Factors Determining the Host Range of Two Tortoise Beetles, *Cassida nebulosa* L. and *C. piperata* Hope (Coleoptera: Chrysomelidae) in Japan

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Abstract: We investigated the relationship between host-plant use by two tortoise beetles, *Cassida nebulosa* and *C. piperata*, in a field and their performance under laboratory conditions. Sixteen plant species were grown in the experimental field with *C. nebulosa* being observed to grow on three chenopodiaceous species (*Chenopodium album*, *C. album* var. *centrorubrum*, and *C. ficifolium*), while *C. piperata* grew on the same three chenopodiaceous species plus three amaranthaceous species (*Amaranthus blitum*, *A. hybridus*, and *A. retroflexus*). Host-plant selection in the field was directly correlated to the larval growth under laboratory conditions. Thus, the two tortoise beetles selected plant species that were suitable as larval food under natural conditions. In the laboratory experiments, the survival period of adults and the number of eggs produced showed that adults have wider food ranges than larvae. Therefore, food quality is less important as a limiting factor for adults compared to larvae. In addition, the field observation showed that *C. nebulosa* laid eggs only on suitable host plant species, whereas *C. piperata* laid eggs on both suitable hosts and non-hosts.

INTRODUCTION

Various factors restrict the host range of phytophagous insects. In general, such factors include plant quality (such as chemistry, nutritional content, toughness, and architecture), plant quantity, spatial or temporal correspondence, and ecological factors (such as interspecific competition and predation or parasitism) [1]. In particular, the relationship between oviposition preference and larval growth has been a central focus in the study of insect-plant interactions [2, 3]. Many insects show a positive correlation between oviposition preference and offspring performance [4-8]. However, some insects show a weak correlation between oviposition preference and offspring performance [2, 9]. For example, the lycaenid butterfly [10], willow-feeding sawfly [11] and willow beetle [12] avoid certain plants as hosts, even though these plants are suitable food for their larvae. Thus, oviposition represents a limiting factor in host-plant use.

Two tortoise beetles, *Cassida nebulosa* L. and *C. piperata* Hope, are oligophagous insects that feed on Chenopodiaceae and Amaranthaceae [13]. However, knowledge remains limited about the host preference of Japanese Cassidinae with respect to Chenopodiaceae and Amaranthaceae plant species. Thus, we studied host-plant use by these two tortoise beetles. Since species interactions are often site-specific, studies using host plants that are allopatric with the insect population cannot inform us about the actual host plant use by insects [14]. Therefore, we used Chenopodiaceae and Amaranthaceae plants that grew sympatrically with the insect population in an experimental field. We then observed how the two tortoise beetles used potential host-plants that were planted in the experimental field.

Sometimes, host-plant use under natural conditions and performance under laboratory conditions are not correlated [15]. Thus, we also studied larval and adult performance with respect to these plants under laboratory conditions to reveal limiting factors in host-plant use.

MATERIALS AND METHODOLOGY

Insects

Two tortoise beetles, *C. nebulosa* and *C. piperata*, were collected from the experimental field of the Graduate School of Agricultural Science, Tohoku University, Sendai, Miyagi Prefecture, Japan. The beetles were reared on the leaves of *Chenopodium album* L. and *C. album* var. *centrorubrum* Makino, which were also collected from the field. In winter, adults were reared on the leaves of spinach, and larvae were reared on *C. album* and *C. album* var. *centrorubrum* grown in a greenhouse. These insects were reared at 24 ± 1°C and 16:8 h light:dark (L:D) photoperiod.

Plants

Nine plant species belonging to the Chenopodiaceae family and seven plant species belonging to the Amaranthaceae family were used.

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Chenopodiaceae

Wild plants: *Chenopodium album* L., *C. album* L. var. *centrorubrum* Makino, *C. ficifolium* Sm., and *C. ambrosioides* L.

Cultivated plants: *Beta vulgaris* L. var. *cicla* L. (chard), *B. vulgaris* L. var. *vulgaris* (table beet), *Bassia scoparia* A. J. Scott, *Salsola komarovii* Iljin, and *Spinacia oleracea* L. (spinach).

Amaranthaceae

Wild plants: *Amaranthus blitum* L., *A. hybridus* L., *A. retroflexus* L., and *Achyranthes bidentata* Blume var. *fauriei* (H. Lév. et Vaniot)

Cultivated plants: *A. tricolor* L., *Celosia cristata* L., and *Gomphrena globosa* L.

All of the listed plants were grown in the experimental field of the Graduate School of Agricultural Science, Tohoku University, Japan.

