

Pollinational-mutualism strategy of *Ficus erecta* var. *beeheyana* and *Blastophaga nipponica* in seasonal Guandaushi Forest Ecosystem, Taiwan

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ABSTRACT. This study investigates pollination mutualism between *F. erecta* var. *beeheyana* and its obligate pollinator *Blastophaga nipponica* using detailed phenology data from the seasonal Guandaushi Forest Station. The symbiotic cycle resembled that of the *F. carica* and *B. psenes* in southern France. *Blastophaga nipponica* emerged from the D-phase syconia of over-winter male crops and entered the receptive male syconia to lay its eggs during the spring male main crop reproductive period. Several weeks later, dozens of offspring emerged and pollinated the receptive syconia of the summer female major crop. A few pollinators entered the receptive male syconia to oviposit, and their offspring wintered inside the male fig as larvae or pupae. The fig trees could control the developmental period of wasp-producing syconia during pollination. The peak of B-phase syconia (pollinators pollinate or set eggs) of both genders appeared earlier than the abundant D-phase syconia (pollinators released) by about two to three weeks. On the other hand, the flowering syconia of both genders occurred abundantly, staggered about two to four weeks after heavy rainfall, and the fly-out pollinators would pollinate or lay eggs during this period. This fig flowering phenology accommodates the shorter life span of the obligate species-special pollen carrier to enter the receptive syconia for effective oviposition or seed-setting. *Ficus erecta* var. *beeheyana* and *B. nipponica* thus have a successful mutualism strategy of pollination at the Guandaushi Forest Station.

Keywords: *Blastophaga nipponica*; *Ficus erecta* var. *beeheyana*; Guandaushi Forest Ecosystem; Mutualism; Pollination.

INTRODUCTION

A total ca. 750 *Ficus* species worldwide are distributed in tropical to subtropical areas (Corner, 1965; Berg, 1989), and each species is typically pollinated by females of its own specific species of fig wasp (Galil, 1973; Wiebes, 1979; Van Noort and Compton, 1996). The relationship between *Ficus* species and their pollinating wasps (Agonidae, Chalcidoidea, Hymenoptera) is considered to be an extreme instance of plant-animal co-evolution (Janzen, 1979). Fig trees are defined by the syconium (syncarp or fig), a unique enclosed inflorescence, which is lined with several dozen to thousands of tiny, unisexual flowers (Berg, 1989; Verkerke, 1989; Tzeng et al., 2001). This is also the arena for interactions with fig wasps. The morphologically specific fig wasp enters the syconia through the bract-lined entrance of the ostiole, often losing their wings and antennae in the process. The pollen-loaded

wasps then pollinate the female flowers. In turn, wasp reproduction is dependent on the fig, as its larvae feed on galling flowers (Ramírez, 1970; Galil, 1973; 1977; Janzen, 1979; Van Noort and Compton, 1996).

Fig trees can be classified as either monoecious or dioecious, with each group comprising roughly 50% of the species (Corner, 1965; Berg, 1989). In monoecious fig trees, male and female flowers line the inner wall of the same syconium. Female flowers, differing in style and length, comprise the imperfect heterostyle (Verkerke, 1989). Additionally, the ovules of female flowers can be pollinated for seed-production and oviposited for fig wasp developing the gall, in which larvae feed (Bronstein, 1988). Several weeks later, adult fig wasps emerge and mate while still in the syconium. The wingless males can then cut a tunnel out of the syconia, often dying inside the natal syconium. The female pollen-carrier emerges from the now-mature male flowers, either through passive ducting or packing special pollen pockets and depart to search for receptive syconia (Galil and Eisikowitch, 1968;

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Bronstein et al., 1990). Because monoecy have syconia, with ripeness is synchronized within an individual tree and are typically asynchronous between trees, the female pollinators flying out of the syconia must search for another receptive syconium on another tree to oviposit and pollinate in (Galil et al., 1970; Janzen, 1979; Wiebes, 1979; Bronstein et al., 1990; Bronstein and Patel, 1992; Thomson et al., 1997).

Dioecious fig species, however, have divided the production of seeds and the rearing of pollinators into two inflorescent types on separate plants: syconia male and female figs. Male and short-style female flowers (gall flowers, for fig wasp ovipositing), line the male syconium while long-style female flowers (seed flowers for seed production) and/or neutral flowers line the female syconium (Weiblen et al., 1995; Tseng, 1999; Tzeng et al., 2001). Short- and long-style female flowers are differentiated by length of style, morphology, structure of stigma and ovary (Verkerke, 1990; Beck and Lord, 1988a; Tseng et al., 2000; Tzeng et al., 2001), and by pollination physiology (Verkerke, 1990; Beck and Lord, 1988b), which displays the perfect heterostyle (Verkerke, 1989; 1990).

Adult female pollinators emerge from D-phase syconia and search for male receptive syconia to oviposit or female receptive syconia to pollinate during their extremely short lifespan ranging from several hours to two days (Kjellberg et al., 1988; Tzeng, 1997; Wu, 1996; Tseng, 1999). After pollination or oviposition, the wasp usually dies inside the syconium it last visited. Otherwise, unvisited syconia are then aborted.

Dioecious figs must produce D- and B-phase male syconia during the same period to maintain a continuous pollinator life cycle (Anstett et al., 1995; Tzeng, 1997; Kameyama et al., 1999), and pollination success is dependent on the continuous cyclical production of pollinators with pollen-entering receptive syconia (Chen, 1998; Tseng, 1999; Harrison et al., 2000). Syconia phenology has been shown to be useful in investigating the influence of climatic fluctuation and biotic interactions in some studies on dioecious figs in seasonal environments which show sexual specialization (Valdeyron and Lloyd, 1979; Spencer et al., 1996; Tzeng et al., 2003; Chang, 2003). Dioecious figs do not necessarily ensure outcrossing (Corlett, 1987), but the fig trees must imitate the morphology, color, and odor of their syconia to keep the fig wasps from distinguishing male from female syconia and, thereby, only setting eggs (Grafen and Godfray, 1991; Ware et al., 1993; Ware and Compton, 1994); they must also be prevented from recognizing the fig phenology between male and female trees (Kjellberg et al., 1987; Kjellberg and McKey, 1989; Spencer et al., 1996; Patel and McKey, 1998; Harrison et al., 2000; Tzeng et al., 2004).

