

The association between *Macaranga* trees and ants in South-east Asia

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Introduction

In south-east Asia, myrmecophytic associations have so far been little investigated. Although the euphorb tree genus *Macaranga* has long been known to contain myrmecophytic ants (Smith 1903) existing information on its association is limited (e.g. Baker 1934; Ong 1978; Tho 1978; Rickson 1980). Nevertheless, the association has often been interpreted as an Asiatic equivalent to similar associations in Africa and America (Janzen 1969; Duviard and Segeren 1974; Buckley 1982). Our study was the first experimental investigation of the biological significance of the *Macaranga* association with ants. We were especially interested to find out what adaptations may have evolved convergently in South-east Asia.

Distribution and habitat

The genus *Macaranga* (Euphorbiaceae) is distributed from Africa to Polynesia and strongly centred in the Malesian region. Many species of this tree genus inhabit disturbed areas such as clearings, gaps, and forest edges. These habitats have enormously increased in extent over the last 100 years and the fast-growing *Macaranga* species have spread and become one of the most conspicuous trees in cleared areas (Whitmore 1967). In West Malaysia, where our study was carried out, 19 of the 27 *Macaranga* species occur in secondary forests.

West Malaysia is situated in the humid tropics with little seasonal variation in temperature. There is no pronounced dry season in the study area but two periods of heavy rainfall. The study areas are primarily covered with mixed dipterocarp forest that has been disturbed by forestry, road building, etc., and hence contains much secondary habitat.

Associated ants

Some of the most common species of *Macaranga* are closely associated with ants of the genus *Crematogaster* (Myrmicinae). In peninsular Malaysia a tight

relationship exists between nine of the 27 *Macaranga* species and a small, non-stinging *Crematogaster*. Most samples from the investigated *Macaranga* plants probably belong to *C. borneensis* which seems to be very variable. Based on these samples, however, several additional, closely related *Crematogaster* species may be involved in the symbiosis in West Malaysia (J. T. Longino, personal communication). In *M. puncticulata* we also found a *Camponotus* (*Colobopsis*). The only myrmecophytic *Macaranga* species which occurs in Thailand (*M. griffithiana*) was also found inhabited by a (different) *Camponotus* (*Colobopsis*) sp. In Borneo other *Crematogaster* species seem to take part in the association; we found a *Crematogaster* species from a different subgenus living in *M. kingii* and D. W. Davidson (personal communication) found several *Crematogaster* species in Bornean *Macaranga*. So the type of community complexity which has been found in other associations may exist (see Chapters 19–21, this volume).

Life history

Young *Macaranga* plants start being colonized by ants when they are about 10 cm tall and occupation occurs all year round. The queen ant searches for an unoccupied plant, sheds her wings, and chews an entrance hole, which she then seals from inside. The importance of the plants for the ants is evident: they provide nesting space inside hollow stems and food in the form of food bodies. A carbohydrate-rich food source is obtained via scale insects cultivated inside the stem. *Crematogaster borneensis* were found to be totally dependent on the host plant: in laboratory tests the workers did not survive away from the plants and in their natural habitat they were never found anywhere else (Fiala and Maschwitz 1990).

Benefits to the plant

There is no indication that the ants contribute to the nutrient requirements of their host plant. We did not find evidence for a net nutrient gain by *Macaranga* plants from the association with ants (Fiala 1988). Only very small amounts of labelled nutrients were taken up by the plant from the hollow internodes. The interior wall of the stem does not show any special absorptive structures. In addition, the ants never leave the plants for foraging or feed on insects that they kill on the plant, so that no nutrient import takes place.

Workers of *Crematogaster borneensis*, however, do protect their host plant against herbivores (Fiala *et al.* 1989). These ants, although seemingly rather defenceless, are very aggressive and, with a mass recruiting system, are able to attack phytophagous insects. Ant-inhabited *Macaranga* plants had a significantly lower percentage of herbivore damage than ant-free specimens (Fig. 18. 1). More than 50 per cent loss of leaf area was observed only in ant-

