Enhancing the weaver ant, *Oecophylla smaragdina* (Hymenoptera: Formicidae), for biological control of a shoot borer, *Hypsipyla robusta* (Lepidoptera: Pyralidae), in Malaysian mahogany plantations

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Enhancing the weaver ant, *Oecophylla smaragdina* (Hymenoptera: Formicidae), for biological control of a shoot borer, *Hypsipyla robusta* (Lepidoptera: Pyralidae), in Malaysian mahogany plantations

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Abstract

The weaver ant is a promising biological control agent of a shoot borer, *Hypsipyla robusta* Moore, on mahogany, but techniques to conserve ant colonies redistributed to mahogany plantations have not yet been developed. The effect of food supplementation and host plant species preference of the weaver ant, *Oecophylla smaragdina* F., was evaluated in a series of field studies.

A simple model was developed to estimate the number of ants within nests on *Khaya ivorensis* A. Chev. (Meliaceae): $\log_{10}$ (Number of ants) = - 1.16 + 1.09 $\log_{10}$ (Nest size). Nest size is calculated from estimated nest height (h) and length ($\hat{l}$) using the formula = $\pi r^2 \hat{l}$, where $r = ½ h$. This model was useful for repeated assessments of ant population levels to evaluate treatment effects. It provides better estimates than previous indirect methods based on nest counts and ant trail counts on plant parts.

Colonies that were relocated without their queens and very small colonies (< 10,000 ants) failed to establish on new host trees, indicating that a minimum ant population and queen needs to be transferred for colony survival. Established colonies consumed more high-protein foods (live mealworms and fish) than high-carbohydrate liquid foods (honey and 'weaver ant formula', which contained sucrose and human muscle-training powder (Enerpro™)). Relocated colonies consumed more weaver ant formula and as many mealworms as established colonies, indicating that existing and relocated colonies require different food supplementation strategies. Decreasing consumption over time and preferential consumption among high-protein food choices (i.e., of mealworms over fish) indicated that ants select and regulate food consumption based on colony needs. Therefore, food supplementation should be as needed. Preliminary indications were that self-sufficiency in trophobiont (honeydew) levels may be achieved in two months after colony relocation.

The optimal colony density that would protect *K. ivorensis* was estimated to be within the range of 6 – 48 colonies per ha based on previous reports for cocoa and cashew, and a consideration of the low damage threshold for mahogany. Substituting chemical control with weaver ants at those application rates gave similar IRRs (Internal rate of return; 11.6 – 12.2 vs. 12.0%) in preliminary financial analyses, and was preferable from an ecological standpoint.

Twenty-nine host plant species were found for Malaysian *O. smaragdina*, of which 11 were new species records for *Oecophylla* spp. Also, there were two new genera and eight new species records for Malaysian *O. smaragdina*. Of eight trophobiont families collected, six species were identified, yielding new trophobiont-host plant species records for four coccoid species and two membracid genera. Screening of several ant-abundant plant species that included preliminary pest risk analyses for trophobionts on *K. ivorensis*, identified *M. citrifolia* as a promising candidate for mixed-planting with this mahogany species.

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Preface

There is some repetition in the following chapters because each was prepared as a separate manuscript for publication in scientific journals.

Chapter 1

Introduction and Literature Review

Cultivation of trees in the family Meliaceae, which include valuable tropical timber species such as *Swietenia* spp. (mahogany), *Cedrela odorata* L. (Spanish cedar) and *Khaya* spp. (African mahogany), have been severely limited by attacks of the mahogany shoot borers (*Hypsipyla* spp., Lepidoptera: Pyralidae) (Newton *et al*. 1993). Anticipating the need to cultivate mahogany due to dwindling natural stands (Verissimo *et al*. 1995) and the high value and demand for mahoganies (Angelo *et al*. 2001; ITTO 2006), various biological, chemical and silvicultural control approaches have been undertaken since the 1920's to address the shoot borer problem (Wylie 2001). These control approaches have not been successful in reducing shoot borer damage to acceptable levels (Wylie 2001). Two major factors combine to make this problem very challenging: 1) *Hypsipyla* spp. biology with their cryptic habit and overlapping generations (Grijpma 1976; Griffiths 2001) and 2) the biology of mahogany with production of multiple leaders following loss of apical dominance after shoot damage. Thus tolerance to damage is very low, i.e., effectively zero (Wylie 2001). This chapter describes characteristics of mahogany and its pest that are pertinent to its management. Previous control approaches are summarized, the characteristics of a promising biological control agent, *Oecophylla smaragdina* F. (Hymenoptera: Formicidae) are described, and critical research areas are identified.

Characteristics of mahogany

The name mahogany refers to timber of the genus *Swietenia* (true mahogany) (Nzokou & Harris 2002), but generally includes the genus *Khaya* (African mahogany) and *Cedrela* (cedar) (Newton *et al*. 1993). These trees belong to the family Meliaceae, which includes other economically important genera such as *Lovoa, Toona, Entandrophragma* and *Chukrasia*, all of which are attacked by mahogany shoot borers (Newton *et al*. 1993). These trees are distributed throughout the tropics and exhibit a high degree of variability within species (Pennington & Styles 1975; Pennington 1981).

Diameters of up to 2.0 m and heights exceeding 40 m can be achieved for mahoganies grown in good conditions (Pennington & Styles 1975). For *Khaya ivorensis* A. Chev, an exotic species to Malaysia, a mean dbh (diam. at breast ht.) of 30 cm and mean height of 30 m is expected in a 20 – 25 yr rotation (Ahmad Zuhaidi *et al*. 2003).

Silvicultural characteristics vary among species, e.g., *Swietenia macrophylla* King is relatively shade tolerant (Lamb 1966) while *K. ivorensis* is a light-demanding, self-pruning species (Ahmad Zuhaidi *et al*. 2006). Trees of most genera are deciduous and flush annually, with intra-specific variation in flushing, fruiting and leaf abscission times (Grijpma 1974, in Newton et al., 1993).

The loss of apical dominance results in production of multiple leaders. If this occurs when the tree is young, before a clear (unbranched) height of at least 6 m is attained, its economic value is greatly diminished (Wylie 2001). Protection is needed for 3 – 5 yr for trees to achieve this merchantable bole length (Wylie 2001). Spontaneous branching has also been reported on *K. ivorensis* trees that are grown in the open (Ahmad Zuhaidi *et al*. 2006).

Characteristics of the mahogany shoot borer

The mahogany shoot borer refers to *Hypsipyla* spp., of which the most important are *H. grandella* (Zeller) occurring in the Americas and *H. robusta* Moore in areas of Africa and the Asia/Pacific region. The taxonomic status of *Hypsipyla* spp. has recently been resolved (Horak 2001) and *H. robusta* is the species found in Malaysia (Marianne Horak, CSIRO, Australia, personal communication, 2005).

These shoot borers are generally limited to feeding on Meliaceous plants of the subfamily Swietenioideae and it is thought to be due to specific adaptation to unique limonoid compounds in trees of that group (Griffiths 2001). Larvae bore into tree shoots (Beeson 1941; Grijpma & Ramalho 1973) and occasionally feed on bark, flowers and fruit (Griffiths, 2001; G.T. Lim, personal observation). The shoot borers have a 1 – 2 month life cycle, but can take up to 5 months if the larvae enter diapause.

Females need to mate only once, after which 200 – 450 eggs are laid over a period of 5 – 8 nights. These eggs are laid singly or in clusters of up to four on the upper leaf surface, particularly around growing shoots (Beeson 1941; Griffiths 2001) and 1 – 3 eggs are laid per tree (Grijpma 1974 in Newton et al., 1993). Adults are strong fliers (Fasoranti 1985). Females can locate distant host trees and adult males can locate distant females and copulate with several females (Griffiths 2001). Three potential semiochemicals have been identified from *H. grandella* ovipositor tips. Of these, Z9, E12-tetradecadienyl acetate is common to both *H. grandella* and *H. robusta* (Borek *et al*. 1991 in Bellas, 2001). The adults appear to be attracted to young trees that are flushing (Howard 1991; Yamazaki *et al*. 1992) and to damaged trees and frass (Griffiths 2001). This attraction may be due to leaf chemistry (Cunningham & Floyd 2004). In addition to this intra-specific preference, *Hypsipyla* spp. have a preferred range of host species, e.g., *K. ivorensis* at 4.5 months after planting was free from *H. robusta* attack in the presence of *Swietenia* spp. (Khoo 2001), indicating the moth prefers the latter. Although the moths are able to disperse, the infestation is usually localized on new shoots as they become available following attack (Griffiths 2001).

Mortality of first instar due to predation and abiotic factors is high because they move around the plant to feed on several locations (Griffiths 2001). Mortality in the remaining 4 – 5 instars is much lower after the larvae tunnel into the shoot blocking the entrance hole with frass and webbing (Ramirez Sanchez 1964). Pupation takes place within the tunnel or in litter at the base of the tree (Beeson 1941; Griffiths 1997). There may be 10 – 12 overlapping generations per year and attack is continuous in regions where the moth does not undergo diapause (Gu & Liu 1984).

Mahogany shoot borer management

Numerous silvicultural control approaches for the mahogany shoot borers have been attempted but have met with limited success. Examples given of successful silvicultural control are frequently conflicting and largely anecdotal, and few reliable recommendations have been given due to lack of experimental evidence (Hauxwell *et al*. 2001a). In general, silvicultural interventions aim to interfere with location of the host plant, reduce host suitability, encourage natural enemies and assist recovery of the trees after attack (Hauxwell *et al*. 2001a). These measures include planting vigorous seedlings at good sites together with insect repellent species or other plant species that could interfere with the ability of the shoot borer to locate the host plant (Hauxwell *et al*. 2001a). These planting approaches could be

followed by post-planting activities that promote vigorous growth, e.g., weeding, and pruning to assist recovery of form after attack (Hauxwell *et al*. 2001a).

Chemical control is generally regarded as not viable from an economic and environmental standpoint (Wylie 2001). Repeated and frequent applications are needed to prevent attack, e.g., once a week for *H. grandella* on *Swietenia humilis* (Goulet *et al*. 2005) and once a month for *H. robusta* on *K. ivorensis* (Ahmad Zuhaidi *et al*. 2006). Efforts to control *H. grandella* used contact sprayed insecticide to target ovipositing females while a systemic granular insecticide was applied for control of tunneling larvae in *H. robusta*. As generations of the pest overlap and the shoot borers are active year-round, continuous protection is needed to prevent any attack (Wylie 2001). Even the more promising controlled-release systemic insecticides cannot kill the larvae quickly enough to prevent any shoot damage (Wylie 2001). Thus, chemical insecticides are anticipated to have limited use in nurseries or as part of an integrated pest management program (Wylie 2001). The use of semiochemicals, specifically synthetic sex pheromones of *H. robusta* did not attract any males (Nakamuta *et al*. 2002). It was assumed that the three compounds isolated from the ovipositor tip of *H. robusta* were sex pheromones, which may or may not be true. Additionally, the synthetic pheromone blend may not have been sufficiently similar to the composition of sex pheromones for the moth. More work is clearly needed here.

Host plant resistance as part of an integrated pest management program has also been discussed (Watt *et al*. 2001) with the recent completion of an international research program on that subject (Cunningham & Floyd 2003). The program reported that *H. robusta* preferred to lay eggs on leaves of open-planted *Toona ciliata* and suggested that managing the light environment (by overstory or gap-planting) could make the trees constitutively less susceptible to attack. Genotypic variation in susceptibility to attack was evident between and within provenances (countries of origin) of all species assessed with some species attacked less than others. However, the infestation rate exceeded acceptable levels in all cases, and the conclusion was that selection or cloning could be used to produce better trees than present provenances (Cunningham & Floyd 2003). Provenances that tolerate attack via strong apical dominance and production of a single main stem following attack could also be evaluated (Watt *et al*. 2001).

Biological control prospects using natural enemies of the shoot borers in classical or conservation biological control are considered poor despite the long list of natural enemies recorded for *Hypsipyla* spp. (Sands & Murphy 2001). The review suggested that the efficacy of parasitoids and predators could be enhanced by freeing them of their native natural enemies, but inundative parasitoid releases were not economically viable. Since there are beneficial moths in the same subfamily (Phycitinae) as *Hypsipyla* spp., e.g., *Cactoblastis cactorum* Berg, which is an important biological control agent of weed cacti, the review (Sands & Murphy 2001) advised host specificity studies in screening for parasitoid biological agent candidates. The conservation of indigenous ant species, e.g., *O. smaragdina* was considered a possible approach to reduce shoot borer attack (Sands & Murphy 2001; Khoo 2001). A review by Hauxwell *et al.* (2001b) reported that the success of entomopathogens for controlling *Hypsipyla* spp. has been limited by the cryptic nature of the larvae, their low density and the low damage threshold of mahogany. This was in spite of significant mortality inflicted by pathogens in the field and laboratory, some of which are commercially available products such as *Bacillus thuringiensis.* The review recommended identifying more pathogens of *Hypsipyla* spp. to screen for potential biological control agents.

Weaver ants

The use of *O. smaragdina* has been proposed for control of *H. robusta* by various authors (Sands & Murphy 2001; Khoo 2001; Lim & Kirton 2003) and a study found that *K. ivorensis* trees from which the ant was excluded had significantly greater shoot borer infestation rates than ant-occupied trees (Lim & Kirton, unpublished data). Application of the weaver ant as a biological control agent is currently an area of active research in Australia (Christian & Peng 2007; Manon Griffiths, Queensland Forestry Institute, Australia, personal communication, 2005) and Malaysia (FRIM 2005).

Oecophylla smaragdina has been successfully used as a biological control agent of insect pests in a number of fruit and cash crop species such as cashew and mango in Australia (Peng & Christian, 2004, 2005, 2006; Peng *et al.* 1995, 1997a, 1999), citrus in Vietnam (Van Mele & Cuc 2000) and cocoa in Malaysia (Way & Khoo 1991). Research is also active in applying the ant on mango in Thailand and Vietnam (ACIAR 2005).

Weaver ants are found in Africa (*Oecophylla longinoda* Latreille) (Ledoux 1950) and in South-East Asia, Australia and western Pacific islands (*O. smaragdina*) (Dodd 1902; Dutt 1912; Chen 1962; Stapley 1980; Van Mele & Cuc 2000). The two species are very similar in their biology and other characteristics (Holldobler & Wilson 1990a) and the following discussion refers to them collectively unless otherwise specified.

The weaver ant is effective as a biological control agent of many defoliating insect pests because it is a vigilant and territorial predator of living creatures in its arboreal domain (Holldobler & Wilson 1990a). Its ability to modify its environment to suit its needs by constructing nests from the living foliage of numerous host plant species allows it to exploit a wide range of habitats (Holldobler 1983a). Larger nests contain brood and reproductives while smaller nests without reproductives are called 'pavilions' (Blüthgen & Fiedler 2002). Final instars produce the silk that binds the colony's nests together (Way 1954a; Vanderplank 1960). Trophobionts such as mealybugs and scale insects are tended by workers for the honeydew that comprises a substantial portion of the ants' diet (Blüthgen & Fiedler 2002). The ants also forage for plant nectar on a diverse number of plant species (Blüthgen *et al*. 2004).

Weaver ants establish large polydomous colonies housed in many nests constructed in the crowns of up to 17 mature trees for *O. longinoda* (Holldobler 1979) and 44 trees for *O. smaragdina* (Holldobler 1983a). A colony may be founded by a single mated queen (Greenslade 1971; Holldobler & Wilson 1983) or multiple queens (Peeters & Andersen 1989), a state which persists in mature Australian colonies (Peng *et al*. 1998a). The mated queen finds a sheltered spot to raise her first brood and her resulting worker offspring then care for subsequent brood (Holldobler & Wilson 1983). The queen, sustained by consuming the trophic egg offerings of her workers (Holldobler & Wilson 1983) produces fertile eggs that are soon distributed to and the offspring raised in nearby nests (Peng *et al*. 1998b).

Weaver ants can be applied to protect plant species that host or provide food resources (trophobiont honeydew and/or plant nectar) to the ant. It involves conserving and augmenting existing colonies or harvesting and redistributing colonies to the trees that require protection. These relocated colonies also need to be conserved and augmented. Practices that aid conservation of the ant include limiting pesticide applications and using pesticides that are less harmful to the ant (Van Mele *et al*. 2002), and supplementing the ants' diet with dried fish during the food-scarce dry season (Van Mele & Cuc 2003). The direct provision of food has also been observed to augment weaver ant populations in a Malaysian

mahogany plantation (Lim Sun Heng. Maju Aik Ltd., personal communication, 2005). However, the types of food preferred by the ant, and other aspects of food supplementation such as timing and duration have yet to be investigated. Additionally, the short- and long-term effects of food supplementation on colonies of the ant on mahogany are not known and ants may be conditioned to supplemented food (Van Mele & Cuc 2003). It is crucial to develop farmer-friendly guidelines for use of weaver ants to protect *K. ivorensis*, and these must detail the types of food to be supplemented, the timing and duration of supplementation, and anticipated effects of supplementation on ant colonies.

Indirect provision of food has been suggested via mixed-planting of alternate host plant species that favor the ant together with the main crop (Way & Khoo 1991; Peng *et al*. 1997b; Van Mele & van Lenteren 2002). The preference of the ant for certain host plant species is due to availability of nectar from active plant nectaries and/or honeydew from trophobionts supported by the plant, and suitable foliage for nest-building (Way & Khoo 1991; Blüthgen & Fiedler 2002). A few host plant species are thought to be preferred by the ant, e.g., mango, guava (Way & Khoo 1991), citrus, clove and cashew trees (Way 1954a). The ant demonstrated an innate attraction to some host plant species over others in a laboratory study (Djieto-Lordon & Dejean 1999). No other studies have qualified or quantified ant preference for various host plant species.

In Malaysia, *O. smaragdina* has been reported nesting on several fruit (Miller 1931; Corbett 1937; Fiedler & Maschwitz 1989), cash crops (e.g., coffee, cocoa, coconut; Miller 1931; Way & Khoo 1991; Way & Bolton 1997), mangroves (Macnae 1968), and forest plants (Fiedler & Maschwitz 1989; Saarinen 2006). The selection of an alternate host plant species candidate for mixed-planting should draw from a larger list of host plant species than what is presently available. Furthermore, screening for candidate host plant species to interplant with mahogany should include a pest risk assessment for the trophobiont species. Information on trophobiont species associated with the ant and the host plants is very limited for both *Oecophylla* spp. The presence of *O. smaragdina*-tended trophobionts on cocoa is not considered detrimental to the crop (Way & Khoo 1991; but see Balakrishnan *et al*. 1992). It is very important to obtain a large selection of host plant species from which several ant-abundant host plant species can be evaluated for suitability to mix-plant with *K. ivorensis.*

Although *K. ivorensis* itself is a host plant of *O. smaragdina* (Khoo 2001), regular nest abandonment has been observed. This abandonment results in periods where the trees are left unoccupied (G.T. Lim, personal observation), and likely results from ants relocating to younger foliage on other trees as the foliage of their current nest ages (Blüthgen & Fiedler 2002). Since mahogany has an extremely low damage threshold for shoot borer attack (Taveras *et al*. 2004), perpetual ant presence at fairly high levels is probably needed to provide satisfactory protection. Minimum ant density on the tree has yet to be estimated for protecting *K. ivorensis.* It is a crucial prerequisite for economic analyses and subsequent cost comparison with other control methods.

Finally, in order to conduct repeated assessments of treatment effects on ant colonies in the field, a non-destructive method of estimating ant population levels is needed. The model should provide a more direct reflection of ant population levels than other indirect estimation methods, e.g., nest counts (Offenberg *et al*. 2004), ant counts on plant parts (Blüthgen & Fiedler 2002), and counts of ant trails on tree stems or branches (Peng & Christian 2005).

Research Objectives

The literature review and introduction (Chapter 1) identified several important deficiencies in current knowledge on applying the weaver ant as a biological control agent of the mahogany shoot borer. These research gaps are addressed with the following objectives:

1) Develop a procedure for direct food supplementation to weaver ant colonies
   a) Identify preferred foods of the ant that are economical and practical to apply.
   b) Examine the effect of food supplementation on establishment of relocated colonies
   c) Determine the cost-effectiveness of supplementing food in applying weaver ants to *K. ivorensis*

2) Identify host plants of the ant with potential for mixed-planting with *K. ivorensis*
   a) Identify host plants and trophobionts for *O. smaragdina* in Peninsular Malaysia.
   b) Perform a pest risk analysis for trophobiont species on ant-abundant host plant species, toward *K. ivorensis*
   c) Compare ant preference among ant-abundant host plant species

3) Develop a method of estimating the number of trophobionts within nests and pavilions.

Chapter 2

Host plants and associated trophobionts of the weaver ant

Introduction

Weaver ants of the genus *Oecophylla* form mutually beneficial relationships with certain trophobionts (Way 1954b; Vanderplank 1960), which are honeydew-producing insects tended by the ants (Gibernau & Dejean 2001). These ants are found in Africa (*Oecophylla longinoda* Latreille) (Ledoux 1950) and in South-East Asia, Australia and western Pacific islands (*Oecophylla smaragdina* Fabricius) (Dodd 1902; Dutt 1912; Chen 1962; Stapley 1980; Van Mele & Cuc 2000). They are arboreal ants that establish large polydomous colonies housed in many nests constructed in the crowns of up to 17 mature trees for *O. longinoda* (Holldobler 1979) and 44 mature trees for *O. smaragdina* (Holldobler 1983a). Their diet consists of trophobiont honeydew, plant nectar and insects, of which they are voracious predators (Nixon 1951; Way 1963). *O. smaragdina* has been successfully exploited as a biological control agent for insect pests of various fruit crops, e.g., cashew, mango and litchi in Australia (Peng *et al*. 1999; Peng & Christian 2005; Leu 2005) and citrus in China (Huang & Yang 1987) and Vietnam (Van Mele & Cuc 2000).

In Malaysia, *O. smaragdina* has been reported nesting on several fruit (Miller 1931; Corbett 1937; Fiedler & Maschwitz 1989), cash crops (e.g., coffee, cocoa, coconut; Miller 1931; Way & Khoo 1991; Way & Bolton 1997), mangroves (Macnae 1968), and forest plants (Fiedler & Maschwitz 1989; Saarinen 2006). The ant has been shown to protect cocoa from the cocoa mirid, *Helopeltis theobromae* Miller (Hemiptera: Miridae) (Way & Khoo 1989). The latter suggested that mixed systems containing crops such as mango, guava and citrus interplanted with cocoa and coconuts could favor the establishment of the ant. Citrus, clove, and cashew trees were observed to be good hosts for *Oecophylla*-tended Coccoidea in addition to having leaves that were suitable for nest-building (Way 1954a). Interplanting of *Oecophylla*-favored host plants with a crop provides more nesting sites and creates a more stable environment with a dependable source of honeydew (Way & Khoo 1991; Peng *et al*. 1997b). Host plant species support the ant-trophobiont relationship by providing floral and extrafloral nectar and harboring the honeydew-producing trophobionts (Blüthgen & Fiedler 2002), both of which were found to play a key role in determining an ant mosaic in Australia (Blüthgen *et al*. 2004).

Oecophylla smaragdina has also been identified as a potential biological control agent of a forest insect pest, the mahogany shoot borer, *Hypsipyla robusta* Moore (Lepidoptera: Pyralidae), in Malaysia, based on a study conducted in a *Khaya ivorensis* A. Chev. plantation (Lim & Kirton 2003). The mahogany shoot borer is the main factor limiting the cultivation of mahogany worldwide. *Hypsipyla grandella* (Zeller) in the Americas and *H. robusta* in Africa and the Asia/Pacific region are the two most important *Hypsipyla* species (Griffiths 2001). The plant species attacked by these shoot borers are from the genera *Swietenia, Khaya, Toona* and *Cedrela* (Meliaceae: Swietenioidea) (Griffiths 2001). Although *K. ivorensis* itself is a host plant of *O. smaragdina* (Khoo 2001), regular nest abandonment has been observed. This abandonment results in periods where the trees are left unoccupied (G.T. Lim, personal observation), and likely results from ants relocating to younger foliage as the foliage of their current nest ages (Blüthgen & Fiedler 2002). Mahogany species have

an extremely low damage threshold for shoot borer attack, which may be as low as one larva per tree (Taveras *et al*. 2004). Therefore, perpetual ant presence on *K. ivorensis* at fairly high levels is probably needed to provide satisfactory protection. Interplanting a second *Oecophylla*-favored host plant with *K. ivorensis* could help augment existing population levels of the ant and also encourage the establishment of newly introduced ant colony 'inoculums'.

The presence of *O. smaragdina*-tended trophobionts on cocoa was not considered detrimental to the crop (Way & Khoo 1991; but see Balakrishnan *et al*. 1992). Nevertheless, screening for candidate host plant species to interplant with mahogany should include a pest risk assessment for the trophobiont species. Interplanted 'nurse' plant species should bear trophobionts with a relatively narrow host plant range that does not include the mahogany species itself (or does not negatively affect it). The trophobiont population should be large enough to produce sufficient supplementary honeydew thus providing meaningful support to the ant population. However, the nurse plant and the trophobiont species associated with it should be less attractive to the ant than the mahogany species requiring protection.

This study was carried out to identify: (1) potential candidates for *O. smaragdina* host plant species to interplant with mahogany in Malaysia, (2) the trophobionts associated with these host plants to obtain preliminary information on the tritrophic interactions among the ant, plants and trophobionts involved.

Materials and Methods

Literature survey

Records of host plants and associated trophobionts of *O. smaragdina* in Malaysia are scarce and a preliminary survey of the literature was carried out to identify potential host plants recorded elsewhere, including host plant records for *O. longinoda*, as there could be an overlap in trophobionts tended by the two species. The literature survey was largely conducted on the CAB (Commonwealth Agricultural Bureau) Direct database that included international archives dating back to 1900. The search term '*Oecophylla longinoda*' and '*Oecophylla smaragdina*' were used to obtain records for the two species. For the purpose of this survey, 'host plants' were those that the ant was reported to nest in, while 'possible host plants' had no confirmation of nesting. Where the abstract alluded to a possible host plant, the original article was reviewed, and where more than one reference was available for a host plant, the earliest mention was recorded, along with associated trophobionts (if any) and country of occurrence.

The plant names were checked against other standardized databases using the GRIN (Online) Taxonomic Nomenclature Checker (TNC) (USDA-ARS 2006). At the date of accession (30 September 2006) the database contained over 18,000 generic and 65,000 specific or infraspecific records of vascular plants and included all currently accepted generic names (over 14,000). However, representation of species in this database was incomplete, especially for non-agricultural plants, so some of the plant names were checked against other sources (RBG 2004; IPNI 2004; DOL 2005; Western Australian Herbarium 2006; APNI 2006). The TNC highlighted species that did not match those in the database and provided up to five possible alternatives, based on which possible spelling mistakes in the original article could be corrected if a close match was found with a matching distributional range and family. Relevant articles cited by the ones found in the database search also provided

additional host plant records. Scale insect trophobiont names were checked against the ScaleNet (Ben-Dov *et al*. 2005) database for scale insects of the world.

Host plant survey

Topographically, Central West Peninsular Malaysia is characterised by extensive coastal plains in the west, and undulating terrain leading to a hilly and mountainous central region. There are mangrove forests along the coast, dipterocarp and peat swamp forests further inland, and agricultural areas with extensive plantations of oil palm, rubber, and other agricultural commodities, including horticultural crops. *Oecophylla* spp. are generally sun-loving (Majer 1972; Begg 1977; Holldobler 1983a; Blüthgen & Fiedler 2002), and *O. smaragdina* is common along the edges of forests, in parks, gardens, and in mangroves in the lowlands of Peninsular Malaysia (Jander & Jander 1979; G.T. Lim, personal observation). Therefore, three habitats (mangrove forests, lowland dipterocarp forests and mixed orchards) were chosen for the survey of *O. smaragdina* host plants to reflect the diversity of plant species in the region, and where the ant is likely to be encountered. A fourth habitat, mahogany plantations, was also selected to obtain preliminary data on ant abundance and trophobiont species that would aid planning for subsequent studies.

Between May to July 2005, three sites for each of the four habitats were surveyed, covering the states of Perak, Negeri Sembilan, Pahang and Selangor. The sites and details of each survey are described in Table 2.1. For the distance of 1 km traveled in the survey for ant-occupied plants, a total 'sampling area' of 2.0 and 0.6 ha was examined at the orchards and other habitats, respectively. A plant was considered a host species only when the ant was confirmed nesting on it, thus excluding plants with no nests, even if the ants tended trophobionts or collected nectar on them. In this study, a 'nest' described any structure built from leaves of a plant species by the ant, on which the ants were visible. It included 'nests' defined by Blüthgen & Fiedler (2002) as structures housing reproductives and brood, and 'pavilions' as leaf structures with no reproductives or brood.

For all ant-occupied trees encountered, we recorded the host plant species and trophobionts found associated with the ant and the number of nests on each tree. Trees were grouped by colony. When trees with nests were next to each other, they were assumed to be of the same colony if their canopies overlapped or if ant trails between the trees were found. When trees with nests were over 10 m apart and ant trails between them were rarely found, the nests were recorded as belonging to different colonies. This method was a simple way to distinguish colonies, but not infallible. The area between trees with nests was thoroughly examined for ant trails but trails joining trees with nests were not always visible and could potentially result in an overestimation of the number of colonies or the number of trees in a colony could be underestimated.

The abundance of ant-occupied trees (number of trees per ha) or ant-occupied tree density was estimated for each site to enable comparison among and within habitats.

$$\text{Ant-occupied tree density} = \left[\frac{\sum(\text{Number of ant-occupied trees in a site})}{\text{'sampling area'}}\right]$$

Trophobionts found on the plants, on the nest surface, and within the nests were placed in vials containing 70% ethanol. They were first located by examining at eye-level the exterior of the nests and extra-floral and floral nectaries of the host plant, where the ant could often be observed tending the trophobionts. Binoculars were used to examine nests that were higher up in the trees and a telescoping clipper was used to retrieve nests to obtain

Table 2.1. Description of sites sampled in four habitats for *Oecophylla smaragdina* host plants in Central West Peninsular Malaysia.

Habitat[1]	Site	Site description
Lowland dipterocarp forest	Commonwealth Forest Park (3°17'N, 101°36'E)	Intensively managed park with groomed paved trails along which sampling was conducted
	Gombak Forest Reserve (3°17'N, 101°46'E)	Minimally managed forest
	Ampang Forest Reserve (3°8'N, 101°47'E)	A loop trail encircling a reservoir, minimally managed
Mangrove forest	Kuala Selangor Nature Park (3°17'N, 101°16'E)	A succession of coastal vegetation, mangrove forest and lowland forest moving away from the estuary. A 300 m section of trail from each of these vegetation types was randomly chosen for a composite sample reflecting vegetation succession.
	Kapar, Klang (3°7'N, 101°22'E)	Two vegetation types: mangrove forest on the seaward side of the bund, and an *Acacia* replanting on the landward side. A composite sample was obtained for these two areas.
	Bagan Lalang, Sepang (2°35'N, 101°41'E)	Two vegetation types: mangrove forest and coastal vegetation
Mahogany plantation	Bukit Hari FRIM (3°14'N, 101°38'E)	Plots and service roadside plantings of *K ivorensis* and *Chukrasia tabularis* A.H.L. Jussieu among plots of other tree species. Zigzag sampling was done within plots and continuous line transect sampling was conducted along service roads to obtain a composite sample.
	Sg Chinoh, Perak (3°53'N, 101°22'E)	*K. ivorensis* (3 – 6 yr) established within an oil palm plantation, minimally managed. Continuous line transect sampling was done along service roads and planting terraces.
	Fivestar, Pahang (3°13'N, 102°25'E)	*K. ivorensis* (5 yr), intensively managed. Zigzag sampling conducted within the plot.
Mixed orchard	Gombak (3°17'N, 101°46'E)	Assorted fruit and other plant species valued by smallholders were planted on their property. The sampling transect cut across the planted areas, maintaining a 10 m distance from housing structures.
	Hulu Langat (3°06'N, 101°48'E)	
	Kuala Selangor (3°17'N, 101°16'E)	

[1] A total distance of 1 km was sampled among vegetation bordering trails or service roads (10 m sample width on each side of and perpendicular to line transect at the orchards and 3 m sample width for the other habitats).

trophobiont samples. Trophobiont samples could not be collected on a few trees where the nests were beyond the 8 m reach of the telescoping clippers. One sample was collected for each tentatively identified species of trophobiont on every tree. Plant species on which the ant was found tending trophobionts but with no visible nests were recorded as additional observations, and trophobionts sampled for identification, but not included in the list of host plant species. Gross identification to family was done by M. Kosztarab (Virginia Tech) for a number of these trophobionts, and were identified at least to family by D.R. Miller (for Coccoidea, Aphididae and Aleyrodidae) and S. H. McKamey (for Membracidae) (USDA-ARS). Plants that could not be identified were collected, and were later identified by Mohd. Asri and Kamarudin Salleh (Botany Section, FRIM).

Habitats were also assessed for homogeneity across sites in stand maturity (tree size or dbh (diam. at breast ht.)), site quality (stand basal area) and tree density (number of trees per ha). These parameters were measured at three points along the sample trail, 250, 500 and 750 m from the starting point. At each point, either the left or right side of the trail was randomly chosen for the measurement of the dbh of trees (> 1.3 m ht.) in a 'fixed plot'. A length of 10 m along the trail, and distance of 3 m from the edge of the trail extending into the trailside vegetation, was demarcated for each fixed plot. This 30 m^2 fixed plot was used for all the habitats except at the orchards, where a 100 m^2 fixed plot was used to account for the large planting distance between the fruit trees at all the orchard sites surveyed.

The basal area (sectional area at breast ht., m^2) for each tree was calculated (after Brack 1999).

$$\text{Basal area, } \quad g = \tfrac{1}{2} [\, \pi (\text{dbh})^2 \,]$$

The sum of the basal area of all the trees in a site was used to calculate stand basal area (m^2 per ha), which is the cross-sectional area of all trees at breast height per ha.

$$\text{Stand basal area} = \frac{10{,}000 [\, \sum (g) \,]}{\text{'fixed plot' size}}$$

Tree density (number of trees per ha) at each sampling point was also calculated from total tree counts in a fixed area plot.

$$\text{Tree density} = \frac{10{,}000 [\, \sum (\text{number of trees in a fixed plot}) \,]}{\text{'fixed plot' size}}$$

Ant-occupied host plant species that were identified as abundant in the various habitats were given a preliminary assessment as to the pest risk of associated trophobionts. The host plant species for scale insects were checked against the host plant species listed in an online database, ScaleNet, for the specific scale insects (Ben-Dov *et al*. 2005).

Statistical analyses

All analyses were carried out using the statistical software Minitab 14® (MINITAB 2007). The results of the literature survey for *O. longinoda* and *O. smaragdina* host plants and associated trophobionts were analyzed using Chi-Square. The two ant species were compared in the distribution of host plant species by trophobiont taxon. For the ant-occupied trees, tree, nest and colony densities (per ha) were analyzed using one-way analysis of variance (ANOVA), with *habitat* as the fixed factor and *site density* as the response variable. The number of trees and nests per colony was analyzed using general linear models with the factors *site* nested within *habitat* in an unbalanced design. Site-descriptive response variables (tree density, tree size and stand basal area) were analyzed this way as well, but excluded a forest site that did not record any trees. Results for all analyses of variance were $\log_{10}(Y+1)$

transformed to achieve normality and equality of variances. All analyses of variance were followed by Tukey's honestly significant difference test to separate treatment means (Zar 1999) at $P \leq 0.05$.

Results

Literature survey

The CAB Direct database search for '*Oecophylla longinoda*' and '*Oecophylla smaragdina*' returned 99 and 228 records, respectively. The literature survey showed that *O. smaragdina* was recorded on 194 plant species in 52 families, with 67 associated trophobiont species in 10 families (Table 2.2), whereas *O. longinoda* was recorded on 74 plant species in 36 families with 54 associated trophobiont species in 10 families (Table 2.3). In addition, there were 88 species (25 families) of possible host plants (i.e., nesting not confirmed) for *O. smaragdina* (Table 2.2). A number of these possible host plants had been reported as host plants also, but the distinction was maintained because their associated trophobiont species were different. Trophobiont association may influence a plant species' suitability as a host plant for the weaver ant.

Figure 2.1 summarizes the number of (confirmed) host plant species and families for the two ant species, and the number of trophobiont species associated with the ant species. There were 18 plant species on which both ant species were reported nesting on but only 11 of these reported trophobiont associations. Of the 11, only *Coffea excelsa* A. Chev. and *Coffea robusta* L. Linden (Rubiaceae) shared a common trophobiont, *Coccus viridis* Green (Coccidae) that both ant species were reported to tend. Since another seven of those 18 plant species have been reported elsewhere (Ben-Dov 2005a) as host plants of *C. viridis* (but not in association with ants), it is possible that there could be undocumented tending of *C. viridis* by both *Oecophylla* spp. on these 7 plant species. Six other trophobiont species were reported for both *Oecophylla* spp. but associated with different host plants, *Planococcus citri* (Risso) (Pseudococcidae), *Coccus hesperidum* L., *Saissetia coffeae* (Walker) and *Parasaissetia nigra* (Neitner) (Coccidae), *Toxoptera aurantii* (Boyer de Fonscolombe), and *Cerataphis lataniae* Boisd. (Aphididae).

The large number of host plant records for *O. smaragdina* compared with *O. longinoda* was in part due to an extensive checklist of host plants of lycaenids (Braby 2000), several of which are obligately tended by *O. smaragdina*, while no lycaenids were reported for *O. longinoda*. Lycaenid host plants consisted of as much as 46.5% of the host plant species recorded for *O. smaragdina*, but contributed only 24.4% to the total number of trophobiont species reported for the ant (Table 2.4). Excluding the family Lycaenidae, there was no significant difference between the two ant species, in the families, and other trophobiont families ($\chi^2 = 1.000$; d.f. = 1, 3; $P = 0.801$).

Host plant survey

The habitat surveys found a total of 29 host plant species (21 families) for *O. smaragdina*, with eight families of trophobionts, six species (four families) of which were positively identified (Table 2.5). Of the 29 host plant species, 21 are new records of *O. smaragdina* host plants in Malaysia. In addition, possible host plant species (where ant-tending of associated trophobionts was observed but no nests were seen) were: for

Table 2.2. Records of *Oecophylla smaragdina* host plants and possible host plants, and associated trophobionts from a survey of the literature (1900 to present). Currently accepted species and family names are used followed by names given in the original article within square brackets [ ], where different.

