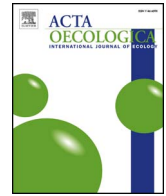




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Adaptive phenology of *Ficus subpisocarpa* and *Ficus caulocarpa* in Taipei, Taiwan

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ABSTRACT

Insect pollination is the main strategy used by Angiosperm plants to transport pollen to another individual. The interaction between entomophilous plants and their pollinators is often mutualistic, with many species pairs being interdependent. In obligate pollination mutualism, the plant relies on its partner for pollination, whereas the pollen vector relies on plant resources. In the mutualism between *Ficus* (Moraceae) and the fig wasps (Hymenoptera, Agaonidae), the plant provides oviposition sites to its exclusive pollinator, which has an extremely short lifespan (a maximum lifespan of few days). This study examined how fig trees maintain their associated pollinator populations by conducting a 45-month phenological survey of 27 and 64 trees belonging to the species *Ficus caulocarpa* and *F. subpisocarpa* in Taipei, Taiwan. The observations indicated that the trees produce figs year-round with no clear seasonal pattern, and are not affected by meteorological factors. On average, about 30% of the trees of both species were bearing figs during the survey. The duration of the fig development was longer during the winter-spring period than during the summer-fall period. The trees displayed strong asynchrony among trees in the population but each crop was synchronous within a tree. However, after wasp emergence, crops lost their synchrony with part of the figs ripening within few days whereas some figs only ripened eight weeks later for *F. subpisocarpa* and four weeks later for *F. caulocarpa*. This study also discusses the implications of fig frugivory and mutualism.

1. Introduction

With the rise and diversification of Angiosperm species, which occurred approximately 115 myr ago (Magallón and Castillo, 2009), pollination by insects (or entomophily) has been extremely successful and currently accounts for approximately 86% of the pollination systems among basal Angiosperm plants (Hu et al., 2008). Animal pollination has been driving the evolution of Angiosperms (Pellmyr, 1992; van der Niet and Johnson, 2012). A vast part of their pollination is done by mutualistic partners (Aslan et al., 2013) with a small number of these mutualisms being obligate (Jaeger and Després, 1998; Holland and DeAngelis, 2001; Kawakita, 2010). One of the best-known examples of obligate nursery pollination mutualism occurs between fig trees (*Ficus*, Moraceae) and the pollinating fig wasps (Hymenoptera: Chalcidoidea: Agaonidae). Among the 800 known *Ficus* species, most pollinating fig wasps are host specific (Berg and Corner, 2005). Approximately half of *Ficus* species are functionally dioecious (Berg and Corner, 2005); for these species, the male trees host the pollinating wasp offspring, whereas the female trees only produce seeds. By

contrast, all figs of monoecious *Ficus* species produces pollinating wasps, pollen, and seeds. At receptivity, the specific pollinating fig wasps enter the figs through the ostiole (the only entrance into the fig), pollinate, and lay eggs simultaneously. After larvae development, mating occurs within the fig and the male fig wasps subsequently cut an exit tunnel through the fig wall, releasing the female wasps. After wasp emergence, the fig ripens and the fig wall turns soft and juicy and becomes attractive to frugivorous animals (Shanahan et al., 2001).

Fig trees are considered keystone species of tropical and subtropical areas (Shanahan et al., 2001), as the food source they provide is crucial to many animal species (Lambert and Marshall, 1991; Nakamoto et al., 2007; Gursky-Doyen, 2010). The importance of fig trees to many frugivores may be explained by strong asynchrony among individuals in their reproductive phenology. In tropical areas, fig tree populations constantly bear figs (Harrison et al., 2000; Kuaraksa et al., 2012); thus, these figs can be consumed by frugivores year-round. Such asynchrony among individuals maintains the pollinator population, allowing them to pass from one crop to the next (Janzen, 1979; Milton et al., 1982; Windsor et al., 1989; Bronstein et al., 1990). By contrast, *Ficus* species

