Timing of diapause induction and overwintering success in the cotton bollworm *Helicoverpa armigera* (Hb.) (Lepidoptera: Noctuidae) under outdoor conditions in temperate Japan

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Abstract

The timing of diapause induction and overwintering success in the cotton bollworm *Helicoverpa armigera* were studied outdoors in Chiba (35°N, 140°E) and Kyoto (35°N, 135°E) prefectures, Japan, using local populations collected from Chiba and Mie (34°N, 136°E) Prefectures, respectively. For comparison, a similar experiment was performed in Chiba using a closely related species, *H. assulta*. Diapause induction in *H. armigera* was stimulated by low temperatures in autumn, and the incidence of pupal diapause increased sharply with little change in photoperiod. In Kyoto, pupae of *H. armigera* overwintered successfully in a state of diapause. However, larvae that had hatched from eggs deposited in late autumn suffered high mortality, presumably from the cold; therefore, the pattern of temperature change in autumn credibly affects overwintering success in *H. armigera*. In contrast, a considerable number of *H. assulta* pupae entered diapause well before autumn, even though those individuals had hatched from eggs deposited during the mid-summer. Thus, *H. assulta* appeared to prepare for overwintering earlier and more successfully than did *H. armigera* in this temperate zone. Differences in diapause induction between the sexes revealed in laboratory experiments with *H. armigera* were not detected under outdoor conditions.

Key words: Diapause induction; *Helicoverpa armigera*; *Helicoverpa assulta*; overwintering success; sexual differences

INTRODUCTION

As global temperatures increase, progressively warmer winters are recorded in the temperate zone, and the climate of Japan is becoming increasingly more suitable for agricultural pests from the tropics and subtropics (Yamamura and Yokozawa, 2002). Many pest species, such as the southern yellow thrips *Thrips palmi* (Thysanoptera: Thripidae; Nagai and Yano, 1999), the American serpentine leafminer *Liriomyza trifoli* (Diptera: Agromyzidae; Abe and Kawahara, 2001), and the southern green stink bug *Nezara viridula* (Heteroptera: Pentatomidae; Musolin and Numata, 2003) have recently invaded agricultural ecosystems in southern temperate Japan.

Another invasive tropical pest species, *Helicoverpa armigera*, has occurred abundantly on commercial crops in the temperate zone of Japan since its outbreak in 1994 (Yoshimatsu, 1995; Casimero et al., 2000). This species has long been observed at low densities in Japan, but has recently become a serious pest. Before the outbreak in 1994, *H. armigera* was suspected to exhibit annual long-distance immigration from the south (Casimero et al., 1999; Zhou et al., 2000). However, *H. armigera* now occurs throughout the year in temperate Japan, and it is highly probable that local populations have established. It is of urgent importance to determine whether this is the case, because if local populations are abundant, the pest status of *H. armigera* in Japan may change (Fitt, 1989).

Diapause is one of the most fundamental seasonal adaptations in insects, and may be coordinated with colonization into new habitats (Tauber et al., 1986; Danks, 1987). *Helicoverpa armigera*
enters into facultative diapause at the pupal stage (Fitt, 1989). In the field, subtropical populations of the species are capable of overwintering in a state of pupal diapause in Africa and Australia (Roome, 1979; Wilson et al., 1979). In Australia, a HEAPS model has been developed based on the local field information and is being used to predict the number of overwintering pupae of *Helicoverpa* moths (Dillon, 1998). However, little field information is available for this species in the temperate zone, where local populations of *H. armigera* are thought to be colonizing. In order to develop similar prediction models in a colonized area in Japan, it is important to understand the seasonal timing of diapause induction in this species under outdoor conditions. Although several laboratory experiments have investigated the basic biology of diapause induction in this species (Qureshi et al., 1999, 2000; Shimizu and Fujisaki, 2002; Kurban et al., 2005), studies in which the seasonal timing of diapause induction has been examined outdoors in the temperate zone are rare (Jiang et al., 1999). Experimental field research that examines the timing of diapause induction and winter survival rates is necessary.

The objectives of this study were to record the timing of diapause induction, to estimate the overwintering success, and to understand their consequences in *H. armigera* under field conditions in temperate Japan. It is worth noting that there is *Helicoverpa assulta*, a closely related species to *H. armigera*, and it has been observed in Japan for decades (Yoshimatsu, 1995). Therefore, *H. assulta* probably originated in the temperate zone, and thus, is expected to exhibit diapause characteristics that are more specifically adapted to the temperate climate than *H. armigera*. We compared characteristics of diapause responses in *H. armigera* with those of local *H. assulta*.

