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Diversity of ant-plant interactions: protective efficacy in *Macaranga* species with different degrees of ant association

Abstract The pioneer tree *Macaranga* in SE Asia has developed manyfold associations with ants. The genus comprises all stages of interaction with ants, from facultative relationships to obligate myrmecophytes. Only myrmecophytic *Macaranga* offer nesting space for ants and are associated with a specific ant partner. The non-myrmecophytic species are visited by a variety of different ant species which are attracted by extrafloral nectaries (EFN) and food bodies. Transitional *Macaranga* species like *M. hosei* are colonized later in their development due to their stem structure. Before the colonization by their specific *Crematogaster* partner the young plants are visited by different ant species attracted by EFN. These nectaries are reduced and food body production starts as soon as colonization becomes possible. We demonstrated earlier that obligate ant partners can protect their *Macaranga* plants against herbivore damage and vine cover. In this study we focused on non-specific interactions and studied *M. tanarius* and *M. hosei*, representing a non-myrmecophyte and a transitional species respectively. In ant exclusion experiments both *M. tanarius* and *M. hosei* suffered significantly higher mean leaf damage than controls, 37% versus 6% in *M. hosei*, 16% versus 7% in *M. tanarius*. *M. tanarius* offers both EFN and food bodies so that tests for different effects of these two food rewards could be conducted. Plants with food bodies removed but with EFN remaining had the lowest mean increase of herbivore damage of all experimental groups. Main herbivores on *M. hosei* were mites and caterpillars. Many *M. tanarius* plants were infested by a shootborer. Both *Macaranga* species were visited by various ant species, *Crematogaster* spp. being the most abundant. We found no evidence for any specific relationships. The results of this study strongly support the hypothesis that non-specific, facultative associations with ants can be advantageous for *Macaranga* plants. Food bodies appear to have lower attractive value for opportunistic ants than EFN and may require a specific dietary adaptation. This is also indicated by the fact that food body production in the transitional *M. hosei* does not start before stem structure allows a colonization by the obligate *Crematogaster* species. *M. hosei* thus benefits from facultative association with a variety of ants until it produces its first domatia and can be colonized by its obligate mutualist.

Key words Ant-plant interactions · Herbivory *Macaranga* · Mutualism · Myrmecophytes

Introduction

Interactions between ants and plants are a key phenomenon in moist tropical ecosystems. Most functional studies on these relationships have been devoted to the question of the protective value of the ants, often with a rather general approach. The extremely high diversity on both the plant and the ant side was often neglected. To understand the evolutionary development of the highly sophisticated obligate and specific mutalistic systems, studies with a comparative focus should be performed. Few data are available, particularly on ant-plant associations in the SE Asian tropics; almost all studies have been conducted in the New World (overview in Beattie 1985; Oliviera and Brandão 1991).

The emphasis of our studies in SE Asia to date has been the tree genus *Macaranga*, which is especially suited for comparative studies since the genus comprises the full range of species from those not regularly visited by a variety of ants to obligate myrmecophytes (Fiala and Maschwitz 1991, 1992a, b; Fiala et al. 1989, 1991). Only the myrmecophytic *Macaranga* species provide nesting space for ants inside stem internodes which become hol-

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low due to degeneration of the pith. The ants obtain food in the form of food bodies produced by the plants, and from scale insects kept inside the plants. Some transitional species (which are, however, true myrmecophytes) are solid as well, but their pith is soft and dry and can be excavated by ants. Non-myrmecophytic species, however, also attract and maintain ants by the offer of food resources: we have verified that actually all species studied so far have extrafloral nectaries (EFN) and produce food bodies.

Most previous experimental work on the functional significance of ant-plant interactions in SE Asia has been conducted on highly developed myrmecophytes such as the *Macaranga* species (Fiala et al.1989, 1991) and on *Endospermum labios* in New Guinea (Letourneau et al. 1993). Only one study from New Guinea concentrates on non-specific associations of several euphorb tree species with various ants attracted by EFN (Whalen and Mackay 1988).

