

Lack of ant attendance may induce compensatory plant growth

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Three levels in ant–plant protection systems need to be considered to fully understand how these symbiotic systems work. Here we present the effect of *Oecophylla smaragdina* ants on (1) the arthropod community, (2) herbivory, and (3) plant performance, within a studied mangrove ant–plant protection system. On *Rhizophora mucronata* trees in Thailand ants successfully colonised ant trees attached with a string to a natural ant tree, whereas they were unable to colonise control trees without this connection. Trees were monitored and arthropods (numbers and composition), leaf damage, leaf turnover and growth rates (stem diameter, tree height and total leaf area) were recorded in two surveys covering a period of 12 months. The number of herbivorous arthropods, but not the number of predators, was significantly lower on ant trees compared to control trees. Likewise, the amount of leaf damage inflicted by the four major groups of herbivores (Chrysomelidae, Tortricidae, Geometridae and Sesarminae) was significantly lower on ant trees compared to control trees and so was the leaf turnover rate. In spite of this, the released herbivore pressure on ant trees did not translate into higher growth rates. In contrast, all growth responses increased more on control trees compared to ant trees. Differences between the two groups were insignificant but leaf area increase was only marginally nonsignificant ($P=0.062$). The results show that ants remove herbivorous arthropods more efficiently than predators but ant-colonised mangroves do not necessarily benefit from this despite the resulting decrease in herbivory.

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Many plant species benefit from the presence of ants. Both the well-studied group of plants that have developed ant attractants (food and domatia; Inouye and Taylor 1979, Odowd 1979, Stephenson 1982, Barton 1986, Smiley 1986, Oliveira 1997, Agrawal and Rutter 1998, Bronstein 1998), as well as plants without attractants (Beattie 1985, Way and Khoo 1992, Peng et al. 1995, 1997a, 1997b, 1999), may perform better when hosting ants, because they are damaged less by herbivores. Within ant–plant protection symbioses it is usually assumed that ants: (1) deter herbivores, leading to (2) reduced amounts of herbivore damage, which

further (3) leads to increased plant performance (Bentley 1977). However, at all three levels alternative outcomes may be possible.

(1) Ants remove herbivorous arthropods from their host plant, yet the removal of animals from other parts of the arthropod community may also be important to the plant. For example, do ants have an asymmetric effect on the herbivore guild compared to the predator guild? If ants deter herbivores more efficiently than they deter other predators, the protection system will be more efficient. More predators left on the plant increases the potential for further herbivore reduction. On the other

hand, if ants remove predators (Del-Claro and Oliveira 2000) preferentially this change is likely to be followed by an increase in herbivore numbers and the result can be harmful to the plant. Thus, the presence of ants can lead either to fewer or to more herbivores.

(2) Next, it is important to consider if the community level in the system is functionally linked to the amount of herbivory experienced by the plants? Will an effect on the community level lead to a significant difference in the amount of herbivore damage experienced by a plant, or alternatively, do we find changes in herbivory without changes in herbivore numbers? For example, ants may protect against herbivory without affecting herbivore numbers if they only disturb herbivore feeding without actually removing the herbivores themselves (Rudgers et al. 2003).

(3) Finally, the last level concerns the link between herbivore damage and plant performance. There may not be a negative correlation between herbivory and plant performance. It has been shown that plants experiencing moderate amounts of herbivory may undercompensate (attacked plants perform less well), compensate (attacked and unattacked plants perform equally), or even overcompensate (attacked plants perform better) from the loss of tissue (Whitham et al. 1991, Huhta et al. 2003). This in turn may result in an advantage, no advantage or even a disadvantage to plants protected against herbivory by ants. In summary, each level of the ant–plant interaction can generate alternative outcomes and a given effect at one level may lead to one out of several effects at the next. Consequently, all three levels need to be considered to fully understand how these ant–plant systems works.

The objectives of this study was: (1) provide information on all three levels in an ant–plant protection system involving the Asian weaver ant (*Oecophylla smaragdina* Fabricius) and its mangrove host tree *Rhizophora mucronata* Lam., and to investigate the effect of ants on the arthropod community, the amount of herbivory and the growth performance of their host plants, and (2) thereby assess which of the alternative theoretical routes between the different levels in the system are actually operating in practice.

