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The impact of a gall midge on the reproductive success of *Ficus benjamina*, a potentially invasive fig tree

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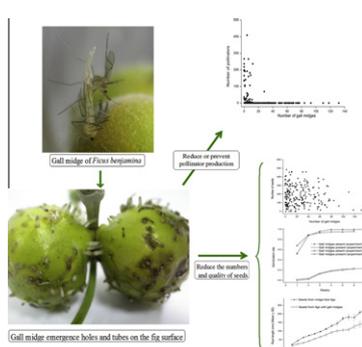
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HIGHLIGHTS

- ▶ We recorded the impact of gall midge on a potentially invasive fig tree.
- ▶ The gall midge decreases the numbers and quality of its host's seeds.
- ▶ It also reduces the number of pollinators, even prevent pollinator production.
- ▶ The host specific gall midge is an excellent candidate biological control agent.

GRAPHICAL ABSTRACT



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ABSTRACT

Fig trees (*Ficus* spp.) are popular ornamental trees that are entirely dependent on a mutualistic association with host-specific pollinating fig wasps for reproduction. They can become naturalized and invasive in countries where the associated pollinator is also established. Figs. (syconia) are also utilized by a diverse community of organisms that are potentially detrimental to the pollinators or seed production. *Ficus benjamina* is a widely-planted fig tree with the ability to establish outside its native range. We examined the impact of an undescribed gall midge species associated with *F. benjamina* within the plant's natural range in Xishuangbanna, south-western China. Observations on the levels of abundance of the midge together with fig abortion and seed germination rates showed that the gall midge had a strong negative effect on reproduction. The gall midge reduced pollinator survival and at high densities eliminated all pollinators, due primarily to premature abortion of figs. Seed numbers were only reduced at high gall midge densities, but seed quality, as measured by germination success and root growth rates, was greatly reduced whenever the gall midge was present. Within its presumed natural range the gall midge appears to be host specific, and given its dramatic impact on host reproductive success, is a potential candidate for the biological control of *F. benjamina*.

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1. Introduction

Ficus (fig trees, Moraceae) is one of the most important plant genera of tropical and sub-tropical forests, with over 800 species worldwide (Harrison, 2005). The diversity and widespread distribution of *Ficus* is reflected in the wide variety of animals recorded as feeding on their figs (syconia), the enclosed inflorescences that are unique to the genus. Over one thousand birds and mammals are known to feed on ripe figs (Shanahan et al., 2001) and they are considered 'keystone' species in tropical rainforests (Herre et al., 2008). Their importance for vertebrates stems from figs being easy to eat and because fig crops are often produced throughout the year, including periods when most other plants are not fruiting. The wide range of species that disperse fig seeds means that introduced fig trees, if they contain viable seed, have the potential to rapidly expand their range.

Maturation of figs (and fertile fig seeds) depends on pollination by host-specific pollinating fig wasps (Hymenoptera, Agaonidae) (Wiebes, 1979). Most fig species are pollinated by females of a single, unique species of agaonid. The female enters the fig via the ostiole, oviposits in some of the ovules and simultaneously pollinates several flowers. Oviposition and development of the larva results in ovule gall induction. On emergence of the next generation a few weeks later, the females mate within the natal fig, collect pollen and then disperse to new figs.

Figs. are also generally exploited by a complex community of host specialized chalcid wasps that do not transfer pollen. These wasps include gall inducing species, inquilines, kleptoparasites and parasitoids of both the pollinating fig wasps and non-pollinating chalcid species (Kerdelhue et al., 2000; Compton et al., 2009). They frequently have a negative impact on the fig–pollinator mutualism by killing pollinators or reducing seed production (Kerdelhue and Rasplus, 1996), but may also benefit the mutualism if they are detrimental to non-pollinating species (eg. a parasitoid of a non-pollinating gall-inducing species). It has been argued that the plant cannot exclude them because any defenses that develop would also harm their pollinators (Cook and Rasplus, 2003).

