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Larval survival of the phytophagous ladybird, *Epilachna yasutomii* (Coleoptera, Coccinellidae), on the blue cohosh, *Caulophyllum robustum* (Ranunculales, Berberidaceae), grown under different environmental conditions

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Larval survival of four local populations of *Epilachna yasutomii* in the southern part of Nagano Prefecture was evaluated on leaves of blue cohosh, *Caulophyllum robustum*, growing at two different sites, Takatoh and Nakatachi. Based on larval survival on leaves of Takatoh *C. robustum*, Takatoh *E. yasutomii* was clearly distinguishable from the three populations in the Minami-Shinano area (Akasawa, Nakatachi and Tenryu). Takatoh *E. yasutomii* developed successfully to emergence on *C. robustum* from both sites, while Minami-Shinano populations showed a very low survival rate when given Takatoh *C. robustum*. Under controlled plant growth conditions, larval survival of Akasawa *E. yasutomii* was significantly reduced when given *C. robustum* leaves, from either site, exposed to direct solar radiation, which suggested that larval survival was influenced by environmental conditions at the growing sites rather than genetic differences between the plant populations. In contrast, Takatoh *E. yasutomii* developed well on *C. robustum* leaves from either site exposed to direct solar radiation. Takatoh *E. yasutomii* appears to have some defensive mechanism that allows it to overcome a substance deterring larval development, which increases in leaves exposed to direct solar radiation.

Key words: *Caulophyllum robustum*; *Epilachna yasutomii*; host plant suitability; plant–insect relationship; sunlight intensity.

INTRODUCTION

Among the phytophagous ladybird group, the *Epilachna vigintioctomaculata* complex, *Epilachna yasutomii* shows the largest geographical variation in host plant preference. The species has a local distribution on some cultivated solanaceous plants and wild plants from various families (e.g. *Caulophyllum robustum* [Berberidaceae], *Scopolia japonica* [Solanaceae], *Panax japonicium* [Araliaceae] and *Chelidonium japonicium* [Papaveraceae]; Katakura 1981, 1986). Previous studies under laboratory conditions have reported that all *E. yasutomii* populations in Japan are able to develop well, in both immature and adult stages, on leaves of the blue cohosh, *C. robustum* (Hoshikawa 1983; Katakura 1986).

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However, a preliminary experiment in 1987 and 1988 showed that larval survival of some *E. yasutomii* populations varied markedly between *C. robustum* grown at different sites in Nagano Prefecture (Y. Shirai, unpubl. data). This suggests the occurrence of varieties in Japanese *C. robustum*, because the blue cohosh, a perennial herb growing mainly in forests, includes only one species, and no subspecies or geographical variation in morphology or chemical components has been reported from Japan (Kitamura & Murata 1961; Tamura 1982; Terabayashi 1989).

Wild host plants of *E. yasutomii* (*C. robustum, P. japonicium* and *C. japonicium*) produce a number of characteristic secondary metabolites, alkaloids or saponins (Mitsuhashi 1988). Secondary metabolites in plants are frequently influenced by environmental factors such as light intensity, soil nutrients and other plant stresses (Waterman & Mole 1989).

Therefore, the environmental factors at sites where plants occur naturally should be taken into account when these plants are used in experiments on host plant suitability or food habits for insects. Regrettably, there has been no phytochemical study of the host plant suitability of the *E. vigintioctomaculata* complex.

The present study was conducted as the first step in a phytochemical approach to understanding the host plant suitability for *E. yasutomii* and other *Epilachna* beetles. First, in order to verify the preliminary result mentioned previously, larval survival was evaluated among four local populations of *E. yasutomii* distributed in the southern part of Nagano Prefecture, using leaves of *C. robustum* taken from two different sites. Further, larval survival was evaluated when *E. yasutomii* was reared on *C. robustum* grown under different environmental conditions with controlled sunlight intensity and temperature. This experiment aimed to elucidate whether genetic differences between plant populations or epigenetic ones, induced by environmental factors at the sites where the plants had grown, caused the differences in host plant suitability for *E. yasutomii* populations.

