, the wasp population will become locally extinct (Harrison, 2000). No tree within the population will be able to reproduce again until wasp pollinators recolonize. Under such circumstances we might expect selection for intra-individual asynchrony to occur, because the reduced dispersal distance will increase wasp survival and ensure a supply of pollinators for the tree. This will be especially true in male dioecious figs, where there is no penalty for self-pollination (Harrison and Yamamura, 2003).

Several monoecious fig species have been shown to have a greater degree of intra-tree asynchrony in seasonal environments (Cook and Power, 1996; Bronstein, 1990; Bronstein, 1992; Hossaert-Mckey and Bronstein, 2001). Moreover, in dioecious figs a high degree of intra-tree flowering asynchrony is known to occur in some species (Patel, 1996; Harrison and Yamamura, 2003), and in at least one case this may permit the cycling of wasps within a single individual (Harrison and Yamamura, 2003). However, direct evidence for the cycling of fig wasp populations within a single fig individual are lacking. In this paper, we study a dioecious fig, *Ficus hirta*, a species that is widely distributed in south China. We use a unique direct method, that of bagging individual plants and thereby creating a closed system comprising a single male tree, to demonstrate that the wasp population can be maintained by the asynchronous syconia production on the plant. The wasps' survival longevity, sex ratio, and flower occupancy rate were all recorded, and we addressed the following questions. 1) Can the pollinating and non-pollinating wasps really survive in this intra-tree system? 2) If so, how many generations they can survive? 3) What changes occur in the flower occupancy rate and wasp sex ratios?

2. Materials and Methods

Species, site and sample collection

Ficus hirta is a widespread, native dioecious fig species in south China. The plants are shrubs or small trees; reaching a height of 1.5 m to 2.5 m. *Ficus hirta* is pollinated exclusively by *Blastophaga javana hilli* in S. China (Wiebes, 1993). Two non-pollinating fig wasps, *Sycoscapter* sp., *Philotrypesis* sp., also live and feed within syconia by ovipositing from the outside of the syconia through the wall with their long ovipositors. The voucher specimens of all the wasps and the trees were lodged in South China Botanical Garden Herbarium.

In the *Ficus* Garden of the South China Botanical Garden (113°18' E, 23°06' N), we selected eight male trees of *F. hirta* and followed their phenology from July 2002 to November 2003. Each week the number of syconia at each of the main developmental stages was recorded. Another

eight male trees were covered by big transparent net bags (mesh size: 80) to create closed, intra-tree systems in December 2002. Before the sample tree was covered, every fig was labeled. Every week we checked the flowering phenology and wasp emergence. If new figs initiated, we labeled them. We defined as the 1st generation of wasps those that emerged from the first cohort of syconia that were initiated after the tree was bagged. The 2nd generation was defined as those that emerged from syconia that were pollinated by the 1st generation, and so on. In every generation, syconia with emerging wasps were collected. We continued the experiment until the intra-tree wasp population went to extinction. Wasps were identified by the authors. Syconia were dissected and the flower occupancy rate was calculated. In this study, only *Blastophaga javana hilli* (pollinating wasp) and *Sycoscapter* sp. (non-pollinating wasp) were involved since on three of the trees very few *Philotrypesis* sp. were found.

This region of China experiences a dry, cool period (winter) from October to April. Hence, our experiment was conducted in the season we predict would be least favorable to wasp survival.

Data analysis

Statistical analyses were performed using SPSS (version 13.0). T-Tests were used to explore the abundance of pollinating-wasps and sex ratio between two generations. ANOVA and Tukey HSD multiple comparison were used to explore differences in longevity, flower occupancy rate, non-pollinating wasp abundance and sex ratios over three generations. Before analysis, the sex ratio data were arcsin transformed. Results are given as mean±SD. A value of p<0.01 was accepted as indicated a significant difference.

3. Results

Receptive syconia and those with emerging wasps were present during the entire study period (Fig. 1). Overlap of the receptive and wasp emerging phases was frequent especially in July and August.

The pollinating wasps were able to survive for up to 2 generations, while the non-pollinating wasps survived up to 3 generations in our eight closed systems. However, the sex ratio, flower occupancy rate and longevity changed substantially between generations (Table 1). The abundance of pollinating wasps of both sexes fell markedly in the 2nd generation, and no pollinating wasps survived to the 3rd generation. Their sex ratio dropped from 0.31±0.05 in the 1st generation to 0.28±0.09 in the 2nd generation, suggesting a marked reduction in the mean number of foundress wasps entering a syconium. For non-pollinating wasps, wasp abundance dropped again markedly from the 1st to the 3rd generation, and none survived to the 4th

Table 1. Parameters of syconia collected from experimentally bagged trees (n=8) of *Ficus hirta*. Each tree was isolated in an individual bag and the wasp production followed until extinction. The number of syconia; number of female and male pollinators (*Blastophaga javana hilli*) and their sex ratio (proportion of male wasps); the number of female and male *Sycoscapter* sp. (a non-pollinator), and their sex ratio; the flower occupancy rate; and the longevity of syconia development (means and standard deviations (SD)). Similar superscript letters for each parameter indicate no significant difference at P<0.01.

