Observations on the Ecology of Weaver Ants (*Oecophylla smaragdina* Fabricius) in a Thai Mangrove Ecosystem and Their Effect on Herbivory of *Rhizophora mucronata* Lam.

Observations on the Ecology of Weaver Ants (*Oecophylla smaragdina* Fabricius) in a Thai Mangrove Ecosystem and Their Effect on Herbivory of *Rhizophora mucronata* Lam.[1]

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ABSTRACT

Ants of the genus *Oecophylla* are predators of other insects and are able to protect a variety of terrestrial plants against pest insects; however, observations on the ecology of these ants in mangrove forests are lacking. General observations on the ecology of *Oecophylla smaragdina* were carried out in a Thai mangrove forest to determine if these ants can protect their host plants in less favorable mangrove habitats. Leaf herbivory and the density of *O. smaragdina* ants were measured on *Rhizophora mucronata* trees at two sites. The results showed a negative correlation between ant density and herbivory. At both sites, the mean percent damaged leaf area was more than four times higher on trees without ants compared to "ant-trees." A significant negative correlation was found between tree mean percent leaf damage and the density of ants on the tree. Furthermore, on trees with ants, there was less herbivory on leaves close to ant nests compared to other leaves on the tree. Most damage was caused by chrysomelid beetles (62%) and sesarmid crabs (25%) and both types of herbivory were significantly reduced on ant-trees.

Key words: ants; ant protection; herbivory; mangrove forest; Oecophylla smaragdina; Rhizophora mucronata; *Thailand.*

IN MANY ANT–PLANT INTERACTIONS, ANTS PROTECT THEIR PLANT PARTNERS against natural enemies. Since ants prey on insects, they have the potential to reduce the number of herbivorous insects on the plants where they forage (Beattie 1985). Indeed, the effectiveness of ants as plant protectors has been shown in numerous studies (Inouye & Taylor 1979, ODowd 1979, Stephenson 1982, Barton 1986, Smiley 1986, Way & Khoo 1992, Oliveira 1997, Peng *et al.* 1997, Ozaki *et al.* 2000). Increased plant fitness in these protection mutualisms is further illustrated by the evolution of many phylogenetically independent plant structures that facilitate the establishment of ant colonies on indi-

vidual plants, *e.g.,* production of domatia, food bodies and/or extrafloral nectaries (Zimmermann 1932, Beattie 1985, Offenberg 2000).

In ant–plant protective mutualisms, ants serve as biological control agents against a variety of different pest species (Way & Khoo 1992). One of the most effective and widely used tropical ant species in this respect is the weaver ant *Oecophylla smaragdina* Fabricius (Way & Khoo 1992). The potential of this species as a biological control agent has been supported by many crop studies in which the ants were reported as being beneficial predators. Such crops include coconut, oil palm, cocoa, coffee, citrus, eucalyptus, mango, cashew nut, and timber tree (Way & Khoo 1992; Peng *et al.* 1995, 1997). These studies have all been carried out in terrestrial habitats. *Oecophylla smaragdina* is also an abundant predator in mangrove habitats where it

nests on a number of different mangrove species (*e.g., Rhizophora* spp., *Ceriops* spp., *Bruguiera* spp., and *Xylocarpus* spp.; Macnae 1968, Clay & Andersen 1996, Veenakumari *et al.* 1997); however, the ecology of ant–plant interactions in mangroves is poorly understood. Several papers have reported studies of ants in mangroves (Simberloff & Wilson 1969; Cole 1980; Johnstone 1981; Cole 1983a, b; Adams 1994; Clay & Andersen 1996; Nielsen 1997, 2000; Ozaki *et al.* 2000; Cogni & Freitas 2002; Durou *et al.* 2002; Wetterer & O'Hara 2002; Cogni *et al.* 2003; Dejean *et al.* 2003). Only two of these studies (Johnstone 1981, Ozaki *et al.* 2000) have tested if the presence of ants leads to reduced herbivory.

