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Interspecific variation and ontogenetic change in antiherbivore defense in myrmecophytic *Macaranga* species

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The present study examined whether or not coexisting congeneric plant species have different defense strategies against herbivores, and the intensity of defense changes ontogenetically. We focused on nine myrmecophytic *Macaranga* species and estimated the intensity of non-biotic and biotic defense by the degree of leaf damage in ant-free and ant-occupied plants, respectively. Ant colonization of myrmecophytic *Macaranga* species occurred in the early stage of plant development (5–50 cm-tall seedlings). Following the colonization, damage by leaf eaters was minimized and stable during the ontogenetic development of the host plants due to protection by ants. In ant-free trees, however, herbivore damage was immense in seedlings and decreased as trees grew. Interspecific comparison of leaf damage and herbivore fauna supported that coexisting congeneric plants differ in their types of non-biotic (chemical/structural) defense: without ant protection, *Macaranga beccariana,* for example, was somewhat resistant to leaf eaters but susceptible to gall-makers, *Macaranga trachyphylla* was heavily infested by generalist leaf eaters, and *Macaranga winkleri* was exploited by ant-predatory birds. Despite these variations in chemical/structural defense, ant-colonized plants were generally well defended by ants against all kinds of herbivores. This suggests that the individual host-specific ant mutualists are well adapted to deter the chemically or structurally adapted herbivores. These results imply that in the history of diversification in the *Macaranga*–ant–herbivore system, a sequence of mutual counter adaptation took place not only between plants and herbivores but also between ants and herbivores.

Key words: ant–plant mutualism; Borneo; *Crematogaster*; herbivore fauna; myrmecophyte.

INTRODUCTION

Many tropical plants are categorized as myrmecophytes (ant-plants, 415 species known worldwide, Benson 1985), which have specialized structures for housing ant colonies. The role of ants in protecting myrmecophytes against herbivores has been investigated ever since Janzen's work on myrmecophytic acacias (Janzen 1966; reviewed by Davidson & McKey 1993). In most of the studies, ants certainly defend their host myrmecophytes against insect herbivores (Janzen 1972 for *Barteria*; Schupp 1986 for *Cecropia*; Fiala *et al*. 1989 for *Macaranga*). However, protection by ants is not always perfect and in some cases ant-occupied plants suffer much herbivory (e.g. de Andrade & Carauta 1982 for *Cecropia*). Why does such variation of the protective efficiency occur? Is there any interspecific or ontogenetic variation of ant protection?

Macaranga species are defended by plant secondary compounds (Sultana & Ilyas 1986; Hnawia *et al*. 1990) and/or by ants (Fiala *et al*. 1989). Fiala *et al*. (1989) demonstrated that ant-occupied *Macaranga* plants suffer less damage by herbivores than ant-free ones, although they made no analysis on variation in damage through developmental stages or among *Macaranga* species. As the inhabitant ants are known to be highly species specific to each *Macaranga* species (Fiala *et al.* 1999; Itino

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et al. 2001a), and the herbivore fauna are different among *Macaranga* species, we hypothesize that the extent or degree of ant protection and plant defensive chemicals are different among *Macaranga* species. We also predict that the degree of biotic and non-biotic defense may change through plant development.

A few authors have documented plant developmental changes in antiherbivore defense. Most of them showed plants are better defended in juvenile than mature stages either by plant chemistry (e.g. Macedo & Langenheim 1989; Bowers & Stamp 1993) or by ants (Heil *et al.* 1997), although Kearsley and Whitham (1989) reported a case where ontogenetic changes in chemical defense had different efficacies against different herbivores. Here, we report ontogenetic change in defense in myrmecophytic *Macaranga* species.

