



# Evaluation of plant quality by *Corythucha marmorata* (Hemiptera: Tingidae) mothers: relationship between oviposition preference and nymphal performance on four sweet potato cultivars and goldenrod

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## Abstract

In novel plant–insect relationships, oviposition preference and nymphal performance determine host range evolution. *Corythucha marmorata*, native to North America and specialist on asteraceous plants, has been reported to exploit sweet potato (Convolvulaceae) in Japan. Here we examined the capability of females to oviposit and of nymphs to grow on both a conventional host (goldenrod, *Solidago altissima*) and novel hosts (four sweet potato cultivars), of which the test insects had virtually no experience of contact at the population level. We then tested whether female preference and offspring performance were correlated. Nymphal survival and development time were always significantly greater on goldenrod, followed by sweet potato cultivars Caroline Lea, Benisengan, Narutokintoki, and Beniazuma in that order. Female oviposition preferences showed a similar order. On higher-ranked plants, the females accepted the plant faster and had higher fecundity. When goldenrod was included in the analysis, nymphal development time and survival rate were significantly related to preoviposition period. When goldenrod was excluded, nymphal survival rate was still significantly related to preoviposition period. These results support the theory that females lay their eggs on the most suitable host to maximize offspring fitness, even though *C. marmorata* had no experience with sweet potato cultivars. As *C. marmorata* is a hemimetabolous insect, in which adults and nymphs have a similar feeding habit and exploit the same habitat, this relationship seems plausible.

**Keywords** Plant–insect relationship · Nymphal survival · Development time · Tingidae · Chrysanthemum lace bug

## Introduction

In novel interactions between herbivorous insects and new host plants, both oviposition preference and offspring performance are important, as they determine the evolution of the host range and host–plant utilization (Thompson 1988; Pearse 2011). Plant choice by adult females can greatly influence offspring survivorship (Shikano et al. 2010) as the offspring need to eat as soon as possible after hatching and usually cannot move far to another host plant. Therefore, mothers are expected to lay their eggs on the most

suitable host to maximize offspring fitness (Jaenike 1978). However, the degree of correlation is still unclear. Some studies of oviposition preference and nymphal performance showed no relationship or even a negative one (Gratton and Welter 1998; Keeler and Chew 2008; Forister et al. 2009), whereas others showed a strong positive relationship (Craig and Ohgushi 2002; Karungi et al. 2010; Zhang et al. 2012; Geng et al. 2012; Dong et al. 2013). Thus, the results may vary among species, and many factors might affect the plant–insect relationship.

These previous studies dealt with herbivorous insects and their conventional host plants, or newly acquired host plants following at least several generations of association. But at the beginning of a relationship between an insect and its potential host, a mother from a population with no prior experience of it needs to evaluate the plant before exploiting it. However, to our knowledge, no study has examined

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preference–performance between an insect and a truly novel plant.

The chrysanthemum lace bug, *Corythucha marmorata* (Heteroptera: Tingidae), is a North American species that feeds exclusively on asteraceous plants (Cartron et al. 2008; Kato and Ohbayashi 2009). Adults and nymphs were found for the first time in Japan in August 2000 feeding on goldenrod, *Solidago altissima*, in Nishinomiya, Hyogo (Kato and Ohbayashi 2009), since then the distribution has broadened rapidly (Kato and Ohbayashi 2009; Hoshino 2011; Ishikawa et al. 2015). They have since been found feeding on *Aster* spp. and *Helianthus* sp. in Shanghai, China, in 2010 (Dang et al. 2012) and in Pohang-si and Changwon-si, Korea, in 2011 (Yoon et al. 2013).

The host plants of *C. marmorata* include several genera of the Asteraceae: *Ambrosia*, *Aster*, *Chrysanthemum*, *Echinops*, *Helianthus*, *Rudbeckia*, *Solidago*, and *Tanacetum* (Drew and Arnold 1977; Tallamy and Denno 1981). Most of the plants in these genera in Japan are invasive species from North America (Ecological Society of Japan 2002). Among them, early successional composites such as *Solidago altissima*, *Ambrosia trifida*, *Artemisia princeps*, *Xanthium canadense*, *Ambrosia artemisiaefolia* and *Bidens pilosa* were found to be damaged by *C. marmorata* (Kato and Ohbayashi 2009). As in other lace bug species, feeding results in white spots on the upper side of leaves, and heavy infestation can cause early leaf drop (Mead 1989; Halbert and Meeker 2001; Ju et al. 2009; Kezik and Eroğlu 2014).

Besides asteraceous species, injuries to sweet potato (Convolvulaceae) have been reported in many prefectures in Japan (Kato and Ohbayashi 2009; Hoshino 2011). Oddly, except for one seemingly accidental example, which recorded the use of *Calystegia sepium* (Wheeler 1987), to our knowledge, there is no scientific or even anecdotal report that they feed on any convolvulaceous plants in their native range. The first record of the use of sweet potato in Japan dates to 2004 (Shiga Pest Control Center 2005). However, its abundance as a host plant is far lower than that of goldenrod, especially in urbanized areas. Therefore, *C. marmorata* individuals found on goldenrod are most likely to have no experience of feeding on sweet potato in urbanized area.

