Temperature tolerance of the diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae) in tropical and temperate regions of Asia

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Abstract

Temperature tolerance was investigated in nine populations of *Plutella xylostella* Linnaeus from tropical and temperate regions of Asia. At all rearing temperatures between 15 and 35°C, no clear differences were observed in female egg production or larval development between tropical and temperate populations. Thus, tropical populations did not show a high-temperature tolerance superior to that of the temperate populations. In all populations, the net reproductive rate (number of new females born per female) largely depended on the number of eggs laid per female, and egg production significantly decreased with increasing temperature ($P < 0.001$). Larval developmental rate also showed a significant positive correlation with temperature ($P < 0.001$). Per cent hatch of eggs and larval survival did not show a significant correlation with temperature: hatching was constant between 15 and 32.5°C, but considerably lower at 35°C. Larval survival was similar between 15 and 30°C, appreciably lower at 32.5°C and declined to 0% at 35°C. Based on these results, environmental conditions under which *P. xylostella* can maintain a high population density throughout the year in tropical and subtropical regions are discussed.

Introduction

The diamondback moth, *Plutella xylostella* Linnaeus (Lepidoptera: Yponomeutidae), a serious pest of cruciferous vegetables, is widely distributed from the tropical to the cool temperate regions of world (CAB, 1967; Talekar & Shelton, 1993; CABI, 1997). In many temperate areas of Japan, *P. xylostella* appears all year round but is less abundant in midsummer (Koshihara, 1986). Egg production and larval survival of *P. xylostella* are inhibited by temperatures above 30°C (Yamada & Umeya, 1972; Yamada & Kawasaki, 1983), and few cruciferous crops are cultivated under such high temperatures (Morishita *et al*., 1995; Shirai, 1996). Thus it has been assumed that the population density of *P. xylostella* in midsummer depends primarily on high temperature conditions.

Using a pheromone census recapture technique Kuwahara *et al*. (1995) reported that *P. xylostella* maintained consistently high population density throughout the year in central Thailand even during the hottest season, March to May, when the monthly mean temperatures were approximately 29 to 31°C. Their findings imply that *P. xylostella* from the tropical region of Thailand may be more adapted to high temperature conditions than would be a population from the temperate region of Japan. Further, Noran & Tang (1997) detected an allozymic difference between highland and lowland populations in Malaysia, suggesting the possibility of geographical divergence in *P. xylostella*.

Although many researchers have studied the thermal response of *P. xylostella* populations from various areas, previous investigations have been conducted separately using different strains, food plants, or procedures, and the respective results have been not evaluated on a similar scale (CABI, 1997). For example, in studies on Japanese and tropical Asian populations, Sarnthoy *et al*. (1989) used a wild

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population from Thailand as a tropical sample but used a laboratory-reared population as the sample from Japan. Umeya & Yamada (1973) evaluated only one Indonesian population as a sample of a tropical region, and documented negligible differences in thermal response between temperate and tropical populations.

Clear geographical variation has been little reported in *P. xylostella* (Zilahi-Balogh *et al.*, 1995; Chang *et al.*, 1997). *Plutella xylostella* is known as a migrant species and appears to migrate from the southern to the northern part of Japan during spring and early summer (Honda *et al.*, 1992). If any difference in thermal response is detected between tropical (or subtropical) and temperate populations, it could be useful evidence in a study of the origins of migrant moths in northern Japan. In the present study, a total of nine populations of *P. xylostella* were tested by uniformly consistent experimental procedures; these included a population from Thailand (Kuwahara *et al.*, 1995), and two Malaysian populations (lowland and highland) (Noran & Tang, 1997), where geographical differences have been implicated. In addition, tropical Vietnamese and Indonesian populations and four Japanese populations were tested, and thermal response, especially with regard to high-temperature tolerance, was evaluated in terms of oviposition and survival by females and of larval development.

Materials and methods

Insects

Fourth stadium larvae and pupae were collected from nine localities: Sapporo, Tsukuba, Kagoshima, Ishigaki, Bangkok, Ho-Chi-Minh, Cameron Highlands, Kuala Lumpur and Selatan (South Kalimantan) (table 1). Among the nine collection sites, Sapporo is the only one where *P. xylostella* is not able to overwinter (Honda *et al.*, 1992). Annual mean temperature, altitude, and other climatic data in table 1 and the text were based on documentation from the National Astronomical Observatory (1997).