#	Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
ANACARDIACEAE					
1	*Anacardium occidentale* L.	*Egropa malayensis* Dist.	MEM	Corbett (1937)	MYS
		Zesius chrysomallus Hubner	LYC	van der Poorten & van der Poorten (2006)	LKA
		-		Peng *et al.* (1997a)	AUS
2	*Buchanania arborescens* (Blume) Blume	*Arhopala micale* Boisduval	LYC	Braby (2000)	AUS
3	*Buchanania obovata* Engl.	*Arhopala centaurus* Fabricius	LYC	Braby (2000)	AUS
4	*Mangifera indica* L.	-	-	Dutt (1912); Soans (1971); De & Pande (; 1988)	IND
		-	-	Peng *et al.* (1997b)	AUS
		-	-	van Mele & Cuc (1999)	VNM
		-	-	Way & Khoo (1991)	MYS
5	*Pleiogynium timoriense* (DC.) Leenh. [*Pleiogynium timorense*]	-	-	Lokkers (1986)	AUS
6	*Spondias dulcis* Sol. ex Parkinson	-	-	van Mele & Cuc (1999)	VNM
ANNONACEAE			-		
7	*Annona glabra* L.	-	-	van Mele & Cuc (1999)	VNM
8	*Annona muricata* L.	Mealybug sp.	PSE	Stapley (1980)	SLB
		Scale insect sp.	COC+	Stapley (1980)	SLB
9	*Polyalthia holtzeana* F. Muell.	-	-	Begg (1977)	AUS
10	*Polyalthia nitidissima* (Dunal) Benth.	-	-	Begg (1977)	AUS

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
APOCYNACEAE						
11		*Alstonia actinophylla* (A. Cunn.) K. Schum.	-	-	Peng *et al.* (1997b)	AUS
12		*Dyera costulata* (Miq.) Hook. f.	-	-	Saarinen (2006)	MYS
13	*	*Ichnocarpus frutescens R.Br.*	-	-	Blüthgen *et al.* (2004)	AUS
14		*Melodinus australis* Pierre	*Milviscutulus* sp.	COC	Blüthgen & Fiedler (2002)	AUS
15		*Plumeria obtusa* L.	-	-	Peng *et al.* (1997b)	AUS
16		*Wrightia pubescens* R. Br.	-	-	Begg (1977)	AUS
ARECACEAE						
17	*	*Archontophoenix alexandrae* (F.Muell.) F.Muell. Ex Benth.	-	-	Blüthgen *et al.* (2004)	AUS
18		*Areca catechu* L.	*Cerataphis lataniae* Boisd.	APH	More *et al.* (2002)	IND
			Icerya aegyptiaca Doug	MAR	More *et al.* (2002)	IND
			-	-	More *et al.* (2002)	IND
19		*Carpentaria acuminata* Becc.	-	-	Peng *et al.* (1997b)	AUS
20		*Caryota mitis* Lour.	-	-	Peng *et al.* (1997b)	AUS
21		*Cocos nucifera* L.	*Laingiococcus painei* Laing	PSE	Phillips (1940)	SLB
			Scale insect sp.	COC	Froggatt (1937)	PNG
			-	-	Phillips (1940); Stapley (1980)	SLB
			-	-	Way *et al.* (1989)	LKA
		Cocos nucifera L. [PALM]	*L. painei*	PSE	Williams (1960)	SLB
			Maculicoccus malaitensis (Cockerell)	PSE	Williams (1960)	SLB
			Mealybug sp.	PSE	Way & Khoo (1991)	MYS
			Mutabilicoccus simmondsi (Laing) *comb. Nov.*	PSE	Williams (1960)	SLB
			Scale insect sp.	COC	Way & Khoo (1991)	MYS
			-	-	Peng *et al.* (1997b)	AUS

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
			-	-	Way & Bolton (1997)	MYS
22	*	*Licuala ramsayi* (F.Muell) Domin	-	-	Blüthgen *et al.* (2004)	AUS
23		*Livistona humilis* R. Br.	-	-	Peng *et al.* (1997b)	AUS
24	*	*Normanbya normanbyi* (W.Hill) L.H.Bailey [PALM]	-	-	Blüthgen *et al.* (2004)	AUS
ASCLEPIADACEAE						
25	*	*Wrightia laevis* subsp. *millgar* (Bailey) Ngan	-	-	Blüthgen *et al.* (2004)	AUS
BIGNONIACEAE						
26	*	*Neosepicaea jucunda* (F.Muell.) Steenis	-	-	Blüthgen *et al.* (2004)	AUS
27		*Tabebuia pallida* (Lindl.) Miers	-	-	Peng *et al.* (1997b)	AUS
BORAGINACEAE						
28		*Cordia curassavica* (Jacq.) Roem. & Schult.	-	-	Simmonds (1980)	MYS
29		*Cordia dichotoma* G. Forst.	*A. micale*	LYC	Braby (2000)	AUS
BURSERACEAE						
30		*Canarium album* Raeusch	-	-	Huang & Yang (1987)	CHN
31		*Canarium australianum* F. Muell.	-	-	Begg (1977)	AUS
CANNABACEAE						
32	*	*Aphananthe philippinensis* Planch. [ULM+]	*Nacaduba berenice* Herrich-Schäffer	LYC	Braby (2000)	AUS
33		*Celtis philippensis* Blanco [*Celtis philippinensis*]	-	-	Begg (1977)	AUS
CAPPARACEAE						
34		*Capparis sepiaria* L.	-	-	Begg (1977)	AUS
CARICACEAE						
35		*Carica papaya* L.	-	-	Fiedler & Maschwitz (1989)	MYS
CASUARINACEAE						

Table 2.2. continued

#	Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
36	*Casuarina* sp.	-	-	Lokkers (1986)	AUS
CHRYSOBALANACEAE					
37	*Maranthes corymbosa* Blume	*A. centaurus*	LYC	Braby (2000)	AUS
38	*Parinari nonda* Benth.	*A. micale*	LYC	Braby (2000)	AUS
CLUSIACEAE					
39	*Calophyllum inophyllum* L.	*A. micale*	LYC	Braby (2000)	AUS
	C. inophyllum L. [*Colophylum inophilum*] [GUTT]	-	-	Peng *et al.* (1997b)	AUS
40	*Garcinia mangostana* L.	-	-	Hill (1983)	AUS
COMBRETACEAE					
41	*Lumnitzera racemosa* Willd.	*Hypolycaena phorbas* F.	LYC	Braby (2000)	AUS
42	*Terminalia arjuna* (Roxb. ex DC.) Wight & Arn.	*Z. chrysomallus*	LYC	van der Poorten & van der Poorten (2006)	LKA
43	*Terminalia catappa* L.	*A. centaurus*	LYC	Braby (2000)	AUS
		Arhopala madytus Fruhstorfer	LYC	Braby (2000)	AUS
*		*Theclinesthes miskini* T.P. Lucas	LYC	Braby (2000)	AUS
44	*Terminalia grandiflora* Benth. [*Terminalia grandeflora*]	-	-	Peng *et al.* (1997b)	AUS
45	*Terminalia melanocarpa* F. Muell.	*A. centaurus, A. madytus, H. phorbas*	LYC	Braby (2000)	AUS
46	*Terminalia muelleri* Benth.	*A. centaurus*	LYC	Braby (2000)	AUS
		A. micale	LYC	Braby (2000)	AUS
47	*Terminalia sericocarpa* F. Muell.	-	-	Begg (1977)	AUS
	Terminalia sericocarpa F. Muell. [*Terminalia seriocarpa*]	*A. centaurus*	LYC	Braby (2000)	AUS
		A. madytus	LYC	Braby (2000)	AUS

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
48		*Terminalia* spp.	Scale insect sp.	COC+	Dodd (1902)	AUS
CONVOLVULACEAE						
49	*	*Ipomoea indica* (Burm.) Merr.	-	-	Blüthgen *et al.* (2004)	AUS
50		*Merremia peltata* Merrill	*Milviscutulus* sp.	COC	Blüthgen & Fiedler (2002)	AUS
			Sextius cf. *'kurandae'*	MEM	Blüthgen & Fiedler (2002)	AUS
DIPTEROCARPACEAE						
51		*Balanocarpus heimii* King	*Anthene emolus goberus* Fruhstorfer	LYC	Saarinen (2006)	MYS
52		*Shorea talura* Roxb.	*Coccus* sp. [*Lecanium* sp.]	COC	Mahdihassan (1976)	IND
EBENACEAE						
53		*Diospyros calycantha* O. Schwarz	-	-	Begg (1977)	AUS
ELAEOCARPACEAE						
54	*	*Elaeocarpus angustifolius* Blume	-	-	Blüthgen *et al.* (2004)	AUS
EUPHORBIACEAE						
55		*Croton schultzii* Benth.	-	-	Begg (1977)	AUS
56		*Croton verreauxii* Baill.	-	-	Begg (1977)	AUS
57	*	*Endospermum myrmecophilum* L.S.Sm.	-		Blüthgen *et al.* (2004)	AUS
58		*Hevea brasiliensis* (Willd. ex A.H.L. Jussieu) Müll. Arg.	*Parasaissetia nigra* (Neitner) [*Saissetia nigra* (Nietn.)]	COC	Anon (1968)	MYS
59	*	*Homalanthus novoguineensis* (Warb.) K.Schum.	-	-	Blüthgen *et al.* (2004)	AUS
60	*	*Macaranga involucrata* subsp. *mallotoides* (F.Muell.) L.M.Perry	-	-	Blüthgen *et al.* (2004)	AUS
61	*	*Mallotus mollissimus* (Geiseler) Airy Shaw	-	-	Blüthgen *et al.* (2004)	AUS
62	*	*Rockinghamia angustifolia* (Benth.) Airy Shaw	-	-	Blüthgen *et al.* (2004)	AUS
FABACEAE						
63		*Abrus precatorius* L.			Begg (1977)	AUS

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
64	*	*Acacia acradenia* F. Muell. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
65	*	*Acacia alexandri* Maslin [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
66	*	*Acacia anceps* DC. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
67		*Acacia aulacocarpa* A. Cunn. ex Benth. [MIMO]	-	-	Peng *et al.* (1997b)	AUS
68		*Acacia auriculiformis* A. Cunn. ex Benth.			Begg (1977)	AUS
	*	*Acacia auriculiformis* A. Cunn. ex Benth. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
			-	-	Peng *et al.* (1997b)	AUS
69	*	*Acacia crassicarpa* A. Cunn. ex Benth. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
70	*	*Acacia flavescens* A. Cunn. ex Benth. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
71	*	*Acacia harpophylla* F. Muell. ex Benth. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
72		*Acacia hemignosta* A. Cunn. ex Benth. [MIMO]	-	-	Peng *et al.* (1997b)	AUS
73	*	*Acacia holosericea* A. Cunn. ex G. Don [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
			-	-	Peng *et al.* (1997b)	AUS
74	*	*Acacia mangium* Willd. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
			-		Peng *et al.* (1997b)	AUS
75	*	*Acacia neriifolia* A. Cunn. ex Benth. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
76	*	*Acacia polystachya* A. Cunn. ex Benth. [MIMO]	*Anthene lycaenoides* C.Felder	LYC	Braby (2000)	AUS
77	*	*Acacia pycnantha* Benth. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
78	*	*Acacia salicina* Lindl. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
79	*	*Acacia saligna* (Labill.) H. L. Wendl. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
80	*	*Acacia tetragonophylla* F. Muell. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
81	*	*Acacia victoriae* Benth. [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
82		*Bauhinia monandra* Kurz [LEGU]	*Pseudococcus lilacinus* Cockerell	PSE	Le Pelley (1943)	PHL
83	*	*Caesalpinia bonduc* (L.) Roxb. [CAES]	*A. lycaenoides*	LYC	Braby (2000)	AUS
84	*	*Caesalpinia crista* L. [CAES]	*A. lycaenoides*	LYC	Braby (2000)	AUS
85	*	*Caesalpinia mexicana* A. Gray [CAES]	*A. lycaenoides*	LYC	Braby (2000)	AUS
86		*Caesalpinia pulcherrima* (L.) Sw. [CAES]	-		Peng *et al.* (1997b)	AUS
87		*Caesalpinia traceyi* L. Pedley [CAES]	*Coccus* sp.	COC	Blüthgen & Fiedler (2002)	AUS
			Sextius cf. *'kurandae'*	MEM	Blüthgen & Fiedler (2002)	AUS
88	*	*Cajanus reticulatus* (Aiton) F. Muell.	*T. miskini*	LYC	Braby (2000)	AUS
89	*	*Calliandra houstoniana* (Mill.) Standl. [MIMO]	*A. lycaenoides*	LYC	Braby (2000)	AUS
90	*	*Calliandra surinamensis* Benth. [MIMO]	*A. lycaenoides*	LYC	Braby (2000)	AUS
91		*Canavalia rosea* (Sw.) DC. [*Canavalia maritima*]	-		Begg (1977)	AUS
92	*	*Cassia auriculata* L. [CAES]	*A. lycaenoides*	LYC	Braby (2000)	AUS
			Z. chrysomallus	LYC	van der Poorten & van der Poorten (2006)	LKA
93	*	*Cassia fistula* L.	*Anthene lycaenoides godeffroyi* (Semper)	LYC	Valentine (1988); Braby (2000)	AUS
	*	*Cassia fistula* L. [CAES]	*A. lycaenoides*	LYC	Braby (2000)	AUS
	*		*Anthene seltuttus* Röber	LYC	Valentine (1988); Braby (2000)	AUS
			H. phorbas	LYC	Braby (2000)	AUS
94		*Castanospermum australe* A. Cunn. & C. Fraser ex Hook.	*H. phorbas*	LYC	Braby (2000)	AUS
95	*	*Cathormion umbellatum* (Vahl) Kosterm.	*T. miskini*	LYC	Braby (2000)	AUS
96		*Dalbergia sissoo* Roxb. ex DC.	*Coccus hesperidum* L. [*Lecanium hesperidum*]	COC	Dutt (1912)	IND

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
			Hilda bengalensis	TET	Dutt (1912)	IND
			Icerya sp.	MAR	Dutt (1912)	IND
			Oxyrhachis tarandus F.	MEM	Dutt (1912)	IND
97		*Delonix regia* (Bojer ex Hook.) Raf. [CAES]	*A. seltutus*	LYC	Braby (2000)	AUS
98	*	*Dendrolobium umbellatum* (L.) Benth.	*A. lycaenoides*	LYC	Braby (2000)	AUS
99		*Entada phaseoloides* Merrill [MIMO]	*Coccus* sp.	COC	Blüthgen & Fiedler (2002)	AUS
			Planococcus citri (Risso)	PSE	Blüthgen & Fiedler (2002)	AUS
			Sextius cf. *'kurandae'*	MEM	Blüthgen & Fiedler (2002)	AUS
100		*Erythrophleum chlorostachys* (F. Muell.) Baill. [CAES]	-	-	Peng *et al.* (1997b)	AUS
101		*Inocarpus fagifer* (Parkinson) Fosberg [*Inocarpus edulis*]	*M. malaitensis, Paraputo leveri* (Green) (*comb. nov.)*	PSE	Williams (1960)	SLB
102	*	*Millettia pinnata* (L.) Panigrahi	*A. lycaenoides*	LYC	Braby (2000), Lokkers (1986)	AUS
			A.seltutus	LYC		
		Millettia pinnata (L.) Panigrahi [*Pongamia pinnata]*	-	-	Lokkers (1986)	AUS
103	*	*Paraserianthes lophanta* (Willd.) I. C. Nielsen [MIMO]	*T. miskini*	LYC	Braby (2000)	AUS
104		*Pueraria phaseoloides* (Roxb.) Bth.	*Catochrysops panormus* Felder	LYC	Ballmer (2003)	THA
			Rapala pheretima Hewitson	LYC	Ballmer (2003)	THA
105		*Saraca thaipingensis* Cantley ex Prain	*A. seltutus*	LYC	Braby (2000)	AUS
		Saraca thaipingensis Cantley ex Prain [CAES]	*A. emolus goberus*	LYC	Fiedler & Maschwitz (1989)	MYS
106		*Schotia brachypetala* Sond.	*A. seltutus*	LYC	Braby (2000)	AUS
107	*	*Senna alata* (L.) Roxb.	*A. lycaenoides*	LYC	Braby (2000)	AUS
			H. phorbas	LYC	Braby (2000)	AUS

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
108	*	*Senna auriculata* (L.) Roxb.	*A. lycaenoides*	LYC	Braby (2000)	AUS
109	*	*Senna gaudichaudii* (Hook. & Arn.) H. S. Irwin & Barneby [*Senna retusa*]	*A. lycaenoides*	LYC	Braby (2000)	AUS
110	*	*Senna surattensis* (Burm. f.) H. S. Irwin & Barneby	*A. lycaenoides*	LYC	Braby (2000)	AUS
111	*	*Sesbania cannabina* (Retz.) Pers.	*T. miskini*	LYC	Braby (2000)	AUS
112	*	*Sesbania javanica* Miq. [*Sesbania javanicus*]	*T. miskini*	LYC	Braby (2000)	AUS
113	*	*Sesbania* sp.	*T. miskini*	LYC	Braby (2000)	AUS
FLAGELLARIACEAE						
114	*	*Flagellaria indica* Linn.	*A. lycaenoides*	LYC	Braby (2000)	AUS
			H. phorbas	LYC	Braby (2000)	AUS
			Scale insect sp.	COC+	Blüthgen & Fiedler (2002)	AUS
LAMIACEAE						
115		*Clerodendrum floribundum* (R.Br.) [VERB]	*H. phorbas*	LYC	Braby (2000)	AUS
116		*Clerodendrum inerme* (L.) Gaertn. [VERB]	*H. phorbas*	LYC	Braby (2000)	AUS
117	*	*Clerodendrum* sp. [VERB]	*A. lycaenoides*	LYC	Braby (2000)	AUS
118	*	*Clerodendrum tracyanum* (F.Muell.) F.Muell. Ex Benth	-	-	Blüthgen *et al.* (2004)	AUS
119	*	*Faradaya splendida* F. Muell. [VERB]	*A. lycaenoides*	LYC	Braby (2000)	AUS
			A. micale	LYC	Braby (2000)	AUS
			H. phorbas	LYC	Braby (2000)	AUS
120		*Tectona grandis* L. f.	-		Dutt (1912)	IND
		Tectona grandis L. f. [VERB]	*P. lilacinus*	PSE	Le Pelley (1943)	PHL
121		*Vitex acuminata* R. Br.	-	-	Begg (1977)	AUS
LAURACEAE						
122		*Cryptocarya hypospodia* F. Muell.	*A. seltutus*	LYC	Braby (2000)	AUS
			A. micale	LYC	Braby (2000)	AUS

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
			Toxoptera aurantii (Boyer de Fonscolombe)	APH	Blüthgen & Fiedler (2002)	AUS
			unidentified immatures	COC	Blüthgen & Fiedler (2002)	AUS
123	*	*Cryptocarya murrayi* F.Muell.	-		Blüthgen *et al.* (2004)	AUS
124		*Endiandra* cf. *monothyra* B.P.M. Hyland	*Coccus* sp., *Milviscutulus* sp	COC	Blüthgen & Fiedler (2002)	AUS
			not collected	LYC	Blüthgen & Fiedler (2002)	AUS
			Sextius cf. *'kurandae'*	MEM	Blüthgen & Fiedler (2002)	AUS
125		*Endiandra microneura* C.T. White	*A. centaurus* group	LYC	Blüthgen & Fiedler (2002)	AUS
			Coccus sp., *Milviscutulus* sp	COC	Blüthgen & Fiedler (2002)	AUS
			T. aurantii	APH	Blüthgen & Fiedler (2002)	AUS
			unidentified	ERI	Blüthgen & Fiedler (2002)	AUS
126		*Litsea glutinosa* (Lour.) C.B.Rob.	-	-	Begg (1977)	AUS
127		*Persea americana* Mill.	-	-	Peng *et al.* (1997b)	AUS
LECYTHIDACEAE						
128		*Planchonia careya* (F. Muell.) R. Knuth	*H. phorbas*	LYC	Braby (2000)	AUS
					Peng *et al.* (1997b)	AUS
LOGANIACEAE						
129		*Strychnos lucida* R. Br.	-	-	Begg (1977)	AUS
LORANTHACEAE						
130		*Dendrophthoe vitellina* (F. Muell.) Tiegh.	*A. centaurus*	LYC	Braby (2000)	AUS
			H. phorbas	LYC	Braby (2000)	AUS
131		*Loranthus* sp. 1	*P. citri* [*Dactylopius citri (Pseudococcus citri)*]	PSE	Green (1913)	IDN
			Saissetia coffeae (Walker) [*Lecanium hemisphaericum (Saissetia hemisphaericum)*]	COC	Green (1913)	IDN
132		*Loranthus* sp. 2	*Z. chrysomallus*	LYC	van der Poorten & van der	LKA

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
					Poorten (2006)	
LYTHRACEAE						
133		*Lagerstroemia speciosa* (L.) Pers.	*A. seltutus, A. centaurus, A. micale*	LYC	Braby (2000)	AUS
134		*Sonneratia caseolaris* (L.) Engl.	Coccid sp.	COC	Macnae (1968)	MYS
MALPIGHIACEAE						
135	*	*Rhyssopterys timoriensis* (DC.) Blume ex A.H.L. Jussieu [*Rhyssopterys timorensis*]	*A. lycaenoides*	LYC	Braby (2000)	AUS
MALVACEAE						
136		*Argyrodendron peralatum* (F.M. Bailey) Edlin ex J.H.Boas [STER]	-	-	Blüthgen & Fiedler (2002)	AUS
137		*Bombax ceiba* L.	-	-	Begg (1977)	AUS
138		*Brachychiton acerifolius* (A. Cunn. ex G. Don) Macarthur [STER]	*A. seltutus*	LYC	Braby (2000)	AUS
139		*Heritiera littoralis* Aiton [STER]	*A. micale*	LYC	Braby (2000)	AUS
140		*Sterculia quadrifida* R. Br.			Begg (1977)	AUS
141		*Taliparititi liliaceum* (L.) Fryxell [*Hibiscus tiliaceus*]	*A. madytus, A. micale*	LYC	Braby (2000)	AUS
			-	-	Tan (2001)	SGP
142		*Theobroma cacao* L.	-	-	Stapley (1980)	SLB
		Theobroma cacao L. [STER]	*M. malaitensis, P. citri*	PSE	Williams (1960)	SLB
			P. lilacinus	PSE	Way & Khoo (1991)	MYS
			Tricentrus sp.	MEM	Way & Khoo (1991)	MYS
MELASTOMATACEAE						
143	*	*Memecylon umbellatum* Kostel	*Rachisphora* sp.	ALE	Jesudasan *et al.* (2004)	IND
MELIACEAE						
144	*	*Dysoxylum mollissimum* subsp. *molle* (Miq.) D.J.Mabberley	-	-	Blüthgen *et al.* (2004)	AUS

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
145	*	*Dysoxylum papuanum* Mabb.	-	-	Blüthgen *et al.* (2004)	AUS
146	*	*Dysoxylum pettigrewianum* F.M.Bailey	-	-	Blüthgen *et al.* (2004)	AUS
147		*Khaya ivorensis* A. Chev.	-	-	Khoo (2001)	MYS
148	*	*Toona ciliata* M.Roem	-	-	Blüthgen *et al.* (2004)	AUS
149		*Vavaea australiana* S.T. Blake	-	-	Begg (1977)	AUS
150		*Xylocarpus moluccensis* (Lam.) M. Roem.	*A. micale*	LYC	Braby (2000)	AUS
151		*Xylocarpus* sp.	Coccid sp.	COC	Macnae (1968)	MYS
MENISPERMACEAE						
152	*	*Pachygone longifolia* F.M.Bailey	-	-	Blüthgen *et al.* (2004)	AUS
153		*Pachygone ovata* (Poir.) Hook. f. & Thomson	-	-	Begg (1977)	AUS
154		*Stephania japonica* Miers	Scale insect sp.	COC+	Blüthgen & Fiedler (2002)	AUS
MORACEAE						
155		*Artocarpus heterophyllus* Lam.	-	-	Saarinen (2006)	MYS
156		*Ficus madurensis* Miq.	-	-	Fiedler & Maschwitz (1989)	MYS
157		*Ficus opposita* Miq.	-	-	Peng *et al.* (1997b)	AUS
158		*Ficus pantoniana* King	*Icerya* sp.	MAR	Blüthgen & Fiedler (2002)	AUS
159		*Ficus religiosa* L.	*C. hesperidum* [*L. hesperidum*]	COC	Dutt (1912)	IND
			H. bengalensis	TET	Dutt (1912)	IND
			Icerya sp.	MAR	Dutt (1912)	IND
			O. tarandus F.	MEM	Dutt (1912)	IND
160		*Ficus septica* Burm. f.	*L. painei*	PSE	Williams (1960)	SLB
161		*Ficus* sp.	*L. painei*	PSE	Williams (1960)	SLB
162		*Ficus* spp.	Scale insect sp.	COC+	Dodd (1902)	AUS
163		*Malaisia scandens* (Lour.) Planch.	-	-	Begg (1977)	AUS
MYRISTICACEAE						

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
164		*Myristica insipida* R.Br.	*Milviscutulus* sp.	COC	Blüthgen & Fiedler (2002)	AUS
			Sextius cf. *'kurandae'*	MEM	Blüthgen & Fiedler (2002)	AUS
MYRSINACEAE						
165		*Aegiceras corniculatum* (L.) Blanco	*H. phorbas*	LYC	Braby (2000)	AUS
166	*	*Ardisia pachyrrachis* (F.Muell.) F.M.Bailey	-	-	Blüthgen *et al.* (2004)	AUS
167	*	*Embelia caulialata* S.T.Reynolds	-	-	Blüthgen *et al.* (2004)	AUS
MYRTACEAE						
168		*Acmena graveolens* L.S. Smith	*Milviscutulus* sp.	COC	Blüthgen & Fiedler (2002)	AUS
169		*Acmena* sp.	*A. micale*	LYC	Braby (2000)	AUS
			H. phorbas	LYC	Braby (2000)	AUS
170		*Corymbia intermedia* (R. T. Baker) K. D. Hill & L. A. S. Johnson	*A. centaurus*	LYC	Braby (2000)	AUS
			Narathura araxes eupolis (Miskin)	LYC	Quick (1974)	AUS
171	*	*Corymbia polycarpa* (F. Muell.) K. D. Hill & L. A. S. Johnson	*T. miskini*	LYC	Braby (2000)	AUS
172		*Corymbia ptychocarpa* (F. Muell.) K. D. Hill & L. A. S. Johnson	*A. centaurus*	LYC	Braby (2000)	AUS
173		*Corymbia tessellaris* (F. Muell.) K. D. Hill & L. A. S. Johnson	*A. centaurus*	LYC	Braby (2000)	AUS
174		*Eucalyptus alba* Reinw. ex Blume	-	-	Lokkers (1986)	AUS
175	*	*Eucalyptus confertiflora* F. Muell.	*T. miskini*	LYC	Braby (2000)	AUS
176	*	*Eucalyptus drepanophylla* F. Muell. ex Benth.	*T. miskini*	LYC	Braby (2000)	AUS
177		*Eucalyptus foelscheana* F. Muell.	-	-	Peng *et al.* (1997b)	AUS
178		*Eucalyptus miniata* A. Cunn. ex Schauer	-	-	Peng *et al.* (1997b)	AUS
179		*Eucalyptus papuana* F. Muell.	-	-	Lokkers (1986)	AUS
180		*Eucalyptus* sp. 1	*A. centaurus*	LYC	Braby (2000)	AUS
181	*	*Eucalyptus* sp. 2	*T. miskini*	LYC	Braby (2000)	AUS
182		*Eucalyptus tectifica* F. Muell.	-	-	Peng *et al.* (1997b)	AUS

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
183		*Eucalyptus tetrodonta* F. Muell.	-	-	Peng *et al.* (1997b)	AUS
184	*	*Eucalyptus torelliana* F. Muell.	*T. miskini*	LYC	Braby (2000)	AUS
185		*Lophostemon lactifluus* (F. Muell.) Peter G. Wilson & J. T. Waterh.	-	-	Peng *et al.* (1997b)	AUS
186		*Lophostemon suaveolens* (Sol. ex Gaertn.) Peter G. Wilson & J. T. Waterh. *[Tristania suaveolens]*	-	-	Lokkers (1986)	AUS
187		*Melaleuca leucadendra* (L.) L.	-	-	Peng *et al.* (1997b)	AUS
188		*Melaleuca quinquenervia* (Cav.) S. T. Blake	*A. centaurus*	LYC	Braby (2000)	AUS
			N. araxes eupolis	LYC	Quick (1974)	AUS
189		*Melaleuca viridiflora* Sol. ex Gaertn.	-		Peng *et al.* (1997b)	AUS
190		*Psidium guajava* L.	*P. lilacinus*	PSE	Le Pelley (1943)	PHL
			Z. chrysomallus	LYC	van der Poorten & van der Poorten (2006)	LKA
			-	-	Jinda (1982); Way & Khoo (1991)	MYS
191		*Ristantia pachysperma* (Bailey) Peter G. Wilson & J.T. Waterh.	*A. micale*	LYC	Braby (2000)	AUS
192		*Syzygium cormiflorum* B.P.M. Hyland	*A. micale*	LYC	Braby (2000)	AUS
			Coccus sp., *Milviscutulus* sp	COC	Blüthgen & Fiedler (2002)	AUS
193	*	*Syzygium cumini* (L.) Skeels	*Rachisphora* sp.	ALE	Jesudasan *et al.* (2004)	IND
			-	-	Begg (1977)	LKA
			-	-	Dutt (1912)	IND
194	*	*Syzygium 'erythrocalyx'* B.Hyland	-	-	Blüthgen *et al.* (2004)	AUS
195		*Syzygium* sp.aff. *erythrocalyx*	*A. micale*	LYC	Braby (2000)	AUS
196		*Syzygium eucalyptoides* (F. Muell.) B. Hyland	-	-	Peng *et al.* (1997b)	AUS
197		*Syzygium jambos* (L.) Alston	-	-	Chanaranothai & Parnell (1994)	THA

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
198		*Syzygium megacarpum* (Craib) N.C.Rathakrishnan & N.C.Nair	-	-	Chanaranothai & Parnell (1994)	THA
199		*Syzygium samarangense* (Blume) Merr. & L. M. Perry	-	-	Chanaranothai & Parnell (1994)	THA
200		*Syzygium sayeri* B.P.M. Hyland	Coccid sp.	COC+	Blüthgen & Fiedler (2002)	AUS
201		*Syzygium suborbiculare* (Benth.) T.G. Hartley & L.M. Perry	-	-	Peng *et al.* (1997b)	AUS
202		*Syzygium tierneyanum* (Benth.) T.G. Hartley & L.M. Perry	*A. micale*	LYC	Braby (2000)	AUS
203		*Syzygium wilsoni* (F. Muell.) B. Hyland	*A. seltutus, H. phorbas*	LYC	Braby (2000)	AUS
204		*Xanthostemon paradoxus* F. Muell.	-	-	Peng *et al.* (1997b)	AUS
OLEACEAE						
205	*	*Jasminum didymum* G.Forst	-	-	Blüthgen *et al.* (2004)	AUS
PANDANACEAE						
206		*Pandanus spiralis* R. Br.	-	-	Peng *et al.* (1997b)	AUS
PASSIFLORACEAE						
207		*Adenia heterophylla* (Blume) Koord.	-	-	Begg (1977)	AUS
PHYLLANTACEAE						
208		*Breynia stipitata* Mull. Arg.	-	-	Begg (1977)	AUS
209	*	*Bridelia tomentosa* Blume [*Briedelia tomentosa*] [EUPH]	*A. lycaenoides*	LYC	Braby (2000)	AUS
210		*Glochidion ferdinandi* (Mull. Arg.) F.M. Bailey [EUPH]	*A. micale*	LYC	Braby (2000)	AUS
211	*	*Glochidion philippicum* (Cav.) C.B.Rob. [EUPH]	-	-	Blüthgen *et al.* (2004)	AUS
PROTEACEAE						
212		*Cardwellia sublimis* F. Muell.	*Austrotartessus* sp.	CIC	Blüthgen & Fiedler (2002)	AUS
			Coccus sp.	COC	Blüthgen & Fiedler (2002)	AUS

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
213	*	*Macadamia integrifolia* Maiden & Betche	*N. berenice*	LYC	Braby (2000)	AUS
214	*	*Macadamia tetraphylla* L. A. S. Johnson	*N. berenice*	LYC	Braby (2000)	AUS
215		*Persoonia falcata* R.Br.	-	-	Peng *et al.* (1997b)	AUS
PUTRANJIVACEAE						
216		*Drypetes lasiogyna* (F. Muell.) Pax & K. Hoffm.	-	-	Begg (1977)	AUS
RHAMNACEAE						
217		*Ziziphus oenoplia* (L.) Mill.	-	-	Begg (1977)	AUS
RHIZOPHORACEAE						
218		*Bruguiera* sp.	Coccid sp.	COC	Macnae (1968)	MYS
219		*Ceriops tagal* (Perr.) C.B. Robb	*H. phorbas*	LYC	Braby (2000)	AUS
220		*Ceriops* sp.	Coccid sp.	COC	Macnae (1968)	MYS
221		*Rhizophora* mucronata (Lam.)	-	-	Offenberg *et al.* (2004)	THA
RUBIACEAE						
222		*Aidia cochinchinensis* Lour. [*Randia cochinchinensis*]	-	-	Begg (1977)	AUS
223		*Coffea excelsa* A. Chev.	*Coccus viridis* Green	COC	Miller (1931)	MYS
224		*Coffea robusta* L. Linden	*C. viridis*	COC	Miller (1931)	MYS
225		*Coffea* sp. 1	*C. viridis*		Balakrishnan *et al.* (1992)	IND
226		*Coffea* sp. 2	*C. viridis* [*Lecanium viridis* Green]	COC	Corbett (1937)	MYS
227		*Ixora klanderiana* F. Muell. [*Ixora klanderana*]	-	-	Begg (1977)	AUS
228	*	*Ixora pavetta* Andrews	*Rachisphora* sp.	ALE	Jesudasan *et al.* (2004)	IND
229		*Morinda citrifolia* L. [COMB]	-	-	Tan (2001)	SGP
230		*Timonius timon* (Spreng.) Merr.	-	-	Begg (1977)	AUS
					Peng *et al.* (1997b)	AUS
231		*Uncaria* sp.	-	-	Fiedler & Maschwitz (1989)	MYS

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
RUTACEAE						
232		*Citrus aurantiifolia* (Christm.) Swingle [*Citrus acida*]	*C. viridis*	COC	Miller (1931)	MYS
233		*Citrus limon* (L.) Burm. f.	-	-	Huang & Yang (1987)	CHN
234		*Citrus maxima* (Burm.) Merr.	-	-	Huang & Yang (1987)	CHN
235		*Citrus reticulata* Blanco	Coccid sp.	COC	Huang & Yang (1987)	CHN
			Mealybug sp.	PSE	Huang & Yang (1987)	CHN
			-	-	van Mele & Cuc (1999)	VNM
236		*Citrus sinensis* (L.) Osbeck	-	-	van Mele & Cuc (1999)	VNM
237		*Citrus* sp. 1	-	-	Dutt (1912)	IND
238		*Citrus* sp. 2	-	-	Greenslade (1971)	SLB
239		*Citrus* spp.	-	-	Way & Khoo (1991)	MYS
240		*Glycosmis trifoliata* (Blume) Spreng.	-	-	Begg (1977)	AUS
241		*Micromelum minutum* (G. Forst.) Seem.	-	-	Begg (1977)	AUS
SALICACEAE						
242		*Flacourtia* sp. [FLAC]	*S. coffeae* [*L. hemisphaericum (S. hemisphaericum)*]	COC	Green (1913)	IDN
SANTALACEAE						
243		*Exocarpos latifolius* R.Br.	-	-	Begg (1977)	AUS
SAPINDACEAE						
244	*	*Alectryon coriaceus* (Benth.) Radlk.	*N. berenice*	LYC	Braby (2000)	AUS
245	*	*Alectryon diversifolius* (F. Muell.) S.T. Reynolds [*Heterodendron diversifolium*]	*N. berenice*	LYC	Braby (2000)	AUS
246	*	*Arytera divaricata* F. Muell.	*N. berenice*	LYC	Braby (2000)	AUS
247		*Arytera pauciflora* S.T. Reynolds	*A. seltutus*	LYC	Braby (2000)	AUS
	*		*N. berenice*	LYC	Braby (2000)	AUS
248	*	*Atalaya hemiglauca* (F. Muell.) F. Muell. ex	*T. miskini*	LYC	Braby (2000)	AUS

Table 2.2. continued

#		Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
		Benth.				
249	*	*Atalaya salicifolia* (A.DC.) Blume	*N. berenice*	LYC	Braby (2000)	AUS
250	*	*Atalaya variifolia* (F. Muell.) Benth.	*T. miskini*	LYC	Braby (2000)	AUS
251		*Cupaniopsis anacardioides* (A. Rich.) Radlk.	*A. seltutus, A. micale, H. phorbas*	LYC	Braby (2000)	AUS
	*		*A. lycaenoides, N. berenice*	LYC	Braby (2000)	AUS
252		*Cupaniopsis sp.*	*A. centaurus*	LYC	Braby (2000)	AUS
253	*	*Litchi chinensis* Sonn.	*A. lycaenoides*	LYC	Braby (2000)	AUS
			-	-	Dutt (1912)	IND
			-	-	Hill (1983); Leu (2005)	AUS
254		*Nephelium lappaceum* L.	-	-	Leu (2005)	AUS
			-	-	Tsuji *et al.* (2004)	IDN
255		*Synima cordierii* Radlk.	*A. seltutus*	LYC	Blüthgen & Fiedler (2002)	AUS
SAPOTACEAE						
256		*Madhuca longifolia* (L.) J. F. Macbr. [*Bassia latifolia*]	*C. viridis*	COC	Miller (1931)	MYS
257		*Manilkara jaimiqui* (C. Wright) Dubard subsp. *emarginata* (L.) Cronquist [*Achras sapota*]	*C. viridis*	COC	Miller (1931)	MYS
258		*Pouteria sericea* (Aiton) Baehni	-	-	Begg (1977)	AUS
SMILACACEAE						
259		*Smilax australis* R. Br.	*H. phorbas*	LYC	Braby (2000)	AUS
	*	*Smilax* cf. *australis*	-	-	Blüthgen *et al.* (2004)	AUS
THEACEAE						
260		*Camellia sinensis* (L.) Kuntze	*Coccus discrepans* Green	COC	Das (1959)	IND
			C. hesperidum	COC	Das (1959)	IND
			Metaceronema japonica (Maskell) [*Eriochiton theae* Green]	COC [ERI]	Das (1959)	IND

Table 2.2. continued

#	Host plant species[1]	Associated trophobiont	Fam[2]	References	Ctry[3]
VERBENACEAE					
261	*Citharexylum subserratum* Swartz	-	-	Peng *et al.* (1997b)	AUS
VITACEAE					
262	*Cissus adnata* Roxb.	-	-	Begg (1977)	AUS
263	*Cissus cordata* Roxb.	-	-	Begg (1977)	AUS
ZINGIBERACEAE					
264	*Achasma* sp.	-	-	Fiedler & Maschwitz (1989)	MYS
VARIOUS FAMILIES					
265	-	*C. hesperidum*	COC	Blüthgen *et al.* (2004)	AUS

[1] Host plants were those on which the ant was reported nesting, while ant presence on plants, without specific mention of nesting indicated possible host plants and these are marked by an asterisk. There was some overlap where a plant species was classified both as a host plant and possible host plant based on different reports.
[2] Families: ALE, Aleyrodidae; APH, Aphididae; CIC, Cicadellidae; COC, Coccidae; ERI, Eriococcidae; LYC, Lycaenidae; MAR, Margarodidae; MEM, Membracidae; PSE, Pseudococcidae; TET, Tettigometridae. Superfamily: COC+, Coccoidea.
[3] Country: Australia (AUS), China (CHN), India (IND), Indonesia (IDN), Malaysia (MYS), Philippines (PHL), Singapore (SGP), Solomon Islands (SLB), Sri Lanka (LKA), Thailand (THA), Vietnam (VNM).

Table 2.3. Records of *Oecophylla longinoda* host plants and associated trophobionts from a survey of the literature (1900 to present). Currently accepted species and family names are used followed by names given in the original article within square brackets [ ], where different.

