國立臺灣大學生命科學院生態學與演化生物學研究所

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正榕與授粉小蜂的物候及族群互動的季節變異

Variation in the phenology and population interactions between *Ficus microcarpa* L. f. and its pollinating wasp, *Eupristina verticillata*

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本論文係楊惠雯君（R96B44009）在國立臺灣大學生態學與演化生物學研究所完成之碩士學位論文，於民國一百年二月十五日承下列考試委員審查通過及口試及格，特此證明

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中文摘要

榕果-榕小蜂的共生關係中，榕樹需仰賴其專一性的授粉蜂傳遞花粉，而授粉蜂也依賴榕果繁衍後代，如何將小蜂族群衍續，對榕樹而言是重要的課題。本研究以台北市的正榕 (*Ficus microcarpa*) 與其授粉蜂之間的物候模式來探討其如何適應季節變化明顯的環境。研究內容分為兩部份，第一部份調查榕果物候及授粉蜂的族群動態以探討環境因子－榕果產量－授粉蜂族群三者的關聯（第二章）。本研究選定國立台灣大學校園周圍的 29 棵正榕植株，自 2008 年 4 月至 2009 年 7 月進行約每週一次的野外調查。每次調查記錄榕果豐度並採集榕果，利用雌花期榕果內的小蜂估算授粉蜂族群量，最後探討氣象因子與各花期榕果量的關聯。結果發現正榕產果高峰主要在春季和夏季，冬季榕果產量十分稀少。正榕的開花物候與氣溫、全天空輻射及雨量皆顯著相關。授粉蜂的族群量在夏季達最高峰，秋季漸減。冬季榕果大多無法授粉，顯示冬季對授粉蜂會造成瓶頸效應，待來年春天時授粉蜂族群再次擴張。第二部份檢視花期不同步性的季節變異和授粉率的關係，並探討此現象在適應上扮演的角色（第三章）。利用第二章的榕果豐度資料，分別將株內不同步性、株間不同步性、族群不同步性量化，比較三者的季節變異；另外分析榕果自花授粉機會的指標──「株內雌雄花期重疊 (intra-tree sexual-phase overlap)」的頻率──在季節間的變異，以及表現此現象的植株在授粉蜂進駐率上是否與其他植株有差異。結果顯示，株內不同步性在春、夏季較高；株間不同步性在冬天較高；而族群不同步性無季節差異。株內雌雄花期重疊在夏季較常發生，授粉蜂進駐率在發生此現象的樹上並未顯著高於其他樹,顯示株內雌雄花期重疊，亦即使小蜂於株內傳播，並非正榕小蜂的渡冬方式。在冬天，正榕小蜂以蟲癭的方式渡過環境較差的日子，並在少數環境較好的日子仍可於株間傳播。此外正榕會連續性的雌花期榕果生產，在春季較常出現，延長雌花期的現象被認為可增加個體和族群的授粉率，本研究提供了此一假說的實際觀察。

關鍵字：正榕、正榕小蜂、物候、授粉生態、互利共生

Abstract

In the mutualistic relationship between fig and fig wasps, the *Ficus* trees are pollinated exclusively by their species-specific pollinating fig wasps. How to sustain the pollinator population is a crucial issue for *Ficus*. This study focused on the phenological patterns between these mutualistic species and explored the adaptive reproduction strategy of a *Ficus microcarpa* population in Taipei, where weather varies seasonally. The study was divided into two major parts: the first section focused on fig phenology and pollinator population dynamics (Chapter two). Field surveys were conducted on 29 *F. microcarpa* trees in one week intervals from April 2008 to July 2009. The number of syconia in each developmental phase was recorded. The number of foundresses inside receptive syconia were counted and used as an index of pollinator population size. The results showed that temperature, solar radiation and rainfall are positively correlated with syconia abundance. Syconia abundance was highest in spring and summer, and decreased to a very low level in winter. The pollinator population exhibited a similar trend but with greater fluctuation. It reached the greatest density in summer and dropped in fall. Receptive figs are poorly pollinated in winter, and thus pollinator population should suffer a bottleneck effect during this season. The pollinator population then recovered the following spring.

The second part of this study explored the pattern of flowering asynchrony and its relationship with pollination rates, and then discussed the potential adaptive reproduction strategy of *F microcarpa* (Chapter 3). I used the syconia abundance data recorded in chapter one to further quantify asynchrony at the intra-tree, inter-tree and population levels. The index for chance of self-pollination (frequency of "intra-tree sexual-phase overlap”) was also counted. In addition, the difference in pollinator colonization rate was tested between trees with sexual-phase overlap and trees without. The results showed that both intra-tree asynchrony and the frequency of intra-tree sexual phase overlap were higher in spring and summer. The pollinator colonization rate was slightly (but not significantly) higher for the trees presenting sexual-phase overlap. The phenomenon of successively (>3 weeks) producing female-phase syconia was more common in spring. Finally, the strategy for *F. microcarpa* to overcome harsh winters and the role of asynchrony in reproductive success were discussed.

Keywords: *Ficus microcarpa*, *Eupristina verticillata*, phenology, mutualism, pollination ecology

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Chapter 1: Grand Introduction

The genus *Ficus* (Moraceae) is one of the largest genera of woody angiosperm (Berg and Corner 2005) including about 750 species in diverse life-from (trees, shrubs, climbers, hemi-epiphyte or holo-epiphyte) occupying large variety of habitats (rainforest understories and canopies, savannahs, riversides, rocky surfaces), and distributed in tropics and subtropics worldwide (Berg 1989). They provide keystone resources in tropical forests (Kalko *et al.* 1996, Korine *et al.* 2000, Shanahan *et al.* 2001).

The fig inflorescence, called syconium, defines the genus *Ficus*. It's an enclosed urn-shaped structure with dozens to thousands of unisexual flowers inside (Tzeng 2004). The fig's pollen can only disperse by their pollinators (Hymenoptera: Agaonidae *sensu* Cruaud *et al.* 2009). The pollinators can exclusively oviposit their eggs in the fig ovules. Half of the fig species are monoecious while others are (functional) dioecious (Berg 1989). Some agaonids wasps actively pollinate the fig and others passively (Kjellberg *et al.* 2001, Cook *et al.* 2004). Besides, the syconia also shelter several non-pollinating fig wasps (NPFW). These non-pollinating fig wasps can be classified into gallers (induce the ovules into galls independently), inquilines (live in the galls induced by other fig wasps but were nutritionally independent of the host larvae) or parasitoids (feed on the host larvae and kill the hosts in the end). Due to its unique structure and complex community, *Ficus* and its fig wasps are striking example of ecology and evolutionary theories such as coevolution theories (Machado *et al.* 2001, Jousselin *et al.* 2008, Rønsted *et al.* 2008), evolution of breeding system (Kjellberg and Maurice 1989, Kerdelhué and Rasplus 1996, Kameyama *et al.* 1999, Harrison and Yamamura 2003, Dunn *et al.* 2008), insect communities (Compton *et al.* 1994, Kerdelhué *et al.* 2000, Peng *et al.* 2005, Marussich and Machado 2007, Tzeng *et al.* 2008), sex-ratio theories (Hamilton 1967, Moore *et al.* 2005, Pereira and do Prado 2005a) , intra-sex competition (Moore and Greeff 2003, Zhen *et al.* 2004, Pereira and do Prado 2005b), and finally the important role of the third layer of insect interaction via the ant species (Schatz and Hossaert-McKey 2003, Schatz *et al.* 2006).

This mutualistic relationship arose in Africa 60 to 90 million years ago (Machado *et al.* 2001, Rønsted *et al.* 2005). This genus has then colonized the five continents (Berg 1989). One of the major challenges when colonizing to higher latitude was the adaptation to the seasonal climates. Due to the short lifespan of winged pollinators (few hours to two days) (Kjellberg *et al.* 1988, Wang *et al.* 2009) and synchronous crops the fig trees exhibit, continuous fig production at the population level is necessary to sustain the wasp population. However, in the seasonal areas, fig production declined in the unfavorable seasons (Kjellberg and Maurice 1989, Spencer *et al.* 1996, Chen *et al.* 2004, Tzeng *et al.* 2006) . Thus, the maintenance of fig wasp population is a crucial problem for both the fig and pollinators. This issue has attracted scholars' attention for more than three decades.

Phenology is the study of periodic plant and animal life cycle events and how these are influenced by seasonal and climatic interannual variations. The five growing stages (Table 1-1) defined by Galil and Eisikowitch (1968) laid a groundwork for studies in fig phenology. Early researches are more qualitative, describing presence or absence of figs and the correspondence with temperature and rainfall, and discussed the importance of inter-tree asynchrony to the fig wasp population (e.g. Corlett 1984, Kjellberg and Maurice 1989, Spencer *et al.* 1996). Recent studies use statistical analysis finding correlation between meteorological variables and quantity of developing phases (e.g. Harrison *et al.* 2000, Yeo and Tan 2009). Besides, many studies from China took the population dynamic of pollinator or non-pollinators into account, and thus drawing larger pictures on the mutualist system. Studies on *Ficus* phenology not only provide insights on the strategy that the figs evolved to adapt local environment, but also provides valuable information to further studies of frugivorous species (Kalko *et al.* 1996, Shanahan *et al.* 2001). As a keystone resource, fig phenology is also linked to the possible impact of climate change on tropic forests (Harrison 2001).

Among all the *Ficus* species, *F. microcarpa* L. f. (subgenus *Urostigma*, section Conosycea) is one of the most widely distributed. It is native to the Eastern and Southern China, Ryukyu Islands (Japan), Indo-China Peninsula, India, Sri Lanka, Papua New Guinea to Northeastern Australia (Chew 1989, Tzeng 2004, Berg and Corner 2005). In Chinese it's called "正榕", or "細葉榕". *Ficus microcarpa* is pollinated by a species-specific pollinating wasp *Eupristina verticillata* Waterston (Waterston 1921). The syconia of *F. microcarpa* shelter more than 20 described non-pollinating fig wasps (Chen *et al.* 1999, Feng and Huang 2010). Its fruits were consumed by more than 200 frugivorous species. Due to its hardness, beauty, and for religious reasons it is widely cultivated in urban areas near their native areas. Besides, *F. microcarpa* has been introduced to tropical and subtropical cities worldwide, including Brisbane, Hawaii, Florida, Mexico and Colombia, Bermuda and Brazil (McKey 1989, McPherson 2005b). In some of these areas, the pollinating fig wasps introduced intentionally or unintentionally have established their populations. In Hawaii and Bermuda, *F. microcarpa* have distinctly weedy tendencies and are likely to invade native plants communities (McKey 1989).

In Taiwan, *F. microcarpa* is a very common roadside tree, and was regarded as "city tree" of Taipei. The first study of its phenology was performed by Hsieh (1992). Hsieh surveyed 84 *F. microcarpa* trees in National Taiwan University campus. Thereafter, Chen *et al.* (2004) surveyed 35 trees of them for six-and-a-half years. Both these studies showed that there are two main fig productions every year: in spring and summer. During winter, only few or even no trees were bearing figs showing the bottleneck undergone by pollinator populations. The maintenance of the pollinator in winter and recovery of the wasp population in spring should be a crucial problem for the *Ficus* trees. Therefore, the first goal in my thesis is to further investigate the phenology of *F. microcarpa* as well as the dynamic of *Eupristina verticillata* populations in Taipei (Chapter 2).

Besides, *Ficus* are well known for its highly intra-tree synchrony. However, different level of intra-tree asynchrony was also noted in some *Ficus* species. Asynchrony of fig development on the same tree can increase the reproductive rate of fig wasps as well as the chance of self-pollination. This phenomenon was interpreted as an important adaptive trait for seasonal area (Janzen 1979). Alternative strategy for adapting seasonality was proposed as lengthened duration of receptive phase by Bronstein and Patel (1992). *Ficus microcarpa* is one of species that have enough individual-level asynchrony to permit self-pollination (McPherson 2005a, Lin *et al.* 2008). Bronstein (1989) proposed that the crop asynchrony may in part contribute to the broad distribution or weedy tendency of *F. microcarpa*. Thus, the second goal of this thesis is to investigate the variation in the degree of asynchrony, self-pollination rate and the wasp colonization rate, and exploring the interrelationship among these three variables in order to discuss the potential benefit/cost of this phenology pattern (Chapter 3).

Tables

Table 1-1. Developmental phases of monoecious figs and corresponding pollinator life stage (modified from Galil and Eisikowitch 1967)

Developmental phase	Characteristic of syconia and relation to fig wasp
Phase A Pre-female	Syconia initiate, enlarge and immature unisexual flowers develop.
Phase B Female	Female flower reach maturity and the syconia become receptive. The bracts at the ostiole withdraw slightly so that the pollen-carrying female pollinators can pass through. The female pollinators which have recently emerged from older syconia penetrate the ostiole, losing their antennae and wings on the way inside. After entering the fig, the female pollinators (foundresses) oviposit into some of the ovules. The other female flowers are pollinated by the pollen on foundress’s body. Foundress then dies inside the syconia.
Phase C Interfloral phase	The pollinated ovules develop into seeds and the oviposited ovules develop into galls, each harboring the wasps’ larvae. This period lasts weeks to months.
Phase D Male phase	The syconia become soft. The male flowers and fig wasps mature simultaneously. Male wasps hatched first, mate with the female wasps. After copulation, male wasps tunnel the fig wall together and finished their life cycle. Female wasps winged soon after. They crawl out of the tunnel with pollen loaded on their bodies in search for the next B-phase syconia.
Phase E Ripe phase	The syconia and seeds ripen, soften, attract frugivores—who disperse seeds through their feces.

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Chapter 2: Phenology of *Ficus microcarpa* L. f. and its pollinator dynamics in Taipei, Taiwan

Abstract

This study focused on the phenology and pollinating wasp dynamics of a *Ficus microcarpa* population in Taipei. From April 2008 to July 2009, field surveys were conducted to collect samples and record the abundance of syconia in each developmental phase. The number of pollinators colonizing each syconium was examined, and used as an indicator of pollinator population. Additionally, the correlation between meteorological factors and the abundance of each developmental phase was tested. The results showed that *F. microcarpa* syconia were present year round but exhibited great seasonal variation. Two main peaks of syconia abundance were observed in spring and summer respectively. Temperature and global solar radiation were the factors most significantly correlated with syconia abundance, and the latter factor played an important role in initiating syconia growth. Rainfall was positively correlated with female and interfloral phase, and with male phase following a one-week delay. Pollinator abundance showed a small springtime increase, reached the highest level in summer, and later declined in winter. Therefore, the pollinator population should suffer a bottleneck effect in winter and recover the following spring. Finally, geographical and temporal variation in *F. microcarpa* phenology and its pollinator population dynamics were explored and discussed through a comparison with previous studies.

Introduction

More than 750 species worldwide belong to the genus *Ficus*; half of them are monoecious while others are dioecious (Berg and Corner 2005). They are considered a keystone resource for some tropical and neotropical forests (Lambert and Marshall 1991, Korine *et al.* 2000, Shanahan *et al.* 2001). They are also widely cultivated in tropical and subtropical cities and provide food resources and/or shelters for urban wildlife (Figueiredo *et al.* 1995). However, some of the introduced trees have invaded local natural communities (McKey 1989).

Ficus reproduction obligately depends on pollinating fig wasps (Hymenoptera: Agaonidae sensu Cruaud *et al.* 2009). A fig (syconium) is an enclosed urn-shaped inflorescence with dozens to thousands of unisexual flowers inside. Monoecious figs have functional male and female flowers inside the same syconium; but they mature at different rates. The only entrance to the syconium lumen is a narrow, bract-surrounded channel, called an ostiole. Each ostiole has evolved to only allow species-specific agaonid wasps entrance (Wiebes 1979, van Noort and Compton 1996). Similarly, the female agaoid wasps can only lay their eggs in these fig ovules. Thus, the reproductive success of both species is dependent on this mutualistic relationship. The system of fig and fig wasp mutualism is a striking example of evolutionary theories on co-evolution, and has received research attention for over three decades (Janzen 1979, Kjellberg *et al.* 2005, Herre *et al.* 2008).

The development of a typical monoecious fig is divided into five phases (Galil and Eisikowitch 1968). In the pre-female phase (A phase), the fig buds emerge, enlarge, and immature female flowers develop. Once the female flowers mature, the syconia go into their female phase (B phase), also known as the receptive phase. During this period, figs emit volatile compounds to attract pollinators (Hossaert-McKey *et al.* 1994, Grison-Pige *et al.* 2002). Pollen-bearing female fig wasps (foundresses) come straggling through the bracts, losing their wings and antennae on their way inside. After entering the fig, the wasps pollinate the flowers and oviposit their eggs in some of the ovules. Several hours to days after the first visit (Chen *et al.* 2004, Wang *et al.* 2009), the interfloral phase (C phase) begins. The pollinated ovules develop into seeds, and the oviposited ovules develop into galls, with a wasp larva growing inside. When both male flowers and wasps are mature the male phase (D phase) begins. Male wasps exit their galls, looking for female wasps to mate with. After copulation, the males dig a tunnel through the fig wall together (Kjellberg *et al.* 2005). Soon after, the female wasps hatch and crawl out of the fig with pollen loaded on their bodies through this channel in search for another receptive fig. The seeds then ripen and the fig walls become thick and soft in the following ripe phase (E phase). In the case of *F. microcarpa*, the whole fig might turn red, yellow or purple to attract frugivores--who disperse seeds through their feces (Kjellberg *et al.* 2005).