Oviposition and survival by females

Each sample was reared for one generation at 26°C, 14L:10D on fully germinated radish seeds using the method of Koshihara & Yamada (1976), and the emerged adults were used in the experiment on female oviposition and survival. For the Kuala Lumpur population only, adults reared for five generations were used. Immediately after emergence, 50 males and 50 females were placed in a mesh cage in darkness, then mated pairs were transferred to a plastic dish (9 cm diameter, 4.5 cm deep) with a fresh cabbage leaf. The dish and cabbage leaf were replaced daily. Eggs laid on the dish and leaves were counted and kept at 26°C until hatching. Six populations (Sapporo, Tsukuba, Kagoshima, Bangkok, Ho-Chi-Minh and Selatan) were evaluated at seven different temperatures (15, 20, 25, 27.5, 30, 32.5 and 35°C), and three populations (Ishigaki, Cameron Highlands and Kuala Lumpur) were evaluated at five different temperatures (15, 20, 25, 30 and 35°C).

Larval development and survival

For six populations (Sapporo, Tsukuba, Kagoshima, Bangkok, Ho-Chi-Minh and Selatan), females and males reared for two or three generations were placed in a mesh cage with a potted young cabbage, and eggs laid on the leaves were collected. Ten hatched larvae were individually reared in a plastic dish (9 cm diameter, 4.5 cm deep) at seven different temperatures (15, 20, 25, 27.5, 30, 32.5 and 35°C). A fresh cabbage leaf was added to the dish every one to two days until the third stadium; daily during the fourth stadium for rearings between 15 and 27.5°C; and daily through the first to fourth stadium for rearings between 30 and 35°C. All experiments were conducted at 16L:8D.

Results

Oviposition and survival by females

Population characteristics, including the days elapsed before 50% oviposition, female longevity, number of eggs laid per female (overall fecundity), and percent hatch are shown in table 2. The days elapsed before 50% oviposition, (i.e. the number of days when the cumulative number of eggs reached 50% of total eggs laid), showed no significant differences among the nine populations at any temperature except at 25°C. At this temperature, the Tsukuba population expressed the shortest period (1.4 days) and Bangkok the longest period (2.6 days) which were significantly different from each other. However, there was no clear relationship that separated the temperate populations (Sapporo, Tsukuba, Kagoshima and Ishigaki) from the tropical populations (Bangkok, Ho-Chi-Minh, Cameron Highlands, Kuala Lumpur and Selatan). Female longevity showed no significant differences among the nine populations at 15°C and 27.5°C. Nor at 20, 25, 30, 32.5 or 35°C was there a clear difference distinguishing temperate from tropical populations. The number of eggs laid per female showed no significant

Table 1. Origin of *Plutella xylostella* populations examined in the present study.

Locality	Latitude	Altitude (m)	Annual mean temperature (°C)	Host plant	Collection date
Sapporo, Japan	43°N	17	8.2	Cabbage	July 25, 1995
Tsukuba, Japan	36°N	20	13.2	Cabbage	October 6, 1994
Kagoshima, Japan	31°N	4	17.6	Cabbage	April 23, 1996
Ishigaki, Japan	24°N	28	23.8	Cabbage	December 18, 1995
Bangkok, Thailand	14°N	20	28.3	Chinese kale	July 21, 1994
Ho-Chi-Minh, Viet Nam	11°N	19	27.2	Cauliflower	March 23, 1997
Cameron Highlands, Malaysia	4°N	1400	17.9	Cabbage	January 30, 1996
Kuala Lumpur, Malaysia	3°N	17	26.5	Chinese mustard	Early February, 1996
Selatan, South Kalimantan, Indonesia	3°S	40	29.0	Cabbage	January 12, 1998

Table 2. Survival and fertility of nine local populations of *Plutella xylostella* at different temperatures[1].

