

# Variable correspondence of female host preference and larval performance in a phytophagous ladybird beetle *Epilachna pustulosa* (Coleoptera: Coccinellidae)

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Genetic and environmental factors causing intraspecific variation of the thistle *Cirsium kamschaticum* Ledeb. as a host plant of the phytophagous ladybird *Epilachna pustulosa* Kôno were investigated through simple food-choice tests and rearing of larvae. Two thistle clones (T1U<sub>1</sub> and T4H<sub>2</sub>) were used, originally growing approximately 12 km apart. A previous study showed that adult female ladybirds preferred T1U<sub>1</sub> to T4H<sub>2</sub>, and that larval performance was better on T1U<sub>1</sub>, when leaves from the clones in situ were examined. The two clones retained their characteristics with respect to beetle preference after transplantation into a common garden. However, the difference between T1U<sub>1</sub> and T4H<sub>2</sub> with respect to larval performance was reduced after the transplantation. When leaves from shoots of T1U<sub>1</sub> exposed to different sunlight intensities were offered, adult female ladybirds did not show obvious preferences. Larval eclosion rates increased significantly with the increase in leaf sunlight intensity exposure. These results suggest strongly that both genetic and environmental factors are involved in interclonal variation of thistle quality in beetle preference and/or performance. It is suggested that the quality of thistle leaves for larval performance is largely affected by environmental factors, while leaf quality for beetle preference may be determined strictly by genetic factors. Under certain conditions, *E. pustulosa* females may behave maladaptively, preferring plants not appropriate for larval growth, or not choosing plants appropriate for the larval growth.

**Key words:** adult preference; *Cirsium kamschaticum*; *Epilachna pustulosa*; larval performance; preference–performance correspondence.

## INTRODUCTION

In many phytophagous insects, the immature stages have little opportunity to change their developmental location (Renwick 1989; Mayhew 1997). Therefore, the fate of the immature insects is largely dependent on host selection by ovipositing females. It is often assumed that ovipositing females will show a strong preference for plants that enhance the performance of their offspring. However, the existing data range from good correspondences between oviposition preferences of

females and larval performance, to very poor correspondences (reviewed by Thompson 1988; Thompson & Pellmyr 1991). Therefore, elucidating the degree of preference–performance correspondences and the factors that cause observed correspondences has been considered to be the crux of understanding the coevolution between phytophagous insects and their host plants (Wiklund 1975; Thompson 1988; Jaenike 1990; Thompson & Pellmyr 1991; Mayhew 1997, 1998).

In the past two decades, much information has been gathered indicating that intraspecific variation in host plants, as well as interspecific differences among hosts, play an important role in shaping insect–plant associations in natural systems (Edmunds & Alstad 1978, 1981; Denno & McClure 1983; Fritz *et al.* 1987; Maddox & Root 1987; Fritz 1990; Price *et al.* 1990; Senn

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*et al.* 1992; Weis & Campbell 1992; Suomela & Nilson 1994; Mopper 1996). Consequently, the problems of preference–performance correspondence have come to be considered not only at the interspecific host–plant level but also at the intraspecific individual host–plant level (Rausher & Papaj 1983; Leather 1985; Karban & Courtney 1987; Taylor & Forno 1987; Damman & Feeny 1988; Craig *et al.* 1989, 2000; Valladares & Lawton 1991; Horner & Abrahamson 1992; Larsson & Strong 1992; Underwood 1994; Larsson *et al.* 1995). At the intraspecific level, both good correspondences (Whitham 1981, 1983; Leather 1985; Damman & Feeny 1988; Anderson *et al.* 1989; Price *et al.* 1990) and poor ones (Karbon & Courtney 1987; Taylor & Forno 1987; Valladares & Lawton 1991; Horner & Abrahamson 1992; Larsson & Strong 1992; Underwood 1994; Larsson *et al.* 1995; Craig *et al.* 1999, 2000) have been found.