As in many hemimetabolous insects, adults and nymphs of *C. marmorata* feed on the same plant species. This means that mothers have an important role in evaluating plant quality for their offspring when they land on a plant and start feeding on it. If this is the case, then how efficiently mothers evaluate a plant by feeding directly is an interesting question, as although the insect has likely never experienced sweet potato, its choice still affects offspring fitness and consequently the expansion of host range to novel plant species.

Here we tested *C. marmorata* oviposition preference and nymphal performance to answer: (1) whether *C. marmorata* is able to feed or oviposit on sweet potato cultivars; (2) if so,

how nymphal performance or oviposition preference differs among test plants; and (3) whether oviposition preference is positively correlated with nymphal performance.

## Materials and methods

### Preparation of test plants

The sweet potato (*Ipomoea batatas* L.) is a dicotyledonous perennial plant that belongs to the family Convolvulaceae. It is widely cultivated throughout tropical and warm regions as it is one of the most important crops in the world (Woolfe 1992). We carried out our experiments on four cultivars of sweet potato, Beniazuma, Benisengan, Caroline Lea, and Narutokintoki. In terms of economic importance, Beniazuma and Narutokintoki are popular cultivars for food, but Caroline Lea and Benisengan are used mainly for livestock feed. From physical appearance, Beniazuma and Narutokintoki leaves have the widest area of leaves compared to Benisengan which has serrated edge and Caroline Lea which has smallest leaf area.

Goldenrod (*Solidago altissima* L.) is a weedy perennial herb that originally comes from North America (Sakata et al. 2015). Due to its fast-growing rhizome, strong roots and its ability to reproduce sexually and asexually, it has spread almost in all prefectures in Japan now (Sakata et al. 2015). This weed can be found in various habitats, for example around roadsides, along riverside banks, railways, poorly managed farm fields or even abandoned houses (Kato and Ohbayashi 2009). In blooming time, its nectar is favored by many wasps, honeybees, bumblebees, and butterflies. In North America, goldenrod is home to over 100 species of insect (Maddox and Root 1990).

We tested nymphal performance and oviposition preference on four cultivars of sweet potato (Beniazuma, Benisengan, Caroline Lea, Narutokintoki) and goldenrod as a control. Sweet potato plants were started from rhizome. Sweet potato rhizomes were placed in dark place to let new shoots grow. About 1–2 weeks newly grown shoots were taken and placed in water until enough roots appear. Before moving them into pots, leaves were checked under stereomicroscope to make sure that no bug infestation is seen. Shoots were planted in greenhouse of the Insect Ecology Laboratory (Tsu, Mie Prefecture, Japan) and watered every day. Sweet potato leaves were then taken for the experiments. Goldenrod leaves were collected from wild-growing plants near the greenhouse.

### Preparation of the insect

Adults of *C. marmorata* were collected from goldenrod on the campus of Mie University, Tsu, Japan (34°44'43.9008"

N; 136°31'19.599" E) and transferred to goldenrod leaves in plastic containers (A-PET material, 430 mL,  $\phi$  129 mm  $\times$  60 mm height), in which they were held in a climate chamber (Nihon Ika Kikai Co., Ltd) at 25 °C and 16L:8D. The stalk of each leaf was wrapped with wet cotton, and water was added every day to prevent the leaves from drying. Eggs laid were observed daily until the emergence of nymphs. The egg development time defined as days from oviposition to egg hatch was assigned to performance tests. For oviposition preference tests, leaves of goldenrod with eggs of *C. marmorata* were collected in the field, kept in the laboratory (25 °C; 16L:8D), and reared until adult eclosion. The emerged adults (0th generation) were then assigned to oviposition preference tests.

### Nymphal performance

Each newly hatched nymph was randomly selected and transferred to one of the test plants with a fine brush in the laboratory (25 °C; 16L:8D). As many as 107 trials on goldenrod, 102 trials on Caroline Lea, 109 trials on Benisengan, 103 trials on Narutokintoki, and 103 trials on Beniazuma were carried out. The nymphs were checked daily to record the nymphal development time defined as days from egg hatch to adult emergence. Totally 97 adults on goldenrod, 68 adults on Caroline Lea, 62 adults on Benisengan, 32 adults on Narutokintoki, and 2 adults on Beniazuma were obtained. When they reached adult stage, body size was measured and sex was recorded. Thus, the sex of nymphs was confirmed using the sex of the emerged adults. Body size was represented by body length (from the tip of the head to the end of the abdomen), head width (from the edge of one eye to that of the other), and the mean of the right and left forewing lengths (from the start of forewing diagonally to its end)

