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Extrafloral nectaries vs ant-Homoptera mutualisms: a comment on Becerra and Venable

Brigitte Fiala, Ökologische Station der Universität Würzburg, Fabrikschleichach, D-8602 Rauhenebrach, FRG.

Becerra and Venable (1989) proposed that the function of extrafloral nectaries (EFNs) may not exclusively be to attract ants which defend plants against herbivores. They questioned the protection hypothesis and proposed that EFNs may also function to defend plants from ant-Homoptera mutualisms. Arguments for their hypothesis were e.g. the lacking universality of ant protection for plants and the negative impact of ant-tended homopterans on their host plants.

In general, effects of homopterans on plants are negative but the damages of ant-homopteran associations are difficult to assess. Becerra and Venable cited a few examples of beneficial by-products of these associations in form of protection for the plants by the visiting ants. However, they considered only facultative interactions.

In most of the highly developed ant-plant mutualisms ants cultivate homopterans while EFNs are absent. Among plant species of 36 genera, for example, which possess permanent domatia formed by hollow stems, only four have EFNs, but in 18 of them ants were recorded to keep homopterans (Huxley 1986). In the eight best-studied obligate myrmecophytic associations (Table 1) most plant partners offer nesting space but no food in form of nectar. The only two exceptions are *Acacia* spp. and *Leonardoxa africana*.

In this respect the genus *Macaranga* (Euphorbiaceae) is especially interesting. In SE Asia it comprises the full range of species which are obligatorily inhabited by ants to those which have only weak and unspecific associations with ants (Fiala et al. 1989, 1990). Most of the facultatively associated *Macaranga* species possess EFNs on the leaf margins and in addition on the lamina. Obligate myrmecophytes in this genus do not secrete sugar-containing fluids (Fiala and Maschwitz, in press) and colonizing ants keep scale insects inside the hollow stems of their *Macaranga* host plants. Contrary to Becerra's and Venable's hypothesis in this case a reduction of nectary production appears to be favoured.

The hypothesis of superiority of extrafloral nectar to honeydew remains to be tested in facultative associations, but my preliminary observations in Malaysia do not support this view. Becerra and Venable list a number of questions which should be addressed experimentally. I will briefly comment here on the first one: Is it generally true that ants neglect Homoptera when an alternative sugar source is available? During studies on the tree genus *Macaranga* in Peninsular Malaysia I looked for plants with EFNs and the occurrence of homopterans on these plants. The main study sites were secondary forests and disturbed habitat which were rich in light-demanding, fast growing plants. Six common species which possess EFNs were studied: *Macaranga gigantea, M. tanarius, Mallotus paniculatus, M. macrostachys, Endospermum diadenum* and *Croton argyratus* (all Euphorbiaceae). I checked 10 specimens each for occurrence of homopterans.

Two to five plants of each species were infested by Homoptera (mostly scales and membracids) despite the presence of EFNs. Other plant species without EFNs in the vicinity were not found with homopterans more often than the above mentioned species (random samples of up to five nearest neighbouring plants; giving a total of over 200 controls). All homopterans on leaves and stems of the plants were visited by various ant species (*Anaplolepis longipes* and three *Crematogaster* spp. were dominant). The ants also visited the extrafloral nectaries on these plants. However, often the ants seemed to prefer honeydew from the homopterans. On a leaf of *Croton argyratus*, for example, almost 2/3 of all ants visited the scale insects on the leaf lamina and only few took notice of the secreted extrafloral nectar. On *Mallotus* ants generally favoured membracids despite

Table 1. Food for ants in obligate myrmecophytic associations.

