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The phenology and potential for self-pollination of two Australian monoecious fig species

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Abstract

In this preliminary study, the reproductive phenology of two monoecious fig species, *Ficus racemosa* and *F. rubiginosa*, was examined in tropical Australia. Syconia (inflorescences) occurred on both species all year round, but pre-floral and interfloral syconia were much commoner than the wasp-receptive and wasp-emitting phases in both species. The temporal overlap of the wasp-receptive and wasp-emitting phases on a single tree indicated that self-pollination was possible in both species and that pollinators may sometimes persist through multiple generations on one tree. This sexual phase overlap was commoner in *F. rubiginosa* than in *F. racemosa*. The two species also differed in their general within-tree asynchrony, with a higher diversity of phases on *F. rubiginosa* than on *F. racemosa*. The time from syconium initiation to ripening was very similar in *F. rubiginosa* (mean = 48.51 days) and F. *racemosa* (mean = 43.53 days). However, there was much more variation within and between trees for *F. rubiginosa*. In addition, the wasp-receptive phase was found to last up to 5 days (mean = 4.38) in *F. rubiginosa*. Such longevity should contribute substantially to local pollinator population persistence. Future work should use genetic studies to determine whether self-pollination is common in these fig species.

Keywords: *Ficus*, Moraceae, fig wasp, phenology, pollination, mutualism

1. Introduction

Fig trees (Moraceae: *Ficus*) and their pollinating wasps (Chalcidoidea: *Agaonidae*) constitute a classical example of insect-plant coevolution (Bronstein and McKey, 1989; Janzen, 1979). Their interaction is an obligate mutualism, in which figs and their fig wasps depend on each other to complete reproduction. Fig ovules are the only place where wasp offspring develop, while female wasps are the only dispersal vectors of fig pollen. Interactions between the two partners occur inside the syconium, an enclosed inflorescence containing hundreds, or even thousands, of unisexual fig flowers.

Galil and Eisikowitch (1968a,b) defined five characteristic phases of syconium development that emphasized the flowering progression and interaction with wasps in monoecious fig species. When new syconia are initiated (phase A, pre-female) all flowers are immature. During female phase (B), female flowers are sexually mature and are pollinated by female wasps that enter the receptive syconia through a narrow tunnel (the ostiole). Following pollination, the ostiole closes and there is a long interfloral (C) phase, during which seeds and wasp offspring mature. Next is the brief male phase (D), when male flowers are mature and liberate pollen that is dispersed by the female wasps that emerge. Finally, the syconium swells and ripens and is often eaten by birds, bats or other frugivores (E phase, postfloral).

It is the short female (B) and male (D) phases that are most important in terms of pollination and pollinator reproduction. Specifically, wasps emerge from D phase syconia and must enter B phase syconia. In many figs this involves dispersal between plants, because there is developmental synchrony of syconia and hence a single tree will not have B and D phases present at the same time. However, few studies have actually quantified the degree of

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within-crop synchrony and tested whether wasps can enter syconia on their natal tree (Bronstein and Patel, 1992). Monoecious *Ficus* species often show traits that limit self-pollination, suggesting it may be detrimental. For example, the temporal separation of male and female phases within a given syconium prevents self-pollination at the spatial scale of the syconium (Bronstein and McKey, 1989). *Ficus* is also well-known for remarkable asynchrony of flowering between trees, such that pollinators leave their natal trees and enter and pollinate receptive syconia on other trees (Anstett et al., 1997; Bronstein and Patel, 1992). Indeed, asynchronous population-level flowering is a necessary condition for the mutualism to persist, because the pollinating wasps have a very short life-cycle.

Although within-tree synchrony is common, individual trees can have syconia at different phases and the potential for B–D phase overlap (Bronstein and Patel, 1992; Cook and Power, 1996; McPherson, 2005). Such within-crop asynchrony was suggested as an adaptive strategy for fig trees to enable their pollinators to survive adverse climatic conditions (Bronstein, 1989; Janzen, 1979) and this idea persists, despite a lack of convincing evidence. It is also clear that syconium phenology often shows some correlation with climatic conditions. For example, decreased flowering frequency in dry and cold seasons (Hill, 1967; Janzen, 1979). The presence of overlapping B- and D-phases on the same tree reduces the size of *Ficus* populations necessary to guarantee pollinator persistence and is of most potential benefit in small isolated populations, where pollinator arrivals may be limiting (Bronstein, 1989; McPherson, 2005). In support of this idea, Smith and Bronstein (1996) found greater within-tree asynchrony in small, isolated populations than in large ones in the neotropical fig species *Ficus insipida* and *F. petiolaris*.

