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Oviposition of the Seed Parasitoid Wasp *Macrodasyceras hirsutum* (Hymenoptera: Torymidae) into Seeds of Nonhost Tree *Ilex latifolia*

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ABSTRACT

Both optimality and physiological state models of oviposition behaviour explain a correlation between host plant appearance and host selection in oligophagous insects. To determine whether monophagous herbivores specialising in a single host species exhibit such correlation, 31 females of the seed parasitoid wasp, *Macrodasyceras hirsutum* Kamijo, whose only host plant is *Ilex integra* Thunb., were released into an enclosed bag containing berries of the nonhost plant, *I. latifolia* Thunb., in late May. Dissection of the 45 berries in August revealed that only one endocarp contained a similar-sized larva to the final instar larvae in *I. integra* seeds. This study indicates that the lack of only one host plant species forces *M. hirsutum* to oviposit into seeds of the nonhost plant, *I. latifolia*, and that a hatching larva develops in an *I. latifolia* seed.

Key words: Host plant, host plant appearance, host selection, *Ilex integra*, plant-herbivore interactions, preference-performance hypothesis.

INTRODUCTION

Host range of phytophagous insects is determined by female oviposition selection among plants and larval performance on the plants. The two traits of insects are affected by environmental conditions such as host plant appearance, toxic substances of host plant, natural enemies, interspecific competition and so on (Jaenike, 1990; Thompson and Pellmyr, 1991; Zangerl *et al*., 2002; Pureswaran and Poland, 2009; Zvereva *et al*., 2010). Both optimality and physiological state models of oviposition behaviour predict that females should be more willing to accept low ranking hosts as current egg load or search time for an oviposition site increases (Jaenike, 1990). The prediction has been confirmed for many oligophagous insects and explains a correlation between host plant appearance and host selection (Thompson, 1988; Jaenike, 1990); however, little is known about a correlation between host plant appearance and host selection by the specialised phytophagous insects.

The seed parasitoid wasp, *Macrodasyceras hirsutum* Kamijo, infests only the fertilised seeds of *Ilex integra* Thunb. and has never been known to infest other plants (Kamijo, 1981; Takagi *et al*., 2010). To determine whether the specialised herbivores exhibit the correlation between host plant appearance and host selection, we investigated the oviposition of *M*. *hirsutum* females into the seeds of the nonhost plant *I*. *latifolia* Thunb., the closely related species to *I*. *integra*, when being deprived of *I*. *integra* seeds. Our objectives were to determine (1) whether *M*. *hirsutum* laid the eggs into the seeds of *I*. *latifolia* in the absence of *I*. *integra* berries and (2) whether *M*. *hirsutum* larvae could develop on the seeds of *I*. *latifolia*.

MATERIALS AND METHODS

Study species

The wasp *M*. *hirsutum* is the specialised seed parasitoid of *I*. *integra*. The larvae eat only the seeds of *I*. *integra* and never damage the berry flesh (Kamijo, 1981). The adults appear twice a year. On emergence, the overwintering generation selectively lays one to five eggs in fertilised seeds from late May through mid-June (Takagi *et al*., 2010). Only one larva develops in each seed. Some of the first-generation larvae (0%–62.5%) develop into adults in August, and the adult females lay the eggs in uninfested developing seeds. Both remaining first- and second-generation larvae overwinter in seeds within berries attached to twigs (Takagi *et al*., 2010). They emerge as an adult between May and June.

The host plant *Ilex integra* and the closely related species *I*. *latifolia* are dioecious, bird-dispersed, broad-leaved evergreen tree species. Both tree species are sympatrically distributed in East Asia (Miyawaki *et al*., 1983; Katsuta *et al*., 1998). They have a similar phenology in anthesis and fruit development. The formation of flower buds is completed at the leaf axils of the current-year twigs by autumn (personal observation by E. Takagi). Flowers emerge from the buds from late March to mid-April in the following year (Katsuta *et al*., 1998). The pistillate flowers of the both species are characterised by four dysfunctional, small stamens and one large superior ovary having four cavities, each of which contains one ovule and is enclosed with endocarp (Katsuta *et al*., 1998). Immediately after flowering in spring, the ovaries of pistillate flowers start to develop into a spherical berry irrespective of pollination (Takagi *et al*., 2010). Individual *I*. *integra* and *I*. *latifolia* trees show marked, yearly fluctuations in berry production (Katsuta *et al*., 1998). In addition, *I*. *integra* changes the sex and the timing of sex change is synchronous in an individual tree (Takagi and Togashi, 2012), whereas the sex change is unknown in *I*. *latifolia*.