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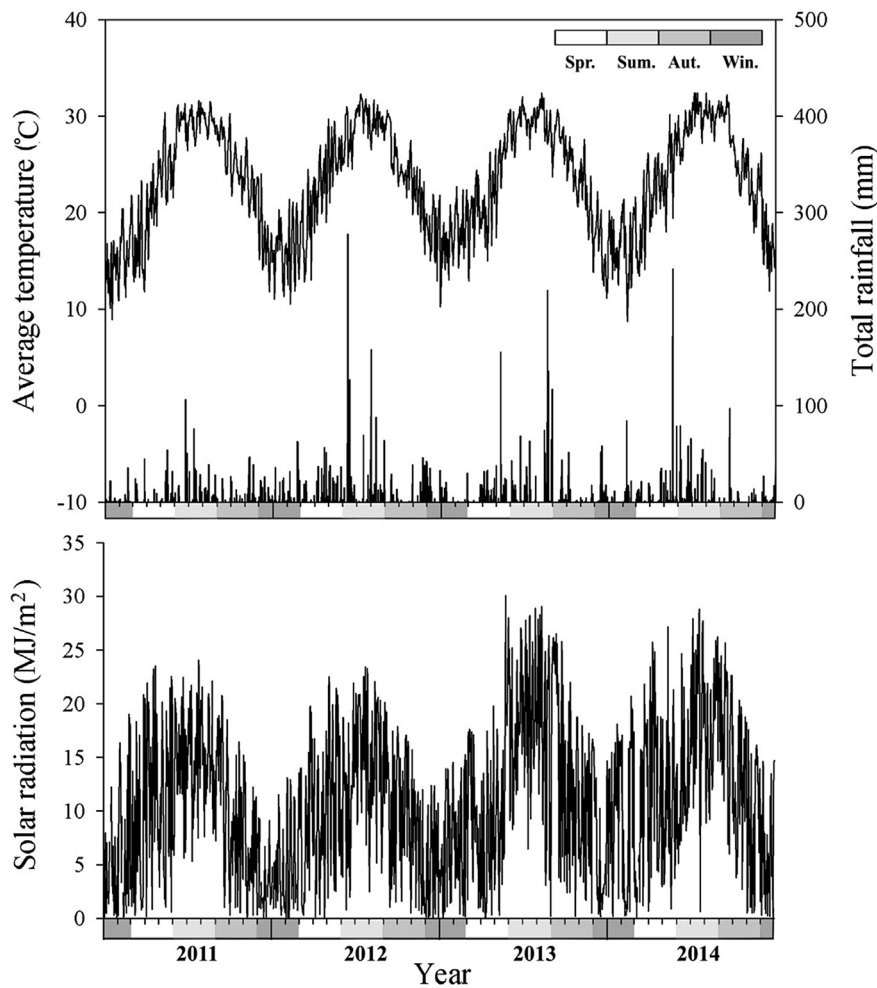


Fig. 1. Meteorological data in Taipei from January 2011 to December 2014.

living in temperate regions may face climatic constraints limiting their capacity to produce crops in the harshest period of the year: an extreme example is the Mediterranean dioecious *F. carica*, which only produces one or two crops per year and in which larval development is arrested during winter (Kjellberg et al., 1987). *Ficus* species may adapt to temperate areas by modifying their year-round phenology: For example, the phenology of the *F. tikoua* northernmost population, in China, has converged towards the phenology of *F. carica* (Zhao et al., 2014). However, in most fig species, the number of trees bearing figs simply decreases during the unfavorable season (Yang et al., 2013; Bain et al., 2014). Additionally, several of the species bear figs at different developmental phases, thus extending the window of receptivity (Yang et al., 2013; Bain et al., 2014). However, in many monoecious species, intra-crown synchrony is very marked (Bronstein et al., 1990): all figs on a tree become receptive to pollination more or less simultaneously and are often mainly pollinated on a single day. In humid tropical regions, asynchrony within the tree population can be constant throughout the year, while in subtropical regions, synchrony within tree may be relaxed (Bronstein et al., 1990; Bronstein and Patel, 1992).

Therefore, in this study, a 45-month survey was conducted to explore whether two monoecious and cauliflorous fig species produce synchronous crops in a subtropical area with clear seasonality. The aim of this study was to determine if the reproductive phenology of the two studied fig species, that have very different climatic affinities, is sufficient to locally maintain the pollinating fig wasp population. Moreover, as fig production is on older wood, and is hence not necessarily linked to vegetative growth, the study investigated if the vegetative and reproductive phenologies are independent from each other. The effects of

meteorological factors on fig production and crop onset were also evaluated.

2. Methods

2.1. Study species and study site

Ficus subpisocarpa Gagnep. (Ex. *Ficus superba* (Miq.) Miq. var. *japonica* Miq.) and *F. caulocarpa* (Miq.) Miq. both belong to section *Urostigma* of subgenus *Urostigma* (Berg and Corner, 2005). The distribution of *F. subpisocarpa* is mostly continental; the subspecies *pubipoda* is restricted to Indochina (from Peninsular Malaysia to Vietnam), whereas the distribution of the subspecies *subpisocarpa* (the subspecies investigated in this study) extends to eastern China, Taiwan, and southern Japan (Berg, 2007). By contrast, *F. caulocarpa* has a more tropical distribution with Taiwan at its northern limit and New Guinea at its southern limit (Berg and Corner, 2005). Both *F. subpisocarpa* and *F. caulocarpa* are monoecious hemiepiphytic trees that can reach up to 12 m and more than 20 m, respectively. A monoecious fig has five developmental phases (Galil and Eisikowitch, 1968): phase A (prefloral), phase B (female wasp receptivity), phase C (development of seeds and wasp larvae), phase D (adult wasp emergence from the fig), and phase E (ripening). These two species are pollinated by fig wasp species belonging to the genus *Platyscapa* (Chalcidoidea, Agaonidae, Agaoninae *sensu* Cruaud et al., 2010), and they produce numerous small ramiflorous figs that attract many frugivores, including bats, birds, primates, and other mammals (Otani, 2001; Su and Lee, 2001; Shanahan et al., 2001; Corlett, 2006; Sreekar et al., 2010).

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