Effects of temperature on oviposition in overwintering females and hatch in first-generation larvae of *Pseudaulacaspis pentagona* (Hemiptera: Diaspididae)

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Abstract

Overwintering females of *Pseudaulacaspis pentagona* (Targioni) entered a reproductive diapause, and the ovary development in females collected before December 22 was retarded at 20°C under short (L10 : D14) and long (L15 : D9) days. In contrast, ovarian eggs in females collected after the beginning of the year developed normally. I examined the effects of temperature on the development of overwintering females that infested tea branches and on the hatch of the first generation at various constant temperatures. The base temperature was determined to be 10.5°C and 10.9°C for 50% of the females to begin laying eggs and for the egg hatch to reach a peak, respectively. Seasonal changes in oviposition of the overwintering generation and hatch of the first generation were monitored from 1998–2002 at Kanaya, Shizuoka Prefecture. When the base temperature was assumed to be 10.5°C and day-degrees (DD) were summed from January 1, 50% of the females began laying eggs when an average of 149 DD had accumulated, and the peak of hatching coincided with an average of 288 DD. The logistic equation $y = 1/[1 + \exp\{-\alpha_0 + \alpha_1 x\}]$ (y, proportion of parous females or hatch; x, DD accumulations; $\alpha_0$ and $\alpha_1$, constants) was used to model a sequence of the population events and to predict the optimum timing of insecticide application for controlling the first-generation larvae of *P. pentagona*.

Key words: *Pseudaulacaspis pentagona*; tea plants; winter diapause; DD accumulations; chemical control

INTRODUCTION

The mulberry scale, *Pseudaulacaspis pentagona* (Targioni) (Hemiptera: Diaspididae) is a destructive and polyphagous insect (Hanks and Denno, 1993) that is the main pest of tea plants in Japan (Kawai et al., 1997). There have been several studies on the biology of *P. pentagona* under field conditions in Japan (Shinano et al., 1976; Terada et al., 1977; Ozawa, 1994, 1995). In most tea-cultivating areas of Japan, *P. pentagona* has three generations a year, but its voltinism fluctuates from two to three generations a year depending on the regional climate (Shinano et al., 1976). Adult females of *P. pentagona* overwinter after copulation, and the overwintering females have underdeveloped ovarian eggs (Yasuda, 1981). However, there have been few studies on the overwintering of *P. pentagona* in tea fields.

Large populations of *P. pentagona* frequently form in tea-cultivating areas and occasionally cause severe damage to tea plants (Kawai et al., 1997). The optimum timing of chemical application to control the insects is limited to 2 to 5 days after the peak of hatching (Tatara, 1999), since most chemicals are only effective when the insects are in the early first instar, before their bodies become covered with wax. Thus, growers must effectively time the chemical application to follow the peak of hatching.

Monitoring methods for determining the peak of hatching have been developed and evaluated (Ozawa, 1994; Tatara, 1999), but it is difficult to determine when those observations should start or whether the peak of hatching occurs during the course of observation based on counting the trapped crawlers. I conducted this study to predict the changes in oviposition of overwintering females and the occurrence of crawlers in the first generation. In this paper, I describe the timing of oviposition and egg hatching under laboratory and field conditions. I also present logistic equations describing a sequence of population events such as oviposition and hatching in nature.

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MATERIALS AND METHODS

Ovarian development in overwintering females. To elucidate the seasonal changes in developmental stages of ovarian eggs in overwintering females of *P. pentagona*, I collected five or six tea branches infested with overwintering females from a tea field of the National Institute of Vegetable and Tea Science (NIVT, 138°08′09″E, 34°48′15″N, 210 m altitude) at about 7-day intervals from November 19, 1997, to April 16, 1998. The females were removed and dissected in a physiological saline solution, and the developmental stages of their ovarian eggs were determined under a binocular microscope. The development in ovarian eggs was categorized into five stages (Y. Asuda, 1981) based on the following criteria: (1) egg cell and nutritional cell not distinguishable; (2) egg cell clearly distinguished from the nutritional cell; (3) egg cell larger than the nutritional cell, and the ovarian egg gourd-shaped; (4) egg cell having almost absorbed the nutritional cell; and (5) ovarian eggs having almost developed eggshells.