To sustain the pollinator population fig trees produce asynchronous crops among trees (Bronstein *et al.* 1990). This cooperation allows pollinators to migrate among trees. Most monoecious fig species present intra-tree synchronization (Hill 1967, Milton *et al.* 1982, Zhang *et al.* 2008), which is thought to prevent self pollination (Janzen 1979, but see Hossaert-McKey and Bronstein 2001). The female winged wasps live from a few hours to two days (Kjellberg *et al.* 1988, Wang *et al.* 2009). They have to find a receptive fig tree within their short lifespan. Thus, continuous fig production at the population level is a crucial problem for the fitness of both the mutualists.

Environmental variations, especially meteorological factors, play a determining role in syconia production levels. Harsh environmental conditions (ex. low temperature, dry season, etc.) dramatically decrease syconia production (Kjellberg and Maurice 1989, Harrison *et al.* 2000, Chen *et al.* 2004, Tzeng *et al.* 2006). On these occasions, pollinating wasp populations might face a bottleneck or even a local extinction (Harrison 2001). To what extent do wasp populations fluctuate with the variation of syconia abundance? Can the wasp population be maintained during harsh periods? If yes, what kind of strategy has been taken? If not, how fast does the population recover during favorable conditions?

The answers to the above questions can be explored through study of fig phenology and the population dynamics of a widely distributed species. Phenological studies conducted in different locations provide an opportunity for a comparison in similar habitats but different climatic zones (Corlett 2006). Long-term phenological comparison can further provides insight on how age differences impact the reproductive ability of trees.

Among all the *Ficus* species, *F. microcarpa* is one of the most widely cultivated urban figs (McKey 1989). Since 1960's its phenology has been documented in at least six locations: Hong Kong (Hill 1967), Singapore (Corlett 1984), Brazil (Figueiredo *et al.* 1995), Taipei (Hsieh 1992, Chen *et al.* 2004), Brisbane (McPherson 2005a), and Guangzhou (Lin *et al.* 2008). These six study sites cover tropical and subtropical areas. Furthermore, the phenology study at Taipei site even has been documented since 1990 (Hsieh 1992) and lasted for 10 years (Chen *et al.* 2004). From these studies, phenological pattern of *F. microcarpa* showed no seasonality in equatorial Singapore (Corlett 1984). Subtropical areas, including Hong Kong, Guangzhou (China), and Taipei

(Taiwan), exhibit seasonal variations (Table 2-2). After six-and-a-half-year survey, Chen *et al.* (2004) found an often decline in syconia production in Taipei in early winter. They also found that pollinator dynamics fluctuated similarly every year. However, the detailed growth and decline of wasp population associated with the fig phenology have not been examined.

Furthermore, the influence of meteorological factors to syconia production can help understanding the adaptation of a *Ficus* population in a habitat. Most previous phenological research on *Ficus* focused primarily on the influence of temperature (Patel 1996, Spencer *et al.* 1996, Chen *et al.* 2004, Tzeng *et al.* 2005, Yeo and Tan 2009) and rainfall (Spencer *et al.* 1996, Harrison 2000, Yeo and Tan 2009). However, van Schaik (1986) demonstrated the importance of solar radiation to plant phenology. It is a reasonable hypothesis given that photosynthesis is powered by the energy of sunlight (Sakai *et al.* 1999). Studies also reported correlation between fig phenology and solar energies (Tzeng *et al.* 2004, Yeo and Tan 2009). To what extent does these variables affect the syconia production?

In this study, I conducted a 14 month survey on fig phenology and foundress dynamics of *Ficus microcarpa* in Taipei. The aims of this study were to (1) update current knowledge on phenology of the same *F. microcarpa* population in Taipei as previous works 10 years ago, (2) investigate the dynamic of pollinating fig wasp populations and its relationship with host phenology.

Materials and Methods

Study Species

Ficus microcarpa L. f. (subgenus *Urostigma,* section Conosycea) is a large evergreen, hemi-epiphytic monoecious tree with abundant aerial roots. Leaves are arranged alternately, lamina elliptic to broadly elliptic. Mature leaves are approximately 8-13 cm. Syconia are axillary, singly or in pairs (Hill 1967, Tzeng 2004, Berg and Corner 2005). Ripe syconia measure about 6-10 mm in diameter, turning from reddish green to pink or purple and are consumed by more than 200 frugivorous species (Shanahan *et al.* 2001). *F. microcarpa* is natively distributed in Eastern and Southern China, the Ryukyu Islands (Japan), Indo-China Peninsula, India, Sri Lanka, Papua New Guinea to Northern and Eastern Australia (Berg and Corner 2005). This species is also native to Taiwan and is a widely cultivated roadside tree in all urban areas. *F. microcarpa* is pollinated by a species-specific pollinating wasp -*Eupristina verticillata* Waterston (Waterston 1921).

Study site and climate

For the phenological study, I surveyed 29 trees along a road about 250 m long near the National Taiwan University campus in Taipei, Taiwan (25°00’43’’N, 121°32’25’’; and 21 m above sea level). This study used the same site as the previous study by Chen *et al.* (2004). Chen *et al.*'s study examined 35 *F. microcarpa* trees, but six of them have since been cut or replaced by other tree species for unknown reasons. These trees are more than 25 years old, with an average height of 7-14 m. These trees are pruned once or twice a year in spring or autumn.

Taipei has a humid subtropical climate. February to October is classified as a very moist period. November to January is classified as a relative moist period (Figure 2-1). The average annual temperature is 22.7 ℃, with an average temperature of 29.4 ℃ in summer and a winter mean of 18.1 ℃ (Taipei meteorological station in Central Weather Bureau; www.cwb.gov.tw). Summers are humid and accompanied by occasional rainstorms and typhoons; while winters are short and mild.

Definitions

A crop is defined as a group of syconia from initiation to maturation. The period that an individual tree does not bear any syconia is called a flowering interval. Four seasons and the corresponding month are: spring: March to May, summer: June to August, fall: September to November, and winter: December to February.

Phenological censuses

Phenological censuses were conducted from May 2008 to July 2009 with 8.2±3.2 (mean±SD) day intervals. During each survey, four units of branch from each tree were cut and sampled at height of two to five meters; and the number of syconia in each phase was recorded. One unit of branch is about 30-50 cm long, with 5-7 twigs. Branches were taken from four different ordinal directions because preliminary observations have shown that different growing stages could be found on different parts of the tree crown.

Meteorological factors

Meteorological variables with a potential influence on syconia production were considered in this study: temperature, rainfall, and global solar radiation. I obtain daily data of the three meteorological factors: average temperature, rainfall, and global solar radiation from the Taipei meteorological station, located 3.7 km away from the study site. Daily temperatures of the days between two surveys were taken average. Daily rainfalls and global solar radiations during two surveys were summed. Kendall's correlation tests were performed for each meteorological variable and the number of syconia in each phase respectively. The correlation between meteorological variables and total syconia quantity was also tested. If the correlation was not significant, a delayed correlations of up to four weeks were then performed.

Indexes of pollinating wasp population

The syconia are regarded as natural bio-traps for pollinators. The number of foundresses in each syconium is used as an indicator of the pollinating wasp population when the syconia were in receiving phase. This indicator is reliable considering based on two assumption (1) I assume that foundress number of a syconium is positively correlated with the wasp cloud in the surrounding environment at the time that the focal syconium is receiving, and (2) although some foundresses could exit from a syconium they entered (Gibernau *et al.* 1996, Chen *et al.* 2001, Appendix I), the vast majority of the observed foundresses should be positively correlated with the actual number of foundresses that had entered the sycona.

Syconia on the sampled branches were taken and cut open for counting foundress number under microscope. Phases of the sampled syconia were also recorded. To ensure all potential pollinators had entered, only syconia in late receptive phase or early interfloral phase were analyzed. Foundresses in 7,291 syconia from 786 branches (28 trees) were counted during the study period.

Several measures of pollinator abundance were calculated by the unit of the same branch:

(1) The occupation rate: the proportion of syconia entered by foundress.

$$\text{Occupation rate} = \frac{\text{number of syconia with pollinators}}{\text{number of total syconia}}$$

Note: this indicator was prone to underestimate the actual proportion of syconia visited by foundresses since the foundresses re-emerged (Gibernau *et al.*, 1996, Appendix I). However, it was positively correlated to actual proportion of visited syconia (Appendix I).

(2) Crowdedness index: mean number of foundresses in occupied syconia on a given branch.

$$\text{Crowdedness index} = \frac{\text{total number of foundresses}}{\text{number of syconia with foundress}}$$

(3) Average foundress number: number of foundresses divided by total sampled syconia.

$$\text{Average foundress number} = \frac{\text{total number of foundresses}}{\text{number of total syconia}}$$

In the analysis for weekly dynamics of the tree variables, interfloral-phase syconia (C phase) were traced back to the week that the focal tree was in receptivity using the phenological data. Foundress data of syconia in the receptive phase during the same week were pooled together.

(4) Pollinator population size: To investigate the approximate size of the pollinator population, this study used the information from above indices as well as the

total syconia quantity. Pollinator population size was estimated as:

$$\text{Pollinator population size} = \sum_{j=1}^{29} \sum_{i=1}^{4} b_{ij} f_{ij} a_{ij}$$

where i represents each side of the tree crown, j represents number of the tree, b_{ij} is the number of syconia-bearing branches at the tree side i, f_{ij} is the number of syconia in the late receptive phase (B phase) or early interfloral phase (C phase) on the day of collection, and a_{ij} is the average number of foundress on the branch. Sometimes, samples for foundress were not taken from one to three sides of the tree crown. Then a_{ij} for these sides were replaced by the average foundress number of all other sides on the same tree. The number of syconia-bearing branches (b_{ij}) was obtained by multiplying the total number of branches on the tree by the proportion of branches with syconia recorded during surveys. The total number of branches was counted using photos taken on November 26, 2010 from one to two sides of the tree. Finally, all 29 concurrently receptive trees were summed together.

Results

Phenology of syconia production

A total of 158 crops were recorded from 29 fig trees. Individual trees produce 5.4±2.7 (mean±SD) crops during the period of 14 month survey, and thus the annual mean crop number was adjusted to 4.7 crops (Figure 2-3). The productivity among trees varied greatly: one tree produced no crops, 50% of them produced seven or eight crops, and 14% of then produced nine crops.

Syconia of *Ficus microcarpa* were present year round on the sampled trees at the population level during observation. But the quantity of syconia varies largely among seasons. Two main syconia production peaks were observed during March to June, 2009 and July to November, 2008 respectively (Figure 2-4). Figure 2-3 demonstrates a trend for individual trees to produce crops during mid-February to May, 2009 and July to October, 2008. However, total crop yield peaked between March to June and July to October (Figure 2-4). The majority of trees started producing their first crop at the end of winter (mid-February), and ceased production before May. During this period five trees started growing a new generation of crops before the previous one had reached maturity. Duration of syconia production lasted four to twelve weeks. Syconia in the pre-female or female phase (A or B phase) were observed over several successive surveys on the same tree in 19 individuals. This indicates continuous production of new syconia for several weeks. Continuous production within the same tree, and the synchronized crop production among different tree accounts for an immense number of pre-female syconia in this period (Figure 2-3). Following spring crop production, all except one tree went into a flowering interval which lasted two to four weeks. The first summer crops started in the second and first week of June in 2008 and 2009 respectively; and the total syconia quantity reaches seasonal maximum at the end of July, 2008. Syconia initiation demonstrated a monthly cyclic undulation trend between July and September, 2008 (Figure 2-4). Before the end of fall, each tree produced one to six crops; at which point the majority of trees went into a long flowering interval lasting two to three month after the fall crops. Syconia production was lowest in December, 2008 and January, 2009. Only two trees in the study site produced crops during this period. The other individuals started the spring crop for the following year when the temperature increased in spring (Figure 2-2, 2-3).

Correlation between syconia abundance and meteorological factors

The number of syconia in each phase showed a significant positive correlation with temperature except for the pre-female phase (Table 2-1). Instead, the number of pre-female syconia only showed a correlation with global solar radiation. Global solar radiation was also positively correlated with abundance of interfloral phase, male phase, and mature phase (Table 2-1). Abundance of female phase and interfloral phase were positively correlated with rainfall. Number of male phase syconia was positively correlated with rainfall after one-week delay. Total number of syconia was correlated with temperature, rainfall and global solar radiation.

Pollinator abundance

Pollinator abundance varied greatly among weeks. Average foundress number varied from zero to six during the survey period. Most syconia contained one to two foundresses; although 12 foundresses in a single syconium were observed once. Occupation rates and crowdedness indexes were high in July when summer crop begins

(Figure 2-5). Average occupation rate was 0.8 and crowdedness indexes are higher than two. This means there were more than two foundresses per syconium. Estimated pollinator population size larger than 30,000 in July 2008; but there was a drastic decline in August. Occupation rates recovered to the previous level observed in July during September and October, but the crowdedness indexes are lower (Figure 2-5). Pollinator indexes were low in November. During this period, pollinator population size was only one-tenth of the July level. Production of female phase was intermittent from December to February and thus resulted in lacks of data in some weeks. Based on available data, occupation rates at this period were low (Figure 2-5). Only one tree (Number 19) that produced receptive syconia in January was pollinated successfully. The situation improved in February, but varied among trees. Estimated pollinator population size was less than 200 during this period. When the first spring crops began the male phase from March to May, occupation rate increased steadily (Figure 2-5). However the crowdedness index remained at one. This indicated that the number of receiving syconia was larger than the pollinator population. Occupation rate decreased drastically in June, although there were some male-phase syconia in the sampling site. Occupation rate, crowdedness index, and estimated population size increased drastically in July. This pattern was observed in both years, revealing that this might not be a sampling error (Figure 2-6).

Average foundress number was positively correlated with the male-phase syconia abundance (Kendall’s rank correlation test, $p < 0.0001$, $\tau = 0.44$). Most syconia that begin the receptive phase in summer or fall were contained a relatively high average foundress number. This corresponds to high abundance of male-phase syconia over the same period. Whereas the male-phase syconia abundance during winter and spring was lower. Thus fewer receptive syconia were pollinated (Figure 2-6). However, some syconia had a higher foundress number even though the male-phase syconia abundance in the sampling site was low. This indicates pollinator migration from outside the local population. These migration events happened at the start of summer crop production in 2008, and also in January of 2009.

Discussion

Fig phenology: Correlation to meteorological factors

As in many other studies, temperature played a determinant role in fig phenology: the number of soconia in each phase showed a significant positive correlation with temperature except for the pre-female phase. Temperature influences the plant metabolism rate and also reflects energy from environment (Sakai *et al.* 1999). Higher syconia production in warmer seasons had been observed in previous studies on *F. microcarpa* in Taipei (Hsieh 1992, Chen *et al.* 2004), as well as other *Ficus* species in seasonal areas (Patel 1996, Spencer *et al.* 1996, Tzeng *et al.* 2003, Tzeng *et al.* 2004).

While most phases were correlated with temperature, pre-female phase (A phase) was only correlated with global solar radiation. This indicates that an increase in solar energy is the environmental cue directly responsible for syconia initiation in *F. microcarpa*. Tzeng *et al.* (2004) also found a positive correlation between initiation of female *F. erecta* var. *beecheyana* syconia and net radiation in Guandaushi Forest Station, Taiwan. Other studies about impact of solar energy to *Ficus* are rare. In fact, increase in solar energy as a possible environmental cue triggering flowering has been documented in other plant species as well (Ng 1977, van Schaik 1986). This phenomenon is reasonable since the accumulation of dry matters after photosynthesis can provide resources for fruit bearing (Sakai *et al.* 1999).

Rainfall is also important for syconia development (C phase). Many studies also reported the correlation of total syconia with rainfall (Patel 1996, Spencer *et al.* 1996, Tzeng *et al.* 2003). During interfloral phase, development of seeds and wasps might results in an energy sink for the fig tree (Ho 2009). Warm and moist conditions are thus favorable for *F. microcarpa* in Taipei. However, negative correlation between temperature and *F. altissima* syconia production was recorded in Xishuangbanna, China (Zhang *et al.* 2008). Fig production of some other *Ficus* populations was also negative correlated with rainfall (Corlett 1993, Harrison 2000). This indicates under different selection pressures, different species and populations might have evolved alternative phenological strategies (Tzeng *et al.* 2005, Zhang *et al.* 2008).