#	Host plant species	Associated trophobiont	Fam[1]	References	Ctry[2]
ANACARDIACEAE					
1	*Anacardium occidentale* L.	*Coccus* sp. nr. *hesperidum* L., *Parasaissetia nigra* (Neitn.) [*Saissetia. nigra* (Nietn.)], *Saissetia zanzibarensis* Williams	COC	Way (1954a)	ZAN
		Pseudococcus sp.	PSE	Way (1954a)	ZAN
2	*Mangifera indica* L.	*Coccus hesperidum* L., *Saissetia* sp. nr. *nigra* (Nietn.), *S. zanzibarensis*	COC	Way (1954a)	ZAN
		Pseudococcus sp., *Rastrococcus iceryoides* (Green) [*Phenacoccus iceryoides* Green]	PSE	Way (1954a)	ZAN
ANNONACEAE					
3	*Annona muricata* L.	*Parasaissetia* sp. nr. *nigra* [*Saissetia* sp. nr. *nigra*]	COC	Way (1954a)	ZAN
		Parastictococcus anonae (Green & Laing) [*Stictococcus anonae* Green & Laing]	STI	Way (1954a)	ZAN
4	*Annona senegalensis* Pers. [*Annona chrysophylla*]	*Isthmia* sp.	TET	Way (1954a)	ZAN
		P. nigra [*Saissetia* sp. ?*nigra*]	COC	Way (1954a)	ZAN
5	*Canangium odoratum* (Lam.) Baill. ex King	*P. anonae* [*S. anonae*]	STI	Way (1954a)	ZAN
APOCYNACEAE					
6	*Rauvolfia mombasiana* Stapf [*Rauwolfia mombasiana*]	*Coccus viridis* Green, *Saissetia* sp. nr. *coffeae* (Wlk.), *Udinia* sp. nr. *catori* (Green) [*Saissetia* sp. nr. *catori* (Green)]	COC	Way (1954a)	ZAN
		Pseudococcus sp.	PSE	Way (1954a)	ZAN
7	*Schizozygia coffaeoides* Baill. [*Schizozygia coffeoides*]	Membracid sp.	MEM	Way (1954a)	ZAN
		R. iceryoides [P. iceryoides]	PSE	Way (1954a)	ZAN

Table 2.3 continued

#	Host plant species	Associated trophobiont	Fam[1]	References	Ctry[2]
ARECACEAE					
8	*Areca catechu* L. [PALM]	*S. zanzibarensis*	COC	Way (1954a)	ZAN
9	*Cocos nucifera* L. [PALM]	*Cerataphis lataniae* Boisd.	APH	Way (1954a)	ZAN
		C. hesperidum, P. nigra [*S. nigra*], *S. zanzibarensis*	COC	Way (1954a)	ZAN
		Planococcus sp., *Pseudococcus cryptus* Hempel [*Pseudococcus citriculus* Green]	PSE	Way (1954a)	ZAN
ASTERACEAE					
10	*Ageratum* sp. [Compositae]	*Parasaissetia* sp. nr. *nigra* [*Saissetia* sp. nr. *nigra*]	COC	Way (1954a)	ZAN
		Pseudococcus sp.	PSE	Way (1954a)	ZAN
BIGNONIACEAE					
11	*Millingtonia hortensis* L. f.	*Udinia* sp. nr. *catori* [*Saissetia* sp. nr. *catori*]	COC	Way (1954a)	ZAN
BORAGINACEAE					
12	*Cordia aurantiaca* Baker [*Cordia aurentiaca*]			Djieto-Lordon & Dejean (1999)	CMR
BURSERACEAE					
13	*Canarium commune* L.	Membracid sp.	MEM	Way (1954a)	ZAN
		S. zanzibarensis	COC	Way (1954a)	ZAN
COLCHICACEAE					
14	*Gloriosa simplex* Linn. [Liliaceae]	*S. zanzibarensis*	COC	Way (1954a)	ZAN
COMBRETACEAE					
15	*Terminalia catappa* L.	Membracid sp.	MEM	Way (1954a)	ZAN
		Saissetia sp	COC	Way (1954a)	ZAN
CUCURBITACEAE					
16	*Momordica foetida* Schumach.	*Saissetia* sp. nr. *coffeae*	COC	Way (1954a)	ZAN
EUPHORBIACEAE					
17	*Alchornea laxiflora*(Benth.) Pax & K. Hoffm.			Holldobler (1979)	KEN
18	*Codiaeum* sp.	*Pseudococcus* sp.	PSE	Way (1954a)	ZAN

Table 2.3 continued

#	Host plant species	Associated trophobiont	Fam[1]	References	Ctry[2]
FABACEAE					
19	*Acacia glauca* (L.) Moench [*Leucaena glauca] [LEGU]*	*C. hesperidum*	COC	Way (1954a)	ZAN
20	*Afzelia quanzensis* Welw. [CAES]	-	-	Holldobler (1979)	KEN
21	*Bauhinia thonningii* Schumach. [LEGU]	*C. hesperidum*	COC	Way (1954a)	ZAN
		Membracid sp.	MEM	Way (1954a)	ZAN
		S. zanzibarensis	COC	Way (1954a)	ZAN
22	*Cassia* sp. [LEGU]	Membracid sp.	MEM	Way (1954a)	ZAN
		S. zanzibarensis	COC	Way (1954a)	ZAN
23	*Delonix regia* (Bojer ex Hook.) Raf. [LEGU]	*P. nigra* [*S. nigra*]	COC	Way (1954a)	ZAN
24	*Gliricidia sepium* (Jacq.) Kunth ex Walp. [LEGU]	*R. iceryoides [P. iceryoides]*	PSE	Way (1954a)	ZAN
		S. zanzibarensis	COC	Way (1954a)	ZAN
25	*Julbernardia magnistipulata* [CAES]	-	-	Holldobler (1979)	KEN
26	*Pithecellobium dulce* (Roxb.) Benth. [*Pithecollobium dulce*] [LEGU]	Membracid sp.	MEM	Way (1954a)	ZAN
27	*Tephrosia vogelii* Hook. f. [LEGU]	*C. hesperidum*	COC	Way (1954a)	ZAN
HYPERICACEAE					
28	*Harungana madagascariensis* Lam. ex Poir.	*C. viridis, Parasaissetia* sp. nr. *nigra* [*Saissetia* sp. nr. *nigra*], *S. zanzibarensis*	COC	Way (1954a)	ZAN
		Pseudococcus sp.	PSE	Way (1954a)	ZAN
		Xiphistes sp.	MEM	Way (1954a)	ZAN
29	*Vismia orientalis* Engl.	-	-	Holldobler (1979)	KEN
ICACINACEAE					
30	*Apodytes dimidiata* E. Mey. ex Bernh.	-	-	Holldobler (1979)	KEN
LAMIACEAE					
31	*Clerodendrum glabrum* E. May	*S. zanzibarensis*	COC	Way (1954a)	ZAN

Table 2.3 continued

#	Host plant species	Associated trophobiont	Fam[1]	References	Ctry[2]
	[*Clerodendron glabrum*] [VERB]				
32	*Tectona grandis* L. f. [VERB]	*C. hesperidum*	COC	Way (1954a)	ZAN
		Membracid sp.	MEM	Way (1954a)	ZAN
33	*Vitex doniana* Sweet [VERB]	*C. hesperidum, Saissetia* sp. nr. *coffeae*	COC	Way (1954a)	ZAN
LAURACEAE					
34	*Cassytha filiformis* L.	*Saissetia* sp. nr. o*leae* (Olivier) [*Saissetia* sp. nr. o*leae* (Bern.)]	COC	Way (1954a)	ZAN
35	*Persea americana* Mill.	*C. hesperidum, S. zanzibarensis*	COC	Way (1954a)	ZAN
LECYTHIDACEAE					
36	*Barringtonia racemosa* (L.) Spreng.	Membracid sp.	MEM	Way (1954a)	ZAN
		Parasaissetia sp. nr. *nigra* [*Saissetia* sp. nr. *nigra*], *Parthenolecanium* sp. nr. *persicae* (Fabricius) [*Coccus* sp. nr. e*longatus* (Sign.)]	COC	Way (1954a)	ZAN
LORANTHACEAE					
37	*Loranthus sansibarensis* Engl.	*Saissetia* sp	COC	Way (1954a)	ZAN
LYTHRACEAE					
38	*Sonneratia alba* Sm. (*Sonneratia caseolaris*) [SONN]	*P. nigra* [*S. nigra*], *Saissetia* sp. nr. o*leae* (Olivier) [*Saissetia* sp. nr. o*leae* (Bern.)]	COC	Way (1954a)	ZAN
MALVACEAE					
39	*Adansonia digitata* L. [BOMB]	Margarodid sp.	MAR	Way (1954a)	ZAN
		Parthenolecanium sp. nr. *persicae* [*Coccus* sp. nr. e*longatus*], *S. zanzibarensis, Udinia* sp. nr. *catori* [*Saissetia* sp. nr. *catori*]	COC	Way (1954a)	ZAN
40	*Durio zibethinus* L. [BOMB]	*Parthenolecanium* sp. nr. *persicae* [*Coccus* sp. nr. e*longatus*], *Udinia* sp. nr. *catori* [*Saissetia* sp. nr. *catori*]	COC	Way (1954a)	ZAN
41	*Grewia glandulosa* Vahl [TILI]	Margarodid sp.	MAR	Way (1954a)	ZAN
		R. iceryoides [*P. iceryoides*]	PSE	Way (1954a)	ZAN
42	*Malvaviscus grandiflorus* H.B. & K.	Coccid sp.	COC	Way (1954a)	ZAN
43	*Theobroma cacao* L. [STER]	*Pseudococcus* sp., *R. iceryoides* [*P. iceryoides (Phenacoccus iceryoides* Green)]	PSE	Way (1954a)	ZAN

Table 2.3 continued

#	Host plant species	Associated trophobiont	Fam[1]	References	Ctry[2]
		Toxoptera sp. *? aurantii* (Boy)	APH	Way (1954a)	ZAN
	Theobroma cacao L.	Stictococcid sp.	STI	Strickland (1951)	CIV
MELIACEAE					
44	*Turraea* sp.	-	-	Holldobler (1979)	KEN
MORACEAE					
45	*Artocarpus heterophyllus* Lam.	*C. hesperidum*	COC	Way (1954a)	ZAN
46	*Ficus* spp.	Margarodid sp.	MAR	Way (1954a)	ZAN
		P. nigra [*S. nigra*], *S. zanzibarensis*	COC	Way (1954a)	ZAN
		R. iceryoides [*P. iceryoides*]	PSE	Way (1954a)	ZAN
MYRTACEAE					
47	*Eucalyptus camaldulensis* Dehnh.	*Coccus* sp. ?*hesperidum, C. viridis, S. zanzibarensis*	COC	Way (1954a)	ZAN
48	*Psidium guajava* L.	*C. viridis, S. zanzibarensis*	COC	Way (1954a)	ZAN
		Pseudococcus sp.	PSE	Way (1954a)	ZAN
49	*Syzygium aromaticum* (L.) Merr. & L. M. Perry [*Jambosa caryophyllus* (*Eugenia aromatica*)]	*Coccus* sp. nr. *hesperidum, C. viridis, Eulecanium* sp., *Parasaissetia* sp. nr. *nigra* [*Saissetia* sp. nr. *nigra*], *Saissetia* sp. nr. *coffeae, S. zanzibarensis*	COC	Way (1954a)	ZAN
50	*Syzygium cumini* (L.) Skeels (*Eugenia jambolana*)	*Coccus* sp. nr. *viridis*	COC	Way (1954a)	ZAN
		Membracid sp.	MEM	Way (1954a)	ZAN
		S. zanzibarensis	COC	Way (1954a)	ZAN
51	*Syzygium jambos* (L.) Alston [*Jambosa jambos* (*Eugenia jambos*)]	*Coccus* sp. nr. *hesperidum, Eucalymnatus tessellatus* (Sign.), *S. zanzibarensis*	COC	Way (1954a)	ZAN
		Membracid sp.	MEM	Way (1954a)	ZAN
52	*Syzygium malaccense* (L.) Merr. & L. M. Perry [*Jambosa malaccensis* (*Eugenia malaccensis*)]	Membracid sp.	MEM	Way (1954a)	ZAN
OLACACEAE					
53	*Olax dissitiflora* Oliv.	-	-	Holldobler (1979)	KEN
OLEACEAE					

Table 2.3 continued

#	Host plant species	Associated trophobiont	Fam[1]	References	Ctry[2]
54	*Jasminum fluminense* Vell.	*S. zanzibarensis*	COC	Way (1954a)	ZAN
OXALIDACEAE					
55	*Averrhoa bilimbi* L.	*Pseudococcid* sp.	PSE	Way (1954a)	ZAN
		S. zanzibarensis	COC	Way (1954a)	ZAN
56	*Averrhoa carambola* L.	*S. zanzibarensis*	COC	Way (1954a)	ZAN
PASSIFLORACEAE					
57	*Passiflora quadrangularis* L.	*P. nigra* [*S. nigra*]	COC	Way (1954a)	ZAN
PHYLLANTHACEAE					
58	*Bridelia micrantha* (Hochst.) Baill.	Membracid sp.	MEM	Way (1954a)	ZAN
	[EUPH]	*P. nigra* [*S. nigra*]	COC	Way (1954a)	ZAN
59	*Uapaca alluminata* [CAES]	-	-	Djieto-Lordon & Dejean (1999)	CMR
RHAMNACEAE					
60	*Ziziphus mauritiana* Lam.	Pseudococcid sp.	PSE	Way (1954a)	ZAN
RHIZOPHORACEAE					
61	*Ceriops* sp.	*P. nigra* [*S. nigra*], *S. zanzibarensis*	COC	Way (1954a)	ZAN
62	*Rhizophora* mucronata (Lam.)	*S. zanzibarensis*	COC	Way (1954a)	ZAN
ROSACEAE					
63	*Eriobotrya japonica* (Thunb.) Lindl.	Coccid sp.	COC	Way (1954a)	ZAN
RUBIACEAE					
64	*Canthium zanzibaricum* Klotzsch	*C. hesperidum, Parasaissetia* sp. nr. *nigra* [*Saissetia* sp. nr. *nigra*], *S. zanzibarensis*	COC	Way (1954a)	ZAN
		Pseudococcus sp.	PSE	Way (1954a)	ZAN
65	*Chassalia umbraticola* Vatke	*C. viridis*	COC	Way (1954a)	ZAN
66	*Coffea excelsa* A. Chev.	*C. viridis, S. zanzibarensis*	COC	Way (1954a)	ZAN
67	*Coffea liberica* Bull. ex K. Shum.	*C. viridis, P. nigra* [*S. nigra*], *S. zanzibarensis*	COC	Way (1954a)	ZAN
			COC	Way (1954a)	ZAN
68	*Coffea robusta* L. Linden	*C. viridis, S. zanzibarensis*	COC	Way (1954a)	ZAN
69	*Polysphaeria* sp.	*C. viridis*	COC	Way (1954a)	ZAN

Table 2.3 continued

#	Host plant species	Associated trophobiont	Fam[1]	References	Ctry[2]
RUTACEAE					
70	*Citrus*, five spp.	*C. lantaniae*	APH	Way (1954a)	ZAN
		C. hesperidum, C. viridis, S. zanzibarensis	COC	Way (1954a)	ZAN
		Icerya seychellarum (Westw.)	MAR	Way (1954a)	ZAN
		P. citri, P. cryptus [*P. citriculus*], *Pseudococcus* sp.	PSE	Way (1954a)	ZAN
71	*Murraya paniculata* (L.) Jack	Coccid sp.	COC	Way (1954a)	ZAN
SAPINDACEAE					
72	*Nephelium lappaceum* L.	*C. hesperidum* L., *Udinia* sp. nr. *catori* [*Saissetia* sp. nr. *catori*]	COC	Way (1954a)	ZAN
		P. anonae [*S. anonae*]	STI	Way (1954a)	ZAN
73	*Paullinia pinnata* L.	Pseudococcid sp.	PSE	Way (1954a)	ZAN
SAPOTACEAE					
74	*Achras zapotilla* (Jacq.) Nutt.	*C. viridis, Saissetia* sp. nr. *coffeae*, *S. zanzibarensis*	COC	Way (1954a)	ZAN

[1]Families: APH, Aphididae; COC, Coccidae; MAR, Margarodidae; MEM, Membracidae; PSE, Pseudococcidae; STI, Stictococcidae; TET, Tettigometridae.
[2]Country: Cameroon (CMR), Cote D'Ivoire (CIV), Kenya (KEN), Zanzibar (ZAN)

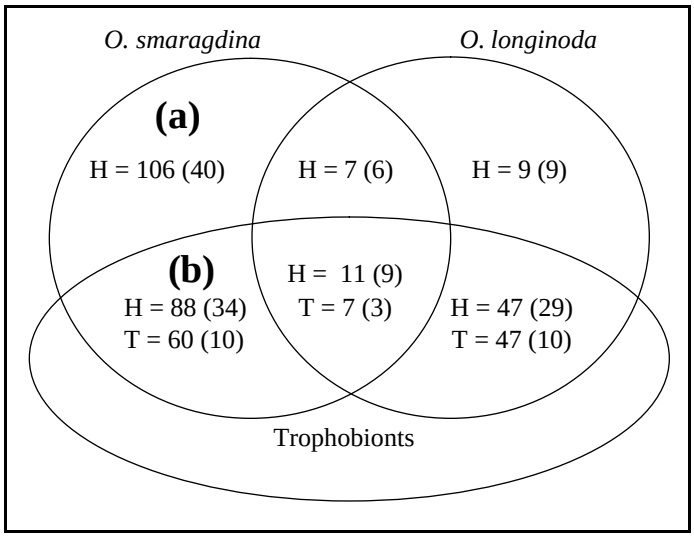

Figure 2.1. Number of host plant species, plant families and trophobiont species reported in the literature for *Oecophylla smaragdina* and *Oecophylla longinoda*. H, number of host plant species; T, number of trophobiont species. The number of families is stated in parentheses. Eighteen host plant species of *O. smaragdina*, which were not hosts of *O. longinoda* were reported with and without trophobionts, thus are repeated in subsets (a) and (b).

Table 2.4. Percentage of host plant species recorded in the literature for trophobionts tended by *Oecophylla smaragdina* and *Oecophylla longinoda*, and the distribution of trophobiont species by family. Number of species in parentheses.

Trophobiont taxon[1]	*O. smaragdina*		*O. longinoda*	
	% host plant species (n = 127)	% trophobiont species (n = 41)	% host plant species (n = 99)	% trophobiont species (n = 27)
Lycaenidae	46.5	24.4	-	-
Coccoidea	41.7	56.1	82.8	81.5
Coccidae	23.6	24.4	56.6	44.4
Pseudococcidae	9.4	19.5	18.2	22.2
Margarodidae	3.1	4.9	4.0	7.4
Eriococcidae	0.8	2.4	-	-
Stictococcidae	-	-	4.0	7.4
Membracidae	7.1	9.8	13.1	7.4
Aphididae	2.4	4.9	3.0	7.4
Tettigometridae	1.6	2.4	1.0	3.7
Cicadellidae	0.8	2.4	-	-
Total	100.0	100.0	100.0	100.0

[1]Scale insect families further grouped under the superfamily Coccoidea.

Table 2.5. Host plant species of *Oecophylla smaragdina* and associated trophobionts recorded in a survey of four habitats in Central West Peninsular Malaysia.

		Host plant species[1]	Trophobionts					NA[4]	Total
			Coccoidea[2]	Membracidae[3]	Lycaenidae	Aleyrodidae	Aphididae		
Lowland dipterocarp forest			6.7	-	-	-	-	-	6.7
*	1	*Bambusa* sp. (Poaceae)	1.7	-	-	-	-	-	1.7
	2	*Cocos nucifera* L. (Arecaceae)	1.7	-	-	-	-	-	1.7
*	3	*Mimusops elengi* L. (Sapotaceae)	1.7	-	-	-	-	-	1.7
*	4	*Samanea saman* (Jacq.) Merr. (Fabaceae)	1.7	-	-	-	-	-	1.7
Plantation forest			13.3	7.5	0.8	-	-	16.7	38.3
	5	*Hevea brasiliensis* (Willd. ex A.H.L. Jussieu) Müll. Arg. (Euphorbiaceae)	0.8	-	0.8	-	-	-	1.7
	6	*Khaya ivorensis* A. Chev. (Meliaceae)	12.5	7.5 (G Tr N)	-	-	-	16.7	36.7
Mangrove			58.1	64.7	19.7	0.8	-	10	153.3
*	7	*Acacia auriculiformis* A. Cunn. ex Benth. (Fabaceae)	18.6 (Ta T *T*)	3.6 (N)	1.9	0.8		6.7 (1.7)	31.7
*	8	*Bruguiera gymnorhiza* (L.) Savigny (Rhizophoraceae)	1.7	-	-	-	-	-	1.7
*	9	*Bruguiera parviflora* (Roxb.) Wight & Arn. ex Griff. (Rhizophoraceae)	1.7	-	-	-	-	-	1.7
	10	*Bruguiera* sp. (Rhizophoraceae)	5.0 (Co)	-	3.3	-	-	-	8.3

Table 2.5 continued

		Host plant species[1]	Trophobionts					NA[4]	Total
			Coccoidea[2]	Membracidae[3]	Lycaenidae	Aleyrodidae	Aphididae		
*	11	*Canthium foetidum* Hiern. (Rubiaceae)	-	1.7	-	-	-	-	1.7
*	12	*Derris trifoliata* Lour. (Fabaceae)	-	3.3	-	-	-	-	3.3
*	13	*Morinda citrifolia* L. (Rubiaceae)	20.5 (C)	22.2 (G *GN*)	7.2	-	-	3.4 (1.7)	53.3
*	14	*Sonneratia alba* Sm. (Lythraceae)	8.1 (E)	4.7	0.6	-	-	-	13.3
*	15	*Taliparitiliaceum* (L.) Fryxell (Malvaceae)	-	26.7	6.7	-	-	-	33.3
*	16	*Vitex pinnata* L. (Lamiaceae)	2.5	2.5	-	-	-	-	5.0
Orchard			5.5	0.7	1.3	-	0.5	1.0	9.0
	17	*Artocarpus heterophyllus* Lam. (Moraceae)	-	-	-	-	-	0.5	0.5
*	18	*Averrhoa bilimbi* L. (Oxalidaceae)	-	0.2 (G)	0.2	-	-	-	0.5
*	19	*Averrhoa carambola* L. (Oxalidaceae)	0.5	-	-	-	-	-	0.5
*	20	*Barringtonia* sp. (Lecythidaceae)	-	0.5	0.5	-	-	-	1.0
*	21	*Canarium megalanthum* Merr. (Burseraceae)	0.5 (Co)	-	-	-	-	-	0.5
	22	*Citrus aurantifolia* (Christm.) Swingle (Rutaceae)	0.3	-	-	-	-	-	0.3
	23	*Cocos nucifera* L. (Arecaceae)	0.5	-	-	-	-	-	0.5
*	24	*Garcinia mangostana* L. (Clusiaceae)	-	-	-	-	-	0.5	0.5
*	25	*Lansium domesticum* Corrêa (Meliaceae)	0.5 (Co)	-	-	-	-	-	0.5

Table 2.5 continued

		Host plant species[1]	Trophobionts					NA[4]	Total
			Coccoidea[2]	Membracidae[3]	Lycaenidae	Aleyrodidae	Aphididae		
	26	*Mangifera indica* L. (Anacardiaceae)	2.5 (Co)	-	-	-	-	-	2.5
*	27	*Nephellium lappaceum* L. (Sapindaceae)	-	-	0.5		-	-	0.5
*	28	*Solanum torvum* Sw. (Solanaceae)	-	-	-	-	0.5	-	0.5
*	29	*Syzygium samarangense* (Blume) Merr. & L. M. Perry (Myrtaceae)	0.5	-	-	-	-	-	0.5
		Total plant abundance	83.5	72.9	21.9	0.8	0.5	27.7	207.3

[1] Cell entries indicate the abundance (number of trees per ha) of a host plant species associated with a trophobiont taxon (number of trees per total habitat area: 6.0 ha for mixed fruit orchard and 1.8 ha for other habitats) followed by trophobiont species in parentheses (tentative identifications italicized). Asterisks denote new host plant species records for Malaysian *O. smaragdina*. Host plant species recorded outside the survey: At mangroves, *Allophylus* sp. (Sapindaceae) and *Terminalia catappa* L. (Combretaceae).
[2]C, Coccidae; Co, *Coccus hesperidium* L.; E, *Exallomochlus* sp.; Ta, *Tachardina aurantiaca* Cockerell; T, *Tachardina* sp.
[3]G, *Gargara* sp.; N, *Nilautama minutispina* Funkhouser; Tr, *Tricentrus* sp.
[4]Not collected. Abundance of plant species where no trophobionts were found is stated in parentheses.

mangroves, *Ficus* sp. (Moraceae) with membracids and *Chromolaena odorata* (L.) R. M. King & H. Rob. (Asteraceae) with mealybugs; and for orchards, *Saccharum* sp. with *Planococcus minor* Maskell and *Exallomochlus* sp. nr. *hispidus* (Pseudococcidae), and *Psidium guajava* with coccids

Of the 21 new host plant records (Table 2.5), 11 were new species records for *Oecophylla* spp.: *Bambusa* sp. (Poaceae), *Bruguiera gymnorhiza, Bruguiera parviflora* (Rhizophoraceae), *Canthium foetidum* (Rubiaceae), *Canarium megalanthum* (Burseraceae), *Vitex pinnata* (Lamiacae), *Mimusops elengi* (Sapotaceae), *Samanea saman, Derris trifoliata* (Fabaceae), *Lansium domesticum* (Meliaceae) and *Solanum torvum* (Solanaceae). From the 11, two are new genera records for *O. smaragdina*, i.e., *Canthium* and *Vitex*, previously recorded as hosts of *O. longinoda*. Two plants from the genus *Canarium* were previously reported as hosts to both *Oecophylla* spp., but *C. megalanthum* is the first specific record for *O. smaragdina.* Likewise, the *Bruguiera* spp. recorded in this study provide the first specific records for *O. smaragdina*, as previous records were to genus only. Also, *Averrhoa bilimbi, Averrhoa carambola* (Oxalidaceae), *Barringtonia* sp. (Lecythidae) and *Sonneratia alba* (Lythraceae) were previously reported for *O. longinoda* alone.

The survey also recorded new trophobiont-host plant associations. *Acacia auriculformis* is a new host plant species record for *Tachardina aurantiaca* Cockerell (Kerridae) in Malaysia. *T. aurantiaca* has been recorded on *Acacia sphaerocephala* Schltdl. & Cham., the sole record for that plant genus, and reported on a total of 17 plants (six families) (Ben-Dov 2005b). This lac scale is listed as an invasive species and mutualistic 'partner in crime' with the yellow crazy ant (*Anoplolepis gracilipes* Fr. Smith), which is a common pest in Malaysian households (Na & Lee 2001) and listed among 100 of the "World's Worst" invaders (O'Dowd 2006).

Three other new records of coccoid-plant associations were of *C. hesperidum* on *C. megalanthum* and *L. domesticum* and *Exallomochlus* sp. (Pseudococcidae) on *S. alba. C. hesperidum* is a highly polyphagous soft scale occurring on over 380 host plants including those from the family Meliaceae, and is a pest of citrus and many other fruit tree species (Ben-Dov 2005c). *Exallomochlus hispidus* Morrison is considered an invasive species (Anon 2005) but not much is mentioned in the literature for the genus. New records of membracid-plant associations were that of *Nilautama minutispina* Funkhouser on *A. auriculiformis, K. ivorensis,* and possibly *M. citrifolia*. A CAB Direct database search showed no records of host plants for this membracid species.

Two other potential new records of trophobiont-plant species associations were of several membracid species in the genera *Gargara* and *Tricentrus*. The *Gargara* spp. that were tended by *O. smaragdina* on *A. auriculiformis, K. ivorensis* and *M. citrifolia* could not be identified to species, as the group needs revision (McKamey, S.H., personal communication). In Malaysia, *Gargara* spp. and *Tricentrus* spp. were recorded with no host plants specified (Goding 1930), and *Tricentrus caliginosus* Wlk. has been reported as a pest of *Uncaria gambir* (Miller 1929).

The largest total number of *O. smaragdina* host plant species was found in the orchard habitat, however the mangroves had the highest abundance of ant-occupied plants (Table 2.5). Five ant-occupied plant species with the highest abundance in their respective habitats were *Morinda citrifolia* (Rubiaceae), *K. ivorensis, Taliparti tiliaceum* (Malvaceae), *Acacia auriculiformis* (Fabaceae) and *Sonneratia alba.* The ant also occurred on *Bruguiera* spp., which were categorized into a single group, as it is difficult to distinguish among the

species of this genus in the absence of fruit or inflorescence (Sheue *et al*. 2005). With the exception of *K. ivorensis*, all the other host plant species were recorded from the mangrove forest. The ant was found nesting in those plants, aggregating on the parts of the plant with nectaries, and actively tending trophobionts that also tended to cluster around extrafloral nectaries and floral nectaries, buds and shoots.

Figure 2.2 summarizes the abundance of ant-occupied trees and characteristics of the ant colonies in the habitats surveyed. Ant-occupied tree density (Figure 2.2.a) was marginally significant for *habitat* (F = 4.00; d.f. = 3, 8; P = 0.052). Density of ant-occupied trees in the mangrove habitat (51 ± 24 trees per ha) was greater (P = 0.042) than that in the forest habitat (2 ± 2 trees per ha), but not from that for the plantation and orchard habitats (mean = 13 and 3 trees per ha; SE = 10 and 1; respectively). Density of ant-occupied trees for the forest, plantation and orchard habitats were also not different.

Nest density (number of nests per ha; Figure 2.2.b) was not significant for *habitat* (F = 3.07; d.f. = 3, 8; P = 0.091). Habitats had a mean nest density of 65 ± 49 nests per ha. Colony density (number of colonies per ha; Figure 2.2.c) was also not significant for habitat (F = 2.77; d.f. = 3, 8; P = 0.110). Habitats had a mean colony density of 7 ± 3 colonies per ha.

The number of trees per colony (Figure 2.2.d) was not significant for *site* nested within *habitat* (F = 1.53; d.f. = 6, 48; P = 0.189), and the response variable was evaluated across *habitat*. The number of trees per colony was not significant for *habitat* (F = 0.26; d.f. = 3, 48; P = 0.856). Habitats had a mean of 1.9 ± 0.4 trees per colony.

The number of nests per colony (Figure 2.2.e) was not significant for *site* nested within *habitat* (F = 2.12; d.f. = 6, 48; P = 0.068), and the response variable was evaluated across *habitat*. The model of nests per colony was not significant for *habitat* (F = 1.95; d.f. = 3, 48; P = 0.135). Habitats had a mean of 6.3 ± 2.6 nests per colony.

Figure 2.3 summarizes site characteristics of the four habitats surveyed. The model of tree density (Figure 2.3.a) was not significant for *site* nested within *habitat* (F = 0.88; d.f. = 7, 22; P = 0.535), and tree density was evaluated across *habitat*. The model was significant for *habitat* (F = 9.95; d.f. = 3, 22; P = 0.000): orchard mean tree density (489 ± 59 trees per ha) was lower than that in forest, plantation and mangrove habitats (mean = 2222, 1556 and 1556 trees per ha; SE = 1198, 401 and 231; respectively).

The model of tree size (Figure 2.3.b) was not significant for *site* nested within *habitat* (F = 2.00; d.f. = 7, 22; P = 0.102), and tree size was evaluated across habitat. The model was significant for *habitat* (F = 17.47; d.f. = 3, 22; P = 0.000): orchard mean tree size (20.5 ± 2.1 cm) was greater than the forest, plantation and mangrove habitats (mean = 2.7, 7.9 and 7.7 cm; SE = 1.5, 2.4 and 0.7; respectively). Mangrove mean tree size was greater than that in the forest habitat, but not different from plantation mean tree size. Plantation and forest mean tree sizes were not different.

The model of stand basal area (Figure 2.3.c) was not significant for *site* nested within *habitat* (F = 2.36; d.f. = 7, 22; P = 0.059), and stand basal area was evaluated across *habitat*. The model was significant for *habitat* (F = 4.60; d.f. = 3, 22; P = 0.012): orchard mean stand basal area (42 ± 23 m^2 per ha) was greater than that for the forest and plantation habitats (mean = 7 and 12 m^2 per ha; SE = 6 and 5; respectively). The difference in mean stand basal area between orchard and mangrove habitats was marginally significant (P = 0.055). Mangrove mean stand basal area was 9 ± 2 m^2 per ha. Forest, plantation and mangrove habitats were not different from each other in mean stand basal area.

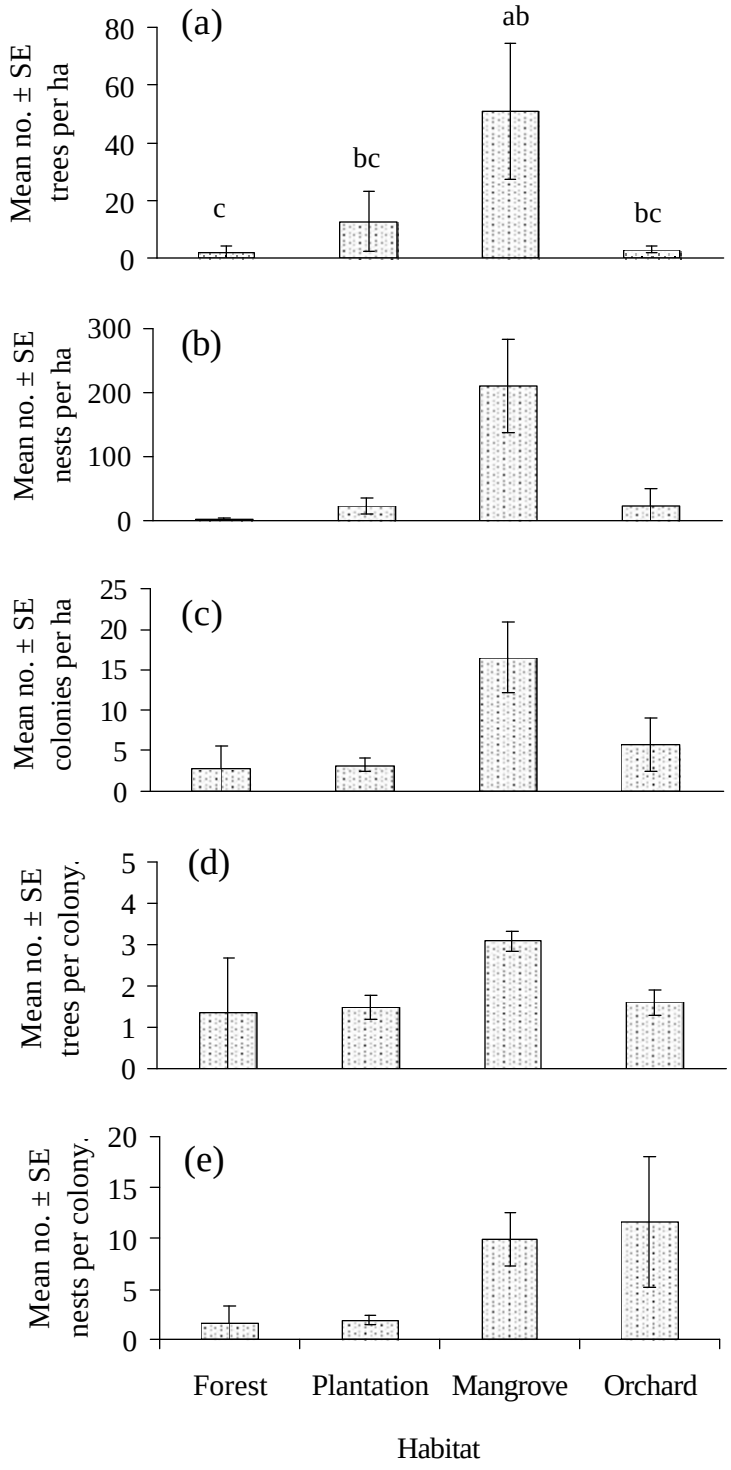

Figure 2.2. Abundance of *Oecophylla smaragdina*-occupied trees and some colony characteristics for four habitats surveyed in Central West Peninsular Malaysia: (a) Mean number of trees (± SE) per ha, (b) Mean number of nests (± SE) per ha, (c) Mean number of colonies (± SE) per ha, (d) Mean number of trees (± SE) per colony, (e) Mean number of nests (± SE) per colony. Only one site recorded ant-occupied trees for the forest habitat. Means with the same letter were not significantly different ($P \geq 0.05$).

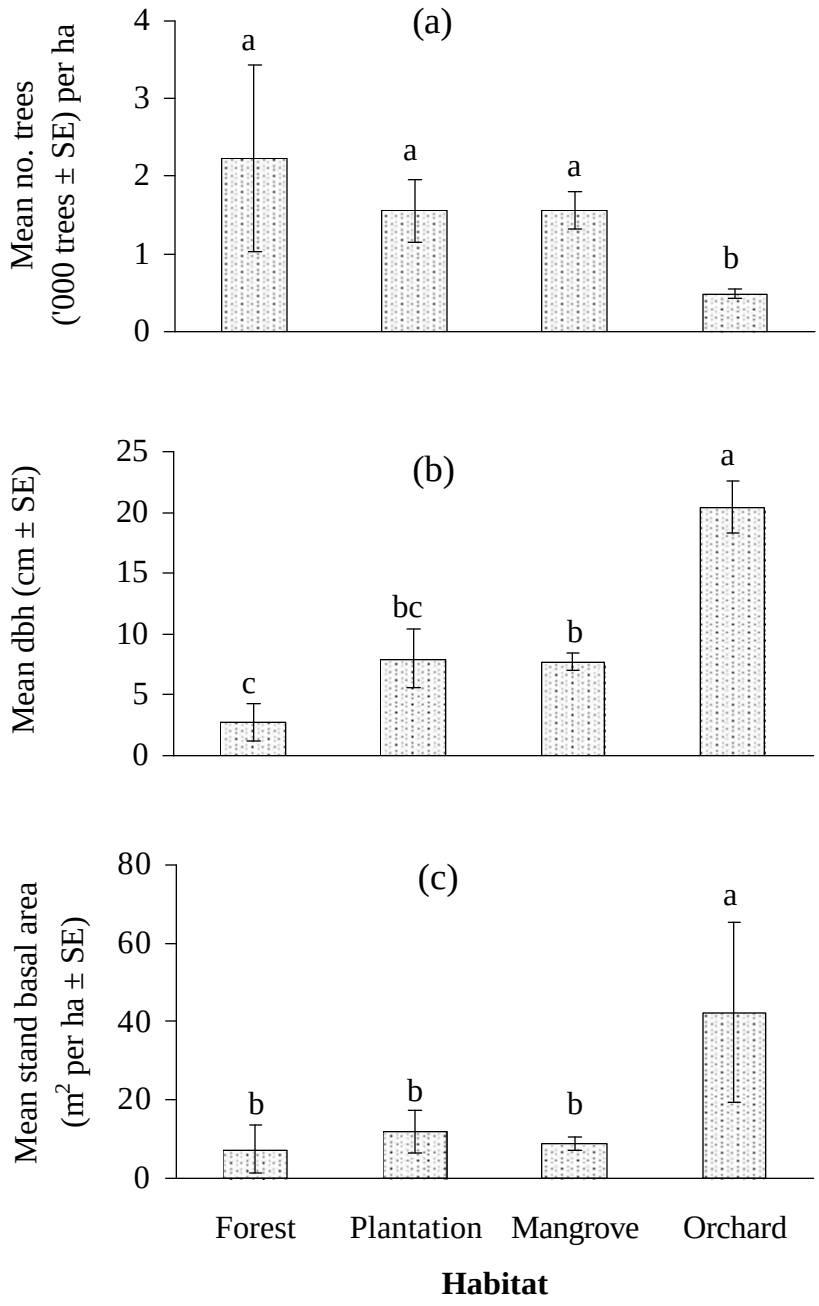

Figure 2.3. Site characteristics (n = 3) of four habitats surveyed for *Oecophylla smaragdina* host plant species in Central West Peninsular Malaysia: (a) Mean number of trees (± SE) per ha, (b) Mean dbh (cm ± SE), and (c) Mean stand basal area (m^2 per ha ± SE). Means with the same letter were not significantly different ($P \geq 0.05$; but includes a marginally significant difference ($p = 0.055$) between mangrove and orchard habitats in (c))

Discussion

Literature survey

The number of host plant species reported for *O. smaragdina* was more than double that for *O. longinoda*, suggesting a greater research interest toward the former or a wider geographic distribution with a more diverse plant community. Recent contributions to the *O. smaragdina* host plant species and trophobiont records (Peng *et al*. 1997b; Braby 2000; Blüthgen & Fiedler 2002) comprised over half the records and reflect the current research interest toward this ant species. On the contrary, the majority of host plant species for *O. longinoda* were reported in 1954a (Way).

The 18 host plant species common to both ant species were largely fruit or cash crop species cultivated in the tropics around the world (Table 2.6) and about half the host plant species reported for either ant species are economically important or of value to human society. Thus, there is a large potential pool of value-added host plant species from which candidates that favor either ant species may be chosen. However, since the trophobionts tended by both ant species were mostly polyphagous and regarded as crop pests, selection of candidates should consider the pest risk of associated trophobionts.

Oecophylla spp. may have similar preferences in the trophobiont families with which they associate. The two ant species appeared to associate with several trophobiont taxa, particularly those from the family Membracidae and superfamily Coccoidea. With regard to the disparity in lycaenid records between the two ant species, the scarcity of records for *O. longinoda*-lycaenid associations may be due to lack of study and not because these associations do not exist.