Previously, we reported considerable intraspecific variation exists in the thistle *Cirsium kamtschaticum* Ledeb. (Asteraceae) as a main host plant of the phytophagous ladybird beetle *Epilachna pustulosa* Kôno (Coccinellidae) (Fujiyama & Katakura 1997). When leaves sampled from the field were offered in laboratory, the thistle showed qualitative intraspecific variation affecting both adult female feeding preference and larval performance of *E. pustulosa*. Furthermore, female beetles preferred the clone on which larval performance was better (Fujiyama & Katakura 1997). Therefore, *E. pustulosa* showed rather good preference–performance correspondence at the intraspecific level of host–plant variation (interspecific level correspondence are rather weak or more complicated: see Fujiyama & Katakura 1997; Yamaga & Ohgushi 1999). This suggests strongly that qualitative intraspecific variation in the thistle has had a large impact on shaping its association with *E. pustulosa*, although the possible effects of other factors (such as thistle abundance and availability, predators, competitors and parasites) cannot be ignored.

However, we know nothing about the mechanisms that cause such intraspecific variation in this thistle. The aim of the present study was to elucidate the factors causing intraspecific variation of *C. kamtschaticum* as a host plant of *E. pustulosa*. We paid special attention to: (i) how genetic and environmental factors affect host–plant leaf quality for the preference and/or performance of *E. pustulosa*;

and (ii) whether/how the factors alter the preference–performance correspondence in the beetle. We focused particularly on the quality of thistle leaves, because leaf quality might be considered to be the principle factor shaping insect–plant associations (Rosenthal & Janzen 1979).

## METHODS

### Insect material

We used post-hibernating adult females (and their offspring) of the so-called Sapporo form of *E. pustulosa*, which is known to occur on *C. kamtschaticum* and on blue cohosh *Caulophyllum robustum* Maxim. (Berberidaceae), when this plant grows together with thistle (Kurosawa 1953; Katakura 1974, 1981). However, no population of *E. pustulosa* exclusively dependent on blue cohosh has been reported (Katakura 1981). This suggests that *C. kamtschaticum* is the main host plant of *E. pustulosa*.

We collected post-hibernating females from thistle plants in Sankakuyama, a western suburb of Sapporo, Hokkaido in northern Japan. All females were sexually mature and had probably copulated and stored sperm before their collection (Katakura 1982).

The beetles were fed the alternative food plants, *Scopolia japonica* Maxim. (Solanaceae) and/or *Solanum japonense* Nakai (Solanaceae) (cf. Katakura 1981), for more than 1 week before the experiments started in order to diminish the possible influence of feeding experience before collection. When the same beetles were used repeatedly in different feeding tests, they were fed *S. japonica* and/or *S. japonense* for more than 24 h prior to each experiment to minimize the influence of preceding tests.

### Manipulations of thistle plants

We used two thistle clones (previously coded as T1U<sub>1</sub> and T4H<sub>2</sub>), originally growing on the campus of Hokkaido University and at Hoshioki, respectively (both locations are in Sapporo and are approximately 12 km apart). The two clones were fully mature, being composed of more than 10 shoots each. They differed distinctly in leaf qualities that affect adult food preference and larval

performance in *E. pustulosa*. Adult females preferred T1U<sub>1</sub> to T4H<sub>2</sub>, and larval performance was better on T1U<sub>1</sub> than on T4H<sub>2</sub>, when leaves from clones in situ were examined (Fujiyama & Katakura 1997).

Because the thistle clones were obtained in somewhat remote locations, both genetic and environmental factors might be postulated as giving rise to the qualitative differences between them. To examine whether and how genetic and environmental factors of *C. kamtschaticum* affect the preference and performance of *E. pustulosa*, we conducted the following two manipulations of the thistle plants.

#### *Transplantation of the two thistle clones*

In the autumn of 1993, we dug up approximately half of the two thistle clones from their original locations, and transplanted the material side by side (about 1 m apart) in an experimental garden on the campus of Hokkaido University. Thus, there were two different thistle clones growing under the same environmental conditions. Hereafter, the two transplanted clones are referred to as T1U<sub>1</sub>(TP) and T4H<sub>2</sub>(TP). All clones in situ and in the experimental garden grew normally from the spring of 1994. Clones in the experimental garden grew mostly intact with the occasional removal of herbivores.

Leaves of the transplanted clones were examined in experiments in 1994 and 1996 for choice tests, and in 1996 for rearing of larvae.

#### *Manipulation of sunlight intensities*

Light conditions are one of two main extrinsic factors that may affect plant quality (Waterman & Mole 1989; the other factor is nutritional condition of the soil). Therefore, in the present study, we investigated the effects of sunlight intensity on thistle leaves, as a representative environmental variable. Under natural conditions, *C. kamtschaticum* grows in a wide range of light conditions from sunny grasslands to within forests (Kadota 1995; N. Fujiyama pers. obs.).

