Coevolution of reproductive characteristics in three dioecious fig species and their pollinator wasps

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Abstract
This study investigates dioecious fig species using a pollinator introduction experiment. Our aims were to determine: (1) whether there was a significant difference in foundress distribution between sexes per fig species; (2) whether fig size and foundress number affect reproductive success of dioecious figs; and (3) who is the 'controlling partner' in the fig/pollinator mutualism. Three dioecious fig species: *Ficus semicordata*, *Ficus hispida* and *Ficus tinctoria* from Xishuangbanna, China, were selected for this experiment. We found that there was no significant difference of the foundress number in female and male figs of *F. semicordata*, *F. hispida* and *F. tinctoria*. Also, the foundress number did not depend on the fig diameter. The numbers and the proportions of fig seeds and female wasp offspring significantly increased with more foundresses; and fig seed number was significantly higher than female wasp offspring in *F. semicordata* and *F. hispida*, but not in *F. tinctoria*. Our results indicate that figs are generally the 'controlling partner' in fig-wasp mutualisms in species with large figs, but not with small figs. Compared with published studies of reproductive success in monoecious figs, the dioecious figs seem to be more efficient in producing both seeds and wasp offspring when there is a high number of foundress.

Keywords: Dioecious figs, female wasp offspring, seeds, foundress distribution, reproduction success

1. Introduction

The species-specific mutualism between *Ficus* species (*Ficus*, Moraceae) and their pollinators is considered a prime example of co-evolution. This mutualism has often been used to examine the costs and benefits of reproductive success to each of the involved parties (Kjellberg et al., 1987; Herre, 1989; Herre and West, 1997; Patel and Hossaert-McKey, 2000), and how ecological and evolutionary factors affect the reproductive success of each partner (Janzen, 1979; Kjellberg et al., 1987; Compton and Hawkins, 1992; Anstett et al., 1997). These studies have revealed conflicts of reproductive interest between the two parties (Herre, 1989; Bronstein, 1992; Weiblen et al., 1995; Herre and West, 1997). So far, most of these issues have only been studied in monoecious *Ficus* (Patel and Hossaert-McKey, 2000).

There are approximately 750 tropical and extra-tropical fig species (*Ficus* spp., Moraceae) that are pollinated by highly specific wasps (Hymenoptera: Chalcidoidea;

Agaonidae) (Hawkins and Compton, 1992; Berg, 2003; Yu et al., 2008). This mutualism is obligate; the fig pollen is dispersed by the wasps and the wasps complete their life cycle inside the figs (Herre, 1989; West et al., 1996). In monoecious figs, the conflict of reproductive interests between the two parties is obvious (Herre, 1989; Yu et al., 2008). The fig wasps pollinate flowers while depositing their eggs in some of the ovaries, i.e. not only do figs invest in producing their seeds but they also support the development of the offspring of the pollinators (Herre, 1989; Bronstein, 1992; Weiblen, 1995; Anstett et al., 1996a,b; Nefdt and Compton, 1996; Herre and West, 1997; Patel and Hossaert-McKey, 2000; Yu et al., 2008). Hypotheses have been raised to attempt to explain the evolutionary stability of the fig-pollinator interaction (Kjellberg et al., 1987; Grafen and Godfray, 1991; Weiblen et al., 1995), but they suffered from lack of empirical data especially for the tropical species (Weiblen et al., 1995). Janzen (1979) raised the question that a proportion of monoecious fig ovaries would be destined for wasps' eggs deposition and another proportion for seed production. To verify this hypothesis, reproductive outputs in terms of seeds and pollinators should be determined (Weiblen et al., 1995). Herre (1989)

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compared seed set and wasp production in 12 monoecious fig species in Panama and found that the reproductive interests of figs and their pollinators are divergent. Indeed fig size and the number of foundresses affect the reproductive success of the involved parties, and the fig seems to be the 'controlling partner' in this mutualism. Nefdt and Compton (1996), Anstett et al. (1997), Herre and West (1997) separately studied the reproductive success in monoecious fig species, and they found that the relative reproductive success of the partners depended on the number of foundresses.

