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Studies of a South East Asian ant-plant association: protection of *Macaranga* trees by *Crematogaster borneensis*

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Summary. In the humid tropics of SE Asia there are some 14 myrmecophytic species of the pioneer tree genus *Macaranga* (Euphorbiaceae). In Peninsular Malaysia a close association exists between the trees and the small, non-stinging myrmicine *Crematogaster borneensis.* These ants feed mainly on food bodies provided by the plants and have their colonies inside the hollow internodes. In a ten months field study we were able to demonstrate for four *Macaranga* species (*M. triloba, M. hypoleuca, M. hosei, M. hulletti*) that host plants also benefit considerably from ant-occupation. Ants do not contribute to the nutrient demands of their host plant, they do, however, protect it against herbivores and plant competition. Cleaning behaviour of the ants results in the removal of potential herbivores already in their earliest developmental stages. Strong aggressiveness and a mass recruiting system enable the ants to defend the host plant against many herbivorous insects. This results in a significant decrease in leaf damage due to herbivores on ant-occupied compared to ant-free myrmecophytes as well as compared to non-myrmecophytic *Macaranga* species. Most important is the ants' defense of the host plant against plant competitors, especially vines, which are abundant in the well-lit pioneer habitats where *Macaranga* grows. Ants bite off any foreign plant part coming into contact with their host plant. Both ant-free myrmecophytes and non-myrmecophytic *Macaranga* species had a significantly higher incidence of vine growth than specimens with active ant colonies. This may be a factor of considerable importance allowing *Macaranga* plants to grow at sites of strongest competition.

Key words: Ant/plant interaction – Myrmecophytes – Protection – *Macaranga* – *Crematogaster borneensis*

Symbiotic associations between myrmecophytic plants and certain ant species are important phenomena in tropical ecosystems. Although the advantages that ants gain from such a relationship are in most cases rather obvious, the benefits for the plants involved are not sufficiently well understood and hence somewhat controversial. However, they have now been well documented in a few cases (reviews: Buckley 1982; Beattie 1985). There appear to be two basic types of associations: 1) Nutrient symbioses which have been described primarily for ant-associated epiphytes in SE Asia and Australia (Janzen 1974a; Huxley 1978; Rickson 1979) and 2) associations where ants protect their host trees against vine-growth and herbivores which have been studied mainly in the neotropics and tropical Africa (Janzen 1967, 1969, 1972; Risch et al. 1977; Letourneau 1983; McKey 1984; Schremmer 1984; Schupp 1986).

In SE Asia there are also myrmecophytic trees, of which the genus *Macaranga* (Euphorbiaceae) is the most widespread. In Peninsular Malaysia nine out of 27 species in this genus occurring mostly in pioneer habitats are associated with ants. According to our studies in the Malay Peninsula only one ant species, *Crematogaster borneensis* (Myrmicinae, subg. *Decacrema*), is involved. These ants live in the hollow stems of their host trees and derive from them food in the form of food bodies and plant fluids via scale insects cultivated inside the stems (Ong 1978; Tho 1978).

Myrmecophytic associations and their evolutionary aspects have been little studied in SE Asia, even though the *Macaranga*/*C. borneensis* system is well suited for such an investigation: *Macaranga* is a very diverse and widely distributed genus, comprising the full range of species from non-myrmecophytes to obligate myrmecophytes. *Macaranga* in SE Asia are generally early seral species which may be regarded as analogues to *Cecropia* in the neotropics (Whitmore 1984). They have been interpreted as myrmecophytes that evolved convergently to similar associations in America and Africa (Janzen 1969; Duviard and Segeren 1974; Buckley 1982; Beattie 1985). This is speculative, however, considering the scarce, mostly descriptive and partly contradictory literature on the *Macaranga*/*C. borneensis* system (Ridley 1910; Blatter 1928; Baker 1934; Ong 1978; Tho 1978).

Taylor (1982) did not find any beneficial role of the ants for the plants. Other authors believe the symbiotic relationship involves nutrient gain or the protection of the plants or both aspects (Baker 1934; Ong 1978; Tho 1978; Rickson 1980; Putz and Holbrook 1988). The protective function of *Crematogaster borneensis* workers has been questioned largely because of their small size and seeming defencelessness. Their lack of a functional sting makes them seem rather inappropriate in protecting the host plant, especially when compared with the aggressive ant species with powerful stings in South America and Africa. However, Rickson (1980) did allude to the rather aggressive behaviour of *C. borneensis* and Putz et al. (1984) provide

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suggestive evidence for protection of host plants against vines.

This study is the first experimental investigation of the *Macaranga-Crematogaster* association and will focus on the potential benefits derived by the plant partner. The biology of the ants, the adaptive responses of the host plant and evolutionary implications will be discussed elsewhere (Fiala and Maschwitz, in prep.). We found that ants do not forage away from their host plants and remove most of the insects they kill on the plant as well as plant material and debris. Within the hollow stems there are no morphological adaptations which might indicate an absorptive function. A preliminary isotope study revealed that only minimal amounts of nutrients could be transported from the interior of the stems to the leaves (Fiala 1988). Thus the nutrient budget for the *Macaranga* host is negative. We therefore concentrate here on the protective role played by ants for their host plants.

Methods and material

Study area

Field investigations were carried out in West Malaysia during the periods of December 1984–March 1985, December 1985–April 1986, January 1987–April 1987 and October–December 1988. West Malaysia is situated in the humid tropics with little seasonal variation in temperature. The study area receives over 2000 mm of precipitation annually with two periods of heavy rainfall (usually October–December and April), but no pronounced dry season. Studies were carried out at three sites:

1. The grounds of the Forest Research Institute Malaysia (FRIM) at Kepong, Selangor (3°14′ N; 101°38′ E; 97 m a.s.l.).
2. Pasoh Forest Reserve, Negri Sembilan (2°59′ N; 102°18′ E; 90 m a.s.l.).
3. Ulu Gombak Field Study Centre, Selangor (3°21′ N; 100°48′ E; 240–500 m a.s.l.).