There was a correlation between the quantity of male phase (D phase) syconia and rainfall after a one-week delay. Most studies referring to this issue showed no direct correlation between male phase and rainfall (Tzeng *et al.* 2003, Tzeng *et al.* 2005, Tzeng *et al.* 2006, Huang 2007, Ho 2009). Another study showed that the peaks of male syconia production and rainfall were staggered (Chen 1998). *Ficus* might avoid growing into male phase during heavy rainfall to benefit wasp dispersal (Tzeng, personal communication). This delay is also advantageous for *F. microcarpa* seed dispersal. Mature phase occurs only one or two days after the male phase and ends quickly. If mature phase were to overlap with a period of heavy rainfall, fewer seed dispersers would be present.

This study found a positive correlation between receptive syconia and rainfall. Response of receptive phase to rainfall seems disadvantageous for pollinator arrival. However, unpollinated syconia remain receptive for one to two weeks (Khadari *et al.* 1995, Chen *et al.* 2004). Receptive syconia might be able to receive pollinator from male-phase syconia after the rain. It might be too presumptive to say that receptive syconia grow in preparation for male-phase syconia. However, a positive correlation between female and male phases was observed in a larger *F. microcarpa* population in Taipei (Hsieh 1992). An overlap between peak productions of male- and female-phase syconia is well documented for certain dioecious *Ficus* species in seasonal areas. Bronstein *et al.* (1990) used simulation models on syconia flowering phenology and subsequently claimed continuous presence of receptive syconia at the population level is necessary to maintain the wasp population. However, previous findings (as well as the present study) showed that some mechanisms might have evolved allowing the two critical phases to have the same rhythm. This reduced both the pollen waste and abortion probability of receptive syconia. It also decreases the actual critical population size (i.e. the number of fig trees needed to sustain a population, proposed by Bronstein *et al.* 1990).

Difference from previous studies in Taipei

The general pattern of *F. microcarpa* syconia production in Taipei is similar with the pattern observed in a previous study of the same sampling site (Chen *et al.* 2004). In both studies, main production occurred in March to June and July to November. However, one major difference from this previous study is the disappearance of the “fig gap”. In Chen *et alter*’s study, there was usually a period, noted as a “fig gap”, that no syconia on the sampled trees were found (Chen *et al.* 2004). This period began in late October or early November and lasted almost two month. This study found syconia presence all year-round. The potential explanations for this change could be (1) higher productivity with age, (2) global warming, and (3) inter-annual variation.

The productivity of a tree may increase with its age. On average higher crop yields and fewer dormant trees were observed in my survey; and some trees that never bore syconia during the previous survey produced crops in 2008 and 2009 (Chen, personal communication). Harrison (2000) found a positive correlation between syconia production and d.b.h. (diameter at breath height) in male *F. fulva* trees. Harrison's result agreed with the age effect on productivity since d.b.h. is an estimation to the trees age (White 1998).

The impact of increased temperature cannot be determined because of the role that age may play on productivity level. Inter-annual variation also exists during Chen *et al*'s survey; they recorded the fig-gap disappearance in one of the years Chen *et al.* concluded the disappearance was caused by warmer temperatures due to El Niño. However, a strong El Niño event occurred in 1997 to 1998 rather than 1996. There were no significant differences in monthly mean temperature between 1996 and the other five years for either the 12 month period or the six months in fall and winter period (paired t-test, $p = 0.415$ for 12 months and $p = 0.984$ for six months, meteorological data from Central Weather Bureau). In fact, the other earlier study on 84 *F. microcarpa* trees in Taipei (Hsieh 1992) also found no gap in syconia production, revealing low winter temperature in Taipei might not be a definite restriction for *F. microcarpa* to grow syconia in the population level.

Geographical comparison

Some similarities on fig phenology of *Ficus microcarpa* can be found when comparing studies in different geographical areas. They are the immense and synchronous spring syconia initiation, the production decline of each phase after spring crop, and a second production peak in July thereafter. The phenomenon of inter-tree synchronous initiation in spring has been recorded on *F. microcarpa* in Hong Kong (Hill

1967) and Brisbane (McPherson 2005a). In Hong Kong, all the observed 20 trees produced a very large crop in April and May (Hill 1967). In Brisbane, although there were marginal differences of female-phase syconia production among seasons, a late spring peak was observed (McPherson 2005a).

This immense production of receptive syconia in spring might seem like a waste of resource because the reduced wasp population after winter could limit pollination success. However, once successfully entering the syconium, the first generation of wasp offspring has a high likelihood of pollinating another syconium. Seven out of eighteen (38%) of the first spring crops went into their male phase during March to April (Figure 2-3). As previously mentioned, the number of receptive syconia is greater than the number of pollinators in this time (occupation rate increased steadily, but the crowdedness index remained at one). This implies that the first generation of wasp offspring has a high likelihood of pollinating another syconium. Thus, the first crop in spring may have higher fitness in their male function.

Pollinator migration

There is a high correlation between average foundress number and abundance of male-phase syconia in the study site (Figure 2-6). This suggests that receptive syconia were predominantly occupied by foundresses from the local wasp population. This observation may seem to contradict current knowledge that monoecious pollinating fig wasps migrate over long distances (Gardner and Early 1996, Harrison 2003, Harrison and Rasplus 2006). A possible explanation is that although pollinating fig wasps are capable of long-distance flight, they prefer to enter syconia more proximate to their natal tree (Kjellberg *et al.* 1988).

In the correlation between average foundress number and male syconia quantity, there are three weeks in which male syconia quantity is low but average foundress number is high. This reveals that the pollinators migrate from trees outside of the sampling area.

Pollinator abundance and the recovery rate

During the study period the pollinator population in Taipei declined in winter and subsequently recovered in spring. Previous studies on foundress number also observed an annual pattern of winter population decline followed by a sping recovery (Chen *et al.* 2004). Reduced availability of crops in winter may lead to a bottleneck effect on the local pollinator population. However, pollinator population recovers fast after the winter decline. On average, one foundress can have 20-80 offspring (Chen 2001). Pollinator population can grow exponentially if there is an abundance of receptive syconia are abundant. The continuous production of crops at the population level in spring provides favorable condition for population growth.

To maintain the pollinator population, *Ficus* populations are under selection pressure to produce few crops in unfavorable seasons. However, crops are less likely to encounter pollinators and thus less likely to be pollinated during colder periods. In my survey, among the receptive syconia collected from four weeks during December and January, only syconia from one of the weeks were pollinated (Figure 2-5). Individuals producing winter crops appear to be unfavorable. However, if these syconia were pollinated, wasp offspring had a high chance of successfully colonizing new patches since an immense number of receptive syconia are produced each spring. Trees that grow winter crops will gain fitness provided there is a sufficient number of receptive syconia the following spring to offset the risk of unpollinated in winter. These individuals play a key role in sustaining the pollinator population.

In this study, only two individuals produced winter crops; one of them produced crops almost all year-round. Continuous production of syconia by individual trees throughout the year was also observed in Hong Kong and Guangzhou (Hill 1967, Lin *et al.* 2008). This phenomenon exists naturally in the *F. microcarpa* population rather than as a consequence of artificial selection in agriculture. However, this phenotype may be more common in urban environments as cultivated *F. microcarpa* may benefit from more available resources (ex. less soil competition and higher illumination, Ho 2009). This phenological adaptive mechanism was seen in dioecious syconia, ex *F. carica* (Kjellberg and Maurice 1989) and *F. erecta* var. *beecheyana* (Tzeng *et al.* 2006).

Through human cultivations, *F. microcarpa* has been widely introduced to Hawaii, Central Australia, and America, and has become an invasive weed to some of the natural communities (McKey 1989). McPherson's (McPherson 2005b) study in Brisbane revealed a possible pattern in the early stages of new colonization: First the local fig tree population increased through occasional pollinator irruptions followed by a local extinction (McPherson 2005b). Once a critical population size is achieved, pollinator population can persist throughout the year, or even expand to other habitats. This present study gave a closer look on population expansion within seasons. *Ficus microcarpa* phenological traits as well as the reproductive potential of their respective pollinators have additive effects on the fitness of both the mutualists. This might be one of the reasons that made these two species successful in many places around the world.

Tables

Table 2-1. Correlations between the number of syconia of five developmental phases of *Ficus microcarpa* and the meteorological factors between two surveys, including mean temperature, total rainfall, total sunshine and total solar radiation in Taipei, Taiwan from April 28, 2008 to July 5, 2009.

Phase		Temperature (°C)	Rainfall (mm)	Global solar radiation (MJ/m^2)
Pre-female (A)	tau	0.128	0.067	**0.191**
	p-value	0.176	0.482	**0.044**
Female (B)	tau	**0.308**	**0.190**	0.146
	p-value	**0.001**	**0.046**	0.124
Interfloral (C)	tau	**0.279**	**0.275**	**0.249**
	p-value	**0.003**	**0.003**	**0.008**
Male (D)	tau	**0.279**	**0.194**	**0.322**
	p-value	**0.003**	**0.041**	**<0.001**
			(one-week delay)	
Mature (E)	tau	**0.350**	0.070	**0.329**
	p-value	**<0.001**	0.469	**<0.001**
Total syconia	tau	**0.002**	**0.008**	**0.003**
	p-value	**0.296**	**0.251**	**0.278**

Table 2-2. Phenology studies on *F. microcarpa*.

Study site	Study year (duration)	Number of trees	Phenology studied	Survey interval	Seasonality	Crops produced by a tree per year	Crop length	Reference
Hong Kong	Jan.-Nov. 1964 (11 months)	20	Leaf, fig	15-30 days	Continuous production by species as a hole and by many individual	1-5 crops, most 3-4	1-4 months	Hill 1967
Singapore	Oct. 1982-Feb. 1984 (16 months)	8	Leaf	7-17 days	No clear pattern	2-6 crops (mean 4.4)	30 days	Corlett 1984
Taipei (Taiwan)	Jan. 1991-Feb. 1992 (14 months)	84	Fig	7-10 days	Continuous production with main peaks in Apr.-Jun. and Jul.-Sep.	0-4 crops, most 2-3	26 days in Jun.	Hsieh 1992
Sao Carlos (Brazil)	Mar. 1991-Feb. 1992 (12months)	19	Fig, leaf, foundress	Twice a month	Continuous production syconia and leaf production were sequentially related	2.26±0.81 crops (mean±SD)	110.75 days	Figueiredo *et al.* 1995
Taipei (Taiwan)	Aug. 1992-Nov. 1998 (76months)	35	Fig, leaf, foundress	7 days	2 gaps: late Apr. to early May. lasting 3 weeks, late Oct. or Nov. lasting 5.8 weeks. Possitive correlation with temparature but rainfall	2.1 crops, with 25% aborted	5.97-10.28 weeks	Chen *et al.* 2004
Brisbane (Australia)	Sep. 1997-Aug. 2001 (47months)	8	Fig (No pollinator)	Once a month	Female phase: Late spring peak; Male phase: more present in warmer months	No records	No records	McPherson 2005a
Guangzhou (China)	Apr. 2005-Sep. 2006 (18months)	10	Fig, wasp, seed	7-14 days	Negative correlation to temperature	1-4 crops, usually 3-4	1-2 months (extended in Oct.-Jan. and Apr.-Jul.)	Lin *et al.* 2008

Figures

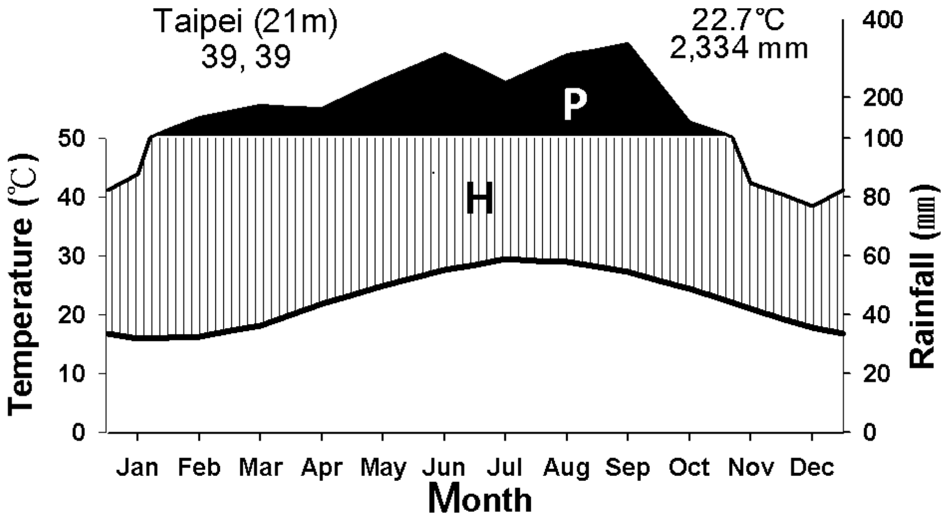

Figure 2-1. Climate diagram of Taipei. Mean monthly temperature, as given on the left axi, is plotted with thick line. Mean monthly rainfall, as given on the right axis, is plotted with thin line. P: very moist period; H: relative moist period. Meteorological data were obtained from Taipei meteorological station in Central Weather Bureau, which is 3.7 km far from sampling site. Data ranged from 1960 to 2009, resource: Central Weather Bureau; www.cwb.gov.tw

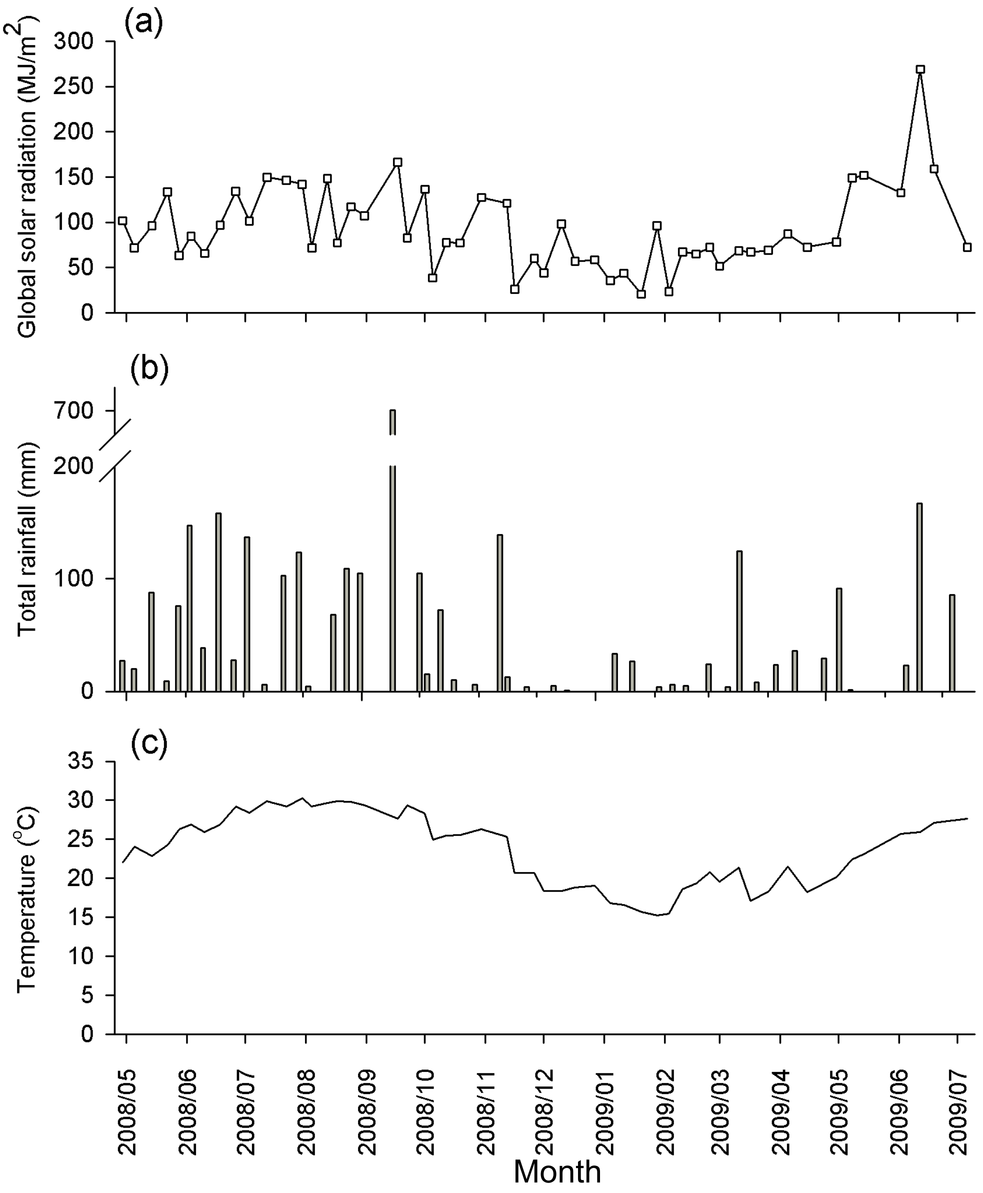

Figure 2-2. Meteorological data between two surveys for Taipei from April 28, 2008 to July 5, 2009. (a) Total global solar radiation. (b) Total rainfall. (c) Mean temperature. Data resource: Central Weather Bureau; www.cwb.gov.tw

