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Acta Oecologica xxx (2017) 1–5

Contents lists available at ScienceDirect

Acta Oecologica

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

Sugar secretion and ant protection in *Ficus benguetensis*: Toward a general trend of fig–ant interactions

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ARTICLE INFO

Article history:
Received 5 December 2016
Received in revised form
22 May 2017
Accepted 8 June 2017
Available online xxx

Keywords:
Ant
Extrafloral nectaries
Ficus
Mutualism
Myrmecophyte
Taiwan

ABSTRACT

The relationship between plants and ants is often mediated by the presence of extrafloral nectaries (EFNs) that attract ants and provide rewards by protecting plants from herbivores or parasites. *Ficus* trees (Moraceae) and their pollinators (Hymenoptera: Agaonidae) are parasitized by many nonpollinating fig wasp species (Hymenoptera: Chalcidoidea) that decrease the reproductive output of the mutualistic partners. Previous studies have shown that ants living on and patrolling *Ficus* species can efficiently deter parasitic wasps. The aim of this study was to verify the presence of EFNs on figs of *Ficus benguetensis* and test the hypothetical protection service provided by ants. Figs in different developmental stages were collected from Fu-Yang Eco Park, Taipei, Taiwan. Sugars on the fig surface were collected and analyzed through high-performance anion-exchange chromatography. Moreover, ants were excluded from the figs to determine the effect of ants on the nonpollinating fig wasps. We identified three oligosaccharides whose relative proportions varied with the fig developmental phase. In addition, results showed that the ant-excluded figs were heavily parasitized and produced three times less pollinators than did the control figs. Finally, the specific interactions of *Ficus benguetensis* with ants and the relationship between figs and ants in general are discussed.

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1. Introduction

Since the early Cretaceous, modern ants have colonized almost all of the Earth's ecosystems (Wilson and Hölldobler, 2005; Moreau and Bell, 2013) and have developed close relationships with many angiosperm groups and species (Weber and Keeler, 2013; Chomicky and Renner, 2015). Ants can provide protection to plants, which in turn reward them with food and/or nesting sites (Webber et al., 2007). The efficiency of this protection has been quantified by meta-analyses, on the basis of which researchers have concluded that the reproductive output of protected plants is increased by almost 50% (Trager et al., 2010), but this value varies depending on many plant- and ant-related factors (Chamberlain and Holland, 2009). The most common reward produced by extrafloral nectaries (EFNs) for ants is the sugar. EFNs are defined as "*nectar secreting glands that are mostly located outside the flowers and are not involved in pollination*" (Heil et al., 2000). EFNs have been reported in almost 4000 plant species across 745 genera (Weber and Keeler, 2013). Among these plants, the *Ficus* genus (Moraceae) is poorly represented, with only three species being actually tested for sugar secretion (Fiala and Linsenmair, 1995; Pemberton, 1998; Blüthgen and Reifenrath, 2003).

Fig trees (*Ficus*) are often patrolled by ants: the presence of ants on fig trees or any type of interaction between the ants and figs or the fig wasps has been documented in approximately 11% of the species (Bain et al., 2014). The *Ficus* species and pollinating wasps from the Agaonidae family (Hymenoptera: Chalcidoidea) are part of an obligate pollination mutualism (Kjellberg et al., 2005). However, this mutualism is parasitized by numerous nonpollinating fig wasps (NPFWs) whose larvae consume either the fig tissue or pollinator larvae (Compton et al., 1994; Castro et al., 2015). These NPFWs have significant negative effects on the reproductive output of the mutualistic partners (Cardona et al., 2013; Wang et al., 2014). Thus, ant protection could improve the seed and pollinator production of parasitized trees. Indeed, studies have shown that in two unrelated *Ficus* species growing in different environments, ants had a highly efficient protective effect on the fig trees they have colonized (Compton and Robertson, 1988; Cushman et al., 1998; Wang et al., 2014; Jandér, 2015). Nevertheless, no study has reported the presence of EFNs and documented their roles in attracting ants and

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http://dx.doi.org/10.1016/j.actao.2017.06.006
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Please cite this article in press as: Lin, S.-Y., et al., Sugar secretion and ant protection in *Ficus benguetensis*: Toward a general trend of fig–ant interactions, Acta Oecologica (2017), http://dx.doi.org/10.1016/j.actao.2017.06.006

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ensuring protection of the figs.