Temperature[2] (°C)	Locality	Days elapsed before 50% oviposition	Female longevity (days)	Number of eggs laid per female	% hatch
15	Sapporo	3.2 ± 1.2 a	10.3 ± 3.4 a	100.6 ± 31.0 b	95.4 ± 4.0 a
	Tsukuba	3.3 ± 1.1 a	11.1 ± 4.4 a	152.5 ± 53.0 a	92.3 ± 7.6 ab
	Kagoshima	4.0 ± 1.6 a	12.3 ± 6.0 a	120.4 ± 48.5 ab	87.1 ± 9.4 b
	Ishigaki	5.5 ± 4.0 a	12.5 ± 5.5 a	117.8 ± 72.9 ab	88.0 ± 16.9 ab
	Bangkok	3.8 ± 1.7 a	13.7 ± 3.9 a	122.0 ± 52.5 ab	90.7 ± 14.8 ab
	Ho-Chi-Minh	4.3 ± 1.4 a	13.4 ± 2.5 a	139.8 ± 49.1 ab	84.9 ± 14.7 b
	Cameron Highlands	4.4 ± 2.1 a	13.8 ± 7.5 a	106.2 ± 57.4 ab	87.5 ± 15.9 ab
	Kuala Lumpur	3.4 ± 1.9 a	11.3 ± 6.1 a	106.5 ± 54.6 ab	82.3 ± 18.6 b
	Selatan	4.4 ± 1.9 a	14.0 ± 5.3 a	123.8 ± 46.6 ab	84.5 ± 14.8 b
20	Sapporo	2.9 ± 2.1 a	6.6 ± 3.8 bc	86.2 ± 31.0 a	94.4 ± 8.9 a
	Tsukuba	2.3 ± 1.2 a	5.6 ± 3.2 cd	90.7 ± 44.7 a	94.6 ± 6.2 a
	Kagoshima	2.6 ± 1.5 a	5.9 ± 3.6 cd	104.6 ± 59.0 a	85.5 ± 21.8 a
	Ishigaki	1.9 ± 0.7 a	3.8 ± 2.0 d	73.1 ± 49.3 a	83.9 ± 18.8 a
	Bangkok	2.6 ± 0.8 a	8.3 ± 2.6 ab	86.2 ± 48.1 a	79.3 ± 26.9 a
	Ho-Chi-Minh	2.4 ± 1.3 a	8.9 ± 1.5 a	98.7 ± 41.5 a	84.0 ± 13.5 a
	Cameron Highlands	2.7 ± 1.4 a	5.7 ± 3.2 cd	109.3 ± 48.0 a	94.3 ± 8.6 a
	Kuala Lumpur	2.7 ± 1.8 a	5.8 ± 3.5 cd	75.4 ± 45.8 a	78.9 ± 23.1 a
	Selatan	2.1 ± 1.0 a	6.3 ± 3.1 bcd	101.3 ± 41.0 a	87.8 ± 10.5 a
25	Sapporo	2.5 ± 1.5 ab	4.3 ± 2.3 bc	57.5 ± 32.2 b	89.0 ± 18.7 ac
	Tsukuba	1.4 ± 0.6 c	2.9 ± 1.2 c	60.5 ± 27.3 ab	89.4 ± 19.6 abc
	Kagoshima	1.6 ± 0.7 bc	3.1 ± 1.7 bc	56.8 ± 29.2 b	85.5 ± 14.8 abc
	Ishigaki	1.6 ± 0.7 bc	2.7 ± 1.3 c	56.2 ± 37.5 b	80.9 ± 18.3 bc
	Bangkok	2.6 ± 1.0 a	5.9 ± 1.8 a	69.8 ± 25.8 ab	81.3 ± 24.6 bc
	Ho-Chi-Minh	2.0 ± 1.0 abc	4.1 ± 2.4 bc	95.2 ± 43.3 a	94.8 ± 9.7 a
	Cameron Highlands	2.1 ± 1.1 abc	3.5 ± 2.3 bc	87.2 ± 49.4 ab	88.1 ± 10.5 abc
	Kuala Lumpur	1.5 ± 0.6 c	3.0 ± 1.0 bc	79.5 ± 42.3 ab	91.4 ± 11.0 ab
	Selatan	2.1 ± 1.2 abc	4.8 ± 2.6 ab	75.8 ± 39.4 ab	74.6 ± 30.3 b
