

**Host Moth Oviposition and Its Induction of Tea Leaves to Arrest
the Egg-larval Parasitoid, *Ascogaster reticulata* Watanabe
(Hymenoptera: Braconidae)**

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**A Dissertation Submitted to
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General Introduction

Over decades, the various kinds of chemical pesticides have become the most important for pest management used in agricultural systems worldwide. Normally, a pesticide must be lethal to the target pests and does not causes resistance in those species; however, it also causes many environmental impacts such as pollutions and contaminations in many areas, as well as the direct impacts on the health of human and animals (reviewed by Aktar et al., 2009). Dichlorodiphenyltrichloroethane (DDT), which is one of the most well-known pesticides discovered by a chemist Paul Müller in 1939, had been debated for a long time. Initially, it was effectively used for the control of several insect-borne diseases such as malaria, typhus, dysentery and typhoid fever. Subsequently, DDT became more available after being introduced as an agricultural insecticide (Berry-Cabán, 2011). In 1962, the use of DDT was cited to be public concerned by Rachel Carson's book, "Silent Spring" and this book prompted public awareness of the environmental impacts of uncontrolled and unexamined use of pesticides. Especially, predatory birds became endangered, nearly to extinction, as well as questions about the effects on human health and ecological system (Carson, 2002). Finally, these concerns resulted in a ban of DDT for agricultural use in the United States in 1972 (Stokstad, 2007) and became worldwide in 2004.

Why the pesticides have been widely used by growers? A main reason is because consumers normally prefer agricultural products based on visual appeal such as color and shape. Many growers are forced to focus on the good appearance of their products more than concern about the contamination of pesticides on their products or the other impacts. Subsequently, large amounts of pesticide used in the last 50 years have caused problems in a pesticide resistance in many species (e.g. Brattsten et al.,

1986; Kaur and Kang, 2015; Mallet, 1989; Talebi et al., 2011). Resistant strains develop through the survival and reproduction of powerful individuals that can survive after exposure to an insecticide. The insecticide resistance cases are usually associated with improved capacity of detoxification enzymes such as cytochrome P-450, carboxylesterases and glutathione-S- transferases (GST), which are referred to a metabolic resistance in pest insects (Brattsten et al., 1986). Moreover, pesticide use has been shown to be associated with a decrease in the population of natural pest control agents (reviewed by El-Wakeil et al., 2013; Fernandes et al., 2010). Thus, the excessive use of agricultural pesticides is concerned and the biological control methods have become more considerable.

What is biological control?

Biological control is the utilization of living organisms, which often referred to as natural enemies or beneficial species, to control pest populations in the ecosystem (Mahr et al., 2008; Rusch et al., 2010; Stoner, 2004). The use of biological control as a choice to suppress the abundance of pest populations is a fundamental philosophy of integrated pest management (IPM; Stern and van den Bosch, 1959). A main objective of biological control is to design methods that can control the population of pests and also establish natural enemies in new areas by improving their environmental living conditions (Mills, 2003; van Driesche et al., 2008). Natural enemies such as predators, parasitoids, and pathogens play an important role in limiting damage caused by native and exotic pests (Hawkins et al., 1997; Memmott et al., 2000).

A parasitoid is one of well-known natural enemies used in biological control of pest insects and the most beneficial insect parasitoids are wasps or flies. Hawkins et al. (1997) reported that parasitoids kill more herbivores than other types of natural

enemies, which are predators and pathogens. Naturally, parasitoids have an immature life stage that develops on or within a single insect host, ultimately killing the host in the mid/late larval and pupal stages. In complex habitat, parasitoids need to locate their hosts and optimize their host location behavior by using visual and chemical cues (e.g. Fisher et al., 2001; Pedigo and Rice, 2009; Schoonhoven et al., 2005; van Driesche et al., 2008).

An example of visual cue utilization by parasitoids was shown in the studies by Morehead and Feener (2000). They reported that *Apocephalus paraponerae*, a parasitic fly of giant tropical ant *Paraponera clavata*, preferred a model of large plastic ants more than the smaller plastic ants. These *A. paraponerae* flies may use ant body size as visual cue when locating hosts at a short distance. Moreover, parasitoids also exploit chemical cues such as kairomones from host insects (e.g. wing scales, secretions) to indicate the presence of a suitable host (reviewed by Afsheen et al., 2008; DeLury et al., 1999; Kainoh et al., 1982; Strand and Vinson, 1982).

Numerous studies have focused on not only interactions between herbivore-plant or herbivore-natural enemy, but also herbivore-plant interaction associated with organisms in other trophic level. The chemicals released by plants when they are damaged by herbivores are called herbivore-induced synomones, which are signals that benefit to both the plant producing the signal for neighboring plants and the parasitoids of herbivorous pest insects (De Moraes et al., 2000; Poppy, 1997; Turlings and Wäckers, 2004; van Driesche et al., 2008). Relationships involving plants, herbivores, and parasitoids are termed “tritrophic interactions,” (Fig. 1) and a better understanding of such interactions can enhance the efficacy of biological control (Dicke and Sabelis, 1987).

