Indirect ant-protection against crab herbivory: damage-induced susceptibility to crab grazing may lead to its reduction on ant-colonized trees

J. OFFENBERG,† D. J. MACINTOSH and M. G. NIELSEN

Institute of Biological Sciences, Ole Worms Allé, Building 135, University of Aarhus, Universitetsparken, 8000 Aarhus C, Denmark

Summary

1. Mangrove trees colonized by weaver ants (*Oecophylla smaragdina*) experience less insect and crab herbivory compared with trees without ants. However, it is unlikely that ants prey on and deter crabs as they do insects. Protection could be indirect if leaves damaged by insects are more susceptible to crab herbivory.

2. In the field and in laboratory tests, leaves with artificial holes simulating leaf beetle-feeding marks were more susceptible than intact leaves to damage by the crab *Episesarma versicolor*.

3. The study further revealed that damaged leaves showed increased susceptibility only to male crab feeding whereas females were indiscriminate, probably because of differences in claw morphology between the sexes.

4. Combined with previous findings at the same field site, these results suggest that ants can indirectly protect trees against crab herbivory by directly removing insect herbivores and thus decreasing the leaf damage they inflict. The system illustrates a complex trophic cascade involving density and trait-mediated indirect interactions.

Introduction

The importance of indirect interactions in biological communities (where one species interacts with a second species via a third; Wootton 2002), such as trophic cascades, has been the focus of an increasing number of ecological studies during the past decade (Wootton 1994; Wootton 2002; Werner & Peacor 2003; Schmitz *et al*. 2004; Preisser *et al*. 2005). In a trophic cascade, predators affect plants indirectly by reducing herbivore density either by consuming herbivores (density-mediated indirect interaction), or by altering herbivore feeding behaviour (trait-mediated indirect interaction). Consequently predator has an indirect positive effect on the plants. Similarly, cascades can exist at higher trophic levels running from top predators to herbivores via penultimate predators (Philpott *et al*. 2004; Schmitz *et al*. 2004). However, indirect interactions may also cascade from a predator via one herbivore to a second herbivore. This may occur if one herbivore induces increased susceptibility (or resistance) to a second herbivore on their common host plant (Haukioja 1990;

Karban & Baldwin 1997; Nykanen & Korechiva 2004), in which case there is a herbivore-mediated, indirect interaction between a predator and a non-prey herbivore. Most examples of induced susceptibility involve herbivores that increase plant susceptibility to members of their own species, and/or induction based on chemical changes in plant tissue that lead to increased susceptibility to herbivore species (Karban & Baldwin 1997; Carrol & Quiring 2003). Few examples have shown interspecific induced susceptibility based on mechanical induction, such as systems where one herbivore makes a plant resource more accessible to a second herbivore (Vesey-Fitzgerald 1960; Bell 1970; Bell 1971; but see Arsenault & Owen-Smith 2002).

It is well known that ants can protect their host plants against a variety of arthropod herbivores (reviewed by Way & Khoo 1992; Agrawal & Rutter 1998; Bronstein 1998). However, only a few studies have examined how protection is actually accomplished, probably because it has been assumed that ants simply prey directly on the herbivores. The few studies addressing the functional basis of ant-plant protection describe mechanisms that are more complex than direct predation. Rudgers, Hodgen & White (2003) show how the presence of ants disturbed the behaviour of lepidopteran

†Author to whom correspondence should be addressed.
E-mail: offenberg@biology.au.dk

larvae, leaving them with less time for feeding and resulting in less herbivory on host plants with ants. Offenberg *et al*. (2004b) show how a chrysomelid beetle avoided feeding on leaves with ant pheromones compared with leaves without pheromones; and Freitas & Oliveira (1996) show that lepidopteran female imagos avoided ovipositing on branches with visual cues of ants (ants made of rubber), presumably in order to reduce ant predation on larvae. In trophic cascades between ants and plants, trait-mediated interactions (TMIs) may increase the benefit of protection by ants (Peacor & Werner 2001; Rudgers *et al*. 2003; Offenberg *et al*. 2004b). Further study on TMIs is desirable: a recent meta-analysis comprising a variety of biological systems surprisingly suggested that TMIs are as strong as, or stronger than, density-mediated interactions, and that the strength of TMIs increases through food chains (Preisser *et al*. 2005).