In the genus *Macaranga* all stages of specificity in the interaction with ants exist. Are these different levels of specificity mirrored in different effectiveness of defence? Do *Macaranga* species without obligate ant partners benefit from these unspecific relationships? In this study we address these questions in two species:

1. The common and widely distributed non-myrmecophyte *M. tanarius*. This species offers the opportunity to compare the attraction value of EFN and food bodies for ants. To date there is little information available on this subject.

2. The transitional species *M. hosei*, which is especially suited for a comparative study. The young plants of this species go through a life history phase in which they do not possess domatia, but have EFN which attract a variety of opportunistic ants. Above heights of 0.7 m they reduce their nectaries, and develop food bodies and domatia which are colonized by a specific obligate mutualist *Crematogaster* species. Thus, the occurrence of both specific and non-specific relationships allows comparison of the effectiveness of different anti-herbivore defences within this species, and between the two *Macaranga* species.

Materials and methods

Organisms

Macaranga has a widespread distribution within the Paleotropics with its centre in the Malesian region. In Malaysia (Peninsula and Borneo) 23 out of the 52 species are inhabited by specific ants, a few small *Crematogaster* species from the subgenus *Decacrema*, mainly of the *C. borneensis* group.

M. tanarius does not provide any nesting space. Saplings usually have small marginal glands as well as five foliar nectaries on the adaxial side of the unlobed leaf blade. Food bodies are scattered over leaf surfaces and petioles and on stems. They are not easily seen in the field but become obvious in the greenhouse and when ants are excluded. Development of EFN and food bodies ceases on leaves of trees > 3–4 m. Leaves of saplings are rather large (diameter about 50 cm) but become smaller (diameter 10 cm) and leathery on mature plants.

Leaves of *M. hosei* are comparatively small (average diameter about 15 cm). Young saplings have two rather inconspicuous EFN on the leaf surface near the petiole insertion. These laminar EFN are usually no longer present on plants taller than 1 m. In contrast to other myrmecophytic *Macaranga* species which become colonized from a size of 10 cm upwards, only 15% of *M. hosei* plants were inhabited below a size of 70 cm (n = 114). Due to an insufficient thickness of the stem in the early stages, this species cannot be colonized until comparatively late in its development. Usually at this size the EFN on the lamina diminish and food body production starts. Food bodies are concentrated and exposed on horizontal stipules. Seventy-eight percent of plants 1.5 m and higher are inhabited by their specific *Crematogaster* ant partner (Fiala and Maschwitz 1991, 1992b).

Study site

The study was conducted in Peninsular Malaysia from 14 January 1991 to 15 March 1991 near the Ulu Gombak Field Study Centre, Selangor (3°21′N, 100°48′C, 240–500 m a.s.l.). The region is situated in the humid tropics with no pronounced dry season and little seasonal variation in temperature.

A large population of *M. tanarius* plants was found in a recently cleared open area (about 900 m^2) near the station (about 80 saplings ranging from 0.5 to 3 m high). Beside *M. tanarius* other typical secondary growth vegetation occurred. Uncolonized saplings of *M. hosei* were studied along a steep logging track in secondary forest 3 km from the field station (the same site as described in Fiala et al. 1989). This trail, which was fairly open and exposed to light with lush plant growth, was kept open by frequent cutting. *M. hosei*, together with other secondary growth specialists like *Mallotus* spp. and *Dicranopteris* spp., grew on a stretch approximately 2 km long.

Experiments

The protective role of ants was tested in ant-exclusion experiments

Of the randomly chosen plants for study, half were selected for ant-exclusion treatment, while the other half served as unmanipulated controls. Pairs of control and experimental plants growing beside each other in the same place were selected wherever possible, to minimize differences in ant colony distribution. However, to avoid one-sided biases in ant density due to special local effects we tried to achieve some spatial variation within both study sites.

Ants were excluded from experimental plants with band of sticky tanglefoot (Tanglefoot Company, USA) placed on tape around the stem base. Control plants were banded with tape only.

At the beginning of the study all *M. hosei* plants were not yet inhabited by their obligate ant partner. Their height varied from 0.3 m to 1.5 m. After 2 months, 7 of these plants had been colonized by their obligate *Crematogaster* ant but ant colonies were still very small (< 30 individuals) and not active on the surface. For comparison, 5 larger plants (> 2 m) inhabited by the obligate *Crematogaster* were monitored in the same habitat. (Sample size could be kept low since herbivore damage of inhabited *M. hosei* had already been studied in detail; Fiala et al. 1989). The leaves of five adult trees of *M. tanarius* were also checked fro herbivore damage.