However, monoecious fig species comprise only half of the fig species in the world, the other half being dioecious. In dioecious fig species, male trees produce figs containing pollen-producing male flowers and short-styled ovaries in which wasps can oviposit. On the other hand, female trees produce figs with only long-styled ovaries that prevent pollinators from ovipositing because their ovipositors are too short to reach the ovaries (Verkerke, 1989; Weiblen et al., 1995; Yu et al., 2008). The evolutionary conflicts between dioecious figs and their pollinators stems from the separation of wasp offspring and seed production between the two sexes of trees (Weiblen et al., 1995, 2001; Harrison and Yamamura, 2003; Yu et al., 2008). The fig wasps can only produce offspring in the male figs, and their offspring is subsequently needed to successful pollination of the female figs (Weiblen et al., 1995; Yu et al., 2008). However, fig wasps entering female figs cannot produce offspring, but just pollinate the flowers. The tension resulting from this conflict of reproductive interests is inherent in the relationship between dioecious figs and their pollinators (Herre, 1989). However, until now, there have been few studies on the fig-fig wasp mutualism and reproductive success in dioecious fig species (Patel and Hossaert-McKey, 2000). Corlett et al. (1990) compared seed set and wasp production between monoecious and dioecious figs in Singapore, by counting the number of wasp offspring and fig seeds, and found that the number of seeds in dioecious figs is higher than that in monoecious figs. Weiblen et al. (1995), Patel and Hossaert-McKey (2000), and Yu et al. (2008) separately studied fig-pollinator reproductive success in dioecious fig species. However, most of the studies on dioecious figs are based on counting the number of seeds and fig wasps in natural figs, and researches on combining the reproductive characteristics with the reproductive success between female and male figs were rare.

Based on reproductive characteristics in monoecious fig species, Herre (1989) comes to the conclusion that 1) fig size and number of foundresses affect the reproductive success of both the wasps and the figs; 2) the natural distribution of foundresses per fruit tends to maximize the reproductive success of the figs more than of the wasps. This suggests that the figs are generally the 'controlling partner' in the mutualism. Compared with monoecious figs,

several questions in dioecious figs remain to be answered. Using three dioecious fig species we will address the following questions: 1) Is there a difference in the foundress distribution between the two sexes? 2) Do fig size and the number of foundresses affect the reproductive success of the partners in the mutualism? And if they do, how does this work, and who is the 'controlling partner' of the mutualism?

2. Materials and Methods

Study sites and species

This study was carried out in the Xishuangbanna Tropical Botanical Garden, Yunnan, China, located at 21°41" N, 101°25" E, and an altitude of approximately 600 m. The climate is characterized by a dry, a rainy and a foggy season, lasting from March to May, June to October, and November to February, respectively. The annual mean precipitation is 1557 mm. The average ambient relative humidity is 86% and the average temperature is 21.4℃ ~22.6℃ (Yang et al., 2000; Zhu and Cai, 2005; Wang et al., 2005).

We studied three dioecious fig species. *Ficus semicordata* Buchanan-Hamilton ex Smith (section *Hemicardia*, subgenus *Sycomorus*) is pollinated by *Ceratosolen gravelyi* Grandi (*Ceratosolen*, Agaonidae, Hymenoptera) and grows to a height of approximately 3–10 m; has an average fig diameter in the receptive phase of 15.8±2.2 mm; and has pendulous fruits placed on prostrate leafless branchlets close to the ground (Zhou and Gilbert 2003). *Ficus hispida* Linnaeus (subsection *Sycocarpus*, section *Sycomorus*, subgenus *Sycomorus*) is a medium-sized free-standing tree pollinated by *Ceratosolen solmsi* Mayr (Agaonidae, Hymenoptera). Male and female figs are produced year-round. Figs are placed axillary on normal leafy shoots and also on leafless branchlets (Yang et al., 2002; Zhou and Gilbert, 2003) and the average fig diameter in receptive phase is 17.27±2.95 mm. *Ficus tinctoria gibbosa* (Blume) Corner (section *Palaeomorphe*, subgenus *Sycidium*) has an average fig diameter in receptive phase of 5.8±0.6 mm and is pollinated by the wasp *Liporrhopalum gibbosae* Hill (*Liporrhopalum*, Agaonidae, Hymenoptera). The figs are axillated on normal leafy shoots and are paired or clustered (Zhou and Gilbert, 2003).