The mangrove crab *Episesarma versicolor* Tweedie lives in burrows in the sediment, but climbs trees during the night to feed on mangrove leaves (Sivasothi 2000). While clinging to a leaf in the canopy, crabs use one claw to seize a leaf edge; they then tear the leaf edge with the serrated dactyls of the claw until a small part of the leaf is detached for consumption, leaving a conspicuous frayed feeding mark. It has been suggested that damaged leaves may be more susceptible to feeding by *E. versicolor* because the crabs prefer to enlarge existing holes made by other herbivores, instead of starting new holes in the leaves (Macintosh *et al*. 1991; Offenberg *et al*. 2004a). The larger claws of male crabs may make them less agile in the canopy, so that pre-existing damage may be more important to them. This leads to the hypothesis that trees with a high density of leaf damage should be more susceptible to subsequent crab damage, particularly by male crabs. Thus trees attended by ants may be indirectly protected against crab grazing as long as the ants are able to reduce the number of herbivores and the leaf damage they inflict. *Rhizophora mucronata* Lam. trees in a Thai mangrove, colonized by the ant *Oecophylla smaragdina* Fabricius, hosted fewer herbivorous insects (Offenberg *et al*. 2005) and showed four times less leaf damage caused by a chrysomelid beetle (Offenberg *et al*. 2004a) that patch-grazes the young expanding leaves, leaving the mature leaves with small (diameter 2–5 mm), circular holes (Macintosh *et al*. 1991; Ng & Sivasothi 1999). Perhaps as a result, the ant-colonized trees also showed reduced crab grazing, but this mechanism was not tested experimentally.

The objective of this study was to test the hypothesis that reduced amounts of crab herbivory on ant-colonized *Rhizophora* trees can result from an indirect interaction between ants and crabs, mediated via leaf beetles. We hypothesized that chrysomelid feeding makes leaves more susceptible to crab grazing by providing existing holes that crabs can enlarge. If beetle feeding indeed mechanically facilitates crab damage, we predict that the increased susceptibility would occur only for suspended leaves, but not for leaves on

the sediment surface where crabs can graze easily. We tested for differences between crab sexes, as male crabs have larger claws than females and therefore may be more constrained when feeding in the canopy.

Materials and methods

The study was conducted within the Ranong Biosphere Reserve in southern Thailand during November–December 2002. Laboratory studies were conducted at the Ranong Mangrove Forest Research Centre, and field studies in the surrounding mangrove forest. A detailed description of the area and the climate is given by Macintosh, Ashton & Havanon (2002).

LABORATORY STUDY

To test the feeding preferences of individual crabs, 23 adult crabs (*E. versicolor*) were caught in the field and their size (carapace width) and sex were recorded. Feeding preferences were then tested in a laboratory experiment where crabs were kept in separate plastic buckets (20 l) covered with a cylinder made of metal mesh net (height above bucket = 50 cm; diameter = 40 cm; mesh size 15 mm) and filled with 15 l mangrove mud collected in the field. The mesh net prevented the crabs from escaping, but allowed them to climb and feed above the sediment. Each day, mangrove water was added to the buckets until the upper level was between the lowest and the highest levels of the sediment. An ambient temperature and light regime was maintained throughout these tests. In choice-preference tests, all crabs were checked for four different types of preference using *R. mucronata* leaves as the only food source: (i) leaf-age preference; (ii) feeding-site preference (suspended *vs* on substrate surface); (iii) preference for leaves with or without holes offered on the sediment surface; and (iv) preference for leaves with or without holes offered on a 'twig' above the sediment. All crabs were tested in the same order.

In the test for leaf-age preference, each crab was offered three leaves taken from a single stem on an *R. mucronata* tree: one newly emerged leaf sampled from the apical leaf position of a shoot (= young leaf); one leaf sampled from an intermediate position with a green leaf (= mature leaf); and one leaf sampled from the lowest position with a yellow leaf (= senescent leaf). As crabs in this initial test strongly preferred mature green leaves (see Results), only mature green leaves were offered in the remaining tests. The two leaves offered to individual crabs in each test were leaves from opposite leaf pairs, and were without any kind of damage. In the test for feeding-site preference, one leaf (randomly selected) was offered on the sediment and the other was placed on a stick (diameter = 2·5 mm) above the sediment to simulate an on-tree leaf. In the third and fourth tests, we made 10 evenly distributed artificial holes (diameter = 3·3 mm) on one of the two leaves (randomly selected) to simulate leaf beetle-feeding