Field Study

Host-plant use by the two tortoise beetles was studied in the experimental field during 2000 and 2001. Nine species of Chenopodiaceae and seven species of Amaranthaceae were randomly planted at the experimental site (7 × 14 m). Plants were initially grown in pots and ten pots per each species were then transplanted to the experimental site at the end of May or the middle of June. In 2000, the plants were transplanted to the experimental site on June 17. In 2001, the plants were transplanted to the experimental site on May 23. Sixteen species were planted in 2001, while just 12 species were planted in 2000 because some plants failed to grow. After transplanting, the wild beetle population appered on these plants at this site. All weeds, except for the plants used for the study, were removed. The study began about one week after transplanting. Every 1 or 2 weeks, the numbers of egg patches, larvae, pupae, and adults of the two tortoise beetle species were counted. However, the eggs of *C. piperata* could not be counted because each egg was laid separately; thus, this parameter was excluded from the analysis. The investigation was carried out until early September of each year.

Larval Growth

A piece of filter paper (90 mm diameter) was placed at the bottom of a petri dish (90 mm diameter) and moistened with purified water (produced by Elgastat Option 4 water purifier, Elga, High Wycombe, UK) to maintain humidity. A test plant leaf was placed on the bottom of the petri dish. Ten larvae that had hatched within a 24-h period were transferred to each leaf. These larvae were reared at 24 ± 1°C under a 16L:8D photoperiod. The leaves were changed every 1-3 days to maintain suitability. The experiment was carried out until all larvae became adults or died. The experiment had 8-10 replicates for each plant.

Performance of Adults on Plants

The experiment was conducted under the same conditions as that used for the larvae experiment in the previous section. Within 24 h of emergence, 10 adults (reared on *C. album* or *C. album* var. *centrorubrum* throughout the larval period) were released into each petri dish. Each day, the number of survivors and eggs were counted. The experiment was carried out until all adults died or all food plants had disappeared. The experiment had 5 replicaes for each plant.

Statistical Analysis

We performed statistical analyses using R v. 3.0.2 for Mac OS X [16]. The number of larvae that survived and the performance of adults (the number of egg batches, eggs, and number of adults that survived at 30, 60, and 120 days after emergence) on 16 plant species were analyzed using the Tukey's HSD test [17] after log transformation [log (x + 0.5)].

RESULTS

Field Study

The distribution of the two tortoise beetles for each plant in the experimental site is shown in Table **1**. *Cassida nebulosa* was mostly found on *C. album*, *C. album* var. *centrorubrum*, and *C. ficifolium*. In exceptional cases, two egg batches and two larvae of *C. nebulosa* were found on *A. bidentata* var. *fauriei* and one larva was found on *G. globosa* in 2000. However, the eggs and larvae did not grow on these plants. In comparison, *C. piperata* was found on all experimental plants, except *S. komarovii* and *C. cristata*. However, only the larvae from the early stages of developmant were observed on *B. scoparia*, *A. tricolor*, *G. globosa*, and *A. bidentata* var. *fauriei*, with none of the pupae being found on these plant species.

Larval Growth

The suitability of the experimental plants for larvae was estimated by the eclosion rate. *Cassida nebulosa* showed high eclosion rates on *C. album*, *C. album* var. *centrorubrum*, and *C. ficifolium*, whereas no adults emerged on amaranthaceous plants (Fig. **1**). *Cassida piperata* showed high eclosion rates on *C. album*, *C. album* var. *centrorubrum*, *C. ficifolium*, *B. scoparia, A. blitum*, and *A. hybridus*. The survival rates on chenopodiaceous plants was similar for both tortoise beetles, whereas the survival rates on amaranthaceous plants were different (Fig. **1**).

