

A true summer diapause induced by high temperatures in the cotton bollworm, *Helicoverpa armigera* (Lepidoptera: Noctuidae)

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Abstract

Summer diapause in the cotton bollworm, *Helicoverpa armigera* (Hübner), which prolongs the pupal stage, particularly in males, is induced by high temperatures. In the laboratory, summer-diapausing pupae of *H. armigera* were induced at high temperatures (33–39 °C) with a photoperiod of LD8:16; winter-diapausing and non-diapausing pupae, cultured at 20 °C with a photoperiod of LD8:16 and at 27 °C, LD16:8, respectively, acted as a control. Retention time of eye spots, weight, and lipid and glycogen levels were compared. At high temperatures, both body weight and energy storage capacity were much higher in summer-diapausing pupae than in non-diapausing pupae reared at 33–39 °C. At temperatures (> 33 °C) high enough to maintain summer diapause, the eye spots of summer-diapausing pupae did not move during the 30-day experiment. However, eye spots of summer-diapausing pupae placed at 30 °C began to move about 10 days after they were transferred, significantly later than in non-diapausing pupae reared at 33–39 °C or non-diapausing pupae reared at 27 °C, which initiated eye spot movement 2 days after pupation. The differences in retention time of eye spots between summer- and winter-diapausing pupae shows that winter diapause is more intense than summer diapause in this insect. The weight loss, and lipid and glycogen metabolism curves indicate that the summer-diapausing pupae's metabolism is very low. We conclude that summer diapause in the cotton bollworm is a true diapause and that the summer diapause enables the cotton bollworm to withstand the high temperatures of summer.

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1. Introduction

The cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), is widely distributed throughout the Old World and is a serious pest that attacks a variety of crops, including cotton, corn, tobacco, hot pepper, tomato, and kidney beans. In most areas of China, this species produces four or five generations a year and overwinters as diapause pupae in the soil. The biology and ecology of *H. armigera* have been described in detail (Fitt, 1989; Zalucki et al., 1986, 1994). Although the effects of pre-winter and winter temperatures and day-length on the induction, maintenance, and termination of winter diapause have been studied (Wilson et al., 1979; Wu and Guo,

1995), little research has been done on summer diapause of the cotton bollworm (Nibouche, 1998; Liu et al., 2004).

Summer diapause (aestivation) is a developmental resting stage that insects use to avoid hyperthermia and other associated physiological stresses (dehydration, starvation) (Ushatinskaya, 1987). It is also an important mechanism for synchronizing life cycles with the growing season (Beck, 1980; Xue et al., 1997). However, the performance of this species at high temperatures has not been thoroughly studied (Hackett and Gatehouse, 1982; Nibouche, 1998). High temperatures are known to induce summer diapause in *H. virescens* (F.) in Arizona (Butler et al., 1985), and a similar phenomenon has also been observed for *H. punctigera* in the Namoi Vally and *H. armigera* in the Ord of Australia (Zalucki, 1990). More detailed evidence for summer diapause in *H. armigera* was lacking until Nibouche (1998) described a “hot thermal diapause” initiated at 37 °C in a population from tropical

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Burkina Faso. In China, summer diapause in the cotton bollworm, induced by high temperatures, has also been demonstrated (Wu and Gong, 2000). Only the prepupae are sensitive to high temperatures and the critical temperature is 33 °C.

The term diapause has been used for developmental delays that allow organisms to survive unfavorable conditions and to synchronize growth and development with favorable conditions. It is important to distinguish between true diapause, in which development is arrested in advance of unfavorable conditions and does not respond immediately to amelioration of the external environment, and quiescence, in which development is temporarily inhibited by an unfavorable environment and may be resumed as soon as the hindrance is removed (Andrewartha, 1952). During diapause, there is a refractory phase (Mansingh, 1971), also known as diapause development (Andrewartha, 1952). During diapause, development is inhibited even if environmental conditions have become favorable again. In addition, diapause-stimuli are perceived before the induction of diapause begins, usually during a stage prior to the one that enters diapause.