Other organisms that feed on developing figs or their pollinators have received much less attention. They include ants that prey on both pollinating and non-pollinating fig wasp adults (Compton and Robertson, 1988), moth and weevil larvae that bore into the figs and kill developing fig wasp larvae and seeds (Janzen, 1979; Bronstein, 1988), nematodes that feed on the figs and the pollinators (Herre, 1993), phoretic mites that feed on galled ovules (Compton, 1993) and several families of flies. The latter include vinegar flies (Drosophilidae) (Lachaise and McEvey, 1990), scuttle flies (Phoridae) with larvae that feed on galled ovules and adult females that prey on pollinator wasps (Compton and Disney, 1991) and several gall midges (Cecidomyiidae). The cecidomyiid larvae either feed within the fig cavity or induce galls in the ovules or fig wall (Felt, 1922, 1934; Williams, 1928; Roskam and Nadel, 1990; Bai et al., 2008).

Fig trees are widely planted as ornamental trees outside their native ranges and several have become significantly invasive in natural and semi-natural habitats in situations where their associated pollinator is also established (Stange and Knight, 1987; Starr et al., 2003). *Ficus benjamina* is indigenous to Asia and Australasia and is commonly planted, both within its native range and elsewhere. Species closely related to *F. benjamina* are significant invasive weeds in the USA and other countries (Oppenheimer and Bartlett, 2000), but because its pollinator has not become widely established, *F. benjamina* mainly represents a potential threat at present (Starr et al., 2003). Natural regeneration of *F. benjamina* has however been reported in Western Australia, where it is described as invading the lower Swan River in Perth (Starr et al.,

2003). It is native in North East Australia, which probably facilitated the introduction of its pollinator. In Florida, *F. benjamina* is found occasionally in disturbed sites across four counties where it has "escaped cultivation" (CAIP database at <http://plants.ifas.ufl.edu/node/161>, accessed January 2011), although the presence of its pollinator has not been confirmed (Stange and Knight, 1987; Boucek, 1988). *F. benjamina* is also commonly-planted in Hawaii, where Starr et al. (2003), recommended that its pollinator be placed on the injurious species list, because of the threat posed if its pollinator were to become established.

Despite the wide range of insects known to destroy fig seeds and eat their pollinators, biological control of fig trees using injurious fig-feeding insects has not been attempted. Predatory and phytophagous cecidomyiids have been used successfully to control a range of insect and plant pests (Meadow et al., 1985; Hinz and Muller-Scharer, 2000; Lloyd et al., 2005; Impson et al., 2008; Gagne et al., 2009; Post et al., 2010). Here we examine the biological control potential of an undescribed gall midge that utilizes the figs of *F. benjamina* in China, focusing on its impact on pollinators, premature fig fall, seed production and seed quality.

2. Materials and methods

2.1. Study site

This study was performed at the Xishuangbanna Tropical Botanical Garden (XTBG) in south-west China (21°55' N, 101°15' E, at about 555 m), at the northern margin of tropical South-East Asia.

2.2. Study species

F. benjamina (Subgenus *Urostigma*, Section *Conosycea* (Berg and Corner, 2005) has a wide distribution across Asia (Corner, 1965). The form which occurs naturally in tropical forests in China is *F. benjamina* var. *nuda*. It is widely planted in cities or gardens as an ornamental plant, both in China and elsewhere. Prolific crops (fig samples from a single fruiting event from a given tree) of small figs are produced in the leaf axils. Fruiting is synchronized within trees but occurs all year round, as different trees producing figs at different times. Mature figs are yellow and average 17.1 mm in diameter (SE = 0.26, n = 31). They are mainly dispersed by birds. *F. benjamina* is monoecious, so individual figs contain both seeds and pollinating fig wasps. It is pollinated by the agaonid *Eupristina koningsbergeri* Grandi, and at XTBG also supports 15 other species of non-pollinating fig wasps belonging to families other than the Agaonidae. Their detailed biology is unknown, but they include putative ovule gallers (three *Otitessellinae* spp. and four *Epicrypsomallinae* spp.), plus inquilines and parasitoids (five *Sycoryctinae* spp., two *Eurytomidae* spp. and one *Ormyridae* sp.).

