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INTEGRATION OF SCALE INSECTS (HEMIPTERA: COCCIDAE) IN THE SOUTH-EAST ASIAN ANT-PLANT (*CREMATOGASTER* (FORMICIDAE)-*MACARANGA* (EUPHORBIACEAE)) SYSTEM.

ABSTRACT

INTEGRATION OF SCALE INSECTS (HEMIPTERA: COCCIDAE) IN THE SOUTH-EAST ASIAN ANT-PLANT (*CREMATOGASTER* (FORMICIDAE)-*MACARANGA* (EUPHORBIACEAE)) SYSTEM.

The coccid colonisers of myrmecophytic *Macaranga* were tested for their trophic integration into the mutualistic *Crematogaster-Macaranga* ant-plant system. Honeydew secretion by these mostly endophytic scale insects was observed in *Coccus caviramicolus* Morrison, *C. penangensis* Morrison, *C. secretus* Morrison, *C. tumuliferus* Morrison, *C. tumuliferus* var. C.84 and in two other *Macaranga* coccid species. However, the use of coccids as protein-rich food by ants under normal and starvation conditions was not observed.

Key words: trophobiosis, ant nutrition, Myzolecaniinae, survival, dumping areas, *C. macarangae*, food-bodies, Pseudococcidae, Malaysia, *Macaranga bancana*, *M. hypoleuca*, *M. bulletii*, *M. winkleri*, *M. triloba*.

INTRODUCTION

Ant-plant systems represent a common type of symbiosis in the tropics. The *Crematogaster-Macaranga* association is probably the most conspicuous ant-plant system in South-East Asia and includes more than 20 plant and at least 9 ant species. The plants provide food in the form of nutrient-rich food-bodies and nesting space for the ants, while the plant-specific ant colonisers defend their host-plant against herbivores and also gnaw off climbers, a behaviour called pruning (Fiala, 1989). The ants rely mainly on plant resources and do not hunt any prey on or around the plants (Fiala & Maschwitz, 1989, 1990, 1992; Fiala *et al.*, 1991). As in many other ant-plant-hemipteran systems (Gullan, 1997), scale insects are found inside almost all ant-inhabited *Macaranga* above a certain size (Heckroth *et al.*, 1998). An exception to this is the two-partner system *Camponotus-M. puncticulata* that can be found as a common understorey tree in peat swamp forests in the Malay Peninsula and Sumatra (Federle *et al.*, 1998). Also other ant-plant systems very often lack scale insects or other hemipterans as trophobiotic partners for the ants (summarised in Davidson & McKey, 1993).

Morrison (1921) and Takahashi (1951) described 6 species of coccids from *Macaranga* species in the Malay Peninsula. Recently, additional collections have been made from West and East Malaysia as well as from Sumatra and the Indonesian part of Borneo and their host-specificity investigated (Heckroth *et al.*, 1998). The *Macaranga* coccids all appear to belong to the Subfamily Myzolecaniinae (Heckroth *et al.*, 1998).

The coccids in the hollow stems of most *Macaranga* species are almost always present in this ant-plant symbiosis, but it is not known in what way they actually contribute to the ant-plant mutualism, since ant colonies can survive and grow without the presence of coccids on their host-plants (Heckroth, unpublished data). Honeydew is a common food source for ants (Davidson & McKey, 1993; Gullan, 1997; Hölldobler & Wilson, 1990). In addition, the use of these trophobionts as prey and, therefore, as a source of protein has been suggested (summarised in Gullan, 1997) because it had been found in non-specific associations (summarised in Gullan, 1997; Pontin, 1978; Way, 1954; 1955; 1963). The consumption of trophobionts by ants in these systems would be a particularly good and resource-saving way of gaining additional protein under normal or starvation conditions and would provide a way of controlling the trophobiont populations.

The aim of this study was to examine the rôle of coccids as a food source for ants in the *Crematogaster-Macaranga* mutualism. The major questions were: (1) do all common coccid species present in the hollow stems of myrmecophytic *Macaranga* provide honeydew for ant colonies; (2) is this honeydew a full diet for both the workers and/or the brood, and (3) are these coccids also used as prey by the ants?

MATERIALS AND METHODS

THE STUDY AREA

The study was conducted at the Ulu Gombak Field Study Centre in the Gombak Valley (Selangor, West Malaysia) and at Poring Hot Springs in Mt. Kinabalu National Park (Sabah; East Malaysia).

