



Original article

Some pollinators are more equal than others: Factors influencing pollen loads and seed set capacity of two actively and passively pollinating fig wasps



Finn Kjellberg^{a,*}, Nazia Suleman^{b,1}, Shazia Raja^{b,2}, Abelouahad Tayou^a,
Martine Hossaert-McKey^a, Stephen G. Compton^b

^a CEFE-CNRS, UMR5175, BP5051, 34033 Montpellier Cédex, France

^b School of Biology, University of Leeds, LS2 9JT, UK

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ABSTRACT

The nursery pollination system of fig trees (*Ficus*) results in the plants providing resources for pollinator fig wasp larvae as part of their male reproductive investment, with selection determining relative investment into pollinating wasps and the pollen they carry. The small size of *Ficus* pollen suggests that the quantities of pollen transported by individual wasps often limits male reproductive success. We assessed variation in fig wasp pollen loads and its influence on seed production in actively pollinated (*Ficus montana*) and passively pollinated (*Ficus carica*) dioecious fig trees.

The ratios of number of male flowers on number of female flowers in a glasshouse-maintained *F. montana* population were highly variable. When fig wasps were introduced into receptive female figs, the resulting seed numbers were strongly linked to the numbers of pollinators that had been seeking access to pollen, relative to the number of anthers in their natal figs. In *F. carica* estimates of the amounts of pollen produced per fig and the quantities of pollen carried by emerging fig wasps suggest that less than 10% of the pollen is transported. Pollinators of *F. carica* that emerged earlier from figs carried more pollen, and also generated more seeds when introduced into receptive female figs.

We show here that all pollinators are not equally valuable and producing more pollinators is not necessarily a good option in terms of *Ficus* male fitness. Previous results on *F. montana* figs showed that only around half of the flowers where pollinators lay eggs produced adult offspring. The amount of pollen collected by young female fig wasps may be a major determinant of their reproductive success.

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“All animals are equal, but some animals are more equal than others”

Animal Farm by George Orwell

1. Introduction

Plant investment in male function includes the cost of pollen production and the cost of traits facilitating pollen dispersal (Bell,

1985). For a given level of resource investment into pollen, there is an obvious trade-off between pollen grain size and pollen grain number. Pollen size results from a trade-off in pollen donor plant strategy between probability of a pollen grain reaching a stigma (increasing with number of pollen grains) and effect of pollen grain size on its capacity to efficiently and rapidly germinate and fertilise an ovule (Yang and Guo, 2004). Generally, entomophilous plants produce heavy, sticky pollen for dispersal by generalist insect pollinators attracted to their flowers.

Among insect-pollinated plants, *Ficus* have achieved a unique feat: breeding pollen vectors is part of the male investment of the plant (Addicot et al., 1990; Anstett, 2001). Indeed, only the insects that have developed within an inflorescence will disperse the pollen of that particular inflorescence. This is not the case for most other nursery pollination mutualisms as for instance the *Yucca-Tegeticula* mutualism (50 plant species, Pellmyr 2003) and the Phyllanthaceae-*Epicephala* mutualism (500 plant species, Kawakita,

* Corresponding author.

E-mail address: Finn.Kjellberg@cefe.cnrs.fr (F. Kjellberg).

¹ Present address: Plant Protection Division, Nuclear Institute of Agriculture (NIA), Tando Jam 70060, Pakistan.

² Present address: The Institute of Plant and Environmental Protection, National Agriculture Research Centre (NARC), Park Road, Islamabad 44000, Pakistan.

2010) in which developing pollinator larvae have to be considered as parasites of the female function of the plant. Therefore, a fig tree is selected to optimise its relative investment into pollinating wasps versus pollen. As each pollinator larva develops at the expense of an ovule, some of the plant ovules have to be considered as male investment, while other plant ovules have to be considered as female investment. Hence optimising investment in male function will translate into variable proportions of anthers relative to female flowers depending on the species (Kjellberg et al., 2001). However, despite intensive studies of the fig-pollinating wasp mutualism (Herre et al., 2008), little is known about variation in quantities of pollen transferred and on ensuing variation in the numbers of seeds that are initiated by individual pollinators. Any factor affecting this efficiency, such as for instance male flower number or pollen grain size, should be under strong selection. *Ficus* are known for their small pollen grain size (Langeveld and van der Ham, in Berg and Corner, 2005). This would suggest that they have evolved under conditions where quantities of pollen transported by individual wasps are limiting male reproductive success. In this contribution we investigate variation in the quantities of pollen transported by individual wasps. Our prediction is that pollen is limiting. Hence we expect that individual pollinators carrying less pollen, or pollinators emerging from figs producing fewer male flowers than average, will achieve the fertilisation of reduced numbers of ovules when they colonise a fig.