© 2005 The Authors
Journal compilation
© 2006 British
Ecological Society,
Functional Ecology,
20, 52–57

marks; the other leaf was left intact (without damage) as a control. Leaf pairs were offered on the sediment and on sticks (diameter = 2·5 mm) above the sediment in tests 3 and 4, respectively. Leaves offered above the sediment were attached to wooden sticks with adhesive tape and the stick was attached to the mesh net 25 cm above the sediment at an angle (≈45° above horizontal) to simulate the natural arrangement of leaves. In each test, leaves were offered in the afternoon and collected the next morning, allowing the crabs to feed overnight. To ensure that sap exudation had ceased from the artificial holes in the treatment leaves, the holes were made several hours before crab feeding began, to exclude the possibility that crabs were attracted to the leaf sap. The area of each individual leaf was measured before and after each test, and the area eaten from each leaf was calculated.

FIELD STUDY

Two field sites characterized by host trees with abundant crab damage on their foliage were selected. The sites were situated at the landward part of the mangrove and were ≈5 km apart. Both sites were dominated by *R. mucronata* and *Rhizophora apiculata* Blume trees. At site 1, most trees were older than 10 years. Site 2 was a newly replanted site with mostly immature trees 1–3 years old. The two sites were searched randomly for opposite mature and undamaged *R. mucronata* leaves until 116 leaf pairs were found on 36 trees. On one of the leaves in each pair, we made 10 holes as described for the laboratory study. The other leaf was left intact as a control. Individual leaf areas were measured on all leaves before the treatment. After 1 day, and again after 21 days, leaf areas were remeasured and the leaf area removed by crabs from individual leaves was calculated. The leaf damage caused by crabs is easily distinguishable from insect herbivory because of the distinctive marks crabs make while feeding. In each leaf pair the preferred leaf was recorded as the leaf with the largest area removed by *E. versicolor*.

STATISTICS

The amount of leaf area eaten from the leaves in the feeding-preference tests was not normally distributed and could not be transformed to obtain variance homogeneity. Therefore a non-parametric approach was applied and the tests were analysed with Wilcoxon's signed rank tests (one-tailed), after the exclusion of non-feeding crabs, to assess if there were significant differences in feeding rate between treatments.

Results

In the feeding tests, mature leaves were much more susceptible to grazing by *E. versicolor* compared with both young and senescent leaves. Seventeen crabs preferred mature leaves; three preferred young leaves; and

three preferred senescent ones. Leaves offered on the sediment were also much more susceptible to the crabs compared with leaves placed on the twig (Wilcoxon signed rank = 93, $n = 19$ crabs, $P < 0.0001$). Nineteen out of the 23 test crabs fed on the offered leaves. Only one crab preferred to feed on the twig above the sediment, whereas 18 preferred to feed on the sediment. The amount of leaf area removed from leaves on the sediment (mean ± SE, 6.65 ± 0.98 cm^2) was >50 times higher than the amount eaten from leaves above the sediment (mean ± SE, 0.12 ± 0.08 cm^2).

Leaves with holes showed increased susceptibility only to male crab feeding, and only when males were feeding above the sediment (Fig. 1). Of the eight females that fed in this test, four preferred leaves with holes, and four preferred control leaves. In contrast, only one of 10 males preferred leaves without holes. Females ate approximately the same amount of leaf material from leaves with and without holes (Wilcoxon signed rank = 2, $n = 8$ crabs, $P = 0.42$), whereas males ate more than three times more leaf material from leaves with holes compared with control leaves (Wilcoxon signed rank = 30, $n = 11$ crabs, $P = 0.002$). The same trend was not seen when leaves were offered on the sediment (Fig. 1b). In this case, the two types of leaf were equally susceptible when exposed to both female and male crabs (Wilcoxon signed rank$_{females}$ = 9·5, $n = 9$
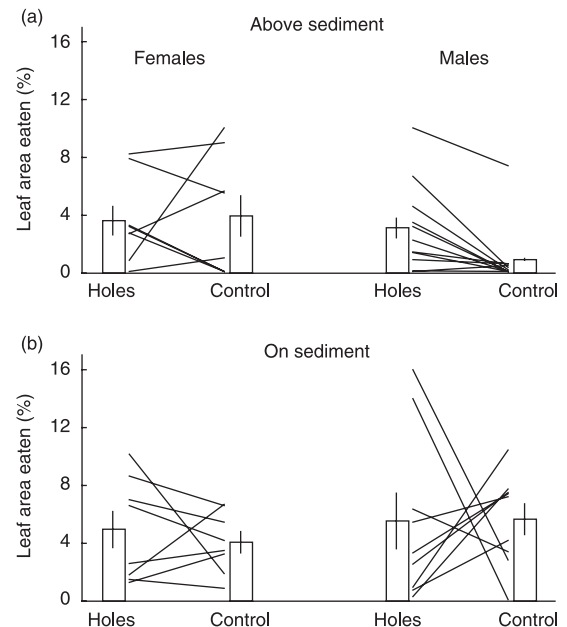