METHODS

Plant materials

At a glance, Takatoh *C. robustum* has a darker green and a harder leaf than *C. robustum* from Nakatachi. Thirty discs (2 cm in diameter) of leaves collected from each site on 6 June 1990 were weighed and showed that Takatoh *C. robustum* was heavier and contained more water than Nakatachi *C. robustum*. In addition, *C. robustum* at Takatoh showed a longer growing period above ground than at Nakatachi; the latter withered in mid-August (Table 1).

A systematic study on the basis of leaf morphology (shape of leaflet) showed no clear differences between the two plant populations (Takatoh and Nakatachi) to distinguish them as different taxa such as species, subspecies or variety (S. Terabayashi, pers. comm. 1992). The present study, therefore, describes the two blue cohosh populations as Takatoh *C. robustum* and Nakatachi *C. robustum*.

Insects

Two survival values (survival rate and development period in the immature stages) were evaluated for four local *E. yasutomii* populations (Takatoh, Akasawa, Nakatachi and Tenryu; Fig. 1). The Takatoh population depends solely on the wild solanaceous herb *S. japonica* (deadly nightshade) in Nakaya, Takatoh (Shirai 1988). Takatoh *C. robustum* growing in Hiji, about 10 km distant from Nakaya, is not used as a host plant by the Takatoh *E. yasutomii* population. In the Minami-Shinano area, south and about 60 km distant from Takatoh, Akasawa and Tenryu *E. yasutomii* populations depend on some cultivated solanaceous plants (potato, tomato and eggplant), while the Nakatachi population feeds only on *C. robustum* (Shirai 1991).

Larval survival on *C. robustum* grown in two native sites

Overwintered beetles of four *E. yasutomii* populations were collected from their respective natural

Table 1 Comparision of blue cohosh, *Caulophyllum robustum* collected from different sites in Nagano Prefecture

Locality	Nakatachi, Minami-shinano (875 m a.s.l.)	Hiji, Takatoh (840 m a.s.l.)
Habitat	Japanese cedar forest with shrub layer	Japanese cedar forest without shrub layer
Phenology		
Sprout	Mid-April	Mid-April
Withering	Mid-August	Early-October
Leaf weight (mg/cm^2)*		
Fresh weight (F)	7.4 ± 0.8	8.8 ± 1.0**
Dry weight (D)	1.4 ± 0.2	2.0 ± 0.2**
Leaf water content (F − D)/D	4.29	3.40

*Mean ± SD ($n = 30$); ** significant differences between two localities at $P = 0.01$ level (t-test).

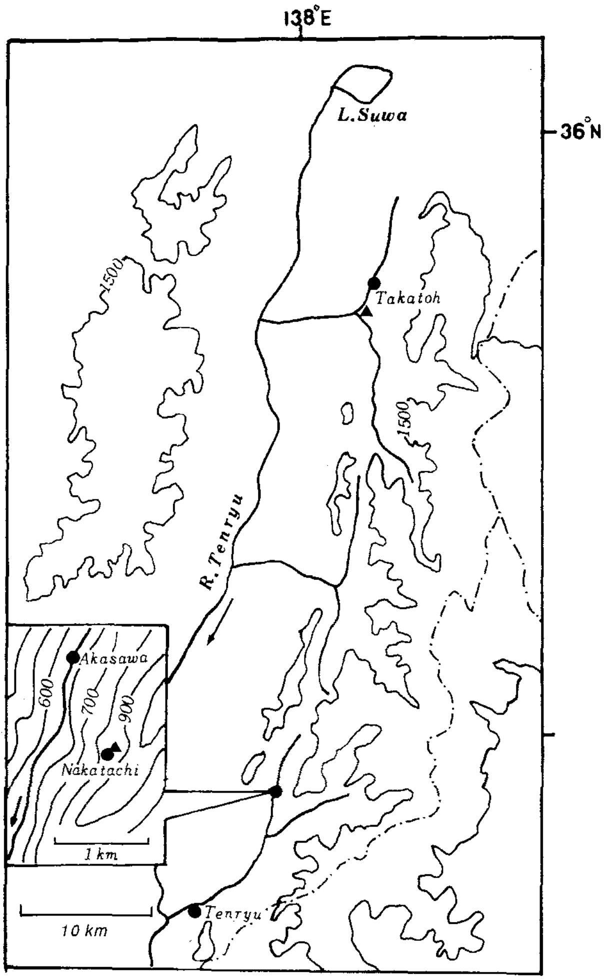

Fig. 1. Locations of the four *Epilachna yasutomii* populations (●) and the blue cohosh, *Caulophyllum robustum* (Berberidaceae) population (▲) used in the present study.