1. TROPHOBIOSIS

Because nearly all of ant-coccid interactions happen inside the plants, trophobiosis cannot usually be observed directly with *Macaranga* coccids. Nonetheless, observations were possible in the following experimental and natural situations, using a dissecting microscope or magnifying glass:

- stimulation of honeydew secretion with a hair: in cut and opened twigs after the removal of all ants (n=23);
- stimulation of coccids by ants: in cut and opened twigs (n=15);
- stimulation of *C. tumuliferus* Morrison (n=5) and morphospecies C.296* (n=6) by ants: in intact *Macaranga hypoleuca* with opened domatia (n=15);
- stimulation of *C. penangensis* Morrison by ants: in intact *Macaranga bullettii* with opened domatia (n=25);
- observations on the occasional aggregations of 1st- and 2nd-instar nymphs on the shoot-tip of *M. hypoleuca* (n=3) (also Khoo, S.G., personal communication) and of *Macaranga winkleri* (n=1).

2. REARING OF ANT WORKERS IN THE ABSENCE OF FOOD-BODIES AND WITH AND WITHOUT COCCIDS.

Sixteen *M. hypoleuca* plants with opened domatia, were each colonised with 15 worker ants, all the ants coming from a single ant colony. Eight of these plants were then also colonised with *C. tumuliferus* coccids *ad libidum*, the other eight plants being left as controls. The control plants were necessary to show whether ants could use any other food source on the plants, such as epiphylls, pollen or plant tissue. After one day, each shoot tip and petiole was covered with a sticky tangle trap (Tangle Foot Company©) to prevent the ants from collecting food-bodies. Dead ants were removed from the plants daily. All coccids were counted to exclude the possibility that they were consumed by the ants.

3. THE FEEDING ON SCALE INSECTS BY WORKERS AND BROOD

i. Offering of coccids as protein-rich food for ant colonies of Crematogaster spec. 6¹:

Scale insects were offered to the ants to observe whether they were eaten, thrown from the plant or accepted as trophobionts under the following conditions:

- intact *C. tumuliferus* (n=25), morphospecies C.296 (n=23) and *C. penangensis* (n=28) were offered to ant-colonies that could obtain honeydew from coccids in an intact plant;
- intact *C. tumuliferus* (n=8), morphospecies C.296 (n=12) and *C.*

*Morphospecies C. 296, C. 41 and C. 84 are undescribed species. These code number was used in Heckroth *et al.* 1998.

¹*Crematogaster* species 6 and 8 are undescribed species. The *Crematogaster* colonisers of myrmecophytic *Macaranga* are separated into 9 species. These code numbers were use in Fiala *et al.* (1999).

penangensis (n=15) were offered to starving ant-colonies which were kept in a container;

- freshly damaged *C. tumuliferus* (n=5), morphospecies C.296 (n=7) and *C. penangensis* (n= 10) were offered to ant-colonies that could obtain honeydew from coccids in an intact plant;

- freshly damaged *C. tumuliferus* (n=5) were introduced to a group of coccids inside an intact plant of *M. hypoleuca* with opened domatia;

- freshly damaged *C. tumuliferus* (n=10), *C. penangensis* (n=15), morphospecies C. 296 (n=7) and C. 41 (n=4) were offered to starving ant colonies of *Crematogaster* species 6¹ and species 8¹, which were kept in a container.

ii. Inspection of (a) dumping-grounds inside Macaranga bancana† and M. hypoleuca plants and (b) colony debris around the plants:

Some internodes along the hollow twigs of myrmecophytic *Macaranga* are obviously used by ants as dumping areas, usually easily recognisable by a dark brown to blackish paste that is generally full of nematodes. In addition, discoloured food-bodies can be found there regularly. If scale insects were consumed by ants in substantial numbers, their antenna, legs, claws and other cuticular structures should be found in these dumping areas and, therefore, this debris was checked under the microscope.