Field observations suggest that B phase syconia are usually pollinated within a few days of receptivity. However, Khadari et al. (1995) found that the duration of receptivity of individual *F. carica* and *F. aurea* syconia protected from pollinator visits lasted from 2 to 3 weeks. Furthermore, syconia of both these species remain receptive for a few days longer when entered by only a single wasp. This is important as simulations show that the length of the receptive (B) phase is perhaps the most important contributor to the persistence of local pollinator populations (Anstett et al., 1995), but it also increases the possibility of self-pollination.

We studied the phenology and potential for self-pollination of two monoecious fig species, *F. rubiginosa* (section *Malvanthera*) and *F. racemosa* (section *Sycomorus*) in Townsville, Australia. *Ficus rubiginosa* is an Australian endemic species that occurs in both open and forest habitats across a wide geographic range (Dixon et al., 2001). It shows within-tree asynchrony in both temperate (Melbourne) and sub-tropical sites (Brisbane) (Cook and Power, 1996; McPherson, 2005), but has not been studied within the tropical part of its range. *Ficus racemosa* is a more widespread species, occurring throughout much of South and East Asia and reaching its southern limit in tropical Queensland (Berg, 1989; Chew, 1989). Some aspects of the phenology of *F. racemosa* have been studied in a sub-tropical area of China (Zhang, 2006), but not in the tropics or in Australia. We specifically asked the questions: (1) What are the seasonal phenological patterns of *F. rubiginosa* and *F. racemosa* in tropical Australia? (2) What is the potential for self-pollination in these species? (3) Do the phenological patterns observed at this tropical site differ significantly from observations of the same species at non-tropical sites? (4) How does developmental phase duration differ between the species?

2. Materials and Methods

Species and study sites

Ficus rubiginosa and *F. racemosa* are both common in the Townsville area of northern Queensland. We recorded the phenology of 24 *F. racemosa* trees and 22 *F. rubiginosa* trees from April 2005 to March 2006. All *F. racemosa* trees belonged to a single large population along the banks of Ross River. *Ficus rubiginosa* trees were chosen from 3 different sites: Ross River (n=4), Castle Hill (n=9) and Cape Pallarenda (n=9), because there were few trees at any one site.

Phenological observations

To study the phenology, we carried out a census of each tree once every two weeks for a period of 12 months. We recorded the presence/absence of each of the developmental phases A–E, following established criteria (Galil and Eisikowitch, 1968a,b; Smith and Bronstein, 1996), and focusing especially on the possibility of B–D phase overlap within a tree, which provides an opportunity for self-pollination (Bronstein and Patel, 1992; Cook and Power, 1996). We recorded the number of syconia in phase B and/or in phase D in each fig tree. Based on these data we were able to understand the progressive change from phase B to D and any overlap between these two phases. Phase A is the developmental phase in which syconia are newly initiated. Phase C is the developmental phase in which syconia have received pollinators.

Developmental phases and initiation mode within a crop

We determined the duration of the different developmental phases in each species by tagging individual syconia on their first appearance (phase A) and following them through to ripening (phase E) from May to July, 2005.

Table 1. The percentage of trees showing combinations of syconium phases, mean number of crops initiated and mean proportion trees flowering, from April, 2005 to March, 2006, and mean length in days of each syconium developmental phase (n=8 syconia) for *Ficus rubiginosa* and *F. racemosa*, from May to July, 2005.

Developmental phases	*F. racemosa* Tree×Census Dates=509	*F. rubiginosa* Tree×Census Dates=388	Syconium phase duration in days	
			F. racemosa	*F. rubiginosa*
A phase	65%	52%	4.38 ± 0.52	3.75 ± 0.71
B phase	41%	34%	2.63 ± 0.74	4.38 ± 1.30
C phase	86%	74%	28.00 ± 2.45	33.63 ± 1.60
D phase	32%	28%	2.50 ± 0.53	2.38 ± 0.52
E phase	43%	22%	6.13 ± 0.83	4.38 ± 0.52
ABCD	7.5%	9.3%	–	–
ABCDE	4.7%	5.7%	–	–
BD	8.4%	11.3%	–	–
Mean crops initiated	3.88	2.02	Total duration =	Total duration =
Mean proportion of trees flowering	85.8%	62.7%	43.63 ± 5.07	48.51 ± 4.65