The benefits experienced with *O. smaragdina* in terrestrial crops may also be applicable to mangroves. A test of this hypothesis would be especially important since reestablishment and management of mangroves has been put on top of environmental agendas in the last decade (Field 1996). For example, major replanting programs are being undertaken in Bangladesh (Siddiqi 1996), Thailand (Aksornkoae 1993), and Vietnam (World Bank 1998). The Coastal Wetlands Protection and Development Project in Vietnam involves reestablishment of a 460 km long mangrove zone in the Mekong Delta (World Bank 1998). Moreover, one of the problems encountered in previous replanting programs is insect herbivory on young mangroves in nurseries and newly established mangrove forests (Field 1996, Macintosh 1996, Ozaki *et al.* 1999). In order to reestablish/manage mangroves successfully, we need more information about the biotic interactions in the system. Ant–plant–herbivore interactions may be an important part of these.

Here, we present observations to test if *O. smaragdina* ants have an effect on herbivores reflected on leaf damage of the economically important mangrove species *Rhizophora mucronata* (Lam.).

MATERIALS AND METHODS

STUDY SITES.—Field observations were carried out in the Ranong Biosphere Reserve on the Andaman Sea coast of southern Thailand (09°50′N, 98°35′E), an area containing *ca* 30,000 ha of mangrove forest. Ranong Province has the highest rainfall in Thailand (4000–5000 mm/yr), with 190 days of rainfall per year on average. There are two main seasons characterized by the dry northeast monsoon from November to February and the wet southwest monsoon from May to mid-October. More information about the climate in Ranong

and a detailed description of the mangrove ecosystem are given in Macintosh, Ashton, & Havanon (2002). Two mangrove sites were found in which it was possible to discriminate between *R. mucronata* trees with and without *O. smaragdina* ants.

Site one was a small island in one of the main channels of the mangrove near the Ranong Mangrove Forest Research Centre. The island is flooded at high tide (water level *ca* 1.5–1.8 m above ground at spring high tide) and covers *ca* 5 ha at low tide. Most of the soil on the island is soft mud with few sandy areas. The site is characterized by dense aggregations of vegetation interspersed with isolated plants and gaps. The vegetation on the island is composed of naturally established trees and scrubs dominated by *R. mucronata, R. apiculata* (Blume), *Avicenia* spp., and *Aegiceras corniculatum* (L.). Additionally, there were some *Sonneratia caseolaris* (L.) and limited ground cover provided by *Acanthus ilicifolius* (L.) and *Derris trifoliata* (Lour.).

Site two was situated at the landward edge of the mangrove, *ca* 6 km from the island site. The site was flooded at high tide with the water level *ca* 1–1.3 m above ground at spring high tides. The soil was soft mud with sandy patches. Parts of the site were planted with *R. mucronata* and *R. apiculata* seedlings in 1999. These young trees were between 1.5 and 2.5 m tall and did not touch each other. The mature vegetation was mainly composed of 5 to 15 m tall *R. mucronata* and *R. apiculata* trees, most of them in dense stands; few solitary trees were present. There was also limited ground cover composed of *A. ilicifolius* and *D. trifoliata.*

THE ANT–PLANT SYSTEM.—*Oecophylla smaragdina* is widely distributed in the Ranong Biosphere Reserve and is one of the most abundant ant species. The species uses many different mangroves as host trees (*e.g.,* species of *Rhizophora, Bruguiera, Ceriops*, and *Xylocarpus*). The ecology of the ants in the mangrove is very similar to their habit under terrestrial conditions. The ants utilize their host mangrove plants for nest building by weaving leaves together and they attend several honeydew-producing trophobionts (homopterans and lycaenid larvae) on the plants. Honeydew, together with arthropod prey, constitutes the major part of their diet. The two most pronounced types of leaf damage on *R. mucronata* trees are caused by leaf beetles and sesarmid crabs. Leaf beetle herbivory on *R. mucronata* originate from the common *Rhyparida wallacei* (Macintosh *et al.* 1991, Ng & Sivasothi 1999). These beetles are especially abundant in nurseries where they cause considerable leaf damage

on *Rhizophora* spp. seedlings (Macintosh *et al.* 1991; J. Offenberg, pers. obs.). Leaf damage made by sesarmid crabs on *R. mucronata* is caused by *Episesarma versicolor* Tweedie and *E. mederi* Tweedie (Macintosh, Ashton, & Tansakul 2002). The crabs climb trees and feed on fresh leaves at night (Cannicci *et al.* 1996, Sivasothi 2000). They feed on a variety of mangrove species on which they leave large distinct feeding marks on the leaves (Macintosh *et al.* 1991).

