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Potential distribution area of the Mexican bean beetle, *Epilachna varivestis* (Coleoptera: Coccinellidae) in Japan, estimated from its high-temperature tolerance

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Abstract

Thermal responses in regard to female oviposition and larval development were investigated in the invasion population of the Mexican bean beetle, *Epilachna varivestis* whose presence was initially confirmed in Yamanashi and Nagano Prefectures, central Japan in 1997. Oogenesis in the female was inhibited when exposed to 27.5°C for five continuous days. Larval development was inhibited markedly at 30°C, and survival rate declined to nearly 0% when exposed to 32.5°C for more than five days. Based on these high-temperature stresses and the 30-year average temperature data in Japan (1961–1990), we estimated the potential distribution area of *E. varivestis* in Japan. It is predicted that *E. varivestis* will be less abundant in the south-western areas of central Japan, while this beetle could survive efficiently and maintain a high population level in the mountainous areas of central Japan, and in almost all of northern Japan (Tohoku and Hokkaido).

Key words: *Epilachna varivestis*, exotic insect, high-temperature, predicted occurrence area

INTRODUCTION

The Mexican bean beetle, *Epilachna varivestis* Mulsant (henceforth abbreviated as MBB), was initially confirmed in the highland areas of Nagano and Yamanashi Prefectures, central Japan in autumn of 1997 (Fujiyama et al., 1998). Up to that time, the MBB had been distributed only in Central and North America (CABI, 1998), and the Japan Plant Protection Station has designated this species as a “foreign pest of major quarantine concern” (JPPA, 1985). As of the summer of 2000, the distribution of MBB has been limited to the above two prefectures (Matsumoto et al., 2000; G. Toyoshima, personal communication), however, severe feeding damage has been found in leguminous crops of the genus *Phaseolus*, mainly the common bean, *P. vulgaris* and the scarlet runner bean, *P. coccineus* (Fujiyama et al., 1998; Funakubo et al., 1998). Abe et al. (2000) reported that the colonized MBB population in Japan could achieve as high a reproductive performance when feeding on the adzuki bean, *Vigna angularis* L. as on *Phaseolus* plants. As the scarlet runner bean and adzuki bean are major crops not only in the highlands of central Japan but also in the northern parts of Japan (Tohoku and Hokkaido), we must closely monitor the invasion by the current MBB population into the northern parts of Japan.

The current distribution of the MBB is limited to highland areas at altitudes of 500 to 1,400 m, with this species being rarely found in lowland areas of less than 500 m, where the daily maximum temperature reaches 35°C in midsummer (Funakubo et al., 1998; Toyoshima and Funakubo, 1998; Matsumoto et al., 2000). Many North American researchers have reported that the reproduction and larval development of MBB were severely inhibited by high temperatures between 27 and 32°C (Bernhardt and Shepard, 1978; Kitayama et al., 1979; Wilson et al., 1982; Fan et al., 1992). The current distribution in Japan is broadly consistent with the above laboratory studies.

The MBB is considered to be native to the plateau region of tropical Central America (southern Mexico and Guatemala) (Biddle et al., 1992), and females do not show a clear reproductive diapause even under short photoperiod (10L–14D) (Elden, 1991). In central Japan at latitudes of 36°N, mating and oviposition are frequently found

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in late September (Fujiyama et al., 1998). Saks (1993) implied that a qualitative change in host plant might be related to the induction of hibernation diapause of MBB. However, between early summer and early autumn when *Phaseolus* beans or adzuki bean have fresh green leaves, we are able to reliably estimate the potential distribution area of MBB in Japan, based solely on the temperature conditions, without incorporating photoperiod or host plant conditions.