The adaptive significance of winter diapause in *H. armigera* is obvious: it allows pupae to survive otherwise lethal winter temperatures (Wilson et al., 1979). However, the adaptive significance of summer diapause of the cotton bollworm has until now remained unclear. The host plants of the pest are usually available in summer, and the only environmental factor that is known to induce summer diapause is high temperature (Wu and Gong, 2000). In many species of moths, including the cotton bollworm, males respond to high temperatures by producing malformed spermatozoa (Guerra, 1972; Wang et al., 1996). Pupal diapause postpones the emergence of adults to less hot conditions. In most temperate parts of China, the hottest times are late July and early August: daily maximum temperatures may reach 40 °C and the temperature of the soil surface is much higher. To avoid hyperthermia and fast depletion of energy reserves as a result of such deleterious high temperatures, the cotton bollworm may enter summer diapause. How prepared is it to enter summer diapause?

Research on the summer diapause of the cotton bollworm to date refers to it as a “hot thermal diapause” (Nibouche, 1998); in his research diapause development was thought to be absent. We investigated summer diapause of the cotton bollworm in terms of diapause development and energy preparation, and as an adaptive mechanism in terms of weight loss and energy metabolism.

2. Materials and methods

2.1. Establishing a laboratory colony

A laboratory colony of *H. armigera* was established by collecting full-grown larvae from cotton growing in the suburbs of Beijing. The larvae were reared on an artificial

diet (Wu and Gong, 1997) at 27 ± 0.5 °C with a photoperiod of LD14:10 to prevent winter diapause. Newly hatched larvae were reared in groups until the 3rd instar, after which they were separated in individual glass tubes (2.0 cm diameter \times 8.0 cm high) to prevent cannibalism. Mature caterpillars were allowed to pupate in moist soil with a water content of about 7%, which is nearly the same moisture at which *H. armigera* pupates in the field. Emerged moths were allowed to mate in cages (50 cm length \times 50 cm width \times 50 cm high) for three days and were provided with a 10% honey solution.

2.2. Criteria for summer diapause

Two characteristics were used to determine whether pupae were in diapause. The first was the retention of pigmented eye spots in the postgenal region (Shumakov and Yakhimovich, 1955). These disappear during the first two days after pupation (mean < 1.6 days) at temperatures ≥ 30 °C in non-diapausing pupae (Wu and Gong, 2000). Pupae showing these eye spots for four days after pupation at 33–39 °C were considered to be diapausing. The second characteristic was the condition of the fat body in the pupal abdomen (Pearson, 1958). The fat body of newly formed pupae is composed of firm rounded lobes and remains unchanged throughout diapause. Its histolysis coincides with movement of the eye spots and is therefore a valid supplementary criterion. Because the eye spots in some pupae can be very faint and are not discernible, it is useful to verify the condition of the fat body in order to determine if pupae have entered diapause.

2.3. Inducing summer- and winter-diapausing pupae and culturing non-diapausing ones at 27 °C

Larvae were reared at 27 ± 0.5 °C and LD16:8 until foundation of the prepupae. Prepupae were transferred to a temperature regime of 33–39 (± 0.5) °C with a photoperiod of LD8:16, the higher temperature for 8 h in the photophase and the lower temperature for 16 h in the scotophase. Prepupae were allowed to pupate in moist soil (water content 7%) to induce summer diapause (80 larvae each of five replicates), and the pupation percentage was recorded. Pupae were checked on the second day after pupation to determine if they were summer-diapausing, and the incidence of diapause and the retention times of eye spots in non-diapausing pupae at 33–39 °C were recorded. Summer diapausing pupae were divided into two groups: one was moved to 30 °C, which terminated diapause, and the retention times of eye spots were recorded; the other was maintained at higher temperatures, 33–39 °C, for later experiments.