Foundress distribution

To count the number of pollinators entering receptive inflorescences in both male and female trees in the three fig species (i.e., the number of foundresses), we sampled figs in August 2004 and from August 2007 to April 2008 in Xishuangbanna Tropical Botanical Garden. We sampled seven trees of *F. semicordata* (5 male, 2 female); 11 trees of

F. hispida (6 male, 5 female); and two trees of *F. tinctoria* (1 male, 1 female). Due to weather conditions only one fruiting female and one fruiting male tree for *F. tinctoria* were appropriate to do the experiment. We collected figs from the trees when the figs were in the B or pre-C phase, which represent the receptive stages and the stage when the galls begin to develop. We harvested between 24 and 165 figs per crop for *F. semicordata*, between 25 and 246 figs per crop for *F. hispida*, and between 11 and 26 figs per crop for *F. tinctoria*. We then cut each fig open and counted the foundresses trapped inside and those struck in the ostiole trying to come out whose head pointed toward the fig entrance (Peng et al., 2005).

Pollinator introduction

On each tree of the three species, three or four fig-bearing branches were selected when figs were in bud. They were enclosed in fine mesh nylon bags to prevent access from pollinators and parasites. When the enclosed figs reached the receptive stage, one, two, three or six foundresses were introduced into randomly chosen receptive figs (Jousselin et al., 2001). We used at least 25 figs for each treatment for each individual tree. After wasp introduction, bags were replaced around the figs until they became mature. When they were in phase D (characterized for male trees by wasp offspring coming out of the ovary; and for female trees by the seeds reaching maturity), the male figs were taken back to the laboratory, where they were each placed in tightly closed muslin bags (20 cm × 15 cm) (Xu et al., 2002; Bai et al., 2006). After the wasps emerged from the figs they were collected and separately placed inside labeled bottles with 75% alcohol. For each fig, the wasp offspring, parasitized ovaries (ovaries from which wasp offspring emerged), unparasitized ovaries (ovaries unaffected by wasps) and bladders (swollen ovaries within which no wasp offspring developed) were counted (Anstett et al., 1996; Yu et al., 2008). For female trees, the enclosed figs were collected and taken back to the laboratory where seeds and ovaries were counted.

Statistical analyses

To determine how foundress numbers varied with sex for each fig species in each crop (here, one crop means the samples in one tree), we used General Linear Model (GLM), Univariate test (SPSS, 16.0), using foundress number as the dependent variable, sex as fixed effects, crop (nested within sex) as a covariate. In another GLM Univariate Test, we used foundress number as the dependent variable, sex as fixed effects, crop (nested within sex) as a random effect, and sycomium diameter as a covariate, to test whether the diameter has effects on foundress distribution in sexes. We used Pearson Correlation statistics to test whether there is positive correlation between foundress numbers and the

numbers of seeds or female wasp offspring in each crop. Then, we used the Independent-Samples T-test, with seed and wasp offspring as the test variables. To test whether there was a significant difference between the mean number of seeds and wasp offspring per foundress within one species, we chose one female tree and one male tree per species.

3. Results

Foundress distribution

Fig. 1 shows proportions of foundress numbers in B- or pre C-phase figs of the three dioecious fig species from XTBG. Foundress numbers ranged from 1 to >6 in male and female figs of *F. semicordata*, *F. hispida* and *F. tinctoria*. In the three species, the mean number of pollinators trapped (foundress number) pre B- or pre C-phase figs (in such sequence as *F. semicordata, F. hispida* and *F. tinctoria*) was 1.6±0.1, 2.5±0.1 and 1.5±0.1 in the males (n=168, 402, 92, all crops combined), and 2.1±0.1, 2.7±0.1 and 1.7±0.2 in the females (n=194, 388, 25, all crops combined). For each of these three *Ficus* species, crops had no effects on the foundress distribution between fig sex (Univariate, *F. semicordata*: $F_{6,362}=3.04$, $P>0.05$, *F. hispida*: $F_{9,709}=0.50$, $P>0.05$ *and F. tinctoria*: $F_{2,92}=0.07$, $P>0.05$). Besides, there was no significant difference for the mean number of foundresses between female and male figs within three *Ficus* species (Univariate, *F. semicordata*: $F_{1,362}=0.05$, $P>0.05$, *F. hispida*: $F_{1,709}=1.99$, $P>0.05$ *and F. tinctoria*: $F_{1,92}=1.38$, $P>0.05$). With respect to the other variables, there was no significant correlation between foundress number and diameter in *F. semicordata* (Univariate, $F_{1,323}=3.76$, $P>0.05$), *F. hispida* (Univariate, $F_{1,409}=2.64$, $P>0.05$), and *F. tinctoria* (Univariate, $F_{1,118}=2.79$, $P>0.05$).