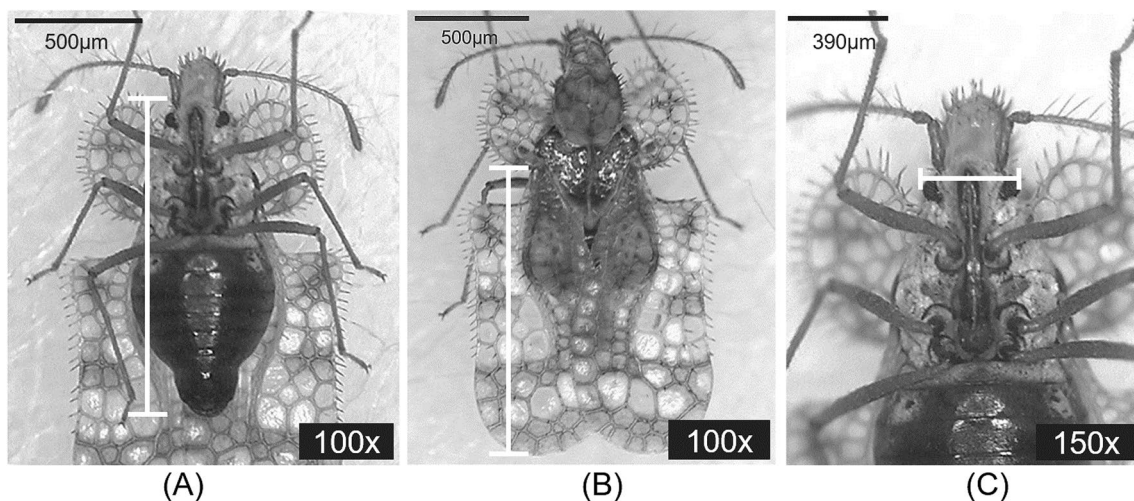
(Fig. 1). All specimens were photographed with a digital microscope (Keyence VH-5000) and measured in ImageJ v. 1.48 g software. Measured individuals were deposited as dry specimens in the Insect Ecology Laboratory, Graduate School of Bioresources, Mie University.

### Oviposition preference

To investigate oviposition preference on the four sweet potato cultivars, we carried out a no-choice preference test at 25 °C; 16L:8D of laboratory condition. After eclosion, the 0th generation individuals were separated into male and female groups and reared for a week on goldenrod leaves. A 1-week-old female and two males were then randomly chosen and put in a plastic container (A-PET material, 430 mL,  $\phi$  129 mm  $\times$  60 mm) with a leaf of one of the test plants. Sample sizes for each treatment were as follows: 31 groups on goldenrod, 31 groups on Caroline Lea, 30 groups on Benisengan, 32 groups on Narutokintoki, and 30 groups on Beniazuma. All containers were checked every day, and the number of eggs laid was recorded from day 1 until the last day of oviposition. Leaves were replaced once a week to prevent deterioration of the leaf from affecting results.

### Statistical analysis

All statistical analyses were performed in R Statistical Computing environment v. 3.4.3 (R Core Team 2018). Nymphal survival rate was expressed as Kaplan–Meier survival curves which were compared by log-rank test with Bonferroni's correction, as the number of combinations was more than two. Mixed-model ANOVAs for egg development time, nymphal development time, and body size indexes were used. In each ANOVA, test plants, sex, and their interaction were



**Fig. 1** Body size measurement of *Corythucha marmorata* adults: **a** body length, **b** wing length, **c** head width

used as explanatory variables. Individuals were assigned as a random factor. Means were compared by Tukey–Kramer multiple comparison test in the ‘multcomp’ package. However, owing to the high mortality and small sample size of individuals reared on Beniazuma, that mean was excluded from the test.

For oviposition preference experiments, preoviposition period (defined as the days from inoculation to the first oviposition) was analyzed using a mixed-model ANOVA, and fecundity was analyzed using a GLMM (‘lme4’ and ‘lmerTest’ package), with test plants as an explanatory variable and the effect of individuals as a random factor. Here, preoviposition period was analyzed for the individuals who laid at least one egg in their life, whereas fecundity was analyzed for all the individuals including those who did not lay eggs. Each combination of test plants was compared by Tukey–Kramer multiple comparison test using ‘multcomp’ package.

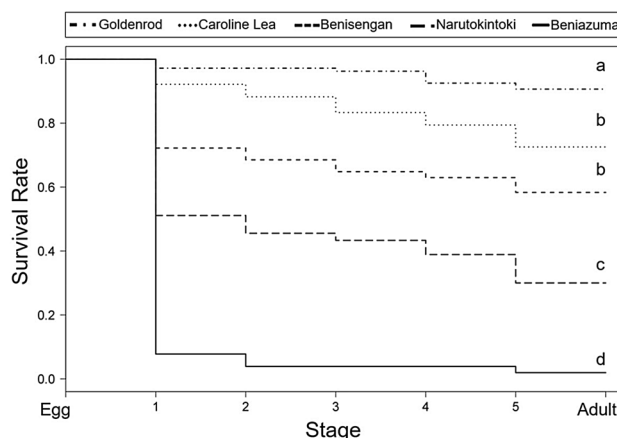
A GLM was used to reveal the relationship between adult preference and nymphal performance. Survival rate and mean of nymphal development time (sex was also incorporated here) were used as response variables, whereas both mean fecundity and mean preoviposition period were used as explanatory variables representing female adult preference.