Host plant survey

Several host plant species that appeared to favor the ant were identified for further evaluation as candidates to interplant with mahogany, i.e., *M. citrifolia, T. tiliaceum, A. auriculiformis, S. alba* and *Bruguiera* spp.. The partial identification of the trophobionts collected on *K. ivorensis* and other host plants precluded conclusive pest risk analyses of trophobionts for *K. ivorensis.* However, the abundance of scale insects found with *O. smaragdina* on healthy-looking *K. ivorensis* in the survey (G.T. Lim, personal observation) suggests that the selection of a host plant species based on ant-preference may be more important than pest risk posed by trophobionts. The preliminary pest risk analyses for identified trophobionts follows.

Morinda citrifolia and *T. tiliaceum* appear promising as these species did not record specific trophobiont associates that are considered pests. It is important that no coccoid trophobionts were found on *T. tiliaceum* because coccoid trophobionts appeared to pose a greater pest risk than membracids. However, *M. citrifolia* had numerous coccoids that were not identified, so the absence of pest coccoids associated with this host plant species cannot be assumed.

Acacia auriculiformis was not an ideal candidate because it supported the pest lac scale *T. aurantiaca* and its attendant pest ant, *A. gracilipes*, which may compete with *O. smaragdina* (Way & Bolton 1997). In its favor, however, is the fact that the lac scale that it supports is unlikely to become a pest of *K. ivorensis* because the host range of *T. aurantiaca* does not include Meliaceous plants. *A. auriculiformis* is also a hardy tree that grows well under a wide range of environmental and soil conditions and has potential for general utility

Table 2.6. Host plant species common to *Oecophylla smaragdina* and *Oecophylla longinoda* reported in the literature.

Host plant species	Family	Common name
Annona muricata	Annonaceae	Soursop, anona
Areca catechu	Arecaceae	Areca
Artocarpus heterophyllus	Moracceae	Jackfruit
Cocos nucifera	Arecaceae	Coconut
Coffea excelsa	Rubiaceae	Coffee
Coffea robusta	Rubiaceae	Coffee
Delonix regia	Fabaceae	Flame tree
Mangifera indica	Anacardiaceae	Mango
Nephelium lappaceum	Sapindaceae	Rambutan
Persea americana	Lauraceae	Avocado
Psidium guajava	Myrtaceae	Guava
Rhizophora mucronata	Rhizophoraceae	Mangrove
Syzygium cumini	Myrtaceae	Java plum, jamun
Syzygium jambos	Myrtaceae	Rose apple
Tectona grandis	Lamiaceae	Teak
Terminalia catappa	Combretaceae	Tropical almond
Theobroma cacao	Malvaceae	Cocoa

timber and for pulp and paper in Malaysia (Ahmad Zuhaidi *et al*. 2002). Interestingly, *T. aurantiaca* is also tended by ants from the genus *Dolichoderus* (Hymenoptera: Formicidae) (Lim *et al*. 2001) of which the species *Dolichoderus thoracicus* Smith is a proven biological control agent in cocoa (Ho & Khoo 1997).

Two mangrove plants, i.e., *Bruguiera* sp. and *S. alba*, are generally limited to mangrove habitats and may not be amenable for interplanting in plantations due to site requirement incompatibility. Additionally, the former harbored *C. hesperidum*, which may pose a pest risk to mahogany. *C. hesperidum* has not been reported on the genus *Khaya* or *Swietenia* (Meliaceae), but has been reported on the genus *Cedrela* and *Toona* (Meliaceae) (Ben-Dov 2005c), so its host range may include *Khaya* and/or *Swietenia* spp. because they are Meliaceous trees.

The host plant species were clearly separated by habitat, with the only overlap being *Cocos nucifera*, which was found in a forest and an orchard site. The data indicated that the selection of habitats for the survey effectively maximized the number of host plant species recorded while keeping redundancy to a minimum. The large number of ant-occupied plants recorded for mangrove species indicate that these plant species may favor the ant, but did not show selection preferences. The host plant survey did not account for the relative abundance of those plant species within their respective habitats. Overall, the results of colony characteristics agreed with a previous report by Holldobler (1983a). Mean colony density (7.1 ± 3.2 colonies per ha) recorded in the present study was within the range of 6 – 25 colonies per ha, but mean colony size (1.9 ± 0.4 trees per colony) was in the lower range of 3 – 21 trees per colony. The mangrove habitat recorded the largest colony (covering 13 trees), while the other habitats had colonies occupying 3 – 5 trees, at most.

The variability in the habitat characteristics in this study reflected their diverse management practices. The orchards, which were managed for fruit production had a significantly lower mean stocking density (489 ± 59 trees per ha) than the other habitats, which were either extensively managed (forest and mangrove) or comprised young stands (plantations). The significantly greater mean tree size (20.5 ± 2.1 cm) and stand basal area (42 ± 23 m^2 per ha) in orchards indicated high stand quality. 'Good' sites tend to have stand basal area values ranging from 10 - 60 m^2 per ha and exceptional sites may have values of up to 150 m^2 per ha (Brack 1999). A stand basal area of 160 m^2 per ha was recorded at one of the orchard sites, which had very mature trees.

The results of the host plant survey suggested that the ant preferred some host plant species over others but were not conclusive. The high number of ant-occupied trees for a particular host plant species in its habitat could also have been because trees of that species were more abundant in that habitat. For example, the high number of ant-occupied *K. ivorensis* trees was likely because the plantations surveyed largely comprised this host plant species. Similarly, the high number of ant-occupied *M. citrifolia* trees in the mangrove habitat could have been due to an abundance of that host plant species rather than preference. Comparing the relative abundance of ant-occupied trees for various host plant species in the same habitat could determine the selection preferences of the ant for those species. The next study addresses this by determining ant preference for three host plant species (*M. citrifolia, T. tiliaceum* and *Bruguiera* spp.), which had the highest number of ant-occupied trees in one of the mangrove sites surveyed.

Chapter 3

Preference of the weaver ant for four plant species in a mangrove habitat

Introduction

The weaver ants, *Oecophylla longinoda* Latreille in tropical forested Africa (Ledoux 1950) and *Oecophylla smaragdina* F. in South-East Asia, Australia and the Western Pacific Islands (Dodd 1902; Dutt 1912; Chen 1962; Stapley 1980; Van Mele & Cuc 2000) are dominant ants in their respective habitats. They form large polydomous colonies housed in many nests constructed in the crowns of a wide range of host plant species (Way 1954a; Holldobler 1979; Holldobler 1983a). These host plants provide the ants with living leaves from which the ants' nests are constructed, and also supply floral and extra-floral nectar that supplements prey items and trophobiont honeydew that form a large part of the ants' diet (Nixon 1951; Way 1963). The host plants also support the trophobiont species that the ants tend, and certain keystone host plant species that hosted a few key trophobiont (homopteran) species were found to influence the distribution of dominant ants, including *O. smaragdina* in an Australian rainforest (Blüthgen *et al*. 2004).

In a survey of four diverse habitats in Central West Peninsular Malaysia that recorded 29 host plant species (21 families) for *O. smaragdina*, five host plant species with the highest abundance (per ha) of ant-colonized trees were identified (Chapter 2). Planting *Oecophylla*-favored host plants with several fruit and cash crops was proposed to create a more stable environment in which the ants can flourish as biological control agents (Way & Khoo 1991; Peng *et al*. 1997b). The preference of the ant toward certain host plant species may be due to the availability of nectar from extra-floral and floral nectaries, honeydew from associated trophobionts, pliable foliage for nest building, and a continuous provision of growing plant tissue that would support honeydew production (Blüthgen & Fiedler 2002).

Likewise, *O. smaragdina*, identified as a promising biological control agent for an important forest insect pest (*Hypsipyla robusta* Moore (Lepidoptera: Pyralidae)) in Malaysia (Lim & Kirton 2003), could establish more successfully if introduced into a mixed-system where *Khaya ivorensis* A. Chev. (the plantation forest tree species that is also a host to the ant) is planted with an alternate favored host plant species (Chapter 2). The ideal candidate for mixed-planting in such a situation should support trophobionts that have a low pest risk toward the crop and be able to support the production of a sufficiently large quantity of honeydew by the trophobionts, thus meaningfully provisioning the *O. smaragdina* population in the area. Additionally, the *O. smaragdina* 'nurse plant' candidate and the trophobiont species associated with it should be highly preferred by the ant yet be less attractive than the mahogany species (and associated trophobiont species), that is in need of the ants' protection (Chapter 2).

The present study evaluated the preference of *O. smaragdina* for three apparently favored host plant species: 1) *Morinda citrifolia* L. (Rubiaceae), 2) *Talipariti tiliaceum* (L.) Fryxell (Malvaceae), and 3) *Bruguiera* spp. (Rhizophoraceae), and a non-host plant species, 4) *Avicennia officinalis* L. (Acanthaceae), as the control. The first three species together with *Acacia auriculiformis* A. Cunn. Ex Benth. (Fabaceae) were identified as having the highest number of ant-occupied trees per ha in the mangrove habitats in which they are usually found (Chapter 2). While this indicated preference, it was not conclusive because it did not take

into the account the relative abundance of those species in the habitat and the present study addresses that question.

Materials and Methods

The study was carried out in July 2005 at the Kuala Selangor Nature Park, Malaysia (3°17'N, 101°16'E). The site was selected because three of the five host plant species identified previously as *O. smaragdina* 'nurse plant' candidates appeared well represented in the area (G.T. Lim, personal observation). Also, the density of ant-occupied trees (11.7 trees per ha; Chapter 2) at the site was moderately high. This site would provide a meaningful number of ant-occupied trees for comparative analyses among host plant species.

The study site was located along a 2.5 km trail bordered by a coastal 'bund' (berm) on one side and a man-made lake and village on the other. Mangroves cover a significant portion on the seaward side of the bund, while secondary forest plant species have succeeded the former mangrove forest on the landward side (Lim *et al*. 2003). A census of host plant species was first undertaken to select blocks where host plant species occurred together and in numbers high enough to permit meaningful comparisons among them. The site was divided into five blocks of 500 m each, and a complete block census of *O. smaragdina* host plant species was conducted for a fixed area plot of 3,000 m^2, i.e., 3 m sample width of the vegetation bordering each side of and perpendicular to the trail. Host plant species were selected for *O. smaragdina* preference evaluation that were represented by a minimum of 20 individuals of each species present in at least all four blocks. Twenty individuals of each host plant species were then randomly sampled from each block. *Bruguiera* spp. were categorized into a single group, as it is difficult to distinguish between the species of this genus, particularly in the absence of fruit or inflorescence (Sheue *et al*. 2005).

Crown width and height were measured with marked measuring poles to calculate crown surface area, which is a surrogate for the photosynthetic area of the tree. Crown surface area could influence the preference of the ant for the tree, because the ant nests were mostly built using young leaves on the crown periphery (G.T. Lim, personal observation). Young leaves are commonly utilized by *O. smaragdina* for nest-building (Majer 1972; Begg 1977; Holldobler 1983a; Blüthgen & Fiedler 2002). Crown width (*D*) was defined as the diameter of the crown at its widest section, and crown depth (*L*) was defined as the length along the main axis of the tree from the tree tip to the base of the crown (Brack 1999). Crown surface area was calculated assuming the crowns were a cylindrical shape, the form of many of the trees censused, although variation in form occurred across and within species. The estimated crown surface area excluded the surface area at the base of the crown and was calculated as:

Crown surface area, $Ca = \pi r^2 + 2\ p r\ (L)$,where $r = \frac{1}{2}D$ (cm)

Ant abundance was inferred from a nest volume index. Nest diameter (*d*) was used to calculate individual nest volume (*v*) assuming a spherical nest shape:

$$v = [4/3\ (\pi\ r^3)], \quad \text{where, } r = \tfrac{1}{2}\ d \text{ (cm)}$$

To account for the possible variation in crown surface area (*Ca*) across the host plant species, a relative nest volume was then calculated by dividing the total volumes of nests on a plant (*V*) by the *Ca* of that plant to obtain the ant abundance index (V_{rel}):

$$V_{rel} = (\sum v) \div Ca$$

Statistical analyses

Analyses of variance were carried out using the statistical software Minitab 14® (MINITAB 2007) and non-parametric analyses were carried out using StatsDirect (StatsDirect 2007). Mean crown surface area of trees in a block, nest counts per tree for all ant-occupied trees across blocks, and mean nest size for ant-occupied trees in a block was analyzed using one-way analysis of variance (ANOVA) with the factor *plant species.* Results for all analyses of variance were $\log_{10}$ transformed to achieve normality and equality of variances. All analyses of variance were followed by Tukey's honestly significant difference test to separate treatment means (Zar 1999), and results were assessed for significance at $P \leq 0.05$. Data for net relative nest volume index per block did not achieve normality or equality of variances after applying the appropriate transformations and were analyzed with the factor *plant species,* using Friedman's test. The Friedman test was followed by Conover's pairwise comparisons between plant species (Conover 1999), and the results were assessed for significance at $P \leq 0.01$. Friedman's test is slightly less powerful than the *F*-test when the number of blocks (< 10) or treatments (< 6) is small (O'Gorman 2001). Finally, the number of trees with trophobionts for ant-occupied vs. non ant-occupied trees was analyzed using Chi-Square.

Results

Based on the fixed area plot census of *O. smaragdina* host plant species in the five blocks along the 2.5 km trail, four blocks were available that contained at least 20 individuals of three of the host plant species to be evaluated, which were narrowed down to *Bruguiera* spp., *M. citrifolia* and *T. tiliaceum* (Table 3.1). However, Block 3 had only 14 *T. tiliaceum* trees, and relative abundance calculations were adjusted accordingly.

Figure 3.1 depicts the relative abundance of the ant in relation to the plant species, and colony and plant characteristics of ant-occupied plants. Net relative nest volume index per block was significant for *plant species* ($T_2 = 12.72$; d.f. = 3, 9; $P = 0.0014$; Figure 3.1.a). With respect to this response variable, *M. citrifolia* (186 ± 113 cm^3 per m^3) was greater than *T. tiliaceum*, *Bruguiera* spp. and the non-host plant *A. officinalis* (mean = 26, 21 and 0 cm^3 per m^3; SE = 17, 10 and 0, respectively). The latter three plant species were not different at $P \leq 0.01$, but both *Bruguiera* spp. and *T. tiliaceum* were different from *A. officinalis* at $P \leq 0.05$.

Mean crown surface area per tree was significant for *plant species* ($F = 8.88$; d.f. = 3, 12; $P = 0.002$; Figure 3.1.b). *M. citrifolia* crown surface area (23 ± 4 m^2) was smaller than that of *Bruguiera* spp and *A. officinalis* but not *T. tiliaceum* (mean = 81, 69 and 51 m^2; SE = 10, 13 and 12; respectively). *Bruguiera* spp. crown surface area per tree was greater than that for *T. tiliaceum* but not different from that of *A. officinalis. A. officinalis* crown surface area per tree was not different from that of *T. tiliaceum*.

Mean number of nests per tree for ant-occupied trees was significant for *plant species* ($F = 7.20$; d.f. = 2, 46; $P = 0.002$; Figure 3.1.c). *M. citrifolia* had fewer nests (2.2 ± 0.1, n = 26) per tree than *Bruguiera* spp. (4.7 ± 2.5 nests per tree, n = 11). The number (3.3 ± 0.7, n = 13) of *T. tiliaceum* nests per tree was not different from *M. citrifolia* or *Bruguiera* spp.

Mean nest size for ant-occupied trees was not significant for *plant species* ($F = 0.61$; d.f. = 2, 7; $P = 0.570$; Figure 3.1.d). *M. citrifolia* nest size (167 ± 46 cm^3) appeared slightly

Table 3.1. Number of representative trees of *Oecophylla smaragdina* host plant species and a non-host plant (*Avicennia officinalis*) along a five-block 2.5 km trail located on a bund in a Malaysian mangrove forest. The boxed section represents blocks of host plant species selected to evaluate preference by the ant.

Plant species[1]	Block[1]				
	1	2	3	4	5
Brugueira spp. (Rhizhophoraceae)	161	218	105	187	735
Avicennia officinalis L.[2] (Acanthaceae)	231	106	84	87	53
Morinda citrifolia L. (Rubiaceae)	25	20	46	22	0
Talipariti tiliaceum (L.) Fryxell (Malvaceae)	40	85	14	20	0
Allophylus sp . (Sapindaceae)	15	13	7	25	0
Sonneratia sp. (Sonneratiaceae)	0	0	7	0	0
Acacia auriculiformis A. Cunn. Ex Benth (Fabaceae)	0	5	0	0	0
Hopea odorata Roxb. (Dipterocarpaceae)	0	0	0	7	0
Ficus sp. (Moraceae)	0	0	16	8	0
Brugueira spp. (Rhizhophoraceae)	472	447	279	356	788

[1]Each block had at least 20 individuals of each plant species, with the exception of *T. tiliaceum* in Block 3.

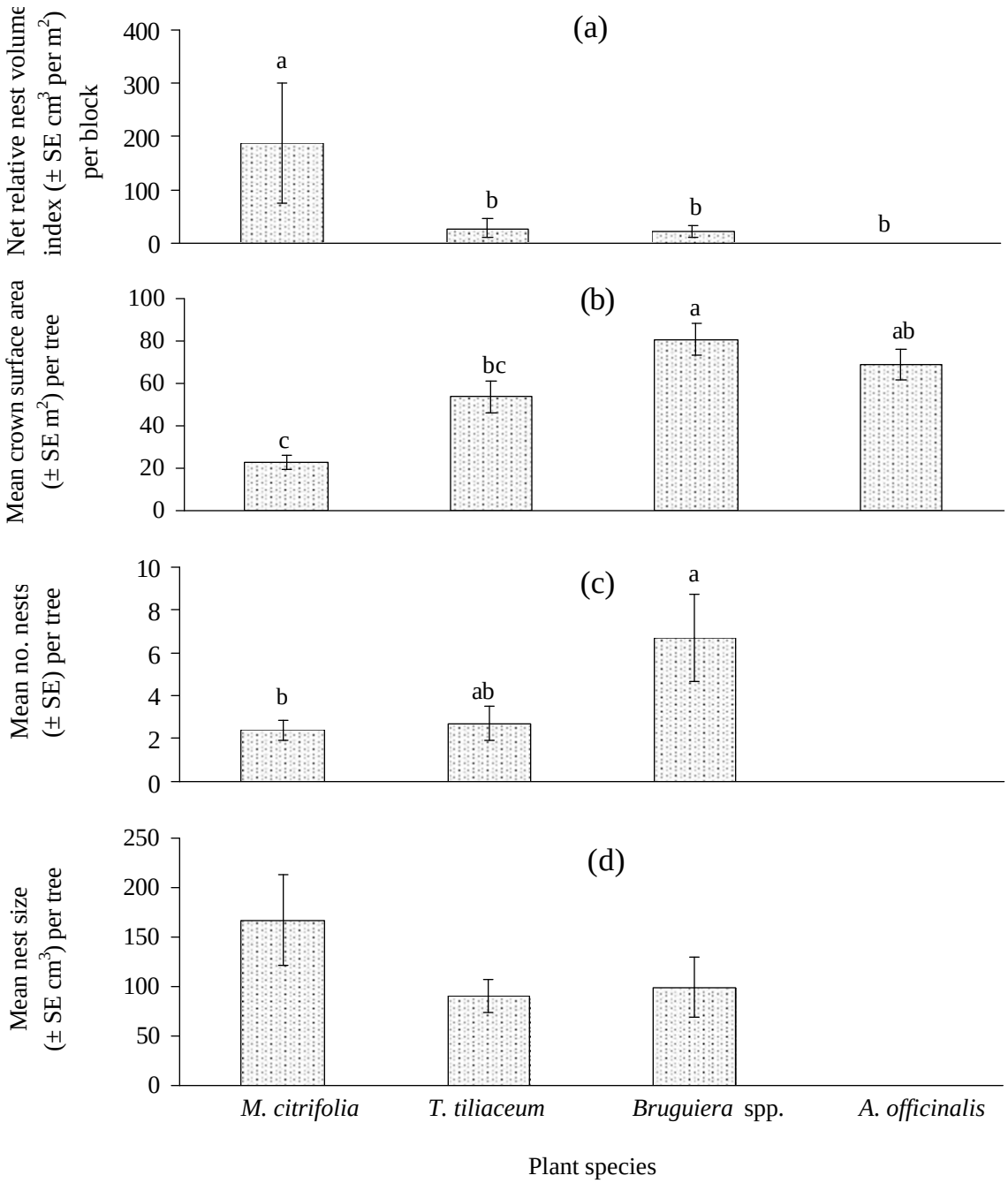

Figure 3.1. Relative abundance of *Oecophylla smaragdina* in relation to three host- and one non-host- plant species (*A. officinalis*) in a Malaysian mangrove, and some colony and plant characteristics of plants occupied by the ant: (a) Net relative nest volume index (cm^3 per m^2 ± SE) per block, (b) Mean crown surface area (m^2 ± SE) per tree, (c) Mean number of nests (± SE) per tree, (d) Mean nest size (cm^3 ± SE) per tree. Means with the same letter were not significantly different at: (a) $P \geq 0.01$ (Friedman test, Conover's pairwise comparisons between samples), and (b-d) $P \geq 0.05$ (one-way ANOVA, Tukey's pairwise comparisons between means).

greater than nest sizes on *Bruguiera* spp. and *T. tiliaceum* trees (mean = 100 and 90 cm^3; SE = 31 and 16, respectively). The largest nest was found on *M. citrifolia* (1,283 cm^3), while the largest nests found on *Bruguiera* spp. and *T. tiliaceum* were 339 and 237 cm^3, respectively.

The presence of trophobionts together with ants could not always be confirmed by collection of samples, because many of the nests were beyond the reach of the telescopic clippers, and examining with binoculars proved challenging. Trophobionts were found on 72% of ant-colonized trees (n = 50) but on only 7% of the 184 host plants not occupied by ants (Table 3.2). The association between ant occupation and trophobiont presence was significant (χ^2 = 103.4; d.f. = 1; P = 0.000). Distribution among host plant species appeared uneven. On ant-occupied *M. citrifolia*, *T. tiliaceum* and *Bruguiera* spp. trees, trophobionts were found on 81, 77 and 45%, respectively, of the time. Trophobionts were found on 9, 8 and 3% of non-ant-occupied *M. citrifolia*, *T. tiliaceum* and *Bruguiera* spp. trees.

Discussion

In this mangrove habitat, *O. smaragdina* was most abundant on *M. citrifolia* (Figure 3.1.a), compared with the other host plant species of the ant and the non-host plant control. It was interesting that *M. citrifolia* had a significantly smaller crown surface area per tree than *Bruguiera* spp. (Figure 3.1.b), yet supported a greater ant population (volume of nests). *Bruguiera* spp. had significantly more nests per tree than the other two host plant species (Figure 3.1.c), which correlated with a greater crown surface area available for nest-building.

However, nests on *Bruguiera* spp. trees tended to be smaller than those on *M. citrifolia*. *T. tiliaceum* generally fell between these two host plant species for all these characteristics. Using the relative nest volume index, which standardized nest volume by each tree's crown surface area (area available for nest-building) appeared to be an appropriate method that facilitated meaningful comparison among these host plant species.

Oecophylla smaragdina appeared to have a strong preference for *M. citrifolia*. This host plant species occurred in lower numbers in the study site compared with other host plant species (Table 3.1), yet the ant was found on more trees of this species (a total of 26 vs. 13 and 11 for *T. tiliaceum* and *Bruguiera* spp., respectively). *M. citrifolia* trees were smaller than the other host plant species assessed, yet supported higher populations of the ant.

Certain characteristics of *M. citrifolia* may favor the ant, particularly with regard to nest-building and food resources. The leaves of *M. citrifolia* are larger and appear more pliable than *Bruguiera* spp. leaves. *O. smaragdina* has been reported to prefer host plant species with leaves within a certain 'normal' size (range: 5 x 8 cm – 20 x 20 cm) and avoid tough-leaved plant species (Blüthgen & Fiedler 2002). Further, pliability of a leaf and the degree to which it bends when pulled determines nest site selection in *Oecophylla* spp. (Holldobler 1983b). *M. citrifolia* was also observed to have extra-floral and floral nectaries around which the ants aggregated, and more ant-occupied *M. citrifolia* trees harbored trophobionts compared with the other host plant species, particularly *Bruguiera* spp. (Table 3.2).

Results of this study indicate that *M. citrifolia* is the most preferred host plant species for *O. smaragdina*, followed by *T. tiliaceum* and *Bruguiera* spp. This plant species is easy to grow, thrives in a wide range of growing conditions, and is cultivated locally for its medicinal value (Lin 2005). Furthermore, the trophobiont species, i.e., *Gargara* sp. and *Nilautama* sp. nr. *minutispina* (Hemiptera: Membracidae), that were identified associating

Table. 3.2. Distribution of trophobionts on three *Oecophylla smaragdina* host plant species in a Malaysian mangrove in relation to presence of the ant.

Host plant species	Ant presence	Trophobiont presence		Total no. of trees
		Yes	No	
M. citrifolia	Yes	21	5	26
	No	5	49	54
T. tiliaceum	Yes	10	3	13
	No	5	56	61
Bruguiera spp.	Yes	5	6	11
	No	2	67	69
Total		48	186	234

with *M. citrifolia* in a previous survey of habitats in Central West Peninsular Malaysia were not noted to pose any pest risk toward *K. ivorensis* in Malaysia and other countries (Chapter 2). With these characteristics in its favor, *M. citrifolia* is proposed for further evaluation of its suitability as a 'nurse plant' for the *O. smaragdina* in mahogany plantations.

Chapter 4

A model for estimating the number of weaver ants inside nests

Introduction

Impressive living-leaf nests are built by the exclusively arboreal weaver ants, of which there are only two extant species, *Oecophylla longinoda* Latreille in tropical Africa and *Oecophylla smaragdina* F. in South-East Asia, Australia and the Western Pacific Islands (Holldobler & Wilson 1990a). *Oecophylla* spp. have been studied for decades throughout their distributional ranges (Dutt 1912; Miller 1931; Ledoux 1950; Way 1954a; Vanderplank 1960; Chen 1962; Holldobler & Wilson 1977). There may be hundreds of nests encompassing a single polydomous colony, established in the crowns of up to 44 mature trees, with a single 'queenright' nest housing unmated reproductives, major and minor workers, trophobionts, brood, and - at least for *O. smaragdina* - multiple queens (Peng *et al*. 1998a, but see also Holldobler & Wilson, 1990b). The queen, sustained by consuming the trophic egg offerings of her workers (Holldobler & Wilson 1983), produces fertile eggs that are soon distributed to and the offspring raised in nearby nests (Peng *et al*. 1998b). 'Barrack' nests (Holldobler 1983a), also known as 'pavilions' (Blüthgen & Fiedler 2002), are clustered around young shoots within the colony's territory. These pavilions shelter worker ants, trophobionts and occasionally final instars, which produce the silk that binds the colony's nests together (Blüthgen & Fiedler 2002). The trophobionts, e.g., mealybugs and scale insects, provide the ants with the honeydew that forms a large part of their diet, which also comprises floral and extra-floral nectar and prey items (Blüthgen & Fiedler 2002; Blüthgen *et al*. 2004).

Adding to the extensive body of knowledge on the behavior, ecology and physiology of these ants, is the recent surge of interest in the application of *O. smaragdina* as a biological control agent. The ant controls insect pests in several fruit and cash crop species, e.g., cashew and mango (Peng & Christian, 2004, 2005, 2006; Peng *et al.* 1995, 1997a, 1999), and cocoa (Way & Khoo 1991). It also shows potential in controlling an important mahogany pest, *Hypsipyla robusta* Moore (Lepidoptera: Pyralidae) (Lim & Kirton 2003). The first record of biological control in 304 A.D. used *O. smaragdina* in citrus orchards in China, where the territorial and aggressive nature of this predator is still harnessed for that purpose (Huang & Yang 1987).

A population of about 50-200 ants per tree has been found to provide sufficient protection against the cocoa mirid, *Helopeltis theobromae* Miller (Hemiptera: Miridae) (Way & Khoo 1991). The release of 15 nests per ha (colonies not differentiated) achieved control of eucalyptus pests in the Solomon Islands (Macfarlane *et al*. 1976). It is likely that a minimum level of ants is needed to deter or destroy pests. Ant abundance is usually estimated indirectly by nest counts, ant trails (Peng *et al*. 1999), or counts of ants on selected plant parts (Way & Khoo 1991; Way & Bolton 1997; Lim & Kirton 2003; Blüthgen *et al*. 2004). Nest counts may not always reflect current ant population levels because these counts may include abandoned nests, which are common, and these empty nests tend to retain their form for a few weeks after the ants have left (Lim, G. T., personal observation). Direct methods to enumerate the ants are almost always destructive (Way 1954b; Greenslade 1971; Begg 1977) or at the very least disruptive to nest inhabitants, e.g., the partial opening of nests for

enumerative purposes (Peng *et al*. 1998a). The present study addressed the need for a non-destructive method of estimating ant abundance based on ant numbers that facilitates repeated, direct evaluation of effects influencing population levels of *O. smaragdina*. Specifically, a model for predicting ant numbers within nests was developed based on selected parameters measured for *Khaya ivorensis* A. Chev. (Meliaceae).

Materials and Methods

The study commenced on July 14, 2005 between 1000 and 1200 h at a plantation of 2 – 5 year-old *K. ivorensis* trees in Trolak, Perak, Malaysia (3°50'N, 97°52'E). Thriving populations of *O. smaragdina* had been previously observed at the study site (Lim & Kirton 2003). Five colonies were found distributed throughout the plantation, with colony boundaries demarcated based on a minimum 10 m distance between colonies or the absence of ant trails between ant-colonized trees less than 10 m apart. Parameters likely to contribute to predicting the model for estimating ant numbers in a nest were measured before the nests on all the trees in the five colonies were harvested for a complete census of their contents. The parameters were: tree height, nest location within the crown column, crown surface area (*Ca*), nest size, the number of (compound) leaves and leaflets in a nest, and ant activity level.

A nest location index (*p*) was calculated to standardize for the variability in the vertical distribution of the nests along the crown column for each tree. It is indicative of the age of the leaf or leaves from which a nest was built, assuming leaf age of 1-12 months from first fully expanded leaf at the apex of the tree to the bottom-most leaf of a tree crown (Lawson *et al*. 2002), where

$$p = \frac{\text{Length from the top of crown to a nest}}{\text{Length of crown column}}$$

Crown surface area (*Ca*) calculation was based on a cylindrical crown shape as in a previous study (Chapter 3), but using crown width and length measurements from scaled photographs of the trees.

Estimated nest size (*s*), was calculated from estimated nest length (*l*) and height (*h*) (± 5 cm). Nest depth was not estimated as it was difficult to obtain a good visual from our vantage point on the ground. Nest depth was assumed to be the same as nest height based on the cylindrical shape of many nests constructed from leaflets spread out along the petiole of the compound leaf.

$$s = \pi r^2 l \text{ , where } r = \tfrac{1}{2} h$$

Ant activity on the terminal 10 cm of the shoot was ranked using binoculars on a scale of 1 – 8. Rank 1 denoted no ants while ranks 2 – 8 denoted 1 – 2, 3 – 4, 5 – 7, 8 – 10, 11 – 15, 16 – 20, and > 20 ants per shoot, respectively. The ants appeared to detect (human) workers approaching five meters away in the undergrowth and swarmed the nest surface. Ranking of ant activity took place for ants in that state. The ants appeared to be concentrated around the entrance of the nest which was usually along the leaf petiole.

Each nest was then cut down using telescoping clippers, bagged and labelled, and taken back to be frozen at the Entomology Section, Forest Research Institute of Malaysia (FRIM). Actual nest size (*s*) was calculated from direct measurements of nest length, height and depth (l x h x d, ± 1 cm^3). The number of leaves and leaflets incorporated into the nest were counted. Entire nests, then their contents, i.e., ants, trophobionts, prey remains, were weighed. Direct counts of the adult major and minor workers, queens and males, and

trophobionts were obtained, as were the pupal forms of the ant castes and larvae. The eggs were weighed but not counted. For every nest, the fresh and dry weights (oven-drying at 40ºC for 48 h) of ants from each caste were obtained in three replicates of 10 ants each.

Mutually exclusive queenright, 'brood', and pavilion nests (pavilions) for each colony were tentatively identified. Queenright nests were those that contained eggs and/or larvae, and a queen or multiple queens, but no pupae. A single queenright nest was expected per colony. This characterization of queenright nests was based on the results of a selective census of 12 *O. smaragdina* queenright nests that found only eggs and early instars together with multiple queens, but no pupae or medium-to-late-stage larvae (Peng *et al*. 1998a). The categorization of queenright nests according to results for Australian *O. smaragdina* was tentative, because a previous survey of Malaysian habitats (Study 2) found brood of all ages, including pupae, in a nest that contained the queen (G.T. Lim, personal observations). 'Brood' nests were identified based on the presence of eggs, larvae and pupae, and the absence of a queen. This formed a broad category covering all nests containing brood without evidence of a queen, but excluding pavilions. Pavilions were identified based on the absence of a queen and eggs or pupae. No eggs have ever been reported in pavilions, but larvae, specifically final-instars, may be expected in pavilion-type nests as they are used in nest-building (Holldobler 1983a; Blüthgen & Fiedler 2002) and therefore are not exclusive to queenright or brood nests.

Statistical analyses

Analyses of variance were carried out using the statistical software Minitab 14® (MINITAB 2007) and non-parametric analyses were carried out using StatsDirect (StatsDirect 2007). Mean nest size, ant counts per nest, major adults : minor adults, and major pupae : minor pupae, were analyzed using one-way analysis of variance (ANOVA) with the factor nest category (levels: pavilion and brood-queen). Binary logistic regression was performed to assess the predictive ability of nest size for nest category. Best subsets regression was used to select the best model predicting ant numbers within a nest that was subsequently tested using multiple regression. Results for all analyses of variance were $\log_{10}$ transformed to achieve normality and equality of variances, except for ant activity. The variable p (nest location index) was $\log_{10}(1+ p)$ transformed. All analyses of variance were followed by Tukey's honestly significant difference test to separate treatment means (Zar 1999) at $P \leq 0.05$.

The data for wet and dry weight of ants by caste did not achieve normality or equality of variances after applying $\log_{10}$ transformations. Therefore, the two variables were analyzed with the factor caste, using Kruskal-Wallis' test. The test was followed by Conover-Inman's pairwise comparisons between plant species (Conover 1999) at $P \leq 0.05$. Friedman's test is slightly less powerful than the F-test when the number of blocks (< 10) or treatments (< 6) is small (O'Gorman 2001). All means are followed by ± SE.

Results

Twenty one nests comprising five colonies were collected from 12 trees, excluding a large nest at the top of a 15 m tree in Colony 4, which was beyond reach. Nest composition by caste, in relation to tentative nest categorization as brood nest or pavilion is given in Table

4.1, which is referred to for the results that follow. The mean number of trees per colony was 2.6 ± 1.2 (n = 5) with a mean of 1.7 ± 0.3 nests per tree (n = 12).

At least one brood nest was identified for three of the five colonies studied, based on the presence of eggs and/or pupae. However, none of these could be confirmed as queenright nests because alate queens were not found in these or other nests. Brood nests in the present study were not distinguished from queenright nests and these two categories were combined as 'brood-queen' nests for comparisons with pavilions. Major workers have been observed to immediately surround dealate queens when the nest structure is compromised, and physically transport them to safety (Peng *et al*. 1998a), and the dealate queen/s may have escaped during harvests of the higher nests in the present study. There were seven brood-queen nests and 14 pavilions. Pavilions always contained adult forms but not immature forms except larvae, which were found 61% of the time (n = 14).

Nests categorized as pavilions were significantly smaller than brood-queen nests ((*F* = 15.96; d.f. = 1, 19; *P* = 0.001; n = 14 and 7, respectively; Figure 4.1) and contained significantly fewer ants (*F* = 25.4; d.f. = 1, 19; *P* = 0.000; n = 14 and 7, respectively; Figure 4.2). There was some overlap as pavilion diameters ranged from 5 – 12 cm while brood-queen nest diameters ranged from 10 – 28 cm (an approximation taking the cube-root of actual nest volume directly measured in the laboratory). Since nest volume estimated in the field from measurements of nest height and length was strongly correlated with nest volume obtained by direct measurements of nest height, length and depth (*r* = 0.95; d.f. = 19; *P* = 0.000, Pearson correlation), estimated nest volume was appropriate to test as a predictor variable in place of actual nest volume.

Likewise, the number of ants in a pavilion ranged from 20 – 2,450 (n = 14) while brood-queen nests contained between 800 – 15,800 ants (n = 7). Consequently, for colonies where both brood-queen nests and pavilions appeared well censused (Colonies 1 and 2), about 9% of the colonies' adults (ca. 20,000) were found in pavilions (Figure 4.3). An average of 18,100 ± 1,800 ants per colony (n = 3) were found in brood-queen nests and 1,900 ± 300 ants per colony (n = 4) in pavilions. The number of immatures housed in brood-queen nests far exceeded the few late-instars found in pavilions. The pavilions for Colonies 1 and 2 contained only 0.1% and 6.1% of the immatures (n = 7,600 and 4,200, respectively).

Further, binary logistic regression showed that ($\log_{10}$) *s*, i.e., nest size alone could be used to predict nest type, i.e., pavilion (*a*) or brood-queen nest (*b*) (*G* = 9.99; d.f. = 1; *P* = 0.002; Log-likelihood = -8.37). The estimated coefficient of -1.22 for *s* (*z* = 2.34; *P* = 0.019; odds ratio = 0.30, 95% CI: lower = 0.11, upper = 0.82) represents the change in log (*a/b*) when *s* is large compared with small *s*. The odds of small nests being brood-queen nests are only 30% that of large nests being brood-queen nests, which is reasonably good. The model appeared to fit the data satisfactorily (χ^2= 8.48; d.f. = 9; *P* = 0.49; Pearson's Goodness-of-Fit test), which was supported by examining the table of observed and expected frequencies. Goodman-Kruskal Gamma and Somer's *D* values of 0.76 and 0.71, respectively, indicated a reasonable predictive ability. However, Kendall's Tau-a was only 0.33, so predictions should be done cautiously.

There were fewer minor workers in pavilions than major workers, while in brood-queen nests it was the opposite. In pavilions, the ratio of adult major to minor workers (2.23 : 1, SE = 1.23; n = 14) was significantly higher (t = 3.11; d.f = 20; *P* = 0.0146) than that in brood-queen nests (0.82 : 1, SE = 0.21; n = 8). The ratio of major to minor pupae in brood-

Table 4.1. Distribution of adult and immature forms of *Oecophylla smaragdina* and its trophobionts in relation to nest and tree for five colonies in a *Khaya ivorensis* plantation in Malaysia. Colony totals follow colony headings in the same row.