The short lifespan of a pollinator (Kjellberg et al., 1988; Wu, 1996; Tseng, 1999) and the receptive syconia can prevent aborting when pollinators do not pollinate

or oviposit on the female flowers during a 2- to 3-week period (Khadari et al., 1995; Tzeng, 1997). Kjellberg et al. (1987) elucidated the stability of the symbiotic relationship between the dioecious figs *F. carica* L. and *Blastophaga psenes* L. and their pollinators during seasonal environments. However, no studies have identified the relationship between the life cycle of the pollinator—with their short-lived escape from D-phase syconia—and the receptive syconia for both genders year round. The goal of the present study is to elucidate the syconia phenology of *F. erecta* Thunb. var. *beeheyana* (Hook. et Arn.) King and determine the relationship between flowering-phase syconia reproduction and the dynamic processes of the obligate pollinator *Blastophaga nipponica* Grandi. under sporadic rainfall. Additionally, this study identifies the pollination-mutualism ecology between a fig and its pollinator in the seasonal environment at the Guandaushi Forest Station.

Studied site

The studied area was located at the Guandaushi Forest Station of the Hue-Sun Experimental Forest Station (24°4' N, 12°80'E), one of the Long Term Ecological Research (LTER) sites in Central Taiwan (Figure 1). During the study period of 1996, the average annual rainfall, relative humidity, and yearly temperature were 2,596.9 mm, 79.1%, and 21.0°C, respectively (data from the station). Most of the rainfall (96.2% of total) occurred during the rainy and typhoon seasons. The average rainfall over ten years was 2,683.3 mm (Figure 2, from 1987 to 1996), and 93.2% occurred during the warm-wet season. According to the classification of Thomthwite, this study area belongs to AB'wa', a wet but warmed wintertrochene klima (Yu, 2001). The vegetation of the site is typical of a warm forest and is characterized by a *Ficus* – *Machilus* vegetation zone at about 500-800 m (Liu, 1968; Su, 1992; Lu and Ou, 1994).

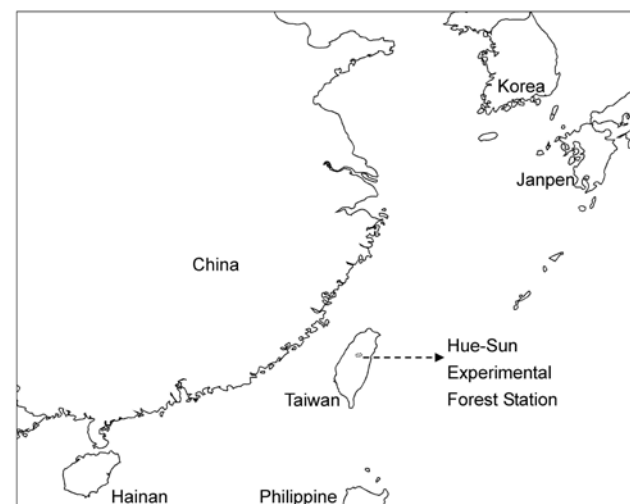


Figure 1. The studied area was located at the Guandaushi Forest Station of the Hue-Sun Experimental Forest Station in Central Taiwan.

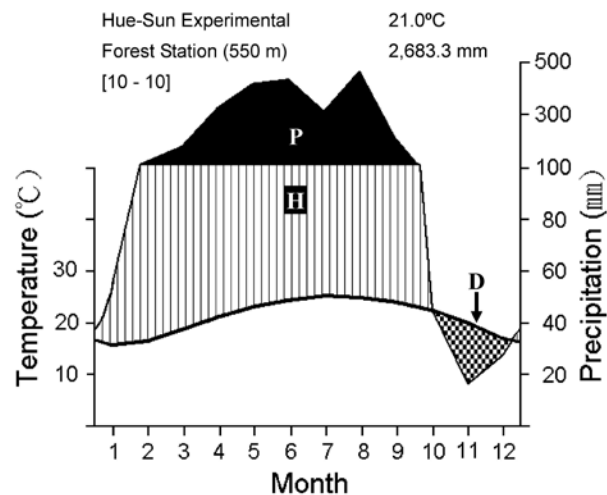


Figure 2. The ecological climate diagram of Hue-Sun Experimental Forest Station; (P) represents perhumid; (H) represents relative humid; (D) represents relative drought.

Biology of *Ficus erecta* var. *beeheyana*

Ficus erecta Thunb. var. *beeheyana* (Hook. et Arn.) King (Figure 7a) is a small semi-deciduous to deciduous tree or big shrub from 2 to 5 m, distributed mainly in southern China, from Ryukyu, Taiwan, Orchid Is., Hong Kong, to the Malay Peninsula (Corner, 1965; Liu et al., 1994; Liao, 1995; Tzeng, 2004). It is a pioneer species, usually occurring in the lowland to medium altitude of disturbed forests, second forests, or along roadsides (Liu et al., 1994; Liao, 1995; Tzeng, 2004). The fig's obligate pollinator is *Blastophaga nipponica* Grandi. (Figure 3a, b) (Chen and Chou, 1997). The non-pollinating fig wasp, *Sycoscapter inubiae* Ishii (Figure 3c, d), which oviposites through the syconium exterior during the C-phase, and its offspring may feed on the pollinator's larvae inside the ovary (Wu, 1996; Tzeng, 1997). The special-species pollinator is also shared with *F. erecta* Thunb. var. *erecta* (Okamoto and Tashiro, 1981; Chen and Chou, 1997).