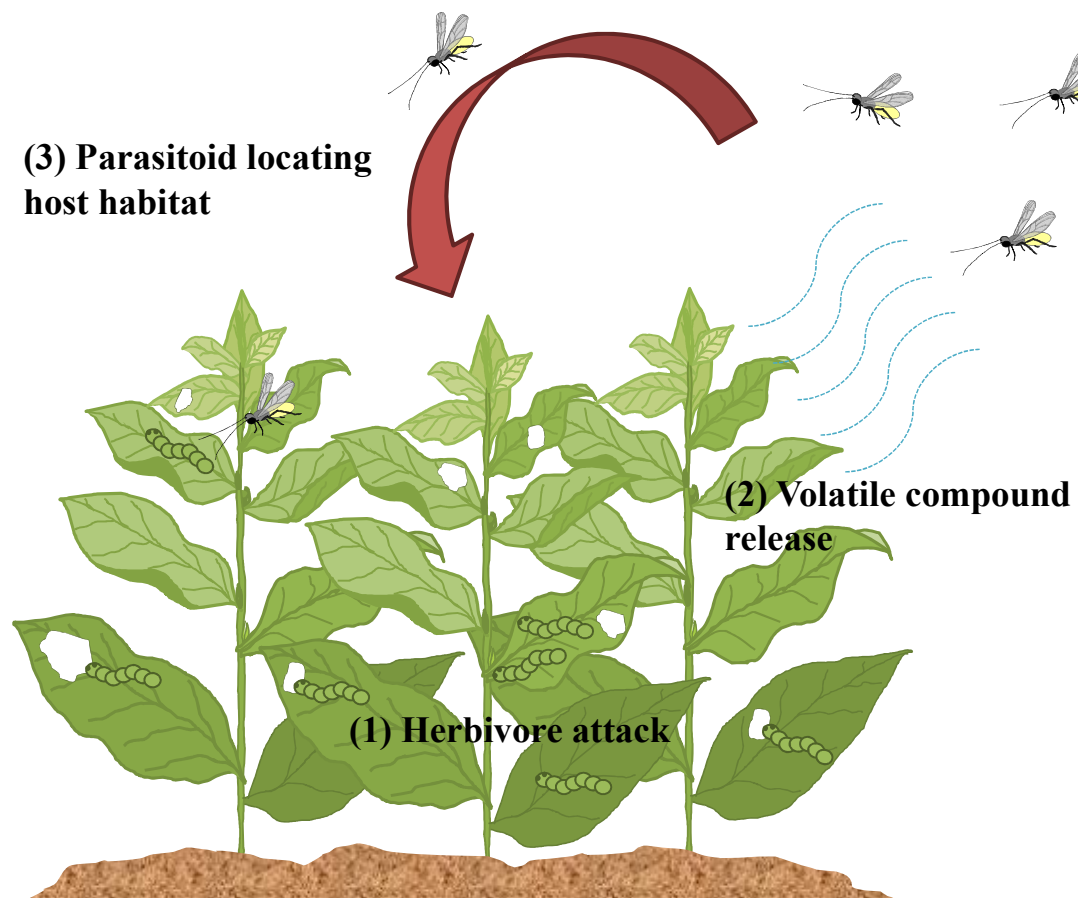


Figure 1. A “Tritrophic interaction” among plants, herbivores and parasitoids

Tea, *Camellia sinensis* (L.), is a major plantation crop for the economies of several countries in Asia and Africa, including Japan and Thailand (Fig. 2). There are many pest insects and diseases (e.g. Muraleedharan, 2002; Commins and Sampanvejsobha, 2008; Das et al., 2010). All parts of the plant, leaf, stem, root, flower and seed are fed on by at least one pest species, causing the impact on productivity, quantity and quality of tea (Hamasaki et al., 2008; Hazarika, 2009).

The smaller tea tortrix *Adoxophyes honmai* is a common pest of tea plants in Japan. Chemical insecticides, a major method to control this species, need to be sprayed in the tea fields several times each year. To reduce the use of insecticides, a mating disruptant has been introduced for controlling a population of *A. honmai* at Shimada in Shizuoka Prefecture since 1983 (Tamaki et al., 1983). However, the infestations increased again after 10 years of annual applications (Mochizuki et al., 2002). Due to appearance of resistance strain, the natural enemies such as parasitoids are an alternative choice to reduce population of this species as a review of Hazarika et al. (2009) suggested that natural enemies normally play a significant role for biological control in tea ecosystems.

One of the parasitoids found in the tea fields is *Ascogaster reticulata*, a solitary egg-larval endoparasitoid of several tortricid species including *A. honmai*. This wasp species can control populations of *A. honmai* by parasitizing host eggs and finally killing their host in the 4th larval stage during egress. Then, they spin cocoons outside the host bodies (Kawakami and Kainoh, 1986; Watanabe, 1967). Host-searching behavior of *A. reticulata* wasps was stimulated by the kairomones from their host, *A. honmai* such as wing scales, excrement (Kainoh et al., 1982). Subsequently, the wasps remained for a longer time in kairomone treated areas than in untreated areas. Not only host kairomones are mainly used by *A. reticulata* to locate their host, but these wasps



Figure 2. Tea field in Shizuoka Prefecture, Japan

also utilize plant chemicals by learning behaviors. They can learn the plant contact chemicals associated with the host egg mass as host-searching cues (Kainoh, 1997), and show an ability to discriminate the chemicals from various species of plants (Seino and Kainoh, 2008). Moreover, they also utilize learned plant chemicals as cues to find their host (Seino et al., 2010). Therefore, better understanding of both host and parasitoid foraging behaviors may increase the effective of parasitoid use in pest management program in the future.

In this thesis, I separated my studies in two chapters. The first chapter, I focused on the effect of leaf age (young and old leaves) on host-selection in *A. honmai* to clarify the oviposition site location by *A. honmai* moths and feeding site location by their neonates on tea plants. The relationship between oviposition preference of adults and the performance of their offspring were observed to show performance of *A. honmai* moths that can choose a suitable oviposition site or not. Also, the ability of parasitoid *A. reticulata* to discriminate volatiles from different ages of leaves was observed to show a possibility of host finding in this species. The second chapter, I mainly focused on the responses of *A. reticulata* to plant chemicals. I speculated that the cues produced by egg-laden leaves or leaves treated with reproductive system may affect host-searching or arresting behaviors in parasitoid *A. reticulata*. To confirm this hypothesis, the system of tea/*A. honmai*/*A. reticulata* was conducted.