27.5	Sapporo	1.4 ± 0.7 a	3.0 ± 1.4 a	68.5 ± 38.5 a	78.2 ± 25.4 a
	Tsukuba	1.5 ± 0.7 a	3.0 ± 1.2 a	67.7 ± 33.1 a	83.3 ± 27.0 a
	Kagoshima	1.2 ± 0.4 a	2.6 ± 1.2 a	72.5 ± 40.4 a	83.8 ± 25.1 a
	Bangkok	1.7 ± 0.8 a	3.5 ± 1.4 a	70.7 ± 38.0 a	80.6 ± 29.5 a
	Ho-Chi-Minh	1.3 ± 0.5 a	3.2 ± 1.4 a	63.7 ± 41.6 a	85.0 ± 21.3 a
	Selatan	1.6 ± 0.8 a	3.4 ± 1.5 a	46.7 ± 27.3 a	83.2 ± 14.5 a
30	Sapporo	1.9 ± 1.0 a	3.1 ± 1.2 b	43.3 ± 22.9 abc	82.8 ± 22.1 ab
	Tsukuba	1.4 ± 0.6 a	2.8 ± 0.9 b	62.3 ± 34.0 ab	88.9 ± 18.1 ab
	Kagoshima	1.5 ± 0.7 a	2.3 ± 1.1 b	38.3 ± 21.2 bc	87.4 ± 19.1 ab
	Ishigaki	1.5 ± 0.7 a	3.1 ± 1.0 b	42.2 ± 27.7 bc	78.0 ± 24.6 abc
	Bangkok	1.6 ± 0.8 a	2.7 ± 1.1 b	54.1 ± 37.1 abc	81.1 ± 20.5 bc
	Ho-Chi-Minh	2.0 ± 0.8 a	4.7 ± 0.9 a	36.5 ± 12.3 c	60.4 ± 25.2 c
	Cameron Highlands	1.4 ± 0.6 a	2.4 ± 0.9 b	74.0 ± 42.5 a	94.8 ± 11.8 a
	Kuala Lumpur	1.6 ± 0.6 a	2.4 ± 0.7 b	54.8 ± 27.7 abc	91.1 ± 10.3 ab
	Selatan	1.4 ± 0.6 a	2.4 ± 1.0 b	56.5 ± 31.1 abc	81.6 ± 27.5 ab
32.5	Sapporo	1.2 ± 0.4 a	1.8 ± 0.7 a	46.7 ± 35.2 a	85.6 ± 15.8 a
	Tsukuba	1.3 ± 0.6 a	2.4 ± 1.1 ab	28.7 ± 21.0 ab	58.0 ± 30.2 c
	Kagoshima	1.1 ± 0.4 a	2.0 ± 0.7 ab	39.5 ± 28.4 ab	78.0 ± 24.2 abc
	Bangkok	1.3 ± 0.6 a	2.8 ± 0.9 b	36.8 ± 21.9 ab	64.0 ± 33.3 abc
	Ho-Chi-Minh	1.1 ± 0.3 a	2.5 ± 0.9 ab	25.7 ± 18.9 b	64.2 ± 28.5 bc
	Selatan	1.5 ± 0.6 a	2.7 ± 1.0 ab	36.5 ± 18.8 ab	79.1 ± 22.3 ab
35	Sapporo	1.1 ± 0.3 a	2.1 ± 0.5 bc	11.7 ± 14.3 bc	25.1 ± 38.4 ab
	Tsukuba	1.0 ± 0.2 a	1.7 ± 0.5 c	18.6 ± 11.2 abc	31.8 ± 28.5 ab
	Kagoshima	1.2 ± 0.5 a	2.2 ± 0.7 bc	11.3 ± 12.7 c	49.0 ± 24.8 ab
	Ishigaki	1.2 ± 0.4 a	1.9 ± 0.4 bc	19.3 ± 13.5 abc	53.5 ± 30.1 a
	Bangkok	1.3 ± 0.9 a	2.3 ± 0.8 bc	14.3 ± 11.1 abc	21.7 ± 35.3 ab
	Ho-Chi-Minh	1.5 ± 0.7 a	3.4 ± 0.8 a	23.7 ± 9.6 a	21.9 ± 29.0 b
	Cameron Highlands	1.2 ± 0.6 a	2.1 ± 0.5 bc	25.2 ± 17.9 a	46.1 ± 29.5 ab
	Kuala Lumpur	1.1 ± 0.4 a	2.1 ± 0.5 bc	25.8 ± 15.5 a	43.2 ± 36.0 ab
	Selatan	1.0 ± 0.2 a	2.6 ± 1.0 b	21.7 ± 12.8 ab	27.5 ± 31.1 ab

