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## *Extrafloral nectaries: a defense against ant-Homoptera mutualisms?*

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**Summary.** We propose that extrafloral nectaries may sometimes function to defend plants from ant-Homoptera mutualisms by weaning ants onto a plant-controlled diet of nectar. According to this hypothesis, extrafloral nectaries can be favored even in the absence of ant defensive behavior. As evidence we cite the following observations: 1) Many studies have shown no net, defensive benefit to plants of nectar feeding ants. 2) Many nectar-feeding ants tend Homoptera which are major plant disease agents and which may profoundly alter plant architecture and physiology. 3) Ants can be distracted from tending Homoptera by feeding them sugar and they may even destroy the Homoptera. 4) Nectar has very similar chemical composition to honeydew and its collection does not require the extensive husbandry that tending Homoptera does. 5) Nectar production has been documented to increase during infestations of Homoptera. 6) It is more difficult to produce chemical defenses against sap feeders than against chewing insects.

The adaptive function of extrafloral nectaries (EFN's) was for a long time the subject of controversy. The polemic was between those who believed that extraflo-

ral nectar had only an excretory function to drain excess sugars (Wheeler 1910) and those who suggested that EFN's function to attract ants which protect the plant from herbivores (Belt 1874, Delpino 1886). The controversy has settled down in the last 25 years because of a paucity of evidence supporting the hypothesis of a physiological (excretory) function of EFN's, and because experimental studies have accumulated showing that, in at least some plants, their presence does indeed provide a safeguard from herbivores (for a review see Bentley 1977a, or Beattie 1985). Thus there is now a general consensus that a mutualistic relationship exists between plants that produce EFN's and their ant defenders. However, there are several inconsistencies in the data which suggest that the ant-attraction hypothesis may not be a universal explanation for the adaptive significance of EFN's. One is that, frequently, ants do not defend plants against herbivores. Also, ants tend mutualistic Homoptera that can be very damaging to plants. The purpose of this paper is to present a comple-

mentary hypothesis that EFN's may function to defend plants against ant-Homoptera mutualisms.

### Ants and plants

Several complex and obligate ant-plant mutualisms have been described which provide the cornerstone of the ant-guard hypothesis (Belt 1874, Delpino 1886, Janzen 1966). The best known example is the relationship between *Acacia cornigera*, the bull's horn acacia, which provides protein, sugar and shelter and the ant, *Pseudomyrmex ferruginea* which aggressively defends the plant (Janzen 1966).

However, in the majority of species producing EFN's, the interaction is facultative and more diffuse (several genera and many species of ants, bees, wasps, flies, etc. may obtain sugar and sometimes amino acids from the EFN's of several species of plants [Schemske 1983, Huxley 1986]). We looked at a sample of 28 papers where the ant-guard hypothesis was tested and unambiguous results were obtained. Twelve (43%) of these studies suggested that, in exchange for nectar, ants provide some protection against leaf feeding (Janzen 1966, Tilman 1978, O'Dowd 1979, Koptur 1979, 1984, Beckmann and Stucky 1981, Stephenson 1982), or seed predation (Bentley 1977b, Inouye and Taylor 1979, Keeler 1981, Schemske 1983, Horvitz and Schemske 1984). Nevertheless, eleven studies (39%) did not find that plants bearing EFN's are better protected, either because ants were not present or because they did not defend (Lukefahr 1960, Blom and Clark 1980, O'Dowd and Catchpole 1983, Tempel 1983, Buckley 1983, Boecklen 1983, Longino 1983, Lawton and Heads 1984, Heads and Lawton 1984, 1985, Koptur and Lawton 1988). Five (18%) showed that plants may or may not be protected, depending on the ant species present or because ants did not tend plants at some sites (Elias and Gelband 1975, Keeler 1977, McKey 1984, Barton 1986, Smiley 1986). There were high levels of herbivory in many of the cases where no effect of ants was observed.

### Ants and Homoptera

Mutualisms with herbivorous Homoptera (some species of aphids, membracids, pseudococcids and coccids) are widespread among ant species that tend EFN's (reviewed in Way 1963 and Buckley 1987). In exchange for honeydew, ants patrol Homoptera, constantly warding off parasites and predators (Way 1963) and may build protective coverings for them (Way 1954). Ants disperse homopterans from plant to plant and move them to better feeding sites within plants (Way 1963, Buckley 1987). Ants also provide brood care to Homoptera and improve their hygiene through removal of contaminating honeydew (Nixon 1951). In addition to providing honeydew, Homoptera are sometimes eaten for solid protein (Way 1954). As a consequence of ant attendance, Homoptera populations can multiply more rap-

idly than when unattended (El-Ziady and Kennedy 1956, Way 1963, Carroll and Janzen 1973) sometimes attaining levels eight-fold higher than in the absence of ants (Skinner and Whittaker 1981). For many species the lack of protection and attendance by ants may result in increased mortality and decreased fecundity (Way 1963).