Chapter 1: Preference-performance linkage in *A. honmai*

1.1 Introduction

Over the past years, numerous studies have demonstrated how different factors influenced phytophagous insect abundance (e.g. Benrey and Denno, 1997; Cornelissen, 2011; Finch and Collier, 2000; Maron and Crone, 2006). These factors include environmental factors, oviposition success of herbivores, quality and quantity of plant resources and effect of natural enemies on survival of herbivores in a complex habitat (Basset, 1999; Maron and Crone, 2006; reviewed by Zalucki et al., 2002). Interactions between herbivores and host plants have become a main area of investigation in recent decades (Bernays and Chapman, 1994). Particularly, many researchers have tested the preference-performance hypothesis (PPH) by analyzing associations between oviposition preference of females for specific plants and performance of their offspring (Clark et al., 2011; Jaenike, 1978; Mayhew, 1997, 2001; Thompson, 1988; Videla et al., 2012).

Although a suitable oviposition site ensures resources for offspring survival and development, there are many factors that affect female oviposition decisions (reviewed by Renwick and Chew, 1994). These include physiological and chemical characteristics of plants (e.g. Badenes-Perez et al., 2014; Bergström et al., 1994; Metspalu et al., 2009; Steinbauer, 2002; Steinbauer et al., 2004), as well as the presence of natural enemies (Carrasco and Kaitala, 2009; De Silva et al., 2011). Not only preferred plant species (e.g. Bruce et al., 2005; Pivnick et al., 1994; Rojas et al., 2000; Späthe et al., 2013), but leaf age also affects the oviposition decision of maternal insects and performance of their offspring (Bittencourt-Rodrigues and Zucoloto, 2005; King et al., 1998; Neck, 1981; Rodrigues and Moreira, 1999; Thomas et al., 2012).

In Lepidoptera, oviposition is particularly crucial because the immature stages have little opportunity to change their developmental habitat (Renwick and Chew, 1994). The fate of offspring depends on the oviposition decision of their parents (Zalucki et al., 2002). Renwick and Chew (1994) indicated that oviposition decisions by gravid moths and butterflies generally follow a sequence of behaviors, i.e. searching, orientation, encounter, landing, surface evaluation and acceptance. Searching behaviors of moths and butterflies have been demonstrated in both field and laboratory observations and plant volatiles play an important role in the orientation of various moths to the appropriate host plants (e.g. Borrero-Echeverry et al., 2015, Feeny et al., 1989, Tasin et al., 2011). Therefore, an understanding of host-searching behavior-associated plant volatiles may lead to a better understanding of host-plant selection by phytophagous insects in different environments.

Although damage caused by larvae of *A. honmai* is widely distributed throughout tea plantations, the mode of oviposition, dispersal of neonates within tea shrubs and their development still remain unclear. Therefore, I focused on the effect of leaf age in oviposition preference of *A. honmai* moths and the performance of their offspring in this study. Moreover, the behavioral responses of *A. reticulata* to volatiles from young and old leaves were observed to investigate the ability of this parasitoid to discriminate volatiles from different ages of tea leaves to increase the possibility of host eggs encounter.

1.2 Plant and Insect Materials

1.2.1 Plant

1. Scientific Classification

Kingdom: Plantae

Order: Ericales

Family: Theaceae

Genus: *Camellia*

Species: *C. sinensis*

Tea, *Camellia sinensis* cv. Yabukita, is a perennial evergreen plant that thrives in the cool, high mountain regions of Central China and Japan. Most tea plants have a growth phase and a dormant period, usually during the winter. New shoots sprout several times per year after plucking.

2. Tea pests and controlled methods

Tea plants are commonly attacked by various species of insect pests. Kawai (1997) reported that most of tea pests in Japan are polyphagous and some of them infest throughout the year causing the reduction of yield and quality of tea. In tea plantation, several insect pests can occur together, so tea growers have to control multiple pests at the same time. An insecticide spraying is commonly used for insect pest control (Takafuji and Amano, 2001), but it has caused insecticidal resistance in several insect pest species (e.g., *Tetranychus kanzawai*, *Homona magnanima*, *Adoxophyes* sp., *Empoasca onukii*). Moreover, the results of an excessive use of pesticides such as serious groundwater pollution have become an issue in tea-growing areas. Therefore,

natural enemies are considerably used with other insecticides. While insecticides are used against pests on new shoots in the summer, natural enemies effectively control pests on mature leaves during the autumn (Kawai, 1997).

3. Plant rearing in laboratory

About 10-year-old potted tea plants, grown from seedlings in clay pots (30 cm in diameter), were kept in a greenhouse at L14 ($25\pm 1^{\circ}\text{C}$):D10 ($20\pm 1^{\circ}\text{C}$) and 40–60% RH (Fig. 3). The plants were watered every alternate day. Pruning was sometimes necessary, but not immediately before the experimental tests. Tea plants were normally pruned in early March and left until they produced new shoots.

Young and old leaves were plucked from tea shrubs and used for the bioassays. Leaf age was determined using color and leaf position within a branch. Figure 4 shows the color criteria for young and old leaves. Intermediate leaves were not used in this study. In addition to color, we used the position of the leaf on a branch to determine the leaf age. Young leaves were located on the top of the branch, whereas old leaves on the bottom of a branch.