## Results

### Nymphal performance

The survival curves of *C. marmorata* nymphs on test plants differed significantly among each combination of plants (log-rank test with Bonferroni correction,  $P < 0.01$ ), except for the combination of Caroline Lea and Benisengan. About 90% of nymphs on goldenrod survived from inoculation to emergence ( $n = 107$ ). Nymphal survival was moderately high on Caroline Lea (73%,  $n = 102$ ) and Benisengan (59%,  $n = 108$ ), moderate on Narutokintoki (30%,  $n = 103$ ), but very low on Beniazuma (2%,  $n = 103$ ). Survival curves dropped sharply after the first instar on Narutokintoki and Beniazuma (Fig. 2), but stabilized thereafter on all test plants.

The total development time from egg to adult eclosion ranged from 22 to 30 days. There was no significant difference among treatments in egg development time of either sex, as all were laid on goldenrod (Table 1;  $P = 0.30$  for sex,  $P = 0.52$  for plant,  $P = 0.60$  for interaction, ANOVA). However, nymphal development time was significantly shorter on goldenrod than on sweet potato (Table 1;  $P = 0.01$  for sex,  $P < 0.001$  for plant,  $P = 0.03$  for interaction, ANOVA), and was shorter on Caroline Lea than on Narutokintoki in females (Beniazuma was excluded from the statistical test due to small sample size). No difference of nymphal



**Fig. 2** Differences among Kaplan–Meier survival curves for nymphal survivorship on different test plants (log-rank test followed by Bonferroni correction,  $P < 0.01$ )

development time was found among sweet potato cultivars in males.

Both female and male adults reared on goldenrod were always significantly larger than those reared on sweet potato (Figs. 3, 4). Their body sizes varied but were not significantly different among sweet potato cultivars. ANOVA showed that sex and test plant had significant effects on all body size parameters, but there was no significant interaction (body length:  $P < 0.001$  for sex,  $P < 0.001$  for plant,  $P = 0.28$  for interaction; head width:  $P < 0.001$  for sex,  $P < 0.001$  for plant,  $P = 0.85$  for interaction; wing length:  $P < 0.001$  for sex,  $P < 0.001$  for plant,  $P = 0.15$  for interaction).

### Oviposition preference

Females never preferred any sweet potato cultivar to goldenrod (Table 2). They showed significantly shorter time to oviposition (2.26 days) and significantly higher fecundity (99.97 eggs) on goldenrod than on sweet potato (4.14 days and 55.39 eggs respectively for the most preferred cultivar, Caroline Lea) (Table 2). They preferred Caroline Lea to Benisengan and Narutokintoki, and were significantly slow to oviposit on Beniazuma (up to 9 days of post inoculation in average), on which they had a shorter lifespan (43% of them died even before laying eggs) and much lower fecundity (Table 2, Fig. 5). The mean fecundity was not different between Caroline Lea and Benisengan, and also between Narutokintoki and Beniazuma (Table 2). The age-specific survival on goldenrod, Caroline Lea and Benisengan dropped only slightly during the early days, indicating low mortality in these test plants (Fig. 5). Mortality in early days on Narutokintoki and Beniazuma was apparent. The age-specific fecundity on goldenrod was higher than those on any of sweet potato cultivars. The mean of net reproductive

**Table 1** Comparison of egg and nymphal development time of *C. marmorata* among test plants

Test plants	Egg development time (mean $\pm$ SD)				Nymphal development time (mean $\pm$ SD)			
	<i>n</i>	Females	<i>n</i>	Males	<i>n</i>	Females	<i>n</i>	Males
Goldenrod	44	11.18 $\pm$ 0.90 <sup>a</sup>	53	11.11 $\pm$ 0.78 <sup>a</sup>	44	12.32 $\pm$ 0.74 <sup>a</sup>	53	12.64 $\pm$ 1.13 <sup>a</sup>
Caroline Lea	35	11.26 $\pm$ 0.78 <sup>a</sup>	33	11.33 $\pm$ 0.60 <sup>a</sup>	35	13.60 $\pm$ 1.19 <sup>b</sup>	33	13.42 $\pm$ 1.30 <sup>b</sup>
Benisengan	32	11.13 $\pm$ 0.61 <sup>a</sup>	30	11.50 $\pm$ 0.82 <sup>a</sup>	32	14.03 $\pm$ 1.47 <sup>b,c</sup>	30	13.77 $\pm$ 1.30 <sup>b</sup>
Narutokintoki	19	11.37 $\pm$ 0.76 <sup>a</sup>	13	11.15 $\pm$ 0.55 <sup>a</sup>	19	14.53 $\pm$ 1.35 <sup>c</sup>	13	14.85 $\pm$ 1.99 <sup>b</sup>
Beniazuma	1	11	1	11	1	19	1	14

Means followed by the same letter are not significantly different (Tukey–Kramer multiple comparison test after mixed-model ANOVA,  $P < 0.05$ )

rate ( $R_0$ ) was highest on goldenrod (81.5), followed by Caroline Lea (40.8), Benisengan (33.2), Narutokintoki (23.2) and Beniazuma (11.4).