Reproductive characteristics of figs and fig-pollinating wasp

For *F. semicordata* and *F. hispida* the crops had significant effects on the number of both seeds and female wasp offspring (Univariate, *F. semicordata*, seeds: $F_{1,288}=26.50$, $P<0.05$, female offspring: $F_{1,126}=11.59$, $P<0.05$; *F. hispida*, seeds: $F_{1,87}=43.80$, $P<0.001$, female offspring: $F_{1,78}=16.34$, $P<0.05$). Fig. 2 shows that there were positive correlations in *F. semicordata* between foundress number and number of seeds (except for seeds number of tree 1) (Correlate, tree2: $r=0.46$, $P<0.001$) or female offspring (Correlate, tree1: $r=0.84$, $P<0.001$, tree2: $r=0.40$, $P<0.05$), *F. hispida* (seeds tree1: $r=0.40$, $P<0.05$, tree2: $r=0.47$, $P<0.005$; female offspring tree1: $r=0.46$, $P<0.001$, tree2: $r=0.35$, $P<0.05$). However, negative correlation was observed between foundress number and
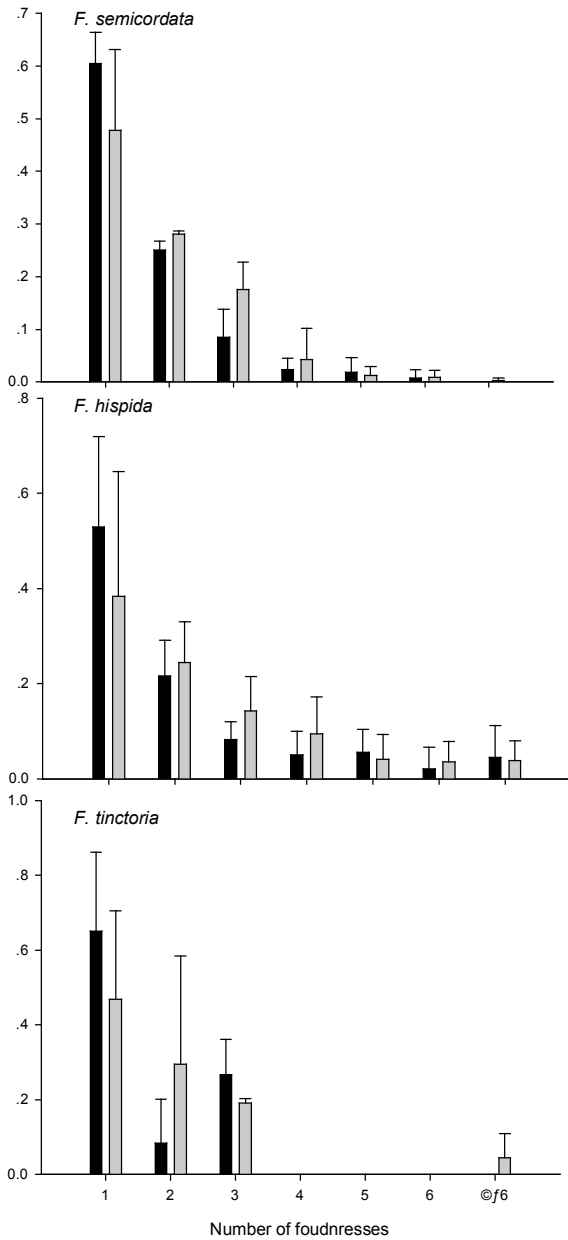
Figure 1. The rank distribution of foundresses over male (black bars) and female (grey bars) figs for the three studied fig species. (*F. semicordata*: male figs 168, female figs 194; *F. hispida*: male figs 402, female figs 388; *F. Tinctoria*: male figs 92, female figs 26)
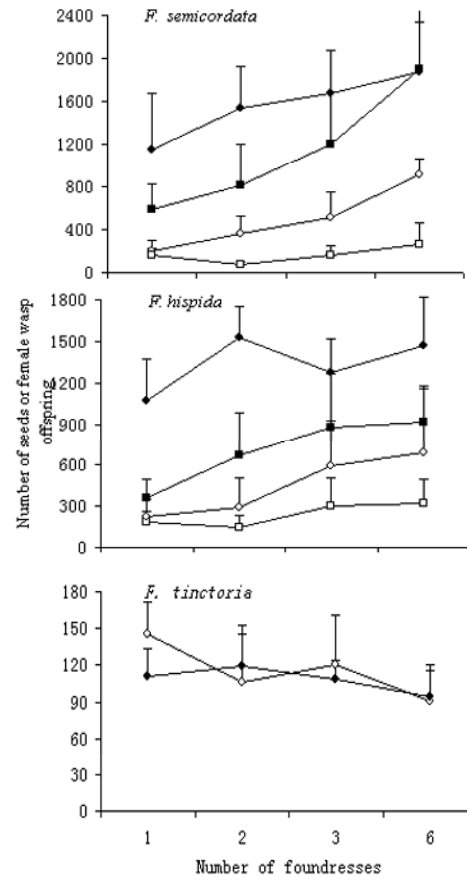