Shimizu and Fujisaki (2002) reported sexual differences in the incidence of diapause in *H. armigera* under laboratory conditions at 18°C: males were more likely than females to enter diapause. These sexual differences may also be expressed in the field. If so, the onset of diapause induction may occur earlier in the season in males than in females. However, there have been no field studies performed in which the timing of diapause induction was recorded for each sex. The expected sexual differences in the timing of diapause induction may be potentially important in the life-history strategy of *H. armigera*. Thus, another objective of this study was to examine sexual differences in diapause induction under natural conditions.

**MATERIALS AND METHODS**

**Insects.** Late-instar larvae of *H. armigera* were collected from tomato fields at four sites in Chiba Prefecture (Kisarazu, 35°22′N, 139°55′E; Narutou, 35°36′N, 140°24′E; Nosaka, 35°39′N, 140°34′E; Tomisato, 35°43′N, 140°20′E) in autumn 1996. To avoid inbreeding depression, individuals were grouped according to collection site, and rotating crossings among field groups were performed to establish the *H. armigera* Chiba population. Another culture of a local *H. armigera* population was established from late-instar larvae collected from cabbage fields in Mie Prefecture (Anou, 34°45′N, 136°27′E) in autumn 2001. Late-instar larvae of *H. assulta* were collected from sweet pepper fields in Chiba Prefecture (Nosaka) in autumn 1999. These two cultures of *H. armigera* and one culture of *H. assulta* were reared continuously under constant conditions of 25°C with a 16L : 8D (h of light : h of darkness) photoperiod. Larvae were placed in individual petri dishes (90-mm diameter), and were provided with an artificial diet (Insecta LFS; Nihon-Nosan Kogyo Co., Ltd., Yokohama, Japan). Larvae from all experiments were fed the same diet. Emerging adults were transferred to an acrylic mating cage (30×30×30 cm) containing cotton wool as an oviposition substrate, and provided with a 10% honey solution.

**Sexual differences in diapause induction under laboratory conditions.** To examine the magnitude of sex-based differences in diapause induction after two generations of rearing in the laboratory, newly deposited eggs of *H. armigera* from the Mie population were reared individually in petri dishes (90-mm diameter) under various photoperiods (11L : 13D, 12L : 12D, 13L : 11D, 14L : 10D, and 15L : 9D) at 18°C. Pupae with eyespots that remained in the same condition for more than 15 days were regarded as diapause individuals (Shumakov and Yakhimovich, 1955). Pupae were sexed according to Butt and Cantu (1962).

**Timing of diapause induction and survival of larvae outdoors.** To examine the seasonal timing of diapause induction, individuals of both the *H.*
armigera and H. assulta Chiba populations were reared outdoors in Chiba Prefecture (Tougane, 35°34′N, 140°19′E) in 1998 and 2000, respectively. For both experiments, newly deposited eggs (88–441 for H. armigera; 123–168 for H. assulta) were collected in the laboratory and immediately transferred to outdoor shelves from late May to early October in 1998 (H. armigera) and 2000 (H. assulta). A group of individuals derived from eggs deposited on the same day were defined as a cohort. Larvae were maintained individually, and pupated in petri dishes (60-mm diameter). After emergence, adults were returned to the laboratory and released into the mating cage. Individuals that remained in the pupal stage and retained eyespots until the following year, regardless of success in emergence, were regarded as diapause individuals; those emerging as adults within the season or died within the season after the disappearance of eyespots were regarded as non-diapause individuals. Larval mortality was calculated as the percentage of individuals that died during the larval stages or during molting to pupae. The incidence of diapause and survival of larvae were calculated for each cohort.