host plants in spring 1989 for the Takatoh, Nakatachi and Akasawa populations and in spring 1991 for the Tenryu population. Hatched larvae from eggs produced by pairs from the same population were assayed. The larvae of the four populations were reared on leaves of both Takatoh and Nakatachi *C. robustum* and larvae of two populations (Takatoh and Nakatachi) were also reared on *S. japonica* leaves. Seven to eight hatched larvae were transferred to a plastic dish (9 cm diameter, 5 cm deep, covered with polyester gauze) and reared to emergence. A fresh leaf was added to the dish at intervals of 1 or 2 days until the third instar and every day during the fourth instar stage. Fresh leaves of *C. robustum* were collected at intervals of about 10 days from the native sites (Takatoh and Nakatachi), and the leaves were kept in a sealed plastic box at 5 °C, which was able to keep them fresh for about 10 days. Leaves of *S. japonica* were taken from a plant grown in the field at the National Institute of Agro-Environmental Sciences (NIAES), Tsukuba. The larvae were reared under constant conditions of 23 °C and about 60% relative humidity, with a light/dark regime of 16/8 h.

Larval survival on *C. robustum* under controlled growth conditions

Control of sunlight intensity

Takatoh and Nakatachi *C. robustum* were transplanted from their native sites to the field at NIAES in mid-May 1991. The plants, in unglazed flower pots (30 cm diameter, 25 cm deep), were placed under trees, where they never received direct solar radiation. During 9 days from 26 May to 3 June, *C. robustum* were grown at four different light intensities (100%, 56%, 36% and 21% of sunlight). The plants were placed in direct sunlight and the treatments shaded with one to three layers of #600 black cheesecloth net. The weather was fine from 26 to 30 May, rainy or cloudy from 31 May to 3 June, and the cumulative solar radiation for the 9 days reached 133.6 MJ m^{-2}. All the pots were watered well every day. Leaves were collected on 3 June 1991, and kept in a sealed plastic box at 5 °C. For Akasawa and Takatoh *E. yasutomii* populations, five to six hatched larvae were transferred to plastic dishes (see previous experiment) and were reared until the fourth instar stage on leaves of *C. robustum* grown under the different sunlight conditions (except the 56% treatment for Takatoh *E. yasutomii*). Leaves were replaced at intervals of 1–2 days. The insects were reared under constant conditions of 25 °C and about 60% relative humidity, with a light/dark regime of 16/8 h.

Control of temperature

Pots of *C. robustum* transplanted from Nakatachi were grown, from 24 May to 5 June 1991 under four different temperature conditions (15, 20, 25 and 30 °C) in the laboratory. The light/dark regime was 16/8 h and the illumination intensity in the photophase was about 500 lx, almost equal to that of shading with three layers of cheesecloth net in the field. All pots were well watered every day. Leaves were collected on 5 June, and kept in a sealed plastic box at 5°C. A larval assay was conducted only for Akasawa *E. yasutomii*, with the same rearing procedure as the former experiment.

The statistical significance of all the results was tested by Mann-Whitney *U*-test ($P = 0.05$) for the larval survival rate, and by *t*-test ($P = 0.05$) for the developmental period.

RESULTS

Larval survival on *C. robustum* grown in two native sites

The survivorship curves and developmental periods for larvae of the four *E. yasutomii* populations reared on leaves of *C. robustum* from the native sites (Takatoh and Nakatachi) are given in Fig. 2 and Table 2, respectively. Takatoh *E. yasutomii* showed a high emergence rate of more than 90% and almost the same developmental periods on *C. robustum* from both sites. The other three *E. yasutomii* populations (Nakatachi, Akasawa and Tenryu) developed to emergence on Nakatachi *C. robustum*, but showed a very low survival rate on Takatoh *C. robustum*. In these three populations, although young larvae could feed on Takatoh *C. robustum* during the initial 5–7 days, most individuals died of miscarriage of exuviation or discoloration. The few individuals that did develop on Takatoh *C. robustum* had a significantly longer developmental period than those reared on Nakatachi *C. robustum* (Table 2).