Material and methods

The study was conducted within the Ranong Biosphere Reserve in southern Thailand in mangrove forest along the Ngao Estuary (9°50'N and 98°35'E). A detailed description of the area and the climate is given by Macintosh et al. (2002). Two sites were selected where it was possible to find gaps within established stands of *Rhizophora* trees. Within these gaps, plots close to established trees with high *O. smaragdina* (hereafter called ants) densities were selected at random. In each

plot, two young *R. mucronata* trees were planted, spaced approximately 1.5 m apart. One tree was randomly assigned as a treatment tree and one as a control. The treatment trees were connected with a nylon string ($\varnothing = 5$ mm) to an existing *Rhizophora* tree with ants, whereas the control trees were left without any aerial connections to other trees. The sites were cleared of weeds and other objects every second week to avoid unintended connections between trees. Eight and 13 tree pairs were planted at sites 1 and 2, respectively. Site 1 was a small island characterised by sandy sediment and low elevation (approx. 1.4 m below spring high tide). Site 2 was located at the foot of a hill and was part of continuous mangrove extending into the mainland. The sediment was muddy and at a higher elevation (approx. 0.3 m below spring high tide) than site 1. Experimental trees were taken from a nursery and were approximately 9 months old (tree height = 131 ± 12.6 cm, mean \pm SD, $n = 42$) at the time of planting. The trees were planted and their sizes measured in February 2002 (t_0). Hereafter they were surveyed two times with six months in between ($t_1 =$ August 2002 and $t_2 =$ February 2003). Four groups of response variables were studied: arthropod communities, herbivory, tree growth and leaf turnover.

Arthropod (insects and spiders) communities

The number of different insects and spiders on individual trees was counted between 09.00 and 12.30 on sunny days by visual inspection of all parts of the tree. In order not to disturb the system, arthropods inside ant leaf nests were not recorded. A few specimens of each species were collected for identification. All trees within a site were inspected on the same day; ant trees and control trees alternately. Night surveys of the arthropod fauna revealed no new species compared to daytime surveys and are not reported on here.

Herbivory

Four different kinds of herbivore damage could be distinguished on the trees. (1) Chrysomelid (Coleoptera) damage consisted of small holes in the leaves made by *Rhyparida wallacei* (Offenberg et al. 2004a, 2004b). The number of holes per leaf on each tree was counted. (2) Tortricid larvae (Lepidoptera) damage was characterised by patch grazing and webbing made by larvae on developing unexpanded leaves. It was not possible to estimate the area of this kind of damage because the larvae were feeding on the still folded opposite leaves. Therefore, the number of attacked shoots on each tree was counted. (3) Geometrid (Lepidoptera) damage was characterised by edge grazing by larvae on mature leaves. The number of leaves eaten was estimated by assigning damaged leaves to one of the following categories: 0–25,

25–50, 50–75 or 75–100% of the leaf eaten. This method was used because it was impossible to measure the area of the damage directly when most of the leaf was missing. (4) Sesarmid crab (Grapsidae) damage consisted of irregular holes torn in the leaves by tree-climbing sesarmids (Offenberg et al. 2004a). The leaf area eaten by these crabs was measured directly in situ using a stereological method described by Gundersen et al. (1988). The area of individual leaves (and their damage) was estimated by counting the number of crosses within the leaf margin when a grid with a known density was placed randomly above it. A grid density of 1.25 crosses cm^{-2} was used.

Tree growth and leaf turnover

Stem diameter (measured 3 cm above the tip of the propagule), tree height (the distance between the sediment and the top of the highest shoot) and total leaf area were measured on each tree. The total leaf area was found by measuring the area of individual leaves nondestructively with the same method that was used to measure crab damage. At each survey a tag was placed beneath the youngest leaf pair on each shoot and the number of leaves below the tag was noted. This allowed us to distinguish between old and new leaves (those produced since the previous survey) and to count the number of leaves lost and produced between surveys.

Data analysis

The arthropod data (excluding *O. smaragdina*) were split into three response variables: total number of arthropods, number of herbivores and number of predators. Table 1 shows the distribution of taxa within the feeding

Table 1. Arthropods observed on trees. The table shows the number of species and distribution of taxa within feeding groups. The table includes both the species identified directly from the community survey and the species causing the feeding marks registered in the herbivory survey.