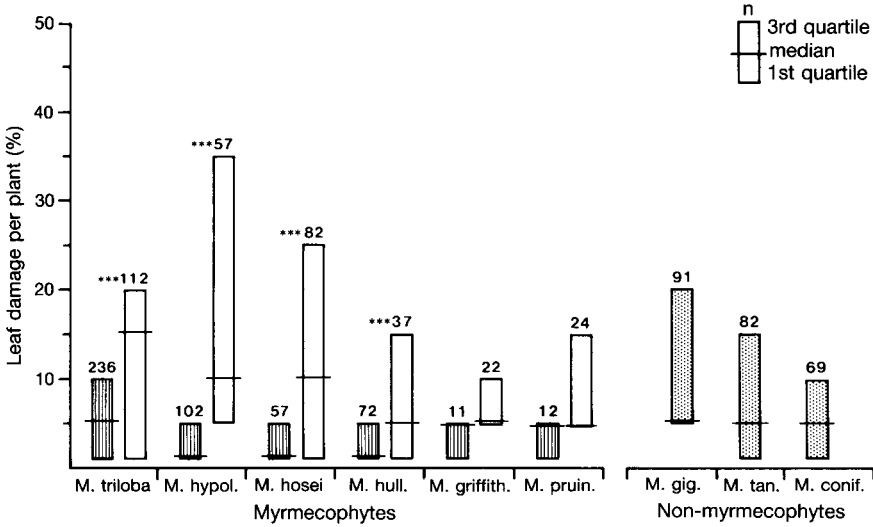


Fig. 18.1. Herbivore damage, as a percentage of leaf area, for ant-occupied (hatched columns) and ant-free (open columns) specimens of myrmecophytic and non-myrmecophytic *Macaranga* species. Differences between ant-occupied and ant-free plants according to Mann-Whitney U-Test: *** = $P < 0.001$. *Macaranga* species: hypol. = *hypoleuca*; hull. = *hulleuti*; griffith. = *griffithiana*; pruin. = *pruinosa*; gig. = *gigantea*; tan. = *tanarius*; conif. = *conifera*.

free plants (e.g. *M. triloba*, Fig. 18. 2). The ants also display a cleaning behaviour which results in removal of herbivores in the earliest developmental stages as eggs (Fig. 18. 3). This contributes significantly to the reduction of herbivore damage.

Still more important is the ants' defence of the host plant against plant competitors, especially vines which are abundant in the well-lit habitats where *Macaranga* grows. The pruning of foreign plant material in contact with the host plant has not been found so far in other *Crematogaster* species. Both ant-free myrmecophytic *Macaranga* species and most of the principally uninhabited *Macaranga* species had a significantly higher degree of vine growth than plants with ants (Fig. 18. 4).

The genus *Macaranga* comprises a full range of species, from those which are not regularly associated with ants to obligate myrmecophytes. This makes the genus especially suitable for interspecific comparison. Most of the myrmecophytic *Macaranga* species have a high percentage of occupation: plants > 1 m are usually colonized to more than 90 per cent. Three species out of the nine myrmecophytes do not seem to be fully adapted and can be seen as transitional. We will briefly introduce two of them: *M. hosei* and *M.*

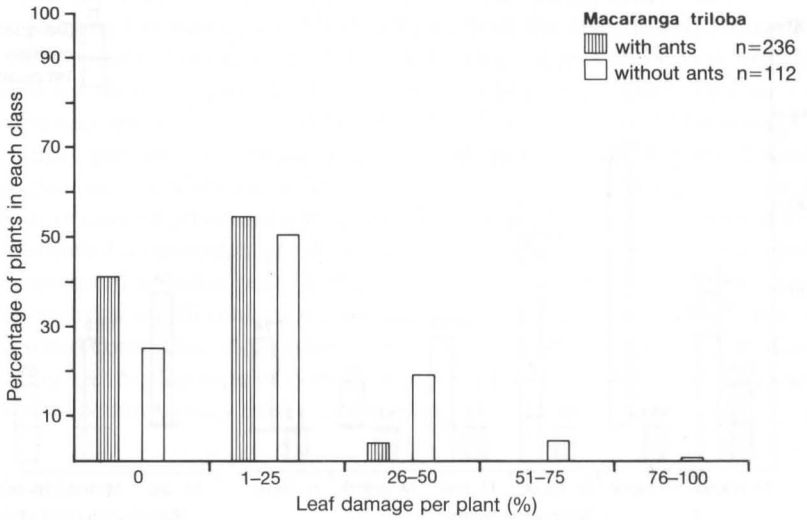


Fig. 18.2. Percentage of herbivore damage on ant-occupied (hatched) and ant-free (open) *Macaranga triloba*.



Fig. 18.3. Worker of *Crematogaster borneensis* removing a lepidopteran egg from the *Macaranga triloba* host plant.