This fig is morphologically gynodioecious and functionally dioecious, with populations comprised of female and hermaphrodite individuals, and this study refers to the two tree sexes as female and male (Tzeng et al., 2001). The syconia are axillary but male syconia are generally born on the older branches while the female syconia are mostly initiated on new branches (Tzeng et al., 2003). The classification of the post-budding period development processes of *F. erecta* var. *beeheyana* is based on Galil and Eisikowitch (1968) and on modifications by Tzeng et al. (2001).

A fig tree can produce one to four crops each year for both genders within the tree, and the syconia productions were seasonally at population level, which responded to the fluctuation of climate and showed sexual difference (Tzeng et al., 2003; Tzeng et al., 2004). The specific pollinator must fly out the D-phase syconium from its natal tree to find another B-phase syconium to set eggs or pollinate in during its short-life span of several hours to

two days (Okamoto and Tashiro, 1981; Wu, 1996; Tzeng, 1997). The phenology of this fig indicated that the syconia production of each gender was adapted to the environment, and it would be helpful for seed production, germination, and maintaining the population of the obligate pollinator, *Bl. nipponica*, respectively (Tzeng et al., 2004).

MATERIALS AND METHODS

Samples selection

A total of 71 trees of *F. erecta* var. *beeheyana* were marked (40 male and 31 female mature trees), from which 30 mature trees (17 male and 13 female) were selected for pollination examination. The figs trees were somewhat closely distributed along the roadside or under a 36-year-old China fir (*Cunninghamia lanceolata*) in an artificial forest at the study site. Two to three branches roughly 50 cm long from one tree or a whole, small tree approximately 2 to 3 m high were selected for each census. The figs, in the form of a shrub to small tree, were 2-5 m high with a diameter at breast height (DBH) of 2-10 cm.

Field observations

Syconia censuses of *F. erecta* var. *beeheyana* were conducted at 5-9 day intervals from November 1995 to April 1997 at the Guandaushi Forest Station. The numbers of all syconia in the developmental stage were counted for each gender during each census. The classification of syconia development was based on the following characteristics: (Table 1, Tzeng et al., 2001) male figs do not have an E-phase, and female figs do not have a D-phase. Although the syconium acts as both flower and

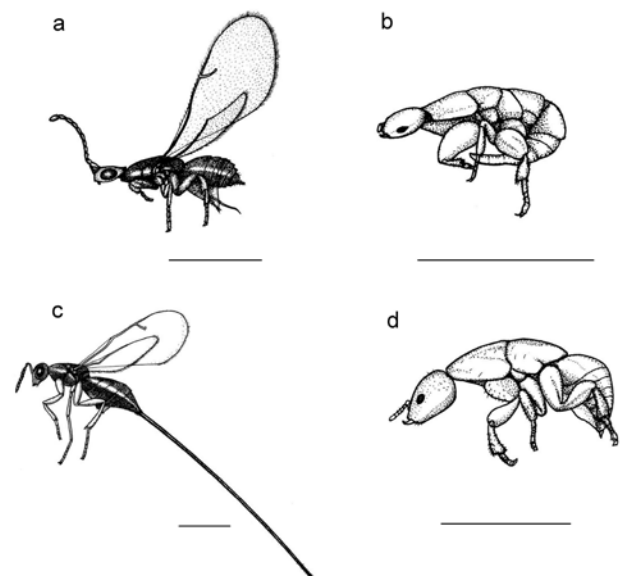


Figure 3. The pollinator of *Blastophaga nipponica* Grandi, and non-pollinating fig wasp of *Sycoscapter inubiae* Ishii. a, c, indicate male wasps; b, d, indicate female wasp; bars indicate 1 mm.

Table 1. Syconia developmental stage, size, and maturity of *F. erecta* var. *beecheana* for both genders.

Phase	Syconium diameter	Syconium maturity
A Pre-female phase	♀: 2 – 6 mm ♂: 2 – 21 mm	The young syconia prior to the opening of the ostiole and with tightly closed ostiolar bracts. Both male and female syconium are orange, red or light green with dark red spots.
B Female or receptive phase	♀: 6 – 8 mm ♂: 9 – 21 mm	Ostiolar bracts loose. Both seed (female syconia) (Figure 7c) and gall (male syconia) female flowers (Figure 7d) are ripe. Pollinators, <i>B. nipponica</i> penetrate into the young syconium (Figures 7b, 8a) and lay eggs into the ovaries of gall flowers (Figures 8b-d) or pollinate with the seed flowers. Both male and female syconia are in red or green color with dark red spot.
C Inter-floral phase	♀: 6 – 8 mm ♂: 9 – 22 mm	Wasp larvae develop within the occupied ovaries, which are transformed into galls in male syconium.
D Male phase	♂: 15 – 30 mm	Male flowers mature, wasps reach the eclosion stage, and the wingless male wasp mates with the female wasp which is inside the gall in the syconium (Figure 7g, h). The female wasps leave the male syconium via the opening ostiole (Figure 7f) with pollen. The male syconia become soft with dark red or purple.
E Mature phase	♀: 9 – 21 mm	Female syconia ripen, becoming dark-purple and soft, sometimes with sweet liquid outside syconium (Figure 7e).

fruit, the true flowering phases of syconia are actively B- and D-phases, together forming the critical phase of syconia development in the mutualistic system. Data were analyzed using SPSS 8.0. Kendall's rank correlation was used to assess between each phenological census and climate at the study site.

RESULTS

Relationship between pollinator life-span and the flowering-phases of syconia

The B-phase male syconia germinated abundantly from the male spring crop during March 1996, matching primarily the mostly D-phase syconia of the 1995 over-winter syconium crop (Figures 4, 5). The peak of the D-phase syconium was delayed by roughly three weeks, after the B-phase syconia of the male trees. The obligate pollinator, *Blastophaga nipponica*, emerged from the D-phase syconia of the 1995 over-winter syconia crop to search for the B-phase of the male syconia to set eggs. The pollinator was observed searching for the B-phase of the male syconia on the same tree or flying away from the host tree to find the B-phase male syconia on other trees.