Feeding group	Taxon	No. of species
Community survey		
Herbivores	Homoptera	6
	Lepidoptera	4
	Coleoptera–Chrysomelidae	3
Predators	Araneae	9
	Heteroptera–Reduviidae	1
	Hymenoptera–Formicidae	3
Algivores	Orthoptera–Gryllidae	1
Unknown	Diptera (imago)	2
Herbivory survey		
Herbivores	<i>Rhyparida wallacei</i> (Chrysomelidae)	1
	Tortricidae	1
	Geometridae	1
	<i>Episesarma versicolor</i> (Grapsidae)	1

groups. For each group the number of individuals per leaf on each tree was calculated at each survey. From the four different types of herbivory data, we calculated for each tree: the mean number of holes made by chrysomelid beetles per cm^2 leaf, the percentage of shoots attacked by tortricid larvae, the percentage of leaves consumed by edge grazing geometrid larvae and the percentage of the leaf area eaten by sesarmid crabs. The damage caused by tortricids was only calculated at t_1 (no new damage at t_2). The number of leaves consumed by geometrid edge-grazing was estimated by multiplying the number of leaves within each damage category by the median of the category and summing the four categories (number of leaves eaten = $\sum_i(m_i \times n_i)$, where i represents the four damage categories, m is the median of the category (0.125, 0.375, 0.625 and 0.875) and n is the number of leaves in the category). The percentage of crab damage was found by dividing the total leaf area of the tree by the area damaged by crabs. Geometrid and crab data were only analysed for site 2 and t_2 since this was the only site and time we observed this damage. By using the size measurements from the trees three different growth rates were calculated. For each tree and time interval ($t_0 - t_1$ and $t_1 - t_2$) the percent increase in stem diameter, tree height and total leaf area was calculated. Leaf turnover was calculated as the number of leaves that were produced and lost during the same time interval. This number was calculated for each tree and for each of the time intervals $t_0 - t_1$ and $t_1 - t_2$. The number of trees with a leaf turnover >0 were found within each treatment group.

Response variables that were detected on both sites and at both surveys (all arthropod response variables, chrysomelid damage and all growth response variables) were analysed with a repeated-measure MANOVA for the effect of treatment and site. The two surveys were used as repeated measures. These response variables were ln-transformed ($\ln [x + 1]$) to obtain variance homogeneity. However, leaf turnover could not be transformed to show variance homogeneity. Therefore, we tested if the probability of losing at least one new leaf was the same within the two treatment groups. Fisher's exact test (one-tailed) was used to evaluate the significance of this probability at each survey. We did not obtain repeated measures on the damage caused by tortricids, geometrids and sesarmids and we only had data from one of the sites on the two latter response variables. To test for the effect of treatment on these responses we used paired one-tailed tests. Sesarmid damage was ln-transformed ($\ln [x + 1]$) to obtain variance homogeneity and tested with a paired t-test. However, it was not possible to transform the data on tortricid and geometrid damage to show variance homogeneity. Therefore, these responses were tested with Wilcoxon's signed rank test. All analyses were done with JMP 3.2.2 (SAS 1995). The p-values obtained from the significance tests were sequentially Bonferroni

corrected (Holm 1979, Rice 1989). Four separate Bonferroni correction analyses were applied; one to each of the four types of response variables (arthropods, herbivory, growth and leaf turnover).

Results

Arthropod community

On experimental ant trees on average $0.8 (\pm 0.39 \text{ se}, n=20)$ ants per tree were registered at t_1 . This number increased to $24.4 (\pm 13.95 \text{ se}, n=20)$ ants per tree at t_2 . In addition, the ants started to build leaf nests on the ant trees at site 2 in late January 2003, with an average of $0.3 (\pm 0.16 \text{ se}, n=20)$ nests per tree at t_2 . Most ants were found at site 2. At site 1, only a few ants were observed sporadically on the ant trees and none during the regular surveys. In general, there was a decline in the ant density on the source trees at this site during all 12 months. The only ant species observed on the ant trees was *O. smaragdina* and these ants were never observed on the control trees. Thus, *O. smaragdina* successfully colonised the ant trees but not the controls.