Performance of Adults on Plants

The eggs of *C. nebulosa* were found on *C. album*, *C. album* var. *centrorubrum*, *C. ficifolium*, and spinach. Only a few or no eggs were found on the other experimantal plants. No eggs were oviposited on amaranthaceous plants (Table **2**). In comparison, most *C. piperata* eggs was laid on *C. album* var. *centrorubrum*, followed by *A. blitum*, *C. album*, and spinach. Only a few or no eggs of either species were found on *A. tricolor*, *C. cristata*, and *G. globosa* (Table **3**). Because *B. scoparia* and *S. komarovii* died off during the study, beetle survival periods were indicated by the number of adults that survived at 30, 60, and 100 days after emergence. Large numbers of *C. nebulosa* survived on *C. ambrosioides*, *C. album* var. *centrorubrum, B. scoparia*, and chard (Table **2**). *Cassida nebulosa* adults lived a long
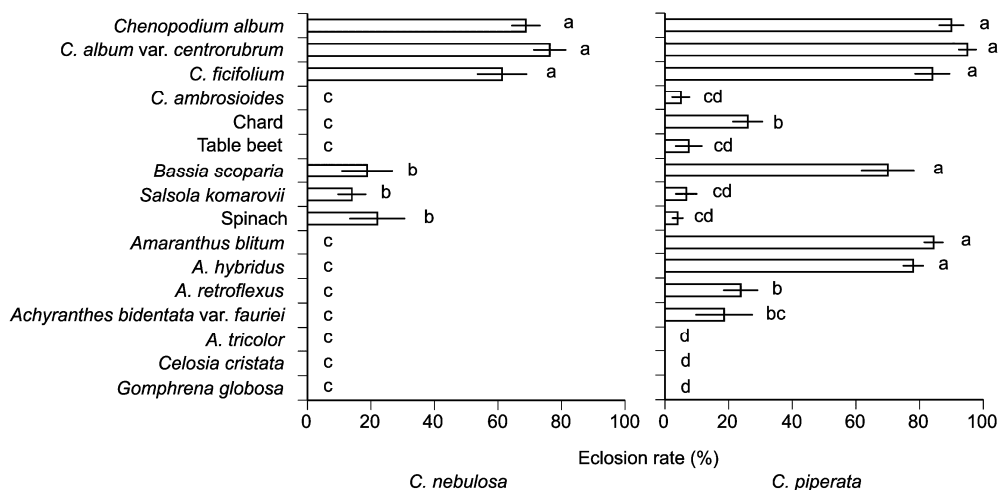
Fig. (1). Eclosion rates of two tortoise beetles on plants belonging to the Chenopodiaceae and Amaranthaceae families. Bars labeled with the same letters on the same series are not significantly different at the 5 % level by the Tukey's HSD test.

Table 1.   Total number of the two tortoise beetles on plants belonging to the Chenopodiaceae and Amaranthaceae families in the experimental field during the study period.

Plants	No. of *C. nebulosa*				No. of *C. piperata*		
	Egg Batches	Larvae	Pupae[1]	Adults	Larvae	Pupae[1]	Adults
Chenopodiaceae							
Chenopodium album	20	303	15	12	56	1	13
C. album var. *centrorubrum*	106	1092	128	28	34	4	10
C. ficifolium	28	342	18	11	37	1	2
C. ambrosioides[2]	0	0	0	0	0	0	0
Chard[2]	0	0	0	0	9	1	1
Table beet	0	0	0	0	7	1	0
Bassia scoparia	0	0	0	0	1	0	0
Salsola komarovii[2]	0	0	0	0	0	0	0
Spinach	0	0	0	0	15	3	2
Amaranthaceae							
Amaranthus blitum	0	0	0	0	113	11	25
A. hybridus	0	0	0	1	67	2	15
A. retroflexus	0	0	0	0	36	3	22
Achyranthes bidentata var. *fauriei*	2	2	0	0	13	0	3
A. tricolor	0	0	0	0	15	0	3
Celosia cristata[2]	0	0	0	0	0	0	0
Gomphrena globosa	0	1	0	0	9	0	2

2000 (29-Jun, 4-Jul, 10-Jul, 19-Jul, 1-Aug, 13-Aug, 24-Aug)
2001 (1-Jun, 8-Jun, 22-Jun, 29-Jun, 7-Jul, 13-Jul, 26-Jul, 10-Aug, 25-Aug)
[1]Pupae = No. of prepupae + No. of pupae
[2]These plants were investigated in 2001 only

Table 2.   Performance of *C. nebulosa* adults on plants belonging to the Chenopodiaceae and Amaranthaceae families.