### Ants, plants, and Homoptera

While the direct effects of Homoptera on plants is strictly negative, the ant-Homoptera mutualism has been termed a "mixed blessing" for plants (Carroll and Janzen 1973). In some cases plants accrue a benefit as a by-product of ant defense from herbivores which outweighs the losses from Homoptera damage (Stout 1979, Messina 1981, Buckley 1987). However, the cost to a plant of a homopteran infestation can be great. Not only do homopteran populations increase when tended by ants, but also, the uptake of phloem sap per individual may increase two to three times (Banks and Nixon 1958). The seed production or vigor of the plant may be considerably reduced because of this metabolic drain (Carroll and Janzen 1973). Homoptera are also known to disrupt developmental and metabolic pathways (Osborne 1972). Some recycle plant hormones or synthesize them from plant metabolites, causing deformation of stems or leaves (Miles and Lloyd 1967). Changes in the shape of organs or plant architecture may slow photosynthesis (Feede 1973; cf. Whitham and Mopper 1985).

Finally, Homoptera are also important vectors of plant diseases, especially those caused by viruses, which can debilitate or kill the host plants. In fact the most important vectors of plant viruses are aphids, followed by leafhoppers and treehoppers which are also tended by ants (Maramosoch 1963, Conti 1985).

### An alternative

We propose that extrafloral nectaries may sometimes evolve for defense against ant-Homoptera associations. In this scenario, the main selective pressure favoring extrafloral nectaries is not protection against herbivores by ants, but the distraction of ants from tending Homoptera by offering a honeydew substitute. This hypothesis is illustrated graphically in Fig. 1 where it is contrasted to the standard ant-guard hypothesis. According to the standard hypothesis, plants, initially without extrafloral nectaries, suffer herbivore damage (Fig. 1a). A mutant plant with extrafloral nectaries attracts ants that provide defense against herbivores, which results in increased plant fitness (though fitness does not reach the point it would in the absence of nectaries and herbivores, due to the cost of nectar production [Fig. 1a]).

In contrast, the ant-distraction hypothesis does not rely on the defensive behavior of ants. It draws a dis-

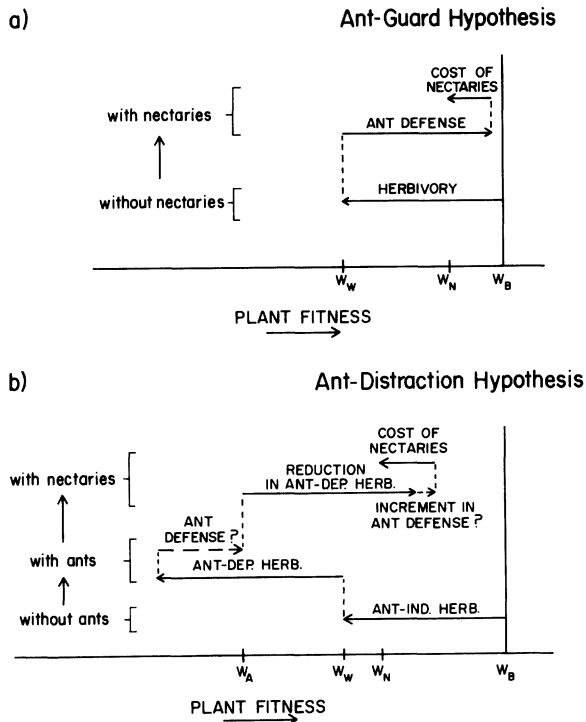


Fig. 1. Effects on plant fitness of changes in the factors considered in the ant-guard hypothesis (a) and the ant distraction hypothesis (b). The fitness of plants without herbivores, ants, or extrafloral nectaries is given as a base fitness,  $W_B$  for both models. The fitness without ants or nectaries (but with herbivores), is indicated as  $W_W$ , that with ants as  $W_A$ , and with nectaries (and presumably ants) as  $W_N$ . Arrows depict changes in fitness due to the indicated factors comparing plants with and without nectaries and ants. For ease of presentation the arrows are drawn for the comparative sequence: plants without ants, nectaries, or herbivores; plants with herbivores; plants with nectaries (and ants), though this is not meant to necessarily imply a historical sequence.

inction between ant-independent herbivores (those that are not tended by ants) and ant-dependent ones (Homoptera), taking into account the potential indirect damaging effects of ants. Plants without extrafloral nectaries may suffer from ant-independent herbivory (Fig. 1b). But many species in which nectaries evolve may already be visited by ants and suffer from ant-dependent herbivore damage, in addition to any damage from ant-independent herbivores. In this scenario, the critical effect of nectaries is to supply ants with a free source of sugar which distracts them from tending ant-dependent herbivores. Notice that plants with extrafloral nectaries may have higher fitness than plants without them even in the absence of antiherbivore defense by ants as long as the benefit of reduced ant-dependent herbivory outweighs the cost of producing nectar and nectaries. Thus the ant-distraction hypothesis is congruent with the numerous studies in which ants apparently do not defend (see above), though it is certainly compatible with ant defense as indicated by the dotted lines in Fig. 1b.