Ficus benguetensis is patrolled, in Taiwan, by 13 ant species and six of them representing more than 97% of the observations: *Lophomyrmex taivanae*, *Crematogaster subnuda formosae*, *Pheidole noda noda*, *Pristomyrmex punctatus*, *Tetramorium nipponense*, and *Technomyrmex albipes brunneus* (Lin et al., 2016). A closely related species, *F. schwarzii*, in Borneo has putative EFNs (that have not been sugar tested) on the figs visited by ants (Harrison, 2014). We observed similar structures on the *F. benguetensis* figs, leading to our investigations regarding the relationship between the *F. benguetensis* mutualism and patrolling ants. Thus, this study aimed to answer several questions regarding ant and fig interactions. First, does *F. benguetensis* produce sugar in EFNs? Second, do ants protect the mutualistic partners from NPFWs? Third, what is the status of *F. benguetensis* in terms of its relationship with ants? Finally, is it a myrmecophyte (a plant which is continuously inhabited by ants during a part of its life (Webber et al., 2007))? To answer these questions, ant exclusion experiments and a chemical analysis of the EFN compounds were performed.

2. Materials and methods

2.1. Study species and biology of the system

Ficus benguetensis Merr. is a functionally dioecious species from the subgenus *Sycomorus* (section *Sycocarpus*), distributed from the Philippines to the Japanese Ryukyu islands (Berg, 2011). The development of *F. benguetensis* male figs can be separated into four phases: the prereceptive phase (A); the receptive phase (B), which is the only period when the female pollinating wasps (*Ceratosolen wui*) can pollinate and lay eggs inside the figs; the interfloral phase (C); and the emergence phase (D), which is the end of the fig life, in which pollen-loaded and mated female fig wasps leave the figs to find a receptive fig. Male *F. benguetensis* trees produce mainly clusters of cauliflorous figs on the trunk or main branches (Fig. 1) whereas figs on female trees develop mainly on the axil of leaves on apical twigs (Lin et al., 2015).

Regarding the other insects associated with *F. benguetensis*, NPFWs (Chalcidoidea: Sycoryctinae: *Sycoscapter* and *Philotrypesis*) lay eggs inside the figs from the outside mostly during the C phase, and ants (Formicidae) mostly visit the figs during the C and D phases (Lin et al., 2015). NPFWs are present only on male trees, and ants are also more abundant on male trees than on female trees (Lin et al., 2015). Therefore, only figs from male trees were collected for sugar analysis. Moreover, honeydew-producing species were not observed during this experiment.

2.2. Sampling and sugar analysis

In July 2014, a total number of 11 figs in the B (two figs from tree 1), early C (two figs from tree 2) and late C phases (seven figs from trees 3, 4 and 5) were collected from five male trees in Fu-Yang Eco-Park, Taipei, Taiwan. The collected figs were immersed in neutral red staining agent for 5 min. The neutral red stain is used to identify organism secretions that turn red after contact with the stain (Koehring, 1930). After immersion, red spots on the fig surface appeared, revealing secretions (Fig. 2).

On the basis of previous findings (Baker et al., 1978; Caldwell and Gerhadt, 1986) that sugars secreted by plants contain mainly oligosaccharides such as sucrose, fructose, and glucose, we performed subsequent analyses to identify these three oligosaccharides. Collected figs (from the B and C phases) were first washed with 2 mL of distilled water, but no sugar was identified in the samples; therefore, they were washed with 2 mL of 70% alcohol. The extracts were then air dried and stored until analysis. The

Fig. 1. A male *Ficus benguetensis* trees with cauliflorous fig clusters on the trunk and main branches.

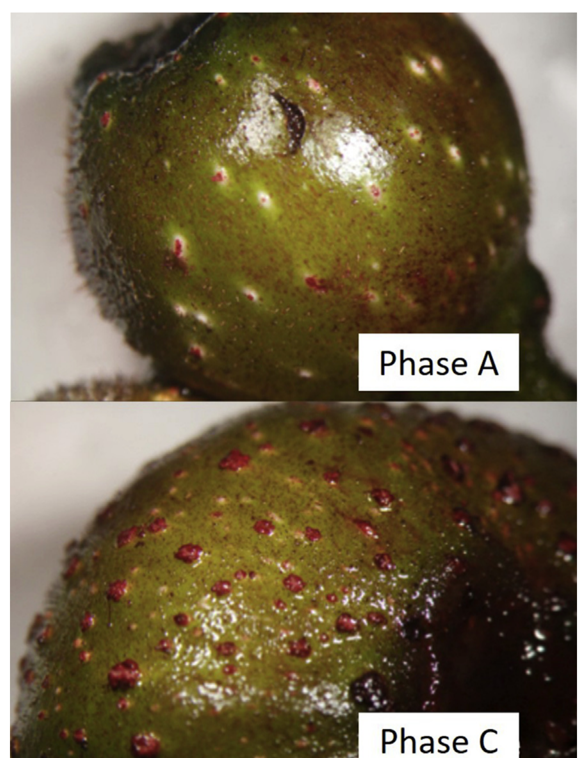

Fig. 2. Preliminary results of neutral red stain. The upper graph shows the fig surface in the A phase and the lower graph shows the fig surface in the C phase.

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