F. benjamina figs at XTBG also support an undescribed species of gall midge (Diptera: Cecidomyiidae), belonging to an undescribed genus near to *Horidiplosis* (J.C. Roskam, personal communication). Its biology was described by Bai et al. (2008). Female gall midges oviposit from the outside through the fig wall, before pollinators have entered the fig. The larvae induce gall development of the ovary and develop singly within a gall cavity. The galls are larger than those induced by the pollinating fig wasps and resemble elongate tubes that radiate out from the centre of the fig and are open distally. When the larvae are mature, the distal end of the gall grows outwards, ultimately extending across the full width of the fig wall and reaching its outer surface. Two or three days before the adult midge emerges, a crown-like ridge is formed around the opening of the gall which causes the surface of the fig to split.

Pupation takes place close to the surface of the fig, with adults typically emerging from a fig over a period of several days. They start to emerge before the pollinating and non-pollinating fig wasps and while the figs are still hard. The gall midge has no known natural enemies.

The Gall midges generally take 1–2 months to complete their life cycle, with development times shorter in summer than in winter. This translates to at least six generations each year, but the adult gall midges have to disperse between trees to find figs at a suitable stage for oviposition, because each individual fig tree has a maximum of three crops annually. There is no evidence of diapause.

2.3. Methods

2.3.1. Natural fig collections

Eight trees were observed every 2 weeks from December 2009 to April 2010. When available, 100 figs at the developmental stage when pupal gall midges are present were removed to determine the proportion of the figs that were occupied by the gall midge. A total of 1800 figs from 18 crops, were sampled. In addition, 207 figs from eight crops were sleeved individually on the trees in fine-mesh bags (20 × 20 cm) to allow the insects to emerge naturally from the figs. Sample sizes ranged from 14 to 41 figs per crop. The sampled figs were individually dissected and the total numbers of female flowers, seeds, 'bladders' (unsuccessful empty galled ovules with unknown original contents), gall midges and adult pollinators were recorded.

2.3.2. Fig abortion

The relationship between the dates when figs were aborted by the trees and the first emergence of gall midges was investigated on one tree between August 25 and September 22 2009. Individual figs were enclosed on the tree in fine-mesh bags (20 × 20 cm) on the first day that one or more gall midges emerged. Each fig was then monitored daily until it was aborted by the tree. A total of 187 figs were sleeved in this manner.

2.3.3. Seed lengths and weights

Thirty seeds were collected at random from each of 10 figs of a single crop that had aborted 4 days after the first gall midges had emerged. This corresponded to the peak date of abortion for the crop. The combined weight of groups of 30 seeds and the maximum length and width of each seed was recorded. These parameters were compared against seeds obtained from 10 midge-free mature figs from the same crop.

2.3.4. Seed germination and seedling growth

Germination rates of seeds were compared using groups of 20 seeds from each of 10 figs with or without gall midges (experiment 1). This was repeated with groups of 10 seeds, where, in addition to germination rates, the growth of the roots that were produced was

also recorded (experiment 2). The germination trials were carried out in petri dishes lined with moistened filter paper in an illuminated incubator maintained at 30 °C with a 12 h day-night cycle. The seeds were checked daily to see if they had germinated and the lengths of the roots of any germinated seeds were recorded weekly. The experiment was terminated when no further seeds germinated and the roots had stopped growing.

2.3.5. Statistical analysis

The influence of gall midges on the presence or absence of pollinators was examined using a generalized linear mixed (GLM) model with binomial errors. Pollinator presence was the dependent variable, gall midge presence/absence (P/A) was the fixed effect, female flower was a random effect and crop (nested within gall midge P/A) was a covariate in the model.