Field experiment

An *I*. *latifolia* tree used in the study was on the campus of the University of Tokyo at Hongo, Tokyo, Japan. On 21 May 2011, two branches were enclosed in two different bags made of polyester gauze (Toray tetoron® Honey queen #9000; Toray Industries Inc. Tokyo, Japan) to isolate the berries from the wild wasp population.

To obtain *M*. *hirsutum* adults, the berries were collected from an *I*. *integra* tree in the Hongo campus on 16 May 2011 and kept at 25 °C under a constant photoperiodic regime of 16:8 h photophase:scotophase. Emerging females were placed singly in Petri dishes in 5 cm diameter and paired with a male for 24 h. The females were observed to copulate with the males soon after being paired.

A total of 31 mated females were introduced into a bag during a period between 21 and 24 May 2011; 6, 13, 4 and 8 females were placed in the bag on 21, 22, 23 and 24 May 2011, respectively. On 15 August 2011, two twigs with berries were harvested from the bag and kept at 5 °C in the dark. All 45 berries were dissected under a microscope to record the presence or absence of endosperm, the degree of endosperm development (well-developed, poorly developed, and unfertilised seeds), and the presence or absence of the wasp in each endocarp. Dissection was completed on 22 August 2011.

To confirm that berries were enclosed before the flight season of *M. hirsutum*, 55 berries were randomly collected from the other bag without introduced wasps on 2 September 2011 and then dissected. In addition, the emergence of *M. hirsutum* females was investigated on the campus daily between 13 May and 22 May 2011. We also investigated the emergence of wasp adults from berries on the specified *I. integra* tree during May and June in 2012 in order to make it clear whether or not the *M. hirsutum* population used in this experiment changed the host plants.

RESULTS AND DISCUSSION

Dissection of 45 *I. latifolia* berries enclosed together with *M. hirsutum* wasps revealed that 180 endocarps contained 30 well-developed seeds, two poorly developed seeds, 147 unfertilised seeds and a single *M. hirsutum* larva, indicating that *M. hirsutum* females oviposited into the seed of *I. latifolia* under the enclosed condition. The *M. hirsutum* larva within the *I. latifolia* seed was similar-sized to the final instar larvae in *I. integra* seeds. Neither eggs nor dead larvae were found. On the other hand, dissection of 55 berries without released wasps revealed that 220 endocarps contained 57 well-developed seeds, 163 unfertilised seeds and the lack of wasp eggs and larvae, indicating that the berries were enclosed before the wasp flight season. Actually, *M. hirsutum* females did not appear before 22 May 2011 at the study site.

In 2012, the following year of experiment, abundant *M. hirsutum* adults were found on berries and leaves of the *I. integra* tree where experimental wasps had been obtained, indicating no host-plant alteration by the wasp population.

Oligophagous insect herbivores sometimes oviposit on plants of nonhost species which are phylogenetically related to their normal hosts, when their hosts are absent or much less abundant (Zhou and Togashi, 2006; Ernst *et al*., 2007; Azerefegne and Solbreck, 2010). The present study shows the oviposition by an *M. hirsutum* population into seeds of a specified tree of nonhost *I. latifolia*. Thus, more researches are necessary to determine within-population and between-population variations in the ability of *M. hirsutum* to use *I. latifolia* as a new oviposition resource. Our study, however, suggests that even specialised phytophagous insects oviposit on the closely-related, nonhost plant species when being derived of the normal host.

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