In the present study, we paid special attention to inhibition by high temperature stress described in the above North American studies and field reports in Japan (Funakubo et al., 1998; Toyoshima and Funakubo, 1998; Matsumoto et al., 2000). In regard to reproduction by female adults and larval development, detailed temperature treatments were designed to determine a critical point of high temperature stress. On the basis of these thermal response experiments and the 30-year average temperature data (henceforth described as the normals) in Japan (1961–1990) (JMA, 1991), we estimated the potential distribution area of MBB where greater attention should be paid to the expansion of the insect's current distribution area and to a possible new invasion by a different exotic population.

MATERIALS AND METHODS

Insects. For the experiments on oviposition by adults and hatching, we collected 50 pairs of MBB adults in common bean fields in Sutama town, Yamanashi Prefecture, in early September 1997. Their progeny were reared for two or three generations in a mesh cage (40×40×40 cm) with a potted kidney bean, *Phaseolus vulgaris* L. var. *humilis*, under the condition of 20°C and 16L–8D photoperiod. In early August 1998, for the experiments on larval survival and development, we also collected 40 pairs of MBB adults in Sutama town, and their progeny were reared for three or four generations in the same manner. All laboratory experiments were conducted under a 16L–8D photoperiod at the National Institute of Agro-Environmental Sciences. Kidney bean plants were grown in the greenhouse and was used as the food plant.

Experiment 1: Female survival and oviposition under constant temperature conditions. When the adults reared in the above-described mesh cage reached 10 days of age, one pair of adults was transferred to a plastic dish (9 cm diameter, 4.5 cm deep) with fresh kidney bean leaf and was maintained at 13 different constant temperatures (5 to 35°C at 2.5°C intervals). The number of eggs laid was counted daily. Twenty dishes were replicated for each temperature treatment. Fresh bean leaves were replaced every other day at temperatures between 5 and 17.5°C, and daily between 20 and 35°C. Randomly selected egg-masses were kept at the same temperature as those in the oviposition experiment until hatching. Percent of hatch at 10, 12.5, 32.5, and 35°C was evaluated using the egg-masses laid between 20 and 25°C.

Experiment 2: Female survival and oviposition under variable temperature conditions. In the same manner as described in the above experiment, egg production and female survival were evaluated at two variable temperature conditions, 30°C×3 h+21.4°C×21 h and 30°C×6 h+20°C×18 h. The daily mean temperature was kept at 22.5°C and a thermophase of 30°C was set at the center of the light phase (16 h) for both temperature conditions. Fresh kidney bean leaves were replaced daily. Randomly selected egg-masses were kept at the same temperature condition as that described in the oviposition experiment until hatching.

Experiment 3: Hatchability of eggs exposed to high temperatures. After emergence, 30 pairs of females and males were introduced into a mesh cage (40×40×40 cm) at 20°C with a potted kidney bean. For periods of 10 and 30 days after emergence, the egg-masses laid on the bean leaves were collected every 12 h and were transferred into a sealed plastic dish (15 cm diameter, 9 cm deep). These dishes were exposed to high temperatures of 27.5, 30, 32.5, 35, and 37.5°C for the following periods, respectively; 1, 3, 6, 12, 18, 24, 36, 48, 72, 96, and 120 h. To prevent drying, water was sometimes added to filter paper in the dish. After the stated times of exposure to high temperatures, the egg-masses were kept at 25°C until hatching. For the control, egg-masses were constantly maintained at 25°C until hatching.

Experiment 4: Larval survival and development under constant temperature conditions. Egg-masses laid by the females reared at 20°C were used. Six hatched larvae were transferred to a plastic dish (9 cm diameter, 4.5 cm deep) and were reared at 13 different constant temperatures (5 to

Table 1. Survival and fertility of *Epilachna varivestis* reared under constant temperature conditions[a,b]