Fig. 1. Amount of leaf area eaten from leaves with (holes) and without holes (control), above (a) and on the sediment (b) by female and male crabs. Each line represents one crab with the points showing the amount of leaf area (percentage of total leaf area) eaten from the two treatments by that crab. Bars shows mean (±SE) in each treatment: (a) $n = 8$, 11 crabs, $P = 0.42$ and 0·002 for females and males, respectively; (b) $n = 8$ and nine crabs, $P = 0.15$ and 0·63 for females and males, respectively. Interaction between leaf preference and feeding site: G-test: $G_{males} = 7.74$; $P = 0.005$; $G_{females} = 0.25$; $P = 0.614$. Significance tests were performed on the absolute amount of leaf area eaten.
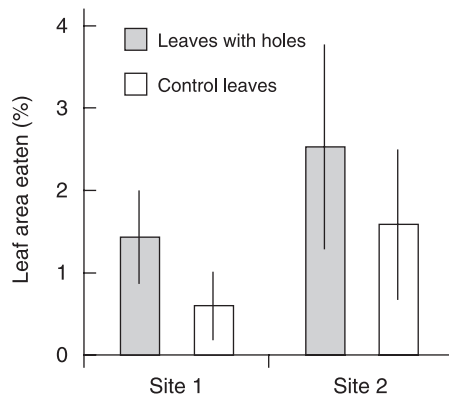
Fig. 2. Mean (± SE) percentage of leaf material eaten from leaves with holes and without holes (control) at two sites in the field. Only leaf pairs that showed crab-feeding marks were included (*n* = 40 and 20 leaf pairs at sites 1 and 2, respectively).

crabs, $P = 0.15$; Wilcoxon signed rank$_{males}$ = −3·5, n = 9 crabs, $P = 0.63$), and both sexes ate approximately the same amount of leaf material from leaves with and without holes. On the sediment, five females preferred the leaf with holes and three the control leaf. Within males, three preferred the leaf with holes and six the control leaf. We found a significant interaction between leaf preference (hole *vs* control leaves) and feeding site (above sediment *vs* on sediment) for males (*G*-test: $G = 7.74$; $P = 0.005$), but not females (*G*-test: $G = 0.25$; $P = 0.614$).

In the field, there were no crab attacks on any of the leaves after the first day. After 21 days, 60 of the 116 leaf pairs had been grazed by crabs. On average, crabs removed approximately twice as much leaf material (Wilcoxon signed rank = 449·5, $n = 60$ leaf pairs, $P < 0.0001$) from leaves with holes (mean ± SE, 1·33 ± 0·41 cm^2) compared with the control leaves (mean ± SE, 0·69 ± 0·3 cm^2). This trend was similar at both sites, although the leaves at site 2 were more heavily grazed (Fig. 2). From the 60 leaf pairs that showed crab grazing, the leaf with holes was most susceptible to crab damage in 45 cases, and the control leaf in 15 cases (*G*-test: $G = 15.7$; $P < 0.0001$).

Discussion

Our results show that when the sesarmid crab *E. versicolor* was feeding above the sediment, damaged mangrove leaves with holes were more susceptible to crab damage than undamaged leaves with an intact lamina. Laboratory experiments revealed that the increased susceptibility of damaged leaves was caused by male, not female crabs. Thus, if females select leaves randomly but males feed preferentially on damaged leaves, this explains why damaged leaves were chosen three times more often in the paired choice tests (assuming a 1 : 1 sex ratio among crabs). In conclusion, our results indicate that male crabs select damaged leaves when they climb trees to feed, whereas females do not discriminate between damaged and undamaged leaves.