Inter-familial or intergeneric difference in plant chemistry is supposed to have evolved against herbivore pressures and caused the counter-evolution of herbivores to the chemistry (Ehrlich & Raven 1964). However, variation in plant defensive strategies among closely related congeneric species has rarely been investigated so far (but see Yano & Ohsaki 1993; Yano 1994). For ant–plant–herbivore systems, Folgarait and Davidson (1994, 1995) documented interspecific variation in plant investment in food bodies (diet for ants) in myrmecophytic *Cecropia* spp. with special reference to light and nutrient conditions. Their reports were, however, from a quantitative viewpoint (comparison of the dry mass of food bodies) and did not include analyses of qualitative difference in defense among plants. Different ant species have often been reported to have different degrees of defensive efficacies (e.g. Horvitz & Schemske 1984; Rico-Gray & Thien 1989), and different chemical or ant defense may have effects against different herbivores (Fowler & MacGarvin 1985). Here, we document interspecific variation in defense among nine *Macaranga* species. The degree of non-biotic and biotic defense was estimated indirectly by the extent of leaf damage of ant-free (chemically/structurally defended) and ant-occupied plants (chemically/structurally and biologically defended), respectively.

The main questions addressed in this study are: (i) does the degree of non-biotic and biotic defense change as plants grow? (ii) is the degree of non-biotic and biotic defense different among *Macaranga* species? and (iii) what specific herbivores attack each *Macaranga* species?

METHODS

Macaranga

Macaranga is a genus of approximately 300 species distributed in the Paleotropics with its center of diversity in the Malesian region. In Borneo, they are a conspicuous component of the secondary forest and forest-gap flora (Davies *et al.* 1998). About 25 of the South-East Asian *Macaranga* species house ants in their stems, and have a range of morphological specialization associated with this symbiosis (Fiala & Maschwitz 1992a, 1992b). These myrmecophytic *Macaranga* species are inhabited by several obligate ant species, mostly *Crematogaster* (subgenus *Decacrema*) species, which are highly species specific to their host *Macaranga* species (Fiala *et al.* 1999). In the study site, the investigated nine *Macaranga* species have close associations with the following morphospecies of ants (Itino *et al.* 2001a). *Macaranga beccariana*, *Macaranga havilandii* and *Macaranga lamellata*: *Crematogaster decamera*; *Macaranga trachyphylla*, *Macaranga bancana*, *Macaranga hullettii* and *Macaranga kingii*: *Crematogaster borneensis*; *Macaranga hosei*: *C.* sp. 4; and *Macaranga winkleri*: *C.* sp. 2. *Macaranga lamellata* is also often associated with *Camponotus macarangae* (Maschwitz *et al.* 1996).

Two types of ant association in *Macaranga* have been identified by Fiala and Maschwitz (1992b): myrmecophytes colonized by ants later in plant development (*M. hosei* in the present study) and earlier-colonized myrmecophytes (the other eight *Macaranga* species investigated in this study). The later-colonized *M. hosei* does not house ants until the sapling grows as high as approx. 70 cm (Fiala *et al.* 1994) because the food-body production starts only at this growth stage (Fiala & Maschwitz 1992a). In earlier-colonized species, however, the food-body production starts earlier, and the seedling internodes swell and the pith degrades so that ant queens can colonize the seedlings that are only 5–10 cm tall.

Study site

The field survey was conducted during August 1993, July–August 1994, August 1995, and March and August 1997 in a lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°20′N, 113°50′E, altitude approx. 60 m). The park receives approximately 4000 mm of rainfall annually, with no pronounced dry season (Sakai *et al.* 1997). We selected nine species of closely related myrmecophytic *Macaranga* species for this study based on their abundance in the study area. They are generally abundant in open habitat like forest gaps or river banks. The habitat of the nine *Macaranga* species overlapped much, so that it was not uncommon to find more than five *Macaranga* species colonizing a single large forest gap, although there is detectable interspecific difference in microhabitat preference (Davies *et al*. 1998).