Temperature (°C)	No. of females	Longevity (days)	No. of eggs laid per female	No. of egg masses[c]	%, hatch[c]
5.0	20	35.9±28.4 bcd	0.0±0.0 a	—	—
7.5	20	93.9±46.4 e	0.0±0.0 a	—	—
10.0	20	194.2±96.8 f	3.5±9.2 a	45	0.0± 0.0 a
12.5	20	229.8±88.1 f	26.1±26.2 b	46	0.0± 0.0 a
15.0	20	187.7±68.3 f	212.8±91.2 c	53	25.0±29.0 b
17.5	20	53.4±11.3 d	265.3±117.1 c	45	82.1±33.5 c
20.0	20	46.7±17.9 d	365.9±270.4 c	18	86.1±33.5 c
22.5	20	41.6±11.9 d	290.0±181.3 c	44	86.9±28.9 c
25.0	20	30.6±11.2 c	215.8±234.1 c	37	82.4±37.7 c
27.5	20	23.3±9.2 b	164.6±153.4 c	33	46.4±48.7 b
30.0	20	19.2±4.5 b	60.0±52.8 b	14	0.7±1.8 a
32.5	20	14.1±2.7 ab	19.9±27.6 ab	28	0.0±0.0 a
35.0	20	12.5±0.9 a	0.0±0.0 a	—	—

[a] Mean±SD. Means followed by different letters are significantly different at the 5% level (Kruskal-Wallis test, Dunn's multiple comparison).

[b] Photoperiod condition: 16L8D.

[c] For 32.5, 30.0, 12.5 and 10.0°C, egg masses laid between 20 and 25°C were used.

—: Not examined.

35°C at 2.5°C intervals). Twelve dished were replicated for each temperature treatment. Fresh kidney bean leaves were replaced every other day until the third stadium, and daily during the fourth stadium.

Experiment 5: Larval survival and development under variable temperature conditions. In the same manner as that described in Experiment 4, larvae were reared under the following five variable temperature conditions: (1) 30°C×1 h+22.2°C×23 h, (2) 30°C×3 h+21.4°C×21 h, (3) 30°C×6 h+20°C×18 h, (4) 30°C×9 h+18°C×15 h, and (5) 30°C×12 h+15°C×12 h. For all variable temperature conditions, the daily mean temperature was kept at 22.5°C and a thermophase of 30°C was set at the center of the light phase (16L). Fresh bean leaves were replaced every other day until the third stadium, and daily during the fourth stadium.

RESULTS

Experiment 1: Female survival and oviposition under constant temperature conditions

Female longevity, the number of eggs laid per female (overall fecundity), and percent hatch are shown in Table 1. Females lived longest at 12.5°C and their longevity decreased with increasing temperatures between 12.5 and 35°C. The largest number of eggs was laid at 20°C and a relatively high egg production was maintained between 15 and 27.5°C. Egg production decreased significantly at temperatures of 12.5°C and lower, and 30°C and higher. None of the females laid eggs at 35°C, and at 7.5°C and lower. Percent hatch showed a high value of about 80–90% between 17.5 and 25°C, but decreased significantly at 15°C and less, and at 27.5°C and higher. At 27.5°C, female survival dropped markedly after the fifth day of temperature treatment, and the female survival and oviposition schedule showed different patterns from those at 22.5 and 25°C (Fig. 1), in which overall fecundity was not significantly different from that at 27.5°C (Table 1). At 30°C, female survival also decreased markedly after the fifth day of temperature treatment.

Experiment 2: Female survival and oviposition under variable temperature conditions

The effects of exposure time at 30°C were evaluated on female survival and egg production because significant inhibition of these traits occurred at 30°C in Experiment 1. No significant differences were seen regarding female longevity, egg production, or percent hatch, between the constant temperature (22.5°C) and two variable temperature treatments (Table 2). Under these two variable tem-