Male sesarmid crabs have relatively larger and heavier claws than females (Macnae 1968). The male claw in *E. versicolor* is noticeably deeper and bears more rounded dactyls than females. For example, the height–length relationship of the propodeus is significantly larger in males (J.O., unpublished data). This sexual differentiation in claw morphology may account for the observed difference in male and female feeding behaviour. By use of their more slender claw, females may be able to pierce the leaf lamina to expose a leaf edge to feed, whereas this may be much harder for a male to achieve. A leaf with holes makes it unnecessary for the male to pierce the leaf to gain access to an internal leaf edge (an edge formed by a hole inside the leaf blade), which may explain why males selected the leaves with holes as opposed to undamaged leaves. A hole inside the leaf blade may be an important feature, as crabs usually grab the external leaf edge (the edge of an intact leaf) with their legs, with their claws pointing to the middle of the leaf. Thus a hole inside the leaf will be situated at an optimal position relative to the claws. In the feeding tests, leaves on the sediment were much more susceptible to damage by *E. versicolor* compared with leaves on sticks (simulating leaves on a tree), suggesting that, in general, crabs find it easier to feed from the sediment compared with on-tree feeding. Difficulty in feeding while balancing on a tree leaf combined with the sexual dimorphism evident in the claws of *E. versicolor* may restrict males to feeding on leaves with holes when they are foraging in trees.

We argue that the induced susceptibility to crab feeding probably originates mechanically, and is unlikely to be chemically based (e.g. originating from induced changes in leaf defence or nutritional value), for three reasons. First, the difference in susceptibility to male and female crab grazing suggests that this is attributable to claw morphology and hence to aspects of leaf handling. Second, the fact that mechanical damage led to differences in crab feeding over short periods suggests a mechanical basis. Mechanical damage often does not induce chemical changes in plants the way insect feeding does (Karban & Baldwin 1997), and the fact that the increased susceptibility followed immediately after the mechanical damage also makes a chemical basis less likely. Third, the fact that mechanical damage mattered only on suspended leaves suggests that it is a matter of food handling. Mechanically based induction leading to increased resistance (e.g. increased density of trichomes and thorns) has been reported in several cases, while the number of cases leading to increased susceptibility is low (Karban & Baldwin 1997). Mechanical induction may also operate between grazing ungulates where larger grazers remove obstructing plant parts and thereby facilitate grazing by smaller species (Vesey-Fitzgerald 1960; Bell 1970; Bell 1971). However, Arsenault & Owen-Smith (2002) conclude that the facilitation between grazers is more likely to be based on regrowth of nutritious new grass (chemically mediated) than on easier access to lower

plant parts (mechanically mediated). The facilitation between leaf beetles and crabs found in this study thus represents a rare case of a mechanically based induction of increased susceptibility between species. Our study is also unusual in that the leaf beetles involved were defoliators, but this type of herbivory has been suggested to be less likely than browsing to induce susceptibility (Haukioja *et al.* 1990; Arsenault & Owen-Smith 2002).

Our results suggest that trees in the field with fewer holes in their leaves will suffer less from crab herbivory. The leaves of *R. mucronata* trees have been found to possess fewer holes made by beetles and also suffer less crab grazing, but only if they were associated with the ant *O. smaragdina* (Offenberg *et al.* 2004a). Fewer holes in leaves on ant-trees arise because the ants prey on (Offenberg *et al.* 2004a), and chemically deter (Offenberg *et al.* 2004b), chrysomelid beetles, which feed on the leaves and leave small circular holes distributed throughout the leaf blade (Macintosh *et al.* 1991; Ng & Sivasothi 1999). As male crabs in this study disliked intact leaves, they probably preferred to forage on trees without ants because of the higher incidence of beetle damage on these trees. Thus, when combined with previous findings, the results of the present study suggest that the presence of ants results in indirect protection against crab herbivory. The possibility, though, that ants have an additional direct effect on the crabs (by direct attacks) cannot be ruled out. Ants can, in some cases, deter large animals such as mammals and birds (Beattie 1985; Haemig 1996), and a recent study (O'Dowd *et al.* 2003) showed that the invading ant *Anoplolepis gracilipes* was able to prey on land crabs on Christmas Island. However, in contrast to the Christmas Island system, mangrove crabs forage on trees only at night when ant activity is lowest and when it is difficult for the ants to use their vision. Moreover, the crabs can easily escape the ants by jumping off the tree if they are harassed. We therefore believe it unlikely that the ants had a strong impact on the crabs in the mangrove.

