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Spatial variation in pollinator gall failure within figs of the gynodioecious Ficus hirta

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Abstract

Figs, the inflorescences of Ficus species (Moraceae), contain numerous uni-ovulate flowers. Male trees of gynodioecious Ficus have figs that support development of pollinator fig wasp offspring (Agaonidae) and rarely produce seeds. Pollinator larvae develop inside galled ovules that expand rapidly after eggs are laid to fill the available space. Galls that fail to support successful larval development can be abundant and failures may influence oviposition behavior and modify realized offspring sex ratios. We examined pollinator reproductive success in figs of the Asian Ficus hirta where we had allowed entry by either one or two foundresses and prevented attack by parasitoids. At the developmental stage when adult offspring were about to emerge from their galls, we recorded where in the figs their galls were located, the distributions of sons and daughters in the galls and whether galls that developed closest to the periphery of the figs were more likely to fail. Foundress number had an effect on gall location, but not total offspring numbers. No spatial variation in the distribution of male and female adult offspring was detected. Overall, over 25% of the galled ovaries failed to support offspring development, and failure rates were independent of foundress number. More peripheral galls were more likely to fail in figs entered by two foundresses. Gall location in gynodioecious figs is determined largely by the extent to which their basal pedicels expand after galling. Competition for nutrients between galls, with those developing shorter pedicels being at a disadvantage, may explain the results. If pedicel length is related to timing of oviposition, then pollinator eggs laid later are less likely to survive.

Key words: fig; fig wasp; mutualism; spatial variation; gall failure; oviposition

Fig trees (Ficus spp., Moraceae), have a largely pan-tropical distribution, and form one of the largest genera of woody plants, with more than 750 species (Berg 2003). The mutualism between fig trees and their pollinating fig wasps (Agaonidae) is one of the most intensively studied of plant-insect interactions. Fig trees have unique enclosed protogynous inflorescences (figs, also called syconia) that depend on fig wasps (Agaonidae) for pollination. They also support diverse communities of non-pollinating fig wasps (NPFW). From one to several adult female pollinator fig wasps (foundresses) enter the figs in order to lay their eggs inside the many ovules that line their inner surface. Once inside, the females lay their eggs by inserting their ovipositors down the styles and they also either actively or passively pollinate them using pollen that they had carried from their natal figs (Weiblen, 2002). The mutualism has persisted largely unchanged for at least tens of millions of years (Ronsted et al., 2005; Compton et al., 2010) and is a model system for studies of coevolution (Weiblen, 2002). The offspring sex ratios of pollinator fig wasps are female-biased and the extent of this bias often varies according to the number of foundress females that share a fig (Hamilton, 1967). As a consequence, fig wasps have also become a model system for studies of sex ratio evolution (Kathuria et al., 1999). Fig wasp offspring sex ratios often broadly correspond to predictions based on optimality theory (Herre et al., 1997) and a simple mechanism of sex ratio adjustment based on variable oviposition site limitation in combination with laying mostly male eggs at the start of an oviposition sequence has been demonstrated in some species (Raja et al., 2008), although this can be modified by interactions with other foundresses sharing a fig (Greeff and Newman, 2011).

Fig trees display two breeding systems: monoecy and functional dioecy. In monoecious fig trees, approximately half of the described species, the trees produce individual inflorescences that perform both female (seed production and dispersal) and male (pollen production and dispersal) functions. Style lengths in these figs are variable and longer-styled flowers are more likely to produce seeds and shorter-styled flowers are more likely to produce pollinator offspring (Compton and Nefdt, 1990;

Ganeshaiah et al., 1995). The preference amongst foundresses for shorter-styled flowers means that most of their eggs tend to be laid in ovules that are initially more central, perhaps in response to selection to avoid NPFW, though other factors may also be important (Compton et al., 1994; Anstett et al., 1996; Jousselin et al., 2004; Yu et al., 2004).