Ant-plant	Food available for ants		
	homopterans	EFN	food bodies
Acacia spp.[1]	−	+	+
Barteria fistulosa[2]	+	−	−
Cecropia spp.[3]	+	−	−
Leonardoxa africana[4]	−	+	−
Macaranga spp.[5]	+	−	+
Ocotea pedalifolia[6]	+	−	−
Piper spp.[7]	−	−	+
Triplaris spp.[8]	+	−	−

References: 1) Janzen 1967, 2) Janzen 1972, 3) Janzen 1969, 4) McKey 1974, 5) Fiala et al. 1989, 6) Stout 1979, 7) Risch et al. 1977, 8) Schremmer 1984.

the high amount of nectar production on the same leaves. A total of 443 ants were counted visiting the EFNs of the above mentioned study plants and 490 ants were visiting homopterans on the same plants. My observations, therefore, do not support the prediction of Becerra and Venable that ants generally neglect homopterans in the presence of EFNs. Buckley (1983) also reported ants on *Acacia decurrens* abandoning EFN when honeydew producing homopterans appeared on the plants.

I do not agree with Becerra's and Venable's view (p. 278) that "extrafloral nectar is superior to honeydew in being highly predictable in space, time, and quality". Nectar is costly to the plants and control over timing and rate of production would therefore be advantageous. Nectar production follows a daily and sometimes seasonal rhythm and is often influenced by external factors such as atmospheric humidity (Fahn 1979). In tropical Malaysia I found that nectar production was often restricted to the early morning hours. Nectar is therefore not a continuously available source of sugar, and honeydew from homopterans may provide a more constant food resource.

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References

Becerra, J. X. and Venable, D. L. 1989. Extrafloral nectaries: a defense against ant-Homoptera mutualisms? – Oikos 55: 276–280.

Buckley, R. 1983. Interaction between ants and membracid bugs decreases growth and seed set of host plant bearing extrafloral nectaries. – Oecologia (Berl.) 58: 132–136.

Fahn, A. 1979. Secretory tissues in plants. – Academic Press, London.

Fiala, B. and Maschwitz, U. Extrafloral nectaries in the genus *Macaranga* (Euphorbiaceae) in Malaysia: comparative studies of their possible significance as predispositions for myrmecophytism. – Biol. J. Linn. Soc., in press.

– , Maschwitz, U., Tho, Y. P. and Helbig, A. J. 1989. Studies of a South East Asian ant-plant association: protection of *Macaranga* trees by *Crematogaster borneensis*. – Oecologia (Berl.) 79: 463–470.

– , Maschwitz, U. and Tho, Y. P. 1990. The association between *Macaranga* and ants in South East Asia. – In: Cutler, R. and Huxley, C. (eds), Interactions between ants and plants. Oxford Univ. Press, Oxford, in press.

Huxley, C. R., 1986. Evolution of benevolent ant-plant relationships. – In: Juniper, B. and Southwood, R. (eds), Insects and the plant surface. E. Arnold, London, pp. 257–282.

Janzen, D. H. 1967. Interaction of the bull's horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. – Univ. Kansas Sci. Bull.: 47: 315–558.

– 1969. Allelopathy by myrmecophytes: The ant *Azteca* as an allelopathic agent of *Cecropia*. – Ecology 50: 147–153.

– 1972. Protection of *Barteria* (Passifloraceae) by *Pachysima* ants in a Nigerian rain forest. – Ecology 53: 885–892.

McKey, D. 1974. Interactions of the ant-plant *Leonardoxa africana* (Caesalpiniaceae) with its obligate inhabitants in a rain forest in Cameroon. – Biotropica 16: 81–99.

Risch, S., McClure, M., Vandermeer, J. and Waltz, S. 1977. Mutualisms between three species of tropical *Piper* and their ant inhabitants. – Am. Midl. Nat. 98: 433–444.

Schremmer, F. 1984. Untersuchungen und Beobachtungen zur Ethoökologie der Pflanzenameise *Pseudomyrmex triplarinus*, welche die Ameisenbäume der Gattung *Triplaris* bewohnt. – Zool. Jb. Syst. 11: 385–410.

Stout, J. 1979. An association of an ant, a mealybug, and an understorey tree from a Costa Rican rain forest. – Biotropica 11: 309–311.