The pollinator's larvae developed in the 1996 main male crop in spring between March and June. Several weeks later the male syconia had successfully developed from C- to D-phase. D-phase syconia were located in the bloom, and the pollinator offspring (second generation) emerged in large numbers primarily from D-phase male syconia while the B-phase syconia were abundant in the main female crop in summer. The female pollinators flew out of their host syconia to search for another B-phase syconia to set eggs. However, most pollinators joined the

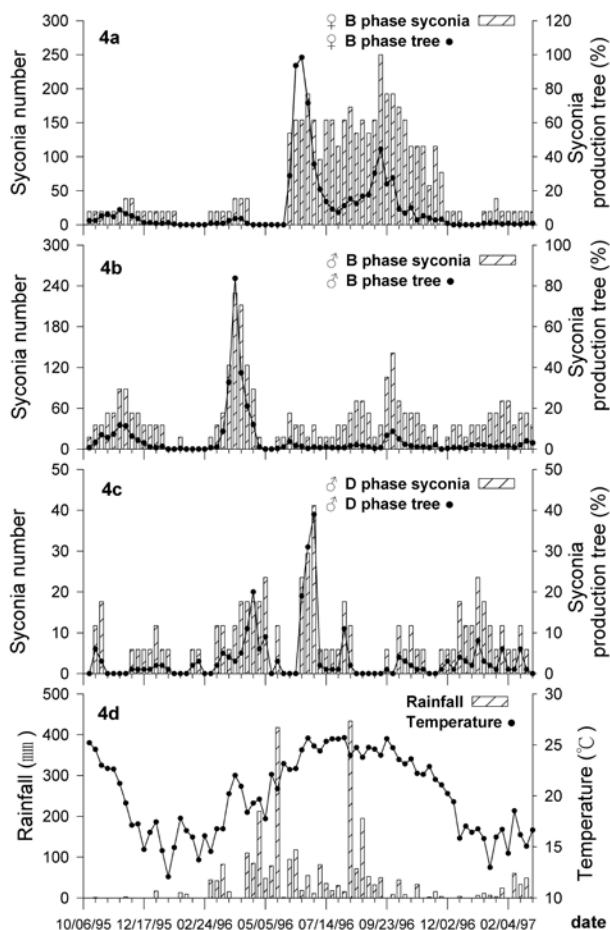


Figure 4. The relationships between rainfall, temperature and flowering syconia production of both genders of *F. erecta* var. *beecheana* at Guandaushi Forest Station from October 1995 to February 1997.

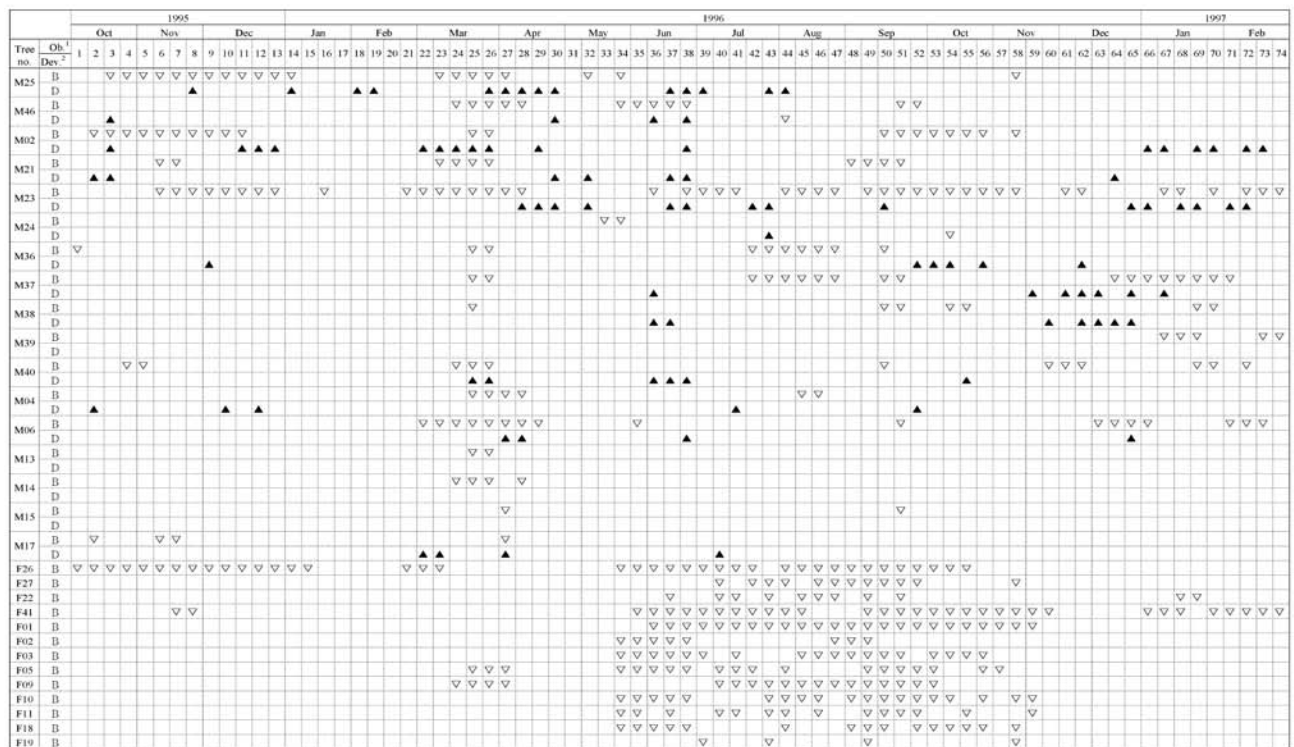


Figure 5. The relationships of flowering syconia production between D- and B-phase syconia of both genders for each sample tree of *F. erecta* var. *beecheana* at Guandaushi Forest Station from October 1995 to February 1997. (▲) indicates female pollinators flying out from D-phase male syconia. (▽) indicate female pollinators entering B-phase syconia.

mass of B-phase female syconia from the main female crop in summer for pollination (Figures 4, 5). A few female pollinators found the B-phase male syconia of the sub-male syconia crop for ovipositing. Some offspring of the third or four generations of pollinators developed in the sub-male syconia crop from September 1996 to February 1997 (Figures 4, 5). The pollinational-symbiotic ecological model is shown in Figure 6.