SAMPLING.—Site one was searched randomly until 12 *R. mucronata* trees without *O. smaragdina* ants (hereafter referred to as ants) were found. These trees were paired with *R. mucronata* trees of similar size (±20% of tree height) harboring at least one ant nest. To collect more information about the variation within ant-trees, the site was searched haphazardly until 6 additional trees with ant nests were found. On all ant-trees, the number of ant nests and the number of leaves used per nest were registered and used as measures of ant density. To test the generality of the main results obtained from site one, additional sampling was conducted at a second site. Site two was searched until 6 *R. mucronata* trees with at least one ant nest were found. These trees were then paired with their closest *R. mucronata* tree without ants.

A method was developed to sample shoots randomly. Six shoots from each tree were sampled by selecting six random 10 cm height intervals (within the range of the particular tree), each combined with a random cardinal angle (30° intervals) for each tree. These "slices" of tree crowns contained from zero to four shoots. If no shoots were found, the shoot closest to the slice was chosen for sampling; otherwise, one of the shoots in the slice was selected randomly. From each shoot, one leaf from all opposite leaf pairs was sampled randomly. On the ant-trees at site one, the shoot closest to an ant nest was recorded for each tree.

HERBIVORY MEASUREMENTS.—On each leaf, the number of feeding marks made by herbivores was counted and the leaf area was measured. Since leaf production of *R. mucronata* shows no seasonality in southern Thailand (Wium-Andersen 1981; J. Offenberg, pers. obs.), sampling time was not related to leafing phenology. Different types of herbivory were distinguished from the morphology of the damage. The area of each type of herbivore attack was measured on all leaves sampled at site one. For example, leaf beetles make small circular holes on the leaf lamina, whereas sesarmid crabs

tear off irregular pieces that leave typical scratch marks (Macintosh *et al.* 1991). At site one, leaf beetles (Chrysomelidae) and sesarmid crabs (Grapsidae) caused the majority of leaf damage (87%). The same pattern was evident at site two; therefore, only these types of herbivory were recorded on samples from this site. Furthermore, since there was a high correlation between the area of leaf beetle feeding marks and the number of feeding marks ($r = 0.93$, $N = 682$) recorded at site one, only the number of feeding marks was recorded at the second site. A stereological method was used for all area measurements. By this method, the area of profiles are estimated by counting the number of points hitting the profile when a grid (with a known density) is placed randomly above it (Gundersen *et al.* 1988). Grid densities of 1.25 and 31.25 points/cm^2 were used for measuring leaf areas and damaged areas, respectively.

DATA ANALYSIS.—For all leaves, the percent damage caused by different herbivores was calculated, followed by calculations of means for individual trees. To obtain normally distributed data and variance homogeneity, percent leaf damage was cubic root transformed [(tree mean % damage)$^{1/3}$] and the effect of ant presence on the trees was analyzed individually for each parameter with a one-tailed paired *t*-test (excluding the six additional unpaired ant trees at site one). Crab damage, however, could not be transformed to symmetrical distributions and was therefore analyzed with permutation tests (Resampling 1999). These tests shuffled the data from the two groups of trees and then drew random samples (10,000 in each test) that simulated a treatment and a control group. The number of times the difference between simulated groups was higher than the difference between the observed groups was divided by the total number of samples; this proportion gave the *P*-value. To test the overall effect of ant presence on crab damage at site one and two, the combined probability test proposed by Sokal and Rohlf (1995) was employed on the two separate permutation tests. At site two, the number of leaf beetle marks/cm^2 leaf were calculated for all leaves and tree means were found. The natural logarithm [ln (tree mean no. of feeding marks/cm^2 leaf)] was calculated to obtain variance homogeneity. To allow comparisons between the sites, the percent of leaf area damaged by beetles at site two was calculated from the regression between the area of feeding marks and the number of feeding marks obtained from site one. To test for a correlation between ant density and herbivory, total
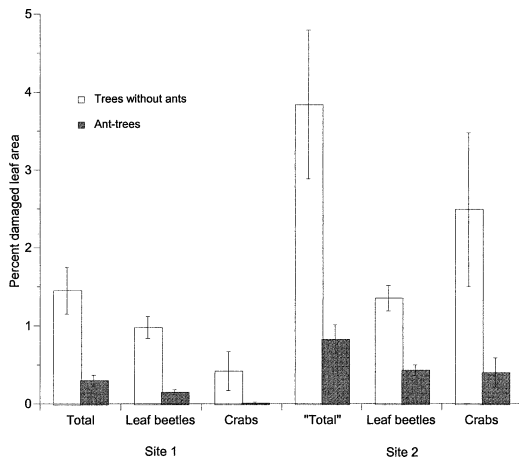
FIGURE 1. Herbivore damage on mangrove trees (*Rhizophora mucronata*) with and without ants. Bars show the mean percent leaf area damaged/removed (±SE) by different categories of herbivores on the two groups of trees at each site. "Total" damage at site two was the sum of leaf beetle and crab damage since these were the only categories recorded at this site. At site one, $N = 12$ trees without ants and $N = 18$ ant–trees. At site two, $N = 6$ for both trees with and without ants.