These areas are primarily covered with mixed dipterocarp forest that has been disturbed by forestry and hence contain much secondary forest habitat. *Macaranga* plants grow mainly along the forest trails and roads that are present in the areas. Surveys were carried out along such roads and logging tracks, which are characterized by plenty of sunlight and lush plant growth. The vegetation comprised many secondary growth specialists, *Musa* and *Dicranopteris* species along with Zingiberaceae and Melastomataceae being most common. Vine growth was prominent along the edges of trails that were 3–7 m broad.

Herbivory

Survey of leaf damage caused by herbivores. Leaf damage was surveyed mostly on young plants (less than 3 m high) of the common and widespread *M. triloba* and to a lesser extent on *M. hosei, M. hypoleuca* and *M. hulletti*, all of which are myrmecophytes. For comparison the non-myrmecophytes *M. conifera, M. gigantea* and *M. tanarius* were surveyed. For each plant, the presence or absence of ants, number of leaves and amount of leaf damage were recorded. We used a millimeter grid to estimate the amount of leaf damage to the nearest 10% leaf area for the proximal eight leaves of each plant. Older leaves often have more herbivore damage but play only a minor role in the energy balance of the plant and were therefore not taken into account. We also noted other types of damage such as missing apices and stem-borer holes as well as presence and location of all animals other than *C. borneensis* (eggs, larvae, imagines).

In each habitat all *Macaranga* plants were surveyed along transects about two km long. As there were no consistent differences between the three study sites in the proportion of colonized plants or the respective amounts of leaf damage, data from all three sites were pooled. In 1987, the development and increase in leaf damage of 20 ant-colonized and 20 non-colonized *M. triloba* plants of about equal size (87 ± 10.7 cm) was followed for six weeks. Due to disturbances only 13 vs. 17 plants remained at the end of this period.

Response of ants to potential herbivores. The response of ants to potential insect herbivores was tested in 66 trials by placing single beetles, lepidopteran caterpillars, grasshoppers and bugs onto *Macaranga* plants with ant colonies. Thirty-six of these trials were done with caterpillars of varying sizes (0.5–4 cm) and taxonomic affinities collected from neighbouring plants and placed onto the upper leaf surface of *M. triloba*, where they were watched for 1 h each. As controls similar herbivores were placed on plants without ants.

To simulate egg laying of potential herbivores we placed insect eggs onto various parts of ant-colonized plants. In 86 trials insect eggs collected from neighbouring plants were placed singly onto stipules, upper stems or the 5–6 upper leaves of 10 *M. triloba* plants. The reaction of the ants was watched continuously for 60 min and at hourly intervals thereafter.

Competition by other plants

Vines are the dominant competitors and plant parasites on *Macaranga* species. We therefore surveyed the amount of vine growth on 977 plants of seven *Macaranga* species. For each plant the height, presence or absence of ants, epiphytes or epiphyll growth, and contact with neighbouring plants were noted. For comparison, the same survey was done for 5–6 structurally similar plants of other species (e.g. *Mallotus* spp., *Endospermum diadenum*) growing next to each of 60 *Macaranga* specimens.

In order to find out whether the ants bite off vines on their host plants we brought live vines in contact with ant-colonized *Macaranga* plants. In a total of 42 trials, vines up to 3 m long were carefully removed (leaving their roots intact) from neighbouring plants and wound around *Macaranga* plants. As a control similar vines were also put onto ant-free *Macaranga* specimens and other similar second growth plants. The vines belonged mainly to the families Fabaceae, Convolvulaceae, Dilleniaceae, Ampelidaceae and Melastomataceae. Most commonly we used *Mikania cordata* (Asteraceae), the dominant vine in the secondary growth habitats studied. Reactions of the ants were observed for a few hours after the manipulation and then checked daily or at longer intervals for several weeks.

Statistics: The non-parametric Mann-Whitney-U test (MW test) was used to test for differences in the means of two samples and the Chi^2 test to distinguish observed from expected frequencies (Zar 1984).

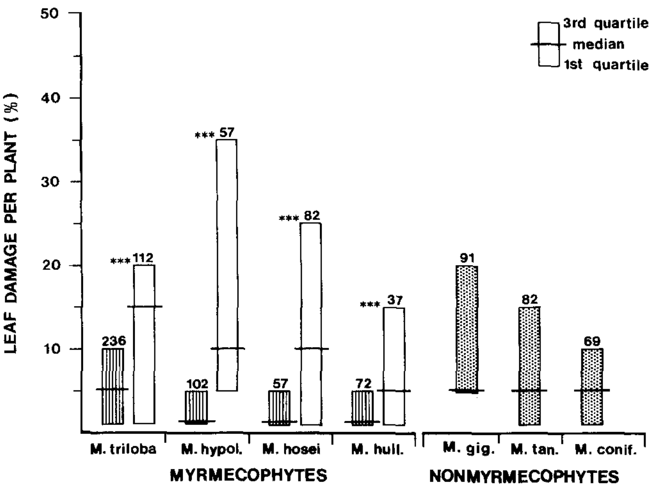

Fig. 1. Herbivore damage in % of leaf area per plant (upper 8 leaves) for myrmecophytic and non-myrmecophytic species. Hatched columns: ant-occupied; open columns: ant-free plants. Numbers above columns are sample sizes. Differences between ant-occupied and ant-free plants according to Mann-Whitney-U-test: ***$=P<0.001$