Some larvae ($n = 240$) were cultured at 20 ± 0.5 °C with a photoperiod of LD8:16 to induce winter diapause. After winter diapause was determined, one group of pupae ($n = 120$) was exposed to 27 °C to terminate diapause, and the retention times of eye spots were recorded. The other

pupae were kept in refrigeration (5 °C) for 100 d and then transferred to 27 °C; the retention times were also recorded.

Non-diapausing pupae from larvae reared at 27 °C and LD16:8 were cultured and checked, and the retention times of eye spots recorded.

2.4. Body weight and weight loss curves

Pupae ($n = 161$) were sampled at high temperatures (33–39 °C), weighed daily with a balance (Sartorius research, 0.1 mg), and checked for the movement of eye spots from the second day following pupation until all the non-diapausing pupae at 33–39 °C had emerged. Then the summer-diapausing pupae were transferred to 30 °C to terminate diapause and weighed daily, and the retention times of eye spots were recorded. The same was done for non-diapausing pupae reared at 27 °C. Daily weight loss was calculated with the formula, $\Delta i = M_i - M_{i+1}$, where i is the pupal age (d) and M is the fresh weight (mg).

2.5. Lipid and glycogen levels and their metabolism curves

On the day when summer diapausing and non-diapausing pupae at 33–39 °C were determined, the energy storage capacity and lipid and glycogen levels were measured. The energy storage capacity in non-diapausing pupae reared at 27 °C was also determined. The changing lipid and glycogen levels in summer-diapausing and non-diapausing pupae at 33–39 °C under high temperatures were also investigated. Non-diapausing pupae at 33–39 °C were tested on their first, third, fifth, seventh, and ninth days; summer-diapausing pupae were tested only on their fifth and tenth days. The following methods of measuring lipid and glycogen levels were used.

Dried pupae were weighed and homogenized, and their lipid content extracted with a chloroform–methanol (2:1) solution (Folch et al., 1957). After centrifugation (2600g for 10 min), the supernatant was removed. The procedure was repeated twice. The resulting pellet was dried at 60 °C for 72 h and the lean dry weight (ldw) determined. Total lipid levels (mg/gDW) and lipid weight (mg) per individual were calculated using the formula

$$[(dw - ldw)/dw] \times 1000 \quad \text{and} \quad dw - ldw.$$

Fresh pupae were homogenized in 2 ml of 70% ethanol and centrifuged (2600g for 10 min). Pooled supernatants from two replications of this procedure were discarded and the remaining pellet was used for isolating glycogen according to the method described in Ohtsu et al. (1992). Two milliliter of 10% (v/v) trichloroacetic acid was added to the residue. The mixture was boiled in a water bath for 15 min and then cooled and centrifuged at 3000g for 15 min. The supernatant was used for glycogen measurement. Glycogen content was determined by the phenol and sulfuric acid method (Dubois et al., 1956). The absorbance was determined at 490 nm on a spectrophotometer (DU650, Beckman, USA). The results were expressed in

mg glycogen g^{-1}dw and mg glycogen/individual using a calibration curve obtained by measuring glycogen standards in seven concentrations ranging from 0.025 to 0.5 mg ml^{-1} .

2.6. Statistical analysis

Statistical analyses of data for retention times, pupal weight, and body water, lipid and glycogen levels of pupae were performed by one-way analysis of variance (ANOVA) (SPSS, 1999), and the means were separated with the Duncan multiple range test (Duncan, 1955). The percentage data were arcsine-transformed before being analyzed, and untransformed data are presented in Table 2.

3. Results

3.1. Effects of high temperatures on pupation and the incidence of summer diapause

In this experiment, only 86.2% ($n = 344$) of larvae pupated at high temperatures (33–39 °C), whereas 99.3% ($n = 396$) of larvae pupated at 27 °C ($F = 18.8224$; $df = 1, 8$; $p = 0.001$). At 33–39 °C, an average of 32.4% ($n = 110$) of pupae entered summer diapause; 63.2% ($n = 91$) of the males and 10.9% ($n = 19$) of the females entered diapause ($F = 49.389$; $df = 1, 8$; $p < 0.001$).