Sunlight intensity was manipulated in 1995 using the thistle clone T1U<sub>1</sub>. We separated shoots of the clone into three groups in early summer and subjected them to three different light conditions. In the first group (T-D1), all shoots were shaded with one layer of black cheesecloth net (creating conditions of 30.8% sunlight relative to direct sunlight; measured by a portable illuminometer (IM-

3; TOPCON, Tokyo, Japan)). In the second group (T-D2), all shoots were shaded with two layers of the same net (creating conditions of 13.1% sunlight relative to direct sunlight). In the third group (T-D0), no shading was provided (100.0% direct sunlight). These conditions were maintained until all experiments were finished. Through this manipulation, we prepared thistle plants that were identical genetically, but differed environmentally.

Leaves of these shoots were offered to adult females in the choice tests not less than 14 days after the start of the manipulation, and were begun to be used for the rearing of larvae 6–8 days after the start of the manipulation.

## Experiments

We examined the degree of female beetle food preference by choice tests, and larval performance by rearing on different food conditions.

It is virtually impossible to distinguish between choice for oviposition and choice for adult food in *E. pustulosa*. Unlike insects such as lepidopterans, for which larval foods are distinctly different from those of adults, both adults and larvae of epilachnine beetles feed on the same part of the same plant species. Hence, it is very difficult to quantify oviposition preference itself in laboratory conditions. For this reason, in the present study, we treated the food choice of ovipositing females as equivalent to the choice of food plant for larvae.

All experiments were carried out under a controlled regime of 16L:8D at 20°C.

#### *Choice tests*

Two pieces of leaves (about 20 cm<sup>2</sup>, each from different clones or differently manipulated shoots) were placed in a transparent polystyrene cage (8.0 cm × 15.5 cm × 3.0 cm), the bottom of which was covered with moist filter paper. We released a female beetle into the cage and allowed it to feed the leaf pieces for 24 h. The leaf areas consumed were measured with the aid of image processing software (NIH Image ver. 1.55; National Institute of Health, Bethesda, USA), after being photocopied and scanned into a computer. Using different females, nine to 15 replicates were carried out simultaneously in each choice test.

Lack of independence was considered between consumed areas on the two leaf pieces offered for

each beetle. Therefore, before statistical analyses, we calculated the subtracted remainder of the consumed area on one leaf piece from the other. Then the remainders were examined through a type of MANOVA (Manly 1993) to detect preferences.

#### *Larval performance*

We gathered egg masses laid by post-hibernating females while they were kept for the above mentioned choice tests.

For rearing on leaves of the transplanted thistle clones, larvae from a single egg mass were divided into two groups, in order to equalize the genetic background of tested insects between food conditions. Larvae were reared individually on leaves of either of the two thistle clones in a transparent polystyrene case (5.5 cm × 6.0 cm × 2.0 cm), the bottom of which was covered with moist filter paper. A total of 35 larvae each, derived from seven females, were reared under the two food conditions.

For rearing on leaves of the shoots exposed to different sunlight intensities, three sets of newly hatched larvae, each containing five individuals from a single egg mass, were prepared and were reared under the three food conditions. Rearing was carried out in transparent polystyrene cages (8.0 cm × 15.5 cm × 3.0 cm), the bottoms of which were covered with moist filter paper. A total of 50 larvae from 10 egg masses derived from 10 females were reared under each food condition.

Throughout the experiments, we provided a sufficient amount of food plant leaves picked every day or every other day. Larvae were reared until emergence. We recorded the eclosion rate (i.e. the percentage of individuals reaching adulthood), the developmental duration (the number of days from hatching to adult eclosion) and the pronotum width of newly emerged adults (a body size index). The eclosion rates were calculated for each replicate (derivation for mother female) in each food condition.

Data were analyzed by one-way ANOVA after adequate transformations of variables. Other non-parametric methods (Mann–Whitney *U*-tests and Kruskal–Wallis tests) were also employed when data were not appropriate for ANOVA. For rearing on leaves exposed to different sunlight intensities, additional pair-wise comparisons were planned to be conducted using the Scheffé method, or non-

parametric tests for multiple comparisons using the Mann–Whitney–Wilcoxon *U*-statistic (Sokal & Rohlf 1995) were to be used when significant difference was detected among the three food conditions.

