Competition among visitors to extrafloral nectaries as a source of ecological costs of an indirect defence

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Abstract: Extrafloral nectar is an indirect, generally ant-mediated, defence mechanism that is particularly common in tropical plants. This study focuses on interactions among different groups of arthropods visiting extrafloral nectaries of the South-East Asian myrmecophilic plant, *Macaranga tanarius*. The diurnal activity patterns of arthropods on nectaries were recorded on two occasions, each plant being used once in an untreated state and once after chemical induction of extrafloral nectar flow. Ants, widely regarded as the most important consumers of extrafloral nectar, made up only 60% of all nectary-visiting arthropods. Striking negative relations became obvious between ants and 'non-ants', among which two (morpho)species of fly (*Grammicomya* sp. and *Mimegralla* sp., both Micropezidae) were most important. On most leaves, either ants or 'non-ants', but not both groups, were present at the same time. Behavioural observations revealed that many flies actively excluded other arthropods, including ants, from the nectaries or leaves. However, the flies had no detectable defensive effect against herbivores. The presence of these 'thieves' of extrafloral nectar therefore can cause ecological costs in terms of reduced presence of ants that consume extrafloral nectar and defend plants.

Key Words: ants, ant–plant, extrafloral nectar, induced defence, *Macaranga tanarius*, Malaysia, myrmecophily, South-East Asia

INTRODUCTION

Many plant species produce extrafloral nectar (i.e. nectar that is not functionally involved in pollination) on their leaves or shoots (Bentley 1977). Extrafloral nectaries are known in at least 66 plant families and occur on species in taxonomically very distant groups, including ferns and flowering plants and – within the latter group – monocotyledons as well as dicotyledons (Elias 1983, Schupp & Feener 1991). Plants bearing extrafloral nectaries can make up ecologically relevant proportions of the vegetation and are particularly common in tropical and subtropical habitats (Blüthgen *et al.* 2000, Fiala & Linsenmair 1995, Oliveira & Brandão 1991, Oliveira *et al.* 1999, Schupp & Feener 1991).

The protective role of extrafloral nectar has long been a matter of discussion, but many studies have now proven that it can play an important role in a plant's indirect defence against herbivores (for reviews, see Bentley 1977, Buckley 1982, Koptur 1992). Given a choice, many ants forage preferentially on plants with extrafloral nectaries (Barton 1986, Koptur *et al.* 1998, Oliveira *et al.* 1999). Their presence reduces numbers of herbivorous insects on these plants and thus lessens damage by herbivores (Barton 1986, Koptur 1984, Koptur *et al.* 1998, O'Dowd 1979, Oliveira *et al.* 1987, Pickett & Clark 1979, Stephenson 1982).

However, interactions among ants and plants bearing extrafloral nectaries often represent rather loose forms of facultative mutualisms, which – due to the necessarily open presentation of extrafloral nectar and the resulting low level of species-specificity – are particularly prone to exploitation by other arthropods. Several authors reported the occurrence of mites and ladybird beetles on extrafloral nectaries of many different plant species (Pemberton 1993, Pemberton & Vandenberg 1993, van Rijn & Tanigoshi 1999). An early observation of obvious competition for extrafloral nectar has been reported by (O'Dowd 1979), who found trigonid bees to consume extrafloral nectar of *Ochroma pyramidale* on plants from which ants had been excluded. Common 'non-ant' visitors that have been observed on extrafloral nectaries include ichneumonid and braconid wasps (Bugg *et al.* 1989, Stapel *et al.* 1997), jumping spiders (Ruhren & Handel 1999), mosquitoes (Foster 1995), neuropterans (Limburg & Rosenheim 2001), and flies (this study).

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Some of these groups of 'non-ant' consumers of extrafloral nectar show a defensive behaviour against herbivores and thus can serve as a true functional 'alternative' to ants in regard to the plants' protection against herbivores (Pemberton & Lee 1996, Ruhren & Handel 1999, van Rijn & Tanigoshi 1999). Others, in contrast, only consume extrafloral nectar without providing the plant with any mutual benefits and thereby behave as parasites. Although there are several reports on the presence of 'non-ant' consumers of extrafloral nectar, none has investigated whether and how these two competing groups interact with each other.