3.2. Comparison of retention time of eye spots

Under temperatures terminating diapause, the retention time of eye spots is one of the characteristics used to determine whether the insect has entered diapause. As shown in Table 1A, average retention times of summer-diapausing pupae, non-diapausing pupae at 33–39 °C and non-diapausing pupae reared at 27 °C were 9.6, 1.6, and 2 d, respectively. Retention times of eye spots were significantly longer among summer-diapausing pupae than non-diapausing pupae at 33–39 °C or non-diapausing pupae reared at 27 °C ($F = 160.897$; $df = 2, 289$; $p < 0.001$).

After both summer and winter diapausing pupae were determined, they were exposed to temperatures to terminate diapause without being exposed to temperatures that would have maintained diapause. Average retention times of eyespots for insects in these two kinds of diapause were 9.6 and 37.4 d, for summer- and winter-diapausing pupae, respectively (Table 1B, $F = 326.713$; $df = 1, 206$; $p < 0.001$). However, retention times did not differ from each other when diapausing pupae were kept at temperatures that maintained diapause for many days ($F = 0.014$; $df = 1, 123$; $p = 0.908$). Under these conditions, the average retention time was about 3 days, significantly longer than the 2 days deserved in non-diapausing pupae reared at 27 °C ($F = 289.026$; $df = 2, 208$; $p < 0.001$).

Table 1
Comparison of retention times of pigmented eye spots

Pupae	<i>n</i>	Retention of pigmented eye spots (d)		
(A) Among summer diapausing, non-diapausing pupae at 33–39 °C and non-diapausing pupae reared at 27 °C				
Summer-diapausing pupae	96	9.56 ± 0.62a		
Non-diapausing pupae at 33–39 °C	110	1.59 ± 0.05b		
Non-diapausing pupae reared at 27 °C	86	1.98 ± 0.01b		
<i>F</i>		160.90		
<i>P</i>		<0.001		
		Retention of pigmented eye spots (d)		
	<i>n</i>	No storage ^a	<i>n</i>	Storage ^b
(B) Between summer and winter diapause				
Summer-diapausing induced by high temperature	96	9.56 ± 0.62	50	3.07 ± 0.21a
Winter-diapausing induced by low temperature	112	37.39 ± 1.32	75	3.08 ± 0.03a
Non-diapausing pupae reared at 27 °C			86	1.98 ± 0.01b
<i>F</i>		160.90		289.026
<i>P</i>		<0.001		<0.001

The data in the table are Mean ± SE and those followed by different letters differ significantly by Duncan's multiple range test ($P < 0.05$).

^aThe diapausing pupae exposed to temperatures terminating diapause, 30 and 27 °C, respectively, once diapause was determined.

^bSummer-diapausing pupae were kept at 33–39 °C for 10 d, winter -diapausing pupae were kept at 5 °C for 100 d.

Table 2
Body weight and energy storage of diapausing and non-diapausing pupae experiencing high temperature

	Non-diapausing pupae at 33–39 °C	Summer-diapausing pupae	Non-diapausing pupae reared at 27 °C	<i>F</i>	<i>P</i>
Fresh body weight (mg) ^a	252.65 ± 2.7 (194)c	269.9 ± 4.3 (41)b	303.5 ± 6.7 (41)a	33.77	<0.001
Water content (% DW) ^b	68.49 ± 0.34 (20)c	67.17 ± 0.26 (20)b	71.67 ± 0.97 (20)a	20.953	<0.001
Lipid					
mg/pupa	27.15 ± 1.26 (20)b	33.76 ± 1.79 (20)a	33.13 ± 2.99 (20)a	4.815	0.013
mg/g DW	360.93 ± 9.22 (20)a	377.03 ± 11.28 (20)a	381.71 ± 8.33 (20)a	0.935	0.4
Glycogen					
mg/pupa	7.05 ± 0.31 (11)b	8.99 ± 0.32 (11) a	9.99 ± 0.30 (11)a	15.478	<0.001
mg/g DW	97.03 ± 4.15 (11)b	103.04 ± 4.35(11)ab	116.48 ± 3.5 (11)a	2.532	0.103

The data in the table are Mean ± SE and the values in parenthesis are the number of samples. The followed different letters indicate significant difference by Duncan's multiple range test ($P < 0.05$).