damage and leaf beetle damage at site one were regressed on ant density measured as the number of leaves used for ant nest construction per tree [ln (no. of nest leaves per tree + 1)]. This method was chosen because the number of leaves used for nest construction is positively correlated with the number of major ant workers (linear regression: ant biomass (g) $= - 0.98 + 0.67 \times$ no. of leaves, $N = 30$, $P < 0.0001$; J. Offenberg, pers. obs.). Furthermore, on all ant-trees at site one, the mean percent total damage and leaf beetle damage were calculated for leaves on the shoot closest to an ant nest and compared with the mean of all other leaves on the tree. The frequency of trees with less damage on leaves close to ant nests was then found and tested against the frequency expected if means had been distributed randomly (Sokal & Rohlf 1995).

RESULTS

SITE ONE.—The overall leaf area damage was 0.76 percent (SD = 0.88, $N = 30$). Despite the low amounts of total herbivory, trees with ants showed significantly ($P < 0.0001$) less damage ($\bar{x} = 0.31\%$, SD = 0.29, $N = 18$) than trees without ants ($\bar{x} = 1.45\%$, SD = 1.04, $N = 12$; Fig. 1 and Table 1). Leaf beetles (62%) and crabs (25%) caused the majority of damage. Overall, they were responsible for 87 percent of the total; however, they only caused 52 percent of the total on ant-trees but caused 97 percent on trees without ants. Leaf beetle damage increased more than six-fold on trees without ants ($\bar{x} = 0.98\%$, SD = 0.49, $N = 12$) compared to ant-trees ($\bar{x} = 0.15\%$, SD = 0.13, $N = 18$). The same comparison revealed a 42-fold increase in crab damage ($\bar{x}_{-ants} = 0.42\%$, SD = 0.85, $N = 12$; $\bar{x}_{+ants} = 0.01\%$, SD = 0.06, $N = 18$), but, with a large variation between trees (Fig. 1 and Table 1). Table 1 shows that leaf beetle damage was significantly different between the two groups ($P < 0.0001$) and the significance level obtained from the permutation test on crab damage was almost significant ($P = 0.052$).

The relationship between leaf damage and ant density is shown in Figure 2. There was a significant negative correlation between ant density and both the total amount of damage [linear regression: (% total damage)$^{1/3} = 1.05 - 0.22 \times$ ln (x + 1); $F_{(1, 28)} = 49.77$, $P < 0.0001$, $R^2 = 0.64$, $N = 30$] and the amount caused by leaf beetles [linear

TABLE 1. *The effect of ant presence on herbivory of* Rhizophora mucronata. *Details about the permutation tests are given in the materials and methods section.*

Paired *t*-tests				
Response variable	Site	df	t-ratio	P
Total damage ($\sqrt[3]{\%damage}$)	1	11	7.27	<0.0001
Leaf beetle damage ($\sqrt[3]{\%damage}$)	1	11	8.49	<0.0001
Leaf beetle damage [ln (scars/cm²)]	2	5	5.98	0.0009