Figure 3. Tea *Camellia sinensis* cv. Yabukita

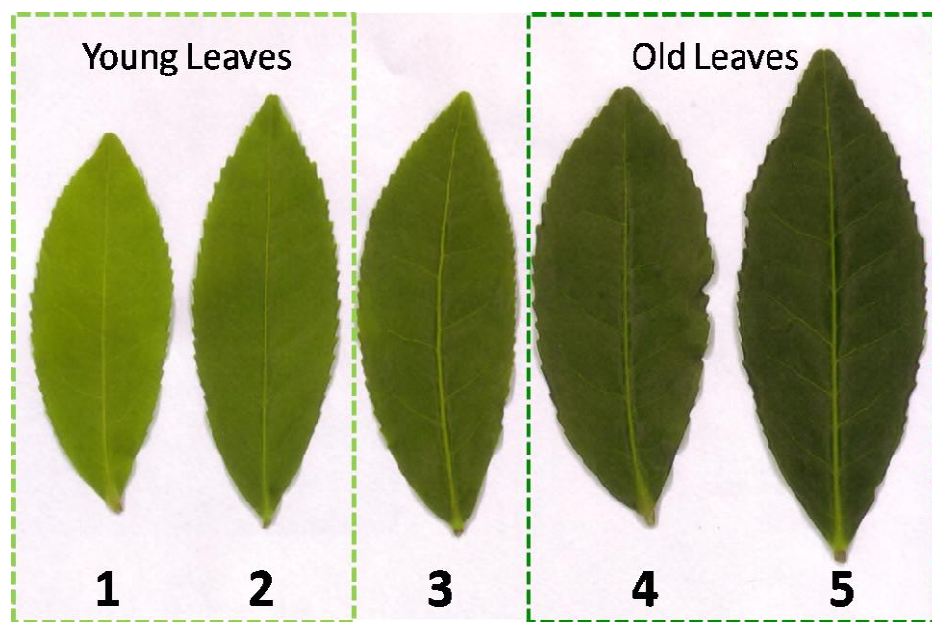


Figure 4. Tea leaf color: Young leaves (1 and 2), Old leaves (4 and 5)

1.2.2 Insects

Host insect, *Adoxophyes honmai*

1. Scientific Classification

Kingdom: Animalia

Order: Lepidoptera

Family: Tortricidae

Genus: *Adoxophyes*

Species: *A. honmai*

The smaller tea tortrix, *A. honmai*, is a polyphagous insect that can feed on many species of plants. It is a serious pest of tea plantations in Japan. It can severely damage immature stages by feeding on the growing leaves and shoots (Hazarika et al., 2009).

2. Species overview

Wingspan of male moth is 15-19 mm. Wings are yellowish and highlighted with dark brown mark. Female moth wingspan is 18-22 mm. Wing color of females is paler than males and highlighted with tawny marks (Fig. 5). Eggs of *A. honmai* are pale yellow (Fig. 6). The larval color is green or yellowish green. Head capsule is yellowish brown (Fig. 7). Larval stage is approximately 18 days at 25°C before entering the pupal stage (Fig. 8). Female moths usually lay egg masses of oval shape, ca. 5 mm in diameter, on the under-surface of tea leaves (Fig. 9).



Figure 5. Adult of *A. honmai* (a: male moth, b: female moth)



Figure 6. *A. honmai* egg mass (a: 1-day old egg mass, b: egg mass ready to hatch)



Figure 7. *A. honmai* larva

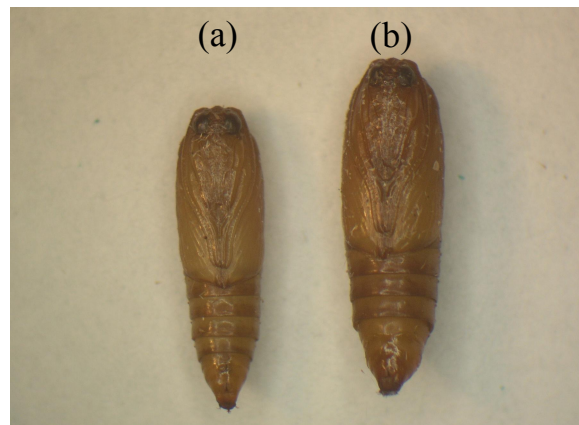


Figure 8. Pupae of *A. honmai* (a: male, b: female)



Figure 9. Egg mass of *A. honmai* on the under surface of tea leaf

3. Host insect rearing

Adoxophyes honmai was reared on an artificial diet as described by Tamaki (1966). The egg masses of the smaller tea tortrix, *A. honmai*, on a sheet of wax paper were cut and transferred to a small Petri dish with a wet filter paper inside bottom. Darkened egg masses before hatching were immediately sterilized with 70% ethanol and washed with distilled water before inoculation of rearing boxes (25x18x8 cm) with an artificial diet and wax papers (9x4.5 cm) inside (Fig. 10). These boxes were kept in an air condition-room at $25 \pm 1^{\circ}\text{C}$ and $60\% \pm 20\%$ RH of a 16L:8D photoperiod. The pupae were collected from rearing boxes about 18 days after inoculation and put in the plastic boxes (25x18x8 cm) with wet absorbent cotton and the top of the box covered with wax paper for female moth oviposition. Egg masses oviposited on wax papers were used for parasitoid oviposition and rearing.



