Tending Ants Protect Honeydew-Producing Whiteflies (Homoptera: Aleyrodidae)

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ABSTRACT We investigated the interaction between the honeydew-producing whitefly *Aleurothrixus aepim* and tending ants on shrubs of *Croton floribundus* (Euphorbiaceae) in a semideciduous forest in southeast Brazil. Whitefly eggs underside leaves were tagged during early March 1998 and randomly divided into two experimental groups: control (ants present, $n = 75$) and treatment (ants excluded, $n = 52$). During the 75-d experiment, honeydew-collecting ants visited 79% of the control groups of *A. aepim.* Adults emerged in significantly greater numbers from control than from treatment groups, the latter being heavily attacked by fungi due to accumulation of honeydew. Complete contamination by fungi was three times more frequent at ant-excluded (39%) than at ant-tended (13%) groups. Control groups with low levels of ant-tending produced significantly fewer adults than those more frequently tended by ants. *Encarsia* parasitoid wasps were more frequently seen on ant-excluded than on control *A. aepim* groups. Predatory arthropods, however, were equally frequent in either experimental group. This is the first experimental study to demonstrate ant-derived protection in honeydew-producing whiteflies. Given that aleyrodid honeydew can cause considerable damage to the host plant, our results suggest that the honeydew-gathering activity by tending ants is an important factor mediating such multitrophic interaction.

KEY WORDS *Aleurothrixus aepim*, *Croton floribundus*, sooty mold, ant-homopteran interactions, mutualism, insect–plant interactions

ANTS ASSOCIATE FREQUENTLY with honeydew-producing homopterans on plant foliage and these associations are often regarded as mutualistic because the continuous collection of the energy-rich honeydew by tending ants can confer a range of benefits to homopterans (Way 1963). The tending activities may extend for 24 h (Del-Claro and Oliveira 1999), and in most cases protection against external predators and parasitoids is the main benefit afforded by ants (Buckley 1987a, 1987b). However, the magnitude of the mutual benefits between ants and homopterans is strongly dependent on the ecological settings in which they occur (Cushman and Whitham 1989, 1991; Cushman and Addicott 1991; Del-Claro and Oliveira 2000).

The presence of honeydew-gathering ants not only affects the behavior of the homopteran's natural enemies, but also excludes them from the host plant (Vinson and Scarborough 1991). In some cases the removal of honeydew reduces physical fouling and the incidence of sooty mold at homopteran groups (Buckley 1987a, 1987b). Demonstration of such beneficial associations has been described primarily for aphid, scale, and treehopper species (Buckley 1987a, 1987b, and included references). To date, no such demonstration exists for ant–whitefly interactions.

Most data on ant–homopteran associations come from temperate regions, and only more recently have these interactions been studied in the Neotropics (Wood 1984; Dansa and Rocha 1992; Del-Claro and Oliveira 1999, 2000). Indeed, most information concerning whitefly species is largely related with agricultural damage, and studies are often restricted to management aspects of a few pest species (see Gerling 1990). In this study we investigated the association between ants and the whitefly *Aleurothrixus aepim* Goeldi in a tropical forest in southeast Brazil. This is the main whitefly species infesting cassava in Brazil (see Bellotti et al. 1999), and in natural forests it is associated with another euphorbiaceous species, *Croton floribundus* Spreng. We used field observations and a controlled ant-exclusion experiment to test the hypothesis that ant protection enhances survival in whitefly groups under natural conditions.

Materials and Methods

Field work was undertaken along trails at the border of a semideciduous forest at the Serra do Japi Reserve (23° 16′ S, 47° 00′ W) near Jundiaí, southeast Brazil. *Croton floribundus* is an abundant species in the study area that frequently supports groups of *A. aepim* on the underside of leaves. We used an ant-exclusion experiment to investigate how ant-tending affects whitefly survival on *C. floribundus* shrubs. Ants were excluded from treatment plants by applying a sticky barrier of Tanglefoot (Tanglefoot, Grand Rapids, MI) to the trunk base. Neighboring foliage providing aerial access of ants to treated plants ($n = 34$) were pruned regularly. Ants had free access to control plants ($n = 51$). During a 75-d period, ant-tended ($n = 75$) and