| Parameter	1st Generation	2nd Generation	3rd Generation	4th Generation
Number of syconia	96	52	21	0
Number of female pollinators	$19.82^a \pm 2.73$	$11.69^b \pm 2.59$	0	0
Number of male pollinators	$8.86^a \pm 1.82$	$4.42^b \pm 1.61$	0	0
Pollinator sex ratio	$0.31^a \pm 0.05$	$0.28^a \pm 0.09$	–	–
Number of female *Sycoscapter*	$15.22^a \pm 2.63$	$10.75^b \pm 2.97$	$6.81^c \pm 2.18$	0
Number of male *Sycoscapter*	$14.34^a \pm 2.59$	$8.19^b \pm 2.75$	$5.29^c \pm 2.10$	0
Sycoscapter sex ratio	$0.49^a \pm 0.06$	$0.43^b \pm 0.09$	$0.44^b \pm 0.13$	–
Flower occupancy rate (%)	$11.34^a \pm 1.49$	$5.19^b \pm 0.77$	$1.78^c \pm 0.59$	–
Longevity of syconia development (days)	$33.00^a \pm 2.08$	$29.43^b \pm 1.62$	$30.86^{ab} \pm 2.12$	–
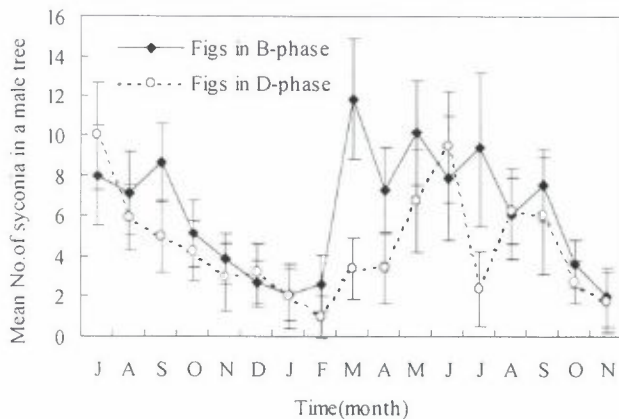
Figure 1. The variation in mean number of receptive-phase (◆) and wasp emerging-phase (○) syconia on eight male trees of *Ficus hirta* during from July 2002 to November 2003 at the South China Botanical Garden.

generation. Their sex ratio dropped markedly from the 1st to the 2nd generation, but there was no significant difference between the 2nd and the 3rd generations. The flower occupancy rate dropped significantly from 11.34±1.49 in the 1st generation, to 5.19±0.77 in the 2nd generation, and 1.78±0.59 in the 3rd generation. The longevity of pollinating wasps, from oviposition to emergence, varied in a narrow range from 33.00±2.08 days to 29.43±1.62 days in these three generations.

4. Discussion

This study demonstrates that single male trees of the dioecious fig species, *F. hirta*, can maintain a local population of pollinating wasps for up to two generations

and non-pollinating wasps for up to three generations, through their asynchronous development of syconia. Moreover, our phenological observations showed that individual trees had a continuous, year-round overlap in receptive and wasp emergence phase syconia. We suggest this completely intra-tree asynchronous phenology may be a strategy to promote wasp persistence in a species that often exists in small local populations in a highly seasonal environment.

Similar individual-level asynchronous phenology has been reported in two other species of dioecious fig, *F. hispida* (Patel, 1996) and *F. cereicarpa* (Harrison, 2000). In *F. hispida* an asynchronous phenology was displayed. Receptivity and wasp or seed production in this species occurred year-round, and there was considerable overlap in timing of male and female inflorescence production. In *F. cereicarpa* a single male tree had a continuous production of new syconia, and therefore potentially maintained a local wasp population, for 18 months.

However, these species occur in less seasonal, tropical sites. In these figs, pollinator dispersal between small-scattered groups or individuals may be limited (Harrison and Rasplus, 2006), and hence the asynchronous phenology may help the plants maintain pollinator production. Intra-tree asynchronous phenology may thus have enabled dioecious figs to occupy new niches in both highly seasonal and aseasonal environments.

Zhen (2004) recently described the oviposition sequences of pollinating and non-pollinating wasps in *F. hispida*. In the receptive phase (only 1–2 days), he found that the pollinating wasp, *Ceratosolen solmsi*, firstly entered and oviposited in the syconium. Then the non-pollinators, *Philotrypesis* sp. and *Apocrypta bakeri*, oviposited through the fig wall over the following 10–15 days. In this study, the non-pollinator, *Sycoscapter* sp., also oviposited from outside of fig wall with its long ovipositor (personal observation). We believe that its ability to utilize

several syconia and its longer adult lifespan explain why their populations persisted longer than the pollinator.

The above results notwithstanding, our experiment showed that the intra-tree system was not sustainable. All the parameters we measured indicted a sharp decline in wasp abundance from one generation to the next, and their ultimate extinction. Thus, trees are still dependent on some wasps arriving from neighboring individuals. It would be interesting to examine the effect of phenology on the evolutionary process by comparing the population genetics of fig species with an intra-tree asynchronous phenology with those that have highly synchronous crop development. Our data also provide the possibility for further studies of population genetics of wasps in this closed intra-tree system.

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