Non-defending users of extrafloral nectar – preventing ants from exhibiting their defensive effect – could reduce the overall efficacy of this indirect defence mechanism and thus could cause important ecological costs (Heil 2002). The data presented here allow a first insight into this complex phenomenon. Our study revealed direct competition leading to temporal exclusion of plant-defending ants from nectaries of West Malaysian *Macaranga tanarius*.

METHODS

Study species

Macaranga tanarius (L.) Muell. Arg. (Euphorbiaceae) is a South-East Asian pioneer tree commonly growing along roadsides and in cleared areas in West Malaysia. The plant produces food bodies on its leaf blades (Figure 1a) and stalks and on the younger parts of the stem (Fiala & Maschwitz 1992). These food bodies contain high amounts of carbohydrates and lipids along with some amino acids and proteins (Heil *et al.* 1998) and are collected by ants from the vicinity. In addition, 5–9 extrafloral nectaries are present on the upper side of the leaf blade (Fiala & Maschwitz 1991) (Figure 1a, b). These secrete extrafloral nectar, an aqueous solution of mono- and disaccharides containing also some amino acids at low concentrations (Heil *et al.* 2000). The presence of ants (Figure 1b), which collect food bodies and extrafloral nectar, results in a significant protection from herbivores (Fiala *et al.* 1989, 1994; Heil *et al.* 2001a).
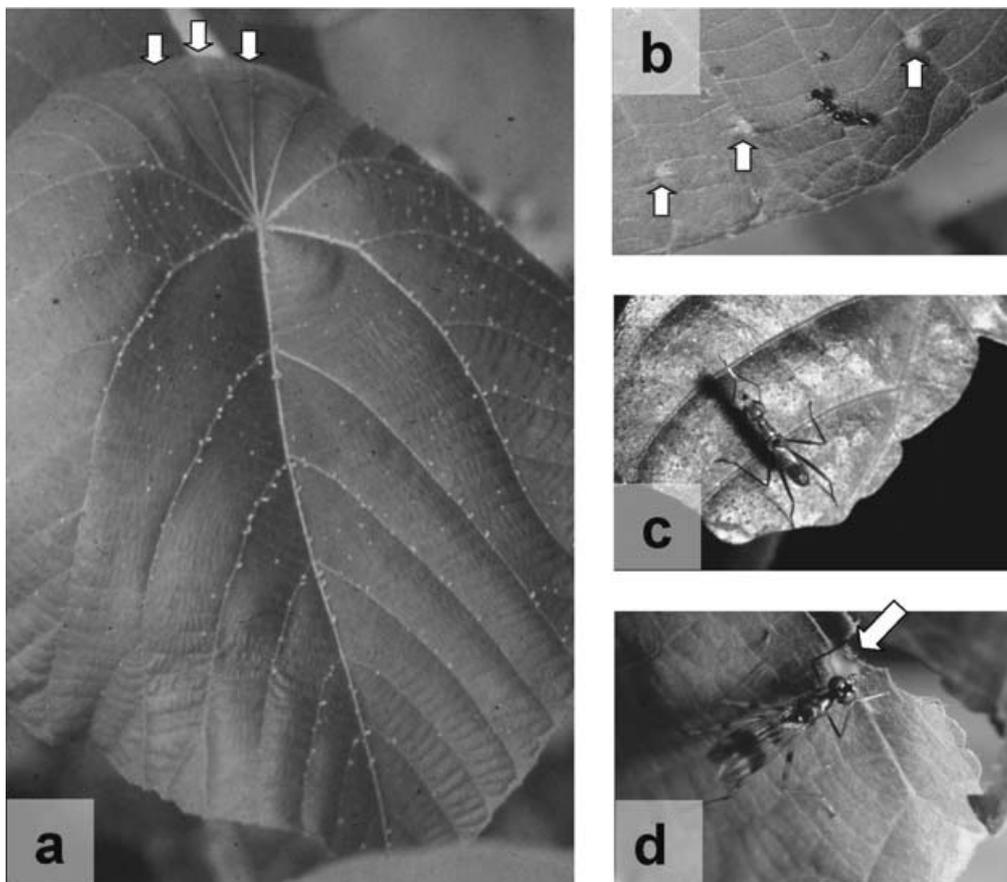
Fig 1. Extrafloral nectaries of *Macaranga tanarius* and their most dominant visitors. Extrafloral nectaries (white arrows) are located on the upper surface of the leaf blade, while food bodies appear along leaf veins (a). During our study, ants (b) and flies such as *Grammicomya* Bigot (c) and *Mimegralla* Rondani (d) were among the most important visitors of the nectaries. Photographs taken by B. Fiala (a), M. Heil (b, d) and K.-E. Linsenmair (c).