The incidence of D-phase syconia was well matched with the abundant B-phase male and female syconia. The largest number of B-phase syconia of both genders developed 2 to 3 weeks before the peak of the D-phase syconia (Figure 4). During the first peak of B-phase male syconia, approximately 80% of male trees bore B-phase syconia, and roughly 50% of male trees bore syconia during the second crop (Figure 4). Roughly 80% of female trees bore B-phase syconia during the summer main crop, and more than half trees bore B-phase syconia during the fall sub-main crop (Figures 4, 5). The frequency distribution of flowering syconia production of D- and B-phase syconia for both genders were similar to the proportional distributions of female and male trees with flowering-phases syconia in each census, a very significant correlation (Table 2). Each male tree produced 1 to 3 (4) generations of pollinator each year (Tzeng et al., 2003) with the B-phase and D-phase male syconia present continuously year round and matching each other (Figures 4, 5, 6).

The relationship between syconia development and weather

The abundant D- and B-phase syconium reproduction of both genders was staggered with heavy rainfall by roughly 2 to 3 weeks although data analysis did not identify a significant correlation between rainfall and reproduction (Table 3). The abundance of D-phase syconia of the 1995 over-winter crop and the B-phase syconium reproduction in the main male crop in spring occurred prior to the heavy rainfall in the rainy season (Figure 4). The main male crop in spring developed to the full-bloom D-phase from June to July between the heavy rainfall of the rainy and typhoon season. Female fig trees bore two peaks of abundant B-phase syconia from June to September (Figure 4). The first peak of the B-phase female syconia occurred between the heavy rainfall of the rainy and typhoon season. The second peak of the B-phase female syconia occurred after the heavy rainfall in the typhoon season.

The receptive syconia were pollinated or oviposited for both male and female trees and developed into C-phase. The abundance of the C-phase syconia of female trees was significantly correlated with temperature and negatively correlated with temperature for the males (Table 3). However, C-phase syconia production was not correlated with rainfall for either gender (Table 3); C-phase syconia were plentiful during periods of heavy rainfall in the rainy and typhoon seasons.

Table 2. Kendall rank correlations (τ) between rainfall, temperature, and developmental syconia production for each observation date of *Ficus erecta* var. *beecheiana* (males/females = 17/13, observation times = 74) at Guandaushi Forest Station from October 1995 to February 1997. Each significance test involves a separate risk of a type I error. NS indicates that means in a given column do not significantly differ at the 5% level.

		♂ D-phase syconia	♂ D-phase tree (%)	♂ B-phase tree (%)	♀ B-phase tree (%)
♂ D-phase syconia	τ		1.000	0.079	-0.066
	ρ		0.000	NS	NS
♂ B-phase syconia	τ	0.121	0.121	0.834	
	ρ	NS	NS	0.000	
♀ B-phase syconia	τ	-0.066	-0.066		1.000
	ρ	NS	NS		0.000

DISCUSSION

Symbiotic relationship between fig and fig wasp

In the Guandaushi Forest Station, the B- and D-phase syconia in the flowering stage were numerous during the specified period. The relationship between *F. erecta* var. *beecheiana* and its obligate pollinator, *B. nipponica*, is a symbiotic-pollination relationship, somewhat similar to the model of *F. carica* and *B. psones* in southern France (Kjellberg et al., 1987). *Ficus erecta* var. *beecheiana*, which shares affinity with *F. carica*, belongs to the subgenus *Ficus*, section *Ficus* (Corner, 1965; Tzeng, 2004), and might have processes similar to *F. carica*.

In a seasonal environment, *F. erecta* var. *beecheiana* produced seasonal and asynchronous crops between its male and female populations, with the males producing syconia earlier than the females by roughly 2 to 3 months (Wu, 1996; Tzeng et al., 2003). At the Guandaushi Forest Station, fig wasps emerged from the D-phase syconia of the 1995 over-winter crop between March and April when the receptive syconia of the main male crop in spring were

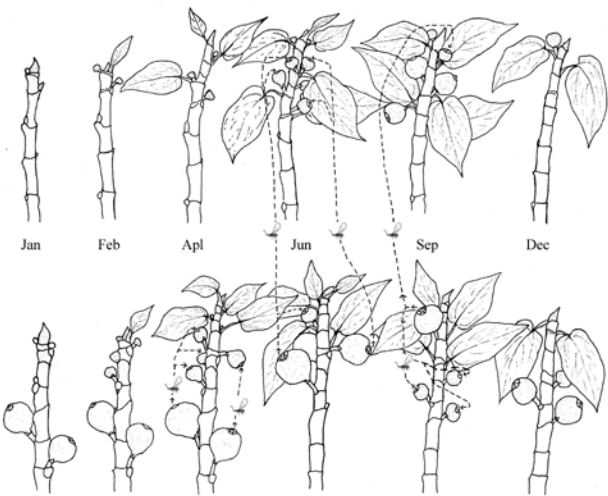


Figure 6. Pollinational-symbiotic ecological modal of *F. erecta* var. *beecheiana* and its obviously pollinator, *B. nipponica* at Guandaushi Forest Station from October 1995 to February 1997. Narrows indicate that female pollinators are flying-out from the D-phase syconium to female syconium.

Table 3. Kendall rank correlations (τ) between rainfall, temperature, and developmental syconia production for each observation date of *Ficus erecta* var. *beecheiana* (males/females = 17/13, observation times = 74) at Guandaushi Forest Station from October 1995 to February 1997. Each significance test involves a separate risk of a type I error. NS indicates that means in a given column do not significantly differ at the 5% level.