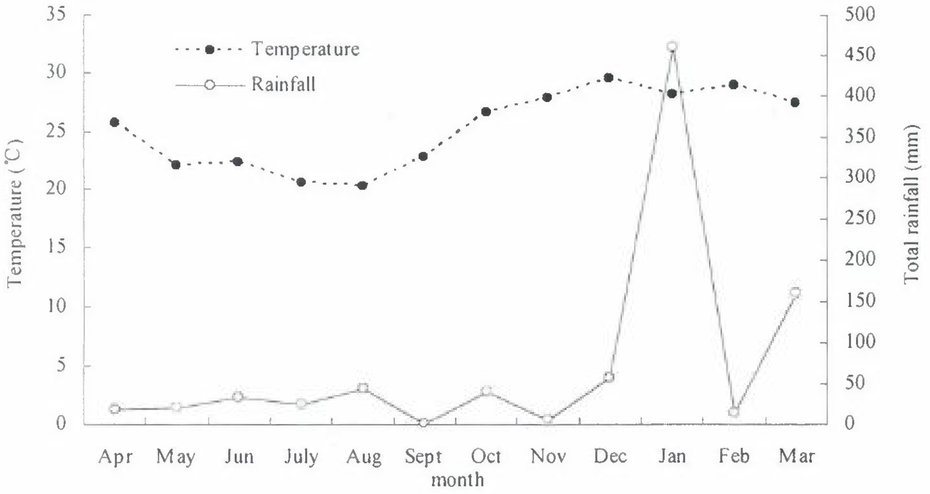

Figure 1. Average temperature and total rainfall in Townsville from April 2005 to March 2006.

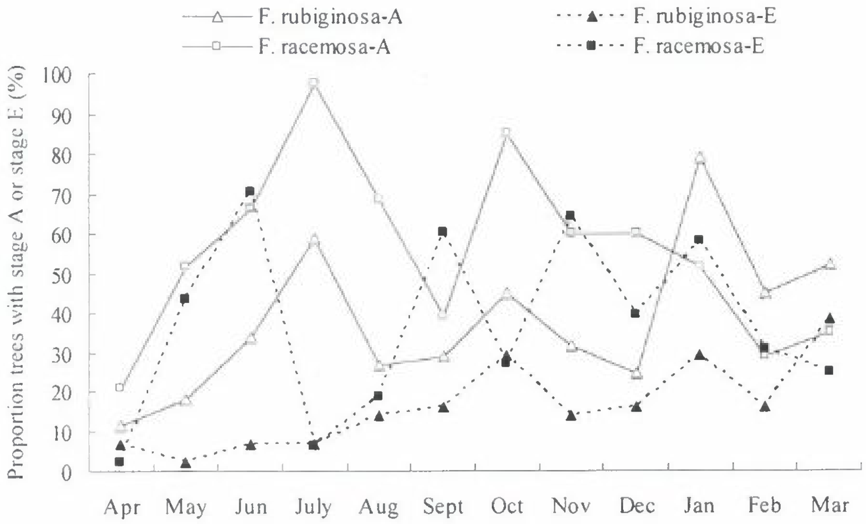

Figure 2. The proportion of trees with young syconia and immature flowers (phase A) and the proportion of trees with ripe fruit (phase E) throughout the year in *F. rubiginosa* and *F. racemosa*.

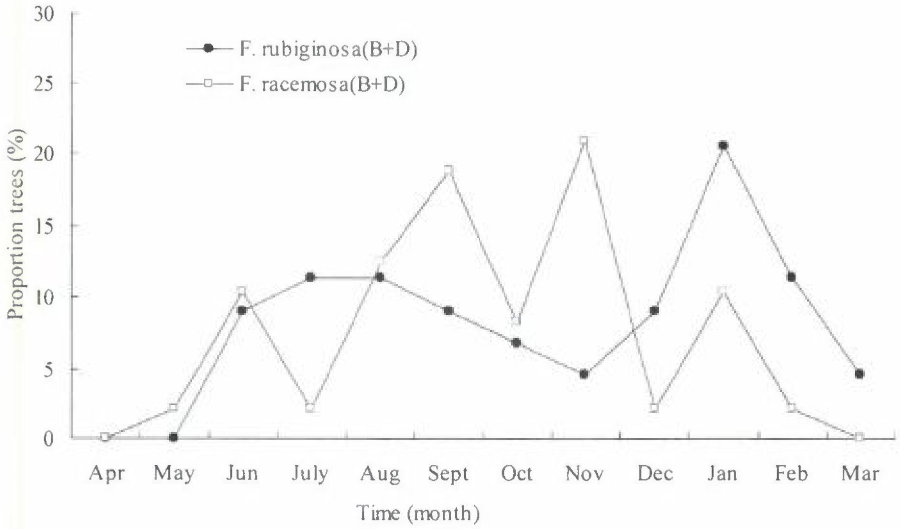

Figure 3. The proportion of trees with self-pollination (B+D overlap) potential in *F. rubiginosa* and *F. racemosa* during the study period.