Table 1. Average amount of leaf damage (% of total leaf area) due to herbivores and growth rate of ant-occupied and ant-free *M. triloba* plants during a period of six weeks

Status	*N*	% leaf damage		% change		Height gain	
		before	after	mean	±s.d.	mean (cm)	±s.d.
With ants	13	3.5	8.6	+ 5.1	(±5.2)	+11.0	(±4.7)
No ants	17	6.6	19.6	+13.0	(±11.8)	+ 9.7	(±5.1)

Results

Leaf damage on plants with and without ants

There were significant differences in the amount of leaf damage between ant-occupied and ant-free specimens of myrmecophytic *Macaranga* species (Fig. 1). Although plants with ants did show leaf damage, it never exceeded 50% of the total leaf area and was on average far less than that of ant-free plants. In two of the three non-myrmecophyte species studied, *M. tanarius* ($n=82$) and *M. gigantea* ($n=91$), leaf damage due to herbivores was greater than in ant-occupied *M. triloba* ($n=236$; $P<0.001$, MW test), but did not differ from ant-free *M. triloba* plants ($n=112$; $P>0.05$). In the third non-myrmecophyte, *M. conifera* ($n=69$), leaf damage was less than in ant-free *M. triloba* ($P<0.05$), but did not differ from that in ant-occupied *M. triloba* ($P>0.05$). *M. conifera* also differed significantly from *M. tanarius* ($P<0.05$), but not from *M. gigantea* ($P>0.05$) in the amount of leaf damage. This indicates that if non-myrmecophytes were attempting to compensate for the lack of ant protection against herbivores by other means, e.g. an increased content of secondary plant compounds, this seems to be effective only in *M. conifera.*

The results of the above survey were supported by longer-term observations of 30 *M. triloba* plants (Table 1): During six weeks ant-free specimens suffered a significantly greater loss of leaf area than ant-occupied plants ($P<0.05$; MW test). This did not, however, seem to significantly affect growth rates ($P>0.05$), although there appears to be a tendency for ant-free plants to grow more slowly – an effect which may reach significance only after longer intervals. The average number of leaves remained almost constant in both groups over the observation period: ant-occupied plants had 9.8 vs. 9.3, ant-free plants 10.2 vs 9.0 leaves at the beginning and the end, resp.

Causes of leaf damage

Insects are the prime herbivores causing leaf damage to *Macaranga* plants. Direct observations and typical damage patterns allowed us to distinguish five main groups:

1. Sap-sucking insects such as Pseudococcidae and Cicadidae occurred on only 3% of the plants investigated ($n=1051$) and caused relatively little damage.

2. Leaf miners (Lepidoptera: Gracillariidae) afflicted an average of 10% of plants both with and without ants. Generally they caused damage to less than 20% of the leaf area. In some cases, however, their mass occurrence resulted in an obviously decreased vitality of the plants.

3. Beetles (Coleoptera) of different families (e.g. Chrysomelidae, Curculionidae, Scarabaeidae) and grasshoppers (Acrididae) were the commonest and most destructive herbivores, about equally common on plants with and without ants. They quickly ate large parts of the leaves, often at night, and were well protected against attacking ants due to their large size and strong sclerotization. On 75% of the ant-occupied plants with herbivore damage this was due to beetles and/or grasshoppers with an average loss of leaf area amounting to 35% per affected plant. Although such damage was generally rather localised to the edges of some leaves, there were instances where leaves were destroyed completely.

4. Lepidopteran larvae, mainly of the families Lymantriidae, Geometridae and Tortricidae, were common herbivores on ant-free plant. Tortricids fed preferentially on *M. hypoleuca* and *M. hosei*, where they lived inside rolled-up, spinned-in upper leaves. On ant-occupied plants caterpillars were rare with the exception of some species of *Arhopala* (Lycaenidae, Theclini). In these cases the ants were servile as they were rewarded from the myrmecophilous organs of the larvae (Maschwitz et al. 1984). Most of the remaining 25% of herbivore-damaged, ant-occupied plants were affected by *Arhopala.* Caterpillars other than *Arhopala* occurred significantly less frequently (1.7%; $n=177$ plants) on ant-occupied than on ant-free plants (18.2%; $n=170$ plants; $\text{Chi}^2=25.0$; $P<0.001$). Two of the three larvae found on ant-occupied plants belonged to a species of Limacodidae, which may have been protected against ants by their dense coat of hair.

5. Severe damage was caused by stem-borers and herbivores feeding on the vegetative apex of the plants. Both types of damage greatly reduced the growth rate and can result in plant mortality. The commonest stem-borers were larvae of a *Rhodoneura* sp. (Thyrididae); curculionids were also involved. Stem-borers were located in 19 out of 235 ant-free *Macaranga* plants, but in none of the 252 ant-occupied plants ($\text{Chi}^2=16.4$; $P<0.001$). Apex damage was found in 8 ant-occupied and 33 ant-free specimens of the same samples ($\text{Chi}^2=13.58$, $P<0.001$).

6. Galls were found on 8% of *M. triloba* (no significant difference between ant-occupied and ant-free) and 6% of

Table 2. Response of *C. borneensis* workers to small caterpillars placed on *M. triloba* host plants (number of observed cases). Observation time: 1 h per trial

No. of trials	Response of ants		Consequence of attacks			
	Attack	No attack	None	Caterpillar		
				leaves plant	is removed	is killed
36	30	6	1	19	5	5

Table 3. Response of *C. borneensis* workers to insect eggs placed on *M. triloba* plants (number of observed cases). Observation time: 1 h per trial

Location of egg	*N*	Eggs discovered	Eggs removed
Upper leaf surface	61	50	43
Underside of leaf	10	7	7
Stem	10	10	10
Stipule	5	5	5
Total	86	72	65

M. tanarius plants. They did not affect plant growth or vitality to a measurable degree, except for five cases where they occurred en masse on all leaves.