Figure 10. Insect rearing boxes with an artificial diet and wax papers inside

Parasitoid, *Ascogaster reticulata*

1. Scientific Classification

Kingdom: Animalia

Order: Lepidoptera

Family: Braconidae

Genus: *Ascogaster*

Species: *A. reticulata*

Ascogaster reticulata Watanabe, a solitary parasitoid wasp, is an egg-larval endoparasitoid of *A. honmai*. The larvae develop inside the body cavity of the host. *A. reticulata*, which allows host to develop after oviposition, is a koinobiont (Kawakami, 1985; van Driesche, 2008). The parasitoids oviposit in host eggs and the parasitized host eggs hatch and host larvae are allowed to develop. Kawakami (1985) found that the parasitoid larvae grow slowly to second-instar larvae when the host larvae are in the 4th-instar, and the 3rd-instar parasitoid larvae egress from the host, then consume their host larval bodies, and spin cocoons for pupation. Newly emerged females need to find hosts for their offspring.

2. Species overview

Female wasps are slightly larger than male wasps. The body color of males and females is black. Antennae are longer than body size. Wings are translucent, and the veins of wings can be observed clearly (Fig. 11).

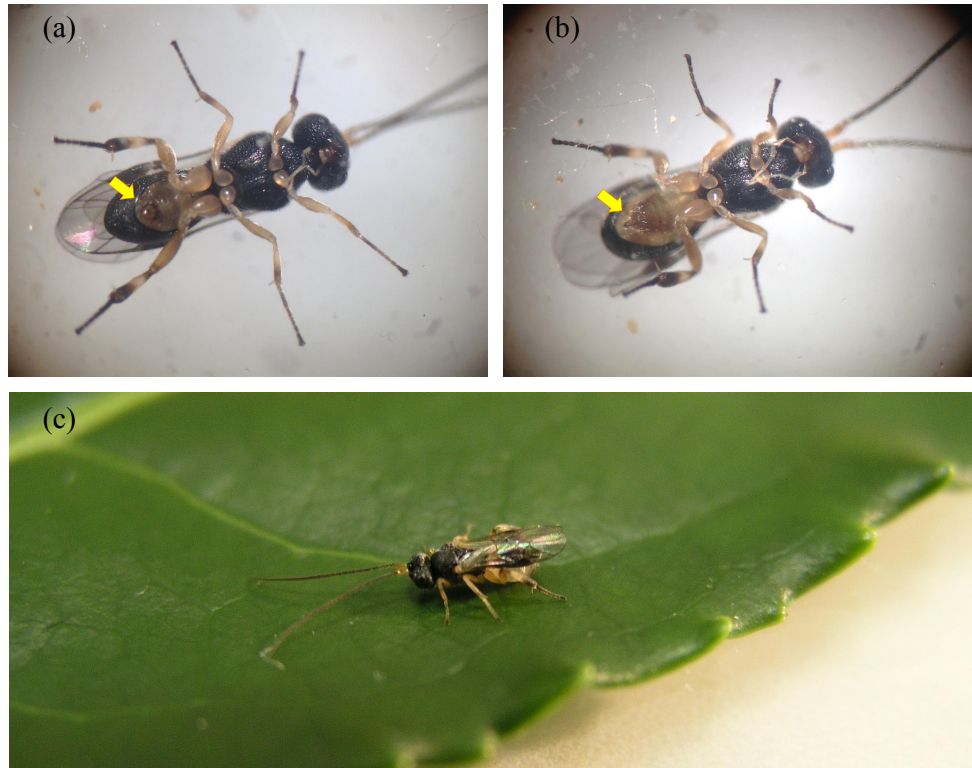


Figure 11. *A. reticulata* wasps (a: male, b: female, c: female *A. reticulata* searching on tea leaves)

3. Parasitoid rearing

The rearing of *Ascogaster reticulata* was based on Kainoh (1988). The egg stage of *A. honmai* was used for starting the rearing and multiplying the parasitoid, *A. reticulata*. The cocoons of parasitoids were maintained in small glass tubes for separation of males and females (Fig. 12). One- to 2-day-old females and 3- to 5-day-old males were used for mating to multiply the next generation (Fig. 13). The adult parasitoids were reared in plastic containers (15 cm in diameter and 8.5 cm in height) with 2x3 cm wet absorbent cottons. A honey drop was applied on the side of the plastic container for food. Each mated female parasitoid was allowed to oviposit on a host egg mass for 30 minutes (Fig. 14). Darkened parasitized host egg masses (Fig. 15) before hatching were immediately sterilized with 70% ethanol and washed with distilled water before inoculating in rearing containers, and cocoons were collected after 18 days of inoculation (as rearing of host; Fig. 16) and put into glass tubes (1 cm diameter and 7.5 length). Adult wasps usually emerged in 2-4 days after putting cocoons into the tubes.