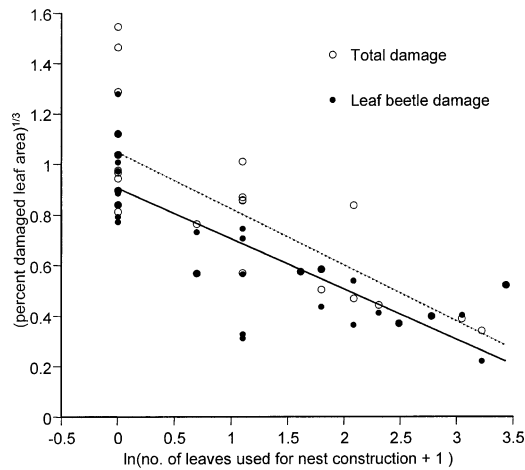| Permutation tests			
Response variable	Site	No. of times simulated difference > observed	P
Crab damage (%)	1	521	0.0521
Crab damage (%)	2	127	0.0127

FIGURE 2.   Linear regressions of total damage and leaf beetle damage on ant density. Data points represent means of individual trees including all trees from site one ($N = 12$ trees without ants, and $N = 18$ ant-trees). Both the regression of total damage ($P < 0.0001$) and leaf beetle damage ($P < 0.0001$) on ant density were significant.

regression: $(\% \text{ leaf beetle damage})^{1/3} = 0.91 - 0.2 \times \ln (x + 1)$; $F_{(1, 28)} = 54.8$, $P < 0.0001$, $R^2 = 0.66$, $N = 30$]. Ant density explained more than 60 percent of the observed variation in herbivory. Excluding trees without ants still revealed a significant negative correlation [linear regression: $(\% \text{ total damage})^{1/3} = 0.92 - 0.16 \times \ln(x + 1)$; $F_{[1, 16]} = 15.07$, $P = 0.0013$, $R^2 = 0.49$, $N = 18$]. Hence, herbivory showed a negative correlation with both ant presence and ant density.

On only 3 out of 18 ant-trees was there more damage on leaves close to ant nests compared to all other leaves sampled on the same tree. This was less than would be expected by a random process (G-test: $G_{\text{adj.}} = 8.4971$, $P = 0.004$, $N = 18$). The same pattern was evident with leaf beetle damage. In only 4 out of 18 trees was there more damage on leaves close to ant nests (G-test: $G_{\text{adj.}} = 5.7249$, $P = 0.0167$, $N = 18$).

COMPARISON OF SITE ONE AND TWO.—At site two, there was 3.3 times more leaf beetle feeding marks per cm^2 leaf on trees without ants ($\bar{x} = 0.5$, SD = 0.15, $N = 6$) compared to ant-trees ($\bar{x} = 0.15$, SD = 0.06, $N = 6$). The percent leaf beetle damage calculated from the relationship between the area and the number of feeding marks at site one showed that there was more leaf beetle damage at site two, both on ant-trees and trees without ants (Fig. 1). Also, there were more crab attacks at site

two and there was a more than six-fold increase in crab damage between ant-trees ($\bar{x} = 0.4\%$, SD = 0.46, $N = 6$) and trees without ants ($\bar{x} = 2.49\%$, SD = 2.43, $N = 6$; Fig. 1). The total (leaf beetle + crab damage) amount of herbivory was 4.6 times higher on trees without ants ($\bar{x} = 3.84\%$, SD = 2.34, $N = 6$) compared to trees with ants ($\bar{x} = 0.83\%$, SD = 0.45, $N = 6$). Both leaf beetle damage ($P = 0.0009$) and crab damage ($P = 0.013$) were significantly different between the two groups of trees (Table 1).

Combining tests of the effect of ant presence on crab damage at sites 1 and 2 showed that the combined effect was significant [$-2 \Sigma \ln (P) = 14.64$, df = 4, $P = 0.006$; Sokal & Rohlf 1995]. Thus, the effect was marginally insignificant at site one, but the result from the second site supported the trend seen at the first site.

