J. Entomol. Res. Soc., 23(1): 01-10, 2021
Doi: 10.51963/jers.v23i1.1846

Research Article
Online ISSN:2651-3579

Host Range Expansion by the Invasive Herbivore *Corythucha marmorata* (Uhler, 1878) is not Caused by Better Quality of New Hosts

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ABSTRACT

Phytophagous insects may become serious pests of crops when introduced into a new place. Better nutritional quality and lower toxicity of new host plants and escape from natural enemies can enhance survival. The chrysanthemum lace bug, *Corythucha marmorata* (Hemiptera: Tingidae), is native to North America, where it exploits mainly goldenrod and its relatives (Asteraceae). It was accidentally introduced into Japan by about 2000. Since then, many reports of injury to sweet potato (Convolvulaceae) and eggplant (Solanaceae) by this species have been published. Here, we tested larval performance on goldenrod, sweet potato, eggplant, and three other known or potential host plants to investigate why the lace bug began to exploit the new host plants. Survival to adult stage was nil on eggplant, extremely low on blue daze (Convolvulaceae) and crown daisy (Asteraceae), moderate on sweet potato, and ca. 80% on goldenrod and sunflower. Developmental time was shorter and adults grew larger on goldenrod and sunflower than on the other plants. These results show that plant nutritional or toxicological qualities are not major factors that facilitate host range expansion of *C. marmorata* in Japan. Possible factors are discussed.

Key words: Tingidae, Asteraceae, Convolvulaceae, specialist herbivore, larval performance, development, survival, biological invasion

Hasegawa, S. & Tsukada, M. (2021). Host range expansion by the invasive herbivore *Corythucha marmorata* (Uhler, 1878) is not caused by the better quality of new hosts. *Journal of the Entomological Research Society*, 23(1), 01-10.

INTRODUCTION

The invasion of insect pests can cause ecological and economic problems (Sydnor, Bumgardner, & Todd, 2007; Basavaraju, Chakravarthy, Doddabasappa, Nagachaitanya, & Yathish, 2010; Gandhi & Herms, 2010). Phytophagous insects may become serious pests of crops even if they are not problematic in their original range. Explanations include escape from natural enemies and from plant resistance. Host shift or host range expansion in new areas also may make them pests (e.g., Bowers, Stamp, & Collinge, 1992; Louda, Kendall, Connor, & Simberloff, 1998; Fukano & Doi, 2013; Davis & Cipollini, 2014).

Most phytophagous insects have limited host range (Bernays & Graham, 1988; Schoonhoven, Van Loon, & Dicke, 2005). Traditionally, insect species that exploit only one plant species, or several species within a genus are called monophagous, while species that exploit several plant species among different genera within a family are called oligophagous, and species that exploit plant species of more than one families are called polyphagous (Bernays & Chapman, 1994), although the trait is not stable (Bernays & Graham, 1988). Host shift and host range expansion by various insects are frequently reported (Tuda et al, 2009; Kohyama, Matsumoto, & Katakura, 2012). Insects introduced for biological control have become pests of non-target native plants (Howarth, 1991; Pemberton, 2000), in most cases adopting new host plants closely related to their original hosts within the same family (Wheeler, 1987; Louda et al.,1997; Pemberton, 2000).

The chrysanthemum lace bug, *Corythucha marmorata* (Hemiptera: Tingidae), is native to North America and is a specialist (mono- or oligophagous species) of asteraceous plants, such as goldenrod (*Solidago altissima*) and sunflower (*Helianthus annuus*). It is the most abundant herbivore on *Solidago* species and several other asteraceous plants, such as *Ambrosia*, *Chrysanthemum*, and *Xanthium* (Wheeler, 1987; Fontes, Habeck, & Slansky Jr., 1994; Kato & Ohbayashi, 2009). It causes chlorosis typical of injury by lace bugs (Root, 1996; Cappuccino, 2000), which suggests that it feeds on leaf cellular materials by sucking (Ishihara & Kawai, 1981). Injury occasionally leads to plant death (Miyatake, 2005).