		♂ B-phase syconia	♂ C-phase syconia	♂ D-phase syconia	♀ B-phase syconia	♀ C-phase syconia
Rainfall	τ	-0.037	-0.076	0.088	0.120	-0.010
	ρ	NS	NS	NS	NS	NS
Temperature	τ	-0.053	-0.185	-0.047	0.521	0.480
	ρ	NS	0.020	NS	0.000	0.000

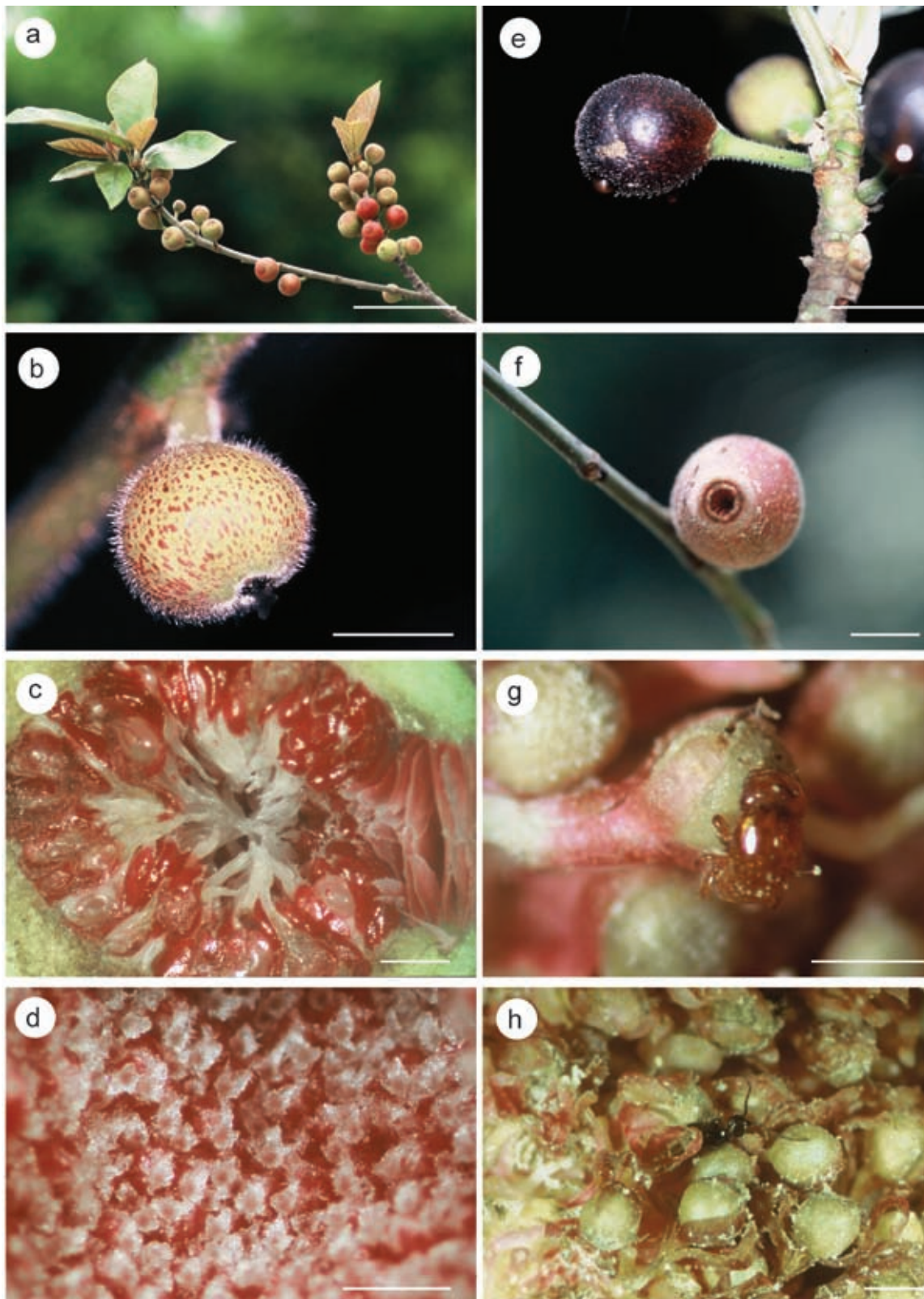


Figure 7. a, Syconia on the branch of *Ficus erecta* var. *beeheyana*; b, *Blastophaga nipponica* inside the B-phase syconium; c, B-phase seed flowers of section syconium; d, stigma of B-phase gall flowers; e, E-phase female syconium; f, Opening ostiole of D-phase syconium; g, Male *B. nipponica* mates with female, which is inside the gall; h, Female *B. nipponica* leaves the gall. Bars indicate 10 cm for Figure 7a, 5 mm for Figure 7b, 1 mm for Figure 7c, d, g, h, and 1 cm for Figure 7e, f.