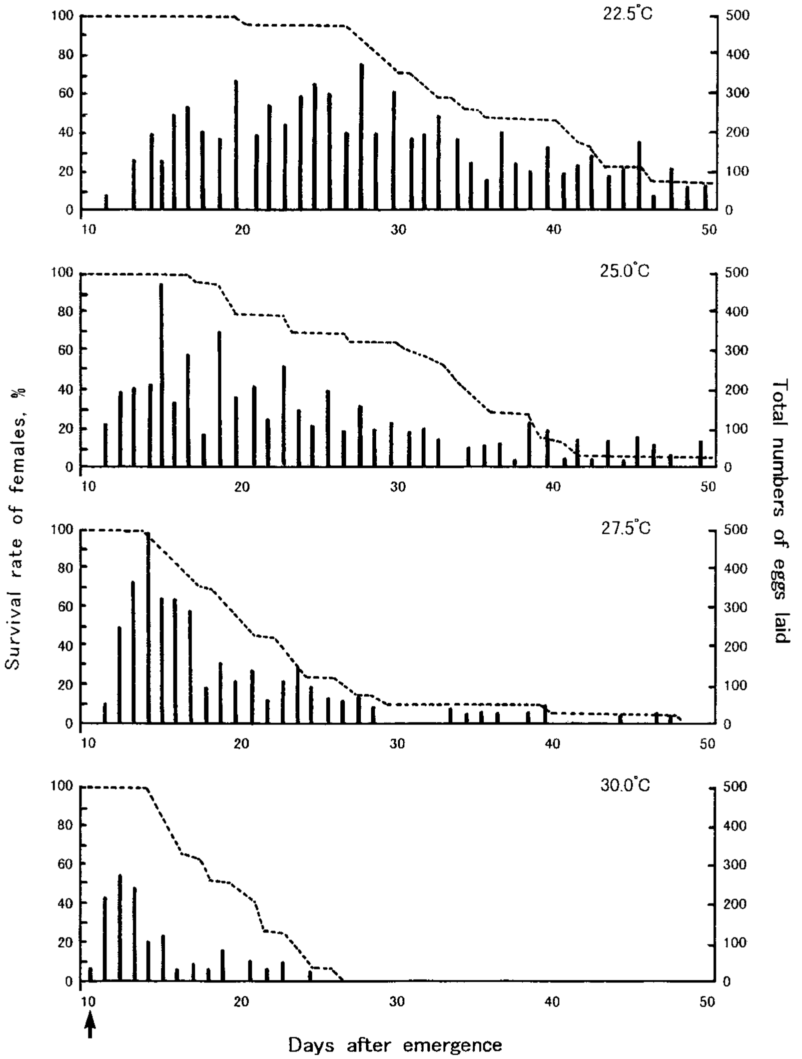

Fig. 1. Survival and oviposition schedules of *Epilachna varivestis* females reared at constant temperatures between 22.5 and 30°C. The histogram shows the total number of eggs laid per day, and the dotted line shows the survivorship curve for females. ↑: Each temperature treatment started at 10 days after emergence.

perature conditions, female survival and fecundity did not decrease at five or six days after the initiation of temperature treatment (Fig. 2).

Experiment 3: Hatchability of eggs exposed to high temperatures

In relation to the control (constant temperature of 22.5°C), a significant decrease in percent hatch occurred when egg-masses were exposed to 30°C for 18 h or more, or 32.5°C for 6 h or more (Table 3). Three hours or more at 35°C and 1 h at 37.5°C also caused significant inhibition of hatching. The egg-masses placed at 27.5°C could hatch normally within five or six days.

Experiment 4: Larval survival and development under constant temperature conditions

The highest emergence rate was seen at 20°C and a high rate of about 80–90% was maintained between 15 and 25°C (Table 4). At temperatures of 27.5°C and higher, emergence rates were significantly decreased mainly because of high mortality during the fourth larval stadium and pupal stages. Most emergent adults were malformed, having distorted elytra at conditions of 30 and 32.5°C, and no larvae reached the second stadium at 35°C. At a low temperature range, the emergence rate dropped significantly at 12.5°C, and most larvae died between the first and second stadium at 10°C. No larvae reached the second stadium at 5 and 7.5°C.