A version of the ant-guard hypothesis that explicitly involves Homoptera was briefly mentioned by Thompson (1982: 432). He suggested that EFN's might have evolved by short-circuiting the ant-homopteran interaction so that the defensive behavior of ants toward Homoptera was transferred to the plants. This differs from our ant-distraction hypothesis which proposes that the main fitness benefit of EFN's is the reduction of homopteran damage.

Several lines of evidence support the ant-distraction hypothesis. Ants can be distracted from tending Homoptera if an alternative source of sugar is offered. In an experiment performed by Way (1954) a solution of honey was supplied to an established colony of *Oecophylla longinoda* tending the coccid *Saissetia zanzibarensis*. Many ants not only deserted the coccids to collect the honey solution but a few of the larger workers began to destroy coccids of all ages. If plants are able to stop or reduce Homoptera damage by giving ants free nectar, there would be a strong selective pressure favoring extrafloral nectaries.

Several investigators have shown that, in general, as better resources become available, ants drop lower value ones from the diet (Addicott 1978, 1979, Sudd and Sudd 1985). From the point of view of ants, extrafloral nectar is superior to honeydew in being highly predictable in space, time, and quality. Also, nectar collection does not require ants to expend as much energy as Homoptera husbandry does: transporting, protecting Homoptera from parasites and predators, making shelters, and brooding their young (Carroll and Janzen 1973). Thus it is reasonable to expect that if EFN's provide ants with resource of similar or higher quality with lower search and handling costs than Homoptera, the latter may be abandoned.

If extrafloral nectar functions as a substitute for honeydew, it might be expected to be similar in its chemical properties. Detailed analyses of extrafloral nectar have shown that it contains the same kinds of sugars and amino acids as honeydew does (Way 1963, Auclair 1963, Bentley 1977a). Even melezitose, a trisaccharide normally synthesized in the gut of homopterans (Kiss 1981), has been found in the extrafloral nectar of some orchids (Bentley 1977a) and *Ochroma pyramidale* (O'Dowd 1979).

Some evidence suggests that plants that are heavily attacked by Homoptera have increased production of extrafloral nectar per unit time. In an experiment with cotton, Homoptera infestation was created by adding thrips, jassids, and whiteflies at different levels of infestation (Mound 1962). Extrafloral nectar production increased 3-4 fold when the sucking insects were present. This suggests that cotton may facultatively adjust the amount of nectar it offers ants as a honeydew substitute.

Why would plants opt to produce nectar instead of toxins as a defense against Homoptera? Chemical defenses may be difficult to utilize against sap feeding

insects since toxins in phloem can disrupt normal plant metabolism (Huxley 1986). Though some toxins have been found in phloem, they are more typically sequestered in special organelles or glands, or synthesized de novo at the time of damage (see McKey 1979, Edwards and Wratten 1985). Thus extrafloral nectaries seem an especially appropriate defense against Homoptera.

### Directions for further investigation

Most investigations to date have involved ant removals. This experimental protocol implicitly assumes that the function of nectaries is ant attraction and that in their absence, ants and their associates are also absent. Given that this may not always be true, sugar removals should be attempted, or perhaps more readily accomplished sugar additions to nectariless plants. Three basic fitness effects should then be measured on plants with and without nectaries or sugar additions: changes in the benefit of ant defense, changes in the level of Homoptera damage, and the cost of producing nectar and nectaries (see Fig. 1b). Nectaries should be favored when any increase in defense by ants plus any benefit of reduced Homoptera damage is greater than the cost of producing nectar.

Our hypothesis focuses attention on a number of questions that should be addressed experimentally: 1) Is it generally true that ants neglect Homoptera when an alternative sugar source is available? 2) Cost-benefit analyses from the point of view of the ants should be performed comparing the cost and benefits of collecting nectar to those of tending Homoptera. 3) Data on the timing and placement of nectar production relative to the timing and placement of Homoptera attack should be collected to determine the generality of the induced response to Homoptera. 4) In addition to exploring the relations between nectaries, ants and ant-independent herbivores, studies should take into account Homoptera and diseases for which Homoptera may be vectors, attempting to measure the magnitude of both direct and indirect effects.

Comparative studies of related species or populations with and without nectaries would shed light on many of the issues raised in this paper. The patterns predicted in Fig. 1b could be tested with such species pairs. For example, the prediction that related species without extrafloral nectar may be tended by ants and have serious infestations of Homoptera could be explored via such comparisons. Such studies would, of course, be even more informative with species pairs for which ancestral and derived conditions could be inferred (Felsenstein 1985). It is safe to conclude that ecological interactions involving EFN's deserve much more detailed study.

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