[1]Mean ± SD. (n = 30). Means followed by different letters at the same temperature are significantly different at the 5% level (Kruskal-Wallis test, Dunn's multiple comparison).
[2]Photoperiod condition: 16L:8D.

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differences among the nine populations at 20 and 27.5°C. Nor at 15, 25, 30, 32.5 or 35°C was there a clear difference distinguishing temperate from tropical populations. Per cent hatch at 20 and 27.5°C showed no significant differences among the populations. Nor did the percent hatch at 15, 25, 30, 32.5 or 35°C clearly distinguish temperate from tropical populations. Thus populations from the tropics could not be distinguished clearly from populations from temperate regions based on the thermal responses studied. Moreover, none of the population characteristics investigated differed significantly between the Cameron Highlands (upland) and Kuala Lumpur (lowland) populations at any temperature.

Larval development and survival

The per cent survival of hatched larvae to adulthood, developmental period, and proportion of emerged female adults are shown in table 3. Survival rates showed no significant differences among the six populations at any temperature except at 30°C. Nor did the survival rate at 30°C indicate a clear distinction between the temperate (Sapporo, Tsukuba and Kagoshima) and the tropical (Bangkok, Ho-Chi-Minh and Selatan) populations. Although each group comprising the six populations maintained a relatively high survival rate between 15 and 30°C, the rate dropped markedly at 32.5°C, and declined almost to 0% at 35°C. At 35°C, most of the larvae had died by the third stadium, and only one individual emerged from each of the Ho-Chi-Minh and Selatan populations. The developmental periods showed some significant differences between populations at each temperature: for example, at 30°C, the four populations (Sapporo, Tsukuba, Kagoshima and Ho-Chi-Minh) developed significantly more slowly than the other two populations (Bangkok and Selatan). However, significant differences did not relate to any distinction between temperate and tropical populations. The proportion of emerged females showed no significant differences among the six populations at 25, 27.5 and 32.5°C. Nor at 15, 20 or 30°C did it differ clearly between the tropical and temperate populations. The mean proportion of females among all six populations ranged from 0.53 to 0.56 between 15 and 30°C, while the mean proportion was 0.42 at 32.5°C. Thus, a reduced larval survival rate and male-biased sex ratio (< 0.5) were observed at 32.5°C.

Larval developmental rate and estimated threshold temperature

The regression equation between temperature in the immature stage (T) and developmental rate (V, a reciprocal of the developmental period), and the threshold temperature for development estimated from V = 0 in the regression equation for each population are shown in table 4. The regression equations were calculated from the data in table 3, but excluded the data obtained at 35°C, when larval development was severely inhibited. For the coefficients of the regression equation, no comparisons among populations showed significant differences. The estimated threshold temperatures, ranging from 6.1 to 8.8°C, did not separate clearly temperate from tropical populations.

Relationship of temperature and reproductive rate

The net reproductive rate (the number of newly emerged females produced by one female) was defined as (the number of eggs laid per female) × (percent hatch) × (larval survival) × (proportion of emerged females). Correlations between these factors and temperature are shown in table 5. The greatest correlation was shown with the number of eggs laid per female ($P < 0.001$); egg production significantly decreasing with increasing temperature. In terms of hatching, the Tsukuba population showed a significant negative correlation with temperature ($0.01 < P < 0.05$) while the other five populations failed to show a significant response to temperature. In no population did the larval survival and the proportion of females show a significant correlation with temperature.

Discussion

Geographical variation of P. xylostella

There are few reports which show that tropical populations of widely distributed species exhibit higher temperature tolerances than conspecific populations from temperate regions (e.g. Chen *et al.*, 1990). This may be because temperate populations actually encounter comparably high temperature conditions during midsummer, and are also exposed to a much broader range of temperatures than are tropical populations (Kimura *et al.*, 1994). In addition, few reports have remarked on any distinct geographical differences in the lower threshold temperature for development. Of the 13 reports which studied geographical variation in threshold temperature, each conducted under uniform experimental conditions, none showed a clear geographical cline (Kiritani, 1997). Tauber *et al.* (1987) obtained the same result with local populations of *Chrysopa oculata* Say (Neuroptera: Chrysopidae). Similarly, in terms of thermal response to larval development in *P. xylostella*, no clear geographical cline was detected between a Java (Indonesian) population and three temperate–region populations from Japan (Umeya & Yamada, 1973). The present study on larval development also showed no clear distinction between populations from tropical and temperate regions (tables 3 and 4).