A GLM model with Poisson errors was used to examine the effect of gall midges on the abundance of pollinators in the figs, with the number of pollinators as the dependent variable, gall midge P/A as the fixed effect, female flowers as a random effect and crop (nested within gall midge P/A) as a covariate. Linear mixed (LM) models examined the effect of gall midges on the numbers of bladders and seeds, with bladders and seeds as dependent variables, gall midges as the fixed effect, female flowers as a random effect and crop (nested within gall midges) as a covariate.

A GLM model with binomial errors compared the germination success of seeds in figs with and without gall midges, with germination as the dependent variable, seed types (from figs with or without gall midges) as the fixed effect, and observation times and replications (nested within seed types) as covariates. The same LM model was also used to compare the root lengths of germinated seeds. With the LMs, *t* values greater than 2 were regarded as significant.

Analyses were performed in R (R version 2.12.1), including Package lme4, and SPSS.

3. Results

3.1. The impact of gall midges on seed and pollinator production

Gall midge occupancy rates in the eighteen *F. benjamina* crops were as high as 100%, and were over 60% in 13 of the crops. Only one crop had no gall midges. There was a tendency for a higher prevalence of gall midges during the colder months (December to February) than in May and June. The contents of 207 midge-occupied figs that had been sleeved *in situ* on the trees (from eight crops) are recorded in Table 1 (sample sizes per crop vary because some bags were damaged). An additional 14 sleeved figs contained no gall midges. Midge-free figs contained 124.7 ± 25.4 (Mean ± SE, *n* = 14) pollinators (both sexes combined). In contrast, figs with gall midges contained only 13.5 ± 3.4 pollinators, with only 15.5% of these figs producing any pollinators at all. Pollinator numbers per fig were significantly reduced in the presence or absence of the

Table 1

The frequency of *F. benjamina* figs containing gall midges (occupancy) at XTBG, China (*n* = 100 figs per crop) and the contents of figs where gall midges were present (14 additional figs lacked gall midges).

| Trees/crops | Sample sizes (occupied figs) | Number of gall midges (Mean ± SE) | Occupancy of pollinators (%) | Number of pollinators (Mean ± SE) | Number of seeds (Mean ± SE) |
|-------------|------------------------------|-----------------------------------|------------------------------|-----------------------------------|-----------------------------|
| 1 | 41 | 45.10 ± 4.06 | 0 | 0 | 229.93 ± 17.91 |
| 2 | 30 | 47.53 ± 4.27 | 0 | 0 | 204.80 ± 19.95 |
| 3 | 32 | 31.72 ± 3.02 | 13 | 13.03 ± 8.17 | 139.31 ± 12.48 |
| 4 | 18 | 13.11 ± 2.14 | 19 | 3.50 ± 2.40 | 71.67 ± 15.05 |
| 5 | 26 | 20.46 ± 3.03 | 22 | 4.27 ± 3.86 | 163.65 ± 19.77 |
| 6 | 14 | 5.50 ± 0.80 | 85 | 82.72 ± 22.23 | 170.50 ± 22.47 |
| 7 | 20 | 10.65 ± 2.36 | 33 | 39.90 ± 23.44 | 279.9 ± 30.07 |
| 8 | 26 | 3.58 ± 0.43 | 32 | 9.35 ± 4.65 | 160.96 ± 23.08 |

