

A gall midge inhabiting the figs of *Ficus benjamina* in Xishuangbanna, south-western China

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Abstract

A new species of gall midge belonging to an undescribed genus (Diptera: Cecidomyiidae) is recorded for the first time inhabiting the figs of *Ficus benjamina* in Xishuangbanna, south-western China. The gall midge larvae develop inside galled ovules and were present in over 86% of the figs, averaging $68 \pm S.E. 6.5$ galls per fig. Figs containing the midge produced fewer seeds and almost no fig wasps. Consequently, it had a major impact on both partners in the fig tree-fig wasp mutualism.

Keywords: Cecidomyiidae, fig wasps, galls, gall midge, mutualism

1. Introduction

Fig trees and their pollinating wasps are a striking example of mutualism between plants and insects. Fig trees (*Ficus* species, Moraceae) depend on pollinator fig wasps of the family Agaonidae to pollinate their flowers and in turn fig wasps require the ovaries of the figs to lay their eggs. Each fig tree species was thought to usually have its own single host-specific pollinating wasp (Cook and Rasplus, 2003), but recent work has revealed that several pollinating fig wasps per host may be common (Machado et al., 2005). Many other insects exploit the mutualism between figs and their pollinators, most notably the often large communities of non-pollinating fig wasps that develop within the figs, but do not transfer pollen (Compton et al., 1994; Bronstein, 1999). Several studies have shown that non-pollinating fig wasps have a negative impact on the production of seeds and of fig pollinating wasps (Compton et al., 1994; West et al., 1996), but it has been argued that the plant cannot exclude them because any defenses they developed would also harm their pollinators (Cook and Rasplus, 2003).

Other insects that feed on the developing figs and exploit the mutualism have received much less attention. These include species of true bugs, Heteroptera (Slater, 1972); beetles (Coleoptera, Perrin, 1992); moths, Lepidoptera (Williams 1928) and flies (Diptera). At least three families of flies are associated with figs. Vinegar flies (Drosophilidae) mainly utilize mature ripe figs (Harry et al., 1996), whereas scuttle flies (Phoridae) have larvae that feed on galled ovules and adult females that eat pollinator wasps (Compton and Disney, 1991). Finally, gall midges (Cecidomyiidae) have larvae that may feed within the fig cavity or develop inside galled ovules or galls in the fig wall (Felt, 1922; 1934; Williams, 1928; Roskam and Nadel, 1990). Here we describe the biology of a previously undescribed gall midge, a *Gen. et Sp. indesc.* near *Horidiplosis*, that is associated with the widespread S.E. Asian fig tree *Ficus benjamina*. J.C. Roskam is preparing a formal description of this new species and genus (personal communication). The taxonomic relationship between this undescribed species and other cecidomyiids associated with figs is unknown. No gall midges have been reported previously from this host.

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2. Materials and Methods

Study site and species

The studies were conducted from August to December, 2005 at Menglun, Xishuangbanna (101°15'E, 21°55'N), in south-western China. Situated at the northern margin of tropical South-east Asia, the climate of Xishuangbanna is tropical, with a rainy season from May to October and a dry season from November to April.

Ficus benjamina (section *Conosycea*) is a large monoecious fig tree native to the area. It is also a popular ornamental tree grown world-wide. At our study site, fruiting is highly asynchronous among trees, but on each tree it produces highly synchronous crops several times a year. The figs are produced in the leaf axils and are red or yellow when mature, reaching 12–25 mm in diameter. It is pollinated by *Eupristina koningsbergeri* Grandi, and at least 12 non-pollinating fig wasps also utilise this host plant in China (Bai et al., 2006).

Methods

In addition to observations on the general biology of the gall midges inhabiting *F. benjamina*, several samples were obtained for quantitative studies. Midge frequencies were estimated based on collections of 368 mature figs collected from six trees between August and December 2005. The figs were then cut open to determine whether or not they contained the prominent midge galls.

The impact of the presence of gall midges on the numbers of seeds and adult fig wasps inside the figs was assessed by comparing the contents of 30 mature figs that had gall midge exit holes with a similar number of figs from the same tree that lacked midge exit holes. The female fig flowers were then scored as either seeds, unhealthy seeds (seed-like in appearance, but often flat ellipses, either empty or full of liquid), fig wasp galls (all species), midge galls, bladders (either liquid-filled or empty galled flowers, possibly where a wasp had failed to develop) and unpollinated flowers. In addition, the contents of a further 60 early mature phase figs with gall midges were counted. These figs were bagged earlier so they could be located after they fell from the trees.

3. Results

Natural history

Adult females of the gall midge are readily distinguished from the males by their orange-red (not grey) abdomens, their retractile ovipositors, an absence of abdominal claspers and by their more cylindrical antennal segments that lack looped circumfila (a unique type of

sensilla found only on cecidomyiid antennae).

Females oviposit from the outside of the figs. The gall midge larvae developed inside galled ovaries, one per gall. Their galls were much bigger than those of the fig wasps and elongate and pocket-like rather than spherical (Fig. 1a). When the larvae were mature, the paler hollow ends of each gall extended across the full width of the fig wall, reaching to the surface (Fig. 1b). A crown-like ridge was formed around the opening of the gall two or three days before the insect finally emerged, and the growth of the gall caused the fig skin to split. Pupation took place close to the surface of the figs, with adults emerging over a period of several days and commencing prior to the emergence of the fig wasps, when the figs were still hard. The period from oviposition to adult emergence was about 25–35 days.