Tree[1] number	Nest[2] type	Adults[3]					Immatures						Grand total	Tropho-bionts[6]
		Maj	Min	Q	M	Total	Maj[4]	Min	Q	Larvae	Eggs (g)	Total[5]		
Colony 1		6133	12583	411	4705	23832	4514	656	12	2464	0.632	7646	31478	688
1 (6.0, 2.0)	B (5.6)	3520	7421	216	2205	13362	2976	656	12	1423	0.611	5067	18429	460
	B (5.0)	1913	4363	168	1630	8074	1538	-	-	1030	0.021	2568	10642	138
	P (3.3)	700	799	27	870	2396	-	-	-	11	-	11	2407	90 (1 M)
Colony 2		12608	6875	201	0	19684	1875	0	295	2023	3.694	4193	23877	261
1 (3.3, 1.7)	B (3.3)	10735	4847	169	-	15751	1875	-	275	-	1.338	2150	17901	86 (20 M)
2 (4.2, 1.4)	B (3.2)	663	918	2	-	1583	-	-	7	798	0.812	805	2388	19 (1 M)
3 (4.5, 2.4)	B (3.4)	323	456	30	-	809	-	-	13	970	1.544	983	1792	8
4 (3.8, 1.1)	P (2.1)	362	255	-	-	617	-	-	-	130	-	130	747	103
5 (3.2, 0.8)	P (1.9)	303	181	-	-	484	-	-	-	98	-	98	582	-
6 (2.8, 0.5)	P (1.9)	157	140	-	-	297	-	-	-	13	-	13	310	8
7 (3.1, 1.0)	P (2.2)	65	78	-	-	143	-	-	-	14	-	14	157	37 (1 L)
Colony 3		5837	9119	-	-	14956	1781	484	-	1242	0.986	3507	18463	1195
1 (11.3, 6.2)	B (6.6)	1363	3464	-	-	4827	1114	-	-	-	0.986	1114	5941	50
	B (7.3)	4474	5655	-	-	10129	667	484	-	1242	-	2393	12522	1145 (1 M)
Colony 4[7]		824	354	-	-	1178	-	-	-	43	-	43	1221	28
1 (2.4, 0.3)	P (1.0)	72	23	-	-	95	-	-	-	4	-	4	99	-
	P (1.0)	56	30	-	-	86	-	-	-	11	-	11	97	-
	P (1.0)	30	4	-	-	34	-	-	-	-	-	0	34	1
	P (0.8)	269	58	-	-	327	-	-	-	-	-	0	327	- (1 M)
2 (4.2, 1.2)	P (3.0)	30	13	-	-	43	-	-	-	-	-	0	43	24 (6 C)
	P (2.9)	367	226	-	-	593	-	-	-	28	-	28	621	3
Colony 5		1048	1575	-	-	2623	-	-	-	214	-	214	2837	17
1 (2.3, 0.3)	P (1.6)	937	1517	-	-	2454	-	-	-	214	-	214	2668	- (1 M)
	P (1.1)	96	49	-	-	145	-	-	-	-	-	-	145	12
	P (1.1)	15	9	-	-	24	-	-	-	-	-	-	24	5

[1]Tree height (m) and base of crown height (m) in parentheses after tree number heading.
[2]Nest type: B, brood-queen nest (indicated by presence of eggs and/or pupae, no dealate queens); P, Pavilions (no eggs, pupae or queens). Height of nest from ground, in parentheses.
[3]Adults: Maj and Min, major and minor workers, respectively; Q, queens (all alate); M, males. Likewise denoted for immature forms.
[4]Major caste pupae were not distinguishable from male pupae and likely include them
[5]Subtotals for immatures exclude eggs, which were not counted.
[6]Number of scale insects in each cell, followed by counts of other trophobionts in parentheses. M, membracid; L, lycaenid; C, mealybug.
[7]Counts exclude a large nest located on a third tree that was beyond reach (>15 m).

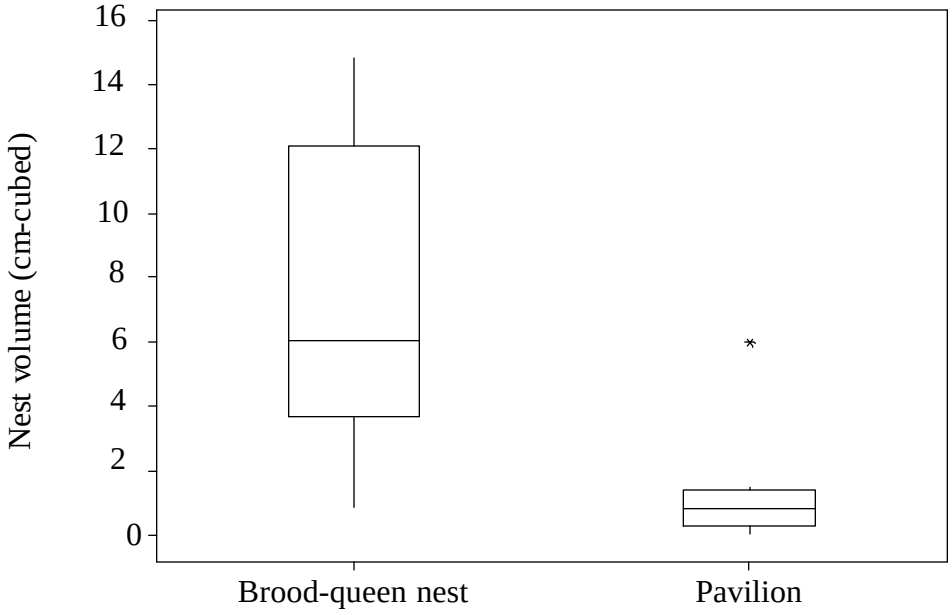

Figure 4.1. Size of *Oecophylla smaragdina* brood-queen nests and pavilions on *Khaya. ivorensis* in Malaysia. Asterisk denotes outlier. Nest sizes were significantly different ($P \leq 0.05$).

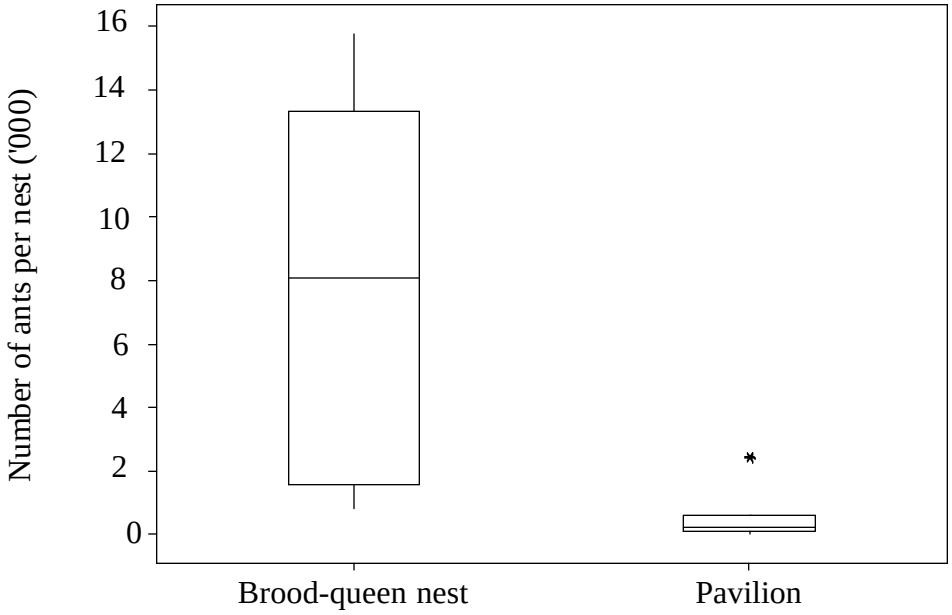

Figure 4.2. Counts of *Oecophylla smaragdina* adults in brood-queen nests and pavilions on *Khaya ivorensis* in Malaysia. Asterisk denotes outlier. Ant numbers were significantly different ($P \leq 0.05$).

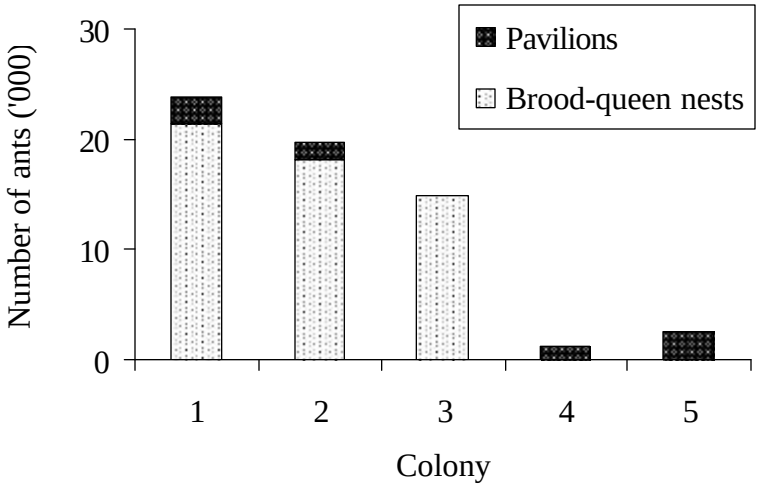

Figure 4.3. Distribution of *Oecophylla smaragdina* adults in relation to colony and nest type for five colonies in a *Khaya ivorensis* plantation in Malaysia. Nest categorization criteria given in text. The nests that could not be harvested for colonies 4 and 5 (> 15 m) were likely brood-queen nests.

queen nests (3.07 : 1, SE = 1.69; n = 2) was also significantly higher (t = 2.49; d.f. = 14; *P* = 0.054) than the ratio of adult major to minor workers in brood-queen nests. It was not uncommon to find major pupae and no minor pupae in those nests (range: 1,100 – 1,900, n = 3). There was a higher major : minor ratio for pupae (3.48 : 1, SE = 1.94; n = 5 nests across 3 colonies) compared with adults (0.74 : 1, SE = 0.14; n = 5 nests across 3 colonies) in the present study.

Our record of weights for *O. smaragdina* castes (Figure 4.4) showed a significant difference between at least two castes in fresh and dry weights (*H* = 33.77, d.f = 3, *P* = 0.000; and *H* = 34.81, d.f. = 3, *P* = 0.000, respectively). This was due to the minors weighing less than the males and majors, which in turn weighed less than queens.

About 87% of the brood-queen nests contained trophobionts (n = 7) while that figure was 71% for pavilions (n = 14) (Table 4.1). Scale insects were were found in 81% of the nests (range = 0 – 1,145, n = 21) and the most common trophobionts. The number of scale insects in a nest was correlated with the number of minor workers (r = 0.69), but less so with the other castes, i.e., major workers, alate queens and kings (r = 0.42, 0.22 and 0.27, respectively). Membracids were found in numbers ranging from 1 – 20, in 6 of the nests, most of which also contained scale insects. Mealybugs were found in one nest, and a lycaenid in another nest.

The visual enumeration of the number of leaves incorporated into a nest underestimated actual leaf numbers, and likewise for the leaflets. Pre-collection counts estimated that nests were built from 1.9 ± 0.4 leaves (n = 21, median: 1, range: 1-9) or 10.3 ± 3.5 leaflets (n = 21, median: 4, range: 1-72). However, nests were actually built from 3.0 ± 1.0 leaves (n = 21, median: 1, range: 1-19) or 22.7 ± 7.6 leaflets (n = 21, median: 5, range: 1-108). This was likely due to difficulties in estimating numbers - particularly of leaflets - incorporated into a nest. However, there was a strong correlation between the estimated and actual values for both leaves and leaflets incorporated into a nest, so estimated values were tested as predictor variables in place of actual values (leaves: r = 0.92, d.f. = 19, *P* = 0.000; leaflets: r = 0.80, d.f. = 19, *P* = 0.000). Estimated leaf count was chosen as the predictor variable as it correlated better with actual counts.

Using best subsets regression, the best two-predictor model included estimated number of leaves incorporated into a nest (*w*) and estimated nest size (*s*). This model had the highest R^2_{adj} (83.4%), lowest Mallows Cp value (0.2) and low S (0.82). The second best fit to the data were possibly one of two three-predictor models that added either ant activity or crown area. The former had a slightly higher R^2_{adj} than the latter (82.6 vs. 82.4%), slightly better Mallows Cp value (2.0 vs. 2.2) and smaller S (8.4 vs. 8.5). Another possible model with the sole predictor *s* had a good R^2_{adj} (80.6%), low Mallows Cp value (1.7) and an S value of 0.89, which was high but not excessively so. The four- and five-predictor models did not have higher R^2_{adj} values, and had higher Mallows Cp and S values, indicating that *nest location* and *crown area* were not very useful in predicting ant numbers within a nest.

Considering the above, the two-variable model comprising *w* and *s* was evaluated using multiple regression. The model was significant (*F* = 51.15; d.f. = 2, 18; *P* = 0.000). The values for R^2 (85.0%) and R^2_{adj} (83.4%) indicated that the model fit the data well, and the predicted R^2 of 80.1% was close to the R^2 and R^2_{adj} values, indicating good predictive ability. However, *w* was not significantly related to ant numbers in a nest (t = 2.04, *P* = 0.056), suggesting a model with only *s* would be more appropriate.

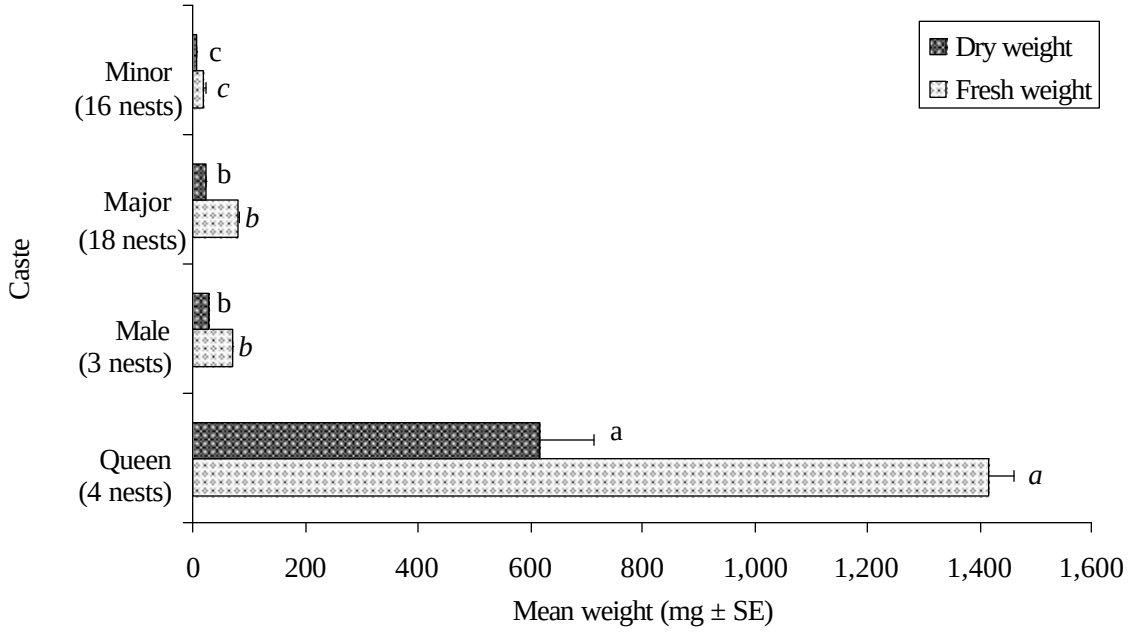

Figure 4.4. Mean fresh and dry weights (mg ± SE) per *Oecophylla smaragdina* individual in relation to caste, for nests taken from a *Khaya ivorensis* plantation in Malaysia. Number of nests in parentheses. Three subsamples of 10 adults were taken from each nest for every caste. Means with the same letter (italicized for fresh weight results) were not significantly different ($P \geq 0.05$). The Kruskal-Wallis pairwise comparison procedure separated castes.

Subsequently simple linear regression showed that the number of ants in a nest could be adequately predicted by the equation: $\log_{10}$ *Ants* = - 1.16 + 1.09 $\log_{10}$ *s*. This was significant at $P \leq 0.05$ ($F = 84.1$; d.f. = 1, 19; $P = 0.000$). The values for R^2 (81.6%) and R^2_{adj} (80.6%) indicated that the model fit the data well, and the R^2_{perd} (77.8%) was close to the R^2 and R^2_{adj} values, indicating good predictive ability. Therefore, this model was chosen for its reasonable predictive ability, parsimony and ease of measurement.

Discussion

A model was developed to estimate the number of ants within nests that has good predictive ability for *O. smaragdina* inhabiting *K. ivorensis* and simple to use since it only requires measurements of two nest dimensions (height and length). This model is anticipated to be very useful for repeated assessments of treatment effects on colonies in the field. The model likely provides a more direct reflection of ant population levels compared with other indirect estimation methods, e.g., nest counts (Offenberg *et al*. 2004), ant counts on plant parts (Blüthgen & Fiedler 2002), and counts of ant trails on tree stems or branches (Peng & Christian 2005). Further, this model may be applicable for general use on weaver ant host plant species with little or no modification and an additional study evaluating this model on other host plant species is on-going (G.T. Lim, unpublished data). The model likely underestimates the total ant population in a nest because the census of nests did not account for ants foraging outside the nest or ants that escaped during nest harvest.

The higher major : minor ratio for pupae (3.48 : 1, SE = 1.94; n = 5 nests across three colonies) compared with adults (0.74 : 1, SE = 0.14; n = 5 nests across three colonies) in the present study was very similar to that reported by Way (1954a). This was attributed to the major workers foraging outside the nest (Way 1954a). The model does not take into account the workers foraging outside the nest. The proportion of workers that forage outside the nest varies diurnally and seasonally (Greenslade 1971).

A higher ratio of major to minor pupae (17.64 : 1, SE = 3.67; n = 3) compared with that for adults (2.81 : 1, SE = 0.96; n = 4) was also reported for a census of four *O. smaragdina* colonies in the Solomon Islands (Greenslade 1971). The results of that census corroborate the significantly higher adult major : minor ratio observed for pavilions compared with brood-queen nests in the present study, as it found that comparatively more of the workers venturing outside the nest were majors, with a major : minor ratio of 5.58 : 1 (SE = 1.93, n = 4). The model estimates only the adult population, and not brood.

Results of the study hint at variable nest-founding behavior between and within *Oecophylla* spp. Each queenright nest for Colonies 1 – 3, which could not be distinguished from the brood nests, would have contained pupae since all the brood-queen nests contained pupae and eggs. This finding would be incongruent with the findings for Australian queenright *O. smaragdina* nests, where as noted previously, eggs, but never pupae, were observed (Peng *et al*. 1998a). However, the results of the present study, together with a previous observation of co-occurring queen and brood of all ages in a Malaysian *O. smaragdina* nest (Lim, G.T, unpublished data), concur with observations for African *O. longinoda* queenright nests (Holldobler & Wilson 1977). Malaysian *O. smaragdina* queenright nest composition may differ from that of Australian *O. smaragdina* as recent phylogenetic analyses have shown that the phylogenetic group that includes Peninsular Malaysia is distinct from the group comprising Australia and New Guinea (Azuma *et al*.

2006). The Australian group established later, after dispersal of the former group through New Guinea and Sulawesi (Azuma *et al*. 2006).

Consequently, subtle behavioral and nest-founding differences between and within *Oecophylla* spp. may exist due to phylogenetic grouping. For example, for *O. longinoda*, a single foundress controls the entire colony (Holldobler & Wilson 1983), and likewise for *O. smaragdina* from the Solomon Islands (Greenslade 1971), which are near New Guinea. Pleometrosis (cooperative colony founding by multiple queens) has been alluded to (Richards 1969), but has yet to be proven for *O. longinoda*. However, pleometrosis (Peeters & Andersen 1989) and also polygyny, (i.e., the occurrence of multiple queens in mature colonies) has been reported for *O. smaragdina* in Australia (Peng *et al*. 1998a). Pleometrosis is advantageous, particularly in nest-building (Peeters & Andersen 1989), and would facilitate the ant's successful establishment in new territories. One proposed scenario suggested the rafting dispersal of nests containing multiple queens from New Guinea and Sulawesi to Australia (Azuma *et al*. 2006). It may also be that *O. smaragdina* is facultatively pleometrotic or that the ant developed this trait in response to a need for more efficient colony founding with regard to inter-island dispersal. The record of single queen colonies for *O. smaragdina* in the Solomon Islands (Greenslade 1971) partially supports this hypothesis because a single mated queen could have been transported from these islands to Australia from which pleometrotic and polygynous offspring came about.

Chapter 5

The preference of the weaver ant for four foods

Introduction

The weaver ant, *Oecophylla smaragdina* F., has been successfully used as a biological control agent of insect pests in a number of fruit and cash crop species such as cashew and mango in Australia (Peng & Christian, 2004, 2005, 2006; Peng et al 1995, 1997a, 1999), citrus in Vietnam (Van Mele & Cuc 2000) and cocoa in Malaysia (Way & Khoo 1991). The ant has also been identified as a potential biological control agent of an important pest of mahogany species, *Hypsipyla robusta* Moore (Lepidoptera: Pyralidae), in Malaysian plantations (Lim & Kirton 2003).

Weaver ants are effective as biological control agents of many defoliating insect pests because they are vigilant and territorial predators of living creatures in their arboreal domain. Their ability to modify the environment to suit their needs by constructing nests from the living foliage of numerous host plant species allows them to exploit a wide range of habitats (Holldobler 1983a). Larger nests contain brood and reproductives while smaller nests that do not contain reproductives are called 'pavilions'. Trophobionts such as mealybugs and scale insects are tended by workers for the honeydew that comprises a substantial portion of the ants' diet (Blüthgen & Fiedler 2002).

The husbandry of weaver ants is both a science and an art, often involving interaction between farmers and extension agents, and combining farmer knowledge with new integrated pest management approaches. Vietnamese citrus farmers have a long-standing tradition of managing the ant and conserving its population by limiting pesticide applications and using pesticides that are less harmful to the ant (Van Mele *et al*. 2002). Chinese citrus farmers use bamboo strips to connect adjacent trees to facilitate dispersal of the ant and increase the area under protection (Huang & Yang 1987). Mixed-planting alternate host plant species that favor the ant together with the main crop has also been recommended (Way & Khoo 1991; Peng *et al*. 1997b; Van Mele & van Lenteren 2002) and planting trials are currently underway to assess their efficacy in conserving weaver ant colonies newly introduced to plantations (G.T. Lim, unpublished data). Supplementing the ants' diet with dried fish during the food-scarce dry season in Vietnam was done to conserve ant populations (Van Mele & Cuc 2003). In Malaysia, locals who wish to rid their yards of this prolific and aggressive ant place meat baits like chicken necks that attract scores of ants, which are promptly set on fire. The application of this traditional knowledge to augment weaver ant populations in a mahogany plantation has been observed to be successful (Lim Sun Heng. Maju Aik Ltd., personal communication, 2005).

Colonies that are newly introduced to new host plants may establish better if provided supplementary food that meets their energy and nutritional requirements. High-carbohydrate foods similar to honeydew and plant nectar may be needed to sustain worker activity during this period when trophobiont population levels on the new host are anticipated to be low. Ants in general prefer sucrose over glucose and fructose (Blüthgen & Fiedler 2004b) and 10% sucrose is considered 'high-quality sucrose', with attractiveness correlated with concentration (Kay 2002). In addition to the foods noted above, *O. smaragdina* has also been reported to prefer complex amino acid mixtures such as the liquid formulation containing a

commercially-available product for human muscle training (Blüthgen & Fiedler 2004b; Nico Blüthgen, Bayreuth University, personal communication, 2006). It is commonly held that for ants, high-protein foods are fed to larvae (Haack *et. al*, 1995). Providing high-protein live crickets and fruit flies to laboratory-reared colonies maintained their vigor (Holldobler & Wilson 1990b). Therefore, provision of such foods may aid colony establishment and expansion as well. The present study evaluated several inexpensive and easily available food sources for their suitability and attractiveness to the weaver ant.

Materials and Methods

A day-long preliminary assessment of ant preference for six food choices carried out on one ant colony at FRIM (Forest Research Institute of Malaysia, Selangor, Malaysia; 3°14'N, 101°38'E). Based on the results of the preliminary assessment, four preferred foods were selected for a subsequent week-long choice test involving six colonies and a week-long, no-choice test involving another 12 colonies. Preference was based on ant counts around the various foods in instantaneous samples taken with a digital camera (Nikon Coolpix® 5700), and the amount taken of each food (g), as described below.

Preliminary study

In the preliminary assessment the following six foods were offered to the ants:

1. 5 g fresh minced mackerel flesh
2. 5 g moistened fish food pellets (50% water)
3. 5 g fresh minced mealworms
4. 35 live mealworms (4.71 g)
5. 15 g honey solution (20% w/w)
6. 15 g 'weaver ant formula'

The mealworms were larvae of *Tenebrio molitor* L. (Coleoptera: Tenebrionidae). The 'weaver ant formula' was a formulated amino acid and sugar solution (15 g cane sugar and 1 g EnerPro™ protein powder by Nutralife (NZ, Ltd.), dissolved in 100 g distilled water (Blüthgen & Fiedler 2004b)). Honey solution was provided as a low-sucrose, high-fructose liquid food alternative to the weaver ant formula. Since the weaver ant formula was high in both sucrose and complex amino acids it was expected to be more attractive to the ants. The fish food pellet was selected for its ease of use and for the balance of animal (krill) and plant food (spirulina) it contained. Mealworms gave a choice of live high-protein prey that could easily be held in bowls. Fresh fish provided a non-living alternative to mealworms that was also lower in fat.

The liquid food choices were placed in the plastic feeding bowls lined with three pieces of filter paper (8.5 mm diam.) to reduce the rate of evaporation and ensure sufficient liquid food for the day-long study. A preliminary 5 h study on evaporative water loss from 1, 2 and 3 filter papers saturated with 5, 10 and 15 g of water, respectively, showed a negative correlation between water loss and the number of filter papers (or amount of water at the start of the study) ($r = -0.957$, $R^2 = 0.915$). One-way analysis of variance (ANOVA) with Tukey's multiple comparisons among means showed that all treatments differed significantly from each other ($F = 221.1$; d.f. = 2, 9; $P = 0.000$), and that using three filter papers gave the lowest mean percent evaporative water loss (mean = 27.0%, SE = 0.8) followed by using two filter papers (mean = 41.5%, SE = 3.3) and one filter paper (mean = 80.7%, SE = 5.5).

The foods were placed in six individual 9 mm diam. plastic feeding bowls on a feeding platform mounted on a 1 m high wood pole. The wood pole was banded at 0.75 m above ground level with Coldfoot® to exclude crawling insects. The platform was positioned outside the radius of the tree canopy in order to exclude ants falling from the tree. A clear plastic cover designed to shelter treatments from rain was affixed to the platform with four bamboo chopstick stands. The plastic cover was affixed 2.6 cm above the platform, which facilitated feeding bowl changes. The ants accessed the center of the base of the feeding platform by crawling from their nest onto a 3 mm thick cotton thread bridge tied to the top of a bamboo chopstick, and down the chopstick through a 3 cm diam. hole in the plastic cover. The various food choices were randomly arranged equidistant from the center of the base of the feeding platform.

The preliminary study ran from 800 to 1600 h on 19 June 2006. The amount of each type of food taken by the ants was obtained from the difference in weight of the food before and after the study. Weight loss due to evaporation was accounted for with a control feeding platform with the same food choices in a serving tray, without ant access to the foods. The ants within the feeding bowls for each of the foods were counted in two instantaneous samples an hour apart.

Choice and no-choice tests

The subsequent choice and no-choice tests used a total of 18 colonies all located within a 1 km radius in the FRIM campus. These colonies occupied many different tree species mainly in and near the FRIM Fruit Arboretum. Ant colonies on neighboring trees were distinguished by staging encounters between ants from those trees. An ant was transferred using soft forceps to a densely populated area of ants on a neighboring tree and it was recorded as belonging to a different colony based on a suite of aggressive behaviors displayed by the resident ants toward the introduced ant (Holldobler & Wilson 1978) or evasive behavior on part of the introduced ant. A captured ant was usually seized by its legs and stretched out in all directions. The ant was designated as from same colony when no evasive or aggressive behavior was observed for or toward the introduced ant. Active antennating of the introduced ant detained by resident ants ultimately resulted in its release. Additionally, trees occupied by the same colony often had overlapping canopies or ant trails on the ground connecting the trees.

For the choice test, conducted between 27 June – 3 July 2006, each of six colonies was provided with four selected food choices, i.e., fresh minced fish (5 g), live mealworms (50 worms), honey solution (15 g) and weaver ant formula (15 g) (Figure 5.1). Each colony represented a replicate. The foods were placed on the feeding platforms at 0830 h and left there until 1430 h. Food was replenished hourly as needed so as to be available *ad libitum*. Digital images of the plastic feeding bowls were taken every hour beginning 0930 h, and the number of ants observed feeding in each bowl was counted. An ant was counted if it was within the perimeter of the rim of the feeding bowl. Counts included ants on the underside of the plastic rain cover, but not on top of it.

Mealworms sometimes were in the other treatment bowls as they were carried in transit to the nest by the ants, and ants carrying them were excluded from the counts of ants in those treatments. The number of remaining worms was also counted. The foods were weighed before and after each feeding period, and weight loss due to evaporation was derived from the control (n = 6). Further, the energetic value and nutrient composition of the

Figure 5.1. Feeding platform providing four food choices to an *Oecophylla smaragdina* colony in a 7 d preference test. The foods were (clockwise from top left) 'weaver ant formula', fresh minced fish, live mealworms and honey solution. The distance from the feeding platform to the nearest nest of the colony was < 3 m.

various foods (Table 5.1) was used to estimate the energetic value of the foods and the amounts of protein and sugar (g) taken by the ants. Where necessary, to ensure those colonies were alerted to the food available, 10 ants were transferred with soft forceps to the feeding bowls.

For the no-choice test, conducted between 5 – 13 July 2006, the four food types were randomly assigned to 12 colonies (three replications each). The method was similar to that for the choice test, but food was given in two bowls per feeding platform to reduce over-crowding at the bowls. Also, a 7 cm diam. polystyrene disk was floated in the liquid food treatments to further reduce evaporation. As direct sunlight caused mealworm mortality in the choice test, extra care was taken in the no-choice test to place the platforms in as much shade as was possible without being directly under the tree canopy.

Additional information was obtained on the microclimatic difference experienced by the worms and ants beneath and outside the plastic cover. A temperature and relative humidity data logger (Hobo®) was affixed with modeling clay within the plastic bowl for a randomly selected mealworm treatment in the no-choice test. A second Hobo® was affixed on the feeding platform outside the plastic cover at the same angle and tilt. Temperature and relative humidity were logged every 15 min. from 0845 to 1430 h for 3 d (1-3 July 2006). The tests were conducted only on days where there was no heavy rain.

Statistical analyses

Analyses of variance were carried out using the statistical software Minitab 14® (MINITAB 2007) and non-parametric analyses were carried out using StatsDirect (StatsDirect 2007). For the choice test, mean weight of foods taken daily per colony over the seven days and mean number of ants counted hourly in feeding bowls per colony over the seven days were analyzed with the factor *food*, using Friedman's test for dependent samples. For the no-choice test, mean weight of foods taken daily per colony over the seven days and mean number of ants counted hourly in feeding bowls per colony over the seven days were analyzed with the factor *food*, using the Kruskal-Wallis test for independent samples. All non-parametric tests were followed by Conover-Inman's pairwise comparisons among *food* (Conover 1999) at $P \leq 0.05$.

For the choice test, mean daily evaporation from foods in each colony's controls over the 3 d was analyzed with the factor *food*, using the Kruskal-Wallis test. For the no-choice test, this response variable was normally distributed and had equal variances, thus was analyzed with the factor *food*, using one-way ANOVA. The paired t-test was used to test for differences in the mean daily feeding platform temperature beneath and outside the plastic rain cover. Further, ambient temperature was analyzed with the factor *day*, using one-way ANOVA. All analyses of variance were followed by Tukey's honestly significant difference test to separate treatment means (Zar 1999) at $P \leq 0.05$. Mean values are followed by ± SE.

Results

Summary statistics of the preliminary study data indicated that live mealworms, minced mackerel, honey solution and the weaver ant formula were preferred by the ants as these foods yielded the highest ant counts and/or greatest weight losses (Figure 5.2). Minced mackerel had similar mean ant counts as minced mealworms, but was chosen over minced

Table 5.1. Nutrient composition and energetic value of four food types provided to *Oecophylla smaragdina* colonies in week-long choice and no-choice tests.

Food[1] (100 g)	Water	Protein	Fat	Ash	Carb.[2]	Fiber	Energy (kcal)
	----------(g)----------						
Fish	70.2	20.1 (53.1)	7.9 (46.9)	1.62	0.0 (0.0)	0	158
Mealworms[3]	62.4	19.8 (40.0)	12.3 (56.0)	1.20	2.0 (4.0)	2.14	244
Honey	83.4	0.1 (0.4)	0 (0)	0.04	16.5 (99.6)	0.04	61
Weaver ant formula[4]	86.2	0.6 (4.1)	0.01 (0.2)	n.a.	13.1 (95.7)	0	53

[1]Data obtained from Nutrient Data Laboratory (2007) for fish (pacific mackerel) and honey, and the granulated cane sugar used in the weaver ant formula.
[2]Carb, carbohydrate.
[3]Data adapted from % nutrients for mealworm larvae (dry matter basis) given by Bernard & Allen (1997), except for the carbohydrate portion, which was deduced consistent with soluble carbohydrates being less than 5% for mealworms (Kasarov 1992). Energy values are calculated from the general factors of 4-9-4 based on industry practices of calculating calories from 4-9-4 kcal per g for protein, fat and carbohydrate, respectively (Nutrient Data Laboratory 2007). For mealworms, this could have resulted in the total energy value (198 kcal) that is different than what would be obtained via the Atwater system for calculating calories (Nutrient Data Laboratory 2007). Cell entries in the columns for protein, fat and carbohydrate state nutrient value per 100 g food followed in parentheses by % contribution to total energy for those three foods.
[4]Weaver ant formula comprised 1g Enerpro™ protein supplement powder and 15 g granulated cane sugar dissolved in 100 g distilled water. Nutritional data for Enerpro™ provided on product label.

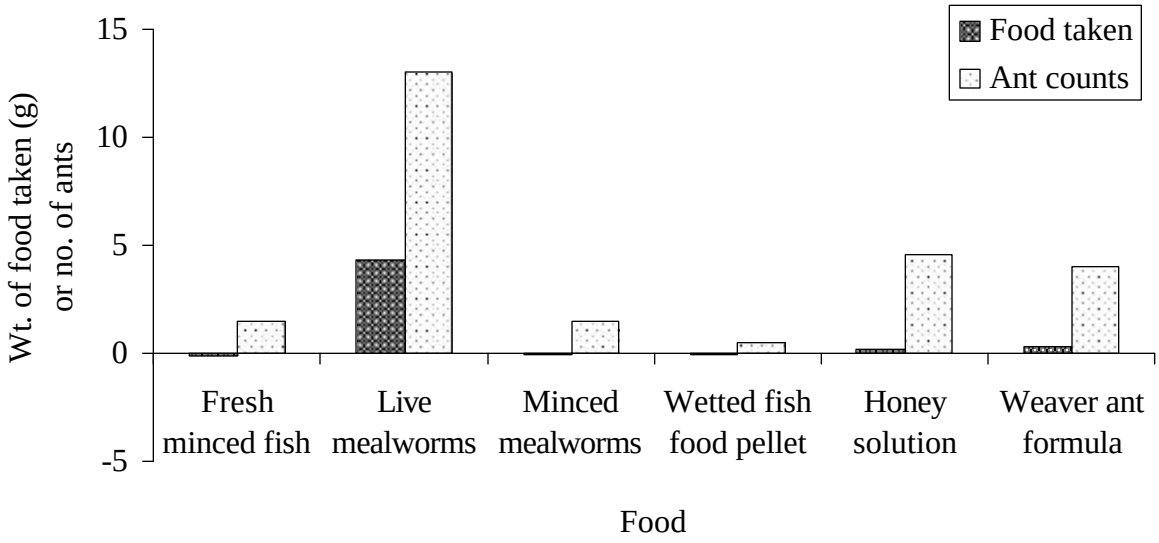

Figure 5.2. Amount of food (g) taken by an *Oecophylla smaragdina* colony and ant counts in feeding bowls in relation to food type in a day-long preliminary study. Preparation of food types described in text.

mealworms as a more practical alternative for the tree farmer to use. The four foods (live mealworms, minced mackerel, honey solution and weaver ant formula) were selected for the subsequent choice and no-choice tests. It appeared that fresh foods were more attractive to the ant than the moistened fish food pellets in the preliminary study. Dry fish food pellets were not taken by the ants.

The choice and no-choice tests are compared using the weight-based method (Figure 5.3) and count-based method (Figure 5.4). Results of the two methods used to evaluate ant preference in the choice and no-choice tests (weight- and count-based methods) are given below.

For the choice test, the weight-based method indicated at least one of the treatments was significantly different from zero (S = 13.2; d.f. = 3; P = 0.0001; Figure 5.3). The amount of live mealworms taken was greater than that of the other foods. Weaver ant formula consumption was greater than that of fish and honey, but fish and honey were not different from each other.

For the choice test, the count-based method also indicated at least one of the treatments was significantly different from zero (S = 13.47; d.f. = 3; $P < 0.0001$; Figure 5.4). Ant counts in the mealworm feeding bowls were greater than that of the other foods and counts in the fish feeding bowls were higher than that in the honey and weaver ant formula feeding bowls. The latter two were not different from each other. It was observed on several occasions that the mealworms were depleted before the next (hourly) replenishment.

For the no-choice test, the weight-based method indicated that live mealworms were the most palatable to the ants but minced fish was readily accepted when no other foods were available. There was a significant difference between at least one of the treatments (H = 8.95; d.f. = 3; P = 0.03; Figure 5.3). The amount of live mealworms taken was not different from that of fish, and both were consumed more than the liquid foods, which did not differ from each other in the amount taken.

For the no-choice test, the count-based method indicated a significant difference between at least one of the treatments (H = 9.6; d.f. = 3; P = 0.022 (adjusted for ties); Figure 5.4). Ant counts in the fish and mealworm feeding bowls were not different from each other, but were both greater than counts in the liquid food feeding bowls, which in turn were not different from each other.

Mealworms in the choice test lost significantly less moisture through evaporation than did the other foods, which were not different from each other (H = 14.57; d.f. = 3; P = 0.002; Figure 5.5). In the no-choice test, there was a significant difference between at least one of the foods (F = 43.3, d.f. = 3, 8; P = 0.000). As in the no-choice test, mealworms lost less moisture through evaporation than the other foods. However, in contrast to the choice-test, evaporative water loss from the honey and weaver ant formula was less than that from fish. The two liquid foods were not different in terms of evaporative water loss.

The mean 'ambient' temperature (ºC ± SE) on the feeding platform recorded from 1-3 June during the no-choice test was 33.3 ºC (± 1.0 ºC, n = 3) and not significantly different (t = 1.54; d.f = 4; P = 0.263) from the mean temperature beneath the plastic cover at 34.4 ºC (± 1.7 ºC, n = 3). Ambient temperatures throughout Day 3 were warmer (35.2 ± 0.4 ºC; n = 22, range: 32.3 - 38.8 ºC) than temperatures throughout Days 1 and 2 (32.2 ± 0.5 ºC, range: 28.3 – 36.6 ºC; and 32.4 ± 0.3 ºC, range: 28.7 – 35.7 ºC, respectively; n = 22) and this difference was significant (F = 15.8; d.f. = 2, 63; P = 0.000). The use of the plastic cover was judged

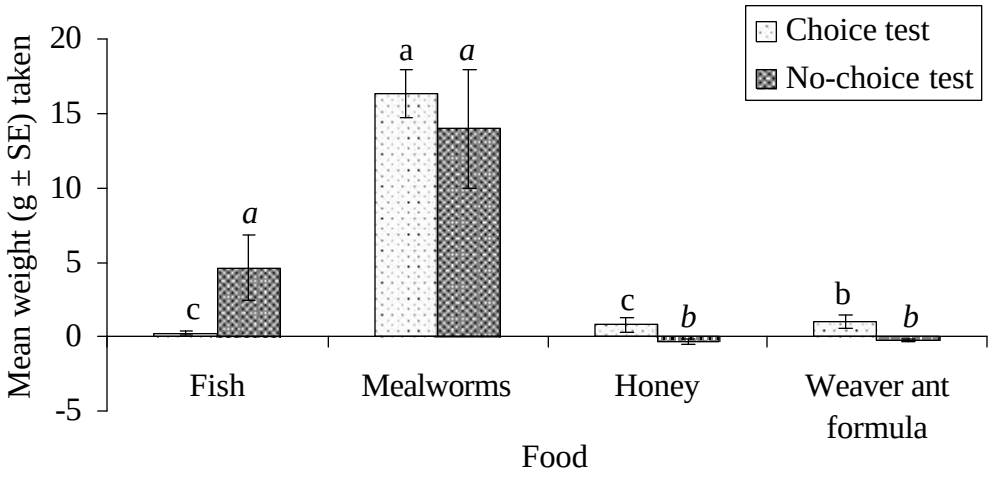

Figure 5.3. Mean amount of food (g ± SE) taken daily by *Oecophylla smaragdina* colonies in relation to four food types in a choice (n = 6) and no-choice test (n = 3) over 7 d. Means with the same letter (italicized for no-choice test) were not significantly different ($P \geq 0.05$). Friedman and Kruskal-Wallis pairwise comparison procedures separated treatment medians for the choice and no-choice test, respectively.