Original number of plants was reduced due to loss of some specimens to trail-clearing activities. At the end of the study period the following groups of plants remained:

A. Untreated control plants
M. hosei n = 23 (138 leaves total initially to 238 leaves finally)
M. tanarius n = 20 (86 to 184 leaves)

B. Ant-exclusion plants
M. hosei n = 24 (139 to 188 leaves)
M. tanarius n = 13 (67 to 144 leaves)

Usually herbivores of *Macaranga* such as beetles and grasshoppers do not gain access to the leaves by climbing up the stem. Common caterpillars developed on the plant from the egg stage and did not leave the plant between feeding periods. Therefore, the probability of excluding at least the most common herbivores together with the ants was rather low.

For *M. tanarius*, two additional sets of experiments were conducted to test for different effects of food bodies on EFN on herbivore damage:

A. On 9 plants (31–62 leaves) ants had free access but EFN were extirpated (being carefully removed from the leaf blade using fine scissors). Earlier tests on 10 plants had shown that leaves were not visibly influenced in their growth process after removal of this very small area of their surface. We carried out control tests (for any detriment caused by the cutting of the leaf tissue) by removing equally large other parts (no EFN) of the leaf blade. We could not find alterations in the attractiveness of these injured plants for ants and other visitors. Plants from which EFN had been removed were used in experiments only after the injured parts no longer lost any plant sap, so as to avoid the release of olfactory cues to herbivores.

B. On 9 other plants (35–64 leaves), ants had free access to plants and EFN were untreated, but food bodies were removed by carefully brushing the plant surface. (Usually a few food bodies were left on the plants because it was difficult to remove them all without damaging the plant surface).

Leaf damage

As a measure of herbivore defence in the relatively short study period, cumulative leaf damage as a percentage of leaf area was estimated to the nearest 5%. The study began with the upper seven leaves which were surveyed during the whole study period. New leaves were included in the survey as soon as they were fully expanded. Percent damage always refers to total leaf area per plant (i.e. new leaves were included). The new leaves were also treated separately to test for possible influences of previously existing damage and as a mean to record development of herbivore damage from the beginning onwards. Initial mean leaf damage of control and experimental plants of *M. hosei* at the beginning of the study was similar, and in *M. tanarius* it differed only slightly (Figs. 1, 2).

An infestation with mites in *M. hosei* became apparent by the increasingly yellow leaf coloration. A totally yellow colour of 50% of the leaf area was arbitrarily classified as 50% damage: usually it then took only a few days before the leaf was dead and fell off the plant.

Leaf damage was monitored at bi-weekly control censuses. All ants and herbivores present were also recorded at these control checks, which took place at various times of the day (and during the night). The non-parametric Mann-Whitney U-test was used to test for differences in the means of two samples.

Results

Ant-exclusion experiments

When ants were excluded, both *M. hosei* and *M. tanarius* suffered significantly greater herbivore damage. The first effects became obvious after 2 weeks. Leaf damage increased much more in ant-exclusion plants than in controls.

In *M. hosei* control plants, mean leaf damage increased by only 6% (from 10% at the beginning of the study to 16% at the end of the study). Experimental plants which had ants excluded suffered an increase in
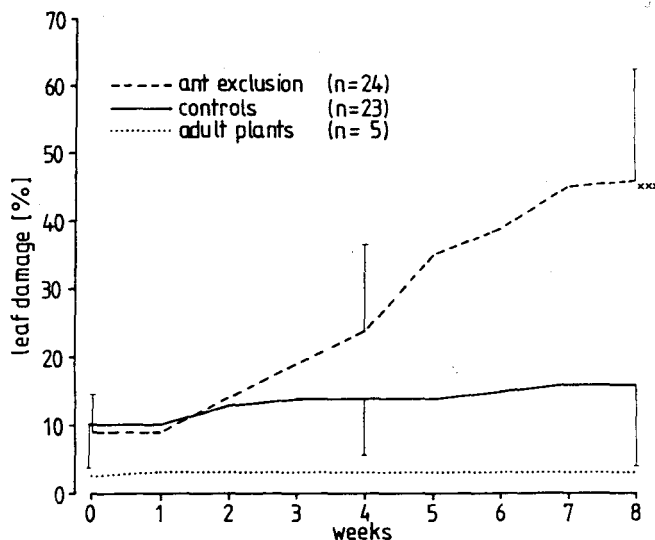