## RESULTS

### Transplanted clones

Distinct preferences for T1U<sub>1</sub> with clones growing in situ (Fig. 1) also occurred after the transplantations (Fig. 2).

The results of the larvae rearing are summarized in Table 1, together with the previous results obtained in 1992 with clones growing in situ for comparisons (cf. Fujiyama & Katakura 1997). As reported before, larvae performed better on T1U<sub>1</sub> than on T4H<sub>2</sub> in the developmental traits, except female pronotum width, when they were reared on leaves from the two clones growing in situ (eclosion rate:  $U = 83.0$ ,  $P = 0.008$ ; developmental duration: d.f. = 1,  $F = 143.873$ ,  $P < 0.001$ ; pronotum width of female: d.f. = 1,  $F = 2.043$ ,  $P = 0.165$ ; pronotum width of male: d.f. = 1,  $F = 8.836$ ,  $P = 0.005$ ). However, differences in larval performance between the clones were reduced after transplantation into the experimental garden; significant differences were not detected, except for developmental duration (eclosion rate:  $U = 16.5$ ,  $P = 0.284$ ; developmental duration: d.f. = 1,  $F = 34.481$ ,  $P < 0.001$ ; pronotum width of female: d.f. = 1,  $F = 0.001$ ,  $P = 0.981$ ; pronotum width of male: d.f. = 1,  $F = 3.161$ ,  $P = 0.088$ ).

### Shoots exposed to different sunlight intensities

Results of choice tests are shown in Fig. 3. No significant preference of *E. pustulosa* female adults was observed in the three combinations examined (T-D0 vs T-D1, T-D1 vs T-D2, and T-D0 vs T-D2; Fig. 3). For the combination of leaves exposed to the most different sunlight intensities (i.e. T-D0 vs T-D2), females tended to choose leaves exposed to higher sunlight intensities ( $P < 0.1$ ; Fig. 3c).

The results of larvae rearing are given in Table 2. There was a significant difference in eclosion rates among the three food conditions (d.f. = 2,

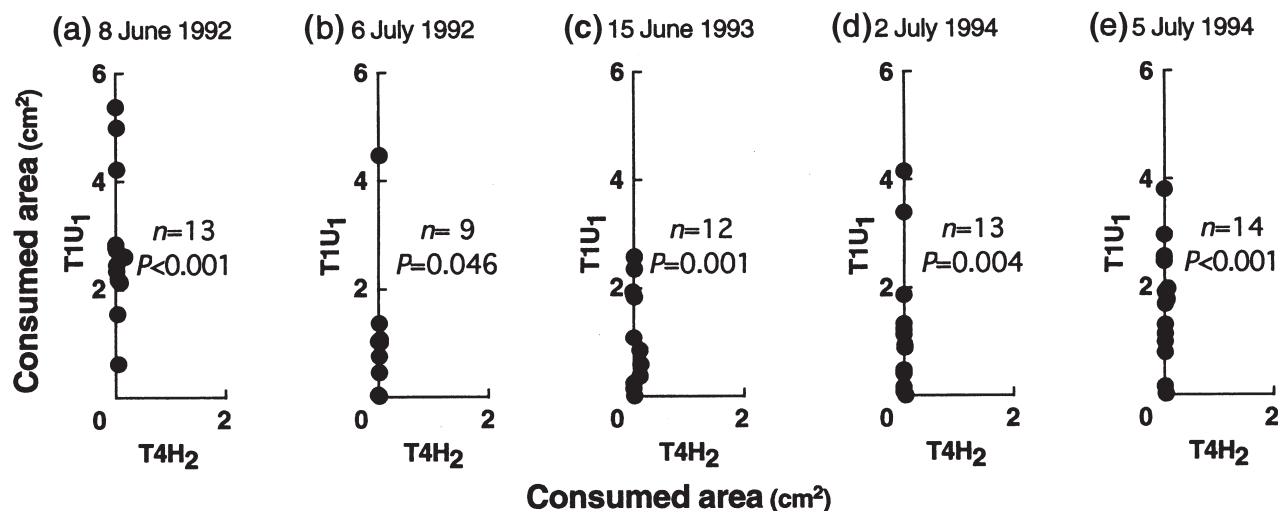


Fig. 1. Choices by post-hibernating adult females of *Epilachna pustulosa* between two thistle clones growing in the original locations (T1U<sub>1</sub> and T4H<sub>2</sub>) examined in different seasons and in different years. (a)–(c) Re-analyses of data in Fujiyama and Katakura (1997); (d) and (e), unpublished data. Each circle represents actual consumed area (in cm<sup>2</sup>) by each beetle. Analyzed by MANOVA (Manly 1993). Significant difference ( $P \leq 0.05$ ) indicates the existence of preference for leaves with larger consumed area.