The data presented here form part of a larger study, which was conducted to test whether production of extrafloral nectar by this species is an induced defence mechanism (Heil *et al.* 2001*b*). The present experiment was conducted in September 1999 in an abandoned oil palm plantation near Tampin, Selangor, West Malaysia. The plantation had been abandoned 3 y before and young pioneer vegetation had therefore developed under the palm trees. The site was rich in young *Macaranga tanarius* saplings.

Experimental design

The activity of arthropods appearing on the five youngest of the completely unfolded leaves of each of 20 different plants was recorded on two occasions (22–23 September 1999 and 1–2 October 1999). Plants were checked every 2 h from noon to 10h00 on the next day for 1 min per leaf, and arthropods appearing on the upper surfaces of the leaf blades were counted. Different functional groups were defined according to the arthropods' current (or known) behaviour, and ants and 'non-ants' were counted separately. All individuals feeding on an extrafloral nectary at least once within the observational time span were defined as 'visitors'. 'Herbivores' were all insect species that were known to feed on *M. tanarius* leaves. Several common species were sorted to morphospecies (or, in the case of ants, genera), as long as these could be determined with the naked eye and from a distance allowing observations without disturbing the animals.

In order to create 'high extrafloral nectar-flow' conditions, the plants were treated with an aqueous (1 mM) jasmonic acid (JA) solution to induce EFN secretion (Heil *et al.* 2001*b*). Each plant was surveyed once in the untreated and once in the induced state. On the first day, 20 similar-sized plants were divided randomly into two groups of 10 plants each. One group served as untreated controls, while in the other group five leaves of each plant were sprayed two times (at 9h00 and at 17h00) with 2.5 ml per leaf of JA solution. In order to exclude any putative effects of the census date or local variations in the availability of ants and 'non-ants', the experiment was repeated 9 d later with the former controls now being induced with JA and vice versa.

Behavioural observations

Striking negative relations among ants and some of the 'non-ant' species became obvious during this study. Quantitatively important 'non-ants' were in particular two morphospecies of fly, *Grammicomya* Bigot (subgenus *Ecdemnodera* Enderlein) and *Mimegralla* Rondani (both Micropezidae). In order to obtain an impression of whether direct interactions were, at least in part, responsible for this phenomenon, observations of the different species' behaviour were conducted both during the regular censuses and in 198 independent cases. Observations during the regular censuses were restricted to the general observational time span of 1 min per leaf and census. In addition, 198 leaves of 35 plants were observed at various dates (several leaves being observed repeatedly). These leaves were selected according to the fact that at least one of these flies was already present on the leaf blade. The flies then were observed until the first other arthropod appeared on the leaf blade. The flies were determined by Bernhard Merz, and voucher specimens are deposited at Muséum d'Histoire Naturelle, Genève, Switzerland.

Defensive effects

In August–September 1999, an experiment was conducted to investigate the defensive efficacy of arthropods attracted by extrafloral nectar of *M. tanarius* (see Heil *et al.* 2001*b* for details). Plants were selected according to similarity in leaf number and plant size, and the three youngest totally unfolded leaves of all plants were marked. The plants then were divided randomly in three groups of 15 plants each. All vegetation with a direct contact to experimental plants was removed. The marked leaves (and the up to three younger leaves that newly emerged during the experiment) of plants in the 'induced' group were treated every 4 d by spraying 2.5 ml of 1 mM aqueous JA solution. From a second group of plants, ants were excluded by applying a ring of sticky resin (Tangletrap®, The Tanglefoot Corp., Grand Rapids, USA. see Heil *et al.* 2001*a* for details). A last group of 15 plants served as untreated controls. Six weeks after the first treatment, the youngest six leaves of all plants were removed and dried and their degree of herbivory was quantified as amount of missing leaf area as described previously (Heil *et al.* 2001*b*).