The North American *S. altissima* was introduced into Japan around 1900 as an ornamental plant (Nakagawa & Enomoto, 1975). It escaped from gardens, spread naturally after World War II (Nakagawa & Enomoto, 1975) and is now a common weed throughout Japan.

In 2000, *C. marmorata* was first reported in Nishinomiya City, Hyogo Prefecture, western Japan, and its geographic range has since expanded rapidly (Tomokuni, 2002; Kato & Ohbayashi, 2009; Hoshino, 2011). Although there is only one report that it utilizes plants other than asteraceous plants in its native range (Wheeler, 1987), in Japan it utilizes non-asteraceous plants such as sweet potato (*Ipomoea batatas*, Convolvulaceae; e.g., Shiga Pest Control Center, 2005; Aichi Prefecture, 2005; Gifu Plant Protection Center, 2005), blue daze (*Evolvulus pilosus*, Convolvulaceae; e.g., Nara Plant Protection Center, 2005; Okayama Plant Protection Center, 2005; Kagawa

Plant Protection Office, 2005), and eggplant (*Solanum melongena*, Solanaceae; e.g., Gifu Plant Protection Center, 2005; Kagawa Plant Protection Office, 2005; Kochi Prefecture Crop Pest Control Center, 2005) as food and oviposition substrate. It can be inferred that *C. marmorata* has expanded its host range to novel plants. This is unusual in that these new hosts belong to different families from that of the original host species.

The central question in insect-plant relationships is what is the key factor which determines the host range of an herbivore. *Corythucha marmorata* may give a clue. The most plausible scenario is that *C. marmorata* enjoys higher larval performance on these new host plants. Here, to examine this hypothesis, we evaluated the quality of novel and original host plants as food for *C. marmorata* in terms of larval performance. In addition to the five species named above, we tested crown daisy (*Glebionis coronaria*, Asteraceae), which is an important vegetable crop in Japan.

MATERIALS AND METHODS

Materials

We collected *C. marmorata* individuals from wild goldenrod growing on the campus of Mie University (Tsu City, Mie Prefecture, Japan) from April 2012 to November 2014. To conduct the experiments with insects as close to wild as possible, we used only descendants two generations after these collected individuals, and therefore made several collections.

We tested goldenrod, eggplant (*cv.* Senryo No. 2), sweet potato (*cv.* Beniazuma), blue daze, sunflower, and crown daisy as food for the lace bug. The goldenrod leaves were collected on campus. The other plants were bought as seeds or seedlings at a DIY store in Tsu City. The plants were grown in pots filled with a ca. 2:1 mixture of *akadama* (granular loam) and leaf litter.

Methods

Adults collected in the field were allowed to reproduce in the laboratory. Larvae were reared to adults in an environmental chamber (25 °C, 16L:8D) on leaves of goldenrod. About six adults (both male and female) were kept in a plastic cup (A-PET, 200 ml, ø 101 mm × 44 mm) with two leaves of goldenrod in the same environmental chamber as before. Each leaf stalk was covered with a piece of sterile cotton soaked with tap water. Any leaf on which eggs were laid was replaced with a new leaf, and was transferred to another plastic cup. Each hatched larva was put individually into a plastic cup and reared on a leaf of one of the six plants in the chamber. All leaves were kept fresh with wet cotton on the stalk, and were checked daily and replaced as necessary. When an individual died, the instar was recorded. As do other lace bugs, this species passes through five larval stages until eclosion. Sex, head width, and body length of adults were recorded. Head width and body length were measured in ImageJ software in photographs taken under a digital microscope (Keyence VH-5000 equipped with a VH-Z25 zoom lens) connected to a PC.

All statistical analyses were performed in R v. 3.5.0 software (R Core Team, 2018). Pairs of survival rate curves were compared by log-rank test. The results were corrected by Bonferroni's method for multiple comparisons. To examine whether developmental time, head width, or body length differed among host plants, we fitted generalized linear models (GLMs) with those as the response variables and plant species as the explanatory variable. Multiple comparisons were conducted using the Tukey–Kramer method. All GLMs had a Gaussian distribution (We show only the result of multiple comparison tests).