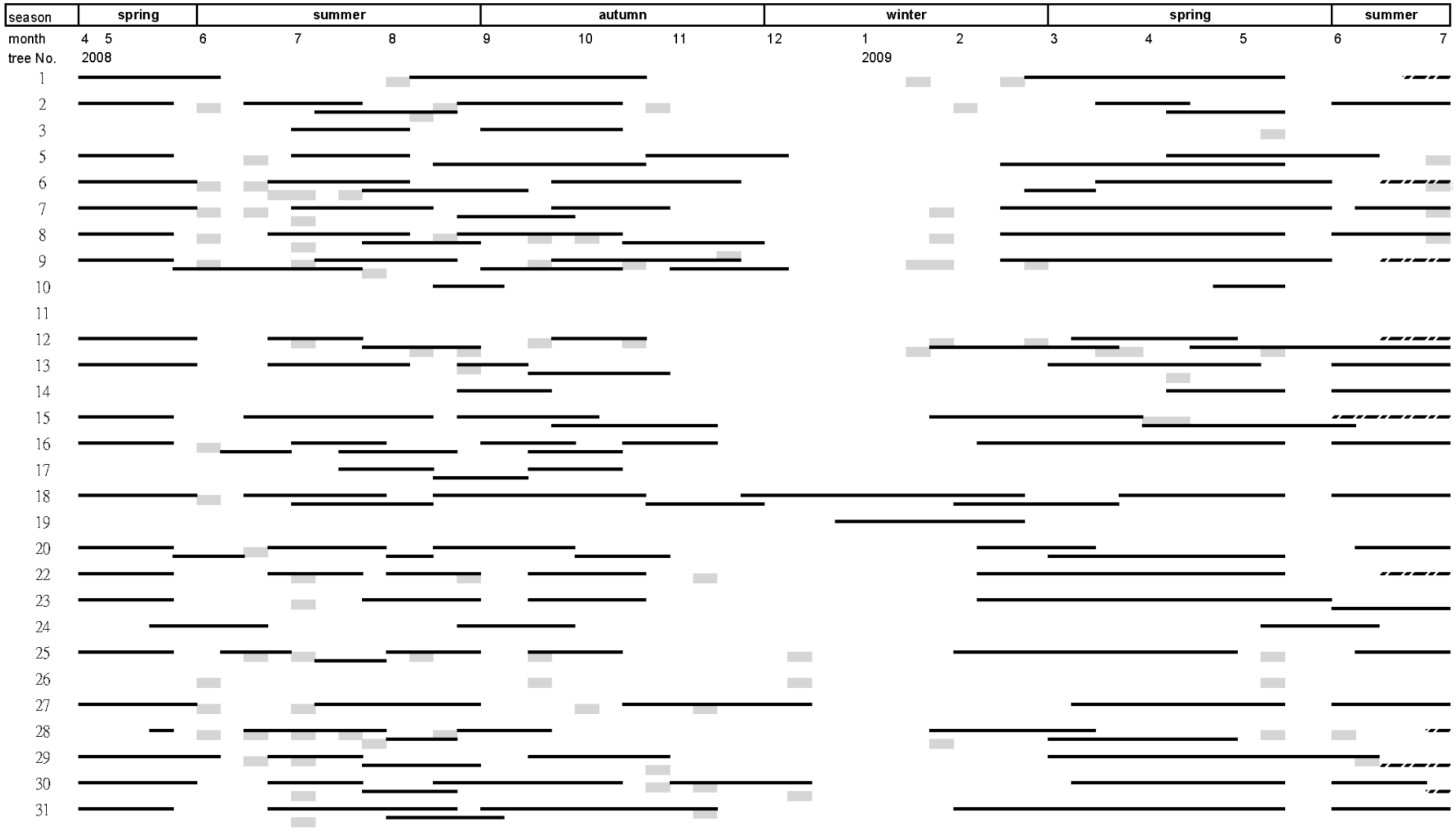

Figure 2-3. Crop productions of 29 trees of *Ficus microcarpa* investigated in Taipei from April 29, 2008 to July 5, 2009. Solid lines (▬) indicates complete crops. Break lines (╌╌) indicate crops that had not mature before the end of survey. Gray blocks indicate mass leaf falling events.

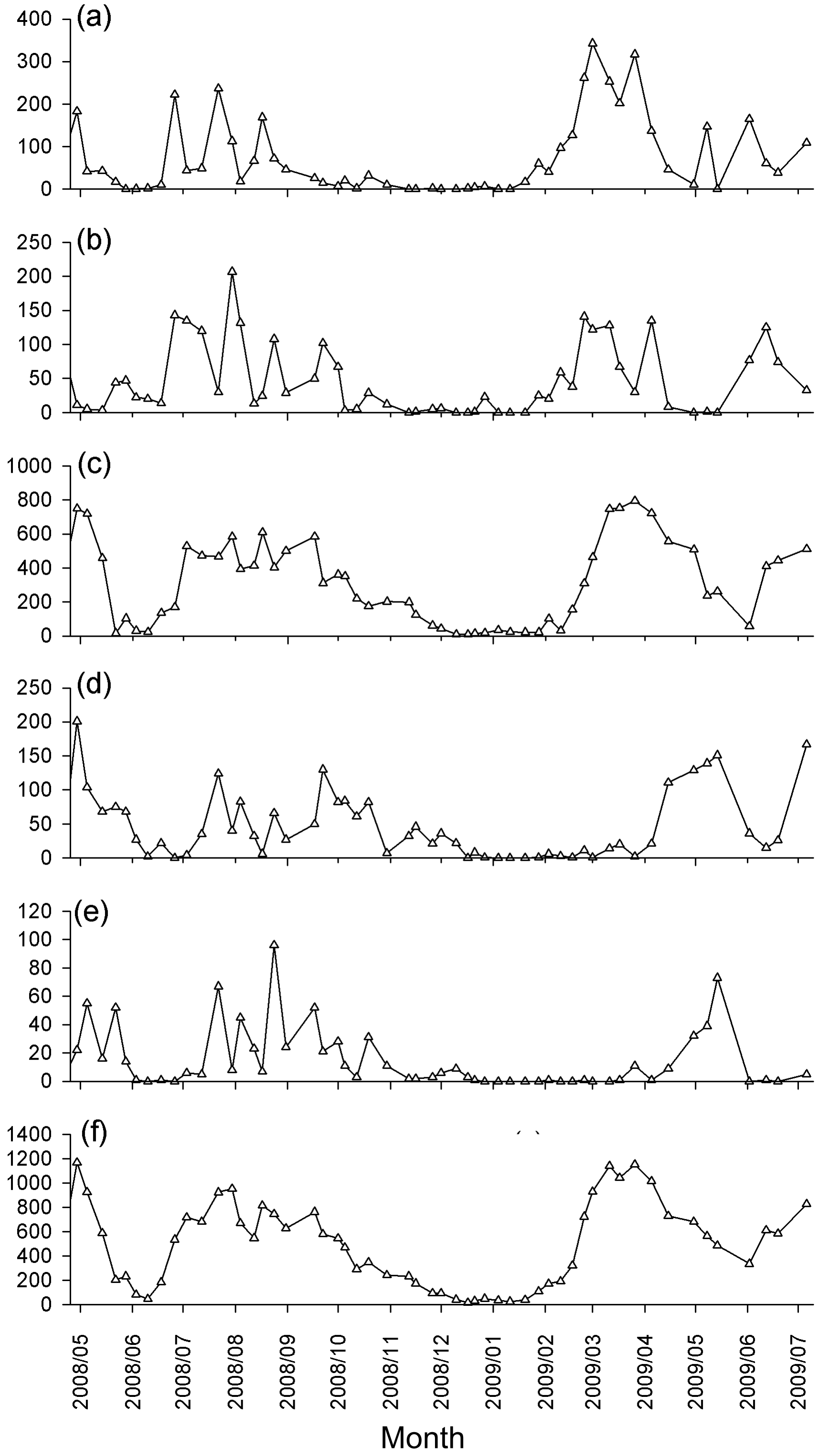

Figure 2-4. Syconia abundance in each phase of *F. microcarpa* in Taipei from April 28, 2008 to July 5, 2009. (a) pre-female phase. (b) female phase. (c) interfloral phase. (d) male phase. (e) mature phase. (f) total syconia.

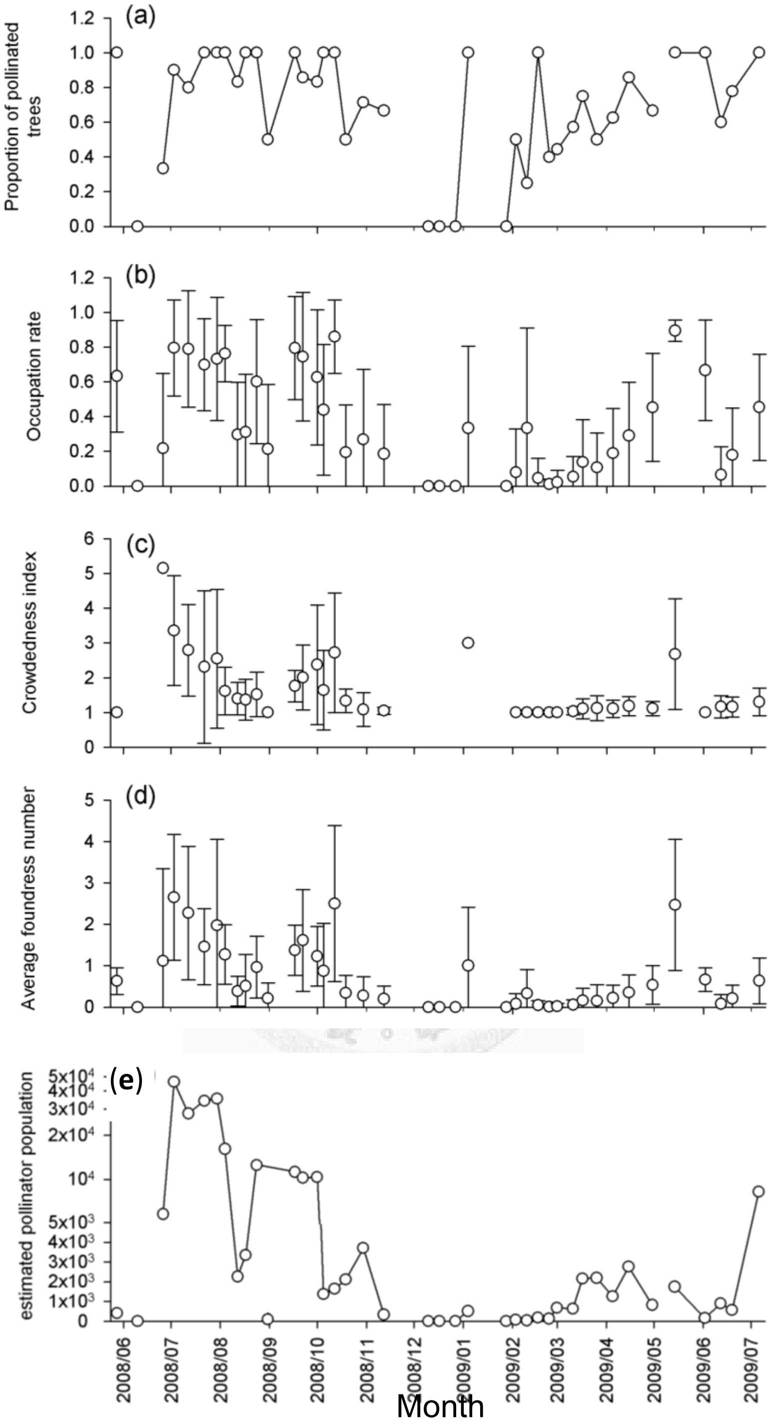

Figure 2-5. Pollinator dynamics of *F. microcarpa* in Taipei from May 27, 2008 to July 5, 2009. (a) Proportion of pollinated tree. (b) Occupation rate (proportion of syconia with pollinators). (c) Crowdedness index (average number of foundress in occupied syconia). (d) Average foundress number. (e) Estimated pollinator population size in study area. Vertical bars in (b), (c) and (d) indicate standard deviation.

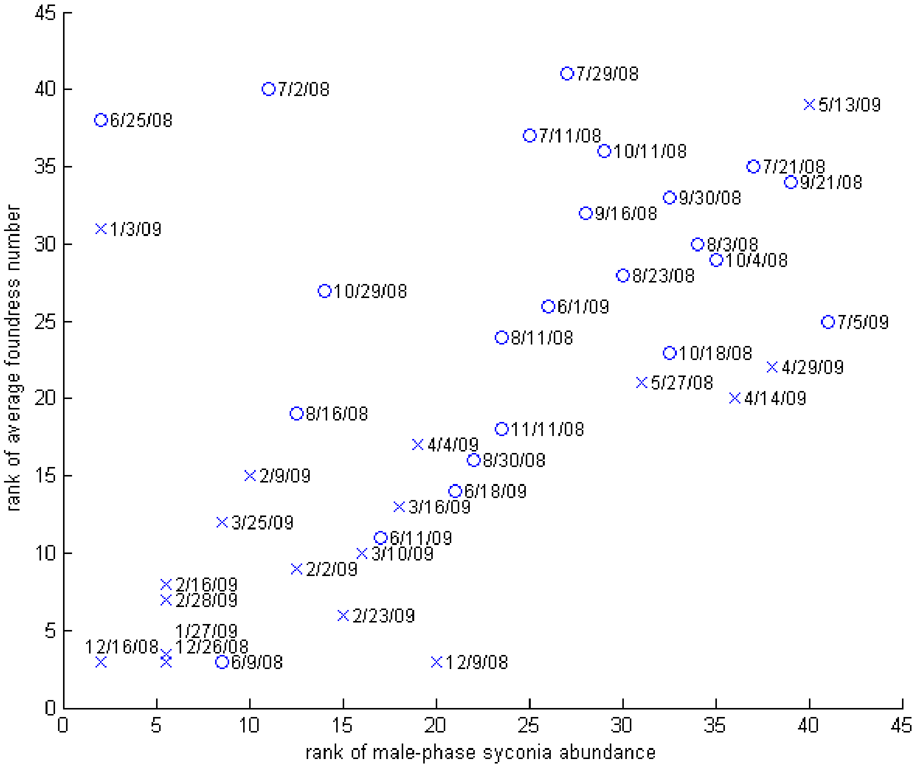

Figure 2-6. A plot of average foundress number versus male-phase syconia abundance. Average foundress numbers for different branches were taken average on the same receptive date. Ranks of the value in the 41 samples were used for the two variables. The higher score of rank corresponds to larger values. Equivalent values were assigned to the same scores. ○: sampled syconia that were receptive in summer or fall; ×: sampled syconia that were receptive in winter or spring. The text labels represent the dates of receptivity for the sampled syconia (Month/date/year).

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Chapter 3: Flowering asynchrony and reproductive strategy of *Ficus microcarpa* (Moraceae) in Taipei, Taiwan

Abstract

Chronological patterns in flowering asynchrony play an influential role in the reproductive success of fig trees as well as fig wasps. Most monoecious *Ficus* trees are reported to have high intra-tree synchrony, but some degree of intra-tree asynchrony has been observed and was hypothesized as an adaptive trait to increase pollinator colonization rate during harsh seasons. The goal of this study was to investigate the seasonal variation of fig flowering asynchrony and its relationship with pollinator colonization rates, and also explore its potential adaptive role for the extremely low *Ficus microcarpa* fig abundance during winter in Taipei. Field phenology of 29 fig trees was regularly surveyed, and the degree of asynchrony by intra-tree, inter-tree and the whole population was quantified. The frequency of sexual-phase overlap (which was regarded as an index for chance of self-pollination) was also counted. Afterwards, the pollinator colonization rate was estimated and compared between trees that presented sexual-phase overlap and trees that did not. The results showed that both the degree of intra-tree asynchrony and the frequency of intra-tree sexual-phase overlap were higher during warmer seasons. Population level asynchrony did not vary seasonally, but inter-tree asynchrony was significantly higher in winter. Nevertheless, the pollinator colonization rate was slightly (but not significantly) higher for the trees presenting sexual-phase overlap. This does not support the hypothesis that intra-tree migration serves as a safety net for fig wasps in winter. The phenomenon of successive (>3 weeks) production of female-phase syconia was found to be more common in spring, and was

accompanied by high quantities of female-phase syconia dropping from the tree. This provided an empirical observation for Bronstein’s hypothesis--which states that an extended duration of receptivity period is an adaptive trait to increase pollination rate and decrease critical population size.

Introduction

Phenological synchronization of plant reproduction plays an influential role on the mutualistic interactions between plants and their associated pollinators, dispersers, or plant-eating species (Augspurger 1983, Bolmgren 1998). Synchronized flowering and/or fruiting may benefit from its massive display effect to attract pollinators and dispersers (Rathcke and Lacey 1985, Hossaert-McKey *et al.* 1994, Galloway *et al.* 2002). Lack of synchrony could be interpreted as adaptive too. Indeed when asynchrony is used as a bet-hedging strategy (by spreading and extending the flowering) plants can decrease the risk of pollination failure (Gillespie 1977, Wells and Lloyd 1991). In the case of dichogamy (i.e. the temporal separation of pollen presentation and stigma receptivity within a flower), synchrony among inflorescences of the same individual can protect against self-pollination and reduce pollen-pistil interference on pollen import and export (reviewed in Lloyd and Webb 1986, Barrett 2002). In this case, asynchrony within-population would be necessary for inter-individual pollen transfer.