A similar experiment was performed to examine the timing of diapause induction in the field using the H. armigera Mie population in Kyoto Prefecture (Sakyo, 35°01′N, 135°44′E) in 2002. Environmental conditions were similar in Mie and Kyoto Prefectures. Newly deposited eggs of the third laboratory generation were transferred into diapause-inducing conditions in the laboratory (15°C, 9L:15D). Pupation occurred from 24 February to 19 March 2002. Diapause induction was confirmed by the retention of eyespots for 15 days after pupation. Thereafter, 150 diapause pupae were transferred to shelves in a mesh cage (3.0L×7.0W×2.6H m), and exposed to outdoor conditions. Adults that emerged from these diapause pupae were transferred to a mating cage placed inside the mesh cage. In successive generations, adult individuals were released into the same mating cage upon emergence. Eggs were collected twice a week until
all adults had died. Enough eggs were collected each time to produce 50 larvae as a cohort, except for 30 August and 22 September 2002, when 100 larvae were produced on each date. Larvae were maintained individually, and pupated in petri dishes (60-mm diameter). Diapause attributes, the incidence of diapause, and larval survival were determined using the same procedures as for the experiments in Chiba described previously. In addition, we recorded the developmental periods and calculated the incidence of diapause for each sex in the experiment at Kyoto.

Temperature data for Chiba in 1998 and 2000, and for Kyoto in 2002, were obtained from the Japan Meteorological Agency (1998, 2000, 2002). The average temperature (middle curve) was calculated as the mean of the maximum (upper curve) and minimum (lower curve) daily temperatures. The minimum, maximum, and average temperatures are shown as 11-day rolling means. The egg and larval periods (open bars) and pupal periods (solid bars) of Helicoverpa armigera cohorts that showed a nearly 50% incidence of diapause are shown with standard deviations. The growth data for Chiba (1998) are approximate (a). Broken lines indicate the lower developmental threshold (13.6°C; Qureshi et al., 1999). (d) The photoperiod includes day-length plus 1 h of twilight. Geographical differences between Chiba and Kyoto were small (<3 min). Photoperiods on 27 August (14 h, 07 min), 8 September (13 h, 41 min), and 21 September (13 h, 13 min) are indicated by arrows.

**Table 1. Logistic regression coefficients (±SE) and tests of the model null hypothesis for the equation predicting the incidence of diapause and overwintering success in Helicoverpa armigera**

<table>
<thead>
<tr>
<th>Parameters in the model: ( P = 1 / [1 + \exp { -(b_0 + b_1 \cdot DATE + b_2 \cdot SEX) }] )</th>
<th>( b_0 )</th>
<th>( b_1 )</th>
<th>( b_2 )</th>
<th>df</th>
<th>( X^2 )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Incidence of diapause</td>
<td>(-16.625\pm1.954^*)</td>
<td>(0.524\pm0.063^*)</td>
<td>(0.064\pm0.167)</td>
<td>2</td>
<td>913.429</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Overwintering success</td>
<td>(2.134\pm0.464^*)</td>
<td>(-0.049\pm0.021^*)</td>
<td>(-0.139\pm0.155)</td>
<td>2</td>
<td>6.576</td>
<td>0.0373</td>
</tr>
</tbody>
</table>

* Model coefficients are significant (Likelihood ratio test, \( p < 0.05 \)).
Japan Meteorological Agency (1998, 2000, 2002); photoperiodic data for Chiba and Kyoto were obtained from the National Astronomical Observatory of Japan.

Overwintering success outdoors. To examine the overwintering success of *H. armigera*, diapause pupae produced in the 2002 Kyoto experiment were maintained under the same conditions in the outdoor mesh cage until they emerged as adults in spring 2003. The overwintering success, determined as the successful emergence in the following year, was calculated for diapause pupae from each cohort, and data were analyzed separately for each sex.

Data analysis. Sexual differences in the incidence of diapause for each photoperiodic regime in the laboratory were tested using Fisher’s exact test. Effects of the time of season and sex on the incidence of diapause and overwintering success outdoors were examined using nominal logistic regression models. The models predicting the incidence of diapause or overwintering success were:

\[ P = \frac{1}{1 + \exp\left(- (b_0 + b_1 \text{DATE} + b_2 \text{SEX})\right)} \]

where *P* is the probability of the incidence of diapause or the overwintering success; \(b_0\), \(b_1\), and \(b_2\) are regression coefficients; and \(\text{DATE}\) and \(\text{SEX}\) are representative independent variables (\(\text{DATE}\): the date when the cohort originated, in days from the date when the cohort showing the first diapause of the season originated; \(\text{SEX}\): 0, male; 1, female). The likelihood ratio test was used to determine the significance of the regression coefficients. All analyses were performed using JMP 4.05 J (SAS Institute, Cary, NC, USA).