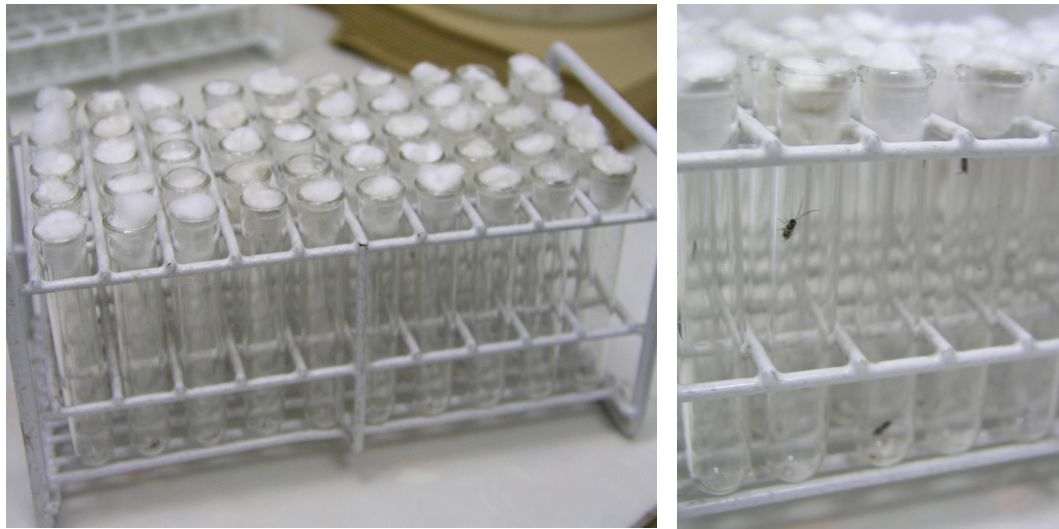


Figure 12. Separation of male and female wasps in 5 ml test tubes



Figure 13. Mating of male and female wasps



Figure 14. *A. reticulata* female wasp in oviposition posture



Figure 15. Darkened parasitized host egg masses



Figure 16. *A. reticulata* cocoons and *A. honmai* pupae collection

Chapter 2: Sex-Specific Elicitor of *Adoxophyes honmai* on Tea Leaf

Arrests the Egg–Larval Parasitoid *Ascogaster reticulata*

2.1 Introduction

Naturally, damages caused by feeding herbivorous insects induce defensive reactions in plants (Karban and Myers, 1989). Recent studies have shown that some plant species respond defensively to herbivore attack, even simply laying eggs on the host plants. Egg deposition by herbivorous insects can stimulate plants to induce direct and indirect defenses with consequences for other species such as natural enemies (Fatouros et al., 2005, 2009, 2012; Hilker et al., 2002; Tamiru et al., 2011).

Direct defenses in plants involve various responses, such as egg deposition triggering hypersensitivity resulting in a necrotic zone at the base of the eggs that detaches them from the plants (Doss et al., 1995, 2000; Fatouros et al., 2012; Shapiro and DeVay, 1987). Egg-laden plants also produce ovicidal substances that cause high mortality in herbivore eggs (Seino et al., 1996; Suzuki et al., 1996). Furthermore, plants produce deterrents for further egg deposition after infestation with the first egg (Blaakmeer et al., 1994; Fatouros et al., 2012). Egg-deposition by herbivores induces indirect defenses in plants with the production of volatile compounds that attract natural enemies of the herbivores (Fatouros et al., 2008; Hilker and Fatouros, 2015; Hilker and Meiners, 2006; Pashalidou et al., 2010). Plants release not only volatile synomones that attract egg parasitoids from long distances (Colazza et al., 2004a, 2004b; Meiners and Hilker, 2000; Tamiru et al., 2011, 2012), but also release contact synomones that are utilized by parasitoids to locate their hosts after they alight on a plant (Fatouros et al., 2005, 2007).

In some tritrophic interactions, oviposition-associated wounding induces synomone production in plants as shown in the studies by Meiners and Hilker (2000), the system of elm (*Ulmus minor*)/elm leaf beetle (*Xanthogaleruca luteola*)/egg parasitoid (*Oomyzus gallerucae*). An elicitor located in the oviduct secretion of elm leaf beetle became active only when it was treated on the damaged leaf surface and it induced elm leaves to produce volatiles that attracted parasitoid *O. gallerucae*. However, system of pine (*Pinus sylvestris*)/pine sawfly (*Diprion pini*)/egg parasitoid (*Chrysonotomyia ruforum*) showed that although oviposition by pine sawfly is associated with wounding on plant surface, only artificial damage on leaf surface caused by needles did not induce the volatile production in this plant species. Thus, the chemical production in plant was mainly induced by an elicitor as similar to the studies of Fatouros et al. (2009) and Pashalidou et al. (2010). *Pieris brassicae* and *Pieris rapae* did not cause any damage while ovipositing, which are clearly different from the egg depositions by elm leaf beetle and pine sawfly. Although there was no damage on leaf surface during their ovipositions, egg depositions by both herbivores induced Brussels sprouts to produce chemicals that arrested the egg parasitoids *Trichogramma brassicae* and *Trichogramma evanescens* (Fatouros et al., 2009; Pashalidou et al., 2010).

Only one study in tritrophic system of tea showed that host-searching and arresting behaviors of these wasps were stimulated by cues produced by egg-laden leaves and the cue induction in tea leaves was not associated with physical wounding caused to the leaf surface by *A. honmai* oviposition (Deshpande and Kainoh, 2012), but the source of elicitor from *A. honmai* is still unclear. Therefore, to confirm the hypothesis that the elicitor that can induce tea leaves to produce cues to arrest parasitoid *A. reticulata* is from *A. honmai* moths and to determine the source of elicitors, I conducted studies on the tritrophic system of tea plant/*A. honmai*/*A. reticulata*. The

effect of egg deposition on tea leaves affecting parasitoid host-searching behavior was observed, as well as the effect of female moth reproductive system homogenates placed on the leaves as an elicitor. The responses of *A. reticulata* wasps to cues from egg-laden leaves or leaves treated with reproductive system homogenates were observed and compared with control leaves. Moreover, to determine whether moth species affects induction in tea plant, the responses of *A. reticulata* wasps on leaves treated with *Homona magnanima* or *Ostrinia furnacalis* reproductive system homogenates were observed and compared with untreated leaves. Based on the results of *A. honmai* oviposition preference in Chapter 1, I decide to conduct all experiments in Chapter 2 by using old tea leaves.

2.2 Plant and Insect Materials

2.2.1 Plant (Tea plant *C. sinensis*)

See the details in Chapter 1.