Both the total number of arthropods and the number of herbivores per leaf were significantly lower on ant trees compared to the controls, however, there was no significant difference in predator numbers between the groups (Fig. 1, Table 2). Also, there was no significant difference in arthropod numbers between the two surveys (Table 2). Considering the average of the two surveys there were 67% more arthropods per leaf (mean \pm se: control = 0.078 ± 0.009 , $n=21$; ant treatment = 0.047 ± 0.008 , $n=20$) and almost twice as many herbivores per leaf (mean \pm se: control = 0.047 ± 0.008 , $n=21$; ant treatment = 0.024 ± 0.004 , $n=20$) on the controls versus ant trees. In contrast there was only

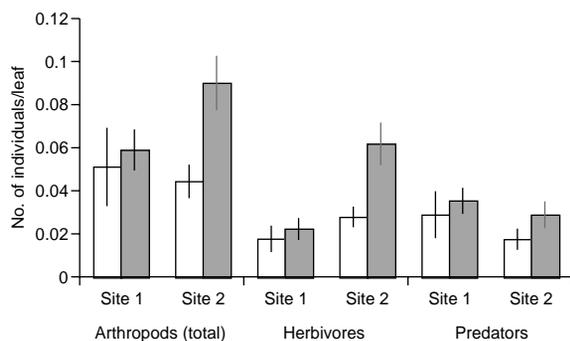


Fig. 1. The number of arthropods on treatment (open bars) and control trees (grey bars) at two sites. The numbers are shown individually for the total number of arthropods, herbivores and predators. Each bar shows the tree mean no. of individuals per leaf averaged between the two surveys (t_1 = August 2002 and t_2 = February 2003); error bars denote $\pm 1 \text{ se}$. At site 1 $N=7$ and 8 in the ant treatment and control groups, respectively; at site 2 $N=13$ in both groups.

46% more predators per leaf (mean \pm se: control = 0.031 ± 0.004 , $n=21$; ant treatment = 0.021 ± 0.005 , $n=20$) on the control trees. Thus, ants reduced the overall number of arthropods on the trees, but the effect was more pronounced on the herbivore guild than on the predators.

Herbivory

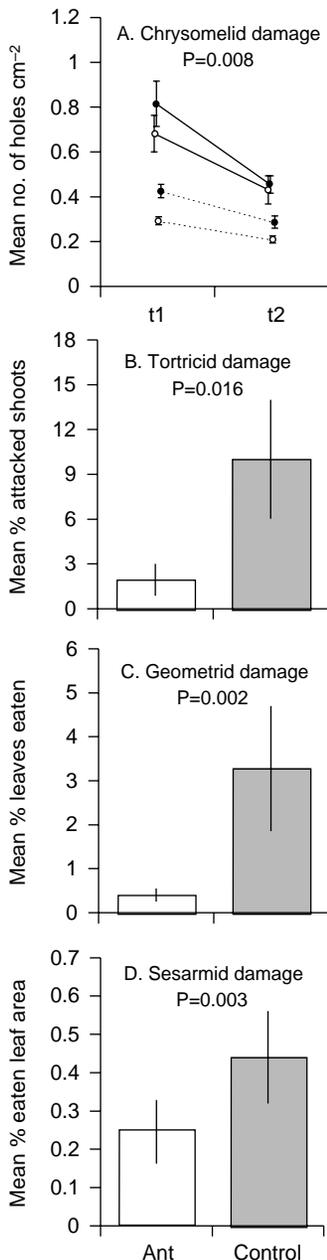
Most chrysomelid damage was observed at site 1 ($P < 0.0001$) and at t_1 ($P < 0.0001$). Overall, there was 29% more ($P = 0.008$) holes cm^{-2} leaf on control trees compared to the ant trees (Fig. 2a, Table 3). Shoots damaged by tortricid larvae were only observed at t_1 . At this time, the proportion of attacked shoots was significantly different ($P = 0.016$) between treatments when data from the two sites were pooled (Table 3). Above five times more attacks were found on control trees compared to the trees with ants (Fig. 2b). Geometrid edge grazing and crab damage were only observed on site 2 and only on the last survey. Again, significantly more damage caused by these two herbivore groups was found on control trees compared to the ant trees ($P = 0.002$ and $P = 0.003$ for geometrid and crab damage, respectively, Table 3). Edge grazing showed a more than eight-fold increase between ant and control trees and there was 76% more crab damage on control trees compared to ant trees (Fig. 2c, d). Thus, ants significantly reduced the amount of damage caused by all four groups of herbivores.