Fig. 1 Mean herbivore damage ($\pm$ SE), as a percentage of total leaf area per plant, for *Macaranga hosei*. Adult plants are inhabited by their obligate *Crematogaster* ants; the other groups are facultatively visited by different non-specific ants. *Asterisks* denote differences between ant exclusion plants and controls according to a Mann-Whitney U-Test: *** $= P < 0.001$. For clarity, SE are only given for the beginning, middle and end of the study

mean damage of 37%, a fivefold difference (9%–46%) (Fig. 1). The difference between control and experimental plants in the increase in damage was highly significant (Mann-Whitney U-test, $P < 0.001$). Damage on leaves of the five adult control plants of *M. hosei* which were already inhabited by their specific *Crematogaster* ant was clearly below that of *M. hosei* saplings (Fig. 1).

In controls, newly expanded leaves had about the same damage as mature leaves, but suffered more damage than mature leaves in the ant-exclusion group (Table 1).

The mean leaf damage increase of *M. tanarius* control plants (Fig. 2) is similar to *M. hosei* controls. Experimental plants with ants excluded had a mean increase in leaf damage of 16%. Although less dramatic than in *M. hosei*, the difference between controls and experimental plants in *M. tanarius* was also significant ($P < 0.001$). On adult trees damage was much lower (only a 4% increase). New leaves when compared to mature leaves in control plants had about the same degree damage, but suffered more damage in experimental plants (Table 1).

M. tanarius plants with EFN removed

These plants had the highest increase of loss of leaf area of all groups (25%, Fig. 2). This loss was significantly greater ($P < 0.001$) than that of control plants, with a mean increase in leaf damage of only 7%. New leaves, however, had a lower mean increase than mature plants, but equal to that of young leaves in ant-exclusion experiments (Table 1).
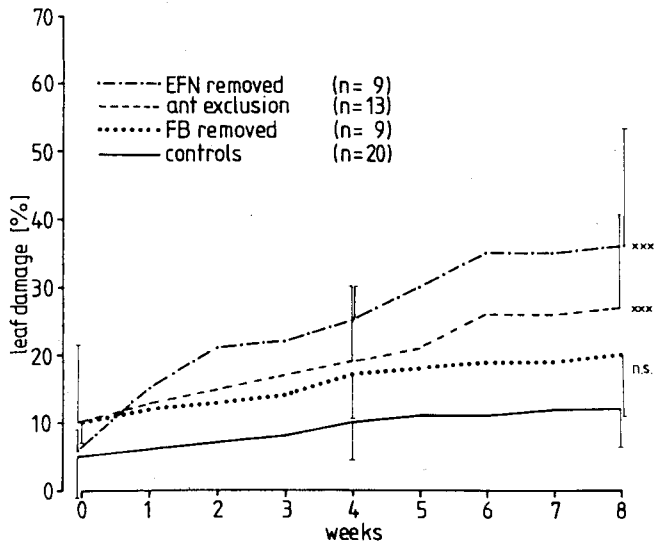
Fig. 2 Mean herbivore damage ($\pm$ SE), as a percentage of total leaf area per plant, for *M. tanarius*. For details of the different experimental groups see text. *Asterisks* denote differences between experimental groups and controls according to a Mann-Whitney U-Test: *** $= P < 0.001$; $ns =$ not significant. For clarity, SE are only given for the beginning, middle and end of the study (*EFN* extrafloral nectaries, *FB* food bodies)