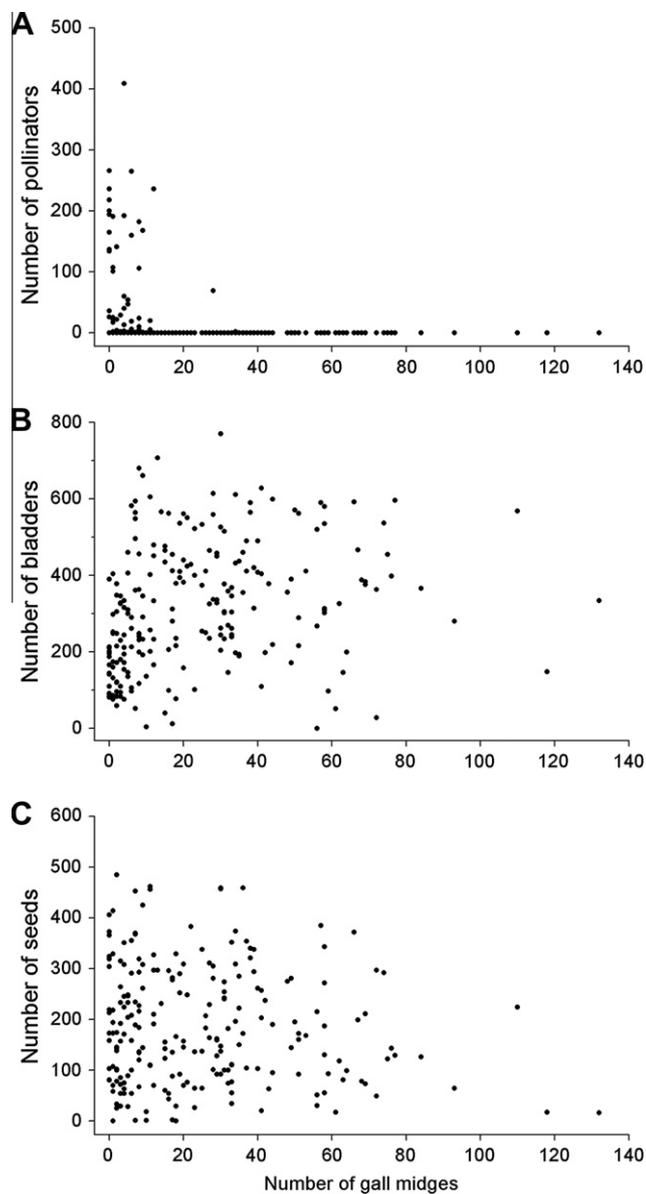


Fig. 1. The impact of gall midges on *F. benjamina* pollinator and seed production. The relationship between gall midge and pollinator numbers (A); the numbers of bladders (B); and the numbers of seeds (C).

midge (Mann–Whitney $U = 451.50$, $P < 0.001$) (Fig. 1A). Pollinating and non-pollinating fig wasp larvae that fail to complete their development resulting in ‘bladders’ being formed. The small number of pollinators present in figs shared with the gall midge was reflected in a corresponding significant increase in the number of bladders (Mann–Whitney $U = 574.00$, $P < 0.001$) (Fig. 1B). Bladder numbers in figs with gall midges averaged 324.9 ± 11.5 , compared with 164.5 ± 21.8 bladders in figs where the midges were absent.

Seed production was not affected in the same way as pollinator production. The 14 midge-free figs averaged 228.6 ± 31.2 seeds per fig, compared with 182.4 ± 8.0 seeds in figs where the midge was present (Mann–Whitney $U = 1100.00$, $P = 0.13$) (Fig. 1C). Almost all (205) of the 207 figs with gall midges contained seeds, but the seeds had no enough time to complete their development because more than 80% of figs were aborted and unripe.