Statistical analysis

Numbers of arthropods appearing on one single leaf could be affected by leaf age (as five different leaves were included from each plant), time of day and induction state. All factors were varied within each individual plant to exclude effects related to plant individuals as completely as possible. A repeated-measures ANOVA (GLM procedure in SPSS) was conducted to test for effects of these factors. Prior to ANOVA procedures, the assumption of sphericity was tested with Mauchly's test. Statistical calculations were conducted with SPSS for Windows 8.0 (SPSS Inc., Chicago, USA). For further graphical data analysis, data

were combined according to the effects as indicated by statistical analyses.

RESULTS

Factors affecting insect numbers

Ants represented *c.* 60% of arthropods visiting the extrafloral nectaries of *M. tanarius* at the study site, while *c.* 17% were two morphospecies of fly (*Grammicomya* sp. and *Mimegralla* sp., see Figure 1c, d). Many more visitors appeared on induced plants than on controls, and ants were present in higher numbers during the night, while 'non-ants' dominated during the day, particularly when plants were in the induced stage (Figure 2).
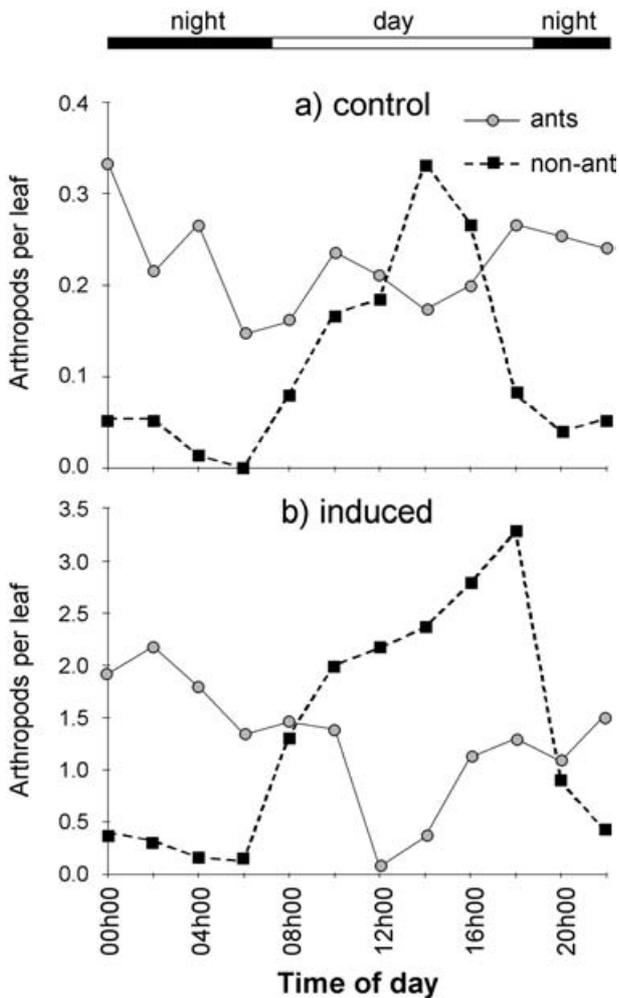
Fig 2. Temporal patterns in the activity of visitors to extrafloral nectaries of *M. tanarius*. Five leaves of each of 20 plants were censused every 2 hours, and numbers of ants and 'non-ants' occurring on each single leaf were averaged for each census. Plants were rotated among treatments, and each plant therewith is presented once in the control stage (a) and once in the stage of induced flow of extrafloral nectar (b).