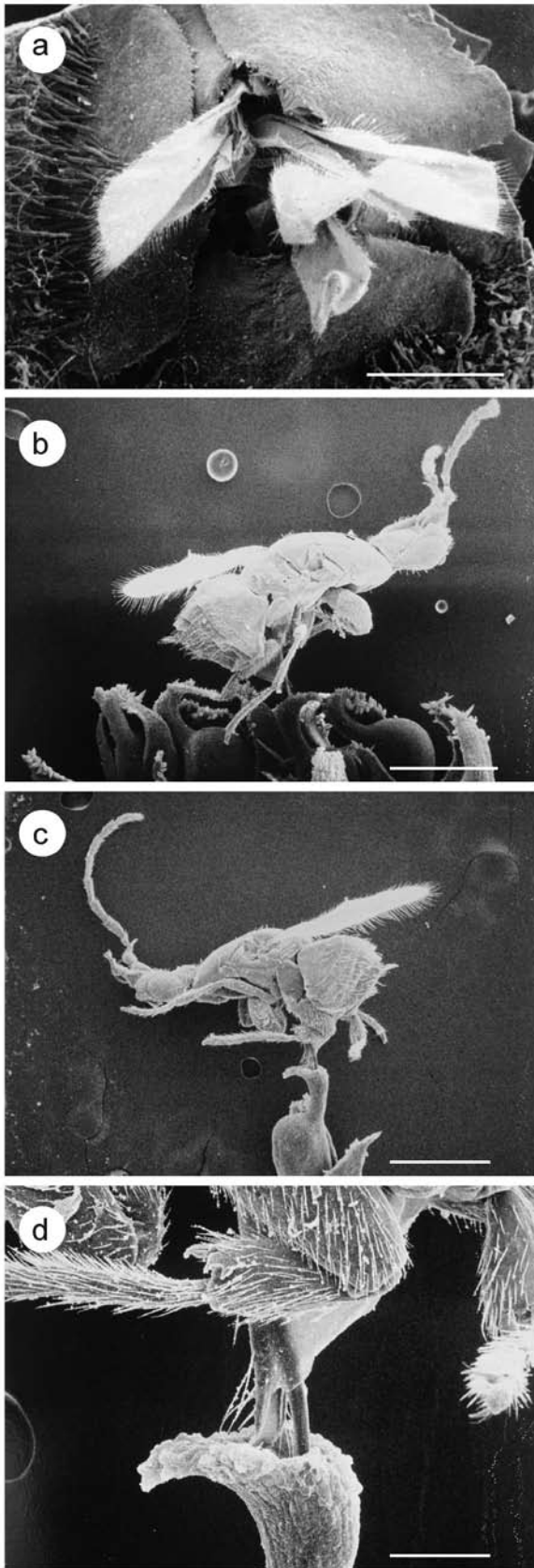


Figure 8. a, Female *B. nipponica* often lose their wings in the ostiole when they penetrate into the B phase syconium; b, c, d, Female *B. nipponica* oviposites on the gall flower. Bars indicate 500 μ m for Figure 8a, b, c and 100 μ m for Figure 8d.

plentiful. Most male fig trees initiated new syconia during the main male crop but bore asynchronous syconia during other periods within the population (Tzeng et al., 2003). Male syconia developed with a similar growth ratio from A-phase to the B-phase when the 1996 over-winter male syconia matured and released countless of fig wasps.

If a female founder enters a B-phase male syconium successfully during the bagged experiment, 100 to 200 offspring could be born during the D-phase syconium several weeks later (Tzeng, 1997). This would extend the pollinator population by an average of 152 times for one founder. In contrast, the average number of progeny (average = 327) inside one D-phase syconium during the 1996 main male crop in a natural state was significantly higher than the one founder's ($T=4.209$, $p=0.000$), despite the larvae of the non-pollinator *S. inubiae*—a parasite—which fed on the larvae of the pollinator inside the ovule (mean number of pollinators=255; $T=3.156$, $p=0.003$) and had a negative relationship with the pollinator (Tzeng, 1997). Conversely, the fig wasp population released from the 1995 over-winter crops was substantially larger than the number of receptive syconia of the 1996 main male crop in spring. Due to creating a good match between D- and B-phase of the male syconia, the pollinator of the 1996 main male crop in spring was extended.

In dioecious figs, wasps can only breed in the gall flowers of male syconium; consequently, pollination of female syconia is always lethal (Kjellberg et al., 1987). Therefore, selection must favor wasps that avoid female trees. The entry of fig wasps into female syconia to extend their population in the short-term offers no apparent benefit (Kjellberg et al., 1987). Hence, to maintain symbiosis dioecious figs must prevent fig wasps from developing the ability to distinguish between male and female syconia. Conversely, syconia display sexual differences at specific times (Valdeyron and Lloyd, 1979; Kjellberg et al., 1987; Kjellberg and Maurice, 1989; Spencer et al., 1996; Tzeng et al., 2003), and fig wasps have acquired the ability to lay eggs in male syconia only. However, male and female syconia have modified their structure, phenology and physiology to prevent the fig wasp from distinguishing between them (Grafen and Godfray, 1991; Wu, 1996). Although there is no evidence that the degree of attraction to female- and male-receptive syconia of *F. erecta* var. *beecheana* is the same for fig wasps, it has been demonstrated that fig wasps do not distinguish between male and female syconia through odor (Ware and Compton, 1994; Hossaert-McKey et al., 1994). Pollen carriers are likely to be attracted by receptive syconia of female trees to pollinate, and surplus pollinators enter B-phase male syconia to lay eggs to further the survival of the pollinator population. In brief, fig trees integrate syconia production phenology and modified characteristics like odor between male and female syconia to maintain their mutualism.

Few pollinators entered by chance the male receptive syconia of the 1996 winter crop, and it was maintained

by larvae or pupa during the C-phase male syconia in the winter. For tiny pollinators with a short life span, cold and rainy weather is fatal (Hill, 1967). However, asynchronous syconia production can maintain and extend the pollinator population under such conditions (Ramírez, 1970). In some male trees, pollinators which escaped from the overwinter syconia emerge from male syconia and quickly begin searching for another B-phase male syconia on the same tree. This can reduce the death ratio and increase the likelihood of the wasp entering a B-phase male syconia during the searching period to oviposit.

Ficus erecta var. *beeheyana* phenologically controls its gender, preventing the species special pollinator, *B. nipponica*, from entering only male syconia. The features of syconia production within a tree or between trees are a form of sexual specialization to maintain the fig wasp populations and attract frugivores for seed dispersal (Tzeng et al., 2003). Researchers have suggested that it is the fig tree, not the wasp, which controls the development time of wasp-producing syconia after pollination occurs (Kjellberg et al., 1987).

Observation results showed that B- and D-phase male syconia were continually present on almost all of the 17 male trees during the study period from Oct. 1995 to Feb. 1997. There were 1 to 3 (4) crops in the male population (Tzeng et al., 2003) and 1 to 3 (4) generations of pollinator success in the study population year round. Although, there was no information on the dynamics of the pollinator population, less than 20 male trees might be the smallest survival population of *B. nipponica*, the obvious pollinator, in the pollination-symbiotic ecological system at the Guandaushi Forest Station.