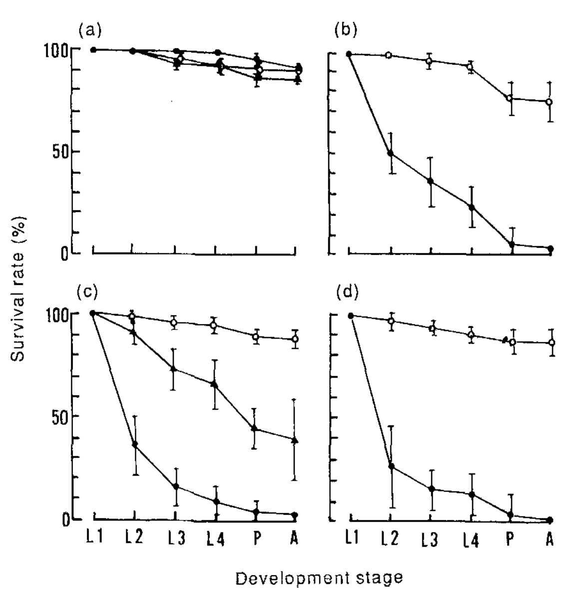

Fig. 2. Survivorship curves during the immature stages in *E. yasutomii* populations, at (a) Takatoh, (b) Tenryu, (c) Nakatachi and (d) Akasawa, reared with different food plants. Vertical bars indicate ±SD. Developmental stage: L1–L4 = first to fourth instar larva, P = pupa, A = adult. Food plants: (○) Nakatachi *C. robustum*; (●) Takatoh *C. robustum*; (▲) Takatoh *Scopolia japonica*.

When reared on *S. japonica* leaves, Takatoh *E. yasutomii* showed the same high survival rate as those on the two types of *C. robustum* (Fig. 2), but developmental periods were significantly shorter (Table 2). Nakatachi *E. yasutomii* showed a low survival rate of about 50% on *S. japonica*, significantly different from those on both *C. robustum*. Larvae of Nakatachi *E. yasutomii* could feed on *S. japonica* leaves, but half the individuals died of miscarriage of exuviation from the second to fourth instar stages. Developmental periods were significantly shorter on *S. japonica* than on Nakatachi *C. robustum* (Table 2).

Larval survival on *C. robustum* grown under different sunlight conditions

Figure 3 shows the survivorship curve from first to fourth instar larva in Akasawa and Takatoh *E. yasutomii*, when larvae were reared on *C. robustum* grown under different sunlight intensities. On Nakatachi *C. robustum*, the survival rate of Akasawa *E. yasutomii* was significantly lower in non-shaded conditions (100% of sunlight) than in the three shaded treatments (56%, 36% and 21%); there were no significant differences among the three shaded treatments. Most of the young larvae could feed on a leaf without shading, but more than half died, mainly of miscarriage of exuviation. A similar tendency was observed on Takatoh *C. robustum*. The developmental period of Akasawa *E. yasutomii* was significantly longer in the non-shaded than in the three shaded treatments of Takatoh *C. robustum*, while there were no significant differences among the four sunlight treaments of Nakatachi *C. robustum* (Table 3).

Takatoh *E. yasutomii* showed high survival rates of more than 80% in every sunlight condition, and no significant difference was found between the non-shaded and shaded treatments in either *C. robustum* (Fig. 3). The developmental period of Takatoh *E. yasutomii* showed no significant differ-

Table 2 Developmental period during immature stages in *E. yasutomii* populations with different food plants