### Preference–performance relationship

The relationship between fecundity and nymphal survival on each plant was marginally significant (Table 3,  $P = 0.08$ ). There were significant (negative or positive) relations between preoviposition period and nymphal survival rate (Table 3,  $P = 0.01$ ), fecundity and nymphal development time (Table 3,  $P = 0.03$ ), and preoviposition period and nymphal development time (Table 3,  $P = 0.01$ ), suggesting that female adults prefer plants on which nymphs can grow better. When goldenrod was excluded from analyses, results were similar, although only preoviposition period and survival rate were significantly related (Table 4,  $P = 0.03$ ).

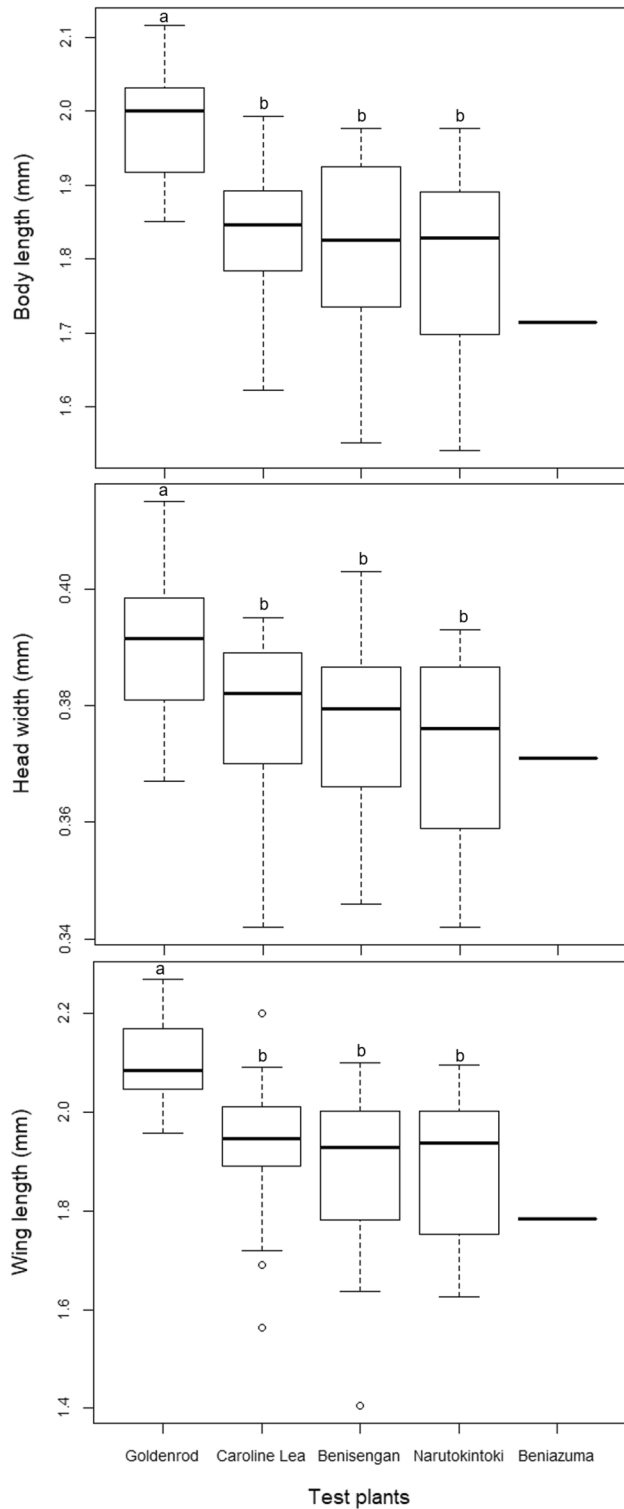
### Discussion

All performance indexes showed that nymphs developed best on goldenrod, followed by Caroline Lea, Benisengan and Narutokintoki, and Beniazuma. This is the first report that sweet potato cultivar can affect performance of *C. marmorata*. However, the strength of the effect differed among offspring traits. Survival rate was significantly and greatly different even among sweet potato cultivars (Fig. 2). Nymphal development time had significant difference between Caroline Lea and Narutokintoki in females (Table 1). On the other hand, body size was significantly and greatly different only between goldenrod and sweet potato (Figs. 3, 4). Among the sweet potato cultivars, we could not detect any significant difference in body size in either sex, but it tended to be smaller on plants on which mortality was higher. Therefore, the inferiority of some sweet potato cultivars appeared first in mortality. Among the survivors, the longer nymphal development time on the inferior cultivars probably compensated for plant quality, explaining why body size did not differ greatly among cultivars. This effect