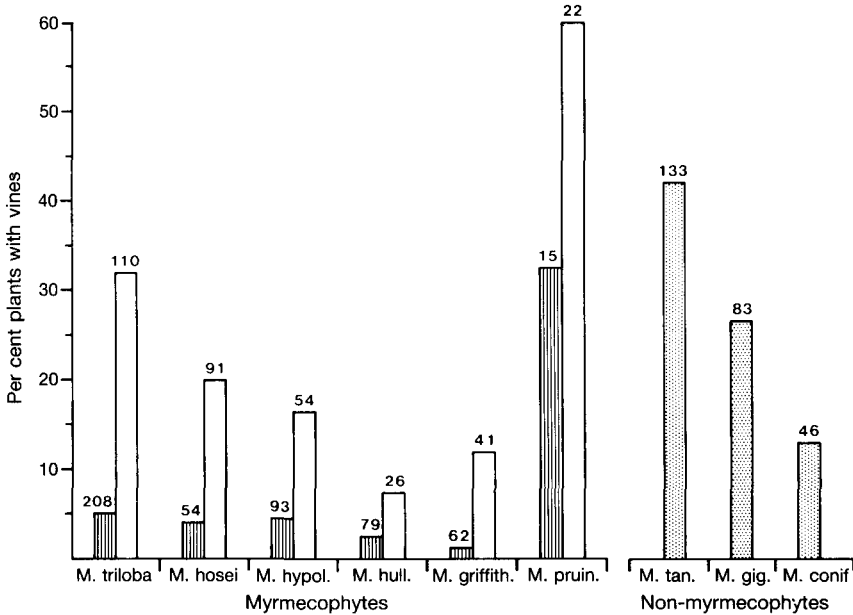


Fig. 18.4. Percentage of plants of myrmecophytic (left) and non-myrmecophytic (right) *Macaranga* species with vines. Hatched columns: ant-occupied; open columns: ant-free specimens. Differences between absolute frequencies according to Chi² analysis: *M. triloba* = $P < 0.001$; *M. hosei*, *M. hypoleuca* = $P < 0.05$; other species n.s. (not significant).

pruinosa, which are morphologically very similar, but differ in habitat. *M. pruinosa* grows in swampy places and *M. hosei* at drier sites. Their percentage of ant inhabitation is lower, and in *M. pruinosa* the effects of ant occupation are less clear cut: only parts of the plants (often the main stems) are inhabited by ants, which is reflected in a greater herbivore damage and vine growth on this species (Figs 18. 1 and 18. 4).

Most of the other myrmecophytic species have food bodies hidden under recurved stipules, as in *M. triloba*. In *M. hosei* and *M. pruinosa* food bodies are exposed on horizontal stipules. The stem interior of these species does not become hollow as in the other myrmecophytes but remains solid with a dry, soft pith. Although cavities can be excavated in the stem interior (Fig. 18. 5), it takes up to four hours for a founding queen to chew her way into the interior and she runs a high risk of predation or parasitoid attack during this time.

We also investigated nine of the *Macaranga* species known as non-myrmecophytes for their possible relationship with ants. Although there are

Table 18.1. Percentage of plants inhabited by *Crematogaster borneensis* for different *Macaranga* species in Peninsular Malaysia. Only plants over 1 m tall are recorded. n = sample size.

Species	n	Percentage of plants occupied by ants
<i>M. hypoleuca</i> Muell. Arg.	56	98
<i>M. hullettii</i> King ex Hook. f.	48	96
<i>M. triloba</i> Muell. Arg.	267	93
<i>M. griffithiana</i> Muell. Arg.	57	89
<i>M. hosei</i> King ex Hook	94	78
<i>M. pruinosa</i> Muell. Arg.	49	51

always ants on the plants (we found at least 24 species in 14 genera) we did not find evidence for any specific association or nesting of ants on these non-myrmecophytic plants. In order to explain this we looked for the presence or absence of morphological or other predispositions to a myrmecophytic way of life. Contrary to earlier assumptions most non-myrmecophytic *Macar-*

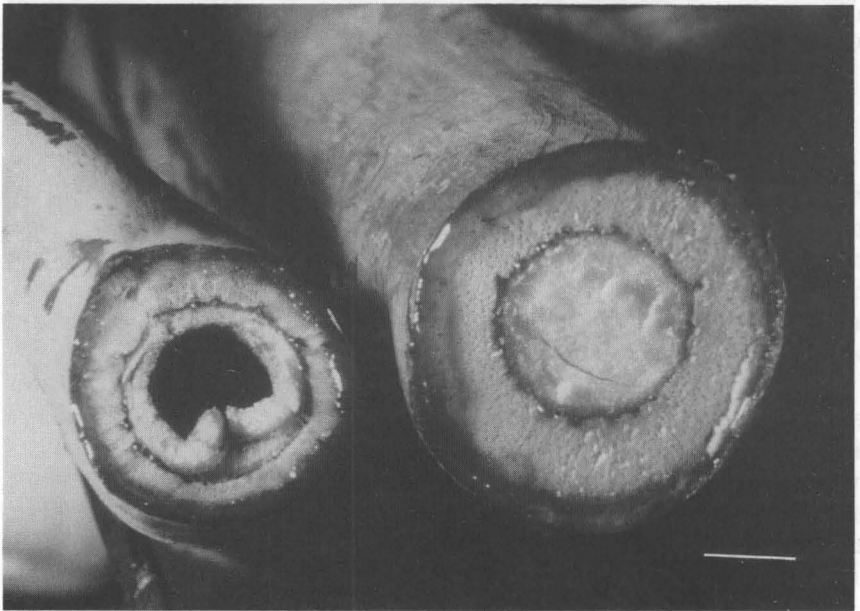


Fig. 18.5. Transverse section through stem of *Macaranga pruinosa*. Younger part of the stem (left side) excavated by *Crematogaster borneensis* ants (scale = 4 mm).