Initially we tagged twenty figs on a single tree each of *F. rubiginosa* and of *F. racemosa*. However, many of the figs were removed by birds, other animals or ants. Furthermore some figs fell before all the developmental phases could be investigated. Thus, we were only able to do a detailed study of and gain complete A–E phase records for eight syconia each of *F. rubiginosa* and *F. racemosa*.

The initiation and duration of developmental phases within one crop were determined by recording the presence of every phase and their co-occurrence in an individual plant. One tree per species was surveyed daily from May to July 2005.

3. Results

Phenology

Townsville experiences a very seasonal climate with a strong summer peak (December–February) in rainfall, but less variation in temperature (Fig. 1). However, while the population-level phenology varied from month to month in both fig species, there were no marked differences (but see below on sexual phase overlap) that corresponded to the strong rainfall peak (Figs. 2–3). There were, however, important differences between the two species in their phenology.

The two species of fig selected for study (Fig. 4) vary in growth, form and size, especially in *F. rubiginosa*. We selected large trees (10–20 m high with trunks of 20–50 cm in diameter). Generally, *F. racemosa* trees bore syconia more often than *F. rubiginosa* trees; indeed all of the *F. racemosa* trees bore syconia during the period from May 2005 to Jan 2006. In contrast, the monthly percentage of *F. rubiginosa* trees with syconia was usually about 50% (Fig. 2). In *F. racemosa* all 24 trees initiated at least one crop during the study period with a mean of 3.9 crops per tree, and ripe fruits were also produced throughout the year (Fig. 2). There was considerable overlap of different phases on the same tree (Table 1), including BD phase overlap (8.4% censuses) and even ABCDE overlap (4.7%).

Not all *F. rubiginosa* trees flowered in the study period and the mean number of crops per tree initiated (2.0) was lower than in *F. racemosa*. Overall, we more often found *F. rubiginosa* trees with no syconia at all (37.3% of censuses) than *F. racemosa* (14.2%). The within-tree asynchrony was higher in *F. rubiginosa*. Thus we found a self-pollination potential, an overlap of phases B and D, in 11.3% of censuses or an overlap of all phases (ABCDE) in 5.7% of the censuses (Table 1). However, in both species, a BD overlap within a tree was relatively common, indicating considerable potential for self-pollination. There was an apparent lack of BD phase overlap in April and May in both species, while it peaked in July and August for *F. racemosa*, but was variable for *F. rubiginosa* (Figs. 2–3).

Developmental phase duration

The total time from syconium initiation to ripening was very similar in the two species (Table 1). The mean length of each phase was also quite similar in the two species, except the crucial receptive B phase, which lasted almost twice as long on average in *F. rubiginosa* (Table 1).

The developmental trajectories of individual syconia were more variable in *F. rubiginosa* than in *F. racemosa*. This is largely due to an extended phase A in *F. rubiginosa* (Fig. 5).

4. Discussion

Our study revealed substantial phenological differences

Figure 4. Growth form of syconia in the fig species studied. *Ficus racemosa* (top) and *F. rubiginosa* (bottom). *See cover illustration.*

between the two fig species studied. Overall, *F. rubiginosa* initiated crops less often and showed more asynchrony than *F. racemosa*. *Ficus rubiginosa* also had a greater proportion of trees without any syconia at a given time. These fig species belong to two distantly related sections of *Ficus* (Chew, 1989) and it is likely that the monoecious habit evolved separately in each. Syconium phenology is probably correlated with phylogeny. Our preliminary observations of *F. obliqua* and *F. macrophylla* lead us to believe that other species in the section *Malvanthera* may also show high within-tree asynchrony.

Two major differences between our study species are in tree size and habitat. *Ficus racemosa* trees are larger (up to 25 m) and grow next to watercourses, while the *F. rubiginosa* trees in our study were smaller (up to 10–15 m) and grow in dry rocky areas. Water availability may be limiting for syconium production and probably contributes to the lower frequency of crops in *F. rubiginosa*. Another factor accounting for the lack of syconia may be the small size of the *F. rubiginosa* trees. *F. rubiginosa* also occurs in rainforests, where the trees achieve a much larger size (up to 15–20 m). It would be interesting to compare the phenology of *F. rubiginosa* at dry and wet sites.

In *F. rubiginosa*, a high level of sexual phase overlap may be a strategy that enables their pollinators to survive when trees grow in less favorable microhabitats, rather than an adaptation to adverse seasons. In other words, within-tree asynchronous phenology may be adaptive for these fig trees as they are thereby able to maintain a local supply of pollinator wasps.