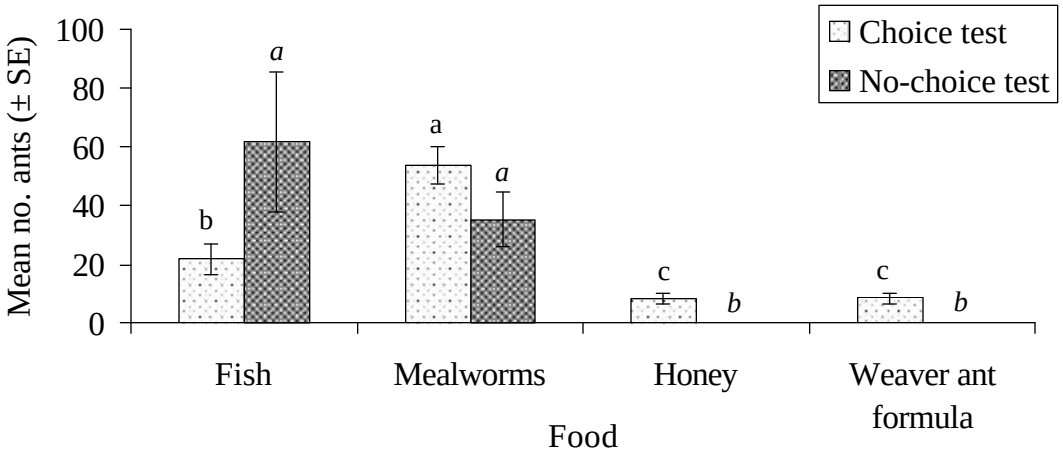

Figure 5.4. Mean counts (± SE) of workers in feeding bowls in relation to four foods provided to *Oecophylla smaragdina* colonies in a choice (n = 6) and no-choice test (n = 3) over 7 d. Instantaneous sampling was done just before the hourly food replenishments. Mean daily ant count over 7 d was calculated from the mean of daily instantaneous samples. Means with the same letter (italicized for no-choice test) were not significantly different ($P \geq 0.05$). Friedman and Kruskal-Wallis pairwise comparison procedures separated treatment medians for the choice and no-choice test, respectively.

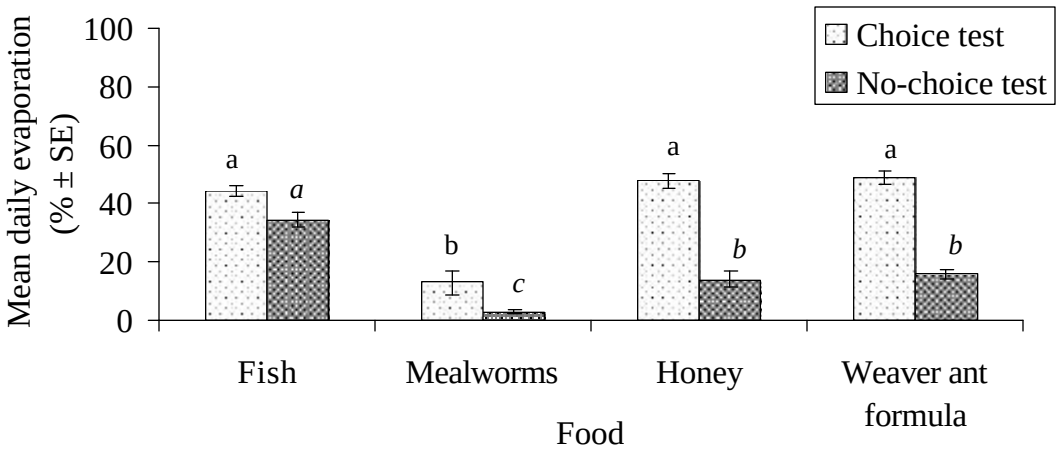

Figure 5.5. Mean daily evaporative water loss (% ± SE) from the controls of four foods tested for *Oecophylla smaragdina* preference in a choice (n = 6) and no-choice test (n = 3) over 7 d. Evaporation was reduced in the no-choice test by floating a food-grade polystyrene disc on the liquid foods. Means with the same letter (italicized for the no-choice test) were not significantly different ($P \geq 0.05$). Kruskal-Wallis pairwise comparison procedure and Tukey's pairwise comparison procedure were used to separate treatment medians and means, respectively, for the choice and no-choice test.

appropriate as it did not seem to deter ant activity, which indicated the temperatures were within the ants' physiological functional temperatures (< 43 ºC).

Observations on foraging behavior of individual colonies or groups of colonies follow. During the choice test, one colony (Colony 1) exhibited a different food consumption pattern than the others (Figure 5.6). Typical colonies tended to sustain a high daily consumption of mealworms (17.4 ± 0.6 worms) over the 7 d and a low daily consumption (0.4 ± 0.4 and 0.7 ± 0.4 g for honey and weaver ant formula, respectively) of liquid foods. Colony 1 had a lower daily consumption (8.7 g) of mealworms and a higher daily consumption (2.8 and 2.5 g for honey and weaver ant formula, respectively) of liquid foods. Mealworm consumption for Colony 1 peaked at 17.3 g on the third day and declined as liquid food consumption increased (Figure 5.7).

In both the choice and no-choice tests, ants in half the colonies discovered the foods on the feeding platforms within an hour of food placement on the first day. Patrolling ants descended via the string bridge to the feeding platforms, investigated the foods offered and returned to recruit more ants. 'Timid' ants from more 'passive' colonies were induced to descend via the string bridge to the platform by tugging the string connecting the nest to the platform. Once established as their territory, the ants maintained a continuous presence on it, even after the last feeding bowls were removed at the end of each day. In the no-choice test all the colonies provided with liquid foods were apparently 'passive'. These colonies were alerted to the food available by transferring ten ants to the feeding bowls. The ants appeared to sample the liquids but did not remain to drink. After they left the feeding platforms via the string bridge presumably rejoining their respective colonies, no other ants were observed on the platforms.

There were three instances of mealworms being preyed upon by birds in the no-choice test and these were deemed missing values in the analyses. There were two such incidences on the fifth and sixth day of the choice test, which was conducted the week before in the same area, and it appeared that the birds learned of the presence of the food over the course of the studies. Other missing values were due to spilled weaver ant formula from one of the replicates on the fifth day of the no-choice test.

It was also observed that taking the fish became harder for the ants as it dried out during the day. The ants were able to take bite-sized pieces of the freshly minced fish but in a few hours it formed a 'skin' through which the ants had difficulty biting. The more persistent ants succeeded in carrying away the entire serving of the minced fish in that form, provided it could be dislodged from the bottom of the feeding bowl.

Discussion

The weight-based method clearly demonstrated the ant's preference/acceptance (in the choice/no-choice test) for live mealworms. Further, this overwhelming preference/acceptance of the ants for the mealworms influenced the outcomes for both tests as discussed below.

First, in the choice test, the intended *ad libitum* provision of the four foods via hourly replenishments was not achieved for the mealworms. The mealworms were rapidly 'consumed' (captured and transported to the nest) and once this resource was exhausted the ants moved on to the next most preferred food, i.e., fish. This behaviour was observed to occur on several occasions, and likely resulted in the preference for fish being overestimated

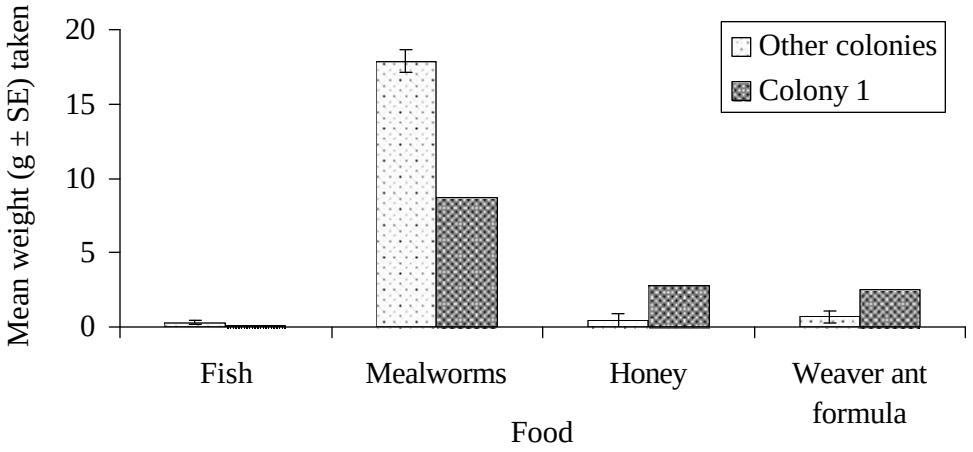

Figure 5.6. Mean weight (g ± SE) of food taken daily by *Oecophylla smaragdina* colonies in relation to four food types in a 7 d choice test. Five colonies with similar patterns of consumption are contrasted with an atypical pattern shown by Colony 1.

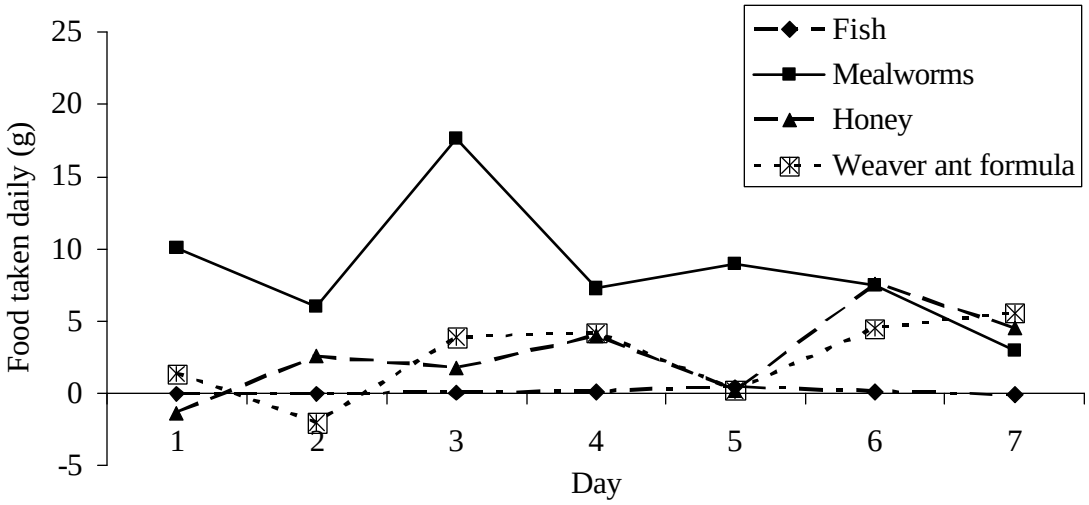

Figure 5.7. Consumption of four foods by an 'atypical' *Oecophylla smaragdina* colony (Colony 1) over seven days of a choice test.

in the choice-test. More fish was taken than would have been the case if mealworms were unlimited. Also, fewer ants were counted in the mealworm feeding bowls because minimal ant presence was maintained in those bowls after they were emptied.

Second, in the no-choice test, the occasional interruption of the mealworm supply in the mealworm treatments resulted in misleadingly low ant counts from those end-of-the-hour instantaneous samples. Thus, the count-based method underestimated the ant's acceptance of mealworms in the no-choice test and erroneously resulted in fish ranking higher than mealworms instead. Perhaps instantaneous samples for the count-based method would have better reflected ant preference if taken shortly after replenishment of the foods. However, the ants' extremely strong preference for the mealworms resulted in a seething mass of ants in those feeding bowls immediately after replenishing the bowls, which was difficult to accurately count.

The count-based method better demonstrated ant preference where liquid foods were offered, compared with the weight-based method. Ants would return to the nest after imbibing the fluid for several minutes and appeared to maintain a consistent presence in those feeding bowls throughout the day, as indicated in the instantaneous snap-shot samples. The weight-based method did not provide a satisfactory reflection of ant preference for liquid foods because the results were too variable. In the choice test the amount of solution taken weighed about 1 g per day but evaporative water loss exceeded 7 g per day while in the no-choice test the estimated amount of solution taken was a negative value (ca. -0.3 g per day) with water loss of over 4 g per day.

The preference/acceptance of the foods in the choice/no-choice tests generally concurred with previous studies where food energetic values (Traniello 1989), carbohydrate : protein ratios, food quality (Kay 2002), seasonal presence of brood (Greenslade 1971; Cannon & Fell 2002) and habituation (Blüthgen & Fiedler 2004b) were used to elucidate ant foraging behavior.

Energy content is typically equated with food value in ant studies (Traniello 1989). From an energetic standpoint, the overwhelming preference of the ants for mealworms could be due to the very high calorific value of the mealworms compared with the other foods (Table 5.1). The results of the choice test suggested that the ants were able to distinguish among the four food choices and selected the food with the greatest energetic value, i.e., mealworms. This was supported by observations of the ants taking fish, which was the next best food in terms of energetic value, during the brief interruptions in mealworm supply. The ants' foraging behavior appeared to be dynamic, with the ants responding quickly and adaptively to resources as these resources became available.

The carbohydrate : protein ratio hypothesis only partly explained the results of the study. Both protein and carbohydrate have been found to influence food selection in ants, which invest more energy foraging for resources that are scarce (Kay 2002). Since prey is generally less abundant than the high-carbohydrate honeydew and/or plant nectar (Stork 1991) that forms the staple resource for *O. smaragdina* (Blüthgen *et al*. 2004), prey should be more attractive to the ant. The consumption of the high-protein foods and the non-consumption of the high-carbohydrate foods in the no-choice test supported the prediction of the carbohydrate : protein hypothesis. However, the overwheliming preference for mealworms over fish was inadequately explained via this line of reasoning because the carbohydrate : protein ratio is higher for mealworms than for fish (Table 5.1). Instead of carbohydrate : protein ratios, the ant's food choices may be better explained by extra benefits

acquired and/or other feeding stimulants.when the amount of protein is similar for those foods. Mealworms had protein content comparable to that of fish, but also contained carbohydrate and 4.4 g (per 100 g) more fat than fish. Based on an industry standard factor of 4-9-4 kcal per g of protein, fat and carbohydrate, respectively (Nutrient Data Laboratory 2007), mealworms provide 40 kcal (per 100 g) more than fish. It is also possible that mealworms contained a feeding stimulant for the ant. Prey kairomones, e.g., cuticular products in adults (Dejean *et al.* 1990), elicit specific behavioral responses in hymenopteran predators (e.g., Dejean *et al.* 1990). Further work is needed to investigate these possibilities.

Ants may also pass up foods if they expect to secure higher-quality foods elsewhere (Kay 2002), and this was possibly why the liquid foods were rejected in the no-choice test and were minimally consumed in the choice test. This may also explain why Colony 1 appeared to consume more liquid food than other colonies (Figure 5.6). Perhaps this colony had limited access to honeydew and plant nectar compared with other colonies and further work is needed to investigate this possibility. The weaver ant formula was a supposedly 'high-quality' liquid food with a 13% sucrose concentration similar to that in a typical honeydew sample, and had a broad complement of amino acids (Table 5.2). However, it was no better than typical honeydew in phenylalanine concentration, which is highly attractive to the ant (Blüthgen & Fiedler 2004b). The honey solution was of 'high-quality' because of its overall sugar concentration of 16%, but sucrose concentration was very low (<1%) and the concentrations of amino acids were far lower than that typically found in honeydew. Based on overall nutritive value it was expected that honey would be less preferred than the weaver ant formula, but the count-based method found no significant difference between them in the choice test.

The foraging behavior of this ant could have also been influenced by colony needs (Greenslade 1971; Blüthgen & Fiedler 2004b). Carbohydrate and protein fulfill different colony needs (Wheeler 1994). Proteins are fed to larvae while workers use sugars for their own metabolic needs (Haack *et. al*, 1995). Foraging activity for high-protein prey is typically higher when brood is being produced (Cannon & Fell 2002). *O. smaragdina* has been observed to bring more prey back to the nest during the wet season (Greenslade 1971). This seasonal variation was attributed to prey abundance rather than brood production although brood was abundant in the wet season (Greenslade 1971).

Finally, the type and quantity of food resource consumed the previous day may have influenced the food consumption patterns of the colonies in this study. Ants provided large quantities of a preferred amino acid solution have been reported to exhibit a significant reduction in attraction to that food after two days and this was attributed to habituation (Blüthgen & Fiedler 2004b). It is more likely that the declining preference for mealworms exhibited by Colony 1 over the 7-day choice test (Figure 5.7) was due to satiation rather than habituation because the other colonies did not show signs of habituation. It is not unreasonable to suppose that Colony 1 had stored up sufficient numbers of mealworm prey in its nests to feed its larvae ('satiation') and thereafter needed more liquid foods, which were lacking in its territory. A similar trend in the number of mealworms taken by the ants for the other colonies could be expected if the *ad libitum* provision continued and this should be substantiated in future work.

Some reasons may be offered as to why the ants rejected the liquid foods when served alone (in the no-choice test) but consumed those foods when served with mealworms (in the choice-test). Results of a previous study suggest that simultaneous presentation of a preferred

Table 5.2. Amino acid and sugar composition of liquid foods (weaver ant formula and honey) offered to *Oecophylla smaragdina* colonies in a choice and no-choice test compared with liquid foods used in a previous study on foraging behavior of nectar-feeding ants

Nutrient (in 100 g)	Weaver ant formula	Honey	"Mix F"[1]	"Mix G"[1]	Unit
Energy	52.8	60.8	na	na	kcal
Protein	0.6	0.1	na	na	g
Total lipid (fat)	0.01	0	na	na	g
Carbohydrate	13.1	16.5	na	na	g
Fiber	0	0.04	na	na	g
Sugars, total	13.1	16.4	15	15	g
Sucrose	13.1	0.18	5	15	g
Glucose (dextrose)	na	7.15	5	–	g
Fructose	na	8.19	5	–	g
Maltose	na	0.29	–	–	g
Galactose	na	0.62	–	–	g
Amino acids, total	0.59	0.05	7.15	1.01	g
Tryptophan	0.003	0.001	–	–	g
Threonine	0.023	0.001	0.480	0.010	g
Isoleucine	0.027	0.002	0.730	–	g
Leucine	0.051	0.002	0.930	0.080	g
Lysine	0.041	0.002	1.000	–	g
Methionine	0.018	0.0002	0.120	0.010	g
Cysteine	0.002	0.001	–	–	g
Phenylalanine	0.032	0.002	0.260	0.080	g
Tyrosine	0.029	0.002	0.360	0.060	g
Valine	0.034	0.002	0.730	0.070	g
Arginine	0.022	0.001	0.600	0.090	g
Histidine	0.020	0.0002	0.740	0.420	g
Alanine	0.022	0.001	–	0.030	g
Aspartic acid	0.037	0.005	–	–	g
Glutamic acid	0.116	0.004	–	0.050	g
Glycine	0.013	0.001	1.200	0.010	g
Proline	0.065	0.018	–	0.020	g
Serine	0.031	0.001	–	0.080	g

[1]"Mix F" was formulated using 15g sugar and 1g total amino acids per 100 g solution and "Mix G" was formulated to mimic the composition of membracid honeydew. Source for these liquid foods adapted from Blüthgen & Fiedler (2004b).

food with a less preferred food may increase the palatability of the latter. Kotler *et al.* (1998) found that bowls of water next to feeding trays lowered the 'giving up density' (GUD) of seeds because water sources increased the seeds' marginal value. The GUD may be used to indicate resource availability (Kay 2002). It may be that the presence of mealworms increased the marginal value of the liquid foods in the choice test. The liquid foods may have been conveniently placed to replenish the ants' energy expended in subduing the mealworms. What little inclination to take these liquid foods that the ants showed in the choice test was amplified in the no-choice test where the main inducement to feeding, i.e., mealworms, was not present. There also may have been a possible repellent effect of the polystyrene foam disk floated on the liquids to reduce evaporation in the no-choice test but not the choice test. However, the use of the polystyrene foam disk in a subsequent study did not appear to deter the ants (G.T. Lim, personal observation). This simple technique reduced evaporative water loss from liquid foods by 60% in the no-choice test compared with the choice test.

It was interesting that the evaporative water loss data were normally distributed in the no-choice test but not in the choice test, leading to their analyses with parametric and non-parametric tests, respectively. The departure of the choice test data from a normal distribution may be attributed to a sharp increase in water loss following death of the mealworms. Mealworms have a cuticle to protect them from evaporative water loss. Thus, evaporative water loss from the mealworms may not have followed a straight line over time, because the worms could regulate cuticular water loss very well right up to the point of death from overheating. The positioning of feeding platforms in the no-choice test likely reduced mealworm death from sun exposure, and resulted in a consistently low evaporative water loss recorded from this food.

The ants may have had an inherent preference for solid vs. liquid foods with protein content being incidental. However, this species has demonstrated a 'trophic plasticity' (Blüthgen *et al*. 2003) partly because it can consume both liquid and solid foods (Kay 2002; Blüthgen & Fiedler 2004b), which may vary in availability from habitat to habitat (Blüthgen *et al*. 2003). Additionally, it is possible that the ants selected foods that were easier to transport for the least energy expended securing and transporting it. The state of the food (solid vs. liquid) was not likely to be as important as the energetic value and protein content discussed earlier but further evaluation of solid vs. liquid food preference is needed to confirm this. Such an evaluation could compare foods in their minced and liquefied states.

The colonies in this study were established, and their dietary needs may differ from colonies moved from their original host plants to mahogany trees. An uprooted colony may need supplemental liquid sugars and/or prey items until it has cultivated enough trophobionts on its new host plant to meet its needs. The establishment success of such colonies in relation to food supplementation will be evaluated in the next study. Based on the present study, the supplemental foods chosen are the weaver ant formula and mealworms. Since there was no difference in preference shown by the ants for either liquid food in the choice test, the weaver ant formula was arbitrarily selected as it provides more nutrients than honey. Furthermore, the weaver ant formula costs less than honey (5 vs. 20 cents per 100 ml serving). Only 1 g of powdered formula was needed per serving, and a $13 (USD) tin would provide 375 g. Mealworms are widely available as bird food in Malaysian pet stores and although more costly than fish ($20 vs. $2 per kg), have better keeping abilities if shaded (ca. 1 wk vs. 2 d; G.T. Lim personal observation) and thus do not require frequent replacement. However, measures may be needed to prevent access of other predators, e.g., birds, to the mealworms.

Chapter 6

The effect of food supplementation on the establishment of redistributed weaver ant colonies

Introduction

The predatory and territorial weaver ant, *Oecophylla smaragdina* F. (Hymenoptera: Formicidae) was recently identified as a potential biological control agent of an important mahogany pest, *Hypsipyla robusta* Moore (Lepidoptera: Pyralidae), in Malaysian plantations (Lim & Kirton 2003). The mahogany shoot borer is the main factor limiting the cultivation of mahogany worldwide and *Hypsipyla grandella* (Zeller) in the Americas and *H. robusta* in Africa and the Asia-Pacific region are the two most important *Hypsipyla* species (Griffiths 2001). Mahogany species, which include trees from the genus *Khaya* and *Swietenia* (Meliaceae) (Goulet *et al*. 2005) have an extremely low damage threshold of as low as one larva per tree (Taveras *et al*. 2004). Therefore, perpetual ant presence on all the trees at sufficiently high levels is probably needed to provide satisfactory protection via predation and/or oviposition deterrence. For a fast-growing species like *Khaya ivorensis* A. Chev., this protection is only needed for the first three to five years (Mayhew & Newton 1998), at the end of which a merchantable height of 8 m is expected (Aminah *et al*. 2005).

Entire colonies that house the living leaf nests of this arboreal ant are harvested and introduced to the environment in which one is seeking protection from arthropod pests. Redistribution of the ants in this manner has been practiced by citrus farmers in China since 300 A.D., in addition to providing bamboo bridges that facilitate the ants' dispersal throughout the orchard (Huang & Yang 1987). Relocated colonies may establish more efficiently if provided supplementary food that meets their energetic and nutritional requirements. The ant's diet comprises honeydew from trophobionts, e.g., scale insects (Hemiptera) in a mutualistic relationship, plant nectar and prey (Holldobler 1983a). High-carbohydrate foods similar to honeydew and plant nectar may be needed to sustain worker activity during this period where trophobiont population levels on the new host are anticipated to be low. The colonies may become less reliant on supplemental high-carbohydrate foods as their cultivated trophobiont populations increase. Consequently, colony expansion may be aided by providing high-protein prey, which is fed to brood (Haack *et al*. 1995). Results of a previous study (Chapter 5) suggested that live mealworms and 'weaver ant formula' (15 g sucrose and 1 g human muscle-training powder by NutraLife®, dissolved in 100 ml water; Chapter 5) can be used as supplemental food for newly relocated colonies.

Additionally, relocated colonies need adequate quantities of young foliage for nest-building and cultivating their trophobiont mutualists. A previous study (Chapter 4) recorded three established single-tree colonies on *K. ivorensis* that were 6.5 m tall (SE = 2.6, range: 2.3 – 11.3 m, n = 3) and supported a mean of 17,600 ants (SE = 8,300, range: 2,800 - 31,500, n = 3). Foliage provided by a single tree appeared adequate for nest-building for these established colonies (G.T. Lim, personal observation).

Finally, relocated colonies may need temporary protection from other ant species during their establishment period (Way & Khoo 1991; Way & Bolton 1997). Suppression of *P. megacephala* with a pesticidal bait resulted in *O. smaragdina* replacing the former and

successfully controlling the coreid, *Pseudotheraptus wayi* Brown (Hemiptera: Coreidae) in coconut (Zerhusen & Rashid 1992). An alternative to pesticides could be the use of a physical barrier to exclude other ant species, e.g., monthly applications of Coldfoot® (clear sticky polybutene gel commercially available as a bird repellent) in a band around weaver ant-occupied trees (G.T. Lim, personal observation). Several ant species have been reported to suppress or destroy *Oecophylla* colonies, e.g., *Pheidole megacephala* Mayr (Hymenoptera: Formicidae; Zerhusen & Rashid 1992) and *Anoplolepis longipes* Jerdon (Hymenoptera: Formicidae; Soans 1971). A resident ant, *Dolichoderus* sp. nr. *affinis* (Hymenoptera: Formicidae), was found to persistently invade harvested weaver ant nests that were placed on platforms in a trial mixed-planting of *Morinda citrifolia* L. (Rubiaceae) with *K. ivorensis* (G.T. Lim, personal observation). These soil-nesting ants, which are generally scavengers that tend trophobionts (Shattuck & Barnett 2007), overwhelmed workers of the weaver ants and preyed on eggs and pupae in that trial planting.

The objective of this study was to evaluate the effect of food supplementation on the establishment of ant colonies introduced to *K. ivorensis.*

Materials and Methods

The study was conducted within a ¼ ha plantation of three year-old *K. ivorensis* at the Bukit Hari Forest Reserve, Selangor (3º14'N, 101º38'E, ca. 100 m a.s.l.). The forest reserve is managed by the Forest Research Institute of Malaysia (FRIM), Selangor, and used for research. The average daily temperature ranges from 27 – 32ºC with annual rainfall between 1800 – 2900 mm. The terrain is undulating and granite underlies shallow reddish loam topsoil. A few of the *K. ivorensis* trees at the study plot were already occupied by weaver ant colonies, indicating conditions favorable to introducing ants to unoccupied trees.

The study was divided into two consecutive periods. The first involved intensive daily monitoring for the first week of the study and the second period involved weekly monitoring for 15 weeks. The initial intensive monitoring was to quantify the consumption of the supplemental foods (mealworms and weaver ant formula, Chapter 5) by ant colonies in the food treatment, and the effects of supplemental food provision on those colonies. It also aimed to promptly identify and address any unforeseen issues arising in the early stage of this pioneering study.

There were three treatments:

1) Food provided to the introduced '*F* colony'
2) No food provided to the introduced '*C* colony'
3) Food with ants and other insects excluded ('evaporation control').

There were six replicates per treatment. Each replicate was assigned randomly to one of 18 trees randomly selected from 50 suitable trees in the study plot. Suitable trees were those whose canopies did not overlap adjacent trees, and that were not already colonized or patrolled by weaver ants or other ant species. In addition, the heights of trees that housed single colonies in Chapter 4 were compared with the heights of the new host trees selected for colony introductions in the present study. The mean height (4.2 m, SEM = 0.5 m) of the eight trees in the present study were not significantly different (t = 0.88; d.f. = 2; P = 0.47; two-sample t-test) from the mean height (6.5 ± 2.6 m) of the three single-tree colonies in Chapter 4.

Colonies were obtained from a *K. ivorensis* plantation at Chinoh River, Perak (3°53'N, 101°22'E; courtesy of Mr Lim Sun Heng, Managing Director of Maju Aik Ltd.). Ant colonies on neighboring trees were distinguished by observing the fate of ants introduced to a neighboring tree's ant colony in staged encounters as described in Study 3, and by visual inspection for ground trails (Chapter 5). Every attempt was made to completely census the colonies to ensure that all nests were accounted for. The total nest volume for each colony was then calculated. Total nest volume of these eight colonies was not significantly different from the three colonies supported by a single tree in Chapter 4 (t = -1.29; d.f = 9; P = 0.23; two-sample t-test with pooled standard deviations). Mean nest volumes for the former and latter colonies were 3.7 ± 0.7 m^3 and 1.9 ± 1.3 m^3, respectively. Since the new host trees selected for colony introductions were similar in size to trees that were previously known to support a single colony, they were deemed adequate for supporting their assigned colony.

In addition to nest volume, the number of ants in a colony was estimated using the regression model developed in Chapter 4 for *K. ivorensis*: $\log_{10}(\textit{Number of ants}) = -1.16 + 1.09 \log s$, where nest size, s = nest height and length. The presence or absence of brood-queen nests was also tentatively identified for each colony. Chapter 4 categorized pavilions as 5 – 12 cm diam. and brood-queen nests as 10 – 28 cm diam. The present study categorized 11 cm diam. (ca. 1331 cm^3) nests as brood-queen nests and nests with diameters < 11 cm as pavilions.

Nests located lower in the tree canopy were harvested using telescoping clippers that had a reach of 10 m. Nests higher up (10 – 15 m) were harvested using a clipper attached to the end of a rubber-wood pole, which was joined to a hollow aluminum pole. Some nests could not be harvested as they were beyond the reach of the harvesting equipment and this was noted. The nests were bagged in breathable draw-string muslin cloth bags measuring 1 x 1 m and immediately placed on wire racks in an air-conditioned all-terrain vehicle. The bags were separated by colony, to reduce possible stress from inter-colony proximity. Where possible, the nests were clipped so that they would drop directly into the bags. The mouth of a bag was held open by a stiff wire hoop attached to the end of a 10 m pole. Easily removable spring-type paper clips temporarily secured the mouth of the bag to the wire hoop. Very high and/or very large nests could not be clipped directly into these open-mouthed bags. However, they remained intact after clipping as their fall was cushioned by the dense undergrowth. The nests were collected on July 18, 2006, in the morning, and promptly transported to the study site for a late afternoon release.

Colonies were randomly assigned for release onto 12 of 18 trees used in the study. Before their release, the release sites were set up for all the trees and supplemental foods readied for the trees that were assigned *F* colonies. Six feeding platforms previously used in Chapter 5 were employed in the present study as the release arenas for each of the *F* colonies. These platforms were 60 x 60 cm plywood boards individually mounted on 1 m high wooden stakes driven into the ground next to their respective trees so that one edge of the plywood board directly contacted the tree stem. Both the tree stems and the wooden stakes were banded with Coldfoot® at 0.75 m above ground level to exclude other crawling insects and to confine the ants to their respective trees. The two supplemental foods were placed in 10 cm diam. plastic feeding bowls set on the platform, one bowl for each food type. For the first week, 15 ml liquid food and 50 mealworms were provided daily to each colony. As with the previous study (Chapter 5) the feeding bowls were sheltered under a clear plastic cover glued to the platform with four bamboo chopstick stands.

All the bags from a colony were placed on their assigned platform in a stacked arrangement around the top of the clear plastic cover that sheltered the feeding bowls. The bags were untied for the ants to disperse onto the tree, and removed after the ants had left the old nests (ca. 3 d). After the bags were removed, the feeding bowls that were previously concealed by them likely became more accessible to birds as many treatments were vandalized. A wire netting was attached with spring-type paper clips to the perimeter of the platform to completely enclose the feeding bowls to ensure that the ants were the sole benefactors of the food. A 20 x 20 cm piece of plastic tarp material was attached to the underside of the netting to shade the mealworms and reduce their mortality. Evaporation controls were set up the same way as for the *F* colonies, but with no ants introduced. The foods were changed every day and the amount (g) taken by the ants was recorded daily for a week. For this first week, the effect supplemental feeding had on the ants was evaluated by comparing ant activity rank on the feeding platform and tree stem of *F* colonies (ranks 0 – 4 denoted 'no ants', 1 – 5, 6 – 10, 11 – 29 and 30 – 50 ants, respectively) with that for the *C* colonies. Dimensions of nests built, i.e., height and length, were recorded as an additional indicator of ant activity. Colonies showing minimal to no activity in the first week were replaced with fresh colonies harvested from a *K. ivorensis* stand near the study site.

Subsequently, the foods were changed during each weekly monitoring session for another 15 weeks. 100 ml of weaver ant formula and 100 mealworms were provided each week. During this period, a more specific method to gauge ant activity was used in place of the ranking approach, i.e., the average number of ants on the uppermost 10 cm of the tree's shoot/s was counted with the aid of binoculars. The amount of supplemental liquid food taken during the week was not measured but counts were taken of ants inside those feeding bowls two days after each food change. This gave an instantaneous sample of ant consumption of liquid food before it curdled (ca. 3 d). As with the first week's monitoring, nest-building was tracked as an indication of colony establishment and/or expansion.

Based on daily observations of the ants in the first week of the study, an important addition to the experimental design was put in place from the second week onward. Each colony's territory was expanded from a single tree to two additional neighboring trees via 2 mm diam. cotton string bridges connecting the trees. We felt that a colony confined to a single tree would be constrained by its limited foraging territory. In addition, colony expansion could be curtailed due to insufficient foliage for nest-building. The foliage on several trees was almost completely used for nest-building and the nests were crowded (G.T. Lim, personal observation). Especially for the *C* colonies, increasing foraging area would better reflect a field situation where an uprooted colony is introduced to a new area and left to forage freely without supplemental feeding. Providing three trees as foraging territory for a colony was a compromise between this ideal scenario and the need to keep the colonies separate, and exclude enemy ant species. The merit of a tree-for-tree approach in gauging foraging area requirements of relocated colonies was evaluated. Post-hoc comparisons in the ratio of crown area : colony size (cm^{-1}) were carried out among colonies in a previous study (Chapter 4), established colonies in the present study (pre-harvest), and the same colonies on their new hosts (post-release). Crown area, which is photosynthetic area well suited for nest-building, was calculated for each tree based on a cylindrical crown shape typical for *K. ivorensis* (Chapter 4).

Statistical analyses

The results were analyzed with the statistical software Minitab 14® (MINITAB 2007). For the first week of intensive monitoring, the two-sample t-test, for normal data with equal variances, was used to test for differences between *F* and *C* colonies in the mean total volume, per colony, of nests built that week, and in the mean ant activity on shoots that week. Additionally, the two-sample t-test was used to test for differences between relocated (present study) and established colonies (no choice test, Chapter 5), in the mean daily mealworm and weaver ant formula consumption per colony nest volume, over the first week. Results for weaver ant formula consumption were transformed: square-root ($\log_{10}(2 + Y)$), to achieve normality and equal variances.

For the longer term assessment, total volume of nests built per colony and ant counts on shoots per colony was analyzed separately using general linear models with food, week and their interaction as factors. Wk 15 – 16 were excluded from the analyses for reasons explained in the following section. The paired t-test was used to test for differences in total crown area per colony occupied by colonies at their former site (pre-harvest) and provided to those colonies at the site they were relocated to (post-harvest). The crown area : nest volume ratio per colony was analyzed using general linear models with factor colony type, which tested for a significant difference among colonies pre-harvest, post-release and Chapter 5 colonies. All analyses of variance were followed by Tukey's honestly significant difference test to separate treatment means (Zar 1999) at $P \leq 0.05$. Additionally, results for ant counts on shoots were $\log_{10}(Y+1)$ transformed to achieve normality and equality of variances. Reported mean values are followed by ± SE.

Results

First week

In the first week of the study, all colonies exhibited some activity around the tree shoots and *F* colonies consumed supplemental food, but only eight of the 12 colonies built nests. The initial size of the introduced colony and/or the absence of any brood-queen nests appeared to affect colony survival and establishment of new nests (Table 6.1) as the two smallest colonies had not constructed any nests in their new host tree by the end of the week. Both of these colonies were also the only two without brood-queen nests. The two partially-collected colonies also did not build any nests. None of these colonies were replaced with new ones at the end of the week because only one suitable replacement colony could be found. Partially-collected colonies and very small colonies were excluded from the subsequent long-term period of the study, leaving four replicates per treatment for that duration. The eight complete colonies were evaluated for treatment differences in nest-building, ant activity, and food consumption in the first week.

Figure 6.1 shows ant activity patterns as measured by food consumption, nest-building, and ant presence, in relation to food supplementation in the first week. *F* colonies showed an increasing trend in nest-building after four days of 'inactivity' and *C* colonies showed a similar, but lower trend (Figure 6.1.a). Mean volume of nests built over the first week by *F* colonies (4,600 ± 2,000 cm^3 per colony) and *C* colonies (1,700 ± 1,200 cm^3 per colony) was not significantly different ($t = 1.31$; d.f. = 6; $P = 0.24$). Mean ant activity rank on shoots over the first week of *F* colonies (2.17 ± 0.4) and *C* colonies (2.17 ± 0.3) was also not significantly different ($t = 0.00$; d.f. = 6; $P = 1.00$; Figure 6.1.b).

Table 6.1. Pre-harvest sizes of 12 *Oecophylla smaragdina* colonies from a *Khaya ivorensis* stand in Perak and 7 days post-release onto individual *K. ivorensis* trees at the study site at Bukit Hari, Selangor.

Treatment	Colony	Pre-harvest		Harvested brood-queen nests and (pavilions) [z]	Post-release nest volume at 7 d (cm^3)
		Nest volume (cm^3)[x]	Ant numbers[y]		
No food provided	1	39,079	29,727	2 (1)	15,427
	2	27,689	19,884	4 (0)	2,396
	3	196	99	0 (1)	0
	4	21,209	16,281	1 (0)	295
	5	54,985 (12,568)	40,341 (7779)	6 (1)	0
	6	19,638	13615	3 (2)	786
	Mean	27,132	19,991	2.7 (0.8)	3,151
Food provided	1	73,052	58,056	4 (0)	786
	2	53,968	39,654	5 (4)	21,307
	3	20,718	14,221	4 (0)	1,571
	4	1,964	1,146	0 (2)	0
	5	40,061	32,127	2 (0)	12,489
	6	43,203 (12,568)	31,644 (8636)	3 (0)	0
	Mean	38,827	29,475	3.0 (1.0)	6,025

[x] Nest volume was the sum total of nest volumes, each of which was calculated with the formula: p r^2 $\hat{I}$, where r = ½ h (r, nest radius; h, estimated nest height; $\hat{I}$, estimated nest length). Cells with parentheses indicate partial collection of the colony and numbers in parentheses are volumes of nests that were successfully collected. All other colonies were collected in full.

[y] Estimated ant numbers from a model developed in Study 3 for the number of ants within an *O. smaragdina* nest on *K. ivorensis*: $\log_{10}$(*Number of ants*) = - 1.16 + 1.09 $\log_{10}$(*Nest volume*). Cells with parentheses indicate partial collection of the colony and numbers in parentheses are estimated ant numbers in nests that were successfully collected. All other colonies were collected in full.

[z] Tentative identification of brood-queen nests as those equal or larger than 1331 cm^3, and pavilions as smaller than 1331 cm^3. Cells contain the number of brood-queen nests followed by number of pavilions in parentheses.