Effects of temperature on ovarian development and oviposition in overwintering females reared on tea branches. About 100 tea branches were collected on November 10 in 1998. The tea branches were vertically inserted into a sponge (Aquaform®) placed in a plastic container (23 cm × 16 cm, 8 cm deep) with water. Then, the overwintering females were reared at one of four different temperatures (15°C, 17.5°C, 20°C, 22.5°C) under a long-day condition (L15 : D9, 15 h of light and 9 h of dark per day). The females were dissected to check the developmental stages of their ovarian eggs on December 20, since they had not laid eggs after 40 days of rearing.

About 100 tea branches were collected on February 4, March 4, April 3, and December 22 in 1998, January 21, February 22, and March 23 in 1999, and February 3, March 3, and April 7 in 2000. Then, the overwintering females were placed in the four different temperatures under L15 : D9, 15 h of light and 9 h of dark per day). The females were dissected to check the developmental stages of their ovarian eggs on December 20, since they had not laid eggs after 40 days of rearing.

Females of *P. pentagona* deposit their eggs beneath their own covers. To trace the egg hatch, a simple method has been developed for use in tea fields (Tatara, 1999): eggs laid by one female are defined as an egg batch; when one or more eggs in an egg batch hatch, the egg batch is regarded as a “hatched egg batch”; when more than 50% of the eggs in a batch hatch, the egg batch is regarded as a “more than half-hatched egg batch”. In the present study, the female’s cover was carefully peeled away using pointed tweezers under a binocular microscope to check egg hatch, and the developmental stages of females and egg batches were divided into parous females, hatched egg batches, and more than half-hatched egg batches by visual inspect. The ratios of the more than half-hatched egg batches deposited by the females collected on April 20, 1998, and April 7, 2000, were examined at 1- to 2-day intervals after the eggs had begun to hatch.

Diapause termination in overwintering females reared on pumpkin fruits. *P. pentagona* eggs of the third generation were sampled from tea fields of the NIVT on September 8, 1999. The eggs were placed on pumpkin fruits in a netted house covered with black cheesecloth for shading and for protection against parasitoids. The pumpkin fruits were used for the laboratory host. The adult females that were reared on pumpkin fruits and grew to the adult stage in the netted house were transferred to incubators at 20°C under a long (L15 : D9) or short (L10 : D14) day condition on November 10, November 24, December 8, and December 22 in 1999 and on January 5 and January 19 in 2000. The development of ovarian eggs and ovipo-
sition of these females were checked at about 7-day intervals.

**Field observations of oviposition and hatch.** I observed the changes in oviposition rates of overwintering females and hatchability of the first generation in tea fields. About six tea branches were collected from the tea fields of the NIVT at 1- or 2-day intervals in April and May from 1998 to 2002. The female’s cover was carefully peeled off using pointed tweezers, and the females and egg batches were divided into nulliparous females, parous females, hatched egg batches, and more than half-hatched egg batches. I counted the number of eggs laid by each female, but I did not count the empty chorions. The nulliparous females were dissected and checked for parasitization, and parasitized females were omitted from the census.

**Data analysis.** I used a logistic equation to describe the relationships between the cumulative ratios of ovipositing females and the census time at 4 different temperatures (STATISTICA/Mac 4.1J; Three’s Company Inc., Tokyo, 1994, using the maximum-likelihood loss function). The logistic equation, also called logit model (Manel and Debouzie, 1995), describes a sigmoid curve expressed as follows:

\[
y = \frac{1}{1 + \exp\left(-\left(\alpha_0 + \alpha_1 x\right)\right)}
\]

where \(\alpha_0\) and \(\alpha_1\) are regression parameters fitted to the data of the proportion of ovipositing females, \(y\), at the various observation times \(x\) (days) under each treatment of 4 different temperatures. The time when 50% of the females began to lay eggs (\(OV_{50}\)) was then estimated as \(OV_{50} = -\alpha_0 / \alpha_1\).