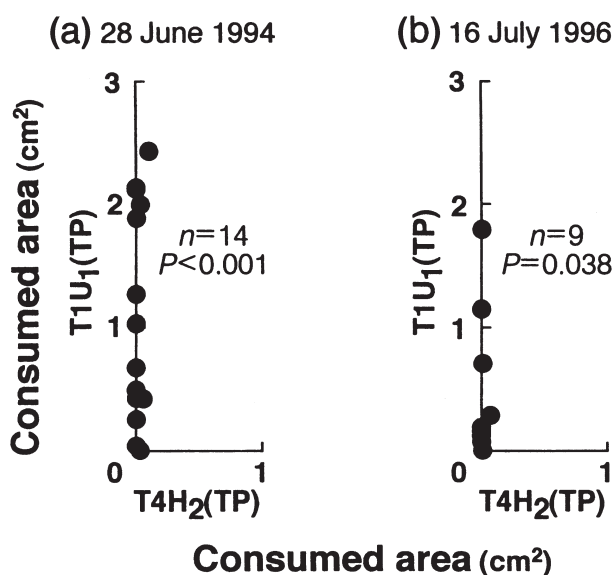


Fig. 2. Choices by post-hibernating adult females of *E. pustulosa* between two thistle clones transplanted into the experimental garden (T1U<sub>1</sub>(TP) and T4H<sub>2</sub>(TP)), examined in different years. For further explanation, see the legend to Fig. 1.

$H = 7.680$ ,  $P = 0.021$ ). Pair-wise comparisons revealed that the difference of the rates between T-D0 and T-D2 was significant (T-D0 vs T-D1,  $U = 78.5$ ,  $P > 0.05$ ; T-D1 vs T-D2,  $U = 53.5$ ,

$P > 0.05$ ; T-D0 vs T-D2,  $U = 81.0$ ,  $P < 0.05$ ). Larval eclosion rates increased with the increase of sunlight intensity for leaves. In the other developmental traits examined, no significant differences were observed (developmental duration: d.f. = 2,  $F = 1.326$ ,  $P = 0.270$ ; pronotum width of female: d.f. = 2,  $F = 0.008$ ,  $P = 0.992$ ; pronotum width of male: d.f. = 2,  $F = 0.166$ ,  $P = 0.848$ ).

## DISCUSSION

### Factors causing interclonal differences in the thistle

Previously, we reported that the *C. kamtschaticum* clone T1U<sub>1</sub> was superior to T4H<sub>2</sub> with respect to both female preference and larval performance of *E. pustulosa* (Fujiyama & Katakura 1997). However, it was not clear whether these differences were caused by genetic or environmental factors, since the two clones were obtained in somewhat remote locations. The two clones were probably exposed to different microenvironments in situ, and were suffering from different levels of feeding by different sets of herbivores.

In this study, transplantation of the two clones to the common experimental garden diminished

**Table 1** Developmental traits [mean  $\pm$  SE (*n*)] of *Epilachna pustulosa* reared on two *Cirsium kamtschaticum* clones growing in their original locations (T1U<sub>1</sub> and T4H<sub>2</sub>) and clones transplanted into the experimental garden [T1U<sub>1</sub>(TP) and T4H<sub>2</sub>(TP)]