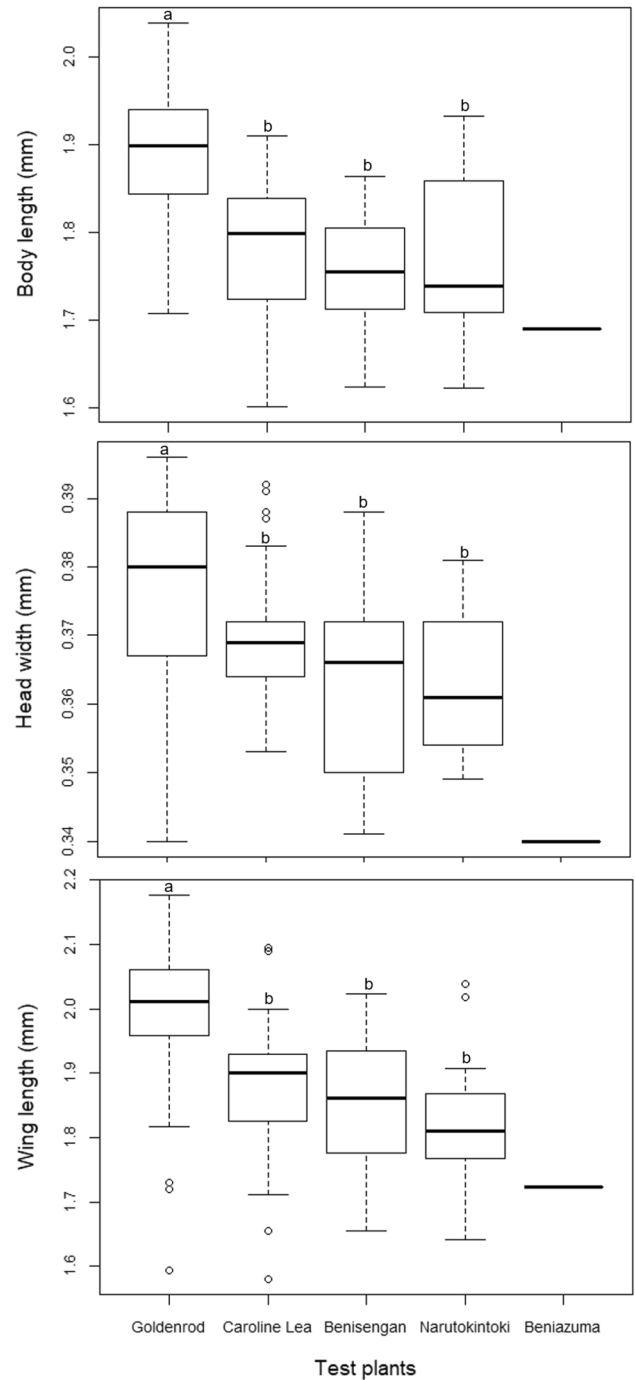
is similar to a longer developmental period in grasshoppers fed on low-nitrogen grass (Berner et al. 2005). However, variation in nutrient content might not be the only reason for the inter-cultivar difference in nymphal development time; as is known in many plant species, chemical defense might also affect development and survival (Mattson et al. 1988; Bernays and Chapman 1994; Poelman et al. 2010).

Before the oviposition preference test, we allowed the females to feed on goldenrod for 7 days after emergence to ensure sexual maturation so at the time of inoculation they were ready to oviposit. In fact, our preliminary data showed that on day 5 after emergence, females had ca. five matured eggs in their ovaries. Therefore, at the beginning of the oviposition preference test, females would have had several matured eggs ready for oviposition. Furthermore, females and males usually copulated within a few hours after we put them together. Nevertheless, females inoculated on inferior plants started their oviposition later than those on goldenrod. This delay of oviposition is therefore not due to any delay of maturation of eggs. Instead, females assessed the quality of the plant for her offspring, and delayed laying eggs.

The hierarchical rank from goldenrod to Beniazuma applied to both oviposition preference and nymphal performance. Our results support the naive expectation that natural selection favors mothers to choose oviposition plant which supports good performance of their offspring, as immature individuals have little opportunity to move to another site (Videla et al. 2012). Adults and nymphs of *C. marmorata*, a hemimetabolous insect, have similar feeding habits and exploit the same habitat like other hemipteran insects (e.g., Dong et al. 2013, Martínez et al. 2017). This characteristic is most likely the reason for our results that females could effectively assess plants for oviposition, indicated by the significant relationship between female preference (preoviposition period) and nymphal performance (mortality). The fact that this insect had no experience of using sweet potato at the population level supports this notion. On the other hand, among some holometabolous insects like butterflies, larval and adult foods are completely different, so female adults may not assess



**Fig. 3** Comparison of female adult body size reared on test plants. Bars with the same letter are not significantly different (Tukey–Kramer multiple comparison test,  $P < 0.05$ )