One of the most known systems in mutualism is on the interaction between fig and fig wasps. More than 750 species worldwide belong to the genus *Ficus* (Berg and Corner 2005). This genus is characterized by an urn-shaped inflorescence, a syconium, that only their species-specific agaonid wasps (Agaoninae, Hymenoptera, sensu Cruaud *et al.* 2009) can enter (Wiebes 1979, van Noort and Compton 1996 but see Cook and Rasplus 2003). Half of *Ficus* species are monoecious while others are dioecious (Berg 1989). Monoecious figs have functional male and female flowers inside the same fig; but they reach maturity at different periods. The female flowers mature first (B phase/female phase), emitting volatile compounds to attract pollinating fig wasps (Hossaert-McKey *et* *al.* 1994, Grison-Pige *et al.* 2002). The pollen loaded pollinators enter the syconia to lay eggs and pollinate the flowers at the same time. After a developmental period, male flowers and the wasp offspring mature simultaneously (male phase). The second generation of female pollinators then emerged from their natal syconia and looking for another receptive syconia.

Due to the short lifespan of pollinators (Kjellberg *et al.* 1988, Wang *et al.* 2009) *Ficus* trees have to provide syconia year-round to sustain the pollinator population (Janzen 1979). Furthermore, most *Ficus* species are synchronous at the individual level that all the inflorescences of a tree are in the same developmental phase (Hill 1967, Milton *et al.* 1982, Yeo and Tan 2009). Thus to ensure successful pollen transfer among trees, some trees have to be in male phase while others are in female phase. Thus, intra-tree asynchrony among individuals should be expected. On this mutualistic partnership, intra-tree synchrony accompanied with population asynchrony has been demonstrated by many studies (e.g. Hill 1967, Wharton 1980, Zhang *et al.* 2008).

Intra-tree synchrony was presumed to be selected for protection against self-pollination (Ramirez 1970, Janzen 1979 but see Hossaert-McKey and Bronstein 2001). However, some degree of asynchrony was recorded in certain monoecious fig species, e.g. *Ficus aurea* (Ramirez 1970, Bronstein and Patel 1992), *F. sur* and *F. burtt-davyi* (Baijnath and Ramcharun 1983, 1988), and *F. rubiginosa* (Jia *et al.* 2008). About 30 years ago, Janzen (1979) proposed that the breakdown of synchrony may an adaptive strategy for maintaining the wasp population in seasonal environments. During hard or cold seasonal areas, syconia production greatly declines (Hill 1967, Galil and Eisikowitch 1968). In addition, mortality rate of fig wasps is expected during inter-tree migration. In this case, intra-tree asynchrony may serve as safety net for the wasp population increasing the wasp survival.

Since Janzen's hypothesis published (1979), the empirical study cases did not all present consistent results with his theoretical work. Some *Ficus* species showed asynchrony both in aseasonal and seasonal areas (Bronstein 1989). However, when comparing the asynchrony level and the plant's geographical distribution, McPherson's study (2005) showed that the species with higher frequency of crop overlap also has wider distributions. Allopatric populations also addressed the importance of asynchrony in adaptation. Smith and Bronstein (1996) studied two species: *F. insipida* and *F. periolaris*, at two different sites in Mexico. They found that both *Ficus* species tended to be more asynchronous at the drier and colder site.

Furthermore, studies of seasonal variation in asynchrony level on sympatric species are inconsistent. Bronstein (1989) argued that if intra-tree asynchrony is a strategy that allowed the wasps to migrate in the same tree in harsh environment, one will expected to observe higher level of asynchrony during unfavorable seasons; but the phenological pattern of *F. sur* in South Africa (Baijnath and Ramcharun 1983) and *F. aurea* in Florida (Bronstein and Patel 1992) showed the opposite situation. Both species exhibited higher level of intra-tree asynchrony in warmer seasons. On the other hand, Jia *et al.* (2008) studied *F. rubiginosa* in tropical Townsville, Australia. A higher rate of intra-tree crop overlap in unfavorable times of the year was observed. This study presented an opposite result to that of *F. aurea* and *F. sur*.

Bronstein (1989) suggested that intra-tree asynchrony, by scattering the fig phase with different timing, can benefit the pollinator colonization rate. However, if the intra-tree asynchrony evolved to increasing the likelihood of pollinator colonization, it should occur more often when the pollinator population level is unpredictable or when pollinator population is very low, rather than in the warm seasons when pollinators are abundant. Therefore, more detailed information on the phenology of *Ficus* trees is required before the Janzen's or Bronstein's hypotheses could be disproved or confirmed and probably new hypotheses have to be theorized to match the empirical reality.

Within tree asynchrony of *F. microcarpa* has been documented in different areas around the world, including Hong Kong (Hill 1967), Singapore (Corlett 1984), Brazil ((Figueiredo *et al.* 1995), Taiwan (Chen *et al.* 2004), Australia (McPherson 2005), and China (Lin *et al.* 2008). Previous studies on *F. microcarpa* phenology in Taipei found seasonal variation in syconia production (Chen *et al.* 2004): more crops were produced in March to May and July to October than the rest of the year. Thus winter is an unfavorable season for the studied trees reproduction. How does *F. microcarpa* wasp population survive through the winter? How does the asynchrony related to adaptive strategy?

This study conducted a phenological survey on *Ficus microcarpa* in Taipei, Taiwan. I investigated the level of asynchrony and its variation among seasons. Two phenomena that were assumed to have benefits were specified (1) sexual-phase overlap and (2) successive presence of receptive syconia. The timing of these two phenomena was examined. To test the presumed benefits of pollinator colonization from asynchrony, I compared the pollinator colonization rates between the trees in which sexual-phase overlap was present. Finally, I will discuss the level, timing and benefits of asynchrony to infer the relation of asynchrony and the adaptation of *F. microcarpa* in Taipei.

Materials and Methods

Study Species

Ficus microcarpa L.f. 1782 (subgenus *Urostigma*, section Conosycea) is a large evergreen monoecious tree, hemi-epiphytic and with abundant aerial roots. Leaves are arranged alternately, lamina elliptic to broadly elliptic. Mature leaves are about 8-13 cm. Syconia are axillary, arranged singly or in pairs (Hill, 1967). Ripe figs are about 6-10 mm in diameter, turning from reddish green to pink or purple at the end of maturation and are consumed by more than 200 frugivorous species (Shanahan *et al.* 2001). *Ficus microcarpa* is natively distributed in the Eastern and Southern China, Ryukyu Islands (Japan), the Indo-China Peninsula, India, and in Sri Lanka, Papua New Guinea to Northern and Eastern Australia (Tzeng 2004, Berg and Corner 2005). This species is native to Taiwan and is a widely cultivated roadside tree in all the urban areas. *F. microcarpa* is pollinated by a species-specific pollinating wasp *Eupristina verticillata* Waterston (Waterston 1921).

Study site and climate

I conducted a 14 month phenological survey on 29 road side *F. microcarpa* trees along a road about 250 m long near the National Taiwan University campus in Taipei, Taiwan (25°00’43’’N, 121°32’25’’; and 21 m above sea level). The trees are more than 25 years old, with an average height of 7-14 m, diameter at breadth height (d.b.h.) ranges from 85.5 to 201.4 cm. Molecular analysis using ten micro-satellite sequences showed that these trees are not cloned at all.

Taipei has a humid subtropical climate. Average annual temperature is 22.7 ℃, and the annual total rainfall is 2334 mm (Central Weather Bureau; www.cwb.gov.tw). The coldest time of the year is from December to February, with an average temperature of 11℃. June, July and August are the hottest months, with an average temperature of 29.4℃. The four seasons are thus defined as: spring—March to May, summer—June to August, fall—September to November, and winter—December to February. Summers are humid and accompanied by occasional rainstorms and typhoons; while winters are short and mild.

Phenological censuses

Phenological censuses were conducted from May 2008 to July 2009 with 8.2±3.2 (mean±SD) day intervals. During each survey, four units of branch were cut and sampled from each tree at height from two to five meters. One unit of branch is about 30-50 cm long, with 5-7 twigs. Branches were taken from four different ordinal directions because preliminary observations have shown that different growing stages could be found on different parts of the tree crown.

Each syconia was assigned to one of the five developmental stages classified by Galil and Eisikowitch (1968): A phase—syconia initiation; B phase—female phase: female flowers mature and emit volatile compounds which attract pollinators. This is the only period during which pollinators can enter the syconia. C phase—seeds and galls develop inside the syconia. D phase—males phase: fig wasp offspring emerge and male flowers mature simultaneously. Female fig wasps loaded with pollen emerge. E phase—Seeds and syconia ripen.

On the other hand, when collecting branch of each tree, I also examined whether there are syconia dropping from the tree. I recoded the presence of ‘dropped B-phase syconia’ if B-phase syconia were found on the ground beneath the tree crown.

Prevalence and degree of intra-tree asynchrony

The prevalence of intra-tree asynchrony was examined by counting the number of phases on each tree was counted. To further clarify the adjacency within each number of phases, “phase interval” was calculated: the numerals one to five were assigned to each development phase (A to E respectively); the “phase interval” is the oldest sampled phase number minus the youngest. If only two neighboring phases were present on an individual tree, then the phase interval is one. If A- and E-phase syconia were present at a given survey, the phase interval is four.

Seasonal variation of intra-tree asynchrony: quantitative measure

To examine the variation of asynchrony among seasons, Simpson’s species diversity index (Simpson 1949) is borrowed for quantitative measure of asynchrony, $\mathrm{D}_{\mathrm{tree,t}}$ (formula 1). In the formula, t is the survey when the samples were collected, and $p_{\mathrm{j,t}}$ is the proportion of syconia at developmental phase j, which consisted of 1 to 5.

$$\mathrm{D}_{\mathrm{tree,t}} = 1 - \sum_{\mathrm{j=a}}^{\mathrm{e}} p_{\mathrm{j,t}}^{2} \qquad (1)$$

The behavior of this formula is similar to the evenness index introduced by Bronstein and Patel (1992): (1) when more different phases are present in one sample, the value is higher; (2) when the proportion of each phase is more evenly distributed, the value is also higher. Theoretically, this index has a maximum value of 0.8 (when there are five developmental phases present and proportions are equal), and a minimum value of zero (when only one phase is present).The validity of this index and differences from the evenness index are discussed in Appendix II.

Population asynchrony

All the syconia observed in the same census were summed up by phase to measure asynchrony at the population level. The population asynchrony, $\mathrm{D}_{\mathrm{population,t}}$, during survey t, was then calculated by formula (2), with $P_{\mathrm{j,t}}$ represents the proportion of syconia that were in phase j.

$$\mathrm{D}_{\mathrm{population,t}} = 1 - \sum_{\mathrm{j=a}}^{\mathrm{e}} P_{\mathrm{j,t}}^{2} \qquad (2)$$

To distinguish the different effects of intra-tree asynchrony and inter-tree asynchrony on population asynchrony, I conducted formula (3). The role of intra-tree asynchrony at time t was calculated by the average value of $\mathrm{D}_{\mathrm{tree,t}}$ and was denoted by $\overline{\mathrm{D}}_{\mathrm{tree,t}}$. The difference between $\mathrm{D}_{\mathrm{population,t}}$ and $\overline{\mathrm{D}}_{\mathrm{tree,t}}$ was regarded as the effect of inter-tree asynchrony. Thus, the effect of inter-tree asynchrony, EI, was then defined as the proportion of population asynchrony resulting from inter-tree asynchronization. It can also be regarded as the reduction of asynchrony from population level to individual level.

$$\mathrm{EI}_{\mathrm{t}} = \frac{\mathrm{D}_{\mathrm{population,t}} - \overline{\mathrm{D}}_{\mathrm{tree,t}}}{\mathrm{D}_{\mathrm{population,t}}} \qquad (3)$$

Sexual-phase overlap and successive presence of B-phase syconia

Asynchrony was presumed to be a strategy by intra-tree sexual-phase overlap or extending receptivity. Thus, I focused on two phenomena in asynchrony: “sexual-phase overlap” and “successive presence of B-phase syconia”, and examine the timing of their occurrence.

First, **sexual-phase overlap** is defined as the co-occurrence of female and male phase syconia. Number of trees in which sexual-phase overlap were present was counted in every survey. However, due to productivity difference among seasons, I standardized the number into a frequency. The frequency of intra-tree sexual-phase overlap is calculated by the number of trees in which sexual overlap occurred over the number of trees in which female or male phase were present.

Second, **successive presence of B-phase syconia** is defined as the presence of B-phase syconia lasting for over three weeks on an individual tree before D phase figs appear. In the case of *F. microcarpa*, unvisited B-phase syconia can persist in this phase for three weeks (Chen *et al.* 2004, Yang, personal observation). Thus, the presence of B-phase syconia for longer than three weeks indicates that the tree produced several cohorts of syconia at different times. In my phenological data, successive presence of B-phase syconia is accompanied by another cohort of A-phase syconia in more than 50% of cases. This confirmed the inference about new syconia production.

Pollinator colonization rate

Sexual-phase overlap was presumed to increase the pollinator encounter rate (Janzen 1979). Thus, I compared the differences of colonization rate between syconia from sexual-phase overlapping trees and others. During the phenological surveys the syconia in the late B or early C phase on the sampled branches were brought back to laboratory and opened for counting the number of female agaonid wasps (foundress) in these syconia under the microscope. Pollinator colonization rate was examined in two aspects: (1) occupancy rate: the proportion of syconia entered by foundresses, and (2) foundress crowdedness: the mean number of foundresses in occupied syconia. These two indicators were calculated based on the syconia and foundress number of the same branch.

Statistical analysis

Statistical analyses were carried out using the statistic program R (version 2.11.1, http://www.r-project.org). To investigate the individual differences on asynchrony, I conducted ANOVA tests to measure the differences in number of phases present simultaneously among trees. Seasonal differences on intra-tree asynchrony and population asynchrony were also tested by performing Kruskal-Walis tests on the level of intra-tree asynchrony ($D_{tree,t}$) and population asynchrony ($D_{population,t}$) among seasons. If the seasonal variation was significant, I performed Wilcoxon signed-rank test for pair-wise differences. The differences in inter-tree asynchrony ($EI_{,t}$) among seasons were measured using ANOVA test. Tukey HSD tests were performed to examine the pair-wise differences.

The seasonal effect of intra-tree asynchrony can be confounded by the individual effect. For example, if some asynchronous trees only grow figs in summer, and some synchronous trees grow figs mainly in winter, then the seasonal effect of intra-tree asynchrony is just the individual differences. Thus, to eliminate individual effects on seasonal difference in asynchrony, eight trees were selected as a control group. These trees were chosen because there were least four samples from different surveys for each season on each tree. Due to non-normality, non-parametric Fredman rank sum test was used. This test is similar the two-way ANOVA test but in non-parametric way. A single tree was regarded as a block, the season was the factor of interest, and the average intra-tree asynchrony index of each season was the dependant variable.

To examine the seasonal difference in the number of trees where sexual-phase overlap was present every survey, the Kruskal-Walis test was performed. Frequency of sexual-phase overlap among seasons was also tested using Kruskal-Walis test. The occurrence of successive presence of B-phase syconia was assigned to either the summer or spring crop according to the first day B-phase syconia developed.

In relation to colonization rate, paired t-tests were conducted to compare the differences between samples from sexual-phase overlapping trees and other individuals from the same date.

Results

Level and frequency of intra-tree asynchrony

I use two indexes to examine the degree of intra-tree asynchrony-- average number of phases and average phase interval. The results showed that intra-tree asynchrony was common phenomenon of surveyed *F. microcarpa* trees. Of all the 913 samples (a unit of sample represents one to dozens of figs from one tree in the same survey), two-third (65.8%) of them was in two or more phases (asynchronous) (Figure 3-1). Furthermore, 34.4% of asynchronous samples were composed by two adjacent phases. In conclusion, 56.8% of the samples were either in one single phase or in adjacent phases. Thus these figs were not likely to take self-pollination. Some *F. microcarpa* trees can be extremely asynchronous: all five developmental phases simultaneously on a single tree was recorded on eight (0.87%) samples (six trees) during the survey.

Regarding the variation among trees, the asynchrony level, indicated by the number of phases occurred simultaneously, showed significant differences among trees (Kruskal-Wallis chi-squared = 111.3277, df = 27, $p < 0.0001$). This indicates that there is individual difference in asynchrony level.