Herbivory and ant predation

Within the 1 km × 1 km study site, *Macaranga* plants (<3.5 m tall) that grew at forest gaps or along river banks were surveyed in the daytime (9.00–15.00 h). Although the selection of sample plants was basically random, some efforts were made to include as many species as possible, and to represent all heights up to 3.5 m. Due to morphological similarity, the *M. beccariana* and *M. hosei* samples may have included a few misidentified samples of very closely related *Macaranga hypoleuca* and *Macaranga pseudopruinosa*, respectively. For each plant, plant height, the presence or absence of worker ants in the hollow stem (in some randomly selected trees, the queen ants were also assessed), the occurrence of each herbivore/predator species on the plants, and amount of leaf damage were recorded.

Macaranga trees were damaged either by generalist herbivores such as leaf-eating grasshoppers (Acrididae), beetles and lepidopteran larvae which feed on other plants as well, or by specialist herbivores such as gall-making Cecidomyidae (Diptera), leaf-eating Phasmatidae (Phasmida), *Arhopala* (Lycaenidae; Lepidoptera) and *Tanaecia* (Nymphalidae; Lepidoptera). The occurrence of generalist herbivores was assessed by percentage leaf damage, which was mostly caused by the generalists, while specialist herbivores were assessed as follows: the occurrence of gall-making Cecidomyidae was assessed by the gall signs and that of leaf-eating Phasmatidae, *Arhopala* and *Tanaecia* was directly assessed (presence of the insects themselves). In addition to herbivores, the occurrence of ant-predatory mirid bugs (Miridae; Hemiptera) and woodpeckers (Picidae; Aves) was assessed directly (mirid bugs) or indirectly (woodpeckers, based on the predation signs). Leaf damage was estimated for the uppermost 10 leaves (if less, all the leaves) to the nearest 10% of leaf area.

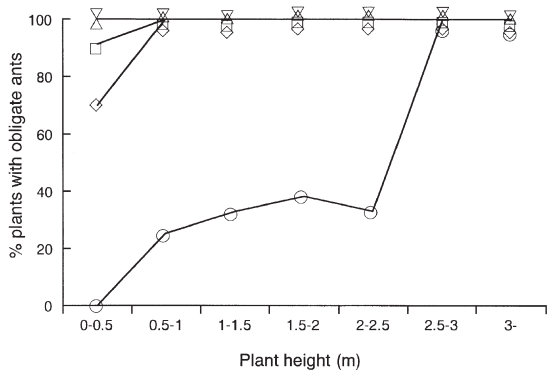

Fig. 1. Ontogenetic changes of percentage obligate-ant occupation in *Macaranga* trees. ▽, *M. beccariana* ($n = 56$); △, *M. bancana* ($n = 44$); □, *M. winkleri* ($n = 42$); ◇, *M. trachyphylla* ($n = 75$); ○, *M. hosei* ($n = 26$).

RESULTS

Timing of ant colonization

Among the five *Macaranga* species with sample size >25, four were colonized by the queen ants early in plant development (Fig. 1). In seedlings (<0.5 m), the ratio of the obligate ant-occupied trees was 100% in *M. beccariana* (5/5) and *M. bancana* (2/2), 91% in *M. winkleri* (10/11), and 72% in *M. trachyphylla* (18/25). Generalist *Crematogaster* ants, which have their mother nest out of the *Macaranga* plants, occupied 9% of *M. winkleri* seedlings (1/11) and 12% of *M. trachyphylla* seedlings (3/25). The other *M. trachyphylla* seedlings (16%, 4/25) harbored no ants. When plants grew to over 50 cm, the four species were always occupied by the obligate ant colonies.

In contrast, *M. hosei* started housing ant colonies later; no seedlings (<0.5 m, 0/2) and only one-third of saplings (0.5–2.5 m, 6/18) harbored obligate ants while other seedlings and saplings harbored no ants at all. Trees taller than 2.5 m ($n = 6$) always harbored the obligate ant colonies (Fig. 1).