ant-excluded ($n = 52$) groups of *A. aepim* were regularly (3-4 d) checked for nymphal hatching and adult emergence, and for the occurrence of sooty mold, parasitoids and predators. Natural enemies were censused during a 2-min inspection of each host plants. We checked ant presence and associated species at control *A. aepim* groups at intervals of 3-4 d, totaling 17 censuses per plant during the 75-d experiment. Ant-tending was considered low if ants occurred less than or equal to the median ant visitation rate in the censuses (≤5 records in 17 censuses), or high if ant records were greater than the median (>5 records). There were no other sugar sources on *C. floribundus* such as extrafloral nectar or honeydew from other homopterans. At the end of the experimental manipulation the emergence rate of adult whiteflies was recorded by counting the number of T-shaped exuviae under a stereomicroscope. Voucher specimens of whiteflies are deposited at the British Museum (Natural History), and of ants at the Museu de Zoologia da Universidade de Sao Paulo, Brazil.

Results

Ants visited 79% of the control groups during the 75-d experiment, and honeydew-gathering by ants persisted on a round-the-clock basis. We recorded 12 ant species: *Brachymyrmex* (two species), *Camponotus* (three species), *Solenopsis* (two species), *Crematogaster*, *Pheidole*, *Procryptocerus*, *Pseudomyrmex*, and *Pachycondyla* (one species each). Whiteflies were tended most frequently by *Brachymyrmex* ants, which were recorded on 29% of the ant-tended groups.

The ant-exclusion experiment unequivocally demonstrates a positive impact of tending ants on whitefly survival (Fig. 1). Despite equal initial numbers of immature nymphs, after 75 d the emergence rate of adult whiteflies was significantly greater at ant-tended whitefly nymphs than at ant-excluded ones (Fig. 1A). In the absence of ants the accumulated honeydew rapidly covered the whiteflies and promoted infection by fungi (*Cladosporium*). Although sooty mold occurred on some ant-tended whitefly groups, complete fungal infection due to honeydew build-up was three times more frequent at ant-excluded (39%) than at ant-tended groups (13%) ($P < 0.01$, χ^2 test). Moreover, despite equal initial numbers of nymphs in groups with different levels (low or high) of ant-tending, adult emergence was significantly greater at groups with high rates of ant visitation (Fig. 1B).

During the censuses of natural enemies, *Encarsia* parasitoid wasps (Aphelinidae) were seen at least once on 40% of the ant-excluded whitefly groups versus 24% of the control groups ($P < 0.05$, χ^2 test). Field observations revealed that tending ants disturbed the approaching *Encarsia* species, keeping them away from the whiteflies. Ant attendance, however, had no effect on the occurrence of predators at whitefly groups. Predatory dipteran (Syrphidae) and beetle (Coccinellidae) larvae were recorded at equal rates in either experimental group ($P > 0.20$, χ^2 test). Only syrphids were seen feeding on the whiteflies.