In gynodioecious fig tree species there is specialization in sexual function, with the development of seeds and pollen-carrying fig wasps taking place on different individual trees. Trees that produce only seed-bearing fruits are functionally female, while others that support the development of pollen-carrying fig wasp progeny are functionally male. Female flowers in figs on male trees produce no seeds and have shorter styles, of relatively uniform length, and stigmas adapted to facilitate oviposition, rather than pollen capture (Verkerke, 1989). This allows oviposition to be rapid, especially in the first few minutes after entry (Raja et al., 2008). The ovules develop into galls that enlarge quickly to fill the available space. Early growth of the galls is likely to be induced by gland products released by females when they probe the ovules in search of oviposition sites, because it occurs before the larvae hatch (Ghana et al., 2015).

The eventual location of galled ovules within developing gynodioecious figs is determined by the degree of extension of the pedicels by which they are attached to the fig wall (Yu and Compton, 2012). Factors determining the extent of pedicel growth are poorly understood. Pedicel extension can be variable between the sexes, resulting in differences in average positions of galls containing male and female offspring. This can lead to sexual differences in mortality rates, because more peripheral galls are more likely to be attacked by parasitoids (Yu and Compton, 2012). More centrally-located galls can also produce larger pollinator offspring than those from more peripheral galls (Peng et al., 2014), which suggests that there are also nutritional advantages for larvae in more central galls, and that if gall failures are linked to nutritional factors they may be less frequent there. The relative ability of pollinators to stimulate pedicel growth inside male figs of gynodioecious species is therefore linked to their survival and can potentially influence their oviposition strategies. The ability to change the internal spatial structure of figs during their development may play a role at fig wasp population and community levels, and influence the stability of the fig and the fig wasp mutualism.

Some galled ovules in figs fail to support the successful development of pollinator offspring. They are referred to as ‘failed’ or ‘empty’ galls or ‘bladders’ Whether eggs were laid inside ovules that developed into empty galls is usually unknown, but there is evidence from the gynodioecious F. montana that a single egg is laid inside each empty gall (Ghana et al., 2012). Empty galls reach about the same size as successful galls, but are typically hollow shells, with no evidence of dead larvae inside. Gall failure is a major source or indicator of larval mortality among pollinator fig wasps and can exceed losses due to parasitoids. These failures of larval development may be due to competition for resources within the figs involving other pollinator galls or gall-forming NPFW. A lack of pollination of the ovule, damage caused by probing parasitoids, or any other factors that lead to damage or insufficient resources being available are other possible causes (Suleman et al., 2013). The significance of nutrition for developing larvae has been demonstrated in experiments where figs were entered by pollen-free fig wasp female and this resulted in less female-biased offspring sex ratios (Nefdt, 1989). The larval mortalities reflected in empty galls can therefore modify realized sex ratios. Male hymenopterans are haploid, and can be more resistant to nutrient shortages than females (Grosch, 1948), which suggests a possible mechanism for this effect.

Here, we describe controlled experiments that examined the relationship between foundress number, pollinator gall location and gall contents in figs of the gynodioecious fig tree F. hirta. The following questions were addressed: in the absence of non-pollinators, how are the ovules containing male and female offspring of pollinator females distributed within the figs, does their position vary according to the number of foundresses, and are gall failures located evenly with respect to distance from the outside of the figs?

Materials and Methods

Study site and species

Our studies were carried out at the South China Botanical Garden (SCBG) in Guangdong Province (N 23°10.246; E 113 °20.938´). The area has a tropical monsoon climate with short winter and a long warm and humid summer. The dry season extends from October to March, and the wet season from April to September. The annual mean temperature was 21.4～21.9℃ (Guangzhou Meteorological Bureau). Maximum temperatures are in July and August and the minimum temperatures in January (Yu et al., 2006).