Seasonal variation of intra-tree asyncrhony

Intra-tree asynchrony index ($D_{tree,t}$) was used to examine seasonal variations. For all the samples, the intra-tree asynchrony index varied from 0 to 0.7517 (the maximum value of this index is 0.8), with an average value of 0.2497 (SD = 0.2304). The level of intra-tree asynchrony varied among seasons (Figure 3-2). The test of within-tree asynchrony among seasons was highly significant (Kruskal-Wallis chi-squared =

34.7409, df = 5, $p < 0.0001$). Pair-wise comparisons showed that intra-tree asynchrony was lower in fall 2008 than in the spring 2008, summer 2008 and spring 2009 (Wilcoxon rank sum test, W=10840.5, 28711 and 13298.5, $p = 0.0031$, $p = 0.0003$ and $p < 0.0001$ respectively). Intra-tree asynchrony values in winter 2008 is also lower than in spring 2008, summer 2008, spring 2009 and summer 2009 (Wilcoxon rank sum test, W=5870.5, 15638.5, 6217 and 3175.5, $p = 0.0007$, $p < 0.0001$, $p < 0.0001$ and 0.0172 respectively).

The phenomenon of intra-tree asynchrony has been observed all along the survey period except during the first two weeks in January (Figure 3-2). During this time, only two trees were bearing syconia, and these syconia were all in C phase. In the following weeks, new crops on one of the two trees as well as on other trees were initiated. Some of these trees produced asynchronous crops and thus the intra-tree asynchrony average recovered quickly to levels previous observed in December

Average intra-tree asynchrony indexes fluctuated with the total number of figs (Figure 3-2). These two variables were positive correlated (intra-tree asynchrony mean= 0.2525 + 0.0003 * total figs, both coefficients are significant at 0.0001 level). In other words, the more figs produced, the asynchrony level increased more. The highest values of intra-tree asynchrony coincided with the largest fig productions. There were two significant drops of the weekly mean intra-tree asynchrony indexes in winter seasons, and these 2 drops corresponded with the weeks in which syconia production was the lowest (Figure 3-2).

The higher level of asynchrony in spring and summer may result from individual differences, and thus eight trees are chosen to controlling the individual effects (see method-statistic analysis for details). The statistic test showed that variation among seasons were also significant (Friedman chi-squared = 17.2857, df = 5, p = 0.0040). This result addressed the effect of seasonality on an individual tree's asynchrony level.

Among these eight trees, seven of them exhibited similar patterns on the seasonal mean asynchrony value: asynchrony values were higher in spring or summer 2008 (all >0.4), and the values decreased in the following two seasons (Figure 3-3).

Population asynchrony and inter-tree asynchrony

Population asynchrony values ($D_{population}$) varied among weeks: ranging from 0 to 0.7402, with an average value of 0.5027±0.1522. Population asynchrony is slightly higher in spring and fall than in fall and winter (Figure 3-4a). However, statistically there were no significant differences (Kruskal-Wallis chi-squared = 3.0664, df = 5, p = 0.6898).

As the intra-tree asynchrony was different among seasons but the population asynchrony was not. The proportion of inter-tree asynchrony to population asynchrony (EI) showed significant differences among seasons (ANOVA, F = 4.4193, df = 5, p = 0.0023) (Figure 3-4b). EI in winter was significantly lower than in spring 2008, summer 2008 and spring 2009 (Tukey's HSD test, p = 0.0246, 0.0010 and 0.0024 respectively). This result indicates that, a relatively higher proportion of inter-tree asynchrony is responsible for population asynchrony in winter than in other seasons.

Sexual-phase overlap and successive presence of B-phase syconia

Although intra-tree asynchrony was frequent, sexual-phase overlap was rare. Samples containing both female and male phase syconia represent 5.6% of the samples.

Of all the syconia in sexual-phases, 12.3% female- and 8.5% male-phase syconia were in samples in which sexual-phase overlap were present. In other words, 12.3% of female-phase syconia have possibility to receive pollinators from the same tree, and the rest 87.7% of female soconia request pollinators from outside.

The number of trees in which sexual-phase overlap was present varied from zero to five per week. The seasonal differences were marginal significant (Figure 3-5a) (Kruskal-Wallis chi-squared = 10.4027, df = 5, $p = 0.0646$) and the average numbers of trees exhibiting sexual-phase overlap was slightly larger in spring and summer than in winter. However, the frequency of intra-tree sexual-phase overlap (calculated as the number of trees in which sexual overlap occurred over the number of trees in which female or male phase were present) did not show a seasonal variation (Figure 3-5b) (Kruskal-Wallis chi-squared = 3.6727, df = 5, $p = 0.5974$).

The phenomena of successive presence of B-phase syconia occurred three times in summer 2008 and six times in spring 2009 (Figure 3-6). B-phase syconia dropping from the tree were also recorded during this period (Figure 3-6).

Pollinator colonization rate

Occupancy rate of samples from trees with sexual-phase overlap was slightly higher than other individuals without, but the difference was not significant (two-sided paired t-test, $p = 0.0978$, n = 44). The foundress crowdedness also showed no significant differences between the two groups of trees (two-sided paired t-test, $p = 0.1776$, n = 44).

Discussion

While most *Ficus* trees are noted for their intra-tree synchrony (Hill 1967, Janzen 1979, Wharton 1980), some species exhibit different levels of intra-tree asynchrony (Bronstein and Patel 1992, Figueiredo and Sazima 1997, Jia *et al.* 2008). This study showed that intra-tree asynchrony is common in *Ficus microcarpa*. Moreover, the level of asynchrony varied among individuals and seasons. Scholars proposed that asynchrony could be an adaptation to seasonal areas: either by sexual-phase overlap (Janzen 1979) or lengthening the duration of receptivity (Bronstein 1989). In the following pages, I first discuss the harsh season strategy of *F. microcarpa* in Taipei. Secondly, I discuss the possible causes and consequences of the two phenomenon (sexual-phase overlap and successive presence of B-phase syconia) and their influence of individual asynchrony to population adaptation.

Harsh season strategy

This research performed a quantitative study on the population asynchrony; and the results showed that population asynchrony was all year-round. This has been also observed in most other *Ficus* populations (e.g. Wharton 1980, Zhang *et al.* 2008), and has been regarded as an evolutionary strategy to ensure wasp migration and pollination success (Bronstein *et al.* 1990).

However, in this current study the population asynchrony dropped to zero in the coldest month. During this time, the only two trees were bearing figs in C phase. This permits pollinator larva to spend few weeks as larvae in the syconia, similarly with the monoecious *F. aurea* (Bronstein and Patel 1992) in seasonal Florida. In fact, winter in Taipei is mild, the lower temperature are caused by cold waves which last several days to one week. *Ficus* trees can extend C phase and enter D phase when environment is suitable. This enables the pollinators to stay in the syconia for the coldest days and emerge at more favorable period between cold waves.

Sexual-phase overlap

Although intra-tree asynchrony was frequent, sexual-phase overlap was rare, accounted for only 5.6% of all the samples. In my observation, this phenomenon occurred when trees grew a new crop right before the former one completed the E phase (Figure 3-6). Johri and Konar (1956) also reported this situation on *Ficus religiosa*: “While one crop is maturing, the next one starts developing”. In addition, sexual-phase overlap occurred more often in summer, but the frequency did not vary among seasons, which reveals that some *F. microcarpa* trees tend to create another crop as long as the environment is suitable. Combining these observations, I suggest that sexual-phase overlap exists because trees are in a rush to produce another new crop; crop overlap is a consequence of reproductive output maximization during favorable seasons.

The trees’ ability to initiate a new crop is related to the resource consumption of the figs. Resource consumption rate in different developing stages can be measured by the syconia’s dry weight, which was not been thoroughly studied in monoecious figs. To my knowledge, the only study was on *F. racemosa* (Zhang *et al.* 2006). But the authors did not provide enough information on the differences among developmental stages. In the case of dioecious figs, the dry weight of male syconia stopped increasing at the end of C phase; while it kept increasing to the end of E phase in female syconia (Harrison *et al.* 2000, Ho 2009). During the end of C phase, wasp larvae entered the pupal stage, and thus the energy intake stopped. A similar situation can be expected in monoecious figs. In monoecious figs, resources are devoted to both seed and wasp larva development. When the larvae enter pupal stages, the trees might have a resource surplus which enables the initiation of new crops. Further studies should be conducted to investigate the resource accumulation in different developmental stages of monoecous syconia.

One possible consequence of intra-tree crop overlap was self-pollination. Before the 1990's, most scholars regarded intra-tree sexual-phase overlap as a cost due to its tendency towards self-pollination. This belief was grounded in two assumptions that (1) figs can increase their pollination rate, and (2) self-pollination is a cost. To my knowledge, there are no studies showing the intra-tree wasp migration in monoecious figs. The first evidence for a fig wasp cycle withen a single tree was in the closed bagging experiment in dioecious *F. hirta* (Jia *et al.* 2007). My results found no significantly higher occupancy rates in trees exhibiting sexual-phase overlap than those that without sexual-phase overlap. On the other hand, to test self-compatibility and its cost in *Ficus*, Hossaert-McKey and Bronstein (2001) did a self-fertilization experiment on *F. aurea*. Their results showed that this species is self-compatible; no negative effects were found on the syconia development or on seed germination. There is no evidence to indicate that intra-tree sexual-phase overlap has a direct cost.

The occupation rate and foundress crowdedness in trees with sexual-phase overlap was not significantly higher than trees without. This result seemed unexpected since most studies suggest that pollinators tend to enter the closest possible tree (Kjellberg *et al.* 1988). In fact, most intra-tree sexual-phase overlap occurred in warm seasons in which pollinators were abundant. This reduced the difference in foundresss number between sexual-phase overlap trees and other individuals. Further studies using mark-recapture experiment or genetic markers are needed to examine the tendency that pollinators migrate within their natal tree.

Successive presence of B-phase syconia

Regarding the probability of receiving pollinators, the duration of receptivity of the fig tree is important. Theoretically, the probability of pollinator colonization is higher when duration of receptivity is longer (Anstett *et al.* 1995). Previous studies have reported that unpollinated syconia remain receptive over 2-3 weeks (Khadari *et al.* 1995, Wang *et al.* 2009, Chen *et al.* 2004). This study suggested that in the case of *F. microcarpa*, receptivity can be extended not only at the syconium level but also at the individual level.

Successive presence of B-phase syconia was more frequent in spring when pollinator abundance was low (see Chapter 2), though this study could not provide a statistical clue. The syconia dropping were also recorded during this time. I suggest that by dropping the unpollinated syconia the trees then have resource to grow a new generation of crop. the duration of receptivity of an individual tree can be prolonged by producing another (or several) cohort of syconia, and thus resulting “successive presence of B-phase syconia”.

This phenomenon can also explain the wide geographical distribution of *F. microcarpa*. Anstett *et al.* (1995) used a simulation model showing that when duration of receptivity is longer, population success (proportion of trees being pollinated or pollinate other trees in the population) is higher. Meanwhile, the critical population size (number of trees needed to sustain a pollinator population) decreased with increasing duration of receptivity. This indicates that a species with longer duration of receptivity, (ex. *F. microcarpa*) can sustain their fig wasps in smaller populations. Bronstein (1989) also addressed that, by reducing critical population size, the crop asynchrony may in part contributed to the broad distribution and/or weedy tendency of *F. microcarpa.* This study hypothesized the mechanism that asynchrony may occur.

Why not asynchrony more often in the population?

Flowering asynchrony is an individual characteristic. The patterns are wide: from the trees producing synchronous crops to year-round crops. This same trend was observed in *F. microcarpa* in other areas (Hill 1967, Lin *et al.* 2008). From the possible benefits of asynchrony, a question arises: why isn't asynchrony more frequent? First, as stated in the introduction, synchronized flowering is beneficial to attract pollinators or seed dispersers, especially in their natural habitat where population densities are low. Second, Hossaert-McKey and Bronstein (2001) suggested that male fitness is higher if its pollen is dispersed to sire other crops, rather than competing locally for ovules in the same individual. Third, asynchrony might increase the rate of non-pollinating wasp infection, since it lengthens the time that wasps can oviposite (Cook and Power 1996). Synchronous crops force the parasitoids disperse to among trees thus reducing the infection rate (Compton *et al.* 1994). Therefore, asynchronous trees exist in the population at a frequency that is selected to let benefits offset cost.

As mentioned in the introduction, studies on variation of asynchrony level among seasons on the sympatric species showed different results. The results of this study are similar to the observations on *F. sur* (Baijnath and Ramcharun 1983) and *F. aurea* (Bronstein and Patel 1992) that higher asynchrony in warmer seasons. But *F.*

rubiginosa showed the opposite pattern (Jia *et al.* 2008): it was more asynchronous during the rainy season, which was regarded as unfavorable. *Ficus obliqua* showed no seasonal differences in asynchrony level (McPherson 2005). Asynchrony might play different roles in different species, due to different habitats and different tolerances to environmental factors. For example, *F. microcarpa* and *F. aurea* syconia reduced their production during colder seasons in Taipei and Florida, while the *F. rubiginosa* and *F. obliqua* showed no seasonal variation among their study sites. Hypothesized reproductive benefits of asynchrony on *F. microcarpa* might not explain other species patterns in different areas.

Although synchronization is regarded as an important trait in pollination ecology and may play a role on adaptation, studies focused on the seasonal variation of asynchrony level in monoecious *Ficus* are scarce. More detailed information on the phenology of *Ficus* trees is required before the general hypothesis can be concluded.

Figures

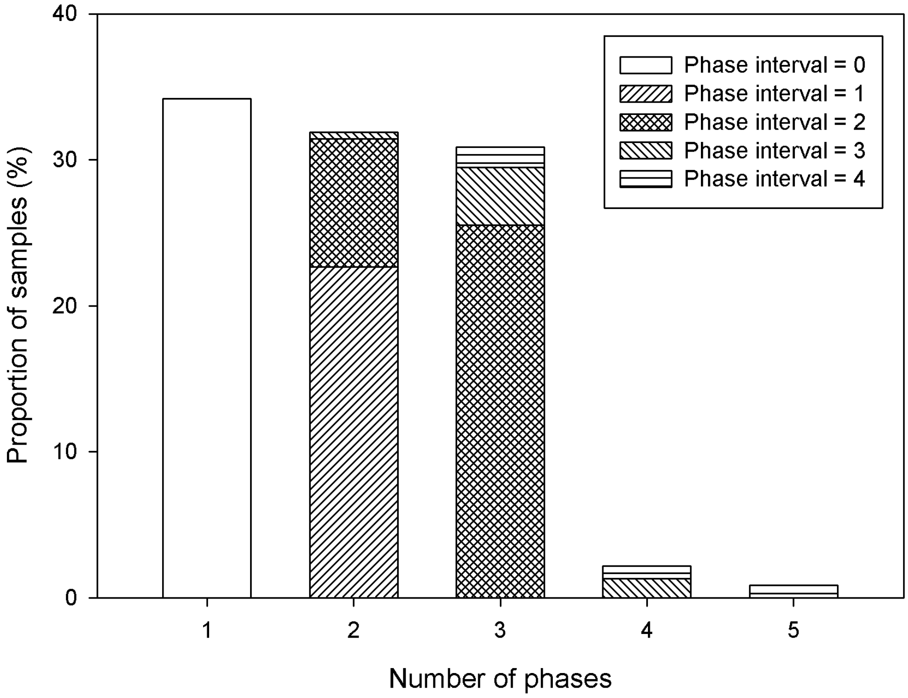

Figure 3-1. Proportion of samples carrying one phase or more, and the phase interval within each number of phases. There are 913 samples from 28 *F. microcarpa* trees on 54 surveys from April 2008 to July 2009.