The degree-day method consists of calculating a lower threshold (base) needed for accumulating degree-days, below which development rate is assumed zero (Manel and Debouzie, 1997). The base temperature (\(T_0\)) for 50% of the females to begin laying eggs was estimated by regressing the values of \(1 / OV_{50}\) on temperature. The velocity \(V(T)\) is a linear function of temperature, \(T\) (°C), as follows:

\[
V(T) = aT + b
\]

where \(-b/a\) and \(1/a\) are the base temperature (°C) and the DD accumulations required for 50% of the females to begin laying eggs, respectively.

For the time when the ratio of the more than half-hatched egg batches reached 50% (\(HH_{50}\)), I used the logistic Eq. (1) to describe the relationship between the proportion of more than half-hatched egg batches and various observation times at 4 different temperatures, and the base temperature and the DD accumulations required for the \(HH_{50}\) were estimated by a linear regression Eq. (2).

The meteorological data were recorded by the Meteorological Monitoring System in Kanaya (MMS-KANAYA, measuring instruments are authorized by the Japan Meteorological Agency), located at NIVT. The air temperature in Kanaya was recorded every minute. The hourly or daily mean temperatures were used to calculate the \(OV_{50}\) of the overwintering generation and \(HH_{50}\) of the first generation of \(P. pentagona\) in the tea fields in each year by the logistic Eq. (1). I also used the logistic Eq. (1) to simulate the relationships between the population events (the proportions of the ovipositing females, hatched egg batches, and more than half-hatched egg batches) and the DD accumulations combining the field data of the five years.

**RESULTS**

**Ovarian development in overwintering females**

Most of the ovarian eggs of the overwintering females remained in the second stage until mid-February (Fig. 1), but some of them had already reached the third stage by January. The ovarian eggs developed rapidly during March and April, and most females had fully developed ovarian eggs in April.

**Effects of temperature on ovarian development and oviposition of overwintering females reared on tea branches**

The overwintering females that had been collected in the tea field on November 10, 1998, and transferred to incubators under various temperature conditions did not lay eggs until December 20. Those females had poorly developed ovarian eggs at 20°C and 22.5°C, but 40.7% and 31.6% of the females that had been reared at 15°C and 17.5°C had ovarian eggs in the third or later stage of development after 40 days of rearing, respectively (Fig. 2).

The effects of temperature on oviposition of the females at the different collection times are shown in Figs. 3, 4, and 5. The preoviposition period tended to decrease as the rearing temperature increased (Figs. 3, 4, and 5). The preoviposition pe-
period in the females collected on April 3, 1998, was shortened compared with the samples of February 4 and March 4 (Fig. 3), and this tendency was also observed in the samples collected in 1999 and 2000 (Figs. 4 and 5). About 50% of the females collected December 22 began to lay eggs after 20 to 30 days of rearing at 22.5°C and 20°C, respectively, but the remaining females did not lay eggs until the end of the rearing test. In contrast, females collected after January 21 developed normally; the ovipositing females increased as the rearing temperature increased (Fig. 4). The fitted curves of the females collected in 2000 also show that the preoviposition period shorted as the rearing temperature increased (Fig. 5).

Figure 6 shows the relationship between the changes in the ratios of the more than half-hatched egg batches and the rearing temperatures. Twenty-five percent of the females had already oviposited by April 20, 1998. The periods of development from the collection time to the time of $HH_{50}$ tended to decrease as the rearing temperature increased. In the females collected on April 7, 2000, the fitted curves for oviposited females and the more than half-hatched egg batches were almost the same shape at each temperature treatment.