The development of figs was described by Galil and Eisikowitch (1968). A-phase describes young immature figs. B- (female) phase receptive figs attract foundresses and allow them to enter, oviposit and pollinate. C-phase is the longest period and is where fig wasp offspring and seeds are developing. D- (male) phase figs are when fig wasp adult offspring mate and females become loaded with pollen before emerging and flying away in search of receptive figs. Finally, E-phase male figs shrivel and eventually fall to the ground, whereas female figs become soft and fleshy and offer a food reward to seed dispersers. Not all galled ovules support the successful development of fig wasp offspring. We refer to galled ovules that failed to support adult offspring as ‘empty galls’.

Ficus hirta Vahl. is a gynodioecious shrub or small tree, found commonly at the edges of forests and on cleared hillsides near habitations. Paired figs are borne along the branches. They are spherical or ellipsoid, with a diameter when mature of 10-20 mm. The production of young receptive figs is continuous throughout the year with figs produced both synchronously and asynchronously on individual plants and at the population level (Yu et al., 2006). Both male and female figs contain about 800 female flowers, and male figs also contain more than 100 male flowers (Yu et al., 2004; Yu et al., 2008). At maturity, the small, red and sweet female fruit are attractive to a variety of birds, which are the main seed dispersers (Corlett, 2006).

The recorded pollinator of F. hirta is Valasia javana (Hill) Mayr (Agaonidae, Agaonidae, Agaoninae）(Cruaud et al., 2010). They are possibly active pollinators (private communication from Finn Kjellberg 2016). At SCBG, more than 70% of F. hirta figs are entered by a single foundress (Yu et al., 2008), but in male figs, foundress numbers can range from 1-9 (mean ± SE = 1.7 ± 1.6: Yu et al., 2008). Pollinator offspring sex ratios under natural conditions are female-biased, but highly variable, with a mean proportion of males of 0.25 (Yu and Compton, 2012). The foundresses are not known to re-emerge from the first fig they enter. Three species of NPFW have also been reported from figs of this species (Mayr, 1885; Nair et al., 1981). At SCBG, NPFW were present in 68% of a sample of 107 figs, with numbers ranging between zero and 298 (mean ± SD = 41.93 ± 55.66 (Yu and Compton, 2012). Adult females of all three species oviposit from outside the figs, and NPFW can have negative effects on both plant and pollinator reproduction (Yu and Compton, 2012).

The influence of foundress number on offspring characteristics

Between June and August 2011, A-phase figs were covered with organdy cloth to prevent access to pollinator and non-pollinator fig wasps. When they became receptive, one or two foundresses that had emerged the same day from D-phase figs that had been bagged earlier were allowed to enter the figs. When two foundresses were introduced they had been obtained from different figs and the second female was introduced at least 30 minutes after the first (Table S1; Supplementary data). The bags were then returned around the figs to prevent entry by additional pollinators and oviposition by non-pollinators.

The figs were removed from the plants and their contents examined 46-51 days after the foundresses had been introduced, once the experimental figs had reached late C-phase and identifiable pupae/adults were present, but had not emerged from their galls. The spatial distribution of the galled ovaries relative to the inside of the fig wall was then measured from the wall to the outermost point of each ovule (Figure 1). If a fig wasp was present in the galls then the sexes of their occupants were then recorded. Details of the offspring from a total of six single-foundress and five two-foundress figs were recorded.

Data analysis

Analytical statistics were generated using SPSS 21.0 (SPSS Inc., Chicago, IL, USA). The total numbers of pollinator offspring, males, female pollinators, sex ratios and abortion rates were compared between one- and two-foundress figs using independent-Samples T Tests. The locations of galls containing male and female pollinators were compared using independent-Samples T Tests for one and two foundress figs respectively. Logistic regression examined the relationship between location of galls and the likelihood gall failure using General Linear Models (GLM) in figs with one or two foundresses.

Results

Pollinator offspring numbers and sex ratios

Figs entered by a single foundress contained an average of around 405 galled ovules, and those entered by two foundresses contained about 366 galled ovules (Table 1). Gall numbers were independent of foundress number, as were total numbers of failed galls, total offspring, male and female offspring and offspring sex ratios (Table 1, T tests, all with $P > 0.05$). Around 25% of the galls failed to produce adult offspring, a high failure rate that was evident in each of the figs (Table 1).