Ontogenetic change of leaf damage

In ant-free trees of five *Macaranga* species where the sample size was enough to conduct a statistical test, Spearman correlation between plant height and percentage leaf damage was all negative from –0.35 (*M. trachyphylla*) to –0.83 (*M. bancana*) and significant in *M. bancana* and *M. hosei*, suggesting that the top leaves of larger plants suffered less herbivory than those of smaller ones (Table 1). In contrast, the ant-occupied plants suffered such little leaf damage throughout all species that no correlation was found between plant height and leaf damage (Table 1).

Interspecific variation of leaf damage

The interspecific comparison of leaf damage was performed by using the Kruskal–Wallis test for the size class 0–1 m of ant-free trees and 0–1 m, 1–2 m and >2 m of ant-occupied trees (Table 1). The interspecific variation was not significant in any size classes of ant-occupied trees but nearly significant in the ant-free trees ($P = 0.07$). The ant-free seedlings of *M. trachyphylla*, *M. bancana* and *M. hosei* suffered severe damage (23–43%) by leaf eaters while *M. lamellata*, for example, suffered little damage.

Herbivores and ant predators

The occurrences of specialist herbivores and ant predators in each *Macaranga* species are summarized in Table 2, together with the information for ecological properties of *Macaranga* species. The characteristics of the *Macaranga*-associated organisms are as follows.

(1) Generalist leaf-eaters: '% leaf damage (eaten)' (Tables 1,2) mostly reflected the damage by generalist leaf-eating insects such as grasshoppers, chrysomelid and scarabaeid beetles, and lepi-

Table 1 Ontogenetic and interspecific comparison of leaf damage (% leaf area, x ± SE (n)) in *Macaranga* species*

	Plant height	% Leaf damage										Kruskal–Wallis H	P
		M. beccariana	*M. havilandii*	*M. lamellata*	*M. kingii*	*M. bulletrii*	*M. trachyphylla*	*M. bancana*	*M. hosei*	*M. winkleri*			
Ant-free trees	0–1 m	16.7 ± 12.0 (3)	–	5.0 ± 2.9 (4)	–	10.0 ± 0 (2)	33.7 ± 6.6 (17)	43.3 ± 11.5 (6)	23.3 ± 6.7 (6)	9.4 ± 3.7 (6)		11.48	0.07
	1–2 m	7.1 ± 7.1 (4)	–	–	–	–	11.2 ± 5.8 (6)	0.5 ± 0.5 (3)	12.8 ± 5.9 (8)	0 (1)		–	–
	>2 m	0 ± 0 (2)	–	–	–	–	–	–	0 ± 0 (2)	0 (1)		–	–
	Spearman correlations	–0.46	–	–	–	–	–0.35	–0.83	–0.72	–0.51			
	P	0.20	–	–	–	–	0.10	0.02	0.01	0.18			
Ant-occupied trees	0–1 m	1.3 ± 1.3 (8)	–	4.0 ± 2.4 (5)	0 ± 0 (2)	3.3 ± 3.3 (3)	3.4 ± 1.3 (38)	2.9 ± 1.8 (6)	–	3.3 ± 3.3 (6)		2.18	0.9
	1–2 m	2.8 ± 1.3 (37)	–	0 ± 0 (4)	0 (1)	2.5 ± 2.5 (4)	2.3 ± 1.7 (42)	4.7 ± 2.2 (16)	0 ± 0 (4)	1.6 ± 1.1 (13)		7.37	0.39
	>2 m	2.0 ± 1.3 (25)	2.0 ± 2.0 (5)	–	0 (1)	5.0 ± 5.0 (2)	2.2 ± 0.8 (28)	3.6 ± 1.8 (8)	5.0 ± 3.4 (6)	0.9 ± 0.9 (11)		4.29	0.75
	Spearman correlations	0.08	–	–0.41	–	–0.05	–0.02	–0.10	0.27	–0.09			
	P	0.49	–	0.24	–	0.90	0.82	0.60	0.41	0.62			