The average syconium development time was very similar (44 or 48 days) in the two species, but varied more in *F. rubiginosa*. This was due largely to some syconia spending a very long time (up to 31 days) essentially "dormant" in A phase (Fig. 4).

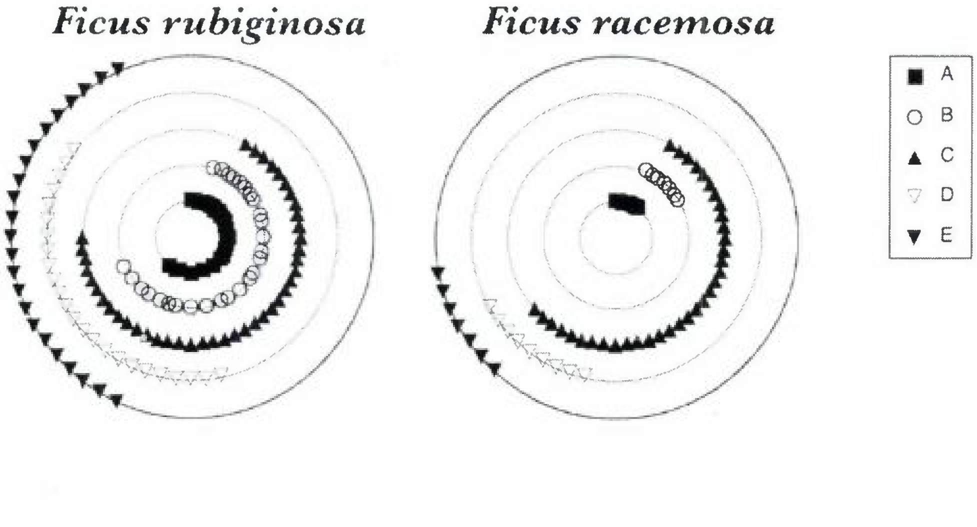

Figure 5. Variation in initiation and duration of developmental phases within one crop in *F. rubiginosa* and in *F. racemosa*. The syconium developmental phases are defined following Galil and Eisikowitch (1968a,b). One circle represents 60 days, the duration of the study period (May to July, 2005). The symbols denote the presence of a phase on a given date, not particular syconia.

Furthermore, in *F. rubiginosa* the receptive B phase was typically longer but more variable. We have also noticed from field observations, and attempts to manipulate foundress numbers, that there is an unusually large variation in the size of B phase syconia often within the same tree in *F. rubiginosa*. The largest ones approach the typical size of a D phase syconium. This size variation is unusual in comparison not only with *F. racemosa*, but also with other sympatric *Malvanthera* fig species (*F. obliqua* and *F. macrophylla* - JMC, pers. obs.).

Neither species showed strong seasonal effects on phenology, and both bore syconia all year round. However, self-pollination potential (BD overlap) did show a seasonal pattern. This was essentially the same in both species, but more marked in *F. racemosa* (Fig. 3). Overlap of the sexual phases B and D was seen in every month except in March, April and May. These months occur at the end of the rainy season and beginning of dry season and are expected to be generally favorable for figs. In contrast, BD overlap is higher in the (relatively) cooler dry-season months in the middle of the year. These patterns seem to support the notion that BD-phase overlap occurs mostly at less favorable times of year. However studies of *F. aurea* in Florida did not support the unfavorable season hypothesis (Bronstein and Patel, 1992) and *F. rubiginosa* in Brisbane shows rainy-season asynchrony (McPherson, 2005), suggesting that asynchrony may be a characteristic of the species rather than of the local conditions. Further study is clearly needed.

Both our study species showed considerable potential for self-pollination – higher than reported in most other studies (Bronstein and Patel, 1992; McPherson, 2005). Using controlled pollination, Hossaert-McKey and Bronstein (2001) showed that selfing had no negative effects on seed set and seed production in *F. aurea*, and suggested that inbreeding avoidance was not a significant factor in fostering outbreeding in this species. Given the considerable potential for selfing in *F. racemosa*, and *F. rubiginosa,* future work should establish whether this actually occurs, using genetic markers. Another question worthy of study is whether there is a demonstrable fitness cost to self-pollination.

Our data also provide benchmarks for further studies of phenological patterns in these two fig species. *Ficus rubiginosa* would be especially suitable for future work, since one could compare phenological patterns at different points in its geographic range, which essentially runs from North to South for 2500 km along the east coast of Australia. This could provide a good test for local adaptation in phenology (Bronstein, 1989).

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