As many as 132 gall midges were reared from a single fig, with average numbers per fig varying between 4 and 40 individuals in different crops (Table 1). There was a significant positive correla-

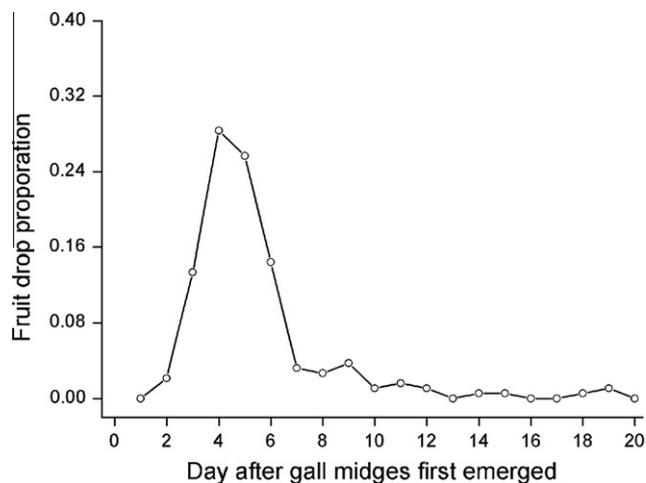


Fig. 2. The timing of fig fall from *F. benjamina* trees, once the first gall midges had emerged.

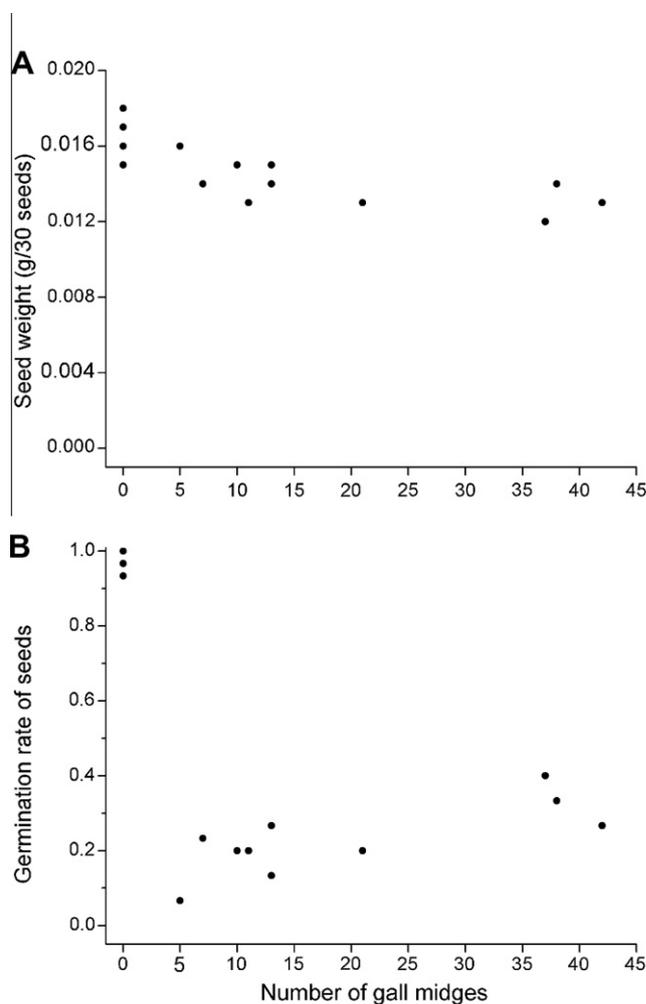


Fig. 3. The effect of gall midges on seed quality: seed weight (A); and germination success (B).

tion between the proportion of figs in a crop where gall midges were present (occupancy) and mean numbers of gall midges per fig (Pearson correlation, $t = 3.73$, $P = 0.009$). Two crops failed to produce any pollinators from figs where gall midges were present

(Table 1). Pollinator offspring were more likely to be present in figs that contained fewer gall midges (GLM: $\beta = -0.18 \pm 0.05$, $P < 0.001$, $n = 207$ figs). Among figs that contained both gall midges and pollinators, increasing numbers of gall midges significantly reduced the numbers of pollinators present, and pollinators were usually entirely absent from figs that contained more than 12 gall midges (GLM: $\beta = -0.05 \pm 0.01$, $P < 0.001$, $n = 39$ figs) (Table 1 and Fig. 1A). Bladders were apparent in figs with even the lowest numbers of galls (Fig. 1B), and consequently gall midge numbers did not have a significant effect on the numbers of bladders present (LM: $\beta = 0.20 \pm 0.33$, $t = 0.61$, $n = 207$ figs).