Plants	Egg Batches (Mean ± SE)[1]	Eggs (Mean ± SE)[1,2]	Survival No. (Mean ± SE)[1]		
			Days After Emergence		
			30	60	100
Chenopodiaceae					
Chenopodium album	21.8 ± 7.3 ab	201.0 ± 70.2 ab	8.8 ± 0.7 a	5.8 ± 0.6 ab	2.4 ± 0.7 ab
C. album var. *centrorubrum*	46.2 ± 18.3 a	464.8 ± 201.4 a	9.4 ± 0.4 a	8.8 ± 0.2 a	5.2 ± 0.4 a
C. ficifolium	48.4 ± 18.3 a	543.6 ± 208.9 a	6.8 ± 0.6 a	2.4 ± 1.0 bcd	0.8 ± 0.6 bc
C. ambrosioides	3.4 ± 2.5 bc	18.0 ± 12.6 bc	9.2 ± 0.4 a	9.2 ± 0.4 a	5.4 ± 1.0 a
Chard	5.6 ± 2.5 abc	30.4 ± 12.8 bc	8.8 ± 0.5 a	7.4 ± 1.0 a	4.8 ± 0.9 a
Table beet	1.2 ± 0.8 c	9.2 ± 5.9 bc	6.4 ± 1.5 ab	1.0 ± 0.4 de	0 c
Bassia scoparia	0 c	0 c	7.8 ± 0.7 a	6.0 ± 0.9 a	4.4 ± 0.5 a
Salsola komarovii	0 c	0 c	8.4 ± 0.2 a	7.2 ± 0.4 a	2.6 ± 1.0 ab
Spinach	23.8 ± 8.4 ab	160.8 ± 60.0 ab	7.0 ± 0.3 a	4.8 ± 0.7 abc	2.2 ± 0.8 ab
Amaranthaceae					
Amaranthus blitum	0 c	0 c	5.8 ± 0.7 ab	2.0 ± 0.5 cd	0 c
A. hybridus	0 c	0 c	8.4 ± 1.2 a	6.2 ± 1.1 ab	2.0 ± 0.8 ab
A. retroflexus	0 c	0 c	0.2 ± 0.2 c	0 e	0 c
Achyranthes bidentata var. *fauriei*	0 c	0 c	5.2 ± 0.7 ab	3.8 ± 0.7 abc	0.8 ± 0.6 bc
A. tricolor	0 c	0 c	0 c	0 e	0 c
Celosia cristata	0 c	0 c	0 c	0 e	0 c
Gomphrena globosa	0 c	0 c	3.2 ± 1.2 b	0.2 ± 0.2 e	0 c

[1]Values followed by the same letters in each series are not signigicantly different at the 5 % level by the Tukey's HSD test.
[2]Eggs indicate the total number of eggs in egg batches.

time on chenopodiaceous plants, except for table beet and *C. ficifolium*, even though amaranthaceous plants (except *A. hybridus*) were not suitable as food (Table **2**). Compared to other plants, fewer *C. piperata* adults survived on *C. ficifolium*, chard, table beet, *C. cristata*, and *G. globosa* (Table **3**).

DISCUSSION

The larvae and pupae of *C. nebulosa* were found on *C. album*, *C. album* var. *centrorubrum*, and *C. ficifolium* in the field. In comparison, large numbers of *C. piperata* larvae and pupae were found on *C. album*, *C. album* var. *centrorubrum*, *C. ficifolium*, *A. blitum*, *A. hybridus*, and *A. retroflexus* in the field. The existence of pupae indicates that *C. nebulosa* larvae develop on three chenopodiaceous plant species, whereas those of *C. piperata* develop on the same three chenopodiaceous plant species plus three amaranthaceous plant species. Therefore, these six species were considered to be the main host plants of the two beetle species. In addition, chard, table beet, and spinach may be potential foods for *C. piperata*, because some pupae and larvae were found on these plants. The two tortoise beetles exhibited different patterns of Chenopodiaceae and Amaranthaceae host-plant use.

In Europe, *C. nebulosa* grows on and harms the leaves of sugar beets [18, 19]. In Japan, although *C. nebulosa* eat sugar beet, only a few larvae reach adult stage on this plant (about 10%) [20]. In addition, *C. nebulosa* from Hokkaido (the northern part of Japan) feed on *A. bidentata* [21]. However, our results showed that *C. nebulosa* was not able to grow on *A. bidentata* var. *fauriei*. Thus, host-plant use differs among phytophagous insect populations [22]. The case of *C. nebulosa* exemplifies this phenomenon.

In general, the oviposition preference and larval performance are the main limiting factors of the host plant use by phytophagous insects [23]. In the experimental field, the eggs of *C. nebulosa* were only observed on three Chenopodiaceae species (*C. album*, *C. album* var. *centrorubrum*, and *C. ficifolium*), with this beetle species also showing a high survival rate on this plant species in the laboratory experiment. The eggs of *C. nebulosa* were not observed on any other plant species, even though a few adults emerged or oviposited on other species in the laboratory experiment. These results show that oviposition is a primary limiting factor for the host range of *C. nebulosa*. In comparison, it was difficult to count the exact number of *C. piperata* eggs in the field which could only be approximated from the

Table 3.   Performance of *C. piperata* adults on plants belonging to Chenopodiaceae and Amaranthaceae families.