RESULTS

Sexual differences in diapause induction under laboratory conditions

Under laboratory conditions, a long-day response was observed in diapause induction in the *H. armigera* Mie population, with significant differences between the sexes, except at 11L:13D (Fig. 1). Critical photoperiods were observed between 14L:10D and 13L:11D, and between 13L:11D and 12L:12D, for males and females, respectively. In males, however, the incidence of diapause at 15L:9D was significantly higher than that at 14L:10D (\(p<0.05\), Fisher’s exact test with Bonferroni correction).

Timing of diapause induction and survival of larvae outdoors

In outdoor experiments with the *H. armigera* Mie population in Kyoto during 2002, non-diapause individuals emerging as adults showed unimodal distributions in all cohorts from eggs deposited before 20 August. Therefore, aestivation induced by high temperatures was not significant in this population, unlike results from laboratory experiments using populations from Bobo-Dioulasso, Burkina Faso (Nibouche, 1998), and Beijing, China (Liu et al., 2004). The developmental periods averaged for each cohort are shown in Fig. 2a. The first incidence of diapause was observed in a cohort that originated on 20 August (Fig. 2b; arrow). The incidence of diapause remained below 20% in cohorts that originated by 27 August, and then sharply increased to 100% in a cohort that originated on 8 September. All individuals derived from eggs deposited thereafter entered diapause.

A significant nominal logistic regression model was developed to predict the incidence of diapause in *H. armigera* (Table 1). While the date on which cohorts originated had a significant effect in the model, sex did not (likelihood ratio test, \(df=1\), \(X^2=0.66, p=0.416\)). The seasonal sharp increases in the incidence of diapause in the two sexes occurred almost simultaneously (Fig. 2b). Larval survival was nearly 100% in cohorts that originated by the end of August (Fig. 2b). However, larval survival then decreased to 0% in the cohort that originated on 25 September. Although non-diapause pupae continued to emerge as adults (Fig. 2a), and those adults oviposited until 17 October (Fig. 2b), all individuals that were derived from eggs deposited after 25 September died before pupation.

In the experiment with *H. armigera* in Chiba during 1998, the first incidence of diapause was observed in a cohort that originated on 21 August (Fig. 3a; arrow). The incidence of diapause remained below 20% in cohorts that originated by 8 September, and then sharply increased to 100% in the cohort that originated on 21 September. All individuals derived from eggs deposited thereafter entered diapause. This sharp increase in the incidence of diapause within 13 days was similar to that which occurred in Kyoto (Fig. 2b). However, the increase in the incidence of diapause was ob-
erved about half a month earlier in Kyoto than in Chiba. Even in the last cohort, which originated on 5 October, 50.7% of the larvae survived and pupated in Chiba in 1998 (Fig. 3a), whereas all larvae derived from eggs deposited after 25 September died in Kyoto in 2002 (Fig. 2b).

In the experiments with *H. armigera* in Chiba (1998) and Kyoto (2002), the cohorts that showed a nearly 50% incidence of diapause experienced decreasing ambient temperatures from their early stages of development (Fig. 4a, c). For example, the minimum ambient temperature fell below 20°C on 30 September 1998 in Chiba and on 17 September 2002 in Kyoto (Fig. 4a, c). This approximately two-week difference corresponded to a similar two-week difference in time when the cohorts that showed a nearly 50% incidence of diapause originated outdoors, i.e., 14 September 1998 in Chiba, and 30 August 2002 in Kyoto (Figs. 2b and 3a). Natural day-length was almost identical in Chiba and Kyoto (Fig. 4d). The incidence of diapause increased from <20% to 100% across only a 30-min shortening of natural day-length (Fig. 4d; arrows: 13 h, 41 min to 13 h, 13 min between 8 and 21 September 1998 in Chiba; 14 h, 07 min to 13 h, 41 min between 27 August and 8 September 2002 in Kyoto).

In the experiment with *H. assulta* in Chiba (2000), the first incidence of diapause was observed in the cohort that originated on 7 August (Fig. 3b; arrow). Approximately 25% and >70% of *H. assulta* individuals entered diapause in cohorts that originated in mid- and late August, respectively. The incidence of diapause increased gradually and reached 100% in a cohort that originated on 13 September, 35 days after the first cohort that showed diapause originated.