Direct ant-herbivore interactions

The ants generally attacked insect herbivores on their host plants by biting with their mandibles. Once attached to an intruder, workers often did not let go and died in the process. Most beetles and grasshoppers were too big and strongly sclerotinized to be seriously affected by the ants. Nonetheless workers were often able to irritate such visitors and to some extent keep them from feeding or even cause them to leave the plant. *C. borneensis* is more effective in fending off small and soft-skinned insects, especially little chitinized larvae. Caterpillars experimentally placed on upper leaves were removed or driven off the host plant at a rate of 80.5% within one hour (Table 2). Usually several ants bit the larva and pulled it towards the edge of the leaf. Interestingly, these larvae were never utilized as food but always dropped from the plant. In control tests on ant-free plants ($n = 20$) larvae only fell off the plants in three cases. The others moved around on the leaves or started to climb down along the stem. Only ten were recorded having left the plant within 60 min ($\mathrm{Chi}^2 = 5.68$, $P < 0.05$).

Ants showed a pronounced cleaning behaviour towards all kinds of foreign objects on their host plant. Insect eggs placed on the leaves were grabbed with forelegs and mandibles and dropped off the plant. Ninety percent of the eggs discovered by the ants were removed within one hour (Table 3). Fourteen eggs were not discovered within one hour, mostly due to little surface activity of the relatively small ant colonies. Of 21 eggs that were not discovered or removed six were on the oldest and two on the second oldest leaves.

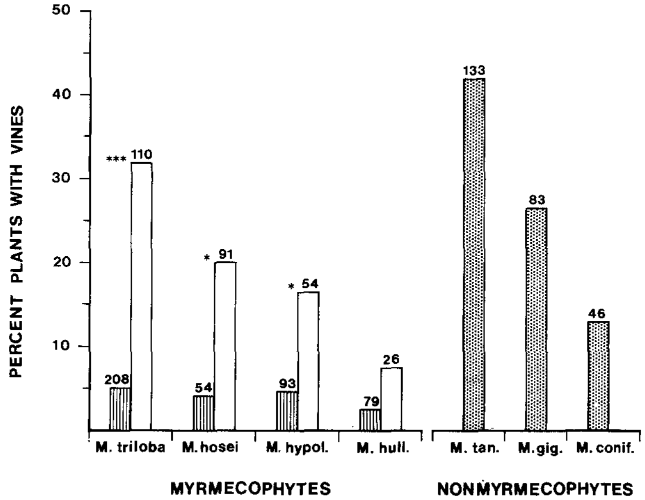

Fig. 2. Percentage of plants with vines of myrmecophytic and non-myrmecophytic *Macaranga* species. Hatched columns: ant-occupied; open columns: ant-free plants. Sample sizes are given above each column. Differences between absolute frequencies according to Chi^2 analysis: $*** = P < 0.001$, $* = P < 0.05$

Highly frequented regions of the plant such as the upper stem and stipules were cleaned of most foreign objects within a few seconds, whereas it took up to two hours when such objects were on the leaves. Checks at later intervals confirmed that even more eggs had been removed by then. Such data are not included in Table 3, because other reasons for the eggs' disappearance could not be excluded.

Competitors of Macaranga *host plants: survey of vine growth*

At all study sites vine growth was abundant. Ant-occupied myrmecophytes of three species were subject to significantly less vine attachment than ant-free conspecifics (Fig. 2; Table 4). Nonmyrmecophytic *Macaranga* species carried significantly more vines than ant-occupied myrmecophytes, but not more than ant-free myrmecophytes ($\mathrm{Chi}^2 = 2.17$; n.s.). Myrmecophytic *M. hulletti* was generally little affected by vines, probably due to its preference for shady sites where vine growth is less predominant. We also compared 60 *M. triloba* specimens with a random sample of 5 to 6 of their nearest neighbouring plants (giving total of over 300 controls). On average, 50% of each sample of these controls carried vines and at some places up to 75% in contrast to only 8% of the ant-inhabited *M. triloba* in this area.

When climbers did occur on ant-occupied plants ($n = 18$) there were mostly single vines growing around the lower parts of the stem or stalks of older leaves. Such areas are little frequented by patrolling ants. Myrmecophytes with a heavy load of vines were either free of ants or had a very young colony, workers of which had not yet started to patrol the exterior of the host plant. Often vines had approached up to a few millimeters yet had not attached themselves to the host plants. Close inspection revealed that in over 50 such cases the tips of the vines had been bitten off by the ants – the terminal parts being black and necrotic. Vines near ant-free *Macaranga* plants never showed this type of damage providing strong evidence that it was caused by the ants and not by other insects that might feed on fresh vine tips.

Table 4. Fate of shoots of 42 vine branches artificially twined around 42 stems of ant-occupied *M. triloba* and *M. hypoleuca*; condition 14 days after manipulation

Condition of vines	*N*	%
Tips dead due to pruning ants	13	31
Tips chewed on by ants	19	45
Tips intact	10	24

Competitors of Macaranga *host plants: experiments*

Seventy-six percent of 42 live vines experimentally brought in contact with host plants were damaged by the ants within two weeks (Table 4). In all of these cases the tips of the vines showed the typical pattern of bite marks from ant mandibles. Plants of both control groups, ant-free *M. triloba* ($n=10$) and *M. hypoleuca* ($n=5$) and non-myrmecophytic neighbours ($n=10$), never showed this type of damage, so toxic chemicals from the plants cannot be the reason.