Diapause termination in overwintering females reared on pumpkin fruits

Most of the females that were transferred to incubators under the condition of a long or short day from November 10 to December 8 remained in the second stage of ovarian development until the end of the rearing test on pumpkin fruits (Fig. 7). About 50% of the females that were transferred to incubators on December 22 developed to the third or a more advanced stage of ovarian development after 6 to 14 days of rearing. However, the remaining females stayed in the second stage of ovarian development until the end of February, and there were no effects of the two different photoperiods. On the other hand, the ovarian eggs in most of the females that were transferred to incubators in January developed rapidly, and the females began to lay

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**Fig. 1.** Seasonal changes in the developmental stages of ovarian eggs in overwintering females of *P. pentagona*. Numbers to the right of the column show the developmental stages of ovarian eggs: 1, egg cell and nutritional cell not distinguishable; 2, egg cell clearly distinguished from the nutritional cell; 3, egg cell larger than the nutritional cell, and ovarian egg gourd-shaped; 4, egg cell having almost absorbed the nutritional cell; 5, ovarian eggs having almost developed their eggshells. Shaded areas show ovipositing females. Sample sizes for each collection time are 34–61 (mean 48.2).

**Fig. 2.** Effects of temperature on the development of ovarian eggs in overwintering females of *P. pentagona* collected on November 10, 1998. The developmental stages of ovarian eggs were observed at 40 days after rearing at the four different temperatures under a long-day condition (L15 : D9). For keys, see Fig. 1. Sample sizes for each temperature treatment are 26–57 (mean 36.5).
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Fig. 3. Relationship between temperature and oviposition in overwintering females of *P. pentagona* collected February 4 (○), March 4 (△), and April 3 (●) in 1998. Sample sizes for each datum point of the females collected on these dates are 21–72 (mean 48.7), 20–67 (mean 53.5), and 13–66 (mean 57.0), respectively.

Fig. 4. Relationship between temperature and oviposition in overwintering females of *P. pentagona* collected on December 22 (○), 1998, and January 21 (△), February 22 (▲), and March 23 (●) in 1999. Sample sizes for each datum point of the females collected on these dates are 8–63 (mean 33.4), 11–71 (mean 33.9), 12–69 (mean 41.8), and 26–120 (mean 49.8), respectively.
Fig. 5. Relationship between temperature and oviposition in overwintering females of *P. pentagona* collected February 3 (○), March 3 (△), and April 7 (●) in 2000. Sample sizes for each datum point of the females collected on these dates are 27–79 (mean 46.4), 21–98 (mean 49.4), and 24–89 (mean 54.3), respectively.

Fig. 6. Effect of temperature on the cumulative percentage of the ovipositing females (open symbols) and the more than half-hatched egg batches (closed symbols) in the first generation of *P. pentagona* collected on April 20 (circles), 1998, and April 7 (triangles), 2000. Sample sizes for each datum point of the females collected on these dates are 34–100 (mean 60.7) and 27–96 (mean 54.3), respectively.
eggs. Thus, winter diapause was terminated in late December. The pumpkin fruit transferred to L15 : D9 at 20°C on January 19 became rotten, and the observation was stopped on February 4.

The base temperatures and DD accumulations estimated by females and eggs reared on tea branches

I calculated the period of development from the time of collection to the time of $OV_{50}$ using the logistic equation (Table 1). The period was shortened with delay in the time of collection. The development periods from the time of collection to the time of $OV_{50}$ and $HH_{50}$ are shown in Table 2. The periods from the time of $OV_{50}$ to $HH_{50}$ in each temperature treatment were not influenced by the collection time, and those periods in the females collected on April 20, 1998, and April 7, 2000, were almost the same.

The base temperature for $OV_{50}$ in the females collected on December 22, 1998, was 3.6°C, a lower value than the base temperature at the other collection times (Table 3), since the females collected before late December remained in winter diapause. The base temperature for $OV_{50}$ varied from 9.5°C to 11.2°C (mean, 10.5°C), depending on the collection time and year, excluding the result for the females collected on December 22, 1998. There was no clear relationship between the base temperature and the collection time each year. The DD accumulations required for $OV_{50}$ also fluctuated from 184.9 to 97.0, excluding the result of the females collected on December 22, 1998. The base temperature and the DD accumulations for the
time from $OV_{50}$ to $HH_{50}$ were 11.0°C and 122 day-degrees for the females collected on April 20, 1998, and 10.9°C and 126 day-degrees for the females collected on April 7, 2000 (Table 3), respectively.