Tree growth

Overall, the mean % diameter increase was higher on control trees compared to the ant trees (mean \pm se: ant trees = 21 ± 2 , $n=20$; control trees = 23 ± 4 , $n=21$) and higher at site 2 compared to site 1 (mean \pm se: site 1 = 17 ± 3 , $n=15$; site 2 = 24 ± 3 , $n=26$, Fig. 3a). Also overall mean % height increase was highest on the control trees compared to the ant trees (mean \pm se: ant trees = 8.2 ± 1.8 , $n=20$; control trees = 13.4 ± 2.1 , $n=21$) and with the largest increase at site 2 (mean \pm se: site 1 = 8.2 ± 2.7 , $n=15$; site 2 = 12.4 ± 1.6 , $n=26$, Fig. 3b). However, the variation observed in % diameter (whole model: $P = 0.31$) and height (whole model: $P = 0.11$) increases could not be explained by the treatment and site effects (Table 4). The mean % increase in leaf area, however, was significantly different between sites ($P = 0.0002$) and surveys ($P < 0.0001$) and there was an almost significant treatment effect ($P = 0.062$, Table 4). Overall, the mean % leaf area increase on site 2 was more than two-fold higher than the increase on site 1 (mean \pm se: site 1 = 143 ± 46 , $n=15$; site 2 = 312 ± 35 , $n=26$) and there was a 1.5-fold increase between ant treatment and control groups (mean \pm se: ant trees = 198 ± 41 , $n=20$;

Table 2. Repeated-measures MANOVA of the effects of ant treatment and site on the ln transformed ($\ln(x+1)$) number of arthropods per leaf. Data from two surveys (t_1 = August 2002 and t_2 = February 2003) were used as repeated measures.

Source	df	Arthropods (total) leaf ⁻¹		Herbivores leaf ⁻¹		Predators leaf ⁻¹	
		Exact F	P	Exact F	P	Exact F	P
Whole model	3	3.65	0.0212	7.66	0.0004	1.3	0.2889
Ant treatment	1	5.03	0.0311	6.11	0.0182	1.69	0.2017
Site	1	1.04	0.3148	10.14	0.0029	1.58	0.2173
Ant treatment × site	1	2.34	0.1342	3.41	0.0729	0.13	0.7179
Time	1	0.67	0.4174	0.28	0.5988	2.11	0.1547



control trees = 301 ± 40 , $n = 21$, Fig. 3c). Thus, all three growth responses showed higher, though marginally insignificant, growth rates on the control trees compared to the trees with ants.

Leaf turnover

The number trees that lost at least one new leaf was highest in the first of the two time intervals ($t_0 - t_1 = 19$ trees, $t_1 - t_2 = 11$ trees). In this interval significantly more trees that lost at least one new leaf belonged to the control group compared to the ant treatment group ($P = 0.018$). Sixty-eight % (13 out of 19 trees) of these trees belonged to the control group and only 32% (6 out of 19 trees) belonged to the ant treatment group. However, between the next two surveys there was no significant difference ($P = 0.76$) between treatment groups. At this time 44% (5 out of 11) of these trees belonged to the control group and 55% (6 out of 11) belonged to the treatment group.

Discussion

The experimental design successfully enabled ants to colonise newly planted small trees by physically linking these trees to natural trees within ant territories. In addition, ants were unable to colonise the control trees

Fig. 2. The amount of damage caused by herbivores on ant treatment and control trees. Four different kinds of herbivory (holes in the leaves made by chrysomelid beetles, shoots attacked by tortricid larvae, edge-grazing by geometrid larvae and holes made by sesamid crabs) were observed. Damage from chrysomelids was present at both surveys (t_1 = August 2002 and t_2 = February 2003) at site 1 and 2. Shoot damage by Tortricidae was only found at the first survey but at both sites and edge-grazing and crab-grazing were only present on site 2 at t_2 . (A) Each symbol shows the tree mean no. of holes per cm^2 leaf area on ant (open symbols) and control trees (solid symbols) at site 1 (solid lines) and 2 (broken lines) at t_1 and t_2 . At site 1 $N_{\text{treatment}} = 7$ and $N_{\text{control}} = 8$; at site 2 $N = 13$ in both groups. (B) Each bar shows the tree mean % attacked shoots. The average for both sites is shown. $N_{\text{treatment}} = 20$ and $N_{\text{control}} = 21$. (C) Bars show tree mean % leaves eaten. $N = 13$ in both groups. (D) Each bar shows the tree mean % leaf area removed. $N = 13$ in both groups. Error bars denote ± 1 se.