The locations of galls within figs

The locations of a total of 4260 galled ovules were recorded. The inner edge of the ovules at late C phase was always at least one mm from the fig wall, because the ovules themselves were about one mm in diameter. The amount of space available declined towards the centre of the (roughly spherical) figs, and this resulted in galls being less numerous in the most central areas of the figs (Figure 2. A-E). The mean distances of the galls from the fig wall was longer in figs entered by two foundresses, as were the distances of galls that contained adult offspring (Figure 2. A-E, Table 2).

The locations of galls that supported the successful development of pollinator offspring (Figure 2. C) were broadly similar to the distribution of galls in general (Figure 1. A). Galls where male (Figure 2. D) and female (Figure 2. E) offspring developed were present throughout the figs, and were separated from the fig wall by a similar range of distances. Mean distances from the fig wall of galls containing male and female offspring were not significantly different in figs entered by one foundress (T = 1.658; P = 0.098) or two foundresses (T = - 1.150; P = 0.250). Within individual figs, mean distances from the fig wall of galls containing male and female offspring in each fig were also generally not significantly different, but there were exceptions (Table 3).

Although some gall failures occurred throughout the figs, the likelihood of gall failure were not uniform (Table 4; Figure 3). In figs entered by a single foundress this trend was not significant (GLM: F = 5.053, P = 0.088), but in figs entered by two foundresses the likelihood of failure among peripheral galls was higher than in more central gall (GLM: F = 49.967, P = 0.002). Within individual figs, mean distances from the fig wall of failed galls were generally not uniform and the likelihood of failure among peripheral galls was higher than in more central gall, but there were exceptions especially in figs entered by one foundress (Table 4).

Discussion

Around half of the female flowers inside the F. hirta figs were galled by the foundress females. The entry of a second foundress shortly after the first did not result in more ovules being galled, although genetic analysis confirmed that both females were contributing to the total number of offspring produced (H. Yu, unpublished). Oviposition sites were not limiting and interference between pairs of foundresses active in the figs at the same time is likely to have been responsible for the large reduction in eggs laid by each female in shared figs. The heads of Valisia javana females suggest that foundresses sharing the same fig are aggressive to each other (Finn Kjellberg, Personal Communication 2016), and any fighting may have also damaged some females. Gall failure rates in the figs were high, implying mortalities among pollinator offspring of around 25%, despite an absence of parasitoids. Although the addition of a second foundress did not alter the number of ovules that were galled, nor their likelihood of failure, it resulted in small changes in the distribution of galls within the figs, which on average were located slightly further from the fig wall. This may have been the result of the two-foundress figs growing slightly larger, if longer pedicel lengths were a result of more resources being drawn to the figs, but given that one- and two- foundress figs contained similar numbers of galls, there is no obvious mechanism to achieve this, unless ovipositing females were committing more resources per gall in shared figs. If there is a trade-off between the number of flowers galled by an individual female and the extent of gall-inducing factors that are deposited into each flower, then average pedicel elongation might be expected to be greater in figs containing two foundresses than in figs where a single female galled a similar number of flowers. In addition, in situations where survivorship is linked to the extent of pedicel elongation, females that achieve greater elongation will be at a competitive advantage in shared figs, and selection may favour females that generate greater gall-induction, even if this risks laying fewer eggs in total. Alternatively, a non-adaptive explanation may be that the slower oviposition rates achieved in shared figs results in more gall-inducing compounds being released each time a foundress oviposits.