The rate and speed at which vines were attacked depended upon the size and activity of the ant colony and location of the vine contact. The closer the point of contact to the apex of the host plant, the sooner the vine was bitten off. Plants other than vines coming into contact with host plants were also bitten off and showed the typical damage pattern described above. Thus *Macaranga* host plants were never interlocked with neighbouring plants but rather stood relatively free. Ants also bit off coloured threads and even damaged tough tape which was initially used to mark study plants, adding further experimental proof for their effective protection of host plants.

Discussion

In concentrating our study on juvenile plants we assumed that this stage is an especially critical one in its eventual development. We agree with O'Dowd (1979) and Schupp (1986) in that the juvenile stage is most susceptible to disturbances. Protection by ants would be most important during this phase. Comparisons between conspecific ant-free and ant-occupied plants are constrained by the fact that ant occupation strongly increases with size/age such that hardly any plants of 3 m or more in height lack ants.

Herbivory

In myrmecophytic *Macaranga* species ant-occupied individuals had significantly less leaf damage than ant-free conspecifics. More than 50% loss of leaf area was observed only in ant-free plants. Myrmecophytes suffered on average less leaf damage from herbivores than congeneric non-myrmecophytes. Thus, even though ant protection against herbivores is far from complete, it does have a pronounced overall effect. This conclusion is supported by the long term observations demonstrating a higher rate of leaf area loss in ant-free *M. triloba* than in ant-occupied ones.

Ant-occupied *Macaranga* plants seemed to be free of herbivory from lepidopteran larvae except for damage caused by *Arhopala* larvae (Lycaenidae), which are tolerated by the ants as a result of their myrmecophilous organs (Maschwitz et al. 1984). On ant-free plants caterpillars caused extensive damage, because they spread over the whole plant, whereas beetles and grasshoppers, which also occurred on ant-occupied plants, mostly ate only parts or all of a few leaves. All cases of 50% or more loss of leaf area were due to caterpillars. We did not observe any herbivory by vertebrates.

These results agree with most observations of defence behaviour against herbivores. *C. borneensis* was most effective in attacks on soft-skinned larvae. However, such cases may not be common, because the intense cleaning behaviour by the ants results in removal of most if not all insect eggs deposited on the host plant. Such cleaning behaviour has been described for other ant-plant symbioses (Janzen 1967, 1969, 1972; Stout 1979; Risch 1982; Letourneau 1983), but is not a universal trait among Formicidae.

Most herbivore damage on ant-occupied plants was caused by large, agile phytophages, which can eat quickly and stay on the plant only briefly. Grasshoppers in particular ate large fractions of a leaf and often left before the ants had time to respond. Although the ability of *C. borneensis* to deter sclerotinized beetles and grasshoppers is rather limited, the ants nevertheless attacked them and often the mere disturbance was enough to chase away even these herbivores.

Although proximate effects of ant protection in *Macaranga* could be demonstrated conclusively, ultimate consequences are more difficult to assess. Contradictory findings have been published with respect to effects of herbivory on productivity and fitness of plants (Owen and Wiegert 1976; review: McNaughton 1979). To quantify lifetime reproductive success long-term surveys of seed production would have to be made for ant-free versus ant-occupied plants. Without long-term experiments with plants that are kept ant-free, this comparison would be impossible, because almost all myrmecophytic *Macaranga* plants have ant colonies before they reach reproductive age. However, our results do demonstrate for young ant-free plants a significantly higher mortality due to stem-borers and higher incidence of severe apex damage than in ant-occupied ones. Also, our observations over six weeks indicated a tendency for faster growth of ant-occupied versus ant-free plants. This difference may take several months to become more pronounced (Janzen 1967). In *Cecropia* a difference in growth rate was only found after four months (Schupp 1986).

Most studies have shown that ants are most active on the upper parts and on young leaves of their host plant (Downhower 1975; Schupp 1981 for *Cecropia*; Bentley 1977a; Stout 1979; McKey 1984 for plants with extrafloral nectaries). This was also true for *C. borneensis* on *Macaranga* (Fiala 1988). This activity distribution results in increased protection of young leaves and the vegetative apices, both being vital and vulnerable parts of the host plant. Apical stem damage in particular results in a lowered growth rate of young rain forest trees, which puts them at a competitive disadvantage and often leads to their death within less than one year (Huffaker et al. 1984). Thus ant protection against apical stem damage and stem-borer attack which can kill young plants within a few weeks, will significantly reduce the mortality of host plants compared to ant-free conspecifics.

C. borneensis was active day and night. Although the average numbers patrolling at night were slightly lower, large numbers were recruited in alarm situations (Fiala 1988). Our observations agree with findings by Janzen (1973), Bentley (1977b) and Windsor (1978) in that a large fraction of herbivore damage in tropical forests occurs at night. Thus the temporal as well as spatial distribution of ants on *Macaranga* guarantees maximum protection of the host plants (Fiala and Maschwitz, in prep.).

Many myrmecophytic plants occur in secondary habitats or tree fall gaps (*Cecropia* and *Acacia*, Janzen 1969, 1974b; *Piper*, Risch et al. 1977; *Ochroma*, O'Dowd 1979; *Triplaris*, Bentley 1977a). Especially *Cecropia* and *Ochroma* are typical pioneer trees with a low branching rate, large leaves and rapid growth. *Macaranga* also belongs to this group and Whitmore (1984, p. 84) called it "the genus par excellence of pioneer trees". Pioneer plants suffer more herbivore damage than primary forest plants (Coley 1983; Dirzo 1984). Coley hypothesizes that pioneer plants are able to tolerate higher herbivore damage because the cost of producing and maintaining leaves is lower. They ought to be able to reach higher production rates due to a relative abundance of light and nutrients and thus be able to offset the effects of increased herbivory. The net photosynthesis rate of *Macaranga hypoleuca* under full sun light was 20 mg CO_2 $dm^{-2}h^{-1}$ (Koyama 1978), i.e. twice as high as in primary forest species under the same light regime.