**Field observations of oviposition and hatching**

Yearly fluctuations in the percentages of parous females, hatched egg batches, and more than half-hatched egg batches are shown in Fig. 8. Overwintering females began to lay eggs in mid-April in 1998, and the number of eggs per female reached a peak of 79 on April 30. The times of $OV_{50}$ in 1998, 1999, 2000, 2001, and 2002 were April 20–22, April 28–30, May 3–5, April 27–29, and April 17–19, respectively, and the times of $HH_{50}$ varied from May 7–9 in 1998 to May 21–23 in 2000. The peak number of eggs per female also varied from 50.1 in 2000 to 101.4 in 2001.

**The day-degree model for oviposition of an over-wintering generation and hatchability in the first generation**

I calculated the DD accumulations from January 1, since the females collected before late December remained in winter diapause and those collected after the beginning of the year developed normally. When the base temperature was 10.5°C (Table 4), the DD accumulations for $OV_{50}$ varied from 147.3 to 152.2 (mean $\pm$ SD: 149.1 $\pm$ 2.03), and those for $HH_{50}$ ranged from 277.9 to 302.9 (mean $\pm$ SD: 287.6 $\pm$ 9.49). When the base temperature was 10.9°C, DD accumulations for the period from the time of $OV_{50}$ to the time of $HH_{50}$ ranged from 122.2 to 147.1 (mean $\pm$ SD: 130.6 $\pm$ 10.1). The values measured for the time of $OV_{50}$ using the mean daily temperatures showed greater fluctuations (mean $\pm$ SD: 119.4 $\pm$ 7.27) than did those measured using the hourly temperatures.
Table 3. The base temperature and DD accumulations required for 50% of overwintering females to start laying eggs ($OV_{50}$) and for reaching 50% more than half hatched egg batches ($HH_{50}$) in overwintering females of *P. pentagona*

<table>
<thead>
<tr>
<th>Collection time</th>
<th>Regression equation $V(T)$</th>
<th>$r^2$</th>
<th>Base temperature ($T_0$, °C)</th>
<th>DD accumulations ($K$, day-degrees)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998. Feb. 4</td>
<td>$V(T) = 0.00597T - 0.064$</td>
<td>0.997</td>
<td>10.8</td>
<td>168.9$^d$</td>
</tr>
<tr>
<td>1998. Mar. 4</td>
<td>$V(T) = 0.00707T - 0.078$</td>
<td>0.998</td>
<td>11.1</td>
<td>142.2$^d$</td>
</tr>
<tr>
<td>1998. Apr. 3</td>
<td>$V(T) = 0.01037T - 0.110$</td>
<td>0.968</td>
<td>10.7</td>
<td>97.0$^d$</td>
</tr>
<tr>
<td>1998. Dec. 22</td>
<td>$V(T) = 0.00197T - 0.007$</td>
<td>0.977</td>
<td>3.6$^b$</td>
<td>518.1$^d$</td>
</tr>
<tr>
<td>1999. Jan. 21</td>
<td>$V(T) = 0.00597T - 0.066$</td>
<td>0.989</td>
<td>11.2</td>
<td>168.7$^d$</td>
</tr>
<tr>
<td>1999. Feb. 22</td>
<td>$V(T) = 0.00587T - 0.057$</td>
<td>0.998</td>
<td>9.9</td>
<td>173.0$^d$</td>
</tr>
<tr>
<td>1999. Mar. 23</td>
<td>$V(T) = 0.00837T - 0.091$</td>
<td>0.992</td>
<td>11.0</td>
<td>120.8$^d$</td>
</tr>
<tr>
<td>2000. Feb. 3</td>
<td>$V(T) = 0.00547T - 0.054$</td>
<td>0.986</td>
<td>9.9</td>
<td>184.9$^d$</td>
</tr>
<tr>
<td>2000. Mar. 3</td>
<td>$V(T) = 0.00597T - 0.061$</td>
<td>0.995</td>
<td>10.4</td>
<td>169.3$^d$</td>
</tr>
<tr>
<td>2000. Apr. 7</td>
<td>$V(T) = 0.00737T - 0.073$</td>
<td>0.992</td>
<td>9.5</td>
<td>130.6$^d$</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>—</td>
<td>—</td>
<td>10.5 ± 0.21</td>
<td>—</td>
</tr>
<tr>
<td>1998. Apr. 20</td>
<td>$V(T) = 0.00827T - 0.090$</td>
<td>0.963</td>
<td>11.0</td>
<td>122.0$^e$</td>
</tr>
<tr>
<td>2000. Apr. 7</td>
<td>$V(T) = 0.00797T - 0.087$</td>
<td>0.978</td>
<td>10.9</td>
<td>126.2$^e$</td>
</tr>
<tr>
<td>Combined$^c$</td>
<td>$V(T) = 0.00817T - 0.088$</td>
<td>0.971</td>
<td>10.9</td>
<td>124.1$^e$</td>
</tr>
</tbody>
</table>