Figure 2. Number of foundresses and the mean number of seeds and female wasp offspring per tree per species. Black circle: mean number of seeds per treatment in female tree No.1. Black square: mean number of seeds in female tree No.2. White circle: mean number of female wasp offspring in male tree No.1. White square: the mean number of female wasp offspring in male tree No.2.

female offspring in *F. tinctoria* (r=-0.41, P<0.005), but it was not for number of seeds (r=-0.24, P>0.05). Also, the number of seeds was significantly greater than that of wasp offspring in *F. semicordata* and *F. hispida* (P<0.001 and P<0.005, respectively). However, there was no significant difference between the number of seeds and wasp offspring in *F. tinctoria* (P=0.467).

The mean number of seeds or female wasp offspring per foundress decreased with more foundresses (Fig. 3), which means that foundresses may only realize part of their reproductive potential due to the high average number of foundresses. Also, mean number of seeds produced per foundress is significantly higher than the mean number of wasp offspring per foundress in *F. semicordata* (P<0.001) and *F. hispida* (P<0.001), but not in *F. tinctoria* (P=0.904).

The proportions of seeds in female figs and female wasp offspring in male figs generally increased with more foundresses in *F. semicordata* and *F. hispida* (Fig. 4). Also, the proportions of seeds in female inflorescences are higher than proportions of female wasp offspring in male inflorescences (see Fig. 3). However, both the number of the total flowers developed in female and male inflorescences decreased with more foundresses in *F. tinctoria*. Yet, the proportion in female inflorescences is much higher than that in male inflorescences (see Fig. 3).

4. Discussion

This study is one of the few on coevolution of reproductive characteristics in dioecious fig species using a pollinator introduction experiment. Previous studies have examined factors affecting the reproductive success of monoecious figs (Janzen, 1979; Bronstein, 1988, 1989, 1992; Herre, 1989, 1996; Anstett et al., 1996). These studies concluded that fig fruit size and the number of foundresses influence the reproductive success of both the wasps and the figs. Our study tests this result in dioecious fig species. Surprisingly, we find that the number of foundress in female figs was not significantly higher than that in male figs and crops had no affects on foundress distribution. Also, the natural distribution of foundresses did not depend on the diameter in the three dioecious fig species; there was a significant increase in the number of both seeds and wasp offspring with foundress number, and the number of seeds was significantly higher than that of wasp offspring in larger figs like *F. semicordata* and *F. hispida*, while it decreased in smaller figs like *F. tinctoria*. Some of these results conflict with Herre's (1989) and Patel and Hossaert-McKey's (2000) results which were based on 12 monoecious and two dioecious figs, respectively.