RESULTS

Larvae reared on goldenrod and sunflower attained significantly higher survival rates than those reared on the other plants (Log Rank Test with Bonferroni correction, $P < 0.01$; Fig. 1). Larvae reared on sweet potato attained a significantly higher survival rate than those reared on blue daze, eggplant, and crown daisy (Log Rank Test with Bonferroni correction, $P < 0.01$). No larvae grew to adult stage on eggplant, and only 2 adults emerged on crown daisy. Larval mortality was extremely high on eggplant (100%), blue daze (89.6%), and crown daisy (96.7%), especially during the first instar (Fig. 1). Larval mortality was higher during the first instar than during the later stages on sweet potato.

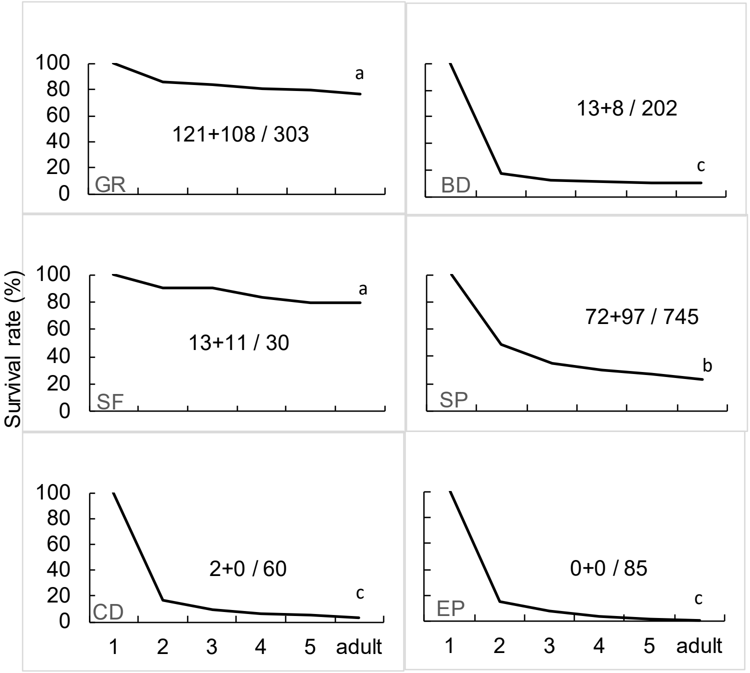

Fig. 1. Larval survival rate by stage on goldenrod (GR), sunflower (SF), crown daisy (CD), blue daze (BD), sweet potato (SP), and eggplant (EP). Survival curves labelled on the right with the same letter are not significantly different (log-rank test with Bonferroni's correction, $P < 0.01$). Equations show

number of emerged females + males over initial number of first instar larvae.

Larvae reared on goldenrod and sunflower had significantly shorter developmental times (both female and male) than those reared on the other plants (Tukey-Kramer multiple comparison test, $P < 0.05$; Fig. 2). There were no significant differences in developmental time among the novel hosts.

Both females and males reared on goldenrod and sunflower had significantly larger head width and body length than those reared on blue daze and sweet potato (Tukey-Kramer multiple comparison test, $P < 0.05$; Figs. 3, 4). Adults reared on sweet potato had no significant differences in head width or body length from those reared on blue daze. Females tended to be larger than males.