Table 2. Survival and fertility of *E. varivestis* reared under two variable temperature conditions[a,b]

Temperature (°C×h)	No. of females	Longevity (days)	No. of eggs laid per female	No. of egg masses	%, hatch
30×3+21.4×21	20	41.0±10.1 a	266.7±146.5 a	39	90.9±14.8 a
30×6+20.0×18	20	38.3±5.5 a	259.5±62.0 a	29	83.0±22.8 a
22.5×24 (constant)	20	41.6±11.9 a	290.0±181.3 a	44	86.9±28.9 a

[a] Mean±SD. No comparison showed significant difference at the 5% level (Kruskal-Wallis test, Dunn's multiple comparison).

[b] Two variable temperature experiments had the same daily mean temperature (22.5°C). All experiments were conducted under a photoperiod condition of 16L8D.

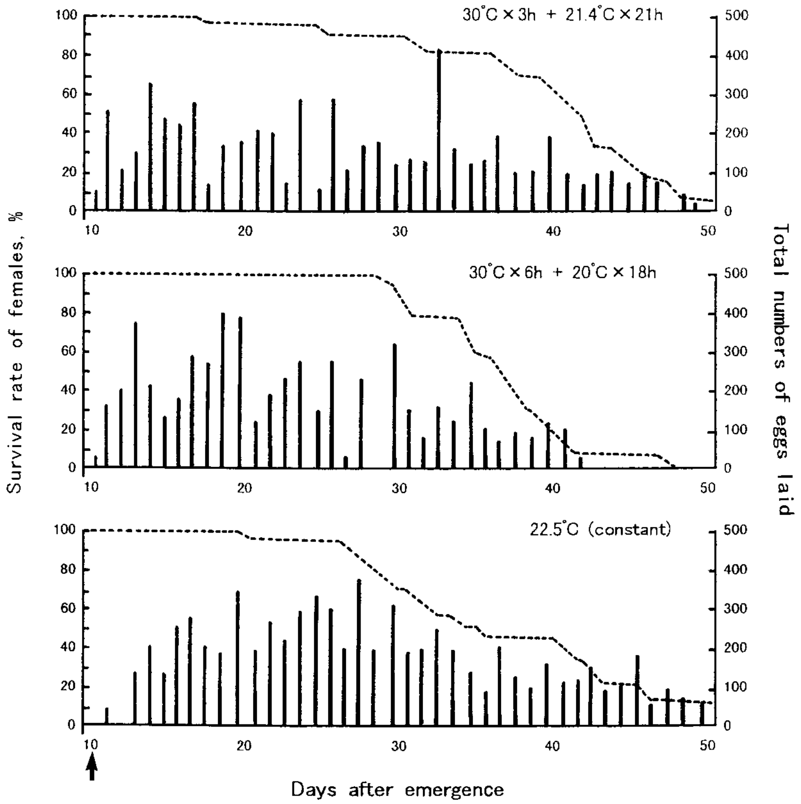

Fig. 2. Survival and oviposition schedules of *E. varivestis* females reared at two variable temperatures (top and middle) and at a constant temperature of 22.5°C (bottom). The histogram shows the total number of eggs laid per day, and the dotted line shows the survivorship curve for females. ↑: Each temperature treatment started at 10 days after emergence.

Experiment 5: Larval survival and development under variable temperature conditions

Because significant inhibition in terms of emergence rate and proportion of malformed adults was found at 30°C in Experiment 4, the effects of exposure time at 30°C treatment were evaluated in regard to larval survival and development. Under the three variable temperature treatments of 30°C for 1, 3, or 6 h, respectively, the emergence rates showed no significant differences between those of the control (constant temperature of 22.5°C). The emergence rate decreased significantly when larvae were exposed to 30°C for 9 h or longer (Table 5). Prolonged developmental periods occurred when larvae were exposed to 30°C for 6 h or longer, but malformed adults were not generated under any variable temperature conditions.

