Biological Control 59 (2011) 228–233

Contents lists available at SciVerse ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

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

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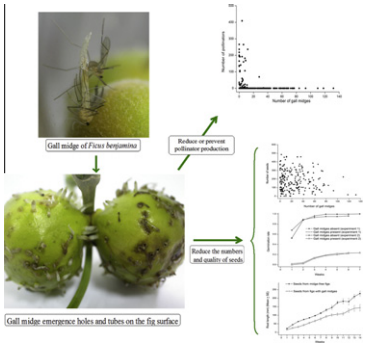
HIGHLIGHTS

- 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



ARTICLE INFO

Article history:
Received 16 February 2011
Accepted 15 July 2011
Available online 30 July 2011

Keywords:
Biocontrol
Cecidomyiidae
Ficus
Fig wasp
Gall midge
Mutualism

ABSTRACT

Fig trees (*Ficus* spp.) are popular ornamental trees that are entirely dependent on a mutalistic 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 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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doi:10.1016/j.biocontrol.2011.07.007

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 Otitesellinae spp. and four Epichrysomallinae 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.