In total, 3813 arthropods were observed visiting the extrafloral nectaries of the 20 *Macaranga tanarius* plants during the censused periods. Among the 3042 arthropods visiting nectaries of induced plants, 1732 were ants, 544 were *Grammicomya* or *Mimegralla* flies and 766 were 'others', including more than 100 further flies (several *Drosophila* and *Musca* spp. and at least one species of a putatively undescribed genus near *Drapetis* Meige, family Hybotidae (B. Merz, *pers. comm.*)). On control plants, only 411 arthropods visited the extrafloral nectaries (238 ants, 93 *Grammicomya* and *Mimegralla* individuals and 80 'others'). Most arthropod groups that appeared on the leaves of *M. tanarius* showed characteristic diurnal activity patterns (Figure 2). Ants, in general, occurred both during day and night, but showed differences at the level of genus and morphospecies, respectively. *Grammicomya* and *Mimegralla* were only active during the day. Herbivorous beetles, in contrast, occurred mostly during the night.

Obviously all groups of consumers of extrafloral nectar were attracted in higher numbers when plants were treated with JA, and ants and 'non-ants' showed different diurnal patterns. Both time of day and induction state significantly affected numbers of nectary visitors (Table 1). Ants were more numerous and were more active during

Table 1. Factors affecting numbers of ants and 'non-ants' appearing on leaves of *M. tanarius*. Repeated-measures analyses on the effects of time of day, leaf position and plant induction state as within-subject variables were conducted separately for ants and 'non-ants' on the complete data set of 2400 single-leaf censuses (i.e. five leaves of 20 plants each censused 12 times within 24 h, each plant being once in the control and once in the induced state).

| Source	df	F	P
Ants			
induction state	1	20.6	< 0.001
error (induction)	19		
time of day	11	5.35	< 0.001
error (time)	209		
leaf position	4	1.37	n.s.
error (leaf)	76		
induction × time	11	5.76	< 0.001
error (induction × time)	209		
Non-ants			
induction state	1	51.5	< 0.001
error (induction)	19		
time of day	11	22.4	< 0.001
error (time)	209		
leaf position	4	0.94	n.s.
error (leaf)	76		
induction x time	11	16.9	< 0.001
error (induction x time)	209		

* Only significant interactions are reported, all other interactions were not significant, n.s. (P > 0.05).

the night (see Figures 2, 3). The decrease in the number of ants and the increase of 'non-ants' during day hours was much more pronounced when plants were in the induced stage, leading to a significant induction × time interaction for both groups of arthropods (Table 1). The patterns of nectary visitors are therefore considered separately for day and night and for both induction states. No ants occurred on most leaves on which 'non-ants' were present, and vice versa (Figure 3). These negative relations could be detected on all plants both at night and in the day (Figure 3a–d) but were more obvious on control plants, which were characterised by low nectar-secretion rates. For example, either only ants or only 'non-ants' occurred in 93% (87 of 94) of single-leaf censuses at which 'visitors' were observed on a leaf of a control plant during the

day (Figure 3a). At night, arthropods occurred in 85 single-leaf censuses on control plants, and no single 'non-ant' was observed on a leaf occupied by one or several ants, and vice-versa (Figure 3b).

Similar, but less exclusive patterns occurred in the large numbers of visitors observed on extrafloral nectaries of induced plants. During daylight hours, 229 of the 321 leaves (= 71%) on which arthropods were observed were occupied only by ants or by 'non-ants', but not both (Figure 3c). At night, arthropods were observed during 313 single-leaf censuses, and 270 of these leaves (= 86%) were occupied exclusively by members of only one group (Figure 3d).