The average numbers of seeds in the dissected figs from the eight crops ranged between 71 and 280. The number of seeds per fig decreased significantly with increasing numbers of gall midges (LM: $\beta = -1.16 \pm 0.22$, $t = -5.22$, $n = 207$ figs), but some figs with large numbers of gall midges still contained seeds (Fig. 1C).

3.2. Fig abortion

Fig. started to fall soon after the first gall midges emerged (Fig. 2), abortions peaked on the fourth day and although some figs persisted for up to 20 days, 94% of the figs had dropped by the 9th day. Fig. that fell in the first few days were unripe and green, and still contained pollinating and non-pollinating fig wasp larvae. The small number of figs that persisted on the trees appeared to mature normally, turning yellow as they ripened and producing adult pollinators before falling.

3.3. Comparisons of seed quality

Seed weights were lower in figs that contained gall midges (Fig. 3A, midge-free figs: mean = 0.017 ± 0.0003 g per 30 seeds, $n = 10$, compared with 0.014 ± 0.0004 g, $n = 10$; Mann Whitney $U = 3.50$, $P < 0.001$). Seeds from midge-free figs were shorter but broader than those from midge-occupied figs, with mean maximum lengths of 1.41 ± 0.007 mm ($n = 300$) in the midge-free figs and 1.45 ± 0.006 mm ($n = 300$) in the figs containing gall midges (Mann Whitney $U = 33568.00$, $P < 0.001$). In contrast, mean maximum widths were 0.90 ± 0.005 mm ($n = 300$) for midge-free figs, and 0.88 ± 0.005 mm ($n = 300$) in figs where gall midges were present (Mann Whitney $U = 39681.50$, $P = 0.012$).

The presence of gall midges significantly reduced the likelihood that a seed would germinate (GLM: $\beta = -6.22 \pm 0.44$, $P < 0.001$) (Fig. 3B). Seeds from mature midge-free figs germinated quickly, with germination rates of 52% and 68% within 1 week (Fig. 4, experiments 1 and 2 respectively) and close to 90% after 2 weeks. No further seeds germinated after 7 or 6 weeks, and final germination rates were 100% and 96%. In contrast, seeds from figs with gall midges germinated more slowly, with less than 5% of the seeds germinating by the second week. Final germination rates of seeds from figs with gall midges were 23% and 22% in experiments 1 and 2 respectively. The roots of seedlings from midge-free figs also developed significantly more quickly than those from figs that had contained gall midges (Fig. 5) (LM: $\beta = -17.09 \pm 1.70$, $t = -10.04$).

4. Discussion

Most pollinating and non-pollinating fig wasps are strictly host plant species-specific (Weiblen, 2002), whereas other insects feeding on fig trees are often more generalist (Basset and Novotny, 1999). *F. benjamina* is one of twelve *Ficus* species belonging to Section Conosycea that grow naturally in the XTBG area. The undescribed gall midge associated with *F. benjamina* has not been found on figs of these closely-related species, suggesting that, like many gall-making species, it is also highly host specific (Vitou

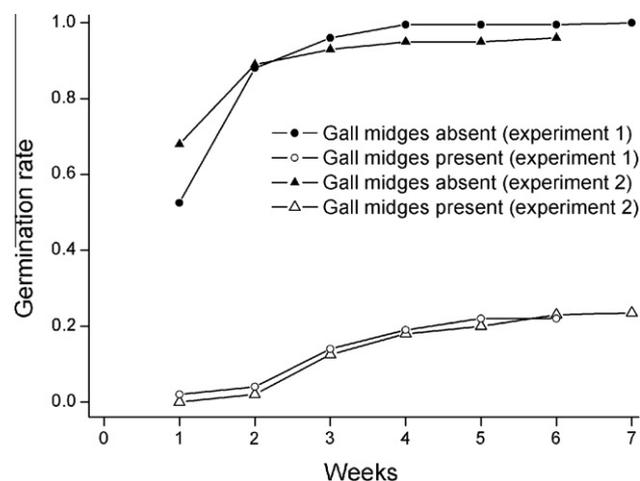


Fig. 4. Germination rates of seeds from figs with and without gall midges.