$^a$ Obtained by linear regression of the data within 15 to 22.5°C ($n=4$), $V(T)$: developmental velocity (day$^{-1}$), $T$: temperature (°C).

$^b$ The base temperature was not included in the mean.

$^c$ The base temperature and DD accumulations were calculated by the mean developmental period of the two tests.

$^d$ The base temperature required for the time from the collection time to the time of $OV_{50}$ (see, Table 1).

$^e$ The DD accumulations required for development time from the time of $OV_{50}$ to the time of $HH_{50}$ (see, Table 2).

Fig. 8. Seasonal changes in the ovipositing females (closed circles), the number of eggs per female (bars + SD), the ratio of the hatched egg batches (open triangles), and the ratio of the more than half-hatched egg batches (open circles) of *P. pentagona* in tea fields. Sample sizes for each observation time of females collected in 1998, 1999, 2000, 2001, and 2002 are 23–100 (mean 59.3), 41–94 (mean 64.5), 27–122 (mean 64.5), 55–75 (mean 64.0), and 62–93 (mean 75.1), respectively.
Table 4. The DD accumulations required for 50% of overwintering females to start laying eggs \((OV_{50})\) and for reaching 50% of the more than half-hatched egg batches \((HH_{50})\) in overwintering females of \(P. pentagona\) in tea fields

<table>
<thead>
<tr>
<th>Year</th>
<th>Base temperature ((^{\circ}C))</th>
<th>(OV_{50}) (day-degrees)</th>
<th>Logistic equation(^d)</th>
<th>(HH_{50}) (day-degrees)</th>
<th>Logistic equation(^d)</th>
<th>(OV_{50}) to (HH_{50})</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>(a)</td>
<td>(b)</td>
<td>(r^2)</td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>10.5(^a)</td>
<td>150.1</td>
<td>-19.6764</td>
<td>0.13113</td>
<td>0.998</td>
<td>286.3</td>
</tr>
<tr>
<td>1999</td>
<td>10.5(^a)</td>
<td>147.3</td>
<td>-14.3586</td>
<td>0.09751</td>
<td>0.967</td>
<td>302.9</td>
</tr>
<tr>
<td>2000</td>
<td>10.5(^a)</td>
<td>148.1</td>
<td>-11.7159</td>
<td>0.07913</td>
<td>0.988</td>
<td>277.9</td>
</tr>
<tr>
<td>2001</td>
<td>10.5(^a)</td>
<td>152.2</td>
<td>-13.5470</td>
<td>0.08900</td>
<td>0.954</td>
<td>282.2</td>
</tr>
<tr>
<td>2002</td>
<td>10.5(^a)</td>
<td>147.8</td>
<td>-14.1421</td>
<td>0.09568</td>
<td>0.981</td>
<td>288.7</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>149.1(\pm)2.03</td>
<td></td>
<td></td>
<td></td>
<td>287.6(\pm)9.49</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Base temperature ((^{\circ}C))</th>
<th>(OV_{50}) (day-degrees)</th>
<th>Logistic equation(^d)</th>
<th>(HH_{50}) (day-degrees)</th>
<th>Logistic equation(^d)</th>
<th>(OV_{50}) to (HH_{50})</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>(a)</td>
<td>(b)</td>
<td>(r^2)</td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>10.9(^b)</td>
<td>136.3</td>
<td>-19.3087</td>
<td>0.14164</td>
<td>0.998</td>
<td>265.4</td>
</tr>
<tr>
<td>1999</td>
<td>10.9(^b)</td>
<td>131.0</td>
<td>-13.7016</td>
<td>0.10458</td>
<td>0.966</td>
<td>278.1</td>
</tr>
<tr>
<td>2000</td>
<td>10.9(^b)</td>
<td>132.5</td>
<td>-11.2022</td>
<td>0.08456</td>
<td>0.986</td>
<td>255.4</td>
</tr>
<tr>
<td>2001</td>
<td>10.9(^b)</td>
<td>137.2</td>
<td>-13.5174</td>
<td>0.09854</td>
<td>0.955</td>
<td>259.4</td>
</tr>
<tr>
<td>2002</td>
<td>10.9(^b)</td>
<td>133.4</td>
<td>-13.8638</td>
<td>0.10394</td>
<td>0.982</td>
<td>264.9</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>134.1(\pm)2.60</td>
<td></td>
<td></td>
<td></td>
<td>264.6(\pm)8.58</td>
</tr>
</tbody>
</table>