The peculiarity of the fig system is due to the distinctive inflorescence of *Ficus* (the fig, or syconium). It is formed like a hollow ball, with its interior lined by florets. These can be staminate, pistillate, or both. The inflorescence is strongly protogynous. Pollen loaded fig wasps (foundresses) enter receptive figs to lay their eggs in the ovules of some flowers, and at the same time pollinate some more flowers. Then larvae and seeds develop. Some weeks later, wasps emerge into the fig cavity and load or become loaded with pollen in their natal fig before leaving it, in search of a new, receptive, fig. Because the pollinating wasps born in a fig transport pollen of that fig, the male reproductive success of a tree depends on the number of pollinators produced and on the quantity of pollen transported by each of these wasps. Hence *Ficus* trees should be selected to adjust the numbers of pollinators produced relative to the quantity of pollen produced per fig in order to maximise the efficiency of their male investment. However, while pollen grain number is already set at fig receptivity (Verkerke, 1986), data on variation in pollinator production per fig show that trees have limited control on this variation, which depends on fig visitation rates by pollinators and the actions of parasites (Herre, 1989). Because of this variance we predict that maximisation of the efficiency of fig tree male investment will result in some wasps carrying sub-optimal quantities of pollen for the tree and/or the insect and in some figs containing more pollen than will be used.

There are two distinct modes of pollen transport, active pollination and passive pollination. When pollination is passive, abundant pollen is shed within the figs and pollinators that developed within a fig get coated with pollen while leaving it. When pollination is active, pollen is not shed. The pollinators move to the anthers, pick pollen with their forelegs and load it into pollen pockets. On entering a receptive fig, they spread pollen on the stigmas, depositing with their forelegs a few pollen grains at each oviposition attempt. Figs of actively pollinated *Ficus* species exhibit lower anther/ovule ratios (Kjellberg et al., 2001). The compromise between quantity of pollen produced and numbers of wasps differs between the two pollination systems. Nevertheless this does not mean that pollination capacity of individual pollinators is not limiting in actively pollinated *Ficus* species. Indeed, some individual active pollinators do not collect any pollen (Jandér and Herre, 2010) and some present only partly filled pollen pockets (Michaloud et al.,

2005). Further, pollen pocket size is variable among pollinator species, and even among pollinator species co-occurring locally within the same figs (JY Rasplus, pers. com.). Because pollen grain size is similar in actively and passively pollinated *Ficus* species (Langeveld and van der Ham, in Berg and Corner, 2005), we predict that pollen loads of individual pollinators are limiting in both pollination systems, and that this has resulted in similar selection for small pollen size.

Fig trees are either monoecious or functionally dioecious (though anatomically gynodioecious). Monoecious fig trees produce figs containing both staminate flowers (that produce pollen) and pistillate flowers that produce either seeds or fig wasps to transport the pollen. Disentangling the role of selection on male versus female function on trait evolution is complicated in plants, as a given trait may contribute both to male and female function (Ashman and Morgan, 2004). This is typically the case for *Ficus*. Indeed, in monoecious species the selective pressures acting on floral ratios are particularly complex to analyse, because female flowers contribute to both male and female reproductive success. Addressing the ratio of wasps to seeds in terms of “how many babies do figs pay for babies” (Janzen, 1979) is misleading as the fig tree is selected to produce female flowers that will host wasps. Further, some of the female flowers may be better suited for seed production and some may be better suited for insect production (Anstett, 2001; Dunn et al., 2008a,b). In dioecious figs, the situation is simpler. Figs produced by female dioecious fig trees have female flowers with long styles that prevent pollinators from laying eggs, so they only produce seeds. In contrast, figs on male trees have pistillate flowers that facilitate oviposition, and produce only fig wasp offspring (and very rarely seeds). In these figs the pistillate flowers therefore contribute only to male reproductive success, via the production of pollen vectors. Hence, in dioecious fig species the effect on male reproductive success of variation in investment in male flowers versus flowers hosting pollinators is much easier to untangle, because of the separation of the sexes.

In this contribution, in order to test the predictions outlined above, we assess variation in the amount of pollen carried by pollinating wasps and its influence on seed production in two dioecious *Ficus* species, one actively pollinated, (*Ficus montana*), and one passively pollinated (*Ficus carica*). We show that all pollinators are not equal and that producing more pollinators is not necessarily a good option for the plants in terms of pollen transfer and hence male fitness.

2. Materials and methods

2.1. *F. montana*

The study was conducted on a glasshouse population of the dioecious *F. montana* and its active pollinator *Kradibia* (= *Liporrhopalum*) *tentacularis* (Grandi) maintained at the Experimental Gardens of the University of Leeds, U.K. The plants originated from seed collected at CIFOR HQ, Bogor, Indonesia and from the Krakatau Islands, Indonesia in 1995 (Moore et al., 2002). An undescribed parasitoid, *Sycoscapter* sp. was also present. The insect populations were established using fig wasps collected from the same locations the following year.

Mature figs of both sexes are between 8 and 12 mm in diameter. Fruiting within plants is typically continuous, with all stages of fig development often present on the same plant throughout the year. Male figs contain mainly female flowers, but also bisexual flowers, which are usually mainly or entirely located around the ostiole. Our counts of ‘male flowers’ refer to these staminate flowers. In *F. montana* each ‘male flower’ presents a single anther so that male flower number and anther number are equal.

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