**Fig. 4** Comparison of male adult body size reared on test plants. Bars with the same letter are not significantly different (Tukey–Kramer multiple comparison test,  $P < 0.05$ )

**Table 2** Preoviposition period and fecundity of *C. marmorata* among test plants

Test plants	Preoviposition period		Fecundity	
	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD
Goldenrod	31	2.26 ± 0.77 <sup>a</sup>	31	99.97 ± 39.59 <sup>a</sup>
Caroline Lea	29	4.14 ± 1.30 <sup>b</sup>	31	55.39 ± 42.49 <sup>b</sup>
Benisengan	29	5.86 ± 2.85 <sup>c</sup>	30	53.73 ± 27.88 <sup>b</sup>
Narutokintoki	22	6.00 ± 3.12 <sup>c</sup>	32	20.47 ± 18.95 <sup>c</sup>
Beniazuma	17	8.59 ± 3.47 <sup>d</sup>	30	11.97 ± 16.34 <sup>c</sup>

Means followed by the same letters are not significantly different (Tukey–Kramer multiple comparison test after mixed-model ANOVA for preoviposition period and GLMM for fecundity,  $P < 0.05$ )

small differences in the quality of the host plant for their larvae. This difference between hemi- and holometabolous species would be one reason why prior research proposed both pros and cons for preference–performance hypotheses (Gratton and Welter 1998; Keeler and Chew 2008; Forister et al. 2009; Craig and Ohgushi 2002; Karungi et al. 2010; Zhang et al. 2012; Geng et al. 2012; Dong et al. 2013).

In many herbivorous insects, it is thought that an adult female tends to choose an oviposition plant based on her experience during her larval stage (Hopkins's "Host-Selection Principle": Hopkins 1917, but see Barron 2001). If this is the case in our study materials, then once eggs laid in sweet potato leaves hatch and the nymphs survive to adulthood, the adults would tend to choose sweet potato. This conditioning of host preference may then lead to the formation of a host race. However, sweet potato would be harvested and disappear from the field during winter, forcing *C. marmorata* to overwinter on goldenrod. Therefore, even if genetic change occurred to favor the use of sweet potato in summer, this change would be weakened in winter, and host race formation, if any, would be slow.

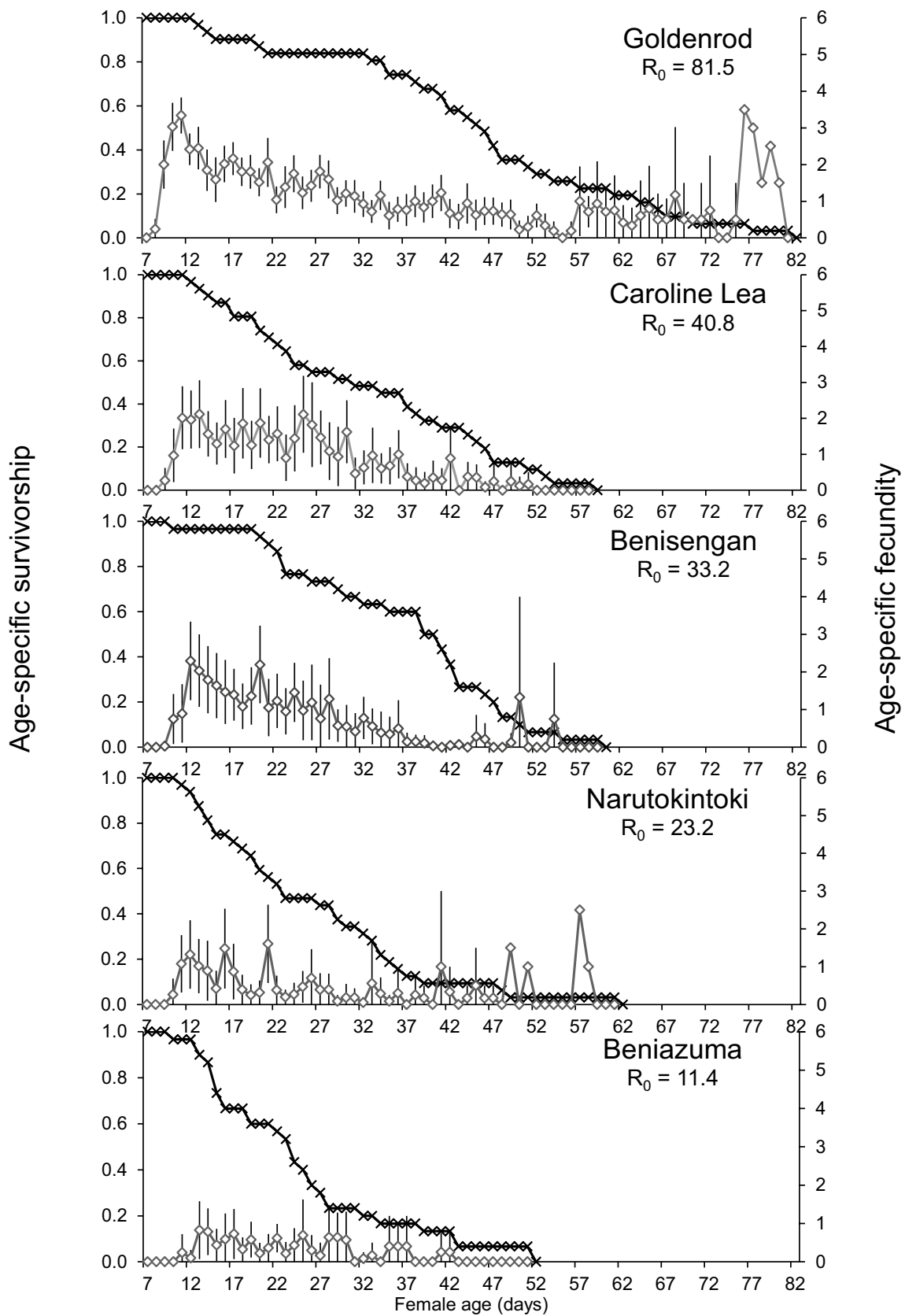
As sweet potato (Convolvulaceae) and goldenrod (Asteraceae) are distantly related (belonging to the orders Solanales and Asterales, respectively), they would have different leaf traits. In fact, our personal observations suggest that trichome density is higher in goldenrod than sweet potato, and C/N ratio is higher in goldenrod. Even so, *C. marmorata* accepted sweet potato to an extent as an oviposition substrate. Thompson and Pellmyr (1991) proposed that such less-selective behavior might be the raw material for host shift. In the field, females may pick several out-of-range