\(^a\) Hourly temperatures were used for the calculation of DD accumulations.  
\(^b\) Daily mean temperatures were used for the calculation of DD accumulations.  
\(^c\) SD represents the standard deviation.  
\(^d\) The logistic equation expressed as: \(y = 1/[1 + \exp\{-(\alpha_0 + \alpha_1 x)\}]\), where \(\alpha_0\) and \(\alpha_1\) are regression parameters fitted to the data of parous females or the ratios of the more than half-hatched egg batches, \(y\), at the various observation time \(x\) (day-degrees).  

Fig. 9. Relationships between population events of \(P. pentagona\) and DD accumulations. The DD accumulations were calculated using the hourly temperatures, and the base temperature was 10.5\(^{\circ}C\). Solid lines represent the fitted curves calculated by the logistic equation \(y = 1/[1 + \exp\{-(\alpha_0 + \alpha_1 x)\}]\) where the samples of 5 years were combined; for further information see the text. Broken lines show the cumulative curves of parous females, hatched egg batches and more than half hatched egg batches in each year. Arrows with the year show rainfall of more than 10 mm over 2 days before and after the DD accumulations had reached 280.
The curves for the proportion of parous females, hatched egg batches, and more than half-hatched egg batches produced by the simulation models and the curves for those in the tea fields are presented in Fig. 9. As initial input values for time, the simulation models required January 1, and a base temperature of 10.5°C for the entire period of development of overwintering females and the first-generation eggs. The simulation model for \( \text{OV}_{50} \) (148.6 DD) predicted time of \( \text{OV}_{50} \) in the field to within 1 day in 4 of 5 years, and the DD accumulations on the day were 149.4–158.3, 147.1–149.0, 146.1–151.5, 144.8–149.2 and 146.2–150.4 in 1998, 1999, 2000, 2001 and 2002, respectively. The simulation model for \( \text{HH}_{50} \) (287.7 DD) predicted time of \( \text{HH}_{50} \) in the field to within 1 day in 3 of 5 years, and the DD accumulations on the day were 278.1–289.0, 302.2–310.2, 276.6–284.6, 285.3–294.5 and 282.1–289.5 in 1998, 1999, 2000, 2001 and 2002, respectively. When tea branches became wet from rain, hatching of \( P. \ pentagona \) was retarded in this study. Therefore, the rainfall of more than 10 mm over 2 days before and after the DD accumulations had reached 280 are shown in Fig. 9. The predicted time of hatching was 2 days earlier than the observed time in 1999 because the heavy rainfalls affected the timing of hatching.