In addition, some debris from the ant colonies was thrown off the plants. To study this, everything that fell from a 50cm high *M. hypoleuca* colonised with a complete ant colony plus 30 adult *C. tumuliferus* was collected in a box for 3 weeks. The box for collecting the debris was surrounded by an insect trap to prevent non-experimental ants from foraging this debris from the surrounding ground. The experiment was conducted indoors to protect the debris from weather conditions. The collected debris was inspected daily.

iii. Observations on colonies in opened plants:

All known typical *Macaranga* coccids can easily be obtained by cutting and splitting a twig of the host-plant and (with the exception of *C. secretus* Morrison) can then be transferred and established at new feeding sites. Once each coccid has withdrawn its stylets, it starts walking. Stylet withdrawal can take from 10 min (many *C. tumuliferus* and morphospecies C. 296) to several hours in *C. penangensis* and *C. macarangae*. Generally, to get a harvest of almost 100% of *C. tumuliferus* and morphospecies C. 296 and 40-60% in *C. penangensis*, live specimens should be kept in the shade under normal dry

†*M. bancana* is now considered as the valid name for the common plant that is well-known as *M. triloba* (J.W.F. Silk, personal communication).

conditions. Sessile 1st-instar nymphs of *C. penangensis* do not remove their stylets and, consequently, cannot be used to colonise a second plant.

For these observations, two opened but living plants were colonised with ant workers and brood. In addition, nymphs of morphospecies C. 296 (n=17) and *C. penangensis* nymphs and adults (n=22) were placed in the internode of one plant. After two days, the leafstalks and shoot tip were covered with a sticky coating to stop the ants from collecting food-bodies. The number of ants, brood and coccids was recorded almost daily. When, after two weeks, the number of ants and brood had dropped to a very low level, fresh brood and ants were added from the original colony. The experiment was conducted for 44 days.

RESULTS

1. TROPHOBIOSIS

Honeydew production in *Macaranga* coccids could be observed in all experimental set-ups. When artificially stimulated with a hair, honeydew production could be observed in *C. caviramicolus* Morrison, *C. macarangae* Morrison, *C. penangensis*, *C. secretus*, *C. tumuliferus*, *C. tumuliferus* var. C. 84, morphospecies C. 296 and morphospecies C. 41. In the absence of honeydew removal by either ants or the experimenter, both *C. penangensis* and *C. tumuliferus* were observed to retract the honeydew droplet after 1-3 minutes. Droplet production after antennation by ants was observed in *C. caviramicolus*, *C. penangensis*, *C. secretus*, *C. tumuliferus* and morphospecies C. 296. Honeydew secretion on the plant surface at the shoot-tip after antennating by ants could be observed in *C. tumuliferus* and morphospecies C. 41. In *C. tumuliferus*, the frequency of honeydew production by coccids on the plant surface was 5 droplets in 5 minutes on a sunny afternoon. On experimentally opened plants, the ants stayed near the coccids most of the time during the 21 days of observation. Honeydew was mostly produced with a frequency of 2-4 droplets per minute and, if not removed by ants or with a hair, was usually retracted after 1-3 minutes.

2. REARING OF WORKERS IN THE ABSENCE OF FOOD-BODIES AND WITH AND WITHOUT COCCIDS.

In the absence of food-bodies and without substitution of lost workers, all workers in plants without coccids had died after 6 days while two-thirds of the workers were still alive and showed no sign of starvation in plants with

Survival of workers with and without honeydew

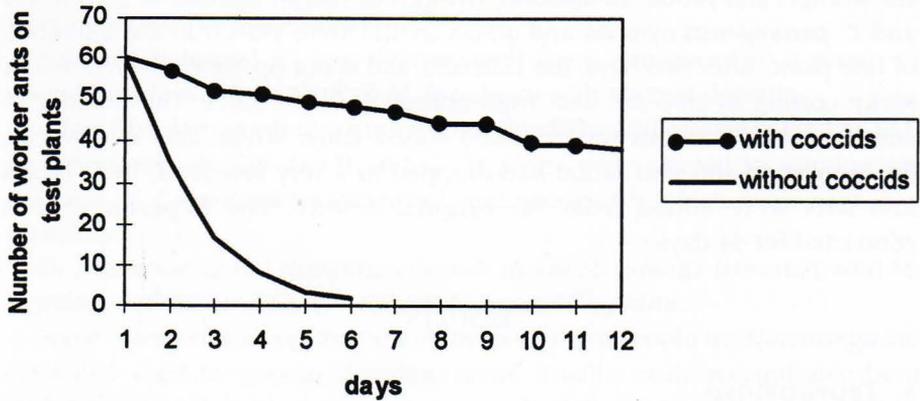


Fig. 1. Worker survival in test plants with ($n=60$) and without ($n=60$) coccids. The ants had no supply of food bodies.

coccids (Fig. 1). The loss of workers in plants with coccids was probably due to normal aging while some ants that died had been caught in the tangle trap. There were no hints that workers in the plants without coccids could use any other food source, such as plant tissue or epiphylls.