Table 1 Comparison of leaf damage increase, as a percentage of leaf area, of newly expanded and mature leaves of *Macaranga hosei* and *M. tanarius* after 8 weeks. (*EFN* extrafloral nectaries, *FB* food bodies)

| | Experimental groups | | | |
	Controls	Ant exclusion	EFN removed	FB removed
M. hosei				
Young leaves	8%	40%	–	–
Mature leaves	6%	19%	–	–
M. tanarius				
Young leaves	9%	22%	21%	14%
Mature leaves	5%	14%	28%	9%

M. tanarius plants with food bodies removed

This group had the lowest mean increase of herbivore damage of all experimental plants (Fig. 2). Damage was slightly, but not significantly, higher than on control plants ($P > 0.05$). New leaves had a higher increase in damage which was, however, also not significant (Table 1). Results were not uniformly low, but two groups could be differentiated: 4 plants had a relatively high mean damage increase of 28.5% ($\pm$ 4.5) versus the less than 12.5% ($\pm$ 3.8) of the other 5 plants. These results were similar to the two other experimental groups and the controls, respectively. This two-peak distribution was not found in any other experimental group. Plants were rather evenly spaced, and there was no correlation between the sites where plants grew and their degree of damage.

Herbivores

Common on both species were beetles (mainly Curculionidae, Scarabeidae) and grasshoppers, most of them nocturnal. In general, they were rarely physically encountered during the course of the brief control checks. However, some left typical feeding marks. For 768 observations on control plants, mobile herbivores such as beetles and grasshoppers were actually found feeding on the plants on only 29 occasions. In addition to the similar general herbivore fauna, there were also distinctive characteristics for each *Macaranga* species.

At the end of the study all surveyed plants were cut and thoroughly investigated. Of 50 surveyed, 32 *M. tanarius* plants were infested by a shootborer (mostly caterpillar or pupa present, sometimes only feeding trails). The caterpillar was identified as the moth *Rhodoneura* species close to *tetragonata* (H. Barlow, personal communication). It was mainly found in the lower part of the stem where it lives in the pith, despite the resin ducts. It also causes severe damage to plant apices that can eventually result in plant mortality.

On *M. hosei* shootborers were quite rare (found only in one of the study plants), which may be due to the relatively small stem diameter of the plants at the sapling stage. More common were caterpillars of Noctuidae, Tortricidae and Geometridae. Nocturnal herbivores such as weevils, scarabeid beetles and grasshoppers were rarely seen feeding, but left typical feeding marks. A large portion of the leaf damage was caused by intensive infestation of pseudococcids, which could cause death (withering) of whole twigs.

The main herbivores on *M. hosei* were mites of at least three different species from 2 families, mainly Tetranychidae. Leaves infested with mites first become yellow, then brown, and usually fell off the plants (on touching) within 2 weeks or even earlier. Mites were present on 19 of the experimental plants with ant exclusion but only on 1 of the control plants. During our study period herbivorous mites were never found on *M. tanarius*.

Associated ants

We found no evidence for any specific relationship between the studied *Macaranga* saplings and visiting ants. Both plant species were visited day and night by various ant species. A total of 21 ant species in 13 genera were found on the leaves during the study period (Table 2). (Due to insufficient taxonomic revision, most SE Asian ants cannot be determined to the species level.) *Crematogaster* were numerically dominant on both *Macaranga* species. At night we encountered most of the species that were also present during daytime; however,

Table 2 Ants visiting *M. hosei* and *M. tanarius*. Ant abundance (number of workers on plants per census): + rare (< 5), + + occasional, + + + common (> 15). Average of 35 censuses

	M. hosei (n = 23)	M. tanarius (n = 20)
Pseudomyrmecinae		
Tetraponera	−	+
Myrmicinae		
Cataulacus sp.	−	+
Pheidole sp.	+	+ +
Monomorium sp.	+	+ + +
Crematogaster		
sp. 1	+ + +	+ + +
sp. 2	+ + +	+ + +
sp. 3	+ + +	+ + +
Dolichoderinae		
3 *Dolichoderus* spp.	+	+ +
Technomyrmex sp.	−	+
Formicinae		
Anaplolepis longipes	+	+ +
3 *Camponotus* spp.	+ +	+ +
Meranoplus mucronatus	+	−
Paratrechina sp.	−	+
Polyrachis		
sp. 1	+ +	+
sp. 2	−	+
sp. 3	−	+
Oecophylla smaragdina	−	+ +

Polyrachis spp. were strictly diurnal whereas one *Camponotus* species was active only at night.