According to Coley's et al. (1985) growth rate theory, species adapted to resource-poor environments should have lower growth rates, less herbivore damage and more defensive structures or chemicals than plants in resource-rich environments. The trend was confirmed in a study of 41 neotropical tree species (Coley 1988). However, *Macaranga hypoleuca* leaves were surprisingly rich in phenol content and hard to digest (Waterman et al. 1988). Such data should be interpreted with care, because that study also demonstrated that soil fertility may strongly influence leaf chemistry. More comparative data will be necessary to evaluate Coley's theory. Young *Macaranga* leaves are not very tough, lack rigid support structures and wilt when loosing turgor pressure. Here ants may well play the role with respect to herbivore protection that chemical compounds or morphological and anatomical adaptations play in other plants. A further advantage of ant defence may be that it is effective against both generalist and specialist herbivores, whereas chemicals are often effective only against one or the other.

In non-myrmecophytic *Macaranga* species one might expect more energy and assimilates to be invested into chemical or mechanical defence. Our data on three non-myrmecophytes show that herbivore damage (8.5–11.5% of leaf area) was only slightly lower than in congeneric ant-free myrmecophytes, but higher than in ant-occupied myrmecophytes. Thus within the genus ant-occupied myrmecophytes are better protected against herbivores than non-myrmecophytes, but these do not seem to be better protected by chemical or mechanical means than ant-free myrmecophytes.

Non-myrmecophytes such as *M. tanarius* and *M. gigantea* we cultivated in the greenhouse did produce large numbers of food bodies. The fact that few food bodies are found in these species in natural habitats (cf. Rickson 1980; Buckley 1982) suggests that visiting ants (and other insects?) harvest them. Ants of several species are often seen on non-myrmecophytic *Macaranga* plants but are not resident there. Since it is generally assumed that ants confer some advantage to plants they visit (Beattie 1985), the situation may represent an evolutionary precursor in the development of obligate myrmecophily.

Putz and Holbrook (1988) (in a very small sample) found a lower herbivore pressure on pioneer plants in Malaysia than in Panama. No matter, whether this result is generally valid, herbivore pressure certainly is an important ecological factor in Malaysia and ant-occupation protects against it.

We conclude that although *C. borneensis* does not provide total protection for its host plants against herbivory, it does ensure that there is less severe herbivore damage as compared with ant-free trees. The cumulative effects of ant presence in deterring diurnal and nocturnal herbivores will be more pronounced than short-term effects.

Protection against plant competitors

Most studies of the function of ants in ant-plant associations have concentrated on their defence against herbivores. In the *Macaranga-C. borneensis* system protection of host plants against plant competitors may be even more important. Our data show that ants bite off vines, remove particles (e.g. spores of epiphyllic plants) from host plant leaves and reduce contact with neighbouring plants. Both ant-free myrmecophytes of three species as well as non-myrmecophytic species had significantly more vine growth than ant-occupied plants. This is in disagreement with Putz and Holbrook's (1988) data, who found no significant difference in vine infestation between *M. gigantea* and *M. triloba*. This may be due to their small sample size.

Experimental establishment of contacts between vines and *Macaranga* plants with and without ants demonstrated clearly that it was the ants, not toxic chemicals, that damaged the vines. Not surprisingly, large and active ant colonies were most effective and soft vine parts were more easily severed than hard parts. Janzen (1969) used the term "allelopathic agents" for ants associated with *Cecropia*, which suppress plant competitors of their hosts by biting off vines and other vegetation coming in contact with it. The same behaviour has been observed in other associations: *Pseudomyrmex-Acacia* (Janzen 1967), *Pachysima-Barteria* (Janzen 1972), *Azteca-Cordia* (Janzen 1969), *Viticola-Vitex* (Janzen 1966), *Pseudomyrmex-Triplaris* (Schremmer 1984), *Pseudomyrmex-Tachigalia* (Wheeler 1921). In contrast, no defence against plant competitors was found in *Petalomyrmex-Leonardoxa* (McKey 1984) and *Pheidole-Piper* (Risch et al. 1977). In addition to biting off vines *Pseudomyrmex triplarinus* and *Pachysima* clear the ground around the base of their host tree from debris and vegetation. Originally this was interpreted as protection against fire (Janzen 1967) which, however, was unlikely in the rainforest plant *Barteria*. Rather it may serve to prevent growth of potential competitors near the host plant.

Such behaviour does not occur in *C. borneensis*. This ant will bite off only plant parts coming in contact with its host tree. Thus only seedlings starting to grow very close to the base of the host plant are likely to be removed. Epiphytes were generally uncommon in the lowland forest of our study sites and did not grow on *Macaranga* at all. In more humid hill and mountain forest where epiphytes are common, myrmecophytic *Macaranga* species are much rarer than in the lowlands. Also, light-rich secondary habitats of *Macaranga* generally have too low a humidity for epiphyte growth.

Vines, the most important competitors of *Macaranga*, are more common in the tropics than in any other floristic region (Richards 1952). They compete with trees for space, light and nutrients and are generally thought to be detrimental for plants on which they grow. Because of their rapid growth rates vines can overgrow other second growth plants and seriously impair their vitality (e.g. Lowe and Walker 1977; Putz 1982, 1984; Putz et al. 1984). This results in lowered resistance to herbivore damage and may increase mortality (Putz 1984). Raup (1978) regards vines as the main factor determining the success of a tree on a clearing. Young *Macaranga* plants are particularly in danger of being overgrown by a carpet of vines, which often share the same habitat along clearings and trails (Kochummen and Ng (1977; Appanah and Putz 1984). Non-myrmecophytic species may have other adaptations (different microhabitat, morphology) to discourage vine growth (Fiala et al., unpublished work).