3. FEEDING ON SCALE INSECTS BY WORKERS AND BROOD.

i. Offering coccids as food for ant colonies

All offered coccids were either thrown off the plants immediately or were found in the experiment nest chambers. None of the surviving coccids showed any sign of damage by ants when checked under the microscope. The coccids that were damaged after they had become established on the plant were thrown off the plant. The development of ant larvae stopped and most of them were thrown off the plants once they had died and showed discolouration. All ants without honeydew died within a few days.

*ii. Inspection of (a) dumping-grounds inside *M. bancana* and *M. hypoleuca* plants and of (b) colony debris around the plants:*

Within the hollow twigs of *Macaranga*, no remains of arthropod origin could be found in the debris which consisted of an amorphous dark-brownish mass. With regard to the debris around the base of the tree, plant tissue from the boring of fresh entrance holes was found around the plant almost every day, especially when new internodes were opened the first

time. Two ants and two coccids were found dead outside the plant. They had probably died inside the plant and were dumped by ant workers. Mature coccids can neither enter or leave the hollow twigs without the assistance of ant workers (Heckroth, unpublished data).

iii. Observations on colonies in opened plants

C. tumuliferus was mostly able to colonise the plants and in only a few cases was it thrown from the plant by ants. However, *C. penangensis* were always thrown from the plants by the ant workers. In the absence of food-bodies, the ant larva stopped development. The coccids developed well and produced offspring. A few ant workers survived the entire 44 days (which is approximately one-third of their life expectancy (Heckroth, unpublished data)) feeding on honeydew.

DISCUSSION

As our results demonstrate, honeydew is a common food source for *Crematogaster* ants on myrmecophytic *Macaranga*. The coccids depend on the removal of this honeydew by the ants and retract the droplet when it is not removed. This shows the high degree of adaptation to life inside the hollow stems of living plants that is a common feature of members of the Subfamily Myzolecaniinae (Gullan & Buckley, 1993; Hodgson, 1994). Honeydew seems to be a full diet for ant workers, which are able to survive on an exclusive nutrition of honeydew for at least 40 days. In the absence of honeydew and without other food, the ants cannot survive longer than five days.

In contrast to our expectations, the coccids were not used as a protein source for the ant colony. Large numbers of coccids were thrown from the plant when they were offered in excess. Under our experimental conditions, *C. tumuliferus* was selectively accepted in the colonies but *C. penangensis* was generally thrown from the plants. This is in contrast to results of our former collections, where *C. penangensis* could be found regularly on *M. hypoleuca* plants although this plant species was most commonly colonised by *C. tumuliferus* (Heckroth *et al.*, 1998). Ants had to accept the loss of large numbers of the brood in the absence of food-bodies because of their inability to use coccids as a protein source. Food-bodies are believed to be the only food source on which an ant brood can be fed, even with coccids as honeydew providers (Heckroth, unpublished results).

In regular colony life, under conditions of food shortage and even when severely starved, no coccids were eaten by the ants. We cannot completely

exclude the possibility that coccids are used as food sometimes but we have found no evidence that coccids are regularly fed on under normal or emergency conditions. Honeydew would appear to be unsuitable for rearing the brood, probably due to its general lack of protein (Crane, 1986a; 1986b; Ewart & Metcalf, 1956). Also, no honeydew producing Sternorrhyncha have been recorded as being eaten by ants in other specific trophobiont interactions, especially in plant-ants. Liefke *et al.* (1998) reported that the ant *Polyrhachis arachne*, which lives in the hollow internodes of bamboo, controls the density of *Kermicus wroughtoni* by either carrying them to other nests of the polydomous colonies or by throwing the crawlers out of the nest, while Moog *et al.* (1998 and pers. communication) found that members of the genus *Cladomyrma*, a common ant-plant genus which generally lives on host plants which do not provide food-bodies and only rarely extrafloral nectar for the ants, were not observed to use food sources other than scale insect honeydew. Preliminary results of J. Moog and H.-P. Heckroth (unpublished) show that the associated pseudococcids are not used as prey.

Further studies will focus on the effect of coccids on colony growth and on their other possible functions in the ant-plant system; this system will also be compared with other ant-plant systems and their scale insects.

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