Emergence from the figs took place mostly at night. Adults wriggled out of the galls while still in their pupal cuticle, which was left partly exposed on the surface of the figs. Eclosion took about 7–15 minutes. Adult males tended to emerge earlier than females and could be seen walking on the surface of the figs where females were emerging (Fig. 1c). Once adult females, still in their pupal cuticles, were protruding from the fig surface by about three-quarters of their length they were grasped by one (or sometimes more) of the males that had been waiting there. The males then flew away with the females (Fig. 1d). The males kept hold of the female until she managed to eclose, and then mated for between 8–15 minutes, after which they disengaged and the male could return to the figs to seek out further female pupae. There was often intense competition between the males on the surface of the figs, with frequent struggles as they attempted to grab the emerging females.

Despite the gall midge activity being mainly at night, ants were common on the *F. benjamina* trees and were often seen capturing the adults. No parasitoids of the gall midges were reared.

Gall midge abundance and impact

Gall midges were present throughout the period from September to December 2005. Eight of the nine crops that were sampled had very high gall midge occupancy rates, and often almost all the figs were attacked (Table 1). The overall occupancy rate was 86.33% ($n = 368$ figs).

The gall midges had a dramatic impact on the other contents of the figs that they occupied. Affected figs contained hardly any fig wasps (28 out of 30 figs whose contents were counted) and about half as many seeds as unaffected figs on the same tree (Table 2). All 30 figs without gall midges produced both fig wasps and seeds. The differences reflected far greater numbers of bladders and unpollinated flowers in the figs with midge galls, but the numbers of unhealthy seeds were similar (Table 2).

Figs occupied by the gall midge contained between 3 and 254 midge galls (mean \pm SE = 67.8 ± 6.5 , $n = 60$ figs)



Figure 1. The gall midge associated with *Ficus benjamina* in Xishuangbanna. (a) (i) A large galled ovule produced by the undescribed gall midge (ii) The smaller galled ovule typical of fig wasps. (b) Gall midge emergence holes on the fig surface. (c) Adult male gall midges waiting for females on D phase figs. (d) Two male gall midges jostling with each other after having jointly carried the same female away from her natal fig. She is still encased within her larval cuticle.

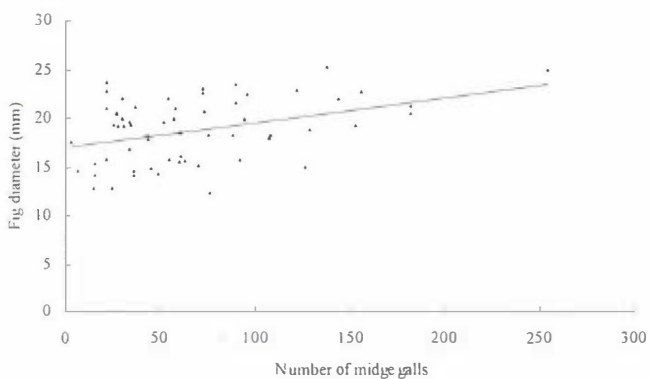


Figure 2. The relationship between the diameter of *Ficus benjamina* figs and the numbers of gall midge galls that they contained.

and because of the large size of their galls, fig diameter at maturity was positively correlated with midge gall density ($r^2 = 0.16$, $p < 0.001$, $n = 60$, Fig. 2).

The impact of the gall midges was progressive, with greater effects in figs that contained more galls. Amongst the 60 figs where midge galls were present (data combined from three trees) there was a very significant negative correlation between midge gall numbers and the numbers of seeds in the figs (Pearson correlation $r = -0.506$, $P < 0.001$), and the numbers of fig wasps (all species combined) (Pearson correlation, $r = -0.521$, $P < 0.001$).

Table 1. Occupancy rates of gall midges in figs of *F. benjamina*.

Trees and samples	Months (2005)	Sample size (figs)	Occupancy (%)
1	September	30	100.0
2	September	25	100.0
3a	September	34	100.0
3b	November	50	100.0
3c	December	50	100.0
4	November	42	19.1
5	November	50	66.0
6a	November	37	91.9
6b	December	50	100.0

Table 2. The impact of gall midges on the contents of *F. benjamina* figs (all the figs were collected from the same tree).

	Midge-free figs (Mean ± SE)	Figs with midge galls (Mean ± SE)
N figs	30	30
Midge galls	—	65.6 ± 11.8
Fig wasps	420.9 ± 29.1	0.2 ± 0.2
Bladders	79.9 ± 10.3	296.0 ± 33.5
Seeds	258.0 ± 22.4	135.5 ± 21.0
Unhealthy seeds	25.6 ± 12.9	28.1 ± 6.1
Unpollinated flowers	343.8 ± 31.9	698.7 ± 41.5
Total female flowers	1128.1 ± 42.6	1224.1 ± 27.3

4. Discussion

Although several other *Ficus* species were producing figs in the Xishuangbanna area at the time of this study, no gall midges were seen, suggesting that this undescribed species is host specific, at least locally. Its biology shares features with the New World species *Ficiomyia perarticulata* Felt which also has larvae that develop in galled ovules (or groups of ovules) and galls that push through the fig wall to the surface (Roskam and Nadel, 1990).

The presence of the midge galls in figs of *F. benjamina* did not seem to deter pollinators from entering the figs, as most of them contained seeds and all contained bladders (ovules assumed to have been galled by pollinators). The gall midge nonetheless had a negative impact on the reproductive success of both partners, but with more severe effects on fig wasp production than seed production. This was despite the midge galls appearing to be concentrated amongst the longer styled flowers of *F. benjamina*, which tend to produce seeds, rather than fig wasps. The large number of bladders in the figs suggest that the main effect of the midge galls may have been to divert nutrient resources away from the other contents of the figs, and that the developing fig wasps were more susceptible to this than the seeds. Interesting future studies would be to determine

the viability of seeds from figs which had contained the gall midge and to see whether pollinator and non-pollinator fig wasps are harmed to the same extent.

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