Vines are also disadvantageous for ant colonies on *Macaranga*, because they provide easy access e.g. for herbivorous insects, foreign ants or folivorous mammals. As described by Davidson et al. (1988) preventing access of other ants to the host plant may be the most important proximate function of pruning behaviour in *Crematogaster*.

Possible nutrient gain by host plants

Nutrient gain through ants has so far been demonstrated for Bromeliaceae (Benzing 1970) and two species of Rubiaceae (Janzen 1974a; Huxley 1978; Rickson 1979). In contrast to speculations by Ong (1978) we did not find any evidence for a net gain of nutrients by *Macaranga* plants from the association with ants (Fiala 1988). This does not exclude that small amounts of nutrients are taken up from the interior of the hollow stem (cf. Rickson and Rickson 1986). Nutrient gains from ants seem to be important especially in epiphytic myrmecophytes which grow in oligotrophic surroundings with low nutrient availability (Huxley 1980, 1986). The ants import organic material and deposit food leftovers within the host plant, from where nutrients can be taken up after partial decomposition by specialized internal roots. For ground dwelling host plants such as *Cecropia* nutrient gain does not seem to be of major importance (Putz and Holbrook 1988). This should be true particularly for second growth and pioneer trees like *Macaranga* which grow in relatively nutrient-rich soils.

Comparison with other myrmecophytic associations

Compared to other myrmecophytic associations the *Macaranga* – *C. borneensis* system seems highly specialized in all respects. The effectiveness of host plant protection by ants is generally variable, but has been demonstrated in all associations studied so far. *Myrmelachista* n. sp. (Stout 1979), *Petalomyrmex phylax* (McKey 1984) and *Pheidole bicornis* (Letourneau 1983) are small ants with limited defence capabilities. They can fight only small insects but do clean the host plant of insect eggs, thus potentially reducing herbivore pressure. Such cleaning behaviour occurs in all ant partners of myrmecophytes. The above-mentioned ant species do not, however, significantly reduce competition from plants.

Aggressive and powerful stingers such as the pseudomyrmecines *Pachysima* and *Pseudomyrmex* effectively defend their host plants *Barteria, Acacia* and *Triplaris*, respectively, against phytophagous insects and even some vertebrates and also clear them of vine growth and other plant competitors (Janzen 1967, 1972; Schremmer 1984). *Azteca* ants on *Cecropia* are somewhat intermediate in the effectiveness of host plant defence (Janzen 1969; Schupp 1986). *C. borneensis* is one of the smallest ant species involved in a myrmecophytic association and morphologically resembles the less aggressive *Pheidole bicornis* and *Petalomyrmex phylax*. Nonetheless it does provide rather effective protection of its host plant against herbivores as well as vine growth. Due to its ability for mass attack and "suicidal" fighting behaviour, *C. borneensis* has effects on its host plants comparable to those of the much more powerful, sting-possessing pseudomyrmecines.

We conclude that the *Macaranga* – *C. borneensis* association of SE Asia evolved convergently and is functionally and in its specificity equivalent to South American and African myrmecophyte systems. Similarities are especially evident between *Macaranga* and the neotropical *Cecropia*. Both possess a similar growth structure with tall stems, large peltate leaves and few branches. Both live in secondary habitats and are fast growing pioneer trees. Neither of them provides extrafloral nectaries, but ants feed on food bodies and plant sap from scale insects cultivated inside the stems. The ant partners of *Cecropia* and *Macaranga* are both rather small and do not sting. They are especially effective in fighting plant competition of their host plants and thus form an important ecological factor for survival in pioneer habitats.

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References

Appanah S, Putz FE (1984) Climber abundance in virgin dipterocarp forest and the effect of pre-felling climber cutting on logging damage. Malay For 47:335–342

Baker JA (1934) Notes on the biology of *Macaranga* spp. Gdns' Bull Straits Settl 8:63–68

Beattie AJ (1985) The evolutionary ecology of ant-plant mutualisms. Cambridge Univ Press, Cambridge

Bentley BL (1977a) Extrafloral nectaries and protection by pugnacious bodyguards. Ann Rev Ecol Syst 8:407–427

Bentley BL (1977b) The protective function of ants visiting the extrafloral nectaries of *Bixa orellana* (Bixaceae). J Ecol 65:27–38

Benzing DH (1970) An investigation of two bromeliad myrmecophytes: *Tillandsia butzii* MEZ., *T. caput-medusae* E. MORREN and their ants. Bull Torrey Bot Club 97:109–115

Blatter E (1928) Myrmecosymbiosis in the Indo-Malayan flora. J Ind Bot Soc 7(3–4):176–185

Buckley RC (ed) (1982) Ant-plant interactions in Australia. W Junk Publ

Coley PD (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol Monogr 53(2):209–233

Coley PD (1988) Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. Oecologia 74:531–536

Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant anti-herbivore defense. Science 230:895–899

Davidson DW, Longino JT, Snelling RR (1988) Pruning of host plant neighbors by ants: an experimental approach. Ecology 69:801–808

Dirzo R (1984) Insect-plant interactions: some ecophysiological consequences of herbivory. In: Medina E, Mooney HA, Vasquez-Yanes C (eds) Physiological ecology of plants in the wet tropics. W Junk Publ, The Hague, pp 209–224

Downhower JF (1975) The distribution of ants on *Cecropia* leaves. Biotropica 7:59–62

Duviard D, Segeren P (1974) La colonization d'un myrmécophyte, le parasolier, par *Crematogaster* spp. (Myrmicinae) en Côte d'Ivoire forestière. Insect Soc 21:191–212