**DISCUSSION**

**Diapause termination and post-diapause development**

Yasuda (1981) reported that female adults of \( P. \ pentagona \) infesting mulberry plants in the Tohoku region (in the northern part of the Japanese main island) overwintered after copulation and the ovarian eggs in overwintering females remained underdeveloped until mid-March. In the same report, Yasuda noted that ovarian eggs in overwintering females of \( P. \ pentagona \) started to develop with the sprouting or the beginning of sap flow in the host plants. Females of \( P. \ pentagona \) in Hungary spend the winter in a facultative diapause stage, and the preovipositional period was longer in the diapausing females collected in January than in those collected in February (Sheble and Kozar, 1996). The results of the present study show that females collected on November 10 did not start to lay eggs until after 40 days of rearing at 20°C (Fig. 2) and that about half of the females collected on December 22 began to lay eggs while the remainder stayed in winter diapause (Fig. 4). The results of the experiments in which overwintering females were reared on pumpkin fruits and transferred to incubators on December 22 also showed that winter diapause in about 50% of the females was terminated (Fig. 7). The data from the overwintering females reared on tea branches and pumpkin fruits suggest that diapause intensity decreases as autumn proceeds, and ends at the end of the year without the intervention of a specific stimulus.

My study focused on monitoring and predicting the population events of oviposition in overwintering females and hatch in the first generation. Overwintering females collected in the period from January to April developed normally, and the period of development for \( \text{OV}_{50} \) became shorter with increases in temperature and with delay in the time of collection. There were no clear differences between the base temperatures at different collection times, excluding the samples of December 22 (Table 3), suggesting that the temperature requirement for post-diapause development did not change after the beginning of the year.

**Prediction of the optimum timing of chemical application for control of the first-generation larvae**

The optimum timing of insecticide application is limited to a short period, 2 to 5 days after the peak of hatching, and the period coincides with the ratio of more than half-hatched egg batches reaching 60 to 90% (Tatara, 1999). The chemical application to control the first-generation larvae is the most effective, since their hatching is more synchronous than those of the other generations (Tatara, 1999). The results of the present study show that the synchronicity in hatching of the first generation is due to the suppression of growth of overwintering females by the winter diapause.

Logistic regression, applied to one stage of development, gives relatively close estimates of stage duration only when the base temperature is known (Manel and Debouzie, 1997). Therefore, as initial inputs, simulation models require values for time and the base temperature. In the present study, I used a base temperature of 10.5°C for both the developmental stages of overwintering females and for the hatch of the first generation. I employed a starting date of January 1 because the reproductive
diapause ends around the end of the year. To calculate the DD accumulations, the hourly temperatures should be used.

The times of setting the sticky trap for determining the peak of hatching or checking the ratios of the more than half-hatched egg batches by collecting tea branches could be determined according to the simulation model for $HH_{50}$. The sticky traps should be set in the tea bushes when the DD accumulations have reached 250 (Fig. 9). Traps should be changed every other day (Tatara, 1999), and the peak of hatching may occur until 7 days after setting traps the DD accumulations have reached 250, because the daily effective temperatures one day before and one day after the $HH_{50}$ were 8.7 ± 1.30 (mean ± SD), and the DD accumulations rose to 310 by 7 days. To check the ratios of the more than half-hatched egg batches, tea branches should be collected on the day after DD accumulations have reached 280.

The present study demonstrates that the logistic equation can be used to accurately describe the hatching curves for the eggs of *P. pentagona* in tea fields. Females and larvae of *P. pentagona* infest tea branches beneath the thick leaf layer, so the culturing methods and the growing stage of tea plants may have affected the microclimatic conditions for growth of the insects. When tea branches become wet from rain, hatching of *P. pentagona* might be retarded. In the present study, heavy rainfalls retarded procession of the cumulative curves of the more than half-hatched egg batches. Despite the inaccuracies caused by fluctuations in temperature and rainfall, the simulation model has been sufficiently precise to account for most of the year-to-year variation in the timing of egg hatching in *P. pentagona*.

REFERENCES