DISCUSSION

In regard to thermal response, particularly the high-temperature tolerance of MBB, survival and

Table 3. Hatchability (%) of egg masses exposed to high temperatures[a]

Exposure period (h)	Temperature (°C)				
	27.5	30.0	32.5	35.0	37.5
0 (Control) 85.0±22.1 (31)[b]					
1	—	68.7±32.7 (23)	70.9±35.4 (22)	65.4±32.2 (24)	28.8±36.9 (21)*
3	—	64.8±42.4 (23)	63.6±40.8 (21)	33.5±40.8 (26)*	4.6±18.1 (25)*
6	—	68.3±48.0 (23)	38.3±41.0 (21)*	14.0±28.5 (20)*	0.0±0.0 (20)*
12	—	69.3±35.5 (22)	34.1±42.3 (22)*	0.0±0.0 (21)*	—
18	—	44.6±45.2 (22)*	10.5±20.1 (22)*	—	—
24	—	35.0±38.9 (22)*	18.9±32.4 (27)*	—	—
36	—	45.0±38.8 (23)*	0.7±3.1 (22)*	—	—
48	—	42.4±41.4 (24)*	0.0±0.0 (28)*	—	—
72	75.0±22.6 (20)	18.1±27.5 (26)*	—	—	—
96	—	11.3±21.5 (27)*	—	—	—
120	80.0±23.7 (17)	0.7±1.8 (14)*	—	—	—

[a] Mean±SD (No. egg masses).

[b] The egg masses of the control were maintained at a constant temperature of 22.5°C. * shows significant difference between the control at the 5% level (by Mann-Whitney *U*-test).

—: Not examined.

Table 4. Larval survival and development of *E. varivestis* reared under constant temperature conditions[a,b]

Temperature (°C)	No. replication	Survival rate (%)			Developmental period (days)	Proportion of malformed adults (%)
		L-2	L-4	Adult		
5.0	12	0.0	0.0	0.0±0.0 c	—	—
7.5	12	0.0	0.0	0.0±0.0 c	—	—
10.0	12	19.5	0.0	0.0±0.0 c	—	—
12.5	12	81.9	29.2	2.8±9.6 c	87.0 a	0.0
15.0	12	98.6	95.8	88.9±13.0 a	55.5±2.7 b	0.0
17.5	12	100.0	97.2	93.1±11.1 a	41.9±1.4 bc	0.0
20.0	12	100.0	95.8	93.5±10.1 a	32.4±0.9 bcd	0.0
22.5	12	100.0	95.8	85.3±15.0 ab	26.9±1.1 cde	0.0
25.0	12	95.8	86.7	76.9±16.9 ab	21.7±0.8 de	0.0
27.5	12	97.2	87.5	62.2±18.2 b	20.1±0.8 e	0.0
30.0	12	100.0	84.7	30.0±34.6 bc	20.6±0.5 e	68.8
32.5	12	77.8	12.5	4.2±14.4 c	20.8 e	100.0
35.0	12	0.0	0.0	0.0±0.0 c	—	—

[a] Mean±SD. Means followed by different letters are significantly different at the 5% level (Kruskal-Wallis test, Dunn's multiple comparison).

[b] Photoperiod condition: 16L8D.

egg production by female adults were inhibited at temperatures of 27°C and higher (Kitayama et al., 1979). Larval development was inhibited at 30°C (Fan et al., 1992) or at 32°C (Wilson et al., 1982), and none of the first stadium larvae were able to reach the next stage when exposed to 32°C for 16 h (Bernhardt and Shepard, 1978). The most favorable temperature is about 22°C for both egg production (Kitayama et al., 1979) and larval development (Wilson et al., 1982). The results of the present study are in good accord with the results of the above reports because egg production and larval development showed appropriate values between 15 and 25°C, and because these traits were significantly inhibited at conditions over 27.5 or 30°C. In addition, the present detailed experiments on ther-

Table 5. Larval survival and development of *E. varivestis* reared under five variable temperature conditions[a,b]