Fiala B (1988) Biologie, Funktion und Evolution eines malaysischen Myrmekophytiesystems: Die Assoziation von *Crematogaster borneensis* (Form.: Myrmicinae) mit Bäumen der Gattung *Macaranga* (Euphorbiaceae). Dissertation, Univ Frankfurt

Huffaker CB, Dahlstein DL, Janzen DH, Kennedy GG (1984) Insect influences in the regulation of plant populations and communities. In: Huffaker CB, Rabb RL (eds) Ecological entomology. Wiley, New York, pp 659–691

Huxley CR (1978) The ant-plants *Myrmecodia* and *Hydnophytum* (Rubiaceae), and the relationships between their morphology, ant occupants, physiology and ecology. New Phytol 80:231–268

Huxley CR (1980) Symbiosis between ants and epiphytes. Biol Rev 55:321–340

Huxley CR (1986) Evolution of benevolent ant-plant relationships. In: Juniper B, Southwood R (eds) Insects and the plant surface. E Arnold Publ, London, pp 258–282

Janzen DH (1966) Coevolution of mutualism between ants and acacias in Central America. Evolution 20:249–275

Janzen DH (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

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

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

Janzen DH (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54:687–708

Janzen DH (1974a) Epiphytic myrmecophytes in Sarawak: mutualism through the feeding of plants by ants. Biotropica 6:237–259

Janzen DH (1974b) Swollen thorn acacias of Central America. Smithson Contri Bot 13:1–131

Kochummen KM, Ng FSP (1977) Natural plant succession after farming in Kepong. Malay For 40:61–78

Koyama H (1978) Photosynthesis studies in Pasoh forest. Malay Nat J 30:253–278

Letourneau DK (1983) Passive aggression: An alternative hypothesis for the *Piper-Pheidole* association. Oecologia 60:122–126

Lowe RG, Walker P (1977) Classification of canopy, stem, crown status and climber infestation in natural tropical forest in Nigeria. J Ecol 14:897–903

Maschwitz U, Schroth M, Hänel H, Tho YP (1984) Lycaenids parasitizing symbiotic plant-ant partnerships. Oecologia 64:78–80

McKey D (1984) Interaction of the ant-plant *Leonardoxa africana* (Caesalpiniaceae) with its obligate inhabitants in a rain forest in Cameroon. Biotropica 16:81–99

McNaughton SJ (1979) Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. Am Nat 113:691–703

O'Dowd DJ (1979) Foliar nectar production and ant activity on a neotropical tree, *Ochroma pyramidale*, Oecologia 43:233–248

Ong SL (1978) Ecology of the ant-association in *Macaranga triloba*. Ph. D. Thesis, Univ Malaya, Kuala Lumpur

Owen DF, Wiegert RG (1976) Do consumers maximize plant fitness? Oikos 27:488–492

Putz FE (1982) Natural history of lianas and their influences on tropical forest dynamics. Ph.D. Thesis, Cornell Univ, New York

Putz FE (1984) The natural history of lianas on Barro Colorado Island. Ecology 65:1713–1724

Putz FE, Holbrook NM (1988) Further observations on the dissolution of mutualism between *Cecropia* and its ants: the Malaysian case. Oikos 53:121–125

Putz FE, Lee HS, Goh R (1984) Effects of post-felling silvicultural treatments on woody vines in Sarawak. Malay For 47:214–226

Raup HM (1978) Discussion in Whitmore TC: Gaps in the canopy. In: Tomlinson PB, Zimmermann MH (eds) Tropical trees as living systems. Cambridge Univ Press, Cambridge, London, New York, pp 136–137

Richards PW (1952) The tropical rain forest. Cambridge, Univ Press

Rickson FR (1979) Absorption of animal tissue breakdown products into a plant stem – the feeding of a plant by ants. Am J Bot 66:87–90

Rickson FR (1980) Developmental anatomy and ultrastructure of the ant food bodies (Beccarian bodies) of *Macaranga triloba* and *M. hypoleuca* (Euphorbiaceae). Am J Bot 67:285–292

Rickson FR, Rickson MM (1986) Nutrient acquisition facilitated by litter collection and ant colonies on two Malaysian palms. Biotropica 18:337–343

Ridley HN (1910) Symbiosis of ants and plants. Ann Bot 24:457–485

Risch S (1982) How *Pheidole* ants help *Piper* plants. Brenesia 19/20:545–548

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

Schremmer F (1984) Untersuchungen und Beobachtungen zur Ökoethologie der Pflanzenameise *Pseudomyrmex triplarinus*, welche die Ameisenbäume der Gattung *Triplaris* bewohnt. Zool Jahrb Abt Syst Tiere 111:385–410

Schupp EW (1981) Interactions between ants and plants: *Azteca* protection of *Cecropia*. M.A. Thesis, Univ South Florida, Tampa

Schupp EW (1986) *Azteca* protection of *Cecropia:* ant occupation benefits juvenile trees. Oecologia 70:379–385

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

Taylor CE (1982) Reproductive biology and ecology of some tropical pioneer trees. Ph.D. Thesis, Univ Aberdeen

Tho YP (1978) Living in harmony. Nature Malaysiana 3:34–39

Waterman PG, Ross JAM, Benett EL, Davies AG (1988) A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. Biol J Linn Soc 34:1–32

Wheeler WM (1921) A study of some social beetles in British Guiana and of their relations to the ant plant *Tachygalia*. Zoologica 3:35–126

Whitmore TC (1984) Tropical rain forests of the Far East. 2nd ed. Clarendon Press, Oxford

Windsor DM (1978) The feeding activities of tropical insect herbivores on some deciduous forest legumes. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithson Inst Press, Washington DC, pp 101–113

Zar JH (1984) Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, New York

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