Table 3. Analyses of the effect of ant treatment on the amount of damage caused by herbivores. Repeated-measures MANOVA analyses the ln-transformed ($\ln [x + 1]$) tree mean no. of holes cm^{-2} leaf area caused by chrysomelid beetles. Damage was found on both site 1 and 2. Two surveys (t_1 = August 2002; t_2 = February 2003) were used as repeated measures. Nonparametric paired test: Wilcoxon signed rank test was applied to the % of shoots attacked by Tortricid larvae (observed only at t_1). The data from site 1 and 2 were pooled in this analysis. Wilcoxon signed rank test was also used to analyse % leaf area eaten by Geometrid larvae. The paired t-test was applied to the ln-transformed ($\ln [x + 1]$) % leaf area eaten by sesarmid crabs. Geometrid and sesarmid damage was only observed at site 2 at t_2 .

Chrysomelid damage (repeated-measures MANOVA):			
Source	df	Exact F	P
Whole model	3	29.59	<0.0001
Ant treatment	1	7.85	0.0080
Site	1	77.07	<0.0001
Ant treatment \times site	1	0.54	0.4654
Time	1	57.73	<0.0001
Tortricid damage (nonparametric paired test):			
Source	N	Wilcoxon signed rank	P
Ant treatment	19 pairs	-13.0	0.016
Geometrid damage (nonparametric paired test):			
Source	N	Wilcoxon signed rank	P
Ant treatment	13 pairs	-34.0	0.002
Sesarmid damage (paired t-test):			
Source	df	t-Ratio	P
Ant treatment	12	-3.34	0.0029

because of their innate reluctance to cross the mangrove sediment. No *Oecophylla* ants were ever seen crossing the sediment in the study site (Davidson et al. 1988, Ozaki et al. 2000).

Lower numbers of arthropods (excluding *O. smaragdina*) were found on ant trees compared to the control trees (Fig. 1, Table 2). On the contrary, the only arthropod species that was more numerous on ant trees compared to control trees was *O. smaragdina*. This ant is known to prey on and deter a variety of other arthropods (Way and Khoo 1992). Thus, the only likely cause to explain the smaller number of other arthropods on the ant trees was the foraging and patrolling by *Oecophylla* worker ants. This is further supported by the higher percent wise reduction in arthropod (total) and herbivore numbers by ants at site 2 where ants were more numerous than on site 1 (Fig. 1); the ant treatment/site interactions, though, was marginally insignificant (Table 2). After splitting the total number of arthropods up into herbivores (excluding ant-attended coccids in leaf nests) and predators it became evident that ants had a more detrimental effect on the herbivore guild compared to the predator guild (Fig. 1, Table 2). Most of the predatory arthropods were spiders living in webs. These spiders may be protected against ants due to their webs, which may explain the lower and insignificant reduction in predators. The asymmetric effect of ants on the two guilds provide valuable insight into the rarely studied mechanisms underlying ant-plant protections (Rudgers et al. 2003) and is of general interest to the studies of ant-plant protection systems since random predation by ants will be of less benefit to the host plant compared to a herbivore biased predation pressure (Beattie 1985, Way and Khoo 1992).

The reduction in herbivore numbers translated into less leaf damage on the ant trees. All the four major

types of leaf damage were reduced significantly by the presence of ants (Fig. 2, Table 3). As in terrestrial systems, *O. smaragdina* seems to be an efficient plant protector able to protect its host trees against a wide range of natural enemies. In this case ants not only protected against three different types of insect herbivory but also against feeding by sesarmid crabs. This pattern is supported by a previous study on mature *R. mucronata* trees (Offenberg et al. 2004a). The study found approximately four times less leaf damage caused by the chrysomelid beetle *R. wallacei* and sesarmid crabs on *O. smaragdina* trees, compared to trees without weaver ants.