In 16 of the 32 *M. tanarius* plants infested by shootborers, their mines were secondarily used by ants which then nested inside the stems. These were mainly *Monomorium* spp. (6 colonies) as well as *Crematogaster* spp. (7 colonies of 2 species) and a *Pheidole* sp. (1 colony). Despite the high number of individuals in these nests, *Monomorium* workers were rarely seen on surface of *M. tanarius* plants. Most abundant were 3 *Crematogaster* spp., as well as 3 different *Camponotus* spp. The *Camponotus* occurred in most cases as single foragers whereas *Crematogaster* often foraged in groups. All ants listed in Table 2 were observed visiting the EFN, but none were observed collecting food bodies.

Our first feeding experiments, offering food bodies to 17 different ant species, showed that these were taken and carried away to the nest, but we could not tell whether they were eaten. Only ants from three species did not accept food bodies: two *Polyrachis* spp. and a *Cladomyrma* species (a specialized ant living exclusively on the tree *Saraca thaipingensis* in the Ulu Gombak area).

Usually food body production on the plants is not very conspicuous. On the plants isolated with tanglefoot, however, food bodies became very numerous. Many food bodies were produced at the base of the stem which gave the impression that they serve to attract ground feeding ants to climb up the plants. On some plants, isolation was interrupted for a short time to test the attractiveness to ants of this unusual offer of large numbers of food bodies. A few hours after ant access was allowed, workers of *Monomorium* were found on the plants. *Monomorium* were recruiting nestmates and soon hundreds of workers were carrying food bodies to the nest. Most of the *Monomorium* ants were not nesting in shootborer holes but came from a nest somewhere in the vicinity of the plants. Collection went on until almost all food bodies which were not too big to be transported by the small workers had been collected. No other ant species was observed to be especially attracted to this unusually large offering of food bodies.

Discussion

Experiments on ant protection

Our previous studies demonstrated that the specific ant partners of the obligate myrmecophytic *Macaranga* species can effectively protect their host plants against herbivore damage and vine infestation (Fiala et al. 1989, 1991). Non-myrmecophytes did not receive any protection against competing plants, and the outcome of defence against herbivore damage appeared to be rather variable in these facultative associations. Despite the production of EFN and food bodies, uninhabited *Macaranga* species had a higher amount of herbivore damage than myrmecophytic species (Fiala et al. 1989). The results of the study presented here, however, strongly support the hypothesis that non-specific association with ants can also provide protection for *Macaranga* plants. After removal of EFN and food bodies, the non-myrmecophytes were subject to even stronger herbivore damage.

The adaptive significance of EFN has been controversial for decades, but in recent years studies mainly from the Neotropics have demonstrated that ants visiting EFN often protect plants against herbivores (overview Beattie 1985; Huxley 1986; Keeler 1989; Koptur 1992). It has been demonstrated that removing nectaries from plants can substantially reduce the number of ants on a plant (Koptur 1979). In New Guinea, Whalen and Mackay (1988) were able to demonstrate the reduction of herbivory on *Macaranga* by ants, but comparable experiments in Australia on euphorb trees did not show an effect (Mackay and Whalen 1991), perhaps due to lower herbivore pressure with increasing latitude, or decreasing productivity of the environment making biotic defence less efficient for the plants.

Problems of proximate and ultimate effects of ant protection have been discussed in Fiala et al. (1989). Of ultimate importance is reproductive success [as was demonstrated by Vasconcelos (1991)]. However, these studies cannot be carried out on woody perennials which need decades to reach reproductive age. The

present study shows that the loss of more than half of the leaf substance in saplings could occur, which certainly leads to reduced growth rate and decreases the competitive ability of this important life-history stage.

M. tanarius in general appeared to have lower leaf damage than *M. hosei*. This might be due to habitat factors, but could also be caused by their different herbivore spectrum.