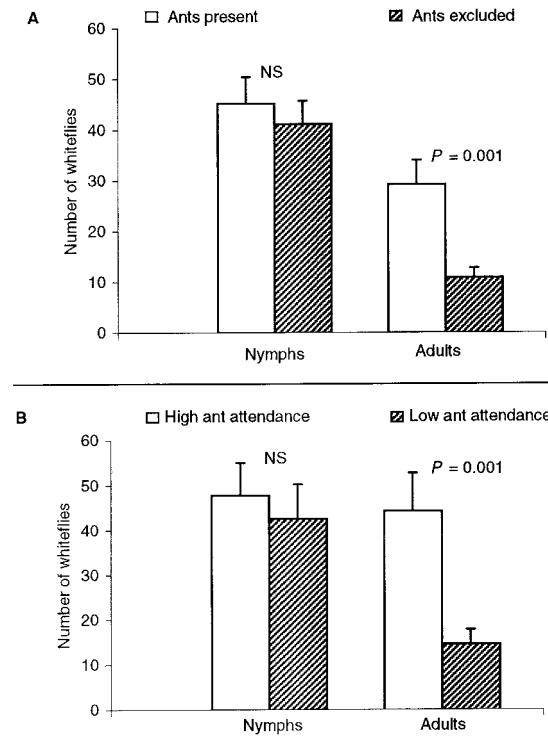

Fig. 1. (A) Mean number (±1 SE) of *A. aepim* whiteflies through time in the presence ($n = 75$ groups) and absence ($n = 52$) of tending ants. Despite equal initial numbers of immature nymphs (Mann–Whitney test, $U = 1918.5$, df = 1, $P = 0.877$), after 75 d of experimental manipulation the emergence rate of adult whiteflies was significantly greater at colonies tended by honeydew-gathering ants than at ant-excluded colonies ($U = 2{,}613.5$, df = 1, $P = 0.001$). (B) Mean number (±1 SE) of *A. aepim* whiteflies through time under high ($n = 37$ groups) and low ($n = 38$) levels of ant-tending. Despite equal initial numbers of immature nymphs ($U = 591$, df = 1, $P = 0.233$), adult emergence was significantly greater under high levels of ant attendance ($U = 379.5$, df = 1, $P = 0.001$). NS, nonsignificant.

Discussion

This is the first experimental study to demonstrate ant-derived protection in honeydew-producing whiteflies. Our field experiments suggest that honeydew removal by tending ants reduces fungal infection at *A. aepim* colonies, and increases the emergence rate of adult whiteflies. Mortality by entomopathogenic *Cladosporium* has also been reported for *A. aepim* infesting cassava cultures in Brazil (Bellotti et al. 1999). Although the infection process by entomopathogenic fungi has been described for several insect species, studies on differential mortality of whiteflies by fungal infection are scarce (Fransen 1990). In contrast to treehoppers, which can inhibit fungal proliferation in the absence of ants through honeydew flicking (Del-Claro and Oliveira 1996), whiteflies are unable to flick away their sugary secretions and suffer increased mortality from fungal attack if unattended by ants. Previous studies have reported

the same kind of benefit to scales from ant-tending (see Buckley 1987b). It is possible that *A. aepim*'s feeding location on the underside of leaves increases the probability that ground-dwelling ants climb onto the host plant and tend the whiteflies, as demonstrated for honeydew-flicking treehoppers (Del-Claro and Oliveira 1996).

The field experiments also showed that the mutualism between ants and *A. aepim* is conditional (Bronstein 1994). Ant-derived benefits to homopterans are greater at high visitation rates by tending ants, because the main service provided by the latter is the continual removal of honeydew. Although we did not detect protection from ants against predators, the frequency of both syrphid and coccinellid larvae at *A. aepim* groups was very low (8.6%). Indeed, Cushman and Whitham (1989) demonstrated that when natural enemies are absent or in low abundance, tending ants have no beneficial effect on treehopper groups. Ants, however, appeared to disturb parasitoids at nymph groups, and *A. aepim* may benefit from protection against these natural enemies, as demonstrated for other ant-tended homopterans (Vinson and Scarborough 1991, Del-Claro and Oliveira 2000).

Although many studies on whiteflies have already been published, it is surprising that ant-whitefly interactions have been negleted until now. One possible reason is that most information concerning whiteflies is usually linked with economically important species, focusing mainly on *Bemisia* species and the greenhouse whitefly, *Trialeurodes vaporariorum* (Byrne and Bellows 1991). Future studies should evaluate the frequency of ant-tending in whiteflies, both in natural and agricultural systems. It is possible that entomologists have neglected this kind of interaction because the management of pest species is largely based on chemical control (see Dowell 1990).

Our data demonstrated that tending ants reduce both fungal infection and parasitoid occurrence at nymph groups, and enhance whitefly survival. Therefore ants may negatively affect plants because whiteflies extract large quantities of phloem sap and excrete honeydew that promote fungal growth, which leads to decreased photosynthetic rate and leaf abscission (see Gerling 1990). However, tending ants may also benefit the plant by eliminating other herbivores (Messina 1981). Additional controlled field experiments are needed to separate the effects of each individual species in ant-whitefly-plant associations, and to better understand the ecological role of ants on plants infested by whiteflies.

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