Foundress distribution

Herre (1989) expected that the number of foundresses per fruit should be low, with less foundresses in male than in female figs. Because female wasps are the only pollinators for figs, the increasing of foundresses entering
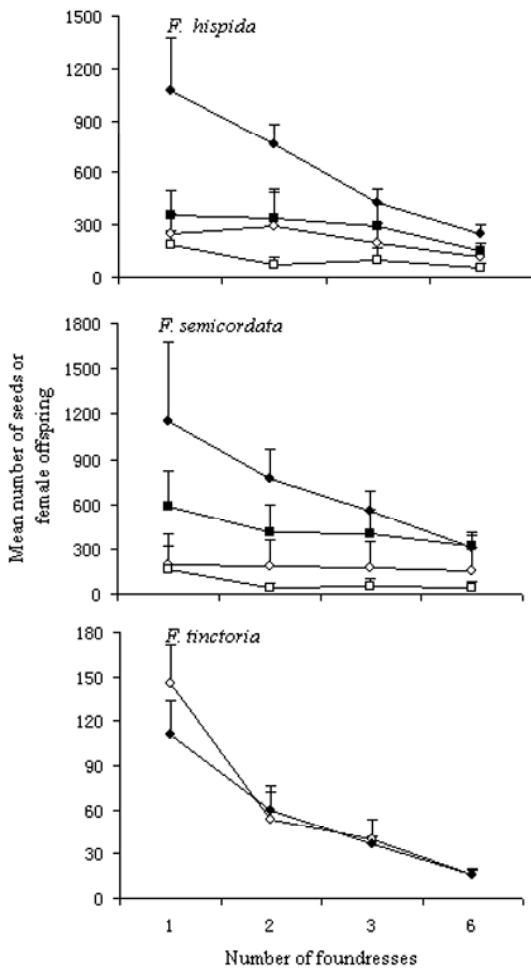

Figure 3. The number of foundresses and mean numbers of seeds or female wasp offspring per tree per species. Black circle: mean number of seeds per treatment in female tree No.1. Black square: mean number of seeds in female tree No.2. White circle: mean number of female wasp offspring in male tree No.1. White square: the mean number of female wasp offspring in male tree No.2.
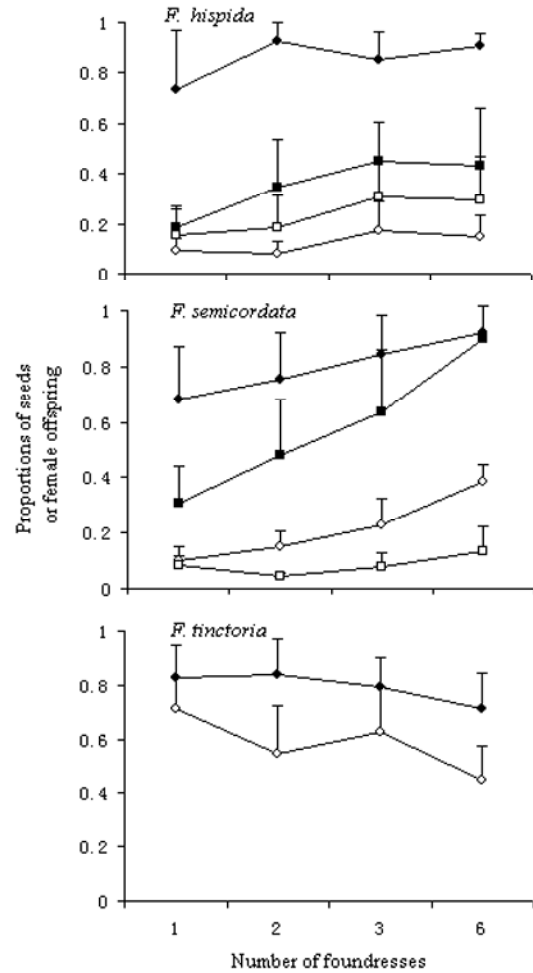

Figure 4. The number of foundresses and the proportions of seeds or female wasp offspring per tree per species. Black circle: mean number of seeds per treatment in female tree No.1. Black square: mean number of seeds in female tree No.2. White circle: mean number of female wasp offspring in male tree No.1. White square: the mean number of female wasp offspring in male tree No.2.

the figs should result in a less female-biased sex ratio (Hamilton, 1979; Frank, 1985; Herre, 1985). This could further lead to a considerable pressure on the fig-pollinator mutualism. In accordance with our results, Patel and Hossaert-McKey (2000) found in *Ficus exasperata* foundress number in female figs was no significantly different from that in male, but the foundress number was higher in females than in male figs in *Ficus hispida*. One reason is they collected figs within the same sex from many crops which may have influence on foundress distribution. However, problems with methodology could have led to the results in the work.

Foundress numbers in these three *Ficus* species did not differ between sexes. One explanation for the lack of sex differences could be that small pollinator population at the beginning of male tree receptivity results in rich, but not overabundant wasp numbers later on at the time of female fig receptivity (Patel and Hossaert-McKey, 2000). Another reason may be the time of the receptive stage for female and male figs seems similarly long (personal observation). Ostiole scales in *F. semicordata* are considerably looser than in *F. hispida* (personal observation), and if the looseness of ostiole scales is close in sexes, they would probably result in similar foundress distribution (Patel and Hossaert-McKey, 2000). For *F. tinctoria* the most important reason could be there exists one interesting phenomenon that pollinators who had entered could come out again later in a certain proportion (Ma et al., in press 2009), so the foundress numbers we collected were just the numbers in the figs in certain time and the results might not reflect the real situation.