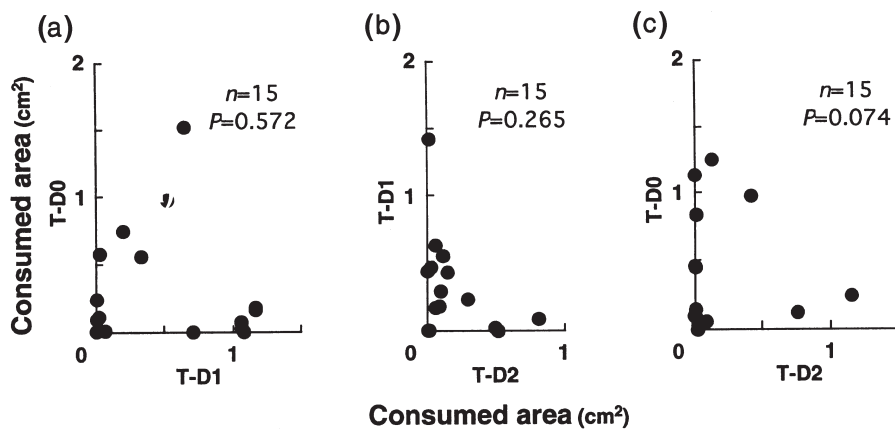
Offered clone	Eclosion rate	Developmental duration (days)	Pronotum widths (mm)	
			Female	Male
T1U <sub>1</sub>	92.0 $\pm$ 4.42 (10) <sup>a</sup>	34.85 $\pm$ 0.342 (46) <sup>a</sup>	3.50 $\pm$ 0.031 (15) <sup>a</sup>	3.36 $\pm$ 0.023 (31) <sup>a</sup>
T4H <sub>2</sub>	64.0 $\pm$ 8.84 (10) <sup>b</sup>	42.69 $\pm$ 0.642 (32) <sup>b</sup>	3.42 $\pm$ 0.049 (12) <sup>a</sup>	3.25 $\pm$ 0.032 (20) <sup>b</sup>
T1U <sub>1</sub> (TP)	82.9 $\pm$ 6.80 (7) <sup>a</sup>	31.90 $\pm$ 0.291 (29) <sup>a</sup>	3.33 $\pm$ 0.075 (12) <sup>a</sup>	3.25 $\pm$ 0.041 (17) <sup>a</sup>
T4H <sub>2</sub> (TP)	71.4 $\pm$ 7.38 (7) <sup>a</sup>	34.76 $\pm$ 0.413 (25) <sup>b</sup>	3.32 $\pm$ 0.029 (16) <sup>a</sup>	3.14 $\pm$ 0.040 (9) <sup>a</sup>

The results for the two thistle clones in situ are re-analyses of data in Fujiyama & Katakura (1997). Figures with the same superscript letters are not significantly different ( $P > 0.05$ ) (eclosion rates, Mann–Whitney *U*-tests; developmental duration and pronotum widths, one-way ANOVA after log-transformation).

**Table 2** Developmental traits [mean  $\pm$  SE (*n*)] of *Epilachna pustulosa* reared on three food conditions of *Cirsium kamtschaticum* leaves that differed in sunlight intensity

Food condition	Eclosion rate*	Developmental duration (days)	Pronotum widths (mm)	
			Female	Male
T-D0	86.0 $\pm$ 7.92 (10) <sup>a</sup>	32.54 $\pm$ 0.342 (43) <sup>a</sup>	3.45 $\pm$ 0.036 (21) <sup>a</sup>	3.33 $\pm$ 0.034 (22) <sup>a</sup>
T-D1	62.0 $\pm$ 10.93 (10) <sup>ab</sup>	32.00 $\pm$ 0.232 (31) <sup>a</sup>	3.44 $\pm$ 0.034 (14) <sup>a</sup>	3.33 $\pm$ 0.026 (17) <sup>a</sup>
T-D2	52.0 $\pm$ 12.37 (10) <sup>b</sup>	33.00 $\pm$ 0.590 (26) <sup>a</sup>	3.44 $\pm$ 0.046 (19) <sup>a</sup>	3.30 $\pm$ 0.056 (7) <sup>a</sup>

\*0.01 <  $P$  < 0.05 by Kruskal–Wallis test. Eclosion rates were analyzed by the Mann–Whitney–Wilcoxon *U*-statistic after Kruskal–Wallis tests. Developmental duration and pronotum widths were analyzed by one-way ANOVA after log-transformation. Figures with the same superscript letters are not significantly different ( $P > 0.05$ ).