Less than 2% of the leaf area was eaten by crabs in the field, and other studies have shown values ranging from 0·5 to 4% depending on the site, and whether or not trees have been associated with ants (Offenberg *et al.* 2004a, 2005; L.H. Kofoed, S. Madsen and K. Olsen, unpublished data). In areas with abundant crabs and leaf beetles the amount of crab herbivory was almost twofold (2·5%) higher than leaf beetle herbivory (≈1·3%) on trees without ants. However, the presence of ants reduced beetle herbivory threefold, which resulted in an even more pronounced sixfold reduction in crab herbivory (Offenberg *et al.* 2004a). Thus the indirect effect of ants on crabs is stronger than the direct effect on the beetles, assuming that ants have no direct effect on the crabs.

Despite the overall low levels of herbivory on mature trees, *E. versicolor* belongs to the group of tree-climbing herbivorous crabs which has a high impact on mangrove dynamics, and which are considered pests in mangrove plantations (Macintosh *et al.* 1991; Ng & Sivasothi 1999; Sivasothi 2000; Ashton 2002). Crab attacks on saplings with few leaves and propagules are detrimental to several mangrove species and can lead to high mortality (J.O., unpublished data; Macintosh *et al.* 1991; Ng & Sivasothi 1999). Consequently, sesarmid crabs have been shown to alter mangrove community structure via seed predation and herbivory (Lee 1998), and therefore play a significant ecological role in mangrove dynamics (Wolcott & O'Connor 1992).

Our results suggest a complex network of direct and indirect interactions which involves both density- and trait-mediated effects between mangrove trees, ants and herbivores. The system illustrates a new behavioural mechanism by which ants may protect their host plants against herbivores without having to interfere with the herbivores directly. Furthermore, this interaction network emphasizes the significance of trait mediation and indirect interactions in community ecology, and the need to address these types of interactions concurrently with direct interactions in order to understand community functioning.

References

Agrawal, A.A. & Rutter, M.T. (1998) Dynamic anti-herbivore defence in ant-plants: the role of induced responses. *Oikos* **83**, 227–236.

Arsenault, R. & Owen-Smith, N. (2002) Facilitation versus competition in grazing herbivore assemblages. *Oikos* **97**, 313–318.

Ashton, E.C. (2002) Mangrove sesarmid crab feeding experiments in Peninsular Malaysia. *Journal of Experimental Marine Biology and Ecology* **273**, 97–119.

Beattie, A.J. (1985) *The Evolutionary Ecology of Ant–Plant Mutualisms.* Cambridge University Press, Cambridge, UK.

Bell, R.H.V. (1970) The use of the herb layer by grazing ungulates in the Serengeti. *Animal Populations in Relation to Their Food Resources* (ed. A. Watson), pp. 111–124. Blackwell Scientific, Oxford.

Bell, R.H.V. (1971) A grazing ecosystem in the Serengeti. *Scientific American* **224**, 86–93.

Bronstein, J.L. (1998) The contribution of ant-plant protection studies to our understanding of mutualism. *Biotropica* **30**, 150–161.

Carrol, A.L. & Quiring, D.T. (2003) Herbivory modifies conifer phenology: induced amelioration by a specialist folivore. *Oecologia* **138**, 88–95.

Freitas, A.V.L. & Oliveira, P.S. (1996) Ants as selective agents on herbivore biology: effects on the behaviour of a non-myrmecophilous butterfly. *Journal of Animal Ecology* **65**, 205–210.

Haemig, P.D. (1996) Interference from ants alters foraging ecology of great tits. *Behavioral Ecological and Sociobiology* **38**, 25–29.

Haukioja, E. (1990) Induction of defenses in trees. *Annual Review of Entomology* **36**, 25–42.