E. yasutomii population	Food plant	*n*	Developmental period (days)* Larva	Pupa	Total
Takatoh	Nakatachi *C. robustum*	16	15.7 ± 1.3^{a}	9.9 ± 0.6^{a}	25.5 ± 1.2^{a}
	Takatoh *C. robustum*	15	15.8 ± 1.3^{a}	9.3 ± 1.1^{ab}	25.1 ± 1.7^{a}
	Takatoh *S. japonica*	11	13.5 ± 1.1^{b}	9.0 ± 0.8^{b}	22.5 ± 1.6^{b}
Nakatachi	Nakatachi *C. robustum*	16	15.8 ± 0.9^{a}	9.9 ± 0.6^{ab}	25.7 ± 1.4^{a}
	Takatoh *C. robustum*	18	21.8 ± 4.5^{b}	10.5 ± 0.7^{a}	29.8 ± 0.4^{b}
	Takatoh *S. japonica*	12	14.2 ± 1.0^{c}	9.2 ± 0.7^{b}	23.1 ± 1.2^{c}
Akasawa	Nakatachi *C. robustum*	12	17.6 ± 1.2^{a}	10.0 ± 0.5	27.6 ± 1.4
	Takatoh *C. robustum*	20	22.5 ± 0.7^{b}	13.0	35.0
Tenryu	Nakatachi *C. robustum*	10	15.1 ± 0.9^{a}	9.6 ± 0.5	24.9 ± 0.9
	Takatoh *C. robustum*	12	23.5 ± 2.4^{b}	10.0	32.5

*Values (mean ± SD) followed by different letters within the same column in the same population are significantly different at $P = 0.05$ level (*t*-test).

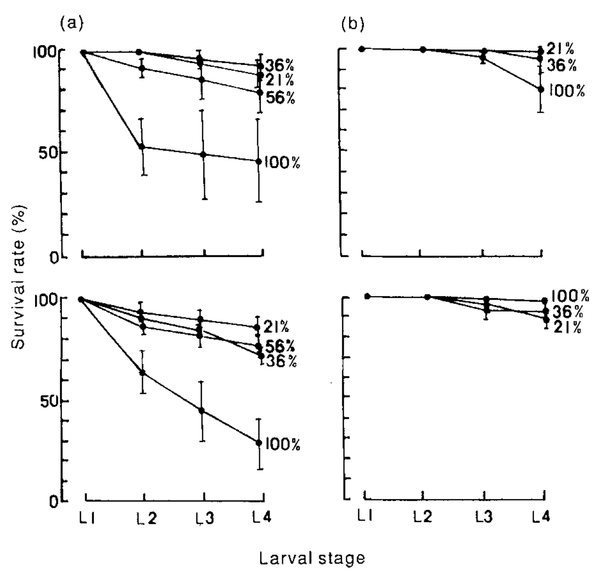

Fig. 3. Survivorship curves during the larval stages in *E. yasutomii* populations at (a) Akasawa and (b) Takatoh, reared on *C. robustum* which had been taken from two different localities: (Nakatachi [top] and Takatoh [bottom]) and exposed to different sunlight intensities (indicated by percentages) at the experimental field. Vertical bars indicate ± SD.

ence between non-shaded and shaded treatments in both *C. robustum* (Table 3).

Larval survival on *C. robustum* grown under different temperature conditions

Figure 4 and Table 4 show the survivorship curves and developmental periods from first to fourth instar larvae of Akasawa *E. yasutomii*, when reared on Nakatachi *C. robustum* grown under four different temperature conditions. Survival rate and developmental period were best on leaves at 15 °C, and were significantly different from those at the other three temperatures (20, 25 and 30 °C). There were no significant differences in survival rate nor in developmental period among the other three temperatures, and all showed a high survival rate of more than 80%.

DISCUSSION

Environmental factors influencing larval survival

The present data (Table 2 and Fig. 2) indicated that a blue cohosh, *C. robustum* on which some *E. yasutomii* populations cannot develop to emergence, exists in Japan. The results (Fig. 2) also showed that the host plant preference of *E. yasutomii* populations in the southern part of Nagano Prefecture distinguishes the Takatoh population from the three populations distributed in the Minami-Shinano area (Nakatachi, Akasawa and Tenryu; see Fig. 1). In addition, inhibition of larval development on *C. robustum* was observed only in these three populations. Therefore, in this section, these three populations are grouped as the 'Minami-shinano population' and environmental factors influencing larval development are considered only for Minami-Shinano *E. yasutomii*.