*Statistical comparison of the leaf damage across the plant species and plant height was performed using Kruskal–Wallis test and Spearman rank correlations, respectively. The rank was assigned to each individual tree.
M. Macaranga.

dopteran larvae, because the specialist leaf-eaters were not common on plants if any. These generalist herbivores or their feeding signs were observed mostly on ant-free plants. Consequently, the leaf damage was more severe in ant-free plants than in ant-occupied plants (Tables 1,2). The leaf damage in ant-free trees was especially high in *M. trachyphylla* and *M. bancana*.

(2) Specialist leaf eaters: Specialist phasmatids, *Arhopala* spp. and *Tanaecia* sp. were generally rare on plants (Table 2). Their infestation rates did not appear to be affected by the ant presence/absence, but by *Macaranga* species: *M. beccariana, M. trachyphylla* and *M. bancana* being considerably infested by the phasmatids and *Arhopala* spp. while others being little infested (Table 2).

(3) Specialist gall-makers: Several species of cecidomyid flies made galls preferentially on *M. beccariana*, *M. lamellata* and *M. hosei* (Table 2). On ant-occupied plants, the galls were only ever found on a few leaves and only in a limited number. When ant-free plants were attacked, however, galls occurred everywhere on most leaves. Judging from the morphology of the galls, the gall flies were more or less host specific.

(4) Predatory bugs: Predatory mirid bugs were specifically found on leaves or in stipules of *M. beccariana*, *M. trachyphylla* and *M. bancana*. Their body size and color patterns are so similar to the symbiont *Crematogaster* ant workers and they walk so swiftly that ants cannot deter them. Once these bugs colonized the plants, the inhabiting ant population decreased and the plant tended to suffer much leaf damage by generalist herbivores. Because of the fact that they mostly attacked ant-occupied trees and often stayed in the stipules where fewer food bodies than usual were found, they appeared to prey on ant workers and/or feed on plant food bodies, like the American *Phyllobaenus* beetles on *Piper* ant-plants (Letourneau 1990).

(5) Woodpeckers: Woodpeckers broke the stems of trees to feed on the inhabiting ants. This damage did not always cause tree death but the damaged shoot usually withered and plants had to grow a new shoot. Such damage by woodpeckers (or some other vertebrates like squirrels) was generally detected in many *Macaranga* species (Table 2), especially in *M. winkleri,* where the stem is softer than the other *Macaranga* species.

DISCUSSION

Ant colonization

Most of the myrmecophytic *Macaranga* species excluding *M. hosei* were colonized by ant queens in the very early stage of plant development (<0.5 m-tall seedlings), as was qualitatively reported elsewhere (Fiala *et al*. 1994). In contrast, *Cecropia*, the neotropical equivalent of *Macaranga*, starts harboring the symbiont ants in saplings of 0.5–1.0 m in height (Folgarait & Davidson 1994). Myrmecophytic *Macaranga* species appear to be good material for further research in the phylogenetic and ecological constraints characterizing the ant colonization.

Ontogenetic change in plant defense

The lack of the ontogenetic change in leaf damage in ant-occupied *Macaranga* species means that once the ant colony is established, even small seedlings are well protected by ants. In ant-free trees, on the contrary, smaller plants were more likely to be infested by leaf eaters (Table 1). Such a pattern is exceptional in non-ant-protected plants, in which younger plants are typically better defended by plant chemistry (reviewed by Bryant *et al.* 1992). Since production of immobile defensive substances (Coley *et al.* 1985) is energetically costly especially for seedlings (Bryant & Julkunen-Tiitto 1995), younger *Macaranga* seedlings may invest less in immobile chemical defense and more into ants, a mobile biotic defense (McKey 1984). Indeed, Heil *et al*. (1997) and Itino *et al.* (2001b) reported that smaller *Macaranga* invested relatively more in the production of food bodies (diet for ants) than the larger plants. These ontogenetic changes in defense in *Macaranga* species forced us to use same-sized plants for the following interspecific comparison.