To date, little is known about the geographical variation in biological traits of *P. xylostella*, except for the study of Zilahi-Balogh *et al.* (1995) which suggested there was a slight difference in pheromone response between Java and Sulawesi Islands populations. Caprio & Tabashnik (1992) detected a measure of allozymic variation between Hawaiian and continental United States populations, whereas according to Chang *et al.* (1997), genetic variance in the mitochondrial DNA cytochrome oxidase-I (COI) sequence was not correlated with geographic location, and differences in COI sequence were very small among populations from Hawaii, Philippines and continental United States. Noran & Tang (1997) reported that lowland and highland populations in Malaysia were genetically distinguishable based on allozyme analysis. This local variation in Malaysia is not likely to be attributable to differences in environmental factors between the two populations, such as altitude or temperature, because the present study did not indicate any significant differences in thermal response

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Table 3. Larval survival and development of six local populations of *Plutella xylostella* at different temperatures[1].

Temperature[2] (°C)	Locality	% Survival from hatched larva to adult	Developmental period (days)	Proportion of emerged female adults (♀/♀+♂)
15	Sapporo	90.0 ± 15.7 a	38.2 ± 2.0 ab	0.51 ± 0.15 ab
	Tsukuba	78.9 ± 21.4 a	42.4 ± 2.9 a	0.63 ± 0.19 a
	Kagoshima	83.9 ± 17.2 a	36.2 ± 2.4 bc	0.52 ± 0.16 ab
	Bangkok	81.1 ± 17.5 a	36.1 ± 1.5 bc	0.55 ± 0.14 ab
	Ho-Chi-Minh	92.8 ± 14.1 a	34.6 ± 1.6 c	0.43 ± 0.15 b
	Selatan	87.2 ± 16.4 a	37.8 ± 1.8 bc	0.59 ± 0.12 ab
20	Sapporo	88.3 ± 12.5 a	21.1 ± 1.6 b	0.51 ± 0.14 ab
	Tsukuba	88.3 ± 14.7 a	21.0 ± 1.1 b	0.56 ± 0.10 ab
	Kagoshima	93.9 ± 12.0 a	23.5 ± 0.8 a	0.55 ± 0.09 ab
	Bangkok	81.7 ± 18.2 a	21.7 ± 1.7 b	0.45 ± 0.10 b
	Ho-Chi-Minh	83.9 ± 11.4 a	21.1 ± 1.5 b	0.49 ± 0.12 ab
	Selatan	82.8 ± 18.1 a	19.1 ± 0.6 c	0.60 ± 0.16 a
25	Sapporo	87.8 ± 11.7 a	14.6 ± 0.8 bc	0.50 ± 0.11 a
	Tsukuba	92.2 ± 11.7 a	16.9 ± 0.8 a	0.55 ± 0.12 a
	Kagoshima	92.2 ± 14.0 a	15.5 ± 0.4 ab	0.54 ± 0.13 a
	Bangkok	85.0 ± 22.0 a	14.2 ± 0.7 c	0.61 ± 0.11 a
	Ho-Chi-Minh	87.2 ± 15.3 a	14.8 ± 0.5 bc	0.53 ± 0.13 a
	Selatan	87.8 ± 13.5 a	13.7 ± 0.7 c	0.59 ± 0.18 a
27.5	Sapporo	83.3 ± 15.0 a	12.9 ± 0.6 a	0.58 ± 0.14 a
	Tsukuba	87.2 ± 19.6 a	11.6 ± 0.9 b	0.51 ± 0.11 a
	Kagoshima	92.8 ± 11.3 a	13.6 ± 0.6 a	0.50 ± 0.13 a
	Bangkok	81.1 ± 24.0 a	11.7 ± 0.8 b	0.60 ± 0.17 a
	Ho-Chi-Minh	90.6 ± 12.6 a	13.2 ± 1.0 a	0.55 ± 0.10 a
	Selatan	95.6 ± 7.1 a	11.1 ± 0.5 b	0.58 ± 0.10 a
30	Sapporo	85.6 ± 18.2 a	12.1 ± 0.5 a	0.53 ± 0.10 b
	Tsukuba	65.6 ± 16.9 b	11.9 ± 1.0 a	0.55 ± 0.12 ab
	Kagoshima	85.6 ± 16.9 a	12.7 ± 0.5 a	0.53 ± 0.11 b
	Bangkok	79.4 ± 26.2 ab	10.7 ± 0.6 b	0.67 ± 0.16 a
	Ho-Chi-Minh	80.6 ± 17.3 ab	12.1 ± 1.0 a	0.58 ± 0.14 ab
	Selatan	88.3 ± 15.4 a	10.4 ± 0.7 b	0.50 ± 0.13 b
32.5	Sapporo	29.4 ± 31.7 a	11.7 ± 1.0 ab	0.47 ± 0.29 a
	Tsukuba	23.3 ± 25.0 a	10.8 ± 0.9 bc	0.30 ± 0.26 a
	Kagoshima	41.7 ± 32.2 a	12.5 ± 0.7 a	0.44 ± 0.23 a
	Bangkok	32.8 ± 35.4 a	11.0 ± 0.8 bc	0.48 ± 0.21 a
	Ho-Chi-Minh	42.8 ± 34.4 a	11.2 ± 1.0 bc	0.46 ± 0.32 a
	Selatan	36.7 ± 36.0 a	10.2 ± 0.9 c	0.39 ± 0.25 a
35	Sapporo	0.0 ± 0.0 a	–	–
	Tsukuba	0.0 ± 0.0 a	–	–
	Kagoshima	0.0 ± 0.0 a	–	–
	Bangkok	0.0 ± 0.0 a	–	–
	Ho-Chi-Minh	0.6 ± 2.4 a	14.0	1.00(♀1)
	Selatan	0.6 ± 2.4 a	8.0	0.00(♂1)