Table 3 Larval developmental period during the first to fourth instar in two *E. yasutomii* populations reared on *C. robustum* grown under different sunlight intensities

E. yasutomii population	*C. robustum*	Relative light intensity (%)	*n*	Developmental period (days)*
Akasawa	Nakatachi	100	9	11.3 ± 1.0[a]
		56	11	11.6 ± 1.1[a]
		36	11	10.5 ± 0.7[a]
		21	12	11.5 ± 0.8[a]
	Takatoh	100	9	12.8 ± 0.6[a]
		56	11	11.1 ± 1.3[b]
		36	11	11.3 ± 0.6[b]
		21	9	11.3 ± 1.0[b]
Takatoh	Nakatachi	100	9	10.1 ± 1.5[a]
		36	9	8.9 ± 0.5[a]
		21	9	8.9 ± 0.3[a]
	Takatoh	100	9	8.8 ± 0.4[a]
		36	9	8.8 ± 0.4[a]
		21	9	8.5 ± 0.4[a]

*Values (mean ± SD) followed by different letters within the same *C. robustum* in the same population are significantly different at $P = 0.05$ level (*t*-test).

The controlled sunlight intensity experiment indicated that there was no difference in the larval survival rate between two *C. robustum* populations. A significant reduction in survival rate occurred only when plants were exposed to direct solar radiation (Fig. 3). These results and a systematic study on *C. robustum* (S. Terabayashi, pers. comm. 1992) suggest that the difference in larval survival rates between the two types of *C. robustum* (Fig. 2) resulted from variation in the environmental conditions where the plant was growing, rather than from a genetic variation between the plant populations.

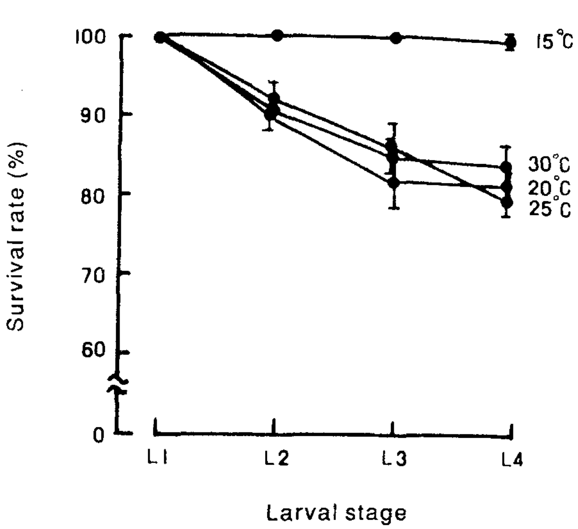

Fig. 4. Survivorship curve during the larval stage in the Akasawa population of *E. yasutomii* reared on Nakatachi *C. robustum* grown under four different temperature conditions in the laboratory. Vertical bars indicate ± SD.

Plant leaf toughness, water content or amount of secondary metabolites are easily influenced by a number of extrinsic environmental factors. Major soil nutrients and incident light intensity, and the interplay between them are the most frequently implicated variables. Temperature (high temperature stress) or drought (water stress) associated with light intensity are also involved (Waterman & Mole 1989). In the present study, effects of soil nutrients or water stress can be discounted, as both *C. robustum* transplanted from the native sites were grown in pots under the same soil conditions and were well watered. Therefore, the most important factor is thought to be sunlight conditions, especially whether the plant is exposed to direct solar radiation or not. Temperature conditions seem to be less important than sunlight conditions, because fatal inhibition of larval development did not occur when reared on leaves grown at a high temperature (30 °C) in shaded conditions in the laboratory (Fig. 4).

Shading to some extent reduces the photosynthetic ability of plants, and plants grown under low light conditions are vulnerable to insect attack

Table 4 Larval developmental period during the first to fourth instar in the Akasawa *E. yasutomii* population reared on *C. robustum* under different temperatures in the laboratory

Temperature (°C)	No. replications	Developmental period (days)*
15	14	9.4 ± 0.7^a
20	9	10.9 ± 0.7^b
25	9	11.7 ± 0.8^b
30	13	11.8 ± 1.4^b

*Values (mean ± SD) followed by different letters are significantly different at $P = 0.05$ level (t-test).