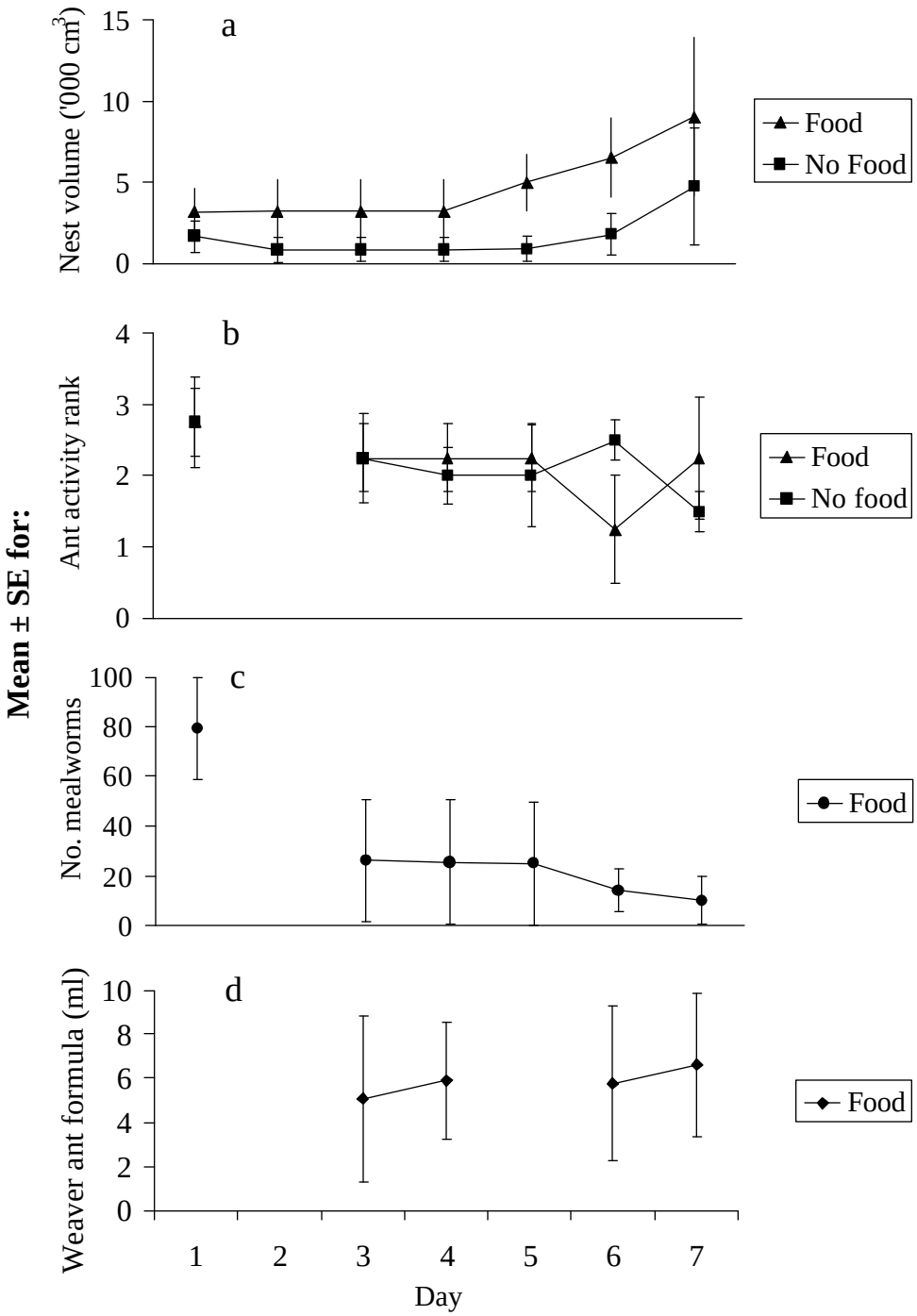

Figure 6.1. Food consumption and activity of relocated *Oecophylla smaragdina* colonies (n = 4) in relation to the first week of food supplementation. For all colonies: (a) Mean nest volume (cm^3 ± SE) per colony, (b) Mean ant activity rank (± SE) on feeding platform and tree (ranks 0 – 4 denoted 'no ants', 1 – 5, 6 – 10, 11 – 29 and 30 – 50 ants, respectively). For food-supplemented colonies: (c) Mean number of mealworms taken (± SE), (d) Mean consumption (ml ± SE) of weaver ant formula. Missing days were due to rain (b – d) and human error (d).

F colonies took a total of 181 ± 66 mealworms per colony (n = 4), or 30 ± 10 worms daily (n = 6; one day missed due to rain). Over 50% of mealworms were taken on the first day, and 'consumption' showed a decreasing trend over the week (Figure 6.1.c). A mean of 4.3 ± 2.2 ml of weaver ant formula was imbibed daily (n = 4; a missing day due to rain, two due to human error; Figure 6.1.d). Notably, when the bags used to transport Colony F_2 (Colony 2 in the food treatment) were emptied on the third day, a large number of mealworms were found 'hoarded' in the bags in addition to many ants that seemed content to remain inside their former nests and forage outside the bags.

Mean daily mealworm consumption per colony nest volume (0.7 ± 0.2 worms per 1000 cm^3) by relocated *F* colonies was not different (t = 1.92; d.f. = 5; *P* = 0.113) than that of established colonies (1.6 ± 0.5 worms per 1000 cm^3) in a no-choice test (Chapter 5). Mean daily weaver ant formula consumption per relocated *F* colony nest volume (0.13 ± 0.05 ml per 1000 cm^3) was significantly greater (t = 3.41; d.f. = 5; *P* = 0.019) than that of established colonies ($-1.9 \times 10^3 \pm 0.8 \times 10^3$ ml per 1000 cm^3).

16 weeks

Following expansion of colony territory from one to three trees per colony, active occupation of the new territory was observed. Figure 6.2 depicts relationships in patterns of ant activity as measured by nest-building, ant counts on shoots, and ant counts on weaver ant formula, in relation to food supplementation, for the study as a whole. Consumption of mealworms was not recorded.

The size of the *F* and *C* colonies fluctuated over time and followed similar trends, with *C* colony size mirroring the apparently greater *F* colony size (Figure 6.2.a). These fluctuations in colony size could be traced back to events that were of possible importance. The extension of each colony's foraging and nest-building area from one to three trees marked the sharp increase in *F* and *C* colony sizes in Week 2.

The disintegration of nests in Weeks 9 and 10 was followed by a bout of nest-building in the subsequent weeks. The nests that disintegrated in Week 10 for colonies C_4 and F_3 were not rebuilt, and these 'expired' colonies were excluded from the analyses from Week 10 onward. Toward the end of the study an invasion of small (ca. 1.5 mm) unidentified red soil-nesting ants on colonies F_2 and F_4 contributed to decreased mean colony size for that treatment. The size of the two colonies decreased from 60,000 cm^3 and 16,000 cm^3 to 6,000 cm^3 and 800 cm^3, respectively, by Week 15 when the invading ants were first noted. Colony F_2 recovered slightly in Week 16 with total nest volume of 8,000 cm^3, but no nests remained for Colony F_4. Therefore, analysis of the results excluded Weeks 15 and 16.

There was no interaction between *food* and *week* for mean total volume of nests built per colony (*F* = 0.18; d.f. = 13, 74; *P* = 0.999), and each factor was evaluated across all other variable levels. Mean total volume of nests built per colony was significant for *food* (*F* = 7.96; d.f. = 1, 74; *P* = 0.01). *F* colonies constructed a greater volume of nests (11,700 ± 1,200 cm^3) than *C* colonies (6,400 ± 800 cm^3). Mean total volume of nests built per colony was also significant for *week* (*F* = 1.94; d.f = 13, 74; *P* = 0.039). Volume of nests built per colony in Week 14 was greater than that in Week 1.

There was no interaction between *food* and *week* for mean number of ants counted on shoots per colony (*F* = 0.43; d.f. = 13, 74; *P* = 0.95; Figure 6.2.b), and each factor was evaluated across all other variable levels. The mean number of ants counted on shoots per colony was not significant for *food* (*F* = 2.24; d.f. = 1, 74; *P* = 0.14). For *F* colonies,

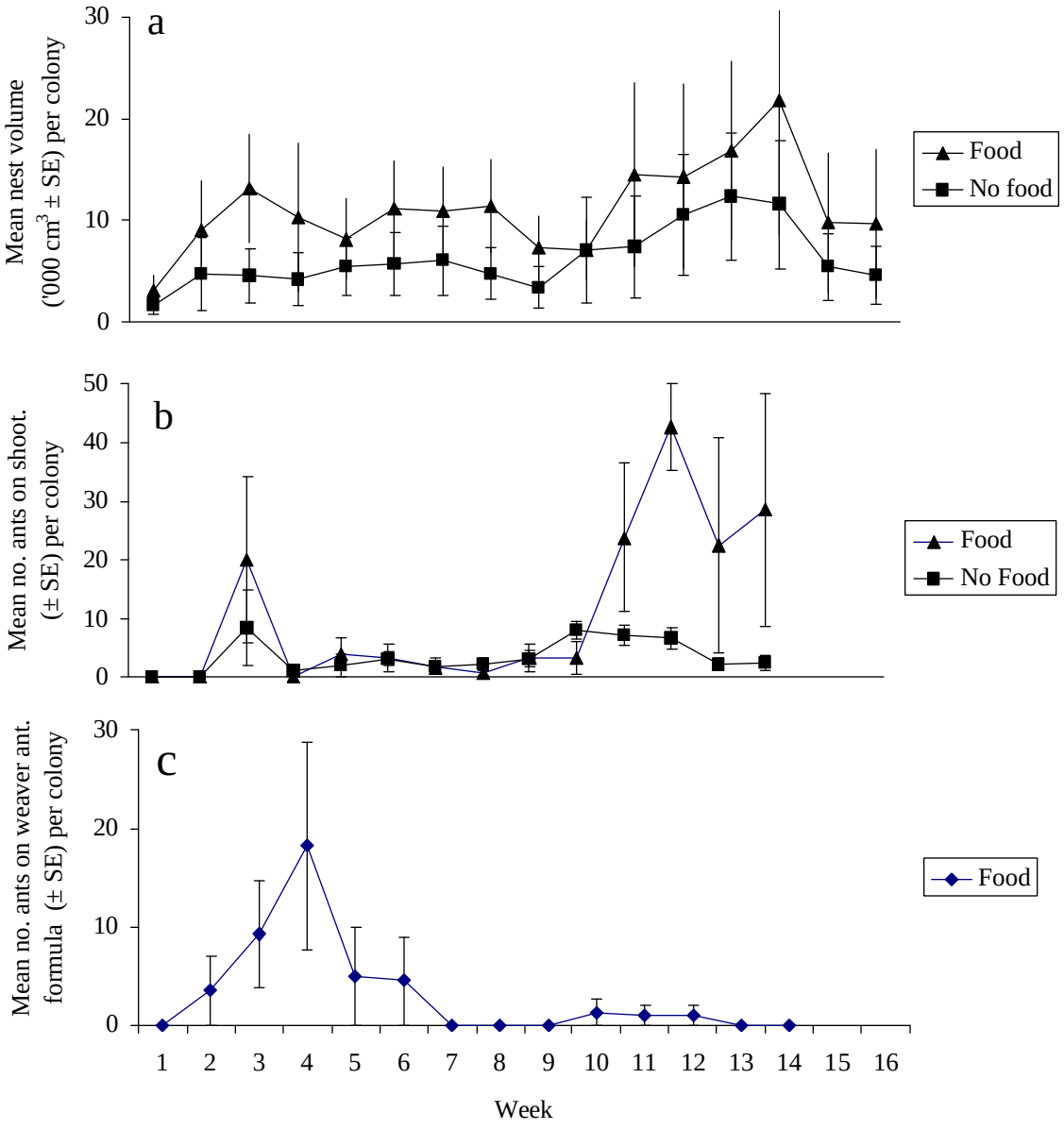

Figure 6.2. Food consumption and activity of relocated *Oecophylla smaragdina* colonies (n = 4) in relation to food supplementation for 16 wk: For all colonies (a) Mean net nest volume (cm^3 ± SE) per colony, (b) Mean number of ants (± SE) on shoots; and for food-supplemented colonies: (c) Mean ant counts (± SE) on weaver ant formula.

8.1 ± 3.9 ants were counted, and 3.0 ± 1.2 ants were counted for *C* colonies. Mean number of ants counted on shoots was significant for *week* (F = 3.14; d.f. = 13, 74; P = 0.001). Fewer ants were counted on shoots in Weeks 1 and 2 compared with Weeks 11 and 12. Ant counts on shoots had a significant positive correlation to colony size (r = 0.68, P = 0.000).

Ants were encountered in the weaver ant formula feeding bowls 20 ± 8% of the sampling times (n = 14, Figure 6.2.c) but their numbers (3.1 ± 1.4 ants) were significantly larger than zero (t = 2.28; P = 0.04; n = 14). They were not encountered from Colony F_1 throughout the 14 weeks, were recorded on two occasions each for colonies F_2 (24 and 34 ants) and F_3 (2 and 14 ants), and recorded eight times for Colony F_5 (range: 3 – 39 ants).

The *F* colonies exhibited an interesting pattern in the type of ant activity recorded. The increase in colony size (Figure 6.2.a) in the first three weeks was accompanied by an upsurge in ant activity on shoots (Figure 6.2.b) and around the weaver ant formula (Figure 6.2.c). This increased ant activity around the shoots was not sustained, but the number of ants visiting the weaver ant formula feeding bowls continued to rise for one week, even after colony size stabilized. Ant activity around that food subsequently diminished, reaching a low level when colony sizes were lowest in Weeks 9 and 10. This was a marked period of nest disintegration and rebuilding (G.T. Lim, personal observation), which would not necessarily have been reflected in the overall nest volume measured for each colony. The subsequent increase in colony size corresponded to an increase in ant activity on shoots. This was not mirrored in ant activity levels around the weaver ant formula, which remained low. Finally, all ant activity showed a declining trend in Weeks 15 and 16, consistent with the observed presence of invading ants.

Damage to the *F* colony platforms was a regular occurrence evident during the weekly monitoring activities. It took place between the third day after each weekly food change and the subsequent food change. Platforms were found toppled, with the wire netting pried apart and feeding bowls scattered far and wide or missing entirely. Every week throughout the study period the platforms had to be repaired and missing feeding bowls replaced. Marks on the affected feeding bowls indicated that birds were responsible. Other damage to tree shoots was consistent with monkeys and it is possible that the resident troops of pig- or long-tailed macaques damaged the feeding platforms as well. As a result, the supply of food to the *F* colonies was available for the first few days after each weekly food change and was not continuous as planned. The platforms placed at the *C* colony trees were not disturbed.

The mean crown area (77 ± 14 m^2 per colony) provided for the eight relocated colonies was not significantly different (t = 1.72; d.f. = 9; P = 0.12) from the crown area (137 ± 32 m^2 per colony) they occupied at their former site. The mean nest volume of the eight colonies that were harvested and subsequently introduced to their new hosts in the present study was 3.6 ± 0.7 m^3 (n = 8). This translated to a crown area : nest volume ratio of 22 ± 2 cm^{-1} for the relocated colonies and 38 ± 7 cm^{-1} for the same colonies at their former site. This ratio was 65 ± 17 cm^{-1} for three colonies in a previous study (Chapter 4). There was a significant difference among pre- and post-harvest and the previous study's colonies in the crown area : nest volume ratio (F = 7.26; d.f. = 2, 16; P = 0.006). The colonies in the previous study (Chapter 4) had a greater crown area : nest volume ratio than that provided to the relocated colonies in the present study but did not differ with what the latter colonies had at their former site.

Discussion

First week

The short term results showed that supplemental food was readily accepted by the *F* colonies, but the immediate benefits of consuming these foods were not apparent. No significant differences were found between the *F* and *C* colonies with regard to the volume of nests built or ant activity on shoots, seven days after release. Although the *F* colony size, i.e., total nest volume per colony, was about two times greater than that for the *C* colonies, the high variability in colony size likely negated the possibility of detection of a significant result.

The availability of sufficient colonies as suitable candidates for introduction to the new host trees limited the number of replications. Of the six intended replicates, only four were found to be ideal candidates, i.e., reasonably large (> 19,000 cm^3 total nest volume per colony or ca. 13,600 ants) and collected in full. The failure of the partially-collected colonies to construct any nests despite having at least 7000 workers each, suggests that nests containing the queen must be included in colony transfers. The queen may have been within the nests that were not collected. Further, a critical ant mass from a colony may be needed to survive the relocation, as (presumably young) colonies with less than 10,000 ants did not establish in these studies. This result is consistent with a previous report that young colonies (< 1.5 yr) and colonies relocated without the queen nest failed to persist (Peng *et al*. 2004).

The ranking method for ant activity on shoots did not distinguish between ants with or without food supplementation. Colony size as indicated by nest volume was not strongly correlated with ant activity on shoots. Ant activity on shoots was variable and depends on the availability of food from or on the shoots, the nutritional needs of the colony and the availability of foods elsewhere. Ants may be active on shoots that have active extra-floral nectaries and trophobionts (Blüthgen *et al*. 2004), and prey (Greenslade 1971). No such activity was observed perhaps because no food was obtainable from the shoots, because the ants had access to better quality foods elsewhere, and/or because the shoots did not provide the type of food the colony required. Ants were rarely seen on the platforms of the *C* colonies, which received no food (G.T. Lim, personal observation). Ants may pass up foods if they expect to secure higher-quality foods elsewhere (Kay 2002) and the foods provided on the feeding platform may have been a better draw if perceived by the ants to be of better quality than that on the shoots. Shoots providing only prey without high-carbohydrate foods like honeydew may not be frequented by a colony that has very little brood. High-protein prey are given to brood while high-carbohydrate foods such as honeydew and nectar are metabolized by workers (Haack *et. al,* 1995).

The short term results of the present study suggest that needs differ between established and relocated colonies of the weaver ant, which may consequently affect worker foraging behavior. The number of mealworms carried away by the *F* colonies was not different than what established colonies took in a week-long no-choice test (Chapter 5), perhaps because brood was present in the nests of both colonies. The sharp decrease in the number of mealworms taken by the relocated colonies by the second day was similar to was observed for one of the established colonies (Chapter 5), and could likewise be because sufficient stores had been accumulated to feed existing brood.

The *F* colonies consumed significantly more weaver ant formula than the established colonies (Chapter 5) possibly because it was the best available high-carbohydrate food source

at that time. Trophobionts were not enumerated in this study, but it is possible that no or very few trophobionts were present on the new host trees of the relocated colonies. Trophobionts normally do not survive well without ant attendance (Delabie 2001) and an earlier study (Chapter 3) found trophobionts on only 7% of the 184 host plants not occupied by ants but on 72% of ant-colonized trees. Since established colonies satisfy their energetic needs with honeydew from cultivated trophobionts in addition to plant nectar (Blüthgen & Fiedler 2002), it was anticipated that the relocated colonies in this study would eventually 'wean off' the weaver ant formula. Established colonies in the previous study (Chapter 5) did not take any weaver ant formula.

16 weeks

The provision of food benefited recipient colonies significantly over a longer period, and colony size, i.e., total nest volume measured for a colony, was able to adequately represent colony growth. The study controlled for major inherent differences among the introduced colonies by excluding partially-collected and unusually small colonies. The extraneous influence of other insects, particularly enemy ant species, was averted by banding tree stems with a sticky barrier and by excluding the last two weeks of data, where this physical deterrent failed to work as it wore off. Birds and possibly monkeys were a nuisance that caused the supply of food to the *F* colonies to be interrupted (ca. 4 d per week) throughout the study period. Further, toppling of the feeding platforms may have resulted in the loss of workers for the *F* colonies if they were present on the platform at that time. The stress experienced by the *F* colonies from being 'harassed' in this manner may have been an additional factor influencing the results. Nevertheless the *F* colonies still showed more colony growth than the C colonies. This difference may have been greater if food supplementation had not been interrupted and if the *F* colonies had not been disturbed.

The decline in colonies invaded by another ant species in Weeks 15 and 16 indicated that the relocated colonies were protected by the physical sticky barrier (Coldfoot®) and were unable to defend their territory up till that time. Weaver ants are generally regarded as dominant ants that exclude other ant species from their territories (Leston 1973; Blüthgen & Fiedler 2004a) but may be vulnerable to attack when newly relocated (Way & Khoo 1991) or if the other ant species are more competitive (Soans 1971; Zerhusen & Rashid 1992). The rapid decline of weaver ant colonies after the invading red ants breached the physical sticky barrier could be because the weaver ants were unable to defend their territory and/or the invading ants overwhelmed the weaver ants by sheer force of numbers. Identifying competing ant species that pose a threat to weaver ant colonies is crucial to formulating strategies to protect the weaver ant and/or to give the it the competitive edge in such confrontations. Colony growth was enhanced by food supplementation in this study, yet the colonies apparently could not mount a vigorous enough defense against the invading ants. Further work should identify all other factors and the extent to which these factors affect colony vigor.

Similar to the short-term results, ant activity on the shoots could not differentiate colonies with regard to food supplementation in the long term. This held true although ant activity was significantly correlated with colony size, (which was able to separate *F* from *C* colonies,) because that positive relationship was weak. The same factors discussed earlier as influencing ant activity on shoots apply here as well.

Simultaneous examination of long term patterns in shoot ant activity, activity around the weaver ant formula, and colony size in relation to food supplementation (Figure 6.2(a-c)) suggested a possible scenario. Initially, ant activity around the shoots and weaver ant formula could have been to secure high-carbohydrate foods and energy for the workers to build new nests. Subsequently however, ant activity on shoots decreased while consumption of weaver ant formula increased. Two possible reasons for these observed consumption patterns were that shoot nectary activity decreased or weaver ant formula was perceived by the ants as a more reliable food source. The subsequent drop in consumption of weaver ant formula as nest-building was at a plateau (Week 5 – 8) is consistent with the period of time it would take for the colonies to cultivate a clutch of scale insects and achieve honeydew sufficiency. Generation time is 67 – 69 d for *Coccus viridis* Green (Hemiptera: Coccidae) (Miller 1931). The period of general nest abandonment of old nests and the subsequent active nest-construction phase near the shoots concurs with observations of *O. smaragdina* constructing nests around shoots to which *C. viridis* moved (Miller 1931) or were transported by the ant (Way 1954b). The abandonment of old nests in the present study (ca. 56 – 70 d) corroborates with the replacement and abandonment rate (56 ± 11 d) of *O. smaragdina* nests observed in Australia (Blüthgen & Fiedler 2002). The practical implication of these observations is that supplementation of weaver ant formula for relocated colonies may be needed for about 2 months, after which trophobiont populations could be high enough to meet colony honeydew needs. Clearly, enumerating trophobiont populations in relation to weaver ant activity is needed to conclusively explain the trends observed.

The duration for mealworm supplementation was not determined in this study since mealworm consumption was not recorded. However, the ants are able to regulate consumption according to colony needs (Greenslade 1971; Wheeler 1994; Cannon & Fell 2002; Kay 2002) and decreased their consumption of mealworms after several days of *ad libitum* provision (Chapter 5 and this study). High-protein mealworms could be provided as needed, which based on previous studies (Greenslade 1971; Cannon & Fell 2002) should be during peaks in brood production. Quantifying consumption of high-protein and high-carbohydrate foods such as mealworms and weaver ant formula, respectively, in relation to brood production is needed before further suggestions are made.

It was fortuitous that the colonies' foraging area was expanded from one to three trees. The initial provision of foraging area and foliage for nest-building was based on a previous study (Chapter 5) that neglected to account for additional foraging area on the surrounding lush vegetation to which those colonies had access. The modified experimental design simulated a field situation where *C* colonies left to forage or cultivate trophobionts without the benefit of supplemental food were evidently not disadvantaged by limited colony territory. Survival of the *C* colonies was not different than that of the *F* colonies, and colony growth of the *C* colonies mirrored that of the *F* colonies, albeit at a lower level. Foliage for nest-building or cultivation of trophobionts appeared sufficient for the colonies on their allocated three trees. The gradual decline in weaver ant formula consumption followed by sustained growth of the *F* colonies was consistent with the colonies having sufficient foliage for nest-building and trophobiont cultivation, at least up to the fourth month.

Based on the above and on my personal observations, a relocated colony should probably be provided with as much foliage as it had access to at its former site, taking into account the restriction of the colony to allocated trees. For example, if the colony occupied a single tree at its former site, relocation could be to several trees of similar size as appeared to

be sufficient in this study. The optimal number of trees to be allocated to each colony needs to be determined in future studies. Allocation could be based on crown area equivalence. An example of the calculations for this allocation method follows. A colony is to be introduced to young mahogany trees (ca. 6 months, 1 m in height) before shoot borer infestations begin (Cunningham & Floyd 2006). It occupies a crown area of 77 m^2 on trees at its former site. The mahogany trees at the new site have a mean height of 1.5 m, height to crown base of 0.7 m, and crown width of 0.7 m, thus have a crown area = $p(0.7/2)^2 + 2p(0.7/2)^2(1.5 - 0.7)$ = 2.14 m^2 per tree. This colony would hypothetically need = 77 / 2.14 = 36 trees in this young plantation based on crown area equivalence. With an initial stocking density of 833 trees per ha, colony density would be 23 colonies per ha.

The minimum ant density per tree required to protect *K. ivorensis* from shoot borer attack has not yet been determined, but some recommendations have been made for cocoa (Way & Khoo 1991) and cashew (Peng *et al*. 2004). A population of about 50 – 200 ants per tree has been found to provide sufficient protection against *Helopeltis theobromae* Miller (Hemiptera: Miridae) in cocoa (Way & Khoo 1991). Cocoa has a conventional planting density of 1096 trees per ha (Pang 2004). What this would translate to is 54,800 – 219,200 ants per ha. Consequently, assuming an average colony size of 28,000 ants (such as in the present study), colony density would be 2 – 8 colonies per ha for such a cocoa plantation. About 20 colonies per ha (10 trees per colony) is recommended for cashew orchards with a final density of 200 mature trees per ha (Peng *et al*. 2004). The colony densities in these managed habitats (i.e., coffee and cocoa,) are slightly higher than the maximum colony densities reported for natural habitats. The largest colony on record occupied 44 mature trees in a mangrove habitat (Holldobler 1983a), i.e., possibly 3.5 colonies per ha based on an arbitrary stocking density of 150 trees per ha and the maximum area of forest occupied by a single colony was 1,500 m^2 (Holldobler 1983a), i.e., 7 colonies per ha.

Based on crown area equivalence, the estimated colony density needed for young *K. ivorensis* could be projected from the recommended 20 colonies per ha for mature cashew trees. Assuming a cylindrical crown shape (Chapter 4) and a crown diam. of 5.5 m and crown height of 5.5 m for 7 year old trees (O'Farrell *et al*. 2002), crown surface area of mature cashew is about 285 m^2 per tree. With each colony applied to 10 trees, each colony could protect about 2850 m^2 of cashew tree crown area. Assuming a crown surface area of 2.14 m^2 for young *K. ivorensis*, the application density would be 133 trees per colony or 6.3 colonies per ha of *K. ivorensis.* Optimal colony density for complete protection is likely higher than this because of the 'zero damage threshold' for mahogany (Wylie 2001). However, a degree of damage is tolerated in a plantation situation, which allows for removal of trees of poor form and diseased trees when thinning(Ahmad Zuhaidi *et al*. 2006). Thus, optimal colony density determination should account for allowable loss in plantations. Preliminary observations indicate that 48 colonies per ha appears more than enough to prevent attack on young *K. ivorensis* (G.T. Lim, personal observation). Perhaps a lower colony density in the range of 6 – 25 colonies per ha, would be a good starting point for future planting trials. Future planting trials should determine the optimal colony density that confers protection to *K. ivorensis* trees.

Preliminary financial analyses gave some idea as to the feasibility of incorporating weaver ants into a *K. ivorensis* planting program in Malaysia. The cost of application and three-year maintenance of 6, 25 and 48 colonies per ha to 40 ha of young *K. ivorensis* was estimated (Table 6.2). Using weaver ants compared favorably with chemical controls

Table 6.2. Preliminary cost estimate for applying and maintaining *Oecophylla smaragdina* as a biological control agent for three years in a 40 ha (833 trees per ha) *Khaya ivorensis* plantation in Malaysia, at three application densities (colonies per ha).

Item	Cost per unit ($, in USD)		Cost per ha ($, in USD) at colony density (colonies per ha)[1]:		
			48	25	6
Feeding apparatus[2]	0.10	ea	5	3	1
Exclusion of other ant species (Coldfoot)[3]	15.00	tube	60	60	60
Harvesting equipment					
Muslin bags	70.00	36 bags	1.75	1.75	1.75
Transporting racks	20.00	4 racks	0.50	0.50	0.50
Telescoping clippers	20.00	ea	0.50	0.50	0.50
Long latex gloves	5.00	box (100 pairs)	0.13	0.13	0.13
Food[4]					
Weaver ant formula	0.05	100 ml serving	125	65	16
Mealworms	0.10	50 worm servin	749	390	94
Labor[5]					
Harvesting and relocating colonies	2.00	colony	96	50	12
Applying Coldfoot	0.08	colony	48	25	6
Feeding colonies	0.08	colony	624	325	78
Grand total			1709	920	269

[1]Conversion rate: 1 USD = 3.75 MYR. Optimal colony density for protection of 100% trees was projected to be within the range of 6 – 48 colonies per ha based on observations for cocoa (2 – 8 colonies per ha; Way & Khoo 1991) and cashew (ca. 20 colonies per ha; Peng *et al.* 2004) and personal observations (48 colonies per ha). Mahogany has a 'zero damage threshold' (Wylie 2001) but a degree of damage is tolerated in a plantation situation, which allows for removal of trees of poor form and diseased trees when thinning (Ahmad Zuhaidi *et al.* 2006). Therefore these colony density projections are conservative.

[2]Estimated cost if purchasing feeding containers that will be secured to the tree. Cost may be lowered, e.g., mealworms placed a covered used tin can with its base perforated and weaver ant formula provided in covered a plastic cup.

[3]Coldfoot® is a clear sticky polybutene gel commercially available as a bird repellent. Applied monthly for 1st year in a 2 cm band around each tree to confine weaver ant colonies to their allocated trees while excluding other crawling insects. About 4 tubes needed per ha.

[4]Weaver ant formula provided weekly for 1st year and mealworms provided weekly for 3 years. Concoction of weaver ant formula detailed in text

[5]Cost of labor $1 per h. Harvesting colonies is a one-time task. Feeding colonies is carried out weekly and estimated to take 5 min per colony.

suggested for Malaysian *K. ivorensis.* The IRR (internal rate of return) for conventionally-grown vs. weaver ant-applied *K. ivorensis* was 12 vs. 11.6 – 12.2% (6 – 48 colonies per ha). IRR calculations were based on substituting chemical control with weaver ant applications in a revenue-expenditure outlay proposed by Ahmad Zuhaidi *et al.* (2006) for a 40 ha plot of *K. ivorensis* in Malaysia (Appendix A).

Using weaver ants could be more effective and sustainable than pesticides. Pesticides are generally ineffective in preventing damage because enough damage is inflicted in the minimal feeding a larvae accomplishes before it succumbs to the toxicant (Wylie 2001). The systemic insecticide recommended to control shoot borers has yet to be formally tested and protection was planned for the first two years only (Ahmad Zuhaidi *et al*. 2006). Even if it proves efficacious against the shoot borer for the first two years, extending protection to the third year would entail higher application rates to maintain toxicant levels in the taller trees, and this is not ecologically viable (Wylie 2001).

Finally, while mahogany farmers could reasonably hope to obtain 25 colonies from surrounding vegetation for redistribution in a 1 ha *K. ivorensis* plantation, a more strategic approach will be needed to supply colonies for larger areas. For a 40 ha plantation, which would need 1000 colonies at that hypothetical colony density application, field-planting could be staggered over several years. Weaver ant colonies were observed to mature at 1.5 – 2.0 yr (Peng *et al*. 2004), so reproductives from the first release could colonize subsequent *K. ivorensis* plantings. Alternatively, colonies could be reared in weaver ant nurseries on preferred host plants that could be redistributed to plantations by harvesting nests. It may also be possible to rear a 'starter' colony by confining a mated queen on the foliage of a single seedling (Way, 1954a), subsequently transporting the entire seedling. Further work is needed to investigate these possibilities.

Chapter 7

Conclusions

The weaver ant, *O. smaragdina,* has shown potential in preventing shoot borer attack in mahogany plantations (Lim & Kirton 2003) and was identified as a natural control in two other forest tree species, i.e., hoop pine (Wylie 1974) and eucalyptus (Macfarlane *et al*. 1976). It has been applied as a biological control agent in various crops (Huang & Yang 1987; Peng *et al*. 1999; Van Mele & Cuc 2000; Peng & Christian 2006), with extensive information on its efficacy in cashew plantations and recommendations on harvesting, transplanting and conserving colonies in cashew plantations (Peng *et al*. 2004). However, very little is currently known about how to enhance its performance in mahogany plantations and this was addressed through a series of field studies.

Model for ant population estimation

A model was developed to estimate the number of ants within nests that has good predictive ability for *K. ivorensis.* Requiring only measurements of two nest dimensions (height and length), this model has simplified estimating ant abundance. This technique has proven very useful for efficiently assessing treatment effects on colonies in the field. It has also provided a non-destructive technique by which population levels of ant colonies can be estimated repeatedly over time. The model should also provide a more direct reflection of ant population levels compared with other indirect estimation methods, e.g., nest counts (Offenberg *et al*. 2004), ant counts on plant parts (Blüthgen & Fiedler 2002), and counts of ant trails on tree stems or branches (Peng & Christian 2005). The model may be applicable for general use on weaver ant host plant species with little or no modification and an additional study evaluating this model on other host plant species is on-going (G.T. Lim, unpublished data).

Harvesting and redistribution

The poor survival rate of partially-collected colonies redistributed to new host plants indicate that nests containing the queen must be included in the transfer. Further, colonies need to contain a critical ant mass to survive the relocation, as (presumably young) colonies with less than 10,000 ants did not establish in these studies. This finding is consistent with a previous report observing that young colonies (< 1.5 yr) and colonies relocated without the queen nest failed to persist (Peng *et al*. 2004). That report suggested applying about 20 colonies per ha for cashew, while 2 – 8 colonies per ha were found to provide protection against pests in cocoa (Way & Khoo 1991). Young *K. ivorensis* trees on which weaver ants were applied at a rate of 48 colonies per ha have remained free of attack up to the present time (G.T. Lim, personal observation). The optimal colony density that could provide protection against the shoot borer in *K. ivorensis* needs to be determined, and may be within the range of 6 – 48 colonies per ha, depending on tree density.

Direct food supplementation

Established colonies were indicated to have different nutritional needs compared with redistributed colonies and these differences may affect (direct) food supplementation strategies for conserving the ant, e.g., duration and timing. Foods preferred by the weaver ant

were identified that were economical and practical to apply, i.e., live mealworms and 'weaver ant formula', which contained sucrose and human muscle-training powder (Enerpro™). Based on these studies, consumption of weaver ant formula is anticipated to be greater in relocated colonies than established colonies, while mealworm consumption may not differ. It is recommended that both foods be provided to the ant colonies initially, tapering supplementation as consumption decreases of either or both foods. These studies indicate that ants regulate their consumption of foods based on colony needs. Initial application rates should be *ad libitum* for relocated colonies (ca. 50 mealworms and 100 ml weaver ant formula every three days) from the onset of transplanting and possibly for up to two months. The duration of food supplementation for relocated colonies has not been conclusively determined.

The differing consumption of supplemented foods between these established and relocated colonies was thought to be due to the presence or absence of cultivated trophobionts and/or active nectaries on host plants. Since the established colonies were on a variety of fruit tree species, whereas relocated colonies were confined to *K. ivorensis*, it is possible that phenological differences, i.e., nectary activity, affected availability of high-carbohydrate resources for the respective colonies. Relocated colonies may have faced a deficit in high-carbohydrate food due to the lack of trophobionts on their new host trees, thus consuming more weaver ant formula. Additional studies that can estimate trophobiont levels (non-destructively) and nectary activity in relation to food consumption are needed for confirmation.

Preliminary financial analysis of applying weaver ants in place of chemical control of the mahogany shoot borer on *K. ivorensis* indicated that applying the ant at rates of 6 – 48 colonies per ha gave an IRR of 11.6 – 12.2%, which was similar to that for chemical control (12%). However, weaver ants were anticipated to provide protection for the entire duration of the critical early stage (3 yr) plantings while chemical control was planned for the first two years only.

Indirect food supplementation

With regard to indirect food supplementation through mixed-planting, the weaver ant was found to nest on a large number of plant species and screening of several ant-abundant species identified *M. citrifolia* as a promising candidate for mixed-planting with *K. ivorensis.* The screening of potential candidates included a preliminary pest risk analysis of the trophobionts identified for the respective host plant species, and concluded that the risk for *M. citrifolia* trophobionts was low with regard to *K. ivorensis.* The ant was found to tend numerous coccoid, membracid and lycaenid trophobionts and the higher incidence of trophobionts on ant-occupied- vs non ant-occupied trees underscores the significance of the weaver ant-trophobiont relationship.

Further study

The model for estimating ant numbers within nests needs to be tested for its general applicability to other host plant species and this work is on-going (G.T. Lim, unpublished data). A model for estimating trophobiont population levels and nectary activity also needs to be developed to better elucidate the tritrophic ant-plant-trophobiont relationship and assess effects of manipulating those components.

The long-term establishment and lifespan of relocated colonies needs to be studied for further financial analysis that weighs the period of protection conferred to mahogany trees against the cost of applying weaver ants. Food supplementation techniques may be refined by better assessment of colonies' nutritional requirements. Again, the ability to gauge food resources available to the ant by estimating trophobiont levels, plant nectary activity and prey availability in relation to colony size, will be important. This work should be conducted over several years in order to simultaneously study seasonal effects on the components of this tritrophic relationship. Optimal colony density that gives complete protection to young *K. ivorensis* also needs to be determined to refine the financial analyses.

The effect of mixed-planting on the establishment and conservation of weaver ant colonies will take the results of these studies a step further. A long-term study on the effect of mix-planting *M. citrifolia* and *K. ivorensis* on relocated weaver ant colonies and mahogany shoot borer attack is on-going (G.T. Lim, personal observation).

Finally, the feasibility of establishing weaver ant nurseries as a strategy to supply colonies to mahogany plantations will need to be determined.

References

ACIAR 2005. *ACIAR. Country Profile: Cambodia, Laos and Thailand (November 2005)*. ACIAR, Canberra, Australia. 86 pp.

Ahmad Zuhaidi,Y., Abdul Rasip,A.G., Rosdi,K., Zainal,T., & Mohd Parid,M. 2006. *Establishment and Management of Khaya ivorensis Plantations.* FRIM Technical Information Handbook No. 37. FRIM, Kuala Lumpur, Malaysia. 27 pp.

Ahmad Zuhaidi, Y., Rosdi, K., Abdul Rasip, A.G., & Hashim, M.N. 2003. Evaluating the performance of *Khaya ivorensis* as a future forest plantation species. Pp. 155-165 in Lee, S.S., Aminah, H., Norini, H., Lim, S.G., & Lim, H.F. (Eds.). *Proceedings of the International Conference on Forestry and Forest Products Research (CFFPR 2003)*, Kuala Lumpur, 6-8 October 2003. FRIM, Malaysia.

Ahmad Zuhaidi, Y., Zakaria, I., & Rosdi, K. 2002. Species for timber plantations. Pp. 13-24 in Krishnapillay, B. (Ed.) *A Manual for Forest Plantation Establishment in Malaysia*. Malayan Forest Records No. 45. FRIM, Kuala Lumpur.

Aminah, H., Besek Intan Zafina, B., Rosdi, K., Rozihawati, Z., Ahmad Fauzi, M.S., & Hamzah, M. 2005. Growth performance of some dipterocarps and non-dipterocarps planted from rooted cuttings. Pp.1-7 in *Proceedings of the 8th Round-Table Conference on Dipterocarps*, Ho Chin Minh City, Vietnam, 15-17 November 2005.

Angelo, H., Brasil, A.A. & Santos, J.d. 2001. Tropical wood: economic analysis of the principal exported forest species. *Acta Amazonica.* 31(2):237-248.

Anon 1968. Scale insects, mealybugs and lac insects. *Planter's Bulletin of the Rubber Research Institute of Malaysia.* 98:146-152.

Anon 2005. *Invasive and Exotic Species: Exallomochlus Hispidus (Morrison) the Cocoa Mealybug*. http://www.invasive.org (accessed 6 November 2006).

APNI 2006. *The Australian Plant Name Index*. ANBG, http://www.anbg.gov.au/apni/apni.html (accessed 30 September 2006).

Azuma, N., Ogata, K., Kikuchi, T. & Higashi, S. 2006. Phylogeography of Asian weaver ants, *Oecophylla smaragdina*. *Ecological Research.* 21:126-136.

Balakrishnan, M.M., Vinodkumar, P.K. & Prakasan, C.B. 1992. A note of green scale-ant association on coffee. *Indian Coffee, Bulletin of the Indian Coffee Board.* 56(10):5-6.