Plants	Eggs (Mean ± SE)[1]	Survival No. (Mean ± SE)[1]		
		Days After Emergence		
		30	60	100
Chenopodiaceae				
Chenopodium album	1275.0 ± 236.0 ab	10.0 ± 0.0 a	7.4 ± 0.6 a	4.6 ± 1.0 ab
C. album var. *centrorubrum*	2314.4 ± 479.0 a	9.4 ± 0.4 ab	8.4 ± 0.7 a	6.0 ± 0.4 a
C. ficifolium	929.6 ± 448.9 abc	6.0 ± 1.4 b	2.8 ± 1.1 b	1.6 ± 0.5 b
C. ambrosioides	190.0 ± 46.1 bc	9.0 ± 0.4 ab	8.6 ± 0.2 a	6.6 ± 0.4 a
Chard	355.8 ± 78.8 abc	7.2 ± 0.2 ab	5.4 ± 0.6 a	1.8 ± 0.9 b
Table beet	279.6 ± 107.9 bc	8.0 ± 0.7 ab	4.6 ± 0.6 ab	1.8 ± 0.7 b
Bassia scoparia	481.0 ± 132.7 abc	6.4 ± 0.9 ab	5.4 ± 1.0 a	3.6 ± 0.6 ab
Salsola komarovii	97.2 ± 22.1 c	8.6 ± 0.6 ab	7.2 ± 0.2 a	4.0 ± 0.4 ab
Spinach	1268.0 ± 368.3 ab	8.6 ± 0.6 ab	6.8 ± 1.2 a	4.0 ± 1.4 ab
Amaranthaceae				
Amaranthus blitum	1583.8 ± 230.7 ab	9.4 ± 0.4 ab	9.2 ± 0.5 a	5.6 ± 0.8 a
A. hybridus	500.8 ± 175.1 abc	8.8 ± 0.2 ab	8.2 ± 0.6 a	6.2 ± 0.6 a
A. retroflexus	433.0 ± 94.6 abc	8.0 ± 0.6 ab	5.4 ± 0.5 a	3.2 ± 0.6 ab
Achyranthes bidentata var. *fauriei*	192.6 ± 68.2 c	9.2 ± 0.5 ab	7.6 ± 0.7 a	3.6 ± 0.6 ab
A. tricolor	7.8 ± 6.6 d	7.6 ± 0.5 ab	6.0 ± 0.8 a	3.8 ± 0.6 ab
Celosia cristata	0 d	0 d	0 c	0 c
Gomphrena globosa	0 d	2.2±0.7 c	0 c	0 c

[1]Values followed by the same letters in each series are not signigicantly different at the 5% level by the Tukey's HSD test.

number of larvae, as larvae are not sufficiently mobile to move to other plants. For this reason, the number of larvae was used to estimate the oviposition preference of this species, rather than the number of eggs. Many *C. piperata* larvae were found on their host plants; however, many early stage larvae were also found on non-host plants. This finding indicates that *C. piperata* lays eggs on both host and non-host plants. Therefore, *C. piperata* does not select specific plants for oviposition. After hatching, the larvae on host plants developed well, whereas those on non-host plants failed to develop. These results show that larval growth is a more important limiting factor for *C. piperata* than ovipositional selection.

We also investigated plant qualities as foods for adults in the laboratory experiment. Both species laid more eggs on host plants. However, adults also exhibited a long life and oviposition on some non-host plants. Thus, the available food range of adults is wider than that of larvae, because the adults could use plants that larvae could not grow on in the laboratory experiments. Therefore, food quality is less important for adults as the limiting factor of their host range than for larval growth or ovipositional behavior.

In addition to the direct insect-plant relationship, previous studies have indicated that external ecological factors limit the host range of phytophagous insects. Such factors include temporal and spatial availability [24, 25], the effect of natural enemies [12, 26-30], competition, or meteorological factors [31, 32]. In the current study, temporal and spatial availability were not limiting factors for the insect and plant population. Other factors were not considered in this study. However, we assumed that these ecological factors were not critical limiting factors because the host ranges of the two species could be explained by the direct insect-plant relationship.

CONCLUSION

Our results showed that ovipositional selection and larval growth were affected by host-plant use. Both species showed positive correlations between oviposition preference and larval performance. However, the two tortoise beetles differed in their specificity of host plant selection. Consequently, *C. nebulosa* plant use was restricted by ovipositional selection, whereas *C. piperata* plant use was restricted by larval growth. The importance of ovipositional selection has been studied in detail for Lepidoptera species, since to adults and larvae use different foods [3]. The current study focused on leaf beetles [12], revealing that ovipositional selection is the important factor in determining the host range

of some leaf beetle species that use the same food as adults and larvae.

CONFLICT OF INTEREST

The authors confirm that this article content has no conflict of interest.

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