Besides, we found that the foundress distribution on both sexes did not depend on the fruit diameters within the fig species. This seems to contradict the prediction made by Herre in 1989 and the results obtained by Anstett (1996a), but this outcome confirms the results of another study on two dioecious fig species (Patel and Hossaert-McKey, 2000). One explanation may be that the female figs try to mimic the size of the male, so that pollinators cannot distinguish between male and female figs. Another explanation could be the differences in diameters among trees, since Anstett's result (1996) were based on different crops among trees, not on figs in the same tree.

Reproductive characteristics of figs and fig-pollinating wasps

In our pollinator introduction experiment the figs of *F. semicordata* and *F. hispida* containing few pollinators tended to have lower numbers of seeds and wasp offspring than those containing more pollinators. These results are comparable with a study by Patel and Hossaert-McKey (2000), but contradict other studies which show a more or less constant proportion of seeds and wasps with foundress numbers varying between one and five (Anstett et al., 1996;

Nefdt and Compton. 1996).

However, in *F. tinctoria*, there was significant decrease in the number of female wasp offspring, again contradicting what was found by Patel and Hossaert-McKey (2000). This may be because the figs in this species are small sized (5.81±0.61 mm) so that one pollinator can use most of the female flower resources. Adding extra foundresses does not result in any increase in fertilized seeds or wasp offspring. The strong local mate competition and the space limitation could even lead to a decrease on wasps' female offspring. Further, the number of female flowers in female figs was significantly lower than those in male figs, which contradicts the result of Yu et al. (2008) in *F. hirta*.

We find that in *F. semicordata* and *F. hispida*, as with most dioecious studies (Harrison and Yanamura, 2003; Yu et al., 2008), female dioecious figs generally produce more seeds than male figs produce female wasp offspring. Furthermore, the proportion of seeds is much higher than the proportions of female wasps in each treatment. This seems to show that female functions of figs are more advantageous than male functions. However, this is contradicted by *F. tinctoria*, of which the mean number of seeds produced is not higher than female pollinator number. This study therefore confirms the prediction raised by Herre (1989) that physically small fruits are very efficient at the production of female wasps, while physically large fig fruits are relatively efficient at producing seeds.

In *F. semicordata* and *F. hispida*, the mean number of seeds or female wasp offspring per foundress significantly decrease, which shows that they may only realize part of their reproductive potential due to the high average number of foundresses. But in each treatment the mean number of seeds is higher than female wasp offspring; then, the average male reproductive potential decreases much faster with more foundresses, then less eggs pollinators can oviposite in the figs, which works against the reproductive interests of the figs (Herre, 1989). Besides, under natural conditions the foundress numbers are low. Therefore, we can conclude that the natural foundress distribution more clearly reflect the reproductive interests of the fig. This seems to indicate that figs are generally the 'controlling partner' in this mutualism in large figs like *F. semicordata* and *F. hispida*, which is similar to the monoecious fig/pollinator mutualism (Herre 1989, 1996), but not in the small figs like *F. tinctoria*.

The results further provide us with some implications for the stability of monoecy and dioecy breeding systems in figs. In comparison with the detailed studies of 12 monoecious fig species in New World made by Herre (1989), we conclude that there is a relatively higher efficiency in producing female wasp offspring in dioecious fig species compared to monoecious species in which average foundress numbers are high (Yu et al., 2008). On the other hand, it seems that it is more efficient to produce both seeds and female wasp offspring when there are low

numbers of foundresses in monoecious fig species (Herre 1989). Therefore, we hypothesize that dioecy arose from a lineage of monoecious fig species that were large and had high numbers of foundresses (Kerdelhue and Rasplus, 1996; Patel and Hossaert-McKey, 2000; Harrison and Yamamura, 2003; Yu et al., 2008). We also expect that reversions to monoecy happened in dioecious lineages with small fruits and few foundresses (Yu et al., 2008). Further, the results and the interpretations presented here should be considered preliminary and tentative; we need further studies, both within and across species, and more studies on comparisons between dioecious and monoecious fig species.

Acknowledgements

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