In the present study the reduction in herbivore numbers suggests that the ant protection, at least partly, results from a direct deterrence effect. Yet, this study did not examine indirect effects, e.g. a disturbance effect (Rudgers et al. 2003), which could potentially be operating in the system as well. On the other hand, the protection against crab feeding was probably based on an indirect effect since crabs prefer to attack leaves with small holes (J. Offenberg, unpubl.). Thus, if ants remove the beetles that cause small holes in the leaves, then they can indirectly reduce the amount of crab herbivory on their host trees.

During the first time interval, leaf turnover on control trees was higher than on ant trees. However, during the next interval there was no significant difference. A possible explanation could be the higher incidence of holes made in the leaves by chrysomelid beetles during the first interval compared to the last (Fig. 2, Table 3). Thus, more damage on control trees, in combination with more damage during the first interval, could generate a significant treatment effect on leaf turnover. The lower damage levels during the next interval may have diluted this effect. This is also supported by the

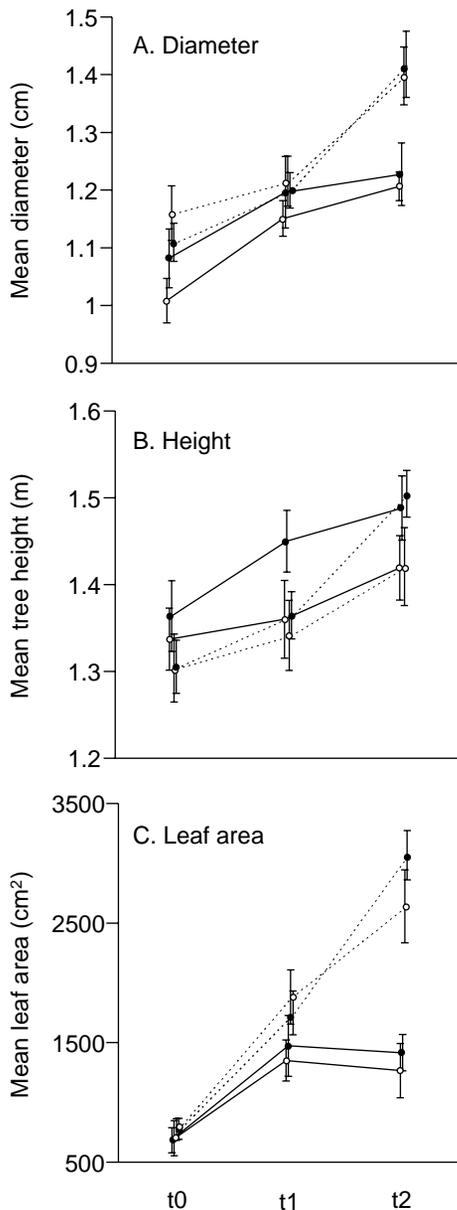


Fig. 3. Mean tree sizes in ant treatment and control groups at site 1 and 2 at three surveys. Mean stem diameter (cm), tree height (m) and total leaf area (cm²) are shown in (A), (B) and (C), respectively. Symbols show tree mean values and error bars denote ± 1 se. Open symbols = ant trees; solid symbols = control trees; solid lines = site 1; hatched lines = site 2; t₀ = February 2002; t₁ = August 2002 and t₂ = February 2003. At site 1 N = 8 in both treatment groups at t₁, however, at t₂, N_{treatment} = 7 (one tree died) and N_{control} = 8. At site 2 N = 13 in both groups on all surveys.

fact that leaf turnover was higher during the first interval when chrysomelid damage was highest. It is therefore likely that the leaf damage caused by chrysomelids increased leaf turnover on the *R. mucronata* trees.