DISCUSSION

At both sites, we found approximately four times more herbivory on trees without ants compared to trees with ants, and at site one, there was a negative correlation between herbivory and ant density both between and within ant-trees. This pattern and the fact that *O. smaragdina* has been observed to be an efficient biological control agent in terrestrial environments (Way & Khoo 1992) suggest that the ants are the direct cause of reduced herbivory. Moreover, we also observed ants attacking *R. wallacei* both in the field and in the laboratory (J. Offenberg, pers. obs.). Although the correlation could have been caused by other factors associated with ant presence, *e.g.,* the spatial distribution of the trees, this seems unlikely because the correlation also applied within trees and ant-trees were paired with their nearest neighbor tree without ants (max. distance between paired trees was 8.9 m).

Both leaf beetles and crabs caused significantly less damage on ant-trees compared to trees without ants. This suggests that the ants protected the trees from overall herbivory and that this effect was mainly due to protection against beetles and crabs. *Rhyparida wallacei* was not only deterred from the trees by the ants but was also taken as prey. It seems unlikely, however, that the ants were able to deter or prey directly on crabs since they are well defended by their hard shells. The lower levels of crab damage on ant-trees, however, can be explained by an indirect protection. Protection against leaf beetles may indirectly protect the leaves against crab attacks if crabs prefer to feed on leaves with holes made by leaf beetles. Macintosh *et al.* (1991), re-

ferring to *E. versicolor* feeding on *R. apiculata*, suggested that crabs may prefer to enlarge already existing holes in the leaves. In this scenario, crabs would select trees without ants because their leaves have more holes made by other herbivores. Thus, the reduced crab damage on trees colonized by ants may be mediated through the interaction between ants and leaf beetles.

The results of this study contrast with the findings of Johnstone (1981). In his survey of leaf damage on 23 different mangroves in Papua New Guinea, he did not find a significant correlation between the density of *O. smaragdina* and the amount of leaf damage; however, there was an increase in mean percent leaf tissue eaten with decreasing ant density. The lack of significance may have been due to the pooling of many different mangroves. If the ants are only able to protect some species, then the pooling of protected and unprotected plants may mask the effect of ants. In fact, since ant-attended lepidopteran larvae attack some mangroves, the opposite correlation could be expected in some cases. Ozaki *et al.* (2000) on the other hand found that two mangrove ant species efficiently protected *R. mucronata* seedlings against the scale insect *Aulacaspis marina* Takagi and Williams, and it has been shown that mangrove ants remove termite baits from their host plants (Cogni & Freitas 2002, Cogni *et al.* 2003). Summarizing these findings and those of the present study suggests that ants play an important role as plant protectors in mangroves.

The overall amount of herbivory at site one was 0.76 percent, which is low compared to the few other studies on mangrove herbivory. The total leaf area damaged by herbivores for a variety of different mangroves species range between 0.24 and 36.1 percent (Johnstone 1981, Lacerda *et al.* 1986, Robertson & Duke 1987, Farnsworth & Ellison 1991, Lee 1991, Feller 2002), excluding rare cases of severe defoliation (Whitten & Damanik 1986, Anderson & Lee 1995). Within this range, *R. mucro-* nata has shown values of 2.6 (Robertson & Duke 1987) and 3.5 percent damage (Johnstone 1981), with other *Rhizopora* spp. ranging between 1.4 and 25.3 percent (Johnstone 1981, Lacerda *et al.* 1986, Robertson & Duke 1987, Farnsworth & Ellison 1991, Feller 2002). At site two, the herbivore pressure was higher than at site one. There was at least 2.4 percent damage (only leaf beetle and crab attacks were recorded), which is close to the result (2.6%) found by Robertson and Duke (1987) in north Queensland, Australia.

In this study, we found a negative relationship between the density of *O. smaragdina* ants and the amount of herbivory on the leaves of *R. mucronata* trees at two different sites in the Ranong mangroves. Considering this finding and the fact that this ant is known to protect their host trees in terrestrial environments (Way & Khoo 1992, Peng *et al.* 1997), we concluded that the ants also protect their host trees in less favorable mangrove habitats. Considering the widespread effort in Southeast Asia to reestablish and manage mangroves, it would be worthwhile to explore if ant protection from herbivorous arthropods translates into increased plant growth and/or survival of young trees. If ants can increase the performance of plantation mangroves, it may be advantageous to optimize ant colonization in newly planted areas and nurseries, *e.g.,* by connecting young trees with lines to assist ant movement between trees.

ACKNOWLEDGMENTS

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