hosts in order to save time in searching for in-range hosts, and so the plant species will be eventually added to their repertoire. In the case of *C. marmorata*; however, the reason might not be to save time, rather, concordance of order of nymphal performance and oviposition preference within sweet potato suggests that females do not lay eggs arbitrarily.

We carried out this study based on previous reports that *C. marmorata* attacks sweet potato in agricultural fields (e.g., Shiga Pest Control Center 2005). However, our laboratory data showed that goldenrod was obviously better than all the sweet potato cultivars as food. A possible explanation for the use of a non-asteraceous low-quality plant, sweet potato, is that goldenrod quality in the field is equal to or lower than that of sweet potato. In Japan, the population density on goldenrod was extremely high especially in short period after invasion (Sakata et al. 2013). One reason for this would be the loss of plant resistance in Japan after release from *C. marmorata* (Sakata et al. 2014). Other factors like escaping from natural enemies also would be important. The consequent high density of *C. marmorata* resulted in heavy injury on leaves of goldenrod (Sakata et al. 2013; pers. obs.). Such heavy injury decreases the quality of plant as food for *C. marmorata* (pers. obs.). We thus suggest that high density of *C. marmorata* on goldenrod in Japan facilitated the use of other plants. However, the reason why it was sweet potato among other many plant species is still unknown.

We conclude that (1) *C. marmorata* is able to feed and lay eggs on sweet potato cultivars; (2) nymphal performance and oviposition preference were higher on goldenrod, and some performance traits differed significantly among sweet potato cultivars; and (3) female adults tended to start oviposition earlier and laid more eggs on plants on which nymphs later grew better. Therefore, host range expansion in this species is likely to be caused by female oviposition preference for sweet potato rather than better survival of nymphs on sweet potato among many other plants arbitrarily chosen by mothers.

There is still much work needed to understand the nymphal performance and oviposition preference of *C. marmorata* in relation to its host plants. Future studies need to focus on how leaf traits and chemical compounds affect *C. marmorata* response (e.g., survival, preference and performance), as the combination of herbivore–host–plant traits and their adaptive capacity will lead to a deeper understanding of how novel interactions are established and maintained (Pearse et al. 2013).



**Fig. 5** Relationship of adult age with survival rate (cross symbol) and age-specific fecundity (unfilled diamond) of *C. marmorata* among test plants. The age-specific fecundity is expressed as number of eggs laid on the day/number of females alive on the day



**Table 3** Relationships of nymphal performance with female preference and sex of nymphs (with goldenrod)

Response variables	Explanatory variables	$\chi^2$	df	P
Survival rate	Fecundity	2.67	4	0.08
Survival rate	Preoviposition period	-6.15	4	0.01
Nymphal development time	Fecundity	-2.86	9	0.03
	Sex of nymphs	-1.11	9	0.30
Nymphal development time	Preoviposition period	3.24	9	0.01
	Sex of nymphs	-1.91	9	0.27

**Table 4** Relationships of nymphal performance with female preference and sex of nymphs (without goldenrod)

Response variables	Explanatory variables	$\chi^2$	df	P
Survival rate	Fecundity	1.78	3	0.22
Survival rate	Preoviposition period	-5.66	3	0.03
Nymphal development time	Fecundity	-1.95	7	0.11
	Sex of nymphs	-1.20	7	0.28
Nymphal development time	Preoviposition period	2.19	7	0.08
	Sex of nymphs	-1.27	7	0.26

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