**Overwintering success outdoors**

Among all diapause pupae (*N* = 234) produced in the outdoor experiment in Kyoto (2002), 75.6% emerged as adults in the following spring (Fig. 2c). The date of oviposition and overwintering success were significantly negatively correlated (Table 1; likelihood ratio test, df = 1, $X^2 = 5.877$, $p = 0.015$); diapause pupae from cohorts that originated earlier in the season showed higher survival rates. However, no significant difference in overwintering success was observed between the sexes (Table 1; likelihood ratio test, df = 1, $X^2 = 0.805$, $p = 0.370$).

Emerging adults mated and deposited fertile eggs.

**DISCUSSION**

There has been some debate as to whether *H. armigera* can overwinter in Japan. While *H. armigera* collected in the temperate zone exhibits diapause ability in laboratory studies (Qureshi et al., 2000; Shimizu and Fujisaki, 2002), it had not yet been determined whether this occurs under natural outdoor conditions in temperate Japan. In addition, it has not been clear whether local populations of *H. armigera* were established in Japan. Because this species has outstanding flight ability (Coombs et al., 1993; Gregg, 1993; Casimero et al., 1999; Zhou et al., 2000), it is probable that populations in Japan reestablish each year by immigration from the subtropics. Our research examined this issue by simulating diapause induction outdoors.

In both outdoor experiments with *H. armigera* in Chiba and Kyoto, sharp increases in the incidence of diapause were observed as the season advanced (Figs. 2b and 3a), and we suggest that this is characteristic of diapause in *H. armigera* in the temperate zone. The seasonal pattern in the incidence of diapause was also similar to that from Nanking, China (Jiang et al., 1999), whereas the incidence of diapause in *H. armigera* was predicted to increase gradually and reach 100% after two months in subtropical Australia (Dillon, 1998). Although our experiments were conducted using different local populations at different sites and in different years, a sharp increase in the incidence of diapause appears to be caused by exposure to low ambient temperatures for two reasons: first, because diapause was observed approximately 13 days later in Chiba than in Kyoto, even though photoperiodic conditions are almost identical in Chiba and Kyoto; and second, the pattern of decreasing ambient temperatures coincided in the two experiments (Fig. 4a, c). In addition, sharp increases in the incidence of diapause were observed with only a <30-min difference in the ambient photoperiod outdoors (Fig. 4d); this sharp increase was not observed in the laboratory between any photoperiods (Fig. 1). Combined changes in environmental factors, such as decreasing temperatures, shortening photoperiods, and fluctuations in daily temperatures throughout the larval stages, induce a higher incidence of
diapause in other *H. armigera* populations (Hackett and Gatehouse, 1982; Kurban et al., 2005), and in other closely related species such as *Helicoverpa punctigera* (Cullen and Browning, 1978), and *Heliothis zea* (Wellso and Adkisson, 1966; Roach and Adkisson, 1970). Such effects must have also influenced the timing of diapause induction in our outdoor experiments.

In a laboratory experiment using a population of *H. armigera* from Okayama in western Japan, Kurban et al. (2005) reported that larvae at the middle of the fifth instar were sensitive to changes in photoperiod under a constant temperature of 20°C. In many insects, the critical photoperiod for diapause induction is mainly determined by temperature during scotophase (Danilevsky, 1965). In our outdoor experiments using *H. armigera*, cohorts that showed a nearly 50% incidence of diapause experienced a minimum ambient temperature below 20°C during the late larval stage (Fig. 4a, c). This suggests that to induce diapause outdoors, *H. armigera* requires a minimum ambient temperature of <20°C during the sensitive stage to cause photoperiodic induction of pupal diapause.

Qureshi et al. (1999) reported that an *H. armigera* population from Okayama rarely entered diapause, even under the constant conditions of 8L : 16D and 25°C, and that all individuals entered diapause at 15°C, even at 16L : 8D. In contrast, Boo et al. (1990) reported that an 85% incidence of diapause occurred in *H. assulta* when individuals were reared under the constant conditions of 8L : 16D and 25°C, and that the critical photoperiod was 12–12.5 h at 25°C. In our experiments, *H. assulta* entered diapause in mid-August, which was much earlier than *H. armigera* (Fig. 3b). Thus, it is likely that the low temperature requirement for diapause induction is characteristic of *H. armigera*, but not of *H. assulta*. Our results have elucidated the difference in ecological expression of diapause-induction characteristics between *H. armigera* and *H. assulta*.