Temperature (°C×h)	No. replication	Survival rate (%)			Developmental period (days)	Proportion of malformed adults (%)
		L-2	L-4	Adult		
30×1+22.2×23	12	98.6	90.6	87.5±13.1 a	24.7±0.5 b	0.0
30×3+21.4×21	12	97.2	90.6	85.5±12.9 a	25.1±1.1 b	0.0
30×6+20.0×18	12	97.2	78.3	61.1±27.8 ab	28.5±1.7 a	0.0
30×9+18.0×15	12	88.9	58.9	27.8±19.2 b	28.1±0.9 a	0.0
30×12+15.0×12	12	90.3	60.3	11.1±21.7 b	27.0±1.0 ab	0.0
22.5×24 (constant)	12	100.0	95.8	85.3±15.0 a	26.9±1.1 a	0.0

[a] Mean±SD. Means followed by different letters are significantly different at the 5% level (Kruskal-Wallis test, Dunn's multiple comparison).

[b] Five variable temperature experiments had the same daily mean temperature (22.5°C). All experiments were conducted under a photoperiod condition of 16L8D.

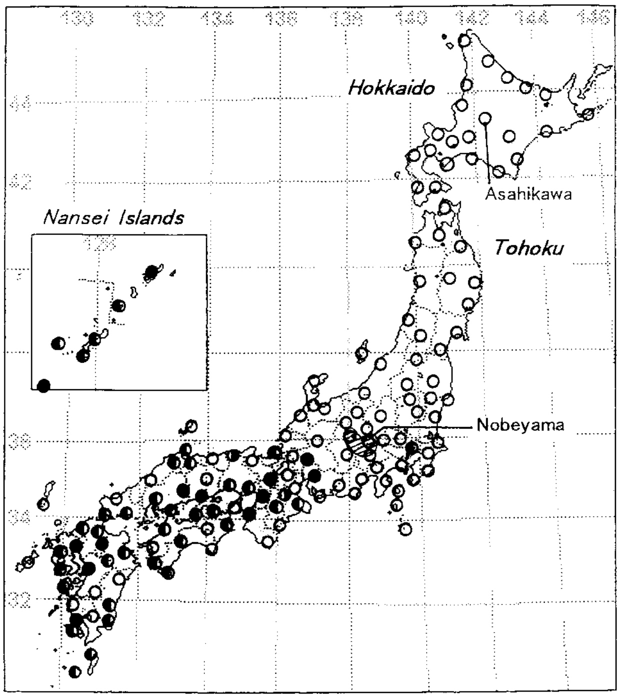

Fig. 3. Potential distribution area of *E. varivestis* in Japan, estimated from thermal response and the 30-year average temperature (the normals). ◐: Normals of pentad mean temperature ≧27.5°C (condition A), ◑: normals of pentad maximum temperature ≧32.5°C (condition B), ●: A and B, ○: neither A nor B, namely the open circles show a potential distribution area for *E. varivestis*. The shaded portion indicates the current distribution as of summer 2000.

mal response revealed that egg production (Table 1) and larval development (Table 4) were markedly inhibited at both lower and higher temperatures outside the favorable temperature range (15–27.5°C). Therefore, there exists a critical temperature point that causes fatal damage to both egg production and larval development of MBB.

For estimation of the insect's potential distribution area, particularly the area where MBB may damage leguminous crops during early summer and autumn in Japan, the temperature indices that it uses must be as practical as possible. First, for the principal temperature index that determines female reproduction, we adopted the normals of the pentad mean temperature ≧27.5°C from the climatic normals in Japan (1961–1990) (JMA, 1991). This is because a significant decrease in percent hatch occurred and females died suddenly after the fifth day of treatment at 27.5°C in Experiment 1 (Table 1, Fig. 1). The pentad corresponds to the five continuous days. Percent hatch in Experiment 3 showed that the high temperature of 27.5°C did not effect embryonic development after egg deposition (Table 3). Therefore, when females were exposed to 27.5°C for five continuous days, oogenesis was physiologically influenced, followed by a significant decrease in hatchability.