Despite the higher numbers of herbivores, more leaf damage and higher leaf turnover on the control trees, these measures did not translate into lower growth rates (Fig. 3, Table 4). In fact, we observed a nonsignificant (though leaf area increase was only marginally insignificant; $P=0.062$) trend in the opposite direction; i.e. higher growth increases in all growth responses on the control trees. The growth responses were most likely not independent, but the results showed that the increase in one response was not balanced by a decrease in one of the other responses. A reduced performance among ant trees could potentially be caused by honeydew producing ant attended herbivores. However, only the honeydew excreting homopteran *Coccus hesperidum* L. and none of the other herbivores found in this study was ant attended. Since *C. hesperidum* only lives inside the ant nests (J. Offenberg, unpubl.) and since ants did not build nests on the experimental trees until January 2003, less than one month before the end of the study, it is very unlikely that these coccids were responsible for a reduced growth among ant trees. Especially since the trend in tree growth was apparent already after the first survey six months earlier (Fig. 3). Moreover, *R. mucronata* do not produce ant attractants. Ant trees could therefore not have been negatively affected by such investments. The trend, however, may be explained by the grazing optimisation hypothesis (McNaughton 1979, Hilbert et al. 1981, Dyer et al. 1986). This hypothesis argues that moderate amounts of grazing, in some cases, may leave plant production unaffected (full compensation) or even increase plant production (overcompensation). Thus, the equal performance shown by the ant-trees and the control trees in the present study may be based on a compensation effect of a magnitude lying somewhere between a full compensation and overcompensation. Several mechanisms underlying compensation phenomenon have been proposed (reviewed by Stowe et al. 2000). In the present case the breakdown of apical dominance due to shoot damage (Huhta et al. 2003) could be a possible mechanism. On control trees, 10 percent of the meristems were damaged by tortricid larvae but only 2 percent were damaged on ant trees. The higher percentage of damaged shoots on control trees may activate dormant buds and lead to more branching and better plant performance as it has been described for other plant species (Huhta et al. 2000a, 2000b, Huhta et al. 2003). The fitness effect of bud activation, though, may be hard to predict. In a longer time perspective trees with activated buds may be out-competed by other trees with stronger apical dominance, especially under conditions with intense competition for light. The complex interplay between ant protection and compensation effects is therefore likely to vary in time and to be conditional (e.g. light competition) making long term interaction outcomes hard to predict.

Table 4. Repeated-measures MANOVA analysing the effects of ant treatment and site on tree growth. The ln-transformed % increase in stem diameter, tree height and total leaf area were analysed separately. Increases were calculated for two intervals ($t_0 - t_1$ and $t_1 - t_2$) and the intervals treated as repeated measures (t_0 = February 2002; t_1 = August 2002; t_2 = February 2003).

Source	df	Diameter increase		Height increase		Leaf area increase	
		Exact F	P	Exact F	P	Exact F	P
Whole model	3	1.25	0.3077	2.18	0.1063	6.97	0.0008
Ant treatment	1	0.04	0.8421	2.93	0.0954	3.72	0.0615
Site	1	2.12	0.1545	2.56	0.1182	17.77	0.0002
Ant treatment \times site	1	1.65	0.2068	0.34	0.5642	0.15	0.7055
Time	1	0.57	0.4561	1.40	0.2439	63.58	<0.0001

Site 2 was characterized by a higher elevation and a direct connection to the mainland compared to the island site (site 1) with a low elevation and more frequent flooding by the tide. Probably because of the proximity to the mainland and a drier habitat, more and also less specialized arthropods were able to survive at site 2. Also, the less frequent inundation by seawater and a more muddy substrate seemed to optimize plant conditions at this site which were lushier than site 1. These differences were reflected by significantly more herbivores and a higher leaf area increase at site 2. Despite the fewer herbivores at site 1, there was more chrysomelid damage caused by *R. wallacei* at this site. This beetle is specialized on mangrove host trees, and thus adapted to a flooded habitat (Macintosh et al. 1991, Ng and Sivasothi 1999) which may explain the high damage levels at site 1.

Ant-plant protection systems do not always follow the most obvious pathway between lower and higher levels in the system. As is generally assumed, ants in this study reduced herbivore numbers, which led to decreased amounts of herbivory. However, the link between herbivory and plant performance followed a less obvious pathway. Protected trees did not perform better than unprotected trees. On the contrary the trend was in the opposite direction. These results are to our knowledge the first to illustrate a possible neutralization of ant protection due to a plant compensation effect. Yet, other studies have illustrated reduced effects of ant protection. A study by Oliveira (1997) revealed a similar complexity whereby ants reduced herbivore numbers on a Brazilian shrub (Caryocaraceae) which led to increased numbers of initial fruits. However, higher abortion rates of initial fruits by ant protected plants (probably caused by plant resource limitations) resulted in equal numbers of final fruits and seed set between ant and non-ant plants. These results emphasize the need to consider simultaneously all the levels within ant-plant systems to fully cover the functional basis and the continuum of possible interaction outcomes between partners.

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