[1]Mean ± SD. (n = 18). Means followed by different letters at the same temperature are significantly different at the 5% level (Kruskal-Wallis test, Dunn's multiple comparison).
[2]Photoperiod condition: 16L:8D.

Table 4. Relationship between temperature (T) and the developmental rate (V) of the larval stage of *Plutella xylostella*.

Locality	Regression[1]	r^2	Threshold temperature (°C)
Sapporo	$V = -0.0235 + 0.0035T$	0.986***	6.7
Tsukuba	$V = -0.0352 + 0.0041T$	0.976***	8.8
Kagoshima	$V = -0.0199 + 0.0032T$	0.985***	6.1
Bangkok	$V = -0.0316 + 0.0041T$	0.980***	7.9
Ho-Chi-Minh	$V = -0.0225 + 0.0035T$	0.997***	6.4
Selatan	$V = -0.0350 + 0.0043T$	0.987***	8.1

[1]For the coefficient of regression equation, no comparisons among localities showed significant difference at the 5% level (t-test).
[2] Significance of r: ***$P < 0.001$ (d.f. = 4)

Table 5. Correlations between rearing temperature and reproductive parameters of six local populations of *Plutella xylostella*[1].

Locality	No. eggs laid per female (A)	Hatching rate (B)	Larval survival rate (C)	Proportion of females (D)	Net reproductive rate (A×B×C×D)
Sapporo	r = –0.943***	r = –0.688ns	r = –0.747 ns	r = –0.116 ns	r = –0.974***
Tsukuba	r = –0.946***	r = –0.767*	r = –0.738 ns	r = –0.617 ns	r = –0.965***
Kagoshima	r = –0.964***	r = –0.637 ns	r = –0.683 ns	r = –0.557 ns	r = –0.959***
Bangkok	r = –0.976***	r = –0.725 ns	r = –0.714 ns	r = 0.055 ns	r = –0.898**
Ho–Chi–Minh	r = –0.974***	r = –0.726 ns	r = –0.739 ns	r = 0.636 ns	r = –0.915**
Selatan	r = –0.982***	r = –0.610 ns	r = –0.667 ns	r = –0.722 ns	r = –0.988***

[1]Significance of r: ***$P < 0.001$; **$0.001 < P < 0.01$; *$0.01 < P < 0.05$; ns$P > 0.05$ (d.f. = 5).

between the lowland (Kuala Lumpur) and the Cameron Highlands populations (table 2), although thermal response in larval development was not examined. In addition, the Sapporo population of *P. xylostella* which is not able to overwinter, did not show a thermal response that was noticeably different from other populations tested (tables 2, 3 and 4).