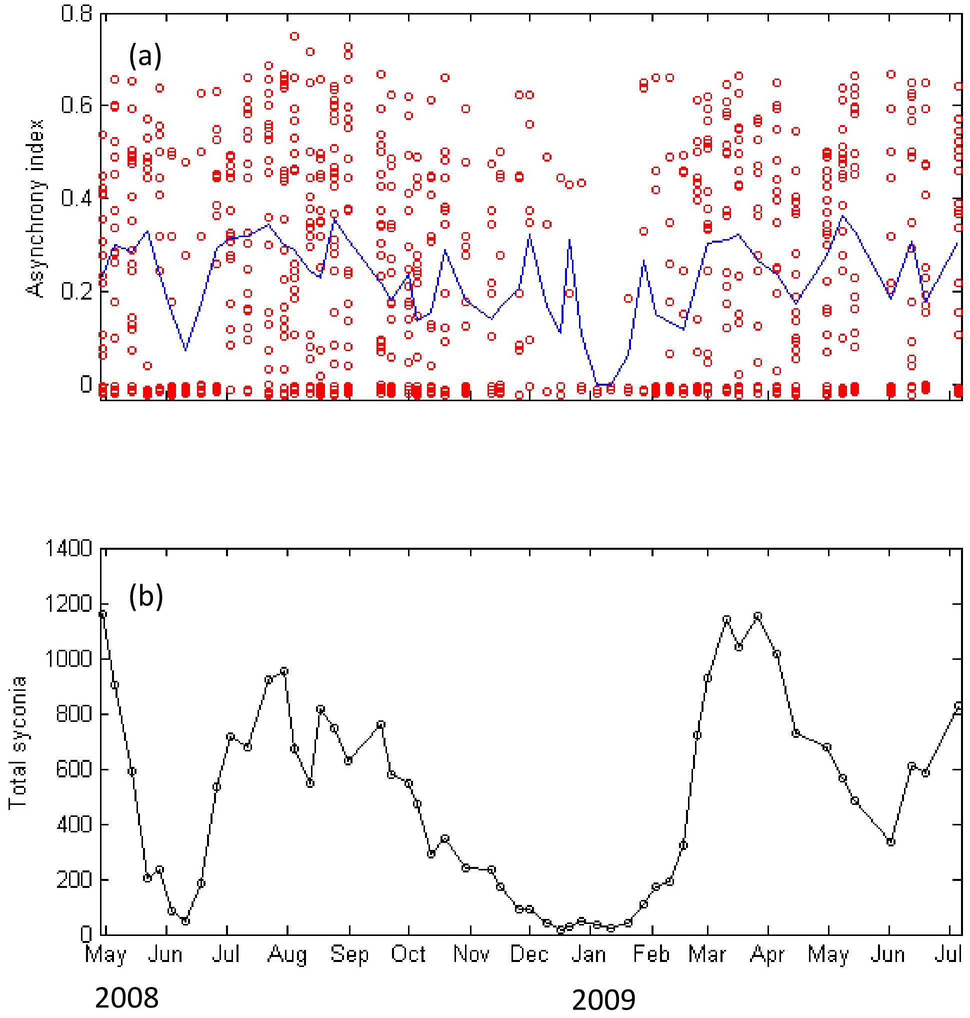

Figure 3-2. Within-tree asynchrony and number of syconia for each survey from May 2008 to July 2009. (a) Each tree Within-tree asynchrony index $D_{tree,t}$ (red circles) and its average $\overline{D}_{tree,t}$ (blue line). The asynchrony index values equal to zero are scattered by minus a small random value (range from 0 to 0.02) for clear presentation. (b) Total number of syconia in each survey.

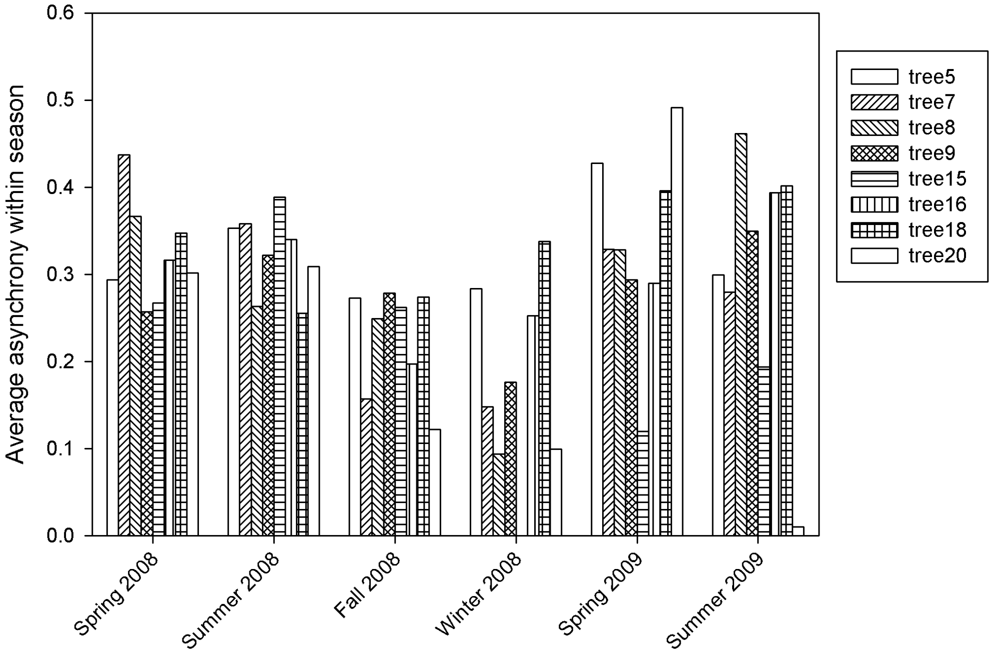

Figure 3-3. Individual asynchrony of eight trees among the six surveyed seasons. Each bar represents average asynchrony index among the samples from each individual in the season.

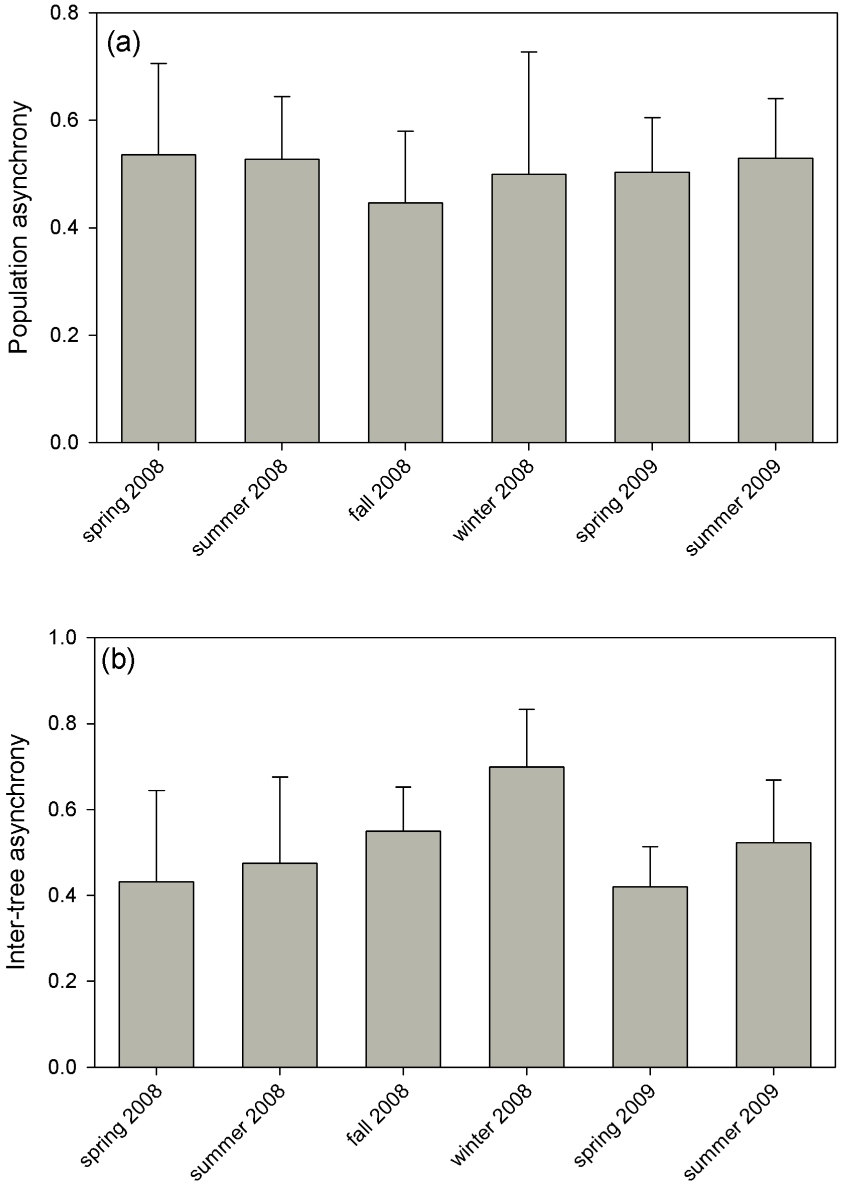

Figure 3-4. (a) Population asynchrony index ($D_{population}$) (b) Inter-tree asynchrony index (IE). Each bar is the average among surveys within each season. Error bars represent standard deviations.

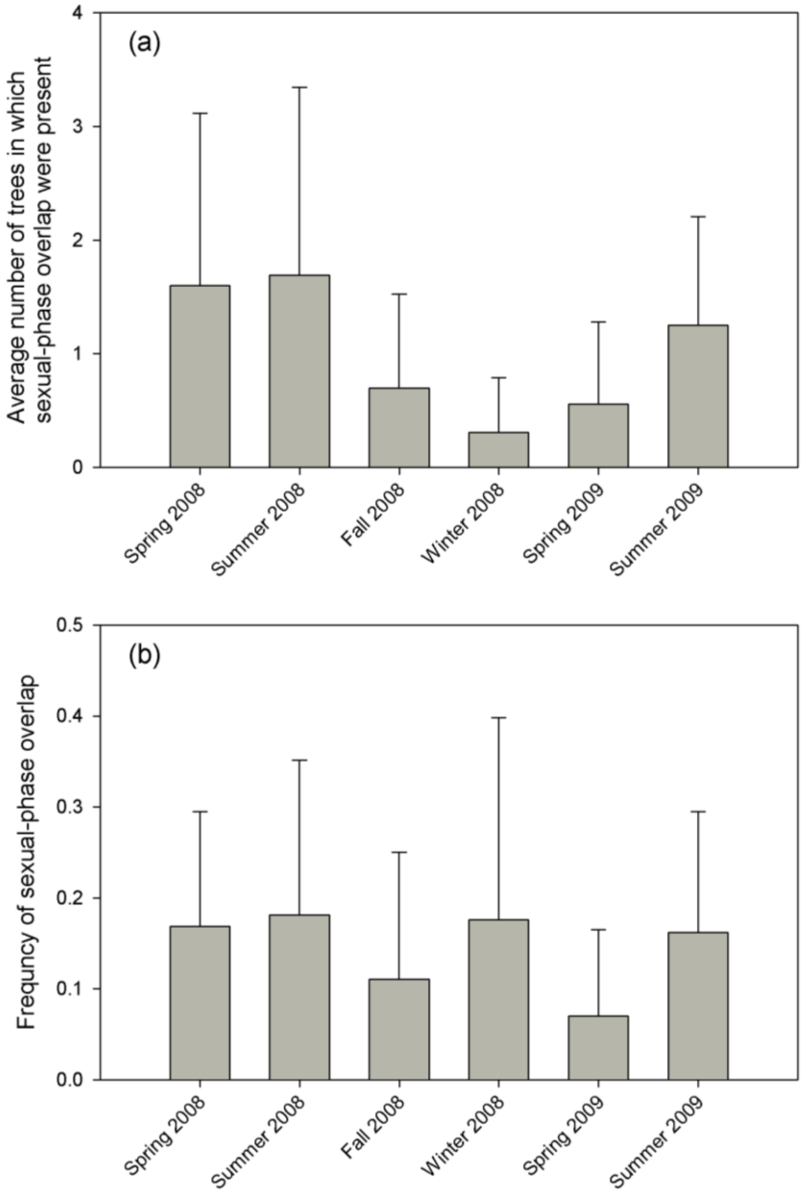

Figure 3-5. (a) Average number of trees in which sexual-phase overlap were present of the surveys in each season. (b) Average frequency of sexual-phase overlap of the surveys in each season.

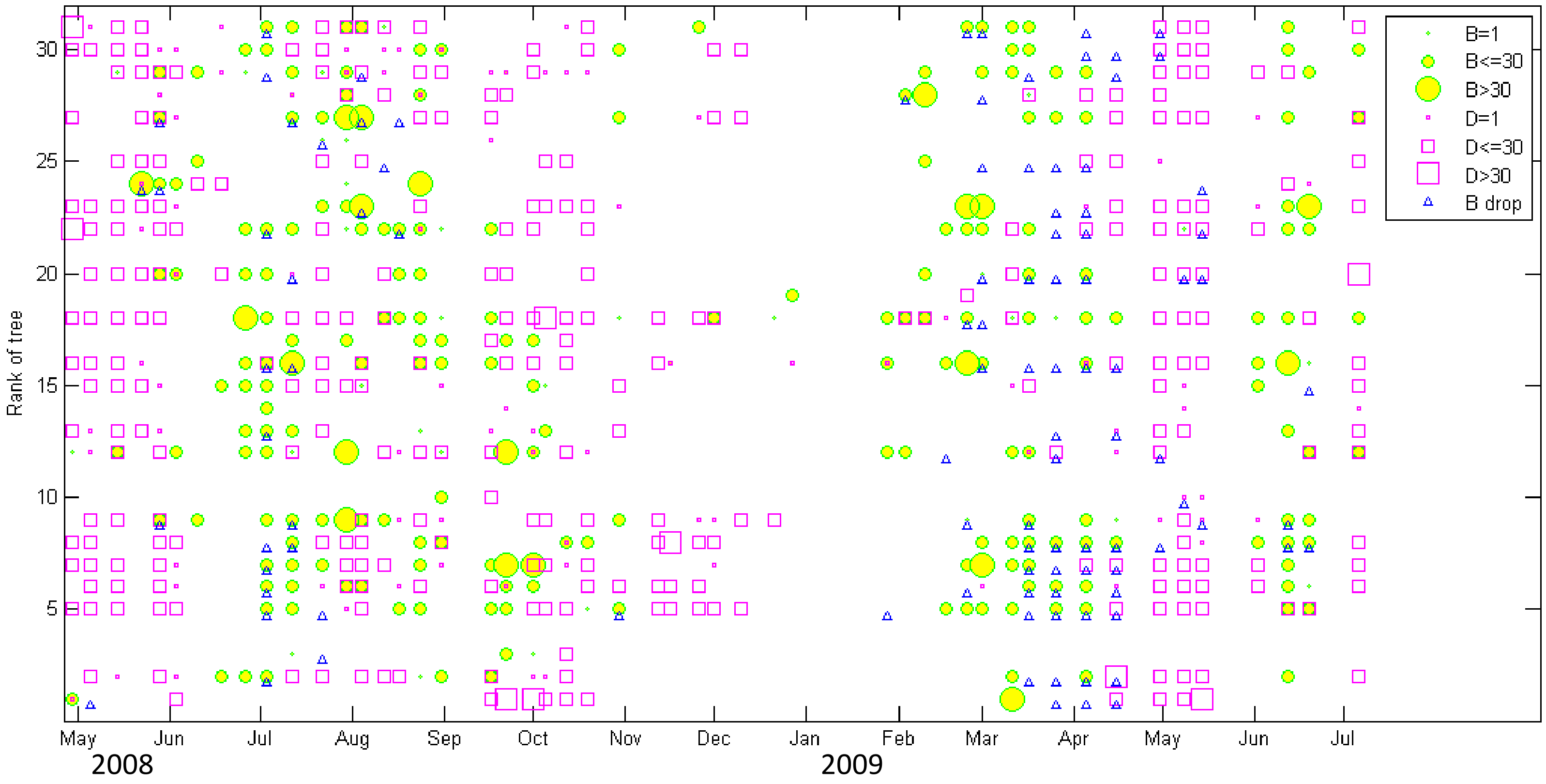

Figure 3-6. A plot of sexual-phase syconia on the tree and dropped B-phase syconia on the ground during each survey from May 2008 to July 2009. Circles, squares and triangles represent B-phase, D-phase syconia on the tree and dropped B-phase syconia on the ground respectively. The three sizes of circles and squares (small, median, and large) represent quantity (1, 2 to 30 and >30 respectively). Note that most within-tree sexual-phase overlap (overlapping of circles and squares) occurred in summer, and most successive presence of B-phase syconia occurred in spring.

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Chapter 4: Grand Summary

1. Syconia of *Ficus microcarpa* were present year round, from April 2008 to July 2009. Two main syconia production peaks were observed during March to June (spring crop) and July to November (summer crop). Syconia production was the lowest in December and January. Each individual tree produced 5.4±2.7 (mean±SD) crops during the period of 14 month survey, which standardized as 4.7 by year.
2. Temperature and global solar radiation were the factors most significantly correlated with syconia abundance, and the latter factor played an important role in initiating syconia growth. Furthermore, abundance of both female phase and interfloral phase were positively correlated with rainfall. Male-phase syconia abundance showed a positive correlation with rainfall when tested with a one-week delay.
3. The pollinator population index was the largest in summer, and subsequently decreased dramatically in fall. During the winter season, when syconia abundance was very low, receptive syconia were poorly pollinated. Pollinators arriving from outside the local population were recorded once. Therefore, the pollinator population should suffer a bottleneck effect in winter and recover the following spring.
4. Intra-tree asynchrony was a commonly observed phenomenon for most of the 29 *F. microcarpa* trees surveyed during the 14 month study period. The level of intra-tree asynchrony varied significantly among seasons, with higher levels recorded during warm seasons, and lower ones recorded in winter. Inter-tree asynchrony was also higher in winter.
5. Population asynchrony was high year-round, except during the coldest month--when

it dropped to zero. During this time, the pollinator larvae stayed inside interfloral-phase syconia.

6. Sexual-phase overlap trees accounted for only 5.6% of all the samples; therefore, the chance of intra-tree inbreeding should be low. More trees exhibited sexual-phase overlap during spring and summer than in winter. The occupation rate of pollinator wasps was slightly (but not significantly) higher in the tree group with sexual-phase overlap than in the tree group without. This does not support Janzen’s hypothesis that intra-tree migration serves as a safety net for fig wasps during winter.
7. Successive presence of B-phase was more frequent in spring when pollinator abundance was low, and was accompanied by high quantities of unpollinated B-phase syconia dropping from the tree. This study offered an empirical observation of extended duration of receptivity, which Bronstein hypothesized as an adaptive trait to increase pollination rate and decrease critical population size.