**Fig. 3.** Choices by post-hibernating adult females of *E. pustulosa* between thistle leaves exposed to different sunlight intensities. (a) T-D0 (not shaded) versus T-D1 (shaded with one layer of black cheesecloth net). (b) T-D1 versus T-D2 (shaded with two layers). (c) T-D0 versus T-D2. For further explanation, see the legend to Fig. 1.

possible influences of habitat-associated physical factors (Khan *et al.* 1986; Larsson *et al.* 1986; Strauss 1990; Shirai 1994) and feeding damage (Parker 1984; Raupp & Denno 1984; Taylor & Forno 1987; Forno & Bourne 1988; Schultz 1988; Reznik 1991). Differences in host-plant age can

also affect the quality of leaves (cf. Craig *et al.* 1986; Price *et al.* 1987, 1990; Caouette & Price 1989; Roininen *et al.* 1993; Stein & Price 1995). However, since both clones used were fully mature, it is also unlikely that the differences between the clones was caused by an age difference. Hence, if

there are differences between the clones after transplantation, they can be considered to be genetic differences (cf. Moran 1981; Service 1984; Leather 1985; Karban 1987, 1989; Maddox & Root 1987; McCrea & Abrahamson 1987; Fritz & Price 1988; Fritz & Nobel 1989; Fritz 1990; Strauss 1990; Horner & Abrahamson 1992; Weis & Campbell 1992; Shen & Bach 1997).

The results obtained in the present study indicate that the characteristics of the two *C. kamtschaticum* clones with respect to beetle preference were well-retained after transplantation (Figs 1,2). For larval performance, on the other hand, the differences seemed to be reduced (Table 1). These results suggest that thistle leaf characteristics for beetle preference are determined more strictly by genetic factors, while qualities for larval performance are less so.

Results obtained by the experiments using shoots exposed to different sunlight intensities are consistent with the results of the transplantation experiments. Adult females tended to prefer leaves of thistle shoots exposed to higher sunlight intensities (Fig. 3c), but the difference was slight and not significant. In contrast, an obvious result was obtained for larval performance; larval eclosion rates increased significantly with the increase in sunlight intensity for the leaves (Table 2). These results indicate that leaf qualities for larval performance probably change more drastically than the characteristics with respect to beetle preference, according to the difference in environmental conditions of the plants.

Thus, the results obtained in the present study suggest strongly that (i) both genetic and environmental factors lead to individual variation among thistle clones as host plants of *E. pustulosa*; and (ii) these two factors could affect thistle leaf qualities for adult preference and for larval performance differently.

### Variable correspondence of adult preference and larval performance

Overall, the quality of thistle leaves for larval performance of *E. pustulosa* seemed to be affected largely by environmental factors, while leaf characteristics with respect to beetle preference may have been determined strictly by genetic factors (cf. Horner & Abrahamson 1992).

The nature of intraspecific variation in *C. kamtschaticum* may be further complicated through genotype  $\times$  environment interactions; it is possible that alternations of phenotypic leaf qualities due to environmental changes are different for each thistle genotype (cf. Strauss 1990; Horner & Abrahamson 1992). Further experiments taking genotype  $\times$  environment interactions into account are necessary for a better understanding of associations between *C. kamtschaticum* and *E. pustulosa*.

The present study showed that the correspondence of adult preference and larval performance in *E. pustulosa* can vary with different experimental conditions. Thus, good correspondence (Fujiyama & Katakura 1997) cannot always be detected if experimental designs are different. Furthermore, good correspondence might deteriorate in a habitat in which environmental conditions are unstable, or in a habitat that has suffered recent disturbance or environmental alternations, because in these habitats, leaf qualities for larval performance may be variable. Under such circumstances, the behavior of *E. pustulosa* females may appear to be maladaptive, as the beetles may prefer plants not appropriate for larval growth, or may not choose plants appropriate for larval growth.

There have been many studies that have attempted to detect good preference–performance correspondence in phytophagous insects (reviewed by Thompson 1988; Courtney & Kibota 1990; Thompson & Pellmyr 1991). However, good correspondence has been confirmed less frequently than expected (Leather 1994; Mayhew 1997). Some authors have reported relatively poor correspondences when they used transplanted host plants, even though good correspondence was expected from foregoing field studies (Horner & Abrahamson 1992; Craig *et al.* 1999, 2000; see also Anderson *et al.* 1989). The relative scarcity of empirical evidence for good preference–performance correspondence might be attributable, at least in part, to different responses of host-plant qualities between those concerning adult preference and those for larval performance, as demonstrated in this study. As Mayhew (1998) emphasized, if good preference–performance correspondence really exists, it may be masked by the experimental methodology employed.

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