(Berenbaum 1988). The phenomenon of sunlight conditions rapidly inducing toughness or secondary metabolism of the host plant, and in turn influencing the survival of insect herbivores has been reported for bread wheat and the white stem sawfly, *Cephus cinctus* (Holmes 1984), nine plant families including the Berberidaceae and the mosquito, *Aedes atropalpus* (Philogene *et al.* 1984), corn and the European corn borer, *Ostrinia nubilalis* (Manuwoto & Scriber 1985), the soybean and the cabbage looper, *Trichoplusia ni* (Khan *et al.* 1986), and willow, *Salix dasyclados*, and the willow beetle, *Galerucella lineola* (Larsson *et al.* 1986).

In the present study, young larvae of *E. yasutomii* could feed on *C. robustum* leaves without inhibiting host searching or feeding behavior, but most larvae died of miscarriage of exuviation or discoloration, when reared on Takatoh *C. robustum* (Fig. 2) or on non-shaded leaves (Fig. 3). From a preliminary chemical approach to *C. robustum* exposed to direct solar radiation, the acid and neutral fractions of the solution extracted from leaves with 80% acetone deterred larval development of *E. yasutomii* at almost the same rate as in the assay using fresh leaves; however, the chemical substance is not yet identified (Shirai & Fujii, unpubl. data). This suggests that an increase in a plant chemical in leaves may deter larval development or exuviation, when the plant is grown under high sunlight conditions, especially with exposure to direct solar radiation.

Caulophyllus robustum contains a number of characteristic secondary metabolites, such as saponin, tannin, alkaloid and terpenoid (Hegnauer 1964; Gibbs 1974). There are still few data about the plant stress-mediated effect of sunlight conditions on insect survival, and interactions among these factors are likely to be very complicated. For future phytochemical examinations, it is important to determine initially whether the interaction is influenced by visible sunlight or by solar ultraviolet light (Berenbaum 1988).

Host plant utilization ability of Takatoh *E. yasutomii*

The host plant range of Takatoh *E. yasutomii* clearly differed from that of Minami-Shinano *E. yasutomii* populations (Nakatachi, Akasawa and Tenryu; Figs 2, 3). Accordingly, Takatoh *E. yasutomii* appears to possess a defensive mechanism to overcome whatever plant substance inhibits larval development of Minami-Shinano *E. yasutomii*.

When plants have a toxicity to insects under high sunlight, herbivorous insects may adopt defensive features, such as behavioral avoidance in time or space to prevent exposure to direct solar radiation (Tallamy 1986), or physiological or biochemical defenses, which enable the insects to avoid or prevent direct exposure to sunlight or photoactivation of plant secondary metabolites (Brattsten 1986). Takatoh *E. yasutomii* may have a superior biochemical defense than Minami-Shinano *E. yasutomii*, such as a metabolic ability for detoxication, because the feeding behavior of larvae was not conspicuously different among the *E. yasutomii* populations.

Takatoh *E. yasutomii* seems to have acquired a higher host plant utilization ability, independent of the interaction between this population and *C. robustum* grown under high sunlight, because Takatoh *E. yasutomii* depends solely on *S. japonica* in nature, and not on *C. robustum*. However, the low survival rate (less than 50%) in Minami-Shinano (Nakatachi) *E. yasutomii* when reared on *S. japonica* (Fig. 2) suggests, in part, that the greater survival ability of Takatoh *E. yasutomii* has resulted from utilizing *S. japonica* as the natural host plant. *Scopolia japonica* produces a number of characteristic secondary plant compounds, such as tropane alkaloids (Mitsuhashi 1988). If the Takatoh *E. yasutomii* has evolved a defensive ability to adapt perfectly to a harmful substance in *S. japonica*, this population may be able to overcome plant substances that occur in *C. robustum* under high sunlight conditions. This hypothesis may be confirmed if the compound produced in *C. robustum* exposed to direct solar radiation is identified as an identical or functionally related substance to that in *S. japonica*.

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