Second, as a practical high-temperature index that determines the inhibition of larval development of MBB, it may be reasonable to use a mean temperature ≧30°C, because the larval mortality rate and proportion of malformed adults were significantly higher at temperatures of 30°C or higher (Table 4). However, there are no locations where a mean temperature over 30°C has been recorded in terms of either pentad, decade, or monthly means from the climatic normals in Japan (JMA, 1991). The maximum temperatures of ≧30°C also fails to provide a reliable and practical temperature index, because no malformed adults were generated when larvae were exposed to 30°C for 12 h in Experiment 5, though larval survival rate decreased significantly under such temperature conditions (Table 5). Therefore, we adopted the pentad maximum temperature of ≧32.5°C as a high-temperature index that brings about fatal damage to larvae of MBB, because the second and third stadium larvae died specifically within 4 and 5 days after the 32.5°C treatment, in contrast to the case of the 30°C treatment in Experiment 4.

In the present study, we did not consider the inhibition of overwintering under winter climatic conditions, because it had been confirmed that MBB had already begun colonization five years earlier in Nobeyama, Nagano Prefecture at an altitude of 1,350 m (Fig. 3) (Fujiyama et al., 1998), where the mean and minimum monthly temperatures were −5.2°C and −11.3°C, respectively, in the coldest month (January). These hard winter conditions nearly correspond to those at Asahikawa, Hokkaido (Fig. 3), located in the northernmost part of Japan, whose mean and minimum monthly temperatures in January are −8.4°C and −13.4°C, respectively (JMA, 1991). Moreover, the MBB is able to survive the winters of New Brunswick and Quebec, Canada at latitudes of 45–46°N (Auclair, 1959; CABI, 1998), where the mean monthly temperature in the coldest month (January) is between −10 and −12°C, which is colder than at Asahikawa, Japan (NAO, 1997). From these reports and field studies, we considered that the reproduction and survival of MBB are not inhibited by the conditions of the winter season in any part of Japan.

Using the mean pentad temperature ≧27.5°C (condition A) and the maximum pentad temperature ≧32.5°C (condition B), the potential distribution area of the MBB was calculated (Fig. 3). Condition A, which inhibits female reproduction, was recorded at 47 locations of 158 meteorological stations in Japan (◐ in Fig. 3), and condition B, which inhibits larval development, was recorded at 15 of 158 stations (◑ in Fig. 3). Thirteen stations experienced both conditions (● in Fig. 3). Although 34 locations experienced condition A only, these locations also appear to be inappropriate areas for larval survival because the maximum pentad temperature was recorded between 30 and 31°C in most of these 34 locations. Based on the data described in Fig. 3, it is estimated that the MBB is unable to survive effectively in the Nansei Islands in the southernmost part of Japan, and that it will be unable to colonize about two thirds of the locations in the south-western parts of Japan. In contrast, it is estimated that almost the entire region comprising the northern parts of central Japan will be very suitable for both the reproduction and larval survival of MBB because most meteorological stations had neither condition A nor B (○ in Fig. 3). If the MBB invades into this area, the beetle could maintain a high population density during early summer and autumn under favorable temperature conditions. The Tohoku and Hokkaido areas belonging to the northern parts of central Japan are more important production areas of the scarlet runner bean and adzuki bean than is the current distribution area of MBB (Yamanashi and Nagano Prefectures), and these areas need to be acutely alert to new occurrences of MBB not only in *Phaseolus* bean fields but in adzuki bean fields (Abe et al., 2000). As the colonized MBB in Japan has little insecticide resistance, this species can be relatively easily controlled by many kinds of synthetic organic insecticides (Funakubo et al., 1998; Toyoshima and Funakubo, 1998). In addition, eradication programs may be successful control measures when a small population of MBB is discovered within a relatively limited area (Armitage, 1956). Therefore, it is important to detect spot occurrence of the MBB in its early stages in northern parts of central Japan.

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