In gynodioecious Ficus species gall location is largely determined by elongation of the pedicels that takes place after oviposition, and is the result of manipulation of plant growth by the ovipositing females (Yu and Compton, 2012). A previous study utilizing naturally-pollinated and NPFW-accessible F. hirta detected spatial variation in the distribution of male and female pollinator offspring, with galls that contained males tending to be more centrally located (Yu and Compton, 2012). No such pattern was detected in these controlled experiments. The concentration of male offspring towards the centre of a fig can result in differential mortality rates that change their realized sex ratio, because female offspring are more likely to be killed by parasitoids (Pereira and Prado, 2005). Our experimental figs were free of NPFW, but the large numbers of empty galls generated under our experimental conditions also had the potential to change the pollinators' realized sex ratios, if the likelihood of gall failure was skewed towards one or other sex.

Ever since the pioneering studies of Galil and Eisikowith (1968), 'bagging' has been the most widely-used experimental technique employed in studies of fig tree pollination (Anstett et al., 1996; Zavodna et al., 2005; Dunn et al., 2011; Kjellberg et al., 2013; Peng et al., 2014; Raja et al., 2015). Bagging involves the placement of fine-mesh bags around developing figs to prevent or manipulate pollinator entry into figs and to prevent or control oviposition by NPFW. Figs that develop within bags may be subjected to atypical physical conditions and may also be more prone to some plant feeders such as mealybugs. Reflecting this, high rates of empty-galls have sometimes been reported from such experiments, sometimes in excess of 30% of all the galls present. The rate of gall failture we recorded in our experiments may therefore have been increased by the presence of the bags around the figs, though failed galls are nonetheless also a feature of most naturally-pollinated figs (Zavodna et al., 2005).

The galled ovules in figs of F. hirta that were developing closer to the periphery of the figs tended to be more likely to be empty than more central galls, especially in figs entered by two foundresses. If eventual pedicel length is related to timing of oviposition, then pollinator eggs laid later are less likely to survive. Later-generated galls can also be more likely to contain female offspring (Yu and Compton, 2012) and realized sex ratios could have been modified as a result, but this was apparently not the case. More peripheral galls have shorter pedicels than more centrally-located galls and their poorer pollinator survival rates may be a reflection of a reduced ability to compete for nutrients with other galls within the figs. Conversely, the spatial pattern we detected may be a reflection of early pollinator mortalities that inhibited subsequent pedicel growth. Whatever the reason, gall failures in figs are widespread and often numerous and as a significant mortality factor for pollinators, their causes and consequences merit further study.

Competition for resources among pollinator offspring developing within shared figs, and in particular variation in competitive ability related to the position of natal galls, also has implications for the host plants, and for the nature of their relationship with pollinator fig wasps. The stability of the mutualism between monoecious fig trees and their pollinators is dependent on a lack of over-exploitation of ovules by the pollinators, because this allows both seeds and pollinator offspring to develop in the same figs (Nefdt and Compton, 1996; Herre, 2008). Lower survivorship and quality of offspring developing in more peripheral galls contributes to this balance between male and female reproductive functions in the plants (Jousselin et al., 2001; Anstett, 2001). Monoecy is believed to be the ancestral condition within the genus Ficus (Weiblen, 2000; Ronsted et al., 2005). Among functionally dioecious species, maximization of fig wasp reproductive success in male figs is advantageous for both partners in the mutualism, and floral characters such as stigma shape and style lengths clearly make oviposition easier for the pollinators. The slightly lower success rate among more peripheral galls therefore seems unlikely to be beneficial for the plant, as well as the insects. The fundamental structure of Ficus inflorescences, with numerous flowers lining the inside of a sphere, generates constraints that reflect a need to fill a space where there is more room available at the periphery than the centre. This is the origin of the style length variation present in figs of monoecious species （and rarely among gynodioecious species as Ficus hispida var. badiostrigosa Corner 1960) and may inherently result in ovules located closer to the fig wall being less favourable for wasp development. That being the case, caution is required when ascribing adaptive significance to any spatial variation in gall success detected within monoecious Ficus speies, with no need to invoke this as evidence of selection for the maintenance of the mutualism.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. The contents of F. hirta male figs that had been entered by one or two pollinator females, with the time intervals between entry of the first and second individuals. Offspring sex ratios are expressed as the proportion of males.

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