Interspecific variation in plant defense and herbivore fauna

Ant-free *Macaranga* plants showed a tendency for interspecific variation in leaf damage by generalist

Table 2 Percentage occurrence (no. infested trees/no. investigated trees) of specialist herbivores, ant predators and woodpeckers in ant-free and ant-occupied *Macaranga* trees with information for ecological properties of *Macaranga* species*

Macaranga species	Ant occupation	*n*	Gall maker Cecidomyidae	Leaf eater Phasmatidae	Leaf eater *Arhopala*	Leaf eater *Tanaecia*	Predatory bug Miridae	Woodpecker Picidae	Symbiont Ant species[a]	Ant Aggressiveness[b]	Position of food bodies[c]	Crown light levels[d]	% leaf eaten[e]
M. bosei	–	16	6	0	0	0	0	0	C4		AL	high	23
	+	10	0	0	0	0	0	0					–
M. beccariana	–	9	44	11	0	0	11	0	CD	+	AL	medium	17
	+	72	22	1	6	0	9	1					1
M. havilandii	–	0	–	–	–	–	–	–	CD		IS, AL	low	–
	+	5	0	0	0	0	0	20					–
M. lamellata	–	4	100	0	0	0	0	25	CD		IS	low	5
	+	9	0	0	0	0	0	0					4
M. kingii	–	0	–	–	–	–	–	–	CB		IS	low	–
	+	4	0	0	0	0	0	0					0
M. hullettii	–	2	0	0	0	0	0	0	CB		IS	low	10
	+	9	0	0	0	0	0	0					3
M. trachyphylla	–	23	0	0	9	0	0	0	CB	++	IS	medium	34
	+	112	2	3	2	2	3	5					3
M. bancana	–	9	0	0	0	0	0	0	CB		IS	medium	43
	+	38	0	3	11	0	26	3					3
M. winkleri	–	8	0	0	0	0	0	13	C2	+++	IS	high	9
	+	30	0	0	0	0	0	23					3

*Statistical comparison of the frequency occurrence between ant-free and ant-occupied trees was performed using Fisher's exact test although in every case no significant difference was detected.
[a]C4, *Crematogaster* sp. 4; CD, *Crematogaster decamera*; CB, *Crematogaster borneensis*; C2, *C.* sp. 2.
[b]After Itioka *et al*. (2000).
[c]AL, surface of apical leaves or stipules, IS, inner side of dome-shaped stipules.
[d]After Davies *et al*. (1998).
[e]After Table 1.

leaf eaters. At least, two potential factors may be responsible for this variation. One is habitat difference. The lower leaf damage of ant-free *M. lamellata*, for example, could be explained by their shady habitat (Davies *et al*. 1998), where the herbivore pressures are expected to be lower. Another factor is the interspecific variation in plant chemical/structural defense. The five *Macaranga* species other than *M. lamellata* and *M. hullettii*, that were used for the interspecific comparison (top row in Table 1), were all light-demanding pioneer species and often coexisted in the same habitat (see Table 2; Davies 1998; Davies *et al*. 1998), but yet, they differed in leaf damage. This suggests that the interspecific difference in chemical/structural defense caused the leaf-damage variation: for example, some species have good defensive substances or structures against leaf-eating herbivores but others do not. Nomura *et al.* (2000) showed experimentally that some of the damage variations among three myrmecophytic and two non-myrmecophytic *Macaranga* species were caused by the variation of chemical and structural defense.

The ant-occupied plants, however, suffered little damage with little interspecific variation, suggesting that, in general, ant protection was effective enough.