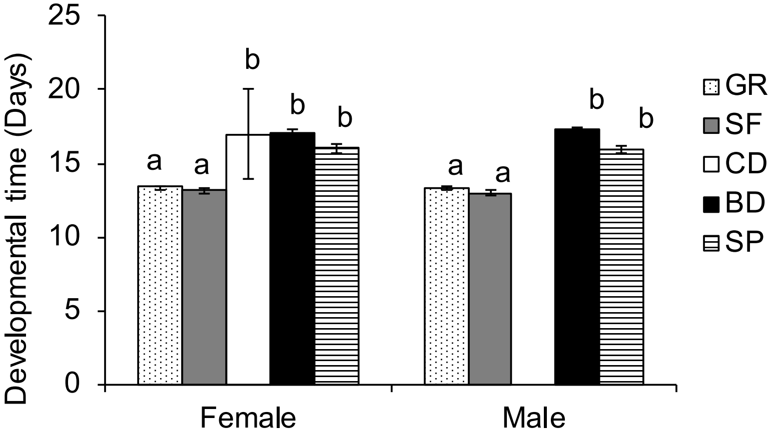

Fig. 2. Developmental time (days, mean ± SE) of females and males. Bars with the same letter are not significantly different within each sex. See Fig. 1 for plant name codes.

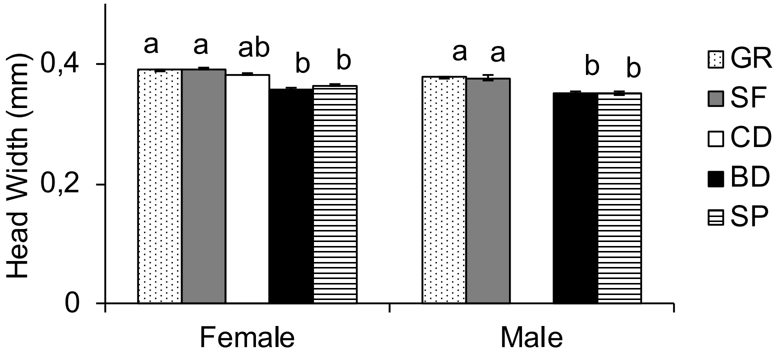

Fig. 3. Head width (mm, mean ± SE) of female and male adults. Bars with the same letter are not significantly different within each sex. See Fig. 1 for plant name codes.

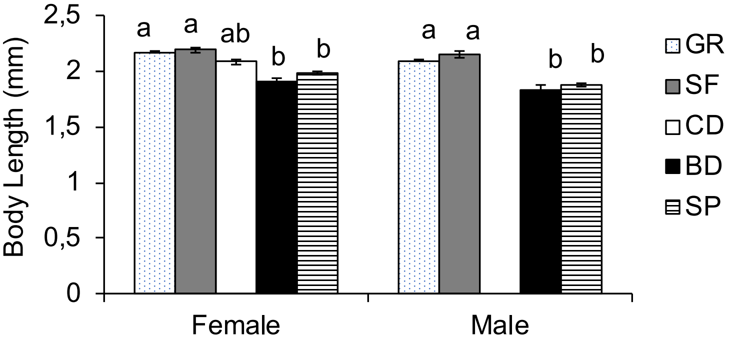

Fig. 4. Body length (mm, mean ± SE) of female and male adults. Bars with the same letter are not significantly different within each sex. See Fig. 1 for plant name codes.

DISCUSSION

As previously reported (e.g., Nara Plant Protection Center, 2005, Chiba Prefecture Agriculture and Forestry Research Center, 2011), *C. marmorata* fed on and grew to adult on sweet potato and blue daze (Convolvulaceae), but not as well as on goldenrod and sunflower. Furthermore, they did not grow to adult on eggplant, even though many records report injury to eggplant by *C. marmorata* (e.g., Gifu Plant Protection Center, 2005; Kagawa Plant Protection Office, 2005; Kochi Prefecture Crop Pest Control Center, 2005). Thus, what has driven the host range expansion is not better larval performance on (intact leaves of) the new hosts. Therefore, our hypothesis that *C. marmorata* expanded its host range to convolvulaceous plants because the plant quality is higher than the original host is not accepted.