anga species do produce food bodies, some also have extrafloral nectaries. Therefore, food availability for potential ant partners does not appear to be a limiting factor. The lack of nesting space on or within the plants probably explains why ants are not present permanently. The stem morphology differs considerably from ant-inhabited species. Most non-myrmecophytes have a solid stem with a hard and wet pith and rings of resin ducts. These secrete large amounts of a sticky gum-like fluid when injured (Fig. 18. 6). This would be an effective barrier to ant colonization.

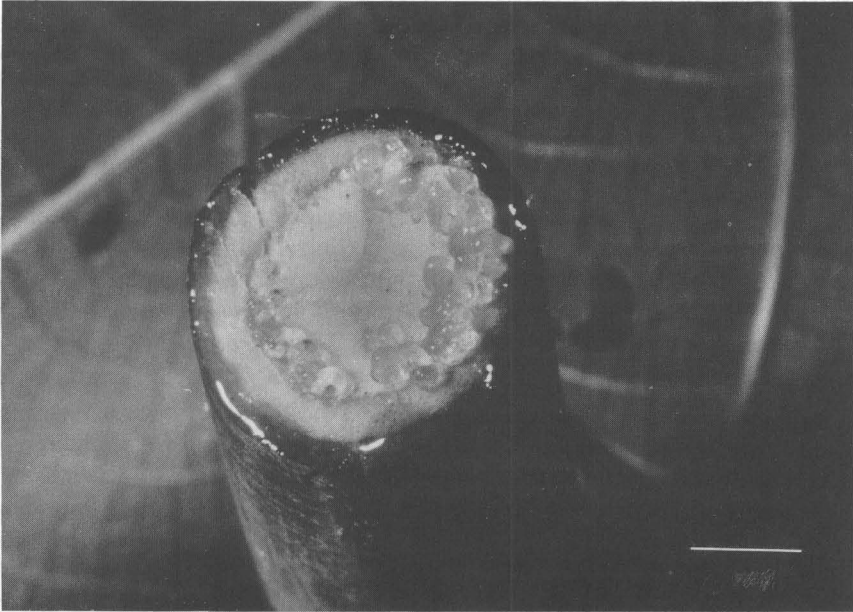


Fig. 18.6. Transverse section through stem of *Macaranga tanarius* Muell. Arg. Secretion of sticky fluid (scale = 4 mm).

As we have seen ant inhabitation offers some advantage for the plants. How do non-inhabited *Macaranga* species cope with herbivory and climber growth? Are there any principal differences between non-myrmecophytes and myrmecophytes? Preliminary evidence suggests that differences exist in habitat requirements and that competitive ability can be achieved by different types of growth. Some species occur exclusively at sites where plant competition and herbivore pressure are lower than in secondary habitats, e.g. in primary forest or at higher altitudes. Species without ants growing in well-lit lowland sites often have certain structures which probably favour them in the face of plant competition, e.g. very large leaves and a broad, roof-like canopy. Both attributes result in shading of the surrounding vegetation and

will inhibit the growth of neighbouring plants. In particular, this is the case with *M. gigantea* and *M. tanarius*. Individuals of *M. gigantea* only 30 cm tall already have leaf widths of up to 40 cm.

Most myrmecophytic species have a much more open and branched canopy. They grow primarily at the interface between forest and openings or roads; these edges are rich in climbers. Here the ants have an important function in suppressing growth of climbers by biting them off. More work is under way on this comparative aspect of the different strategies of all Malaysian *Macaranga* species. This will also involve investigations of defence mechanisms against herbivores, to assess effectiveness of herbivore protection in non-myrmecophytic *Macaranga*. Thus, the relationships between ants and plants are not only curious examples of symbiotic mutualisms, but show patterns and complexity paralleling those in other ecological systems, as pointed out in Chapter 20.

In summary, it can be said that the ecology of ant-associated *Macaranga* trees is modified compared to uninhabited congeners and that these adaptations influence their competitive ability. A broader perspective on ant-plant associations may lead to new insights in colonization patterns in plants. In some features *Macaranga* resembles the pioneer tree genus *Cecropia* (Cecropiaceae) in Central and South America and may be regarded as an Asiatic analogue of this neotropical system. The *Macaranga*-*C. borneensis* association is equivalent to myrmecophytic systems in South America and Africa in its specificity and symbiotic character.

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