Appendix I

Re-emergence of pollinator and correlation between occupation rate and actual pollination rate

Objective and methods

To estimate re-emergence rate of foundress and to know whether the remaining foundress is a good indicator of pollinator colonization, 117 branches that with number of figs larger than 10 was examined carefully (2141 syconia in total). I denoted the each foundress as either (1) successful—the foundress had entered the syconium successfully. Her whole body was in the syconium or at the ostiole with her head pointing outward; (2) unsuccessful foundress—the foundress was stuck when entering the syconium. Some parts of the body were at the ostiole and her head orientated towards the syconium lumen; or (3) unidentifiable—the body of the foundress was parallel to the bracts at the ostiole. Among the successful foundresses, I also denote those whose heads were orientated outward to see if it was a common tendency toward re-emergence. On the other hand, when no successful foundresses were observed in the syconium, the tanning of the stigmas and styles was regarded as an evidence of pollination. The syconia either with successful foundress inside or with tanning of the stigmas and styles were regarded as pollinated syconia.

On each branch, the pollination rate was calculated as pollinated syconia over the total syconia sampled on the branch. The occupation rate, as defined in Chapter 2, was the proportion of syconia occupied by foundress. The average foundress was the total number of foundress over the total number of syconia. The correlation between pollination rate and occupation rate of the branches was established using binomial variance models (Generalized Linear Models with logit link function in R). Furthermore, the correlation between pollination rate and average foundress was also performed. In both models, pollination rate was the dependant variable.

Results

The results were summarized in table A1-1. Among all the syconia examined, pollinated syconia accounted for 56.2%. Syconia without successful foundress accounted for 9.6% among all pollinated syconia, ranging from 0% to 73% of each branch. Of all the foundresses, the unsuccessful ones accounted for 16.2%. Note that this rate overestimated the actual death rate when passing through the ostiole, because the actual number of foundress that had visited the syconia was underestimated. The foundress with their head pointing outward accounted for 35.7% of all successful foundresses, indicating the tendency toward re-emergence.

The pollination rate increased with the occupation rate ($p < 0.001$). This indicates that, although the foundresses re-emerge from the syconia, occupation rate can still be an indicator to the actual pollination rate. The pollination rate also increased with the average foundress number ($p < 0.001$). Assuming that the pollination rate increases with actual pollinator abundance, the remaining number of foundresses in the syconia can reflect the actual pollinator abundance.

Tables

Table A1-1. Summary of the situation of syconia and foundress.

Situation of syconia or foundress	Number of syconia or foundress	Proportion (%)
Total syconia	2141	
Pollinated	1204	56.2
Pollinated syconia without successful foundresses	205	9.6
Total foundress	2399	
Successful	1650	68.8
Foundresses with head pointing outward among the successful ones	857	35.7
Unsuccessful	389	16.2
Unknown	360	15.0

Figures

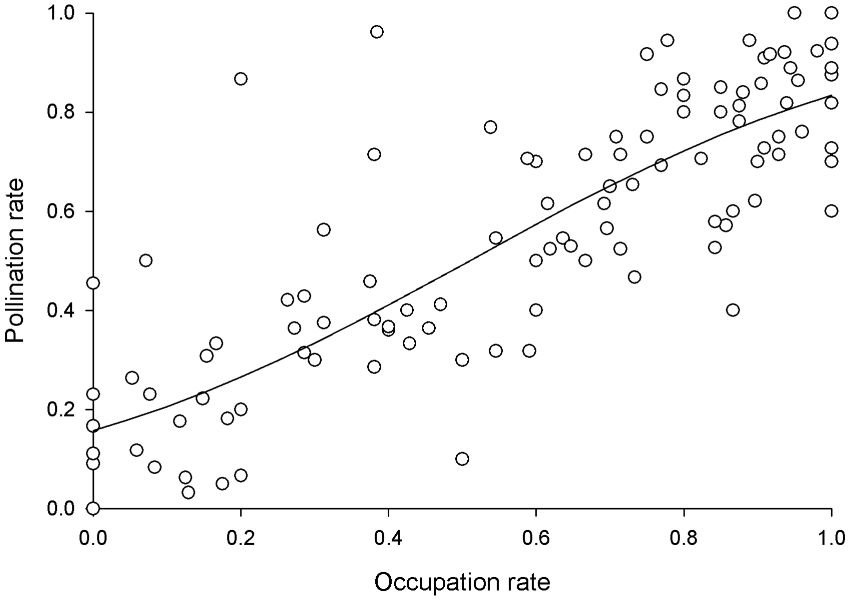

Figure A1-1. White circles show the observed pollination rate in relation to pollination rate. Curves show the pollination rate estimated from logistic regressions (pollination rate = 1/1+exp(-1.6764+3.2904*occupation rate)) using a logit link.

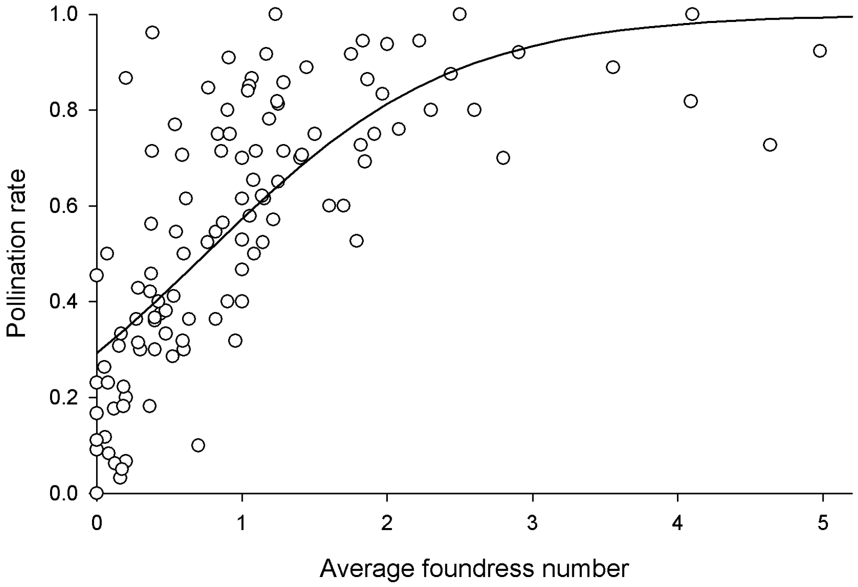

Figure A1-2. White circles show the average foundress number in relation to pollination rate. Curves show the pollination rate estimated from logistic regressions (pollination rate = 1/1+exp(-0.082+1.1757*average foundress number)) using a logit link.

Appendix II

Validity of Asynchrony index

In this thesis I defined “asynchrony” as the abundance of each flowering phase. According to this definition, we expect the asynchrony index to follow these principles:

1. When there is only one phase present on a tree (or among all the sampled syconia), the asynchrony index = 0.
2. If two phases are present on a tree, and the proportion of a second phase syconia is small, the index is close to zero. With an increase in the number of second phase syconia, the difference between the two proportions decreases, so the asynchrony index should be higher. Thus, the evenness index should reach its maximum value when the proportions of both phases are equal.

Here I use a graph to explain. Assume there are only two phases present on one sample, say p_i and p_j respectively. Since there are only two phases, $p_j = 1 - p_i$. Because there is only one variable, we can demonstrate the concept on a 2D graph. If the x-axis represents p_i and the y-axis represents the asynchrony index value, then we expect the curve to be convex (Figure A2-1), and reach maximum at $p_j = p_i = 0.5$.

Now assume a third phase is present. If we first regard it as a constant c, then $p_j = 1 - c - p_i$ and again can be demonstrated on a 2D graph. There are more phases now so the asynchrony value should be larger. Thus a 3-phase curve is higher than a 2-phases one. If c is near zero, the curve should be close to the 2-phases one. The larger c is, the higher the curve will be (Figure A2-1).

Brostein and Patel (1992) are the first scholars to quantify the asynchrony level on monoecious *Ficus* tree. The following formula is the evenness index that they proposed:

$$\mathrm{Evenness} = 1 - \sum_{i=0}^{5} \frac{|\mathrm{p_i} - 0.2|}{1.6}$$

Where i=1, 2, 3, 4 or 5 represent each flowering phase, p_i is the proportion of syconia in phase i. This index assumes that the most "even" situation occurs when that a tree bears the same number of syconia in all five phases. In this situation, the proportion of each phase is equal to 0.2. Thus evenness reaches its maximum.

Graphically, this index follows the two principles outlined at the start of the appendix (Fig. A2-2); but it's equal to the same value when the difference among proportions is relatively small. For example, when there are two phases on the tree, which represents 32% of all cases in my observations, the evenness equals 0.25 as long as the proportion of each phase is between 0.2 and 0.8. This equality can be easily proved algebraically. A similar situation occurs when three phases are present. This equality means the index loses sensitivity within these situations.

Furthermore, the length of each growing phase is different. The frequency where we observe a phase is positively correlated with the length of that phase. Smith and Bronstein (1996) proposed another index to adjust for differences in the length of developmental phases:

$$\mathrm{Evenness} = \sum_{\mathrm{i=a}}^{\mathrm{k=X}} p_{\mathrm{i}} \ln\left(\frac{p_{\mathrm{i}}}{\pi_{\mathrm{i}}} - \frac{k-1}{2n}\right)$$

Where i represent each flowering phase,

k = the number of fig development phases

p_i= the proportion of syconia in phase i

π_i = the expected proportion in each developmental phase based on the average length of that phase

n = the total number of syconia in each sample

X was not defined in the article.

This index is zero when there is only one phase on a tree (k=1). However, the term within the natural log falls below zero easily, resulting in an imaginary number. On the other hand, this equation was modified by G-statistic (Sokal and Rohlf, 1995). In fact, the logic of G-statistic was to measure the "deviation from expected proportions". This is not equal to synchrony level. For example, assuming the expected length of each phase was as follows: A=0.5 weeks, B=0.7 weeks, C=1.8 week, D=0.6 weeks, and E=0.4 weeks. Then the proportion of each phase is 0.125, 0.175, 0.45, 0.15 and 0.1 respectively. If a tree presents only one phase, the G-statistic value changes depending on which phase (ex A phase value=3.69, C phase value=3.14). Thus the "synchronous" events mapped to different values. Therefore, this thesis did not apply this index into the asynchrony index.

In this thesis, I introduced Simpson's species diversity index as a measure of asynchrony:

$$\mathrm{D}_{\mathrm{tree},\mathrm{t}} = 1 - \sum_{\mathrm{j}=\mathrm{a}}^{\mathrm{e}} p_{\mathrm{j},\mathrm{t}}^{2}$$

The behavior of this equation is similar to that of the evenness index introduced by Bronstein and Patel (1992) in relation to the two principles (Figure A2-3), but does not have problem of equality. Thus I used this index as a measure of asynchrony.

Figures

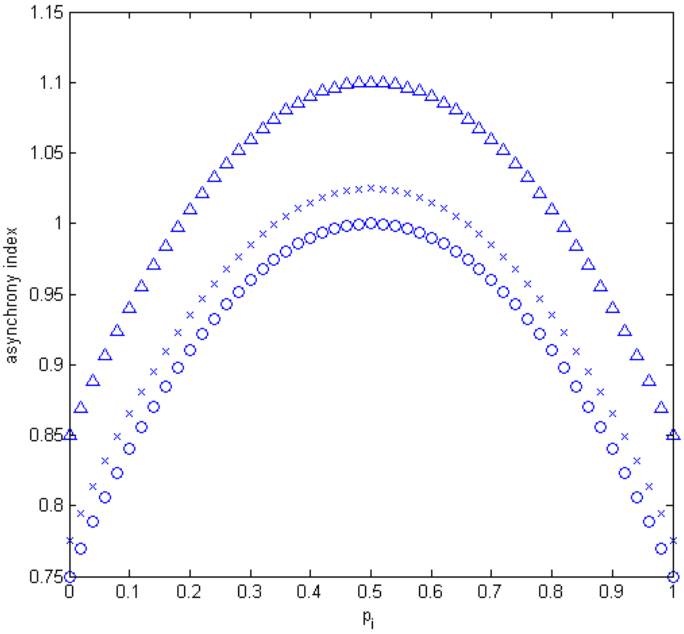

Figure A2-1. Hypothetic curves that fits the two principles of asynchrony index. Circles: the case that only two phases are present in a sample. Crosses: the case of three phases and one of the proportions, c, is near zero. Triangles: the case that three phases and c is relatively larger.

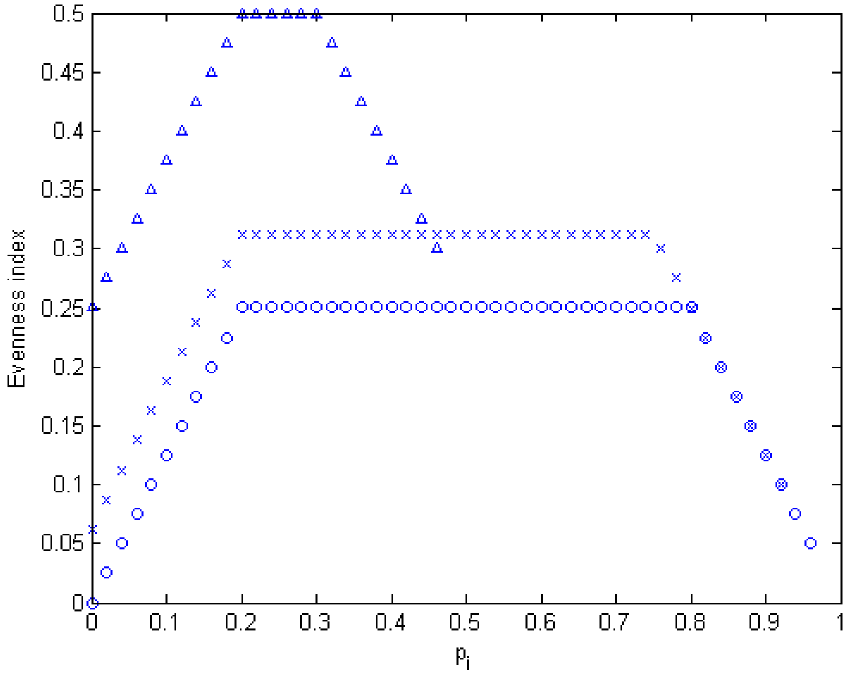

Figure A2-2. The curve of Evenness index by Bronstein and Patel (1992). Circles: the case that only two phases are present in a sample. Crosses: the case of three phases and one of the proportions, c, is 0.1. Triangles: the case that three phases and c is 0.5.

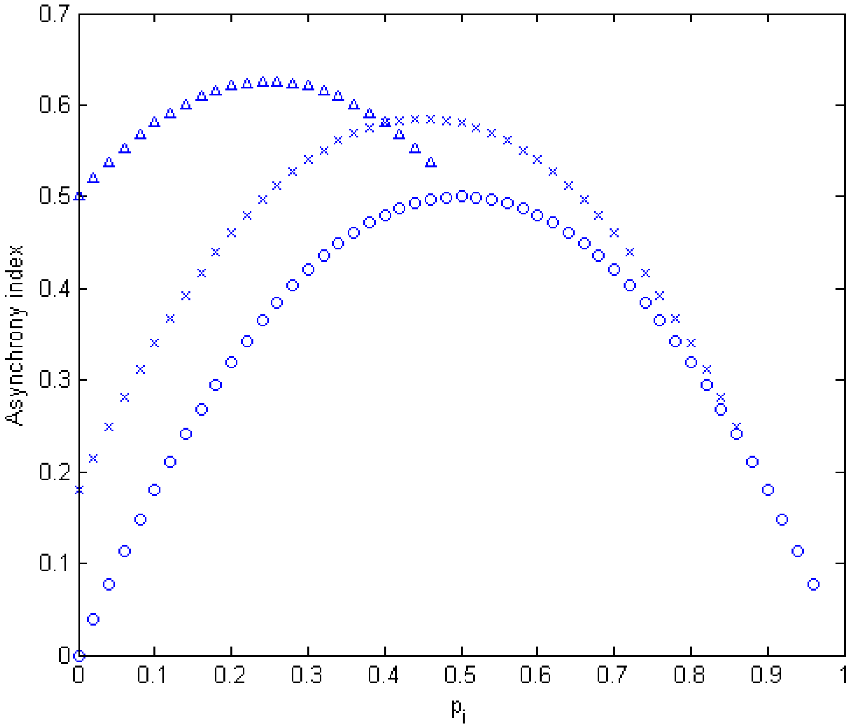

Figure A2-3. The curve of asynchorny index used in this thesis. Circles: the case that only two phases are present in a sample. Crosses: the case of three phases and one of the proportions, c, is 0.1. Triangles: the case that three phases and c is 0.5.

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