Interspecific differences in herbivore fauna further suggest variation in plant defense strategies among *Macaranga* species. *Macaranga beccariana* and *M. lamellata* (BEC group), for example, were prone to attacks by specialist gall-making flies (Table 2), *M. trachyphylla* and *M. bancana* (TRA group) tended to be infested by generalist leaf eaters (Table 1), and *M. winkleri* (WIN group) suffered damage by birds that foraged for ants inside the stem (Table 2). Itioka *et al*. (2000) showed that the symbiont ants were more aggressive in the order of *Crematogaster* sp. 2 (associated with WIN group), *C. borneensis* (TRA group) and *C. decamera* (BEC group), while Nomura *et al.* (2000) documented that the intensity of chemical/structural defense was stronger in the opposite order (i.e. BEC group was chemically/structurally best defended). These facts may explain the pattern of the differentiation in herbivore fauna among the three *Macaranga* groups as outlined below.

First, the WIN group is so well defended by the ants that they have evolutionarily escaped from constantly attacking specialist insect herbivores (see Table 2), although, experimentally, ant-excluded plants were severely attacked by generalist insect leaf eaters (Itioka *et al.* 2000). In contrast, however, they were prone to attacks by birds (Table 2). Although the thin-walled hollow stem permits a wider inner space, which harbors an active ant colony, it is, at the same time, easily destroyed and exploited by birds (T. Itino, unpubl. obs., 1994) even though the birds may hesitate to attack next time due to the ant aggressiveness. In short, the WIN group is nearly completely defended by ants (so they do not have specialist herbivores) although they are chemically/structurally defenseless.

The BEC group, on the other extreme, are poorly defended by ants but better defended by chemicals and structures than the WIN group (Itioka *et al*. 2000; Nomura *et al*. 2000). Although most generalist herbivores, including the ant-predatory birds, are inaccessible to the plants due to the chemical/structural defense, specialists like gall-making flies, phasmatids, *Arhopala* larvae and ant-predatory mirids, constantly attack the BEC group (Table 2). Thus, the important function of the mutualist ants, in this case, is thought to minimize the damage by these specialists.

As an intermediate, the TRA group is nearly completely defended from birds by its harder stem structure and from the specialist gall flies by its ant protection. However, some groups of leaf eaters seem to have adapted to attack the TRA group constantly, taking advantage of the imperfect chemical and biotic defense. All in all, the three *Macaranga* groups are shown to have different types of defense, although our data sets have some limitations of quantification (relying on ant/herbivore occurrence rather than their abundance).

Other than the chemical/structural and biotic defensive properties, ecological properties of plants such as position of food bodies or crown light levels, appear to be correlated with the degree of herbivory to some extent: food-body production at apical leaves seems to be correlated with gall-maker infestation, and higher crown light levels appear to have some effects on increased herbivory (Table 2).

Although ant–myrmecophyte associations have greater specialization than other animal–plant

mutualisms (pollination and seed-dispersal systems) (Fonseca & Ganade 1996), the ultimately high species-to-species specificity in the *Macaranga-Crematogaster* system is exceptional among myrmecophytes (Fiala *et al*. 1999). Fonseca and Ganade suggested that, in an Amazonian ant-plant community, myrmecophytic plants are not so specialized toward ant partners as ants are toward plants because plants receive fewer fitness benefits and are less dependent on ants, but with the ants in turn relying heavily on specific plant partners. However, in the *Macaranga* system, herbivores exert a major impact on plants (this study, see also Fiala *et al*. 1989). The degree of mutual dependence of *Macaranga* plants and ants seems so high and symmetric that reciprocal specialization seems to have occurred. Such reciprocal adaptive radiation and specialization among herbivores, plants and ants may result in diversification of defense strategies in *Macaranga* species. The coexistence of several *Macaranga* species in a small spatial scale might also be explained by such interspecific difference in defensive strategies (i.e. species coexistence due to the competition for enemy-free space; Lawton 1986).

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