Due to the generally higher number of ants present during the night (Figure 2, 3), cases with one or a few ants,
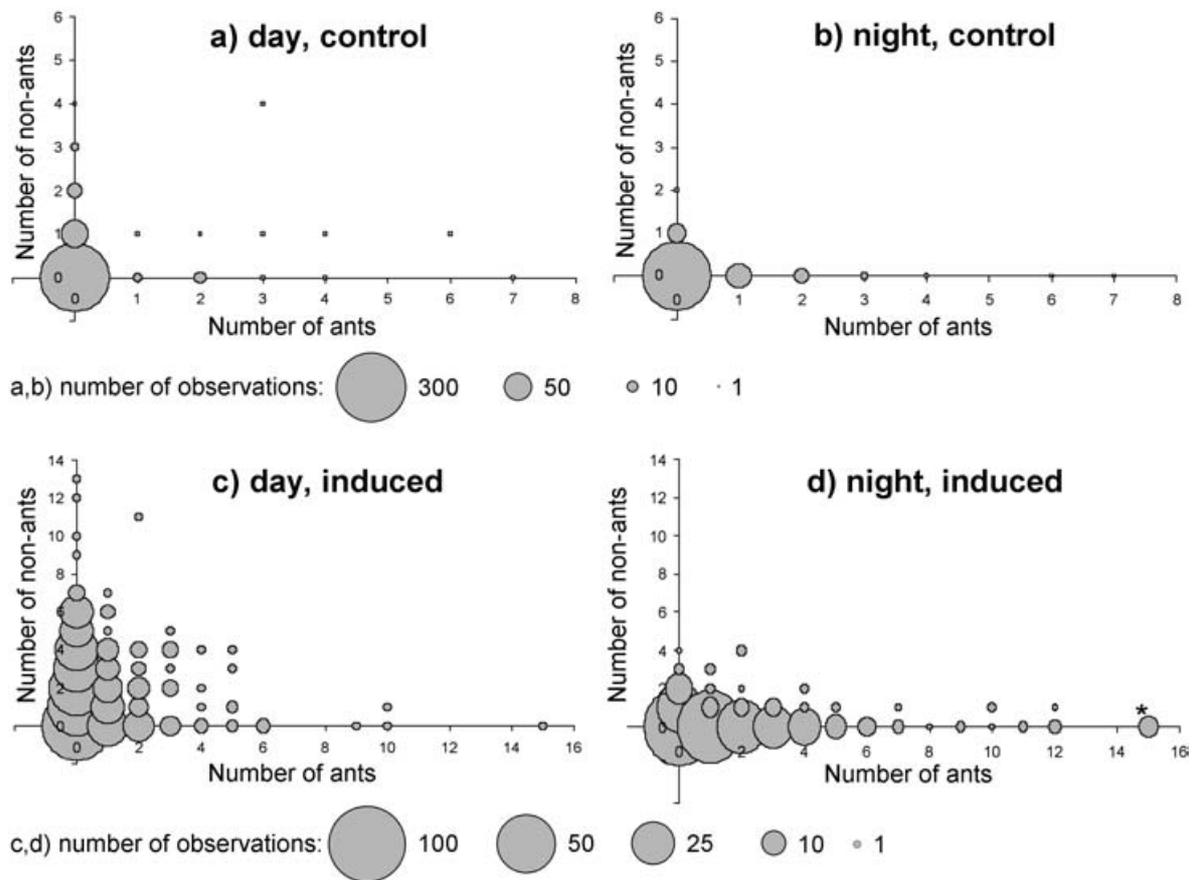
Fig 3. Negative relations between ants and 'non-ants' visiting the extrafloral nectaries of *Macaranga tanarius*. Numbers of ants and 'non-ants' appearing together and at the same census on one single leaf are plotted separately for 'day' (censuses 10h00, 12h00, 14h00 and 16h00) and 'night' (censuses at 22h00, 24h00, 02h00 and 04h00) and separately for the control and the induced state of the respective plant (plants were rotated among the treatments, data from both dates are combined). Arthropods were counted as 'appearing' on a leaf as soon as they landed or crawled on the leaf blade and had obvious physical contact with it. The censuses conducted during dusk (18h00 and 20h00) and dawn (6h00 and 8h00) were omitted to present clear day/night patterns, since appearance and disappearance of arthropods showing a clear diurnal rhythm took place during these time spans (see Figure 2). The size of symbols represents the number of individual leaves on which a given combination of numbers has been observed. A circle at coordinates x = 0 and y = 3 thus symbolizes the occurrence of one or several cases in which 0 ants and 3 'non-ants' appeared at one census on one single leaf. See inserts for relation between number of observations and circle size. * In (d), nine cases in which 15 or more ants co-occurred with 0 'non-ants' are plotted together in order to avoid a too long x-axis.

but no 'non-ants', dominated during night (Figure 3b, d), while the reverse pattern occurred during daylight hours (Figure 3a, c). These patterns resulted, at least in part, from direct interactions among these functional groups (see below).