Plutella xylostella is known to be an active flier or migratory species in many parts of the northern hemisphere (Shirai, 1995). Presumably this species can migrate overseas and moves frequently between lowland and highland areas even in the tropics. It is thus unlikely that clear geographical difference in thermal response would be generated in such a highly mobile species.

Plutella xylostella *in central Thailand*

Kuwahara *et al.* (1995) suggested that a population of *P. xylostella* originating from central Thailand might be better adapted to high temperatures than a temperate population, because it maintained a higher adult density even during the hottest season when monthly mean temperatures reached 29 to 31°C. In the present study on egg production and larval development, however, there was no evidence of geographical differences in thermal response between tropical and temperate populations. In both tropical and temperate populations, larvae developed well between 15 and 30°C, but their development was severely inhibited at 32.5°C. Wakisaka *et al.* (1992) also reported that the net reproductive rate and intrinsic rate of natural increase of a population from central Japan maintained almost identical values between 25 and 30.5°C, and declined considerably at 33°C.

In general, insect development is extremely inhibited by high temperatures immediately above the optimal temperature range (Huey & Kingsolver, 1989; Denlinger & Yocum, 1998). In the present study, temperatures over 33°C had a fatal influence on egg production and larval development of *P. xylostella*. In Bangkok, Thailand, the monthly mean temperature ranges from 29 to 31°C; even though in the hottest season from March to May, it does not exceed 33°C. It is therefore unlikely that fatal damage to *P. xylostella* from high temperatures occurs frequently under field conditions in central Thailand. Conversely, a higher net reproductive rate can be achieved between 29 and 31°C, as larval developmental periods are extremely short at such high temperatures (tables 3 and 4; Wakisaka *et al.*, 1992), although egg production by females decreases with temperature increase.

In Selatan, South Kalimantan, it is hottest in August and September, when the monthly mean temperature reaches 30 to 31°C, and *P. xylostella* is found infrequently in the field. It is thought that population density of this species has declined since the cultivation of cruciferous crops has been impeded by severe dry conditions, with monthly rainfall less than 100 mm (K. Nakasono, personal communication). In the Cameron Highlands, at altitudes of 1400 to 1500 m, where mean temperature is approximately 18°C throughout the year, cruciferous crops are always grown and *P. xylostella* is abundant throughout the year (Ooi, 1986; Syed *et al.*, 1997). In the Java Islands, Indonesia, a higher prevalence of *P. xylostella* is concentrated in the vegetable crop growing area in the highlands at altitudes of 800 to 1300 m (Sastrodihardjo, 1986). In North Vietnam, *P. xylostella* becomes most abundant in the cooler season during December and January, when cruciferous crops are most frequently cultivated (Trinh, 1997). In the southern part of Japan, *P. xylostella* temporarily declines in numbers in midsummer, since at that time monthly mean temperatures reach 27 to 28°C and cruciferous crops are little cultivated (Koshihara, 1986; Morishita *et al.*, 1995). Thus, population density of *P. xylostella* in midsummer largely depends on whether cruciferous crops are widely cultivated during this season.

Among the Asian tropical lowland regions, the Chao Phraya delta in central Thailand where Kuwahara *et al.* (1995) studied is unusual, in that *P. xylostella* is abundant throughout the year including midsummer. In the present study, the Bangkok population from the Chao Phraya delta did not show a significantly superior high-temperature tolerance compared with that of the other tropical lowland populations (Ho-Chi-Minh, Kuala Lumpur and Selatan). In the Chao Phraya delta, the largest-scale irrigation system among tropical savanna areas was constructed in the early 1970's (Kaida, 1973). This irrigation and water system made mass cultivation of vegetables possible even during the dry season, and as a result, *P. xylostella* became a major pest throughout the year in this area (Rushtapakornchai & Vattanatangum, 1986). In tropical and subtropical regions, it is predicted that *P. xylostella* may achieve higher population densities throughout the year than at present, if cruciferous crops are cultivated more frequently in midsummer or during the dry season as a result of the construction of large-scale irrigation systems.

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