^aBody weight recorded on the second day after pupation.

^bThe data of percentages were arcsine-transformed before analysis and the untransformed data are shown in the table.

3.3. Body weight, water content, and the dynamics of weight loss in pupae

Body weights were recorded starting the second day after pupation (Table 2). Mean body weights of summer-diapausing, non-diapausing pupae at 33–39 °C, and non-diapausing pupae reared at 27 °C were 269.9, 252.6, and 303.5 mg, respectively, showing significant differences ($F = 33.777$; $df = 2, 273$; $p < 0.001$). Non-diapausing pupae reared at 27 °C were significantly heavier than summer-diapausing pupae, which were in turn slightly, but significantly, heavier than non-diapausing pupae at 33–39 °C.

Summer-diapausing pupae contained less water than did non-diapausing pupae at 33–39 °C ($F = 9.30$; $df = 1, 38$; $p = 0.004$), i.e. 67.2% and 68.5%, respectively. Both

contained less water compared to non-diapausing pupae reared at 27 °C (71.7%).

Before summer-diapausing pupae were transferred to 30 °C, their weight loss curve was lower than that of the others (non-diapausing pupae at 33–39 °C and non-diapausing pupae reared at 27 °C) (Fig. 1). When summer-diapausing pupae were exposed to 30 °C temperatures, their weight loss per day remained at low levels for the first three days and then increased quickly, a pattern similar to that of non-diapausing pupae reared at 27 °C. Moreover, the summer-diapause-terminated pupae took 3 days more to turn into adults compared to non-diapausing pupae at 33–39 °C and non-diapausing pupae reared at 27 °C, suggesting that diapause development occurred.

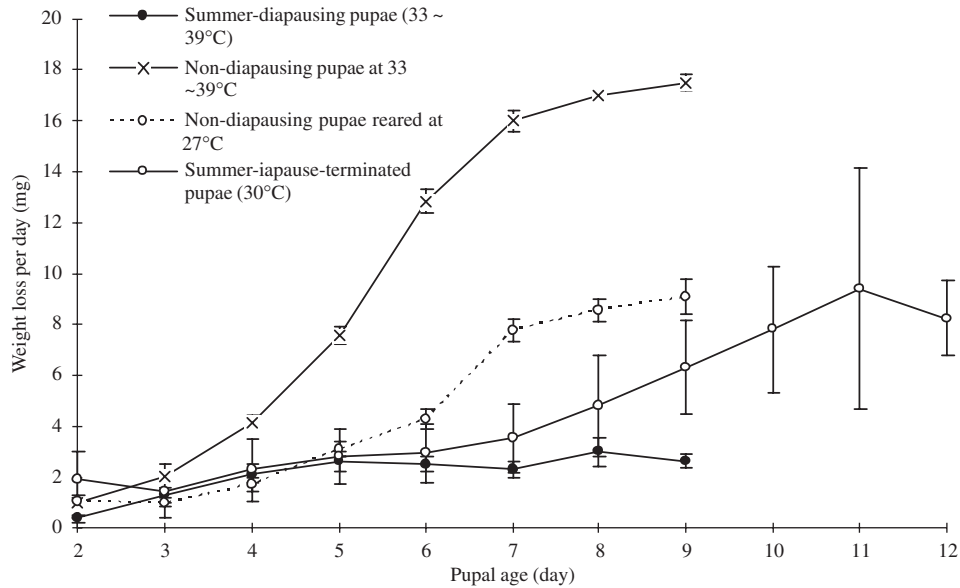


Fig. 1. Curves of weight loss of pupae of *H. armigera* among different groups. Age of summer-diapause-terminated pupae was expressed with $10 + i$; i is days after pupation. The bar indicates Mean \pm SE and samples tested per group were not smaller than 50.