Behavioural observations

Observations of the behaviour of arthropods appearing on leaves of *M. tanarius* at the study site revealed that *Grammicomya* sp. (Figure 1c) and *Mimegralla* sp. (Figure 1d) showed an aggressive behaviour towards other arthropods. Both morphospecies occurred on the upper side of single leaf blades and regularly visited the extrafloral nectaries. The flies actively kept the whole leaf blade, or at least an area with a diameter of *c*. 15–20 cm, free of intruders. Among 144 leaves that were occupied (at least for the whole census time of 1 min per leaf) exclusively by these flies during the regular controls, 54 were occupied by a single *Grammicomya* and 23 by a single *Mimegralla*. Twenty-five leaves carried 2–4 *Grammicomya* flies, 15 leaves 2–4 *Mimegralla* flies, and on 27 leaves 2–5 flies of both morphospecies occurred together.

In most (> 85%) of the observations (n = 314) in which a foreign arthropod appeared on the upper, nectary-bearing surface of a leaf within the area occupied by one of these flies, the 'resident' fly opened its wings and moved quickly towards the 'intruder'. These movements were mainly by running, but short flights of several cm were observed as well. This behaviour was directed against both conspecifics and members of other species. Within-species interactions included short direct fights, which were never observed in interactions of the flies with other species. Within-species interactions ended predictably with the departure of the smaller individual; while in interactions among similar-sized flies the originally resident individual had an obvious advantage. In contrast, most of these flies successfully defended their leaves (or their occupied area of the leaves) against insects from other species. Smaller ants (mostly *Crematogaster* and *Pheidole* spp.) entered the occupied leaves in 143 cases and were quickly driven away by the resident flies. However, the flies even deterred several considerably larger arthropods: this was the case in 67 of the 82 cases in which larger arthropods such as larger flies, small butterflies, or ants (58 cases) were observed to intrude an area occupied by a fly. However, the flies were not able to deter large beetles (four cases) or grasshoppers (11 cases).

The aggressive behaviour of these flies was seldom directed against herbivores. Most herbivores that were of quantitative relevance at the study site were grasshoppers and beetles, along with some caterpillars of different species. While the grasshoppers were too large to be attacked by the flies, beetles were mainly active during
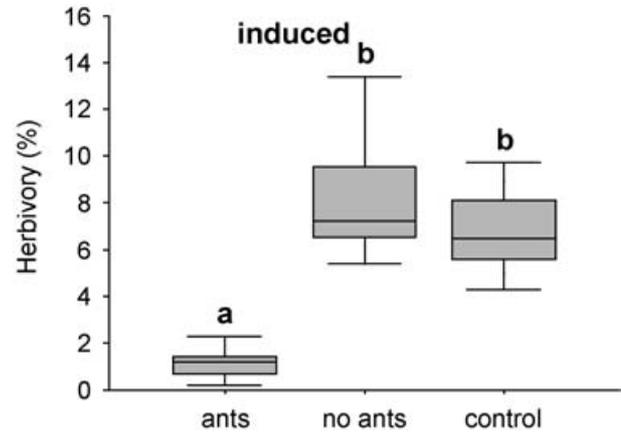
Fig 4. Effects of induction of extrafloral nectar flow and ant exclusion on herbivory of *M. tanarius*. Herbivory is presented as per cent of missing leaf area (averaged for the six youngest leaves of 15 plants per treatment) and is plotted separately for induced plants to which ants had access ('ants'), for those from which ants had been excluded ('no ants'), and for untreated control plants. Bars marked by different letters are significantly different (P < 0.01, according to Kruskal–Wallis test for independent samples) (data in part from Heil *et al.* 2001*b*).

night and fed from the leaf's lower surface, thereby being separated spatially and temporally from the flies, which were strictly restricted to the day and only defended the upper leaf surface. In contrast, ants of different species were observed both during day and night, patrolling the upper and the lower leaf surface, and were repeatedly observed to attack herbivorous insects, even when these were much larger than the ants.