On the two convolvulaceous plants, most larvae died during early development, especially in the first instar. However, most of those that passed through this stage survived. Therefore, most of the larvae might not have recognized these plants as food and starved to death. On the other hand, most of the individuals that recognized a plant as food were able to feed and develop on it, though some might be killed by poor nutrition. Herbivorous insects distinguish their hosts mainly by chemical compounds (Ehrlich & Raven, 1964; Futuyama & Agrawal, 2009). The azalea lace bug *Stephanitis pyrioides* (Hemiptera: Tingidae) distinguishes azalea varieties by leaf surface lipids (Balsdon, Espelie, & Braman, 1995). The Convolvulaceae are only distantly related to the Asteraceae (Angiosperm Phylogeny Group, 2009), and so their chemical components would be different. However, as some individuals fed on them, some of the chemicals could be similar to those of the original hosts. Such similarity might accelerate host range expansion to different families from the original hosts (Tuda et al, 2014).

Some previous studies have reported low larval performance in some phytophagous insects on novel host plants due to physiological non-adaptation (Bowers et al, 1992;

Keeler & Chew, 2008; Dai, Lu, Zhang, & Ding, 2014), whereas others suggested that pre-adaptation can contribute to similar performance as on the original hosts (Fox & Caldwell, 1994; Leclaire & Brandl, 1994; Newman, Borman, & Castro, 1997). Here, we found higher survival rate, shorter developmental time, and larger head width and body length on goldenrod and sunflower than on the novel plants. Even though the adults reared on novel hosts recognized the plant as food, the shorter developmental time and larger sizes show that the original hosts are more suitable than the other four species for the development of *C. marmorata*. Thus, *C. marmorata* has not yet adapted to the novel hosts.

Many studies, including ours, show that the suitability of novel plants for development may be not critical in host range expansion (e.g., Dai et al, 2014). One factors that is more important for range expansion would be high oviposition preference for novel plants. Adult females of some species lay eggs even on plants on which their offspring perform poorly (Gratton & Welter, 1998; Thompson, 1988b), as *C. marmorata* does. Yet even if the offspring performance is low, if some grow to the adult stage, those female adults may prefer their natal host plant (Hopkins' host selection principle). Therefore, such apparent mistakes in oviposition can be the first step toward a host shift (Thompson, 1988a; Thompson & Pellmyr, 1991; Davis & Cipollini, 2014). Even if most of the offspring on a novel plant die, even limited success may make the mother's oviposition on it adaptive.

Despite the many reports of injury by *C. marmorata* on eggplant, larvae did not complete their development to adult stage. This suggests that female adults cannot assess the unsuitability of eggplant for the larvae correctly in the field, and the injury found was mostly made by adults because the larvae would die soon after egg hatch. If this was the case, addition of eggplant to the host plants of *C. marmorata* would not occur in near future.

The sunflower and crown daisy belong to the same family as the goldenrod, Asteraceae. On sunflower, the survival rate was mostly the same as that on goldenrod. On the other hand, only two male adults were obtained from 60 larvae on crown daisy. As Asteraceae is a large family with large phylogenetic diversity (Mandel et al, 2019), it is not surprising that only a part of this family is suitable as the host of *C. marmorata*.

We used leaves with no or very low damage of sap feeding by *C. marmorata* for the experiment. This might have led our conclusion differently from what is occurring in nature, as injury level become high in summer and autumn, when the population density become high (Kato & Ohbayashi, 2009). When relative quality of the goldenrod become lower than the other plants, females may choose novel plants such as sweet potato. Investigation on larval performance on damaged leaves would be required.

Although *C. marmorata* is considered a specialist herbivore of several asteraceous plants, it has expanded its host range to distantly related plants in its introduced range. Many insects have been introduced as biological control agents all over the world (Howarth, 1991; Pemberton, 2000). Our results suggest that invasive species can have an unpredictable impact on native environments. When non-native organisms are introduced as biological control agents, circumspect research about the agent ecology is necessary before introduction.

ACKNOWLEDGEMENT

We thank Dr. T. Tsuchiya of the Organization for the Promotion of Regional Innovation of Mie University for helpful discussion on sweet potato varieties. We thank the editor and two anonymous reviewers for their positive comments, which improved the manuscript greatly.

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Received: January 10, 2020 *Accepted: February 12, 2021*