2.2.1 Insects

Host insect A. honmai and parasitoid A. reticulata rearing

See the details in Chapter 1.

Non-host insects

- Oriental Tea Tortrix *Homona magnanima* Diakonoff (same host plant of *A. honmai*)

1. Scientific Classification

Kingdom: Animalia

Order: Lepidoptera

Family: Tortricidae

Genus: *Homona*

Species: *H. magnanima*

H. magnanima (Fig. 30) is an economically important pest, which often occurs together with the smaller tea tortrix *Adoxophyes honmai* in the tea field of Japan. The

severe damages such as leaf fold and feeding activity by this species, especially tea shoots and leaves, shows the impacts on tea products.

2. Insect rearing

The colony of *H. magnanima* was obtained from NARO Institute of Vegetable and Tea Science (Shimada, Shizuoka, Japan). This species was sexed from the pupal stage and separately reared until adult emergence. Male and female moths were kept in rearing boxes (25×18×8 cm) containing moist cotton and 3 pieces of folded wax paper for female moth oviposition. These boxes were kept in an air condition-room at 25±1°C and 60% ± 20% RH of a 16L:8D photoperiod.

- Tropical corn borer *Ostrinia furnacalis*

1. Scientific Classification

Kingdom: Animalia

Order: Lepidoptera

Family: Crambidae

Genus: *Ostrinia*

Species: *O. furnacalis*

The Asian corn borer (ACB; Fig. 31) *O. furnacalis* is the most serious insect pest of corn, *Zea mays* in many countries including Japan and Thailand (Patanakamjorn, 1975). The larvae feed on all parts of the plant, especially ears and stalk (Nafus and Schreiner, 2008). Serious damage occurs when corn stalks are heavily infested by this species causing many stems break from larval burrowing.



Figure 30. Adult female of *H. magnanima*



Figure 31. Adult female of *O. furnacalis*

Egg masses, which averaged 21 eggs per egg mass (Areekul et al., 1964), are found on the under surface of the corn leaves, while the neonates, after hatching, normally stay on the upper surface of leaves that is not far away from the sites of hatched eggs (Patanakamjorn, 1975). Neonates of *O. furnacalis* feed on rolled leaves of corn. The damaged size that caused by this species gradually increase as the larval growth. Third instar larvae finally tunneled into the stalk through corn sheaths and continued to feed inside until they are full-grown (5th instar larvae) and pupate close to their feeding sites (Areekul et al., 1964).

2. Insect rearing

In this laboratory, the colony of Asian corn borer, *O. furnacalis*, was obtained from Japan Plant Protection Association Ibaraki Research Institute (Uchiku, Ibaraki, Japan) and reared on an artificial diet (Silk Mate 2M, Nosan Corporation, Yokohama, Japan) in an air condition-room at $25 \pm 1^\circ\text{C}$ and $60\% \pm 20\%$ RH of a 16L:8D photoperiod. This species were sexed from the pupal stage and separately reared until adult emergence. Male and female moths *O. furnacalis* were kept in a cylinder chamber (13 cm in diameter, 33 cm long) that was covered inner side with wax paper for oviposition and 10% sugar solution was also put in the chamber as a food source of moths.

General Discussion

Many concepts of host-plant selection indicate factors that affect oviposition of herbivorous insects (e.g. Bernays and Chapman, 1994; Finch and Collier, 2000; Jaenike, 1978; Mayhew, 1997; Thompson, 1988). Diurnal insects such as butterflies generally rely on visual cues with shape, size and color of plants to locating host plants for oviposition from the long distance (Honda, 1995; Rausher, 1978; Rausher and Papaj, 1983; Vasconcellos-Neto and Monteiro, 1993; Wiklund, 1984), while moths use odor cues under low light during scotophase to find appropriate host plants (De Moraes et al., 2001; Gupta and Thorsteinsons, 1960; Späthe, 1981; Thöming and Norli, 2015).

Naturally, the oviposition step of herbivorous insects in Lepidoptera is crucial because the neonates in some species are often immobile, so that the fate of them depends on maternal insects making a proper choice of plants as food resources (Renwick and Chew, 1994). An error in oviposition is one of the mortality factors of larvae hatching from the eggs laid on unsuitable host plants (Zalucki et al., 2002). Adult females normally lay eggs where their offspring can survive and develop best (Jaenike, 1978; Schoonhoven et al., 2005; Videla et al., 2012), as in the term “mother knows best” (Valladares and Lawton 1991), whereas females with non-adaptive behaviors choosing inappropriate host plants resulting in a suboptimal environment for offspring development is referred to “bad motherhood” (Mayhew, 2001; Scheirs et al., 2000).

However, some species in lepidopteran families have shown that the young larvae can disperse and locate on a new suitable host by spinning silk and ballooning passively downwind (Moore and Hanks, 2004). Therefore, the survival of these larvae may depend on not only oviposition decision of maternal insects, but also the offspring locomotory abilities as similar to the oviposition-feeding preference of *A. honmai*.

Adoxophyes honmai moths prefer to oviposit on old leaves, whereas their offspring preferred feeding on young leaves (Fig. 44). Therefore, neonates, which show high locomotory abilities, rapidly move up to the top of tea plants and start feeding soft leaf tissues. In addition, there are many new shoots located between leaves and stalk of tea plants, some of neonates chooses to enter and feed inside those shoots. From this physiology of tea plants and feeding preference of *A. honmai* neonates, it may be one reason why the damages caused by this species widely spread in tea bushes not only on the top of the branch. Although old leaves are difficult to feed by young larvae by resulted in the slow growth rate, it does not cause the high impact on the offspring survival and larvae can develop to pupal stage as same as the development of larvae that feed on young leaves.