Defensive effects

After 6 wk, plants on which extrafloral nectar secretion had been regularly induced had accumulated a significantly lower degree of herbivory than did control plants (Figure 4). This effect was however restricted to those plants to which ants had free access. The herbivory of plants from which ants (but not flying insects) had been excluded was even higher (yet not significantly different) than that of totally untreated control plants.

DISCUSSION

Although many studies have demonstrated an effective indirect defence against herbivores that is mediated by extrafloral nectary-visiting ants (see Introduction, and Bentley 1977, Koptur 1992 for reviews), several studies did not find any protective effects (Freitas *et al.* 2000, Mackay & Whalen 1998, O'Dowd & Catchpole 1983, Rashbrook *et al.* 1992, Tempel 1983). We report here that interactions among different groups of visitors of extrafloral nectaries can be an important reason for the

unpredictability of defensive effects related to the presence of extrafloral nectaries.

Numbers of ants and 'non-ant' visitors observed at the extrafloral nectaries on leaves of *Macaranga tanarius* were negatively related to each other (Figure 3), pointing to a mutual exclusion of these two groups of arthropods. This exclusion takes place on the scale of the single leaf: no ants occurred on most individual leaves on which 'non-ants' were present, and vice versa. In general, such negative correlations could result from direct interactions between the two groups regarded, or from other, external factors (such as site effects leading to a dominance of either of both groups). Our study was conducted at one site, and each plant was investigated once in the 'control' and once in the induced state. The abundance of ants and 'non-ants' differed among leaves of the same plant and during the same census, and also among different surveys of the same leaf. No hints of effects of microsite or plant individual could therewith be observed. Moreover, both numbers of ants and 'non-ants' showed marked diurnal patterns, with ants dominating at night, while other arthropods (in particular two morphospecies of flies, *Grammicomya* sp. and *Mimegralla* sp.) dominated during the day (Figure 2). The decrease in the number of ants was however more dramatic when high numbers of aggressively behaving flies occurred on induced plants (Figure 2b). Induction of nectar flow generally attracts ants as well (*pers. obs.*), this pattern therefore leads to the conclusion that the flies effectively excluded ants from the nectaries.

This interpretation is confirmed by behavioural observations, which revealed that direct interactions between individual animals had a considerable influence on the taxonomic composition of the extrafloral nectar consumers. 'Non-ants' were an important driving force in these interactions. In particular *Grammicomya* and *Mimegralla* (Figure 1c, d) have regularly been observed to actively deter other nectary visitors, including ants, from occupied leaf surfaces. This is in contrast to most other reports on negative relations among ants and other arthropods: in these cases, ants in general were the more dominant partner in the interaction (Halaj *et al.* 1997, Mackay & Whalen 1998).

In general, arthropods from several taxonomic groups appear at extrafloral nectaries, but ants seem to be the most important defenders. Most studies reporting protective effects of extrafloral nectar have in fact been ant-exclusion studies, which used sticky resin to exclude ants, but not flying consumers, from the experimental plants. *Ochroma pyramidale* suffered from a significant increase in herbivore damage when ants were excluded, although other nectar collectors still had access to the plant (O'Dowd 1979). The same holds true for the species studied here. Ant exclusion from *M. tanarius* leads to a dramatic increase in herbivore damage (Heil *et al.* 2001*a*), and the induction of extrafloral nectar secretion did

reduce herbivory only in plants to which ants had access (Figure 3). From these observations it becomes clear that the flying consumers of extrafloral nectar (which still had access to the nectaries) have little, if any, defensive effect against herbivores.

The negative relationship between ants and non-ants that has been detected in our study thus means a negative relationship between better and less-good defenders. The true role of the aggressive behaviour of these flies is unclear. Proximate reasons could be, among others, the defence of a reliable food source or the protection of attractive mating sites. However, its net effect for the extrafloral nectar-producing plant is reduced protection against herbivores. Being visited by these 'thieves' of extrafloral nectar can thus cause an important ecological cost in terms of reduced presence of defending ants.

ACKNOWLEDGEMENTS

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