Haukioja, E., Ruohomäki, K., Senn, J., Suomela, J. & Walls, M. (1990) Consequences of herbivory in the mountain birch (*Betula pubescens* ssp. *tortuosa*): importance of the functional organization of the tree. *Oecologia* **82**, 238–247.

Karban, R. & Baldwin, I.T. (1997) *Induced Responses to Herbivory*. University of Chicago Press, Chicago, IL/London.

Lee, S.Y. (1998) Ecological role of grapsid crabs in mangrove ecosystems: a review. *Marine and Freshwater Research* **49**, 335–343.

Macintosh, D.J., Aksornkoae, S., Vanucci, M. *et al.* (1991) *Final Report of the Integrated Multidisciplinary Survey and Research Programme of the Ranong Mangrove Ecosystem*. UNDP/UNESCO Regional Project: Research and its Application in the Management of the Mangroves of Asia and the Pacific (RAS/86/120) UNDP/UNESCO. Funny Publishing Ltd Partnership, Bangkok, Thailand.

Macintosh, D.J., Ashton, E.C. & Havanon, S. (2002) Mangrove rehabilitation and intertidal biodiversity: a study in the Ranong mangrove ecosystem, Thailand. *Estuarine Coastal and Shelf Science* **55**, 331–345.

Macnae, W. (1968) A general account of fauna and flora of mangrove swamps and forests in Indo–West-Pacific Region. *Advances in Marine Biology* **6**, 73–270.

Ng, P.K.L. & Sivasothi, N., eds (1999) *A Guide to the Mangroves of Singapore II*. Singapore Science Centre, Singapore.

Nykanen, H. & Korechiva, J. (2004) Damage-induced changes in woody plants and their effects on insect herbivore performance: a meta-analysis. *Oikos* **104**, 247–268.

O'Dowd, D.J., Green, P.T. & Lake, P.S. (2003) Invasional 'meltdown' on an oceanic island. *Ecology Letters* **6**, 812–817.

Offenberg, J., Havanon, S., Aksornkoae, S., Macintosh, D. & Nielsen, M.G. (2004a) Observations on the ecology of weaver ants (*Oecophylla smaragdina* Fabricius) in a Thai mangrove ecosystem and their effect on herbivory of *Rhizophora mucronata* Lam. *Biotropica* **36**, 344–351.

Offenberg, J., Nielsen, M.G., Macintosh, D., Havanon, S. & Aksornkoae, S. (2004b) Evidence that insect herbivores are deterred by ant pheromones. *Proceedings of the Royal Society of London, Series B* **271** (Suppl.), S433–S435.

Offenberg, J., Nielsen, M.G., Macintosh, D., Havanon, S. & Aksornkoae, S. (2005) Lack of ant attendance may induce compensatory plant growth. *Oikos* **111**, 170–178.

Peacor, S.D. & Werner, E.E. (2001) The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences, USA* **98**, 3904–3908.

Philpott, S.M., Maldonado, J., Vandermeer, J. & Perfecto, I. (2004) Taking trophic cascades up a level: behaviorally-modified effects of phorid flies on ants and ant prey in coffee agroecosystems. *Oikos* **105**, 141–147.

Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005) Scared to death? The effect of intimidation and consumption in predator–prey interactions. *Ecology* **86**, 501–509.

Rudgers, J.A., Hodgen, J.G. & White, J.W. (2003) Behavioral mechanisms underlie an ant–plant mutualism. *Oecologia* **135**, 51–59.

Schmitz, O.J., Krivan, V. & Ovadia, O. (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* **7**, 153–163.

Sivasothi, N. (2000) Niche preferences of tree-climbing crabs in Singapore mangroves. *Crustaceana* **73**, 25–38.

Vesey-Fitzgerald, D.F. (1960) Grazing succession among East African game animals. *Journal of Mammalogy* **41**, 161–172.

Way, M.J. & Khoo, K.C. (1992) Role of ants in pest management. *Annual Review of Entomology* **37**, 479–503.

Werner, E.E. & Peacor, S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**, 1083–1100.

Wolcott, D.L. & O'Connor, N.J. (1992) Herbivory in crabs: adaptations and ecological considerations. *American Zoologist* **32**, 370–381.

Wootton, J.T. (1994) The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* **25**, 443–466.

Wootton, J.T. (2002) Indirect effects in complex ecosystems: recent progress and future challenges. *Journal of Sea Research* **48**, 157–172.