Not only host insects such as butterflies and moths utilize both visual and chemical cues to locate the suitable host plants, but parasitoids also use them to find their host insects (Gupta and Thorsteinsons, 1960; Honda, 1995; Morehead and Feener, 2000; Späthe, 1981). The visual cues are usually used by insects from the short or long distances, whereas chemical cues play the major role after insect landing (Berneys and Chapman, 1994; Morehead and Feener, 2000; Renwick and Chew, 1994). Paré and Tumlinson (1999) suggested that female parasitoids, especially larval parasitoids that prefer parasitizing on young larvae, may face with the task if they rely only on visual cues to find their hosts. Normally, the young larvae prefer to stay on the hidden places difficult to detect by their eyes from the long distance. Therefore, the chemical cues from damaged plants may increase the chances of parasitoids to encounter hosts in tritrophic system.

In the case of egg-larval parasitoid *A. reticulata*, it is difficult to find host egg masses by visual cues of parasitoid because *A. honmai* prefer to oviposit on the under

surface of tea leaves. This parasitoid species may mainly rely on the chemical cues from tea plant. Although, this species cannot utilize the volatiles produced by egg-laden leaves (Deshpande and Kainoh, 2012), it is possible that female wasps can find their host eggs based on their performance to discriminate the volatiles from different ages of leaves (Fig. 44). From a small scale of my experiments in this laboratory, these wasps may use the volatiles from old leaves to locate landing sites on tea plants. After that, wasps may easily receive cues from egg-laden or intact leaf surface after they alight on the upper surface of old leaves and then continue finding host eggs for their progeny.

Finally, I conclude that cues that are produced from tea plant are; (1) essential for host insect *A. honmai* adults to find suitable habitats for their offspring by using plant volatiles and (2) important cues for parasitoids to locate hosts from the long distance by old leaf volatiles and after landing on the plant by cues from leaf surface that are induced by egg deposition of *A. honmai*.

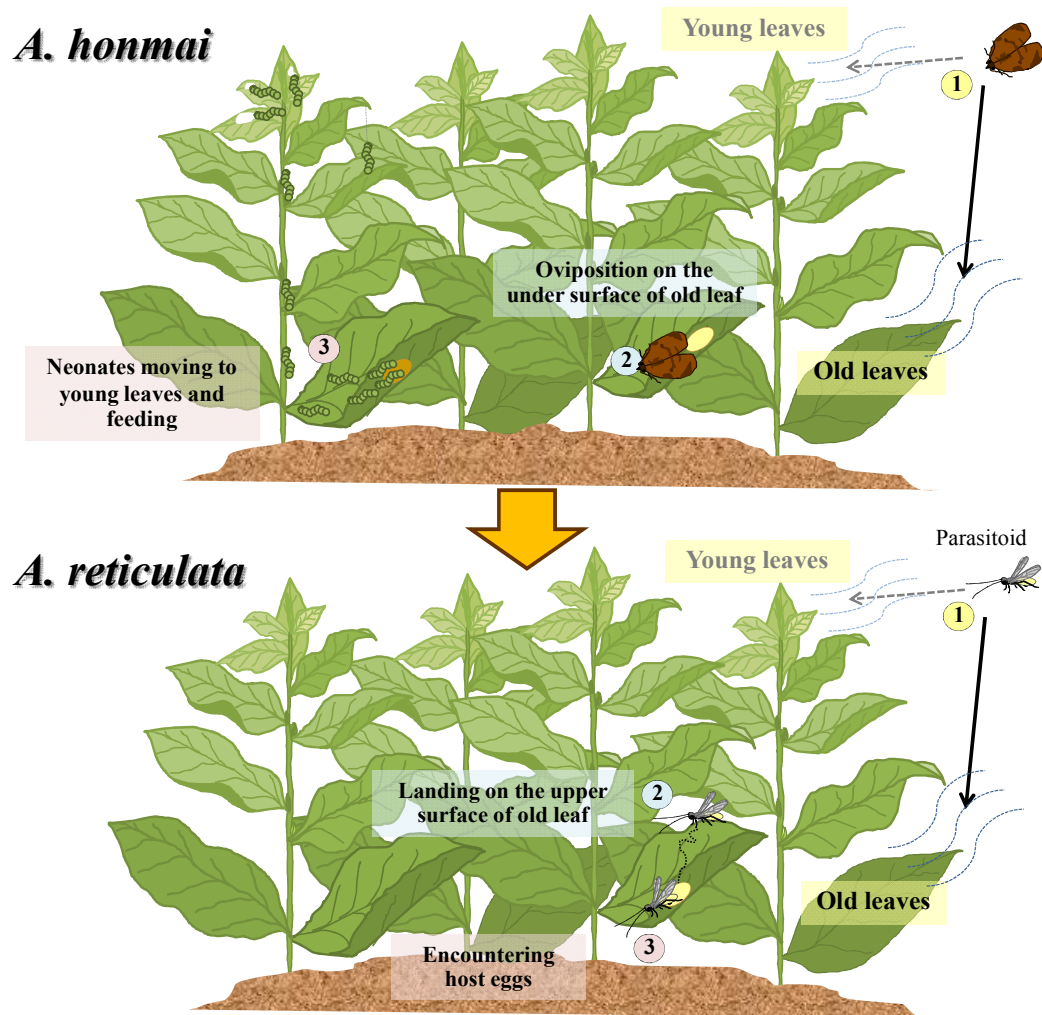


Figure 44. Summary of the studies

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