Ballmer, G.R. 2003. Observations on resource partitioning among ants (Hymenoptera: Formicidae) and lycaenid larvae (Lepidoptera: Lycaenidae) associated with *Pueraria phaseoloides* in South Thailand. *ScienceAsia* 29:197-202.

Beeson, C.F.C. 1941. *The Ecology and Control of the Forest Insects of India and the Neighbouring Countries.* Variant Press, Dehra Dun. 1007 pp.

Begg, R.J. 1977. The effects of Cyclone "Tracy" on the ant *Oecophylla smaragdina*. *Journal of the Australian Entomological Society.* 16:289-295.

Bellas, T. 2001. Semiochemicals of *Hypsipyla* shoot borers. Pp. 116-117 in Floyd, R.B. & Hauxwell, C. (Eds.). *Proceedings of an International Workshop on Hypsipyla Shoot Borers in Meliaceae*. ACIAR Proceedings Series No 97, Kandy, Sri Lanka, 20-23 August 1996. ACIAR, Canberra.

Ben-Dov, Y. 2005a. *ScaleNet, Coccus Viridis Green*. http://www.sel.barc.usda.gov/catalogs/coccidae/Coccusviridis.htm (accessed 1 November 2006).

Ben-Dov, Y. 2005b. *ScaleNet, Tachardina Aurantiaca Cockerell*. http://www.sel.barc.usda.gov/catalogs/kerriida/Tachardinaaurantiaca.htm (accessed 1 November 2006).

Ben-Dov, Y. 2005c. *ScaleNet, Coccus Hesperidum L*. http://www.sel.barc.usda.gov/catalogs/coccidae/Coccushesperidum.htm (accessed 1 November 2006).

Ben-Dov, Y., Miller, D.R., & Gibson, G.A.P. 2005. *ScaleNet: Query Index*. http://www.sel.barc.usda.gov/scalenet/query.htm (accessed 1 November 2006).

Bernard, J.B. & Allen, M.E. 1997. *Feeding Captive Insectivorous Animals: Nutritional Aspects of Insects As Food*. Nutrition Advisory Group Handbook No. Factsheet 3. Nutrition Advisory Group, Accessed online Jan 10, 2007. 7 pp.

Blüthgen, N. & Fiedler, K. 2002. Interactions between weaver ants *Oecophylla smaragdina*, homopterans, trees and lianas in an Australian rain forest canopy. *Journal of Animal Ecology*. 71(5):793-801.

Blüthgen, N. & Fiedler, K. 2004a. Competition for composition: lessons from nectar-feeding ant communities. *Ecology*. 85(6):1479-1485.

Blüthgen, N. & Fiedler, K. 2004b. Preferences for sugars and amino acids and their conditionality in a diverse nectar-feeding ant community. *Journal of Animal Ecology*. 73:155-166.

Blüthgen, N., Gebauer, G. & Fiedler, K. 2003. Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. *Oecologia*. 137(3):426-435.

Blüthgen, N., Stork, N.E. & Fiedler, K. 2004. Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. *Oikos*. 106(2):344-358.

Borek, V., Kalinova, B., Valterova, I., Hochmut, R. & Vrokoc, J. 1991. Sex pheromone gland volatiles from *Hypsipyla grandella* females. *Acta Entomologia Bohemoslovaca*. 88:181-186.

Braby, M.F. 2000. Family Lycaenidae. Pp. 617-856 in *Butterflies of Australia*. Their identification, biology and distribution. Volume 2. CSIRO Publishing, Canberra.

Brack, C. 1999. *Forest Measurement and Modelling: Stand Basal Area*. ANU, Australia, http://sres.anu.edu.au/associated/mensuration/s_ba.htm (accessed 18 February 2006).

Cannon, C.A. & Fell, R.D. 2002. Patterns of macronutrient collection in the black carpenter ant, *Camponotus pennsylvanicus* (De Geer) (Hymenoptera: Formicidae). *Environmental Entomology*. 31(5):977-981.

Chantaranothai, P. & Parnell, J.A.N. 1994. The breeding biology of some Thai *Syzygium* species. *Tropical Ecology*. 35(2):199-208.

Chen, S. 1962. The oldest practice of biological control: the culture and efficacy of *Oecophylla smaragdina* Fabr. in orange orchards . *Acta Entomologica Sinica*. 11(4):401-407.

Christian, K. & Peng, R.K. 2007. *Green Ants As Biological Control Agents in Agroforestry. Research Projects Program 1.1. Pest and Diseases.* RIRDC, Charles Darwin University, Australia. http://www.cdu.edu.au/ehs/research/TEDS/weeds_pests_and_diseases.html (on-going, accessed 7 March 2007).

Conover, W.J. 1999. *Practical Nonparametric Statistics.* 3rd edition. Wiley, New York. 584 pp.

Corbett, G.H. 1937. *Division of Entomology. Annual Report for the Year 1936.* No. 26. Dept. Agr., South Seas and Federated Malay States, Gen. Ser. Dept. Agr. Straits Settl.. 48 pp.

Cunningham, S.A. & Floyd, R.B. 2003. *Final Report (January 1 1999 - Dec 31, 2002): Insect Resistance and Silvicultural Control of the Shoot Borer, Hypsipyla Robusta, Feeding on Species of Meliaceae in the Asia-Pacific Region. ACIAR Project FST/97/24*. CSIRO, Canberra, Australia. 169 pp.

Cunningham, S.A. & Floyd, R.B. 2004. Leaf compositional differences predict variation in *Hypsipyla robusta* damage to *Toona ciliata* in field trials. *Canadian Journal of Forest Research.* 34(3):642-648.

Cunningham, S.A. & Floyd, R.B. 2006. *Toona ciliata* that suffer frequent height-reducing herbivore damage by a shoot-boring moth (*Hypsipyla robusta*) are taller. *Forest Ecology and Management.* 225(1-3):400-403.

Das, G.M. 1959. Observations on the association of ants with coccids of tea. *Bulletin of Entomological Research.* 50:437-448.

De, K. & Pande, Y.D. 1988. Bionomics and some behavioural aspects of mango stone weevil, *Sternochetus gravis* (Fabricius) (Coleoptera: Curculionidae). *Entomon.* 13(1):17-24.

Dejean, A., Corbara, B. & Oliva-Rivera, J. 1990. Evidence for a form of apprenticeship in the prey capture behaviour of *Pachycondyla* (=*Neoponera*) *villosa* (Formicidae, Ponerinae). *Behaviour*. 1990(115): 175-187

Delabie, J.C. 2001. Trophobiosis Between Formicidae and Hemiptera (Sternorrhyncha and Auchenorrhyncha): an Overview. *Neotropical Entomology*. 30(4):501-516.

Djieto-Lordon, C. & Dejean, A. 1999. Tropical arboreal ant mosaics: innate attraction and imprinting determine nest site selection in dominant ants. *Behavioral Ecology and Sociobiology*. 45(3/4):219-225.

Dodd, F.P. 1902. Notes on the Queensland green tree ants (*Oecophylla smaragdina*). *Victorian Naturalist*. 18:136-140.

DOL 2005. *Plant Systematics.Org.* DiversityofLife.org, http://132.236.163.181/index.html (accessed 30 September 2006).

Dutt, G.R. 1912. Life histories of Indian insects, IV (Hymenoptera): *Oecophylla smaragdina* F. *Memoirs of the Department of Agriculture in India (Entomology)*. 4:254-260.

Fasoranti, J.O. 1985. Influence of flight on the mating behavior of the mahogany shoot borer *Hypsipyla grandella* (Zeller) (Lepidoptera: Pyralidae). *Turrialba*. 35:300-303.

Fiedler, K. & Maschwitz, U. 1989. The symbiosis between the weaver ant, *Oecophylla smaragdina*, and *Anthene emolus*, an obligate myrmecophilous lycaenid butterfly. *Journal of Natural History*. 23(4):833-846.

FRIM 2005. *Annual Report of the Forest Research Institute of Malaysia (FRIM)*. FRIM. http://info.frim.gov.my/cfdocs/infocenter/annualreport/2005/files/AR2005.pdf (accessed 7 March 2007), Selangor, Malaysia. 123 pp.

Froggatt, J.L. 1937. *Promecotheca antiqua* Wse. Leaf pest of coconuts. *New Guinea Agricultural Gazette* 3(2):21-22.

Gibernau, M. & Dejean, A. 2001. Ant protection of a Heteropteran trophobiont against a parasitoid wasp. *Oecologia*. 126(1):53-57.

Goding, F.W. 1930. Membracidae in the American Museum of Natural History. *American Museum Notivates.* 421:1-27.

Goulet, E., Rueda, A. & Shelton, A. 2005. Management of the mahogany shoot borer, *Hypsipyla grandella* (Zeller) (Lepidoptera:Pyralidae), through weed management and insecticidal sprays in 1- and 2-year-old *Swietenia humilis* Zucc. plantations. *Crop Protection*. 24:821-828.

Green, E.E. 1913. Remarks on Coceidae collected by Mr Edward Jacobson, of Samarang, Java, with descriptions of two new species. *Tijdschrift voor Entomologie*. 55(4):311-318.

Greenslade, P.J.M. 1971. Phenology of three ant species in the Solomon Islands. *Journal of the Australian Entomological Society*. 10(4):241-252.

Griffiths, M. 1997. *The Biology and Host Relations of the Cedar Tip Moth, Hypsipyla Robusta Moore (Lepidoptera: Pyralidae) in Australia*. University of Queensland, Brisbane (Ph.D. dissertation).

Griffiths, M.W. 2001. The biology and ecology of *Hypsipyla* shoot borers. Pp. 74-80 in Floyd, R.B. & Hauxwell, C. (Eds.). *Proceedings of an International Workshop on Hypsipyla Shoot Borers in Meliaceae*. ACIAR Proceedings Series No 97, Kandy, Sri Lanka, 20-23 August 1996. ACIAR, Canberra.

Grijpma, P. 1974. *Contributions to an Integrated Control Programme of Hypsipyla Grandella (Zeller) in Costa Rica*. Wagenigan, Netherlands (Ph.D. dissertation) *in* Griffiths, M.W. 2001. The biology and ecology of *Hypsipyla* shoot borers. Pp. 74-80 in Floyd, R.B. & Hauxwell, C. (Eds.). *Proceedings of an International Workshop on Hypsipyla Shoot Borers in Meliaceae*. ACIAR Proceedings Series No 97, Kandy, Sri Lanka, 20-23 August 1996. ACIAR, Canberra.

Grijpma, P. 1976. Resistance of Meliaceae against the shoot borer *Hypsipyla* with particular reference to *Toona ciliata* M.J.Roem.var. *australis* (F.v.Muell)C.D.C. Pp. 69-78 in Burley, J. & Styles, B.T. (Eds.) *Tropical trees: Variation, breeding and conservation*. Linnaean Society, London.

Grijpma, P. & Ramalho, R. 1973. *Studies on the Shoot Borer Hypsipyla Grandella (Zeller). Lep., Pyralidae.* IICA Miscellaneous Publication No. 101. edition. IICA, San Jose, Costa Rica. 17 pp.

Gu, M.B. & Liu, Y.F. 1984. A preliminary study on *Hypsipyla robusta* (Moore). *Kunchong Zhishi*. 21:118-120.

Haack, K.D., Vinson, S.B. & Olson, J.K. 1995. Food distribution and storage in colonies of *Monomorium pharaonis* (L.) (Hymenoptera: Formicidae). *Journal of Entomological Science* 30:70-81.

Hauxwell, C., Mayhew, J., & Newton, A. 2001a. Silvicultural management of *Hypsipyla* species. Pp. 151-163 in Floyd, R.B. & Hauxwell, C. (Eds.). *Proceedings of an International Workshop on Hypsipyla Shoot Borers in Meliaceae*. ACIAR Proceedings Series No 97, Kandy, Sri Lanka, 20-23 August 1996. ACIAR, Canberra.

Hauxwell, C., Vargas, C., & Opuni Frimpong, E. 2001b. Entomopathogens for control of *Hypsipyla* spp. Pp. 131-139 in Floyd, R.B. & Hauxwell, C. (Eds.). *Proceedings of an International Workshop on Hypsipyla Shoot Borers in Meliaceae*. ACIAR Proceedings Series No 97, Kandy, Sri Lanka, 20-23 August 1996. ACIAR, Canberra.

Hill, D.S. 1983. *Agricultural Pests of the Tropics and Their Control*. Cambridge. 524 pp.

Ho, C.T. & Khoo, K.C. 1997. Partners in biological control of cocoa pests: mutualism between *Dolichoderus thoracicus* (Hymenoptera: Formicidae) and *Cataenococcus hispidus* (Hemiptera: Pseudococcidae). *Bulletin of Entomological Research*. 87:461-470.

Holldobler, B. 1979. Territories of the African weaver ant. *Zeitschrift fur Tierpsychologie*. 51:201-213.

Holldobler, B. 1983a. Territorial behavior in the green tree ant (*Oecophylla smaragdina*). *Biotropica*. 15(4):241-250.

Holldobler, B. 1983b. The evolution of communal nest-weaving in ants [Oecophylla]. *American Scientist*. 71:490-499.

Holldobler, B. & Wilson, E.O. 1977. Weaver ants. *Scientific American*. 237(6):146-154.

Holldobler, B. & Wilson, E.O. 1978. The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). *Behavioral Ecology & Sociobiology*. 3:19-60.

Holldobler, B. & Wilson, E.O. 1983. Queen control in colonies of weaver ants (Hymenoptera: Formicidae). *Annals of the Entomological Society of America*. 76(2):235-238.

Holldobler, B. & Wilson, E.O. 1990a. Weaver ants. Pp. 618-629 in *The Ants*. Belknap Press, Cambridge, Massachussets.

Holldobler, B. & Wilson, E.O. 1990b. Collecting, culturing, observing. Pp. 630-633 in *The Ants*. Belknap Press, Cambridge, Massachussets.

Horak, M. 2001. Current status of the taxonomy of *Hypsipyla ragonot* (Pyralidae: Phycitinae). Pp. 69-73 in Floyd, R.B. & Hauxwell, C. (Eds.). *Proceedings of an International Workshop on Hypsipyla Shoot Borers in Meliaceae*. ACIAR Proceedings Series No 97, Kandy, Sri Lanka, 20-23 August 1996. ACIAR, Canberra.

Howard, F.W. 1991. Seasonal incidence of shoot infestation by mahogany shoot borer (Lepidoptera: Pyralidae) in Florida. *Florida Entomologist*. 74:150-151.

Huang, H.T. & Yang, P. 1987. The ancient cultured citrus ant. *BioScience*. 37(9):655-671.

IPNI 2004. *The International Plant Names Index*. http://www.ipni.org (accessed 29 October 2006).

ITTO 2006. *Tropical Timber Market Report*. Vol. 11, No. 16. ITTO, Japan. 17 pp.

Jander, R. & Jander, U. 1979. An exact field test for the fade-out time of the odor trails of the Asian weaver ants *Oecophylla smaragdina*. *Insectes Sociaux.* 26(3):165-169.

Jesudasan, R.W., Claver, M.A., Priyakumari, C.J. & Ragupathy, E. 2004. Some ethological observations in whitefly and ant interaction. *Journal of Applied Zoological Research.* 15(1):17-21.

Jinda, L. 1982. The weaver ants, *Oecophylla longinoda, Oecophylla smaragdina*, Malaysia. *Nature Malaysiana*. 7(1):16-17.

Kasarov, W.H. 1992. Tests of the adaptive modulation hypothesis for dietary control of intestinal nutrient transport. *American Journal of Physiology (Regulatory, Integrative and Comparative Physiology).* 263:496-502.

Kay, A. 2002. Applying optimal foraging theory to assess nutrient availability ratios for ants. *Ecology*. 83(7):1935-1944.

Khoo, S.G. 2001. *Hypsipyla* shoot borers of Meliaceae in Malaysia. Pp. 24-30 in Floyd, R.B. & Hauxwell, C. (Eds.). *Proceedings of an International Workshop on Hypsipyla Shoot Borers in Meliaceae*. ACIAR Proceedings Series No 97, Kandy, Sri Lanka, 20-23 August 1996. ACIAR, Canberra.

Kotler, B.P., Dickman, C.R. & Brown, J.S. 1998. The effects of water on patch use by two Simpson Desert granivores (*Corvus coronoides* and *Pseudomys hermannburgensis*). *Australian Journal of Ecology*. 23:574-578.

Lamb, F.B. 1966. *Mahogany of Tropical America: Its Ecology and Management*. The University of Michigan Press, Ann Arbor, Michigan. 220 pp.

Lawson, G., Friend, A.D., Smith, R.I., & Dick, J.M. 2002. *Functional Classifications, Physiological Ecology, and Options for Parameterising and Modifying the Hybrid Forest Model for Application to Indonesian TMF* . No. 1. Institute of Terrestrial Ecology, UK. 62 pp.

Le Pelley, R.H. 1943. An oriental mealybug (*Pseudococcus lilacinus* Ckll.) and its insect enemies. *Transactions of the Royal Entomological Society of London.* 93:73-93.

Ledoux, A. 1950. Rechercher sur la biologie de la fourmi fileuse (*Oecophylla longinoda* Latr.). *Annales des sciences naturelles.Zoologie et biologie animale.* 12:333-461.

Leston, D. 1973. The ant mosaic - tropical tree crops and the limiting of pests and diseases. *PANS* 19:311-341.

Leu, A.F. 2005. Organic lychee and rambutan production. Pp. 241-254 in Chomchalow, N. & Sukhvibul, N. (Eds.). *Proceedings of the Second International Symposium on Lychee, Longan, Rambutan and other Sapindaceae Plants* . Acta Horticulturae 665, Chiang Mai, Thailand, 25-28 August, 2003. ISHS, Thailand.

Lim, A.T., Khoo, S.S., Yeap, C.A., Norsham, Y., Hijjas, A., & Chitra, D. 2003. *A Visitor's Guide to Kuala Selangor Nature Park*. Leong, H.Y. & Hijjas, A.(Eds.) Malaysian Nature Society Selangor Branch, Selangor, Malaysia. 105 pp.

Lim, G.T. & Kirton, L.G. 2003. A preliminary study on the prospects for biological control of the mahogany shoot borer, *Hypsipyla robusta* (Lepidoptera: Pyralidae), by ants (Hymenoptera: Formicidae). Pp. 240-244 in *Proceedings of the International Conference on Forestry and Forest Products Research (CFFPR 2001): Tropical*

Forestry Research in the New Millenium - Meeting Demands and Challenges, Kuala Lumpur, 1-3 October 2001. FRIM, Malaysia.

Lim, K.K.P., Murphy, D.H., Morgany, T., Sivasothi, N., Ng, P.K.L., Soong, B.C., Tan, H.T.W., Tan, K.S., & Tan, T.K. 2001. *A Guide to the Mangroves of Singapore*. Ng, P.K.L. & Sivasothi, N.(Eds.) Singapore Science Center, Singapore. 168 pp.

Lin, K.W. 2005. Ethnobotanical study of medicinal plants used by the Jah Hut peoples in Malaysia. *Indian Journal of Medical Sciences.* 59(4):156-161.

Lokkers, C. 1986. The distribution of the weaver ant, *Oecophylla smaragdina* (Fabricius) (Hymenoptera: Formicidae) in Northern Australia. *Australian Journal of Zoology*. 34:683-687.

Macfarlane, R.J., Jackson, G.V.H. & Morten, K.D. 1976. Die-back of *Eucalyptus* in the Solomon Islands. *Commonwealth Forestry Review.* 55:133-139.

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.

Mahdihassan, S. 1976. Mixed infection of lac. *The Journal of the Bombay Natural History Society*. 74(3):551-552.

Majer, J.D. 1972. The ant mosaic in Ghana cocoa farms. *Bulletin of Entomological Research.* 62:151-160.

Mayhew, J.E. & Newton, A.C. 1998. *The Silviculture of Mahogany*. Volume 95. CABI. 226 pp.

Miller, N.C.E. 1929. Division of Entomology. Annual Report for 1929. *Bulletin of the Department of Agriculture, Straits Settlements and Federated Malay States, General Series* 3:50-61.

Miller,N.C.E. 1931. *Coccus (Lecanium) Viridis Green: the "Green Scale" of Coffee*. 7 edition. Federated Malay States Government Press, Malaya (Malaysia). 29 pp.

MINITAB 2007. *MINITAB Statistical Software Release 14.20*.

More, P.S., Desai, B.D., Jalangaonkar, V.N. & Mule, R.S. 2002. Record of pests infesting arecanut, (*Areca catechu* Linneaus) and their seasonal incidence in Konkan region of Maharashtra. *Indian Journal of Arecanut, Spices and Medicinal Plants.* 4(3):120-122.

Na, J.P.S. & Lee, C.Y. 2001. Identification key to common urban pest ants in Malaysia. *Tropical Biomedicine.* 18(1):1-17.

Nakamuta, K., Matsumoto, K. & Kotulai, J.R. 2002. Field trapping of the mahogany shoot borer, *Hypsipyla robusta* (Lepidoptera: Pyralidae), with synthetic sex pheromones in Sabah, Malaysia. *JIRCAS Journal.* 10:9-12.

Newton, A.C., Baker, P., Ramnarine, S., Mesen, J.F. & Leakey, R.R.B. 1993. The Mahogany shoot borer: Prospects for control. *Forest Ecology and Management.* 57:301-328.

Nixon, G.E.J. 1951. *The Association of Ants With Aphids and Coccids*. CAB, London. 37 pp.

Nutrient Data Laboratory 2007. *USDA National Nutrient Database for Standard Reference*. No. Release 19. USDA-ARS, Accessed online at http://www.nal.usda.gov/fnic/foodcomp/search/ on Jan 10, 2007.

Nzokou, P. & Harris, S.A. 2002. Differentiating mahogany wood from allied timbers. *Journal of Tropical Forest Products.* 8(1):98-111.

O'Dowd, D. 2006. *Global Invasive Species Database: Anoplolepis Gracilipes.* http://www.issg.org/database/species/ecology (accessed 5 November 2006).

O'Farrell,P., Armour,J., & Reid,D. 2002. *The Effect of Nitrogen on Cashew in North Queensland*. No. Publication No. W02/001 (Project No. DAQ-257A). Rural Industries Research and Development Corporation (RIRDC), Canberra. 39 pp.

O'Gorman, T.W. 2001. A comparison of the F-Test, Friedman's test, and several aligned rank rests for the analysis of randomized complete blocks. *Journal of Agricultural, Biological, and Environmental Statistics.* 6(3):367-378.

Offenberg, J., Havanon, S., Aksornkoae, S., MacIntosh, D.J. & Nielsen, M.G. 2004. 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(3):344-351.

Pang, J.T.Y. 2004. Rootstock effects of cocoa in Sabah, Malaysia. *Experimental Agriculture.* 40:445-452.

Peeters, C. & Andersen, A.N. 1989. Cooperation between dealate queens during colony foundation in the green tree ant, *Oecophylla smaragdina*. *Psyche.* 96(1-2):39-44.

Peng, R.K. & Christian, K. 2004. The weaver ant, *Oecophylla smaragdina* (Hymenoptera: Formicidae), an effective biological control agent of the red-banded thrips, *Selenothrips rubrocinctus* (Thysanoptera: Thripidae) in mango crops in the Northern Territory of Australia. *International Journal of Pest Management*. 50(2):107-114.

Peng, R.K. & Christian, K. 2005. The control efficacy of the weaver ant, *Oecophylla smaragdina* (Hymenoptera: Formicidae), on the mango leafhopper, *Idioscopus nitidulus* (Hemiptera: Cicadellidae) in mango orchards in the Northern Territory. *International Journal of Pest Management.* 51(4):297-304.

Peng, R.K. & Christian, K. 2006. Effective control of Jarvis's fruit fly, *Bactrocera jarvisi* (Diptera: Tephritidae), by the weaver ant, *Oecophylla smaragdina* (Hymenoptera: Formicidae), in mango orchards in the Northern Territory of Australia. *International Journal of Pest Management.* 52(4):275-282.

Peng, R.K., Christian, K. & Gibb, K. 1995. The effect of the green ant *Oecophylla smaragdina* (Hymenoptera: Formicidae), on insect pests of cashew trees in Australia. *Bulletin of Entomological Research.* 85:279-284.

Peng, R.K., Christian, K. & Gibb, K. 1997a. Control threshold analysis for the tea mosquito bug, *Helopeltis pernicialis* (Hemiptera: Miridae) and preliminary results concerning the efficiency of control by the green ant, *Oecophylla smaragdina* (Hymenoptera: Formicidae) in northern Australia. *International Journal of Pest Management.* 43(3):233-237.

Peng, R.K., Christian, K. & Gibb, K. 1997b. Distribution of the green ant, *Oecophylla smaragdina* (F.) (Hymenoptera: Formicidae), in relation to native vegetation and the insect pests in cashew plantations in Australia. *International Journal of Pest Management.* 43(3):203-211.

Peng, R.K., Christian, K. & Gibb, K. 1998a. How many queens are there in mature colonies of the green ant, Oecophylla smaragdina (Fabricius)? *Australian Journal of Entomology*. 37(3):249-253.

Peng, R.K., Christian, K. & Gibb, K. 1998b. Locating queen ant nests in the green ant, *Oecophylla smaragdina* (Hymenoptera, Formicidae). *Insectes Sociaux*. 45(4):477-480.

Peng, R.K., Christian, K., & Gibb, K. 1999. The effect of levels of green ant, *Oecophylla smaragdina* (F.), colonisation on cashew yield in northern Australia. Pp. 25-28 in Loke, W.H. (Ed.). *Symposium on Biological Control in the Tropics*, MARDI, Serdang, Malaysia, 18-19 March 1999. CABI, Serdang, Malaysia.

Peng, R.K., Christian, K., & Gibb, K. 2004. *Implementing Ant Technology in Commercial Cashew Plantations and Continuation of Transplanted Green Ant Colony Monitoring*. RIRDC Publication No W04/088. RIRDC, Australia, http://www.rirdc.gov.au/reports/NPP/04-088.pdf (accessed 6 March 2007). 72 pp.

Pennington, T.D. 1981. *A Monograph of Neotropical Meliaceae in Flora Neotropica Monograph 28: Meliaceae. pp 360-390.* The New York Botanical Gardens, New York.

Pennington, T.D. & Styles, B.T. 1975. A generic monograph of the Meliaceae. *Blumea*. 22(3):419-540.

Phillips, J.S. 1940. Immature nutfall of coconuts in the British Solomon Islands. *Bulletin of Entomological Research*. 31:295-316.

Quick, W.N.B. 1974. Early stages of the life cycle of *Narathura araxes eupolis* (Miskin) (Lepidoptera: Lycaenidae). *The Victorian Entomologist*. 4:24-24.

Ramirez Sanchez, J. 1964. *Investigacion Preliminar Bore Biologia Ecologia y Control De Hypsipyla Grandella Zeller.* Boletin del Instituto Forestal Latino-Americano de Investigacion y Capacitacion No. 16. 77 pp.

RBG 2004. *Flora Zambesiaca*. Board of Trustees of the Royal Botanic Gardens, Kew, http://www.rbgkew.org.uk/floras/fz/intro.html (accessed 30 September 2006).

Richards, O.W. 1969. Colony-founding in the ant, *Oecophylla longinoda* (Latr.) (Hym., Formicidae). *Entomologist's Monthly Magazine*. 105:203.

Saarinen, E.V. 2006. Differences in worker caste behaviour of *Oecophylla smaragdina* (Hymenoptera: Formicidae) in response to larvae of *Anthene emolus* (Lepidoptera: Lycaenidae). *Biological Journal of the Linnean Society*. 88:391-395.

Sands, D.P.A. & Murphy, S.T. 2001. Prospects for the biological control of *Hypsipyla* spp. with insect agents. Pp. 121-130 in Floyd, R.B. & Hauxwell, C. (Eds.). *International Workshop on Hypsipyla Shoot Borers in Meliaceae . Proceedings of an International Workshop on Hypsipyla, Kandy, Sri Lanka, 1996*. ACIAR Proceedings Series No. 97, 121. ACIAR, Canberra.

Shattuck, S.O. & Barnett, N.J. 2007. *Genus Dolichoderus. Australian Ants Online.* CSIRO, Australia, http://www.ento.csiro.au/science/ants/dolichoderinae/dolichoderus/dolichoderus.htm (accessed 6 March 2007).

Sheue, C.R., Yong, J.W.H. & Yang, Y.P. 2005. The *Bruguiera* (Rhizophoraceae) species in the mangroves of Singapore, especially on the new record and the rediscovery. *Taiwania*. 50(4):251-260.

Simmonds, F.J. 1980. Biological control of *Cordia curassavica* (Boraginaceae) in Malaysia. *Entomophaga*. 25(4):363-364.

Soans, A.B. 1971. A case of intergeneric competition and replacement in the ants, *Oecophylla smaragdina* Fabricius and *Anoplolepis longipes* Jerdon (Hymenoptera: Formicidae). *The Journal of the Bombay Natural History Society*. 68(1):289-290.

Stapley, J.H. 1980. *Using the Predatory Ant, Oecophylla Smaragdina, to Control Insect Pests of Coconuts and Cocoa*. Information circular of the South Pacific Commission No. 85. SPC. 7 pp.

StatsDirect 2007. *StatsDirect Statistical Software Version 2.6.2*.

Stork, N.E. 1991. The composition of the arthropod fauna of Bornean lowland rain forest trees. *Journal of Tropical Ecology*. 7:161-180.

Strickland, A.H. 1951. The entomology of swollen shoot of cacao. II. The bionomics and ecology of the species involved. *Bulletin of Entomological Research*. 42:65-103.

Tan, R. 2001. *Mangrove and Wetland Wildlife at Sungei Buloh Wetlands Reserve: Weaver Ants.* http://www.naturia.per.sg/buloh/inverts/weaver_ants.htm (accessed 14 October 2006).

Taveras, R., Hilje, L., Hanson, P., Mexzon, R., Carballo, M. & Navarro, C. 2004. Population trends and damage patterns of *Hypsipyla grandella* (Lepidoptera: Pyralidae) in a mahogany stand, in Turrialba, Costa Rica. *Agricultural and Forest Entomology*. 6:89-98.

Traniello, J.F.A. 1989. Foraging strategies of ants. *Annual Review of Entomology*. 34:191-210.

Tsuji, K., Hasyim, A., Harlion & Nakamura, K. 2004. Asian weaver ants, *Oecophylla smaragdina*, and their repelling of pollinators. *Ecological Research*. 19(6):669-673.

USDA-ARS 2006. *Taxonomic Nomenclature Checker - GRIN [Online]*. http://pgrdoc.ipgri.cgiar.org/taxcheck/grin/index.html (accessed 30 September 2006).

Valentine, P. 1988. *Australian Tropical Butterflies.* Frith & Frith, Queensland, Australia. 71 pp.

van der Poorten, M. & van der Poorten, N. 2006. *Butterflies and Dragonflies of Sri Lanka*. http://www.srilankaninsects.net/Butterflies/Lycaenidae/Redspot/RedSpot.htm (accessed 30 September 2006).

Van Mele, P. & Cuc, N.T.T. 1999. Predatory ants in orchards in the Mekong Delta of Vietnam. Pp. 118-122 in Loke, W.H. (Ed.). *Symposium on Biological Control in the Tropics*, MARDI, Serdang, Malaysia, 18-19 March 1999. CABI, Serdang, Malaysia.

Van Mele, P. & Cuc, N.T.T. 2000. Evolution and status of *Oecophylla smaragdina* as a pest control agent in citrus in the Mekong Delta, Vietnam. *International Journal of Pest Management*. 46(4):295-301.

Van Mele, P. & Cuc, N.T.T. 2003. *Ants As Friends: Improving Your Tree Crops With Weaver Ants.* CABI Bioscience. 67 pp.

Van Mele, P., Cuc, N.T.T. & Van Huis, A. 2002. Direct and indirect influences of the weaver ant *Oecophylla smaragdina* on citrus farmers' pest perceptions and management practices in the Mekong Delta, Vietnam. *International Journal of Pest Management*. 48(3):225-232.

Van Mele, P. & van Lenteren, J.C. 2002. Survey of current crop management practices in a mixed-ricefield landscape, Mekong Delta, Vietnam - potential of habitat manipulation for improved control of citrus leafminer and citrus red mite. *Agriculture, Ecosystems & Environment.* 88(1):35-48.

Vanderplank, F.L. 1960. The bionomics and ecology of the red tree ant, *Oecophylla* sp., and its relationship to the coconut bug *Pseudotheraptus wayi* Brown (Coreidae). *Journal of Animal Ecology.* 29:15-33.

Verissimo, A., Barreto, P., Tarifa, R. & Uhl, C. 1995. Extraction of a high-value natural resource in Amazonia: The case of mahogany. *Forest Ecology and Management.* 72:39-60.

Watt, A.D., Newton, A.C., & Cornelius, J.P. 2001. Resistance in mahoganies to *Hypsipyla* species - a basis for integrated pest management. Pp. 89-95 in Floyd, R.B. & Hauxwell, C. (Eds.). *Proceedings of an International Workshop on Hypsipyla Shoot Borers in Meliaceae*. ACIAR Proceedings Series No 97, Kandy, Sri Lanka, 20-23 August 1996. ACIAR, Canberra.

Way, M.J. 1954a. Studies of the life history and ecology of the ant *Oecophylla longinoda* Latreille. *Bulletin of Entomological Research.* 45:93-112.

Way, M.J. 1954b. Studies on the association of the ant *Oecophylla longinoda* (Latr.) with the scale insect *Saissetia zanzibarensis* Williams. *Bulletin of Entomological Research.* 45:113-134.

Way, M.J. 1963. Mutualism between ants and honeydew-producing Homoptera. *Annual Review of Entomology.* 8:307-344.

Way, M.J. & Bolton, B. 1997. Competition between ants for coconut palm nesting sites. *Journal of Natural History.* 31(3):439-455.

Way, M.J., Cammell, M.E., Bolton, B. & Kanagaratnam, P. 1989. Ants (Hymenoptera: Formicidae) as egg predators of coconut pests, especially in relation to biological control of the coconut caterpillar, *Opisina arenosella* Walker (Lepidoptera: Xyloryctidae), in Sri Lanka. *Bulletin of Entomological Research.* 79(2):219-233.

Way, M.J. & Khoo, K.C. 1989. Relationships between *Helopeltis theobromae* damage and ants with special reference to Malaysian cocoa smallholdings. *Journal of Plant Protection in the Tropics.* 6:1-11.

Way, M.J. & Khoo, K.C. 1991. Colony dispersion and nesting habits of the ants, *Dolichoderus thoracicus* and *Oecophylla smaragdina* (Hymenoptera: Formicidae), in relation to their success as biological control agents on cocoa. *Bulletin of Entomological Research.* 81(3):341-350.

Western Australian Herbarium 2006. *FloraBase (Ver 2.1.3) - The Western Australian Flora.* Department of Environment and Conservation, http://florabase.calm.wa.gov.au/ (accessed 30 September 2006).

Wheeler, D.E. 1994. Nourishment in ants: patterns in individuals and societies. Pp. 245-278 in Hunt, J.H. & Napela, C.A. (Eds.) *Nourishment and evolution in insect societies.* Westview Press, Boulder, Colorado, USA.

Williams, D.J. 1960. The Pseudococcidae of the Solomon Islands. *Bulletin of the British Museum (Entomology).* 8:387-430.

Wylie, F.R. 1974. The distribution and life history of *Willonia isodoxa* Prout (Lepidoptera: Geometridae), a new pest of hoop pine in Papua New Guinea. *Bulletin of Entomological Research.* 63:649-659.

Wylie, F.R. 2001. Control of *Hypsipyla* spp. with pesticides: A review. Pp. 109-115 in Floyd, R.B. & Hauxwell, C. (Eds.). *International Workshop on Hypsipyla Shoot Borers in Meliaceae . Proceedings of an International Workshop on Hypsipyla, Kandy, Sri Lanka, 1996.* ACIAR Proceedings Series No. 97, 120. ACIAR, Canberra.

Yamazaki, S., Ikeda, T., Taketani, A., Vasquez Pachecho, C. & Sato, T. 1992. Attack by the mahogany shoot borer, *Hypsipyla grandella* Zeller (Lepidoptera: Pyralidae), on the Meliaceous trees in the Peruvian Amazon. *Applied Entomology and Zoology.* 27:31-38.

Zar, J.H. 1999. *Biostatistical Analysis.* 4th edition. Prentice Hall, Englewood Cliffs, N.J. 931 pp.

Zerhusen, D. & Rashid, M. 1992. Control of the bigheaded ant *Pheidole megacephala* Mayr. (Hym., Formicidae) with the fire ant bait "AMDRO" and its secondary effect on the population of the African weaver ant *Oecophylla longinoda* Latreille (Hym., Formicidae). *Journal of Applied Entomology*. 113(3):258-264.

Appendix A.1 Revenue and expenditure outlay for a 40 ha *Khaya ivorensis* plantation in Malaysia in a 20 yr rotation. Table adapted from Ahmad Zuhaidi *et al*. (2006).

Item	$, in USD, per ha[1]
Revenue[2]	
10 yr thinning	851
15 yr thinning	1512
20 yr harvest	32120
Capital Expenditure[3]	
Land preparation (clearing, ditches)	432
Planting (lining, handling, holing, planting)	444
Seedlings	333
Developing major and feeder roads	92
Building culverts	47
Maintenance costs	
Weeding[4]	123
Climber cutting (in 2nd yr)	10
Pest control[5]	200
Fertilizer[6]	311
Road maintenance[7]	10
Thinning at 5 yr	67
Thinning at 10 yr[8]	102
Thinning at 15 yr	181
Administrative costs	
Worker enumeration (annual increment 6%)	147
Log Extraction Cost at 20 yr	1288

[1]Conversion rate: 1 USD = 3.75 MYR.

[2]Final stand density was estimated at 322 trees per ha at 20 yr with marketable log volume of 0.75 m^3 per tree = 242 m^3 per ha. Estimated log volume from 10 and 15 yr thinnings were 21.3 and 37.8 m^3 per ha, respectively. Estimated market price per m^3 log at 10, 15 and 20 yr was $40, 40 and 133, respectively. Initial density: 833 trees per ha.

[3]Planting costs estimated at 53 cents per tree; Seedlings cost 40 cents per tree with initial planting density of 833 trees per ha; 50 m per ha of major roads constructed at a cost of $1.10 per m and 74 m per ha of feeder roads constructed at a cost of 53 cents per m.

[4]Weeding cost for yr 1, 2, 3 and 4 estimated at $40, 30, 30 and 13, respectively

[5]Ten applications of carbofuran per yr at $10 per application, for first two yr. Substituting this with weaver ants at 6, 25 and 48 colonies per ha would cost $269, 920 and 1,709, respectively, over three yr (Table 6.2).

[6]Fertilizer applied in yr 1 and 2 – 4 at a rate of 100 and 200 g per tree, respectively.

[7]Road maintenance carried out annually from yr 2 - 7.

[8]Thinning cost estimated at $4.80 per m^3 log for yr 10 and 15.

Vita

Grace Lim was born in Kuala Lumpur, Malaysia and grew up in a small village on the outskirts of the city. She obtained her high school education at Bukit Bintang Girls' School from Form 1 to 5, followed by pre-university education at St. John's Institution, both in the heart of Kuala Lumpur. She pursued a Bachelor of Agricultural Science degree at Putra University of Malaysia (UPM) in Selangor. Upon graduation, Grace took a position as research officer at the Entomology Unit of the Forest Research Institute of Malaysia (FRIM). While under employment at FRIM, she pursued a Master of Agricultural Science degree again at UPM under the advisement of Drs Khoo Kay Chong, Yusof Ibrahim (UPM) and Laurence Kirton (FRIM). She completed her thesis research on the bionomics of the teak skeletonizer, an important pest of teak in Malaysia. After graduation, Grace was awarded the Fulbright Fellowship to pursue a Doctor of Philosophy degree in Entomology at Virginia Polytechnic and State University, Blacksburg, USA, under the advisement of Drs Scott Salom and Loke T. Kok. Dr Laurence Kirton was her FRIM co-advisor. During her time in the US, she served as a panelist on the Graduate Honor System investigative and judiciary boards of Virginia Tech and assisted in conducting educational tours of the Entomology Department of Virginia Tech. She is currently a member of the Entomological Society of America, the Gamma Sigma Delta Honor Society of Agriculture and International Organisation of Biological Control.