A “temporal gap” between D- and B-phase syconia production

This study has identified a temporal gap between the mass production of B- and D-phase syconia in *F. erecta* var. *beeheyana* at the Guandaushi Forest Station. This phenomenon was somewhat similar to that of *F. carica* (Kjellberg et al., 1987) in southern France. However, the temporal gap of *F. erecta* var. *beeheyana* differed from *F. carica* in the number of receptive syconia since both genders were developed earlier than the highest number of D-phase syconia while female pollinators emerged, i.e., the emergence of fig wasps from the delayed syconia (D-phase) occurred earlier than the maturation of the undelayed syconia (B-phase) in which the fig wasp oviposited in *F. carica* (Kjellberg et al., 1987).

The highest D-phase syconia occurred roughly 2 to 3 weeks after the peak of B-phase male and female syconia in *F. erecta* var. *beeheyana*; i.e., the *B. nipponica* were released from the D-phase male syconia later than female syconia of both genders. During the delay period of D-phase syconia, a few female syconia were entered by pollinators, released from male syconia. This phenomenon has been observed in other dioecious figs, such as *F. erecta* var. *beeheyana* (Wu, 1996), *F. formosana* (Subg. *Ficus*,

Tseng, 1999), *F. irisana* (Subg. *Sycidium*, Chen, 1998), and *F. ampelas* (Subg. *Sycidium*, Chang, 2003).

Kjellberg et al. demonstrated that a temporal gap was a selective pressure favoring the fig wasp's pollinational-symbiotic system, concluding that it is characteristic of *F. carica* (Kjellberg et al., 1987). However, the receptive syconia were not visited and were aborted while dozens of wasps emerged before the development of receptive syconia in *F. carica* in Southern France. This might be a result of long artificial culture and small size samples (four males and three females) of *F. carica* employed in southern France (Kjellberg et al., 1987).

Was the phenomenon of D-phase syconia, which were in abundance after the B-phase syconia, stable in the symbiotic system? Because the D-phase syconia only lasted for a few days (Tzeng et al., 2001), emerging pollinators had to search for another receptive syconia in which to lay their eggs or pollinate during their short life-spans of several hours to 2 days (Ramírez, 1970; Janzen, 1979; Baijnath and Ramcharun, 1983; Kjellberg et al., 1988; Chen, 1994; Wu, 1996; Chen, 1998; Tseng, 1999). Observational results indicated that *B. nipponica* survived 1 to 2 days, and generally less than 1 day during the cold winter (Wu, 1996; Tzeng, 1997). There were no receptive syconia to enter for ovipositing or pollinating if the D-phase syconia developed earlier than B-phase syconia. Therefore, it is not beneficial for pollinators to emerge before receptive syconia develop.

B-phase syconia of both tree genders remain on the tree for roughly 2 to 3 weeks longer than D-phase syconia. In the monoecious species *F. aurea* (Bouchaib et al., 1995), female syconia can survive on the branch for 2 to 5 weeks, as long as for dioecious species (Bouchaib et al., 1995; Ware and Compton, 1994; Chen, 1998; Tseng, 1999). The extended receptive period of the syconia may be a result of the developmental asynchrony of female flowers inside the syconia (Tzeng et al., 2001); however, temperature is the principal factor (Bouchaib et al., 1995).

Although, extending the receptive period wastes the resources of the trees, a prolonged B-phase provides increased likelihood for the uncertain flowering period, low-density population, and seasonal-efficiency of *Ficus* for pollination or oviposition (Bouchaib et al., 1995). It is a critical factor allowing fig and fig wasp to maintain their pollinational-symbiotic ecological system in a required minimum number of trees (Bronstein et al., 1990; Anstett et al., 1995; Bouchaib et al., 1995; Kameyama et al., 1999). To ensure the future of this relationship, the short-lived pollinator must enter the B-phase syconia before they fade. The fig wasps will die before they enter a receptive syconia to oviposit or pollinate if the receptive syconia have developed prior to the fig wasp emergence.

That the abundance of receptive syconia occurred before the numerous of pollinator eclosion (D-phase syconia) is a flowering characteristic of *F. erecta* var. *beeheyana*. Comparing the cost of a prolonged B-phase with the successful pollination/oviposition and delayed

peak production of D-phase, it showed that dozens of wasps which emerged after the peak of receptive syconia would benefit evolution between the short life-span of *B. nipponica* and *F. erecta* var. *beecheana* in seasonal Guandaushi Forest Ecosystem. In one big enough population, it might present another strategy on the pollination-symbiosis ecological system in the seasonal environment for other fig species and its obvious pollinator. And it has to more research in pollination-symbiosis to understand the co-evolution of fig and fig wasp.

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關刀溪森林生態系牛奶榕授粉共生生態之研究

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本研究探討關刀溪森林牛奶榕與牛奶榕小蜂之授粉共生生態。研究結果得知：牛奶榕與牛奶榕小蜂的授粉模式與法國南部之無花果相似。由越冬雄榕果發育而羽化的牛奶榕小蜂，進入雄株春季主要花季雌花期雄榕果內，產卵在短花柱雌花子房以擴大其族群。其後裔隨後於雄花期春季主要花季羽化，絕大多數進入了雌株夏季主要花季的雌花期雌榕果，為牛奶榕長花柱雌花授粉，少數進入雌花期雄榕果內產卵。牛奶榕小蜂以幼蟲或蛹在榕果內度冬，延續授粉蜂的族群。在授粉的過程中，牛奶榕可以控制種子及牛奶榕小蜂在榕果內的發育時間；即牛奶榕雌、雄株的雌花期榕果，其最大生產量要比牛奶榕小蜂孵化的雄花期雄榕果發生最大量的時期早 2~3 星期。而雌、雄花期榕果生產的最大生量要比降水晚 2~4 星期，大多數的牛奶榕小蜂在此時期羽化，可以比較安全的進入雌花期榕果進行授粉或產卵。生命短暫而專一性的牛奶榕小蜂，其生活史適應著牛奶榕的開花物候，彼此間於季節性變化的關刀溪森林生態系中具有一個良好的共生授粉關係。

關鍵詞：牛奶榕；牛奶榕小蜂；授粉；共生；關刀溪森林生態系。