Attractive value of food bodies

Almost no information exists on the attractive value of food bodies in comparison with EFN. In *M. tanarius*, most leaf area reduction occurred on plants where ant access was excluded or EFN extirpated (despite of the presence of food bodies). Plants which had their food bodies removed but on which EFN were still present suffered on average less damage. However, two distinct groups of leaf damage could be differentiated: a portion of the experimental plants in which food bodies remained but EFN were removed suffered rather high damage. The presence of food bodies alone appeared to be less attractive for ants. On the other hand, five specimens of this group had a mean leaf damage which was similar to that of controls, which may indicate that these food rewards are differentially used by several ant species with different protective value for the plants. Only a *Monomorium* species was observed to exploit an unusually rich offer of food bodies on *M. tanarius*. They were usually rather shy and not very active on the surface, and may therefore be of low protective value for the plant. However, Australian *Monomorium* species are reported to defend resources using topically applied alkaloid venoms (Jones et al. 1988).

There are indications that food bodies are only attractive for specialized ants (Fiala and Maschwitz 1990, 1992a; Davidson et al. 1991). There may exist a dietary adaptation of ants for this kind of plant food.

Diversity of interactions

Although much information exists on the ant associates of extrafloral nectaries in the Neotropics (overview, e.g. Oliviera and Brandão 1991), almost no comparable data are available from SE Asia. Our investigations in Malaysia provide the first insights into non-specific ant-plant interactions of this tropical region. Saplings of both *Macaranga* species were visited by a large number of different ant species, indicating a low specificity of the relationship (21 species from 13 genera). The study of Whalen and Mackay (1988) on ant visitors of *Macaranga* species in New Guinea revealed only 14 different species out of 8 genera. *Crematogaster* spp. were again numerically dominant.

The association with ants in *M. tanarius* ceases as the age of *M. tanarius* plants increases. Above a height of about 3–4 m, EFN and food body production usually stop in this species. A very different development occurs in *M. hosei*. Juvenile plants < 1.5 m lack domatia but attract a variety of ants by EFN. As soon as the stem diameter becomes large enough to allow a colonization by its obligate *Crematogaster* partner, EFN production stops. At about the same time, or a few weeks earlier, food body production for the specialized ant partner starts. A similar phenomenon has been described for the myrmecophyte *Barteria fistulosa* where only juvenile plants without domatia have EFN (McKey 1988). However, in *Barteria* no food body production occurs. The fact that juvenile plants of *M. hosei* initially offer extrafloral nectar, whereas food bodies are provided only a short time before obligate colonization can take place, indicates that, in general, extrafloral nectar is more attractive for unspecialized ant associates.

Even if non-specific interactions already provide some protection for *M. hosei* plants, defence by their obligate *Crematogaster* partner is much more effective. Variation and effectiveness of the particular local ant fauna can be minimized in obligate, specific mutualisms. Ant-inhabited specimens had average damage of less than 5% (this study; and in Fiala et al. 1989, with a sample size of $n = 57$). The relationship with unspecialized ants, however, helps the plants to survive a life stage which is likely to be a critical one (Schupp 1986; Fiala et al. 1989), until the special ant partner is aquired. The shift toward obligate colonization in *M. hosei* is favourable especially with regard to plant competition. Only obligate *Crematogaster* ants destroy vines growing on *Macaranga*, which is a very important advantage in their open habitats (Fiala et al. 1989, 1991). *M. tanarius* can achieve competitive ability by a different type of growth (Fiala et al. 1991; Fiala 1991).

M. hosei has developed two types of relationship with ants to its advantage, each type restricted to plants of a different age class. In the juvenile phase, a variety of unspecialized ants are attracted mainly by EFN, which provide protection against herbivores. Later age classes have obligate *Crematogaster* partners which feed on special food bodies and reduce herbivore damage and vine cover.

The *Macaranga* species presented here are only one example of the ecological diversity of ant-plant interactions which can be found within this most interesting tree genus. This study had demonstrated the importance of non-specific interactions between *Macaranga* spp. and ants, in addition to protection by specialized plant-ants. The relative importance of various plant rewards to different guilds of ants seems to result in different degrees of effectiveness of anti-herbivore protection for the plants. Further work should concentrate on comparative ecology of ants as well as that of plants, to reveal patterns and functional significance of variation among ant-plant systems.

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