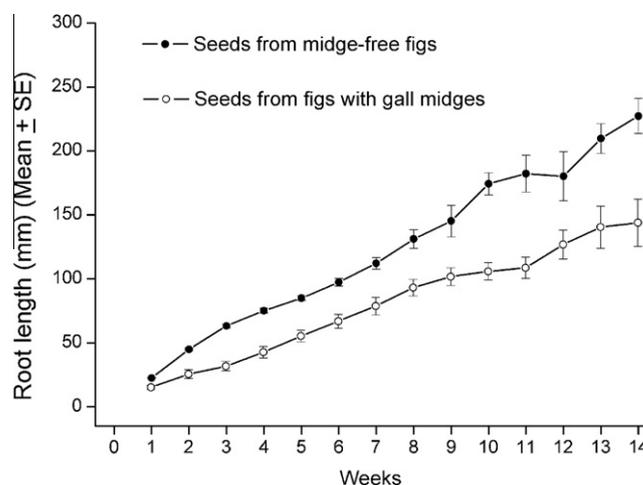


Fig. 5. Root growth of seeds from figs with and without gall midges.

et al., 2008). Although galls similar to those on *F. benjamina* began to appear on *Ficus curtipes*, *Ficus glaberrima* and *Ficus microcarpa* figs at XTBG in 2008 (all three species belong to Section Conosycea), genetic studies (Y.-Q. Peng, unpublished) have shown that these are caused by a second species of gall midge with a slightly broader host range, which appears to have recently colonized the area.

The gall midge associated with *F. benjamina* colonized most, or even all, of the figs in a crop within its native range at XTBG. It also reached high densities within individual figs, benefiting from an absence of parasitoids. The impact of gall midges on the male reproductive success of the host trees was substantial in all eight crops that were surveyed, with figs containing 12 or more midge galls almost never producing any adult pollinators. This resulted in pollinators being entirely eliminated from two of the crops and greatly reduced in the others. The reduction in pollinator production was linked to an increase in the number of bladders, suggesting that the larvae had died before they completed their development. Pollinator failure may partially reflect competition for nutrients with the much larger gall midge galls, but was primarily the result of early abortion of figs colonized by the gall midge, before both pollinating and non-pollinating fig wasps had time to complete their development. At this stage the figs are still hard and green, and not attractive to birds, so the seeds are also less likely to be dispersed. The impact of the gall midges on seed

production was more subtle, with the numbers of seeds only declining slightly in figs that contained more gall midges. However, seeds from figs that had aborted prematurely due to the presence of the gall midge rarely germinated and developed roots at a slower rate than seeds from figs that had lacked gall midges.

The undescribed gall midge from the figs of *F. benjamina* displayed extreme host specificity, never being found in figs of other closely-related *Ficus* species growing in the same botanic garden in China. The gall midge has been present at high densities at XTBG for at least 5 years (it may have been present earlier and have gone un-noticed). It locates most of the fig crops produced there and colonizes most of the figs, where it can reach densities of more than 100 galls per fig. Even at far lower densities, the gall midges have a major impact on the reproductive success of the figs they colonize, substantially reducing the numbers of both pollinators and viable seeds, primarily by causing premature abortion of the developing figs. It is also independent of the pollinating fig wasp, being able to develop in figs that no pollinators have entered. This combination of characters makes the gall midge an excellent candidate biological control agent, available as and when *F. benjamina* becomes of more widespread conservation concern.

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