In the subtropics, where autumn temperatures are mild and decrease gradually (Danilevsky, 1965), diapause induction stimulated by low temperatures should function as a method of seasonal adaptation in *H. armigera*. In contrast, in the temperate zone, autumn temperatures are more severe, and decrease unpredictably. Under these conditions, both *H. armigera* and *H. assulta* are subject to high larval mortality, as shown in our experiments. However, compared to *H. armigera*, more individuals of *H. assulta* are able to enter diapause before larval mortality increases. In *H. armigera*, photoperiodic responses in diapause induction are observed only at temperatures near 20°C (Qureshi et al., 1999), whereas *H. assulta* shows photoperiodic responses within a wider and higher temperature range (20–25°C; Boo et al., 1990). Consequently, it is suggested that *H. assulta* is sensitive to the critical photoperiod for a longer period of time during the season than *H. armigera*, and that *H. assulta* is better adapted to the climate of the temperate zone than is *H. armigera*.

We imply that low temperatures significantly cause larval mortality in *H. armigera*. The lower temperature threshold for larval development in *H. armigera* is 13.6°C (Qureshi et al., 1999). The dates when the average ambient temperature reached below 13.6°C were 15 November 1998 in Chiba, and 28 October 2002 in Kyoto (Fig. 4a, c; broken lines). Insects do not die immediately when the ambient temperature reaches below the lower developmental threshold; however, the difference in the dates on which these low temperatures occurred seems responsible for the difference in larval mortality between Chiba and Kyoto (Fig. 4a, c). Therefore, *H. armigera* should cease to deposit eggs early in the diapause-inducing season to avoid such high larval mortality and to gain higher overwintering success (Fig. 2c, Table 1). Diapause pupae of *H. armigera* undergo a process of cold acclimation during which their trehalose content as a cryoprotectant increases (Izumi et al., 2005). If pupae are produced too late, there may be not enough time for this cold acclimation to occur. Thus, *H. armigera* requires temperature low enough (<20°C) for diapause induction, but temperatures too low (<13.6°C) can affect survival rates prior to pupation. This dilemma represents maladaptation of the species in the temperate zone.

The results from our laboratory experiments confirmed previous findings that males have a higher incidence of diapause in three local populations (Shimizu and Fujisaki, 2002). However, in contrast to laboratory observations, there were no significant sexual differences in the timing of diapause induction in *H. armigera* that developed outdoors (Figs. 1 and 2b, Table 1). Nibouche (1998) and Liu et al. (2004) found that only male individu-
als of *H. armigera* entered diapause induced by high temperatures under laboratory conditions. The egg hatching in offspring from males that had entered diapause at high temperatures was significantly higher than from non-diapause males (Liu et al., 2004). Butler et al. (1985) also reported similar sexual differences in summer diapause in *Heliothis virescens*. In the case of *H. virescens*, males that entered diapause at high temperatures had higher sperm viability, suggesting a male-specific adaptive benefit of diapause (Butler et al., 1985). Although we did not detect diapause induced by high temperatures in *H. armigera* in Kyoto, male-specific summer diapause is expected to occur in the subtropics or tropics, where the ambient temperatures are generally higher. If there are similar male-specific adaptive benefits of winter diapause, individual males ought to enter diapause earlier or show higher incidences of diapause than females, or the overwintering success will be higher in males. The reason why sexual differences in diapause induction were not detected outdoors remains unclear; however, we suppose that combined changes in environmental factors such as those mentioned previously in this paper masked any sexual differences, or pleiotropic expression of high-temperature-induced diapause resulted in sexual differences under laboratory conditions.

In the present experiments, eggs were randomly collected from stock cultures of confined female adults of various ages. Through this procedure, the consistency of the starting materials with the source materials is probably affected (Danks, 2000). Furthermore, it is also possible that the present result occurred due to a lack of variation in diapause response within the original population. It is proposed to examine diapause induction for more comminuted lines within a local population.

When the ambient temperature favorably decreases in autumn, *H. armigera* enters diapause and, as long as the temperature is suitable for development, larvae can become diapause pupae, resulting in high overwintering success. The individuals that succeeded in overwintering can establish a local population in temperate Japan. Furthermore, if a low temperature favorable for diapause induction, but at the same time, high enough for larval growth, occurs early and remains at this level until late autumn, more diapause pupae are expected to be produced. Recent global warming has increased the probability of warm winters and warm autumns, with temperatures suitable for successful diapause induction in *H. armigera*. Such changes benefit this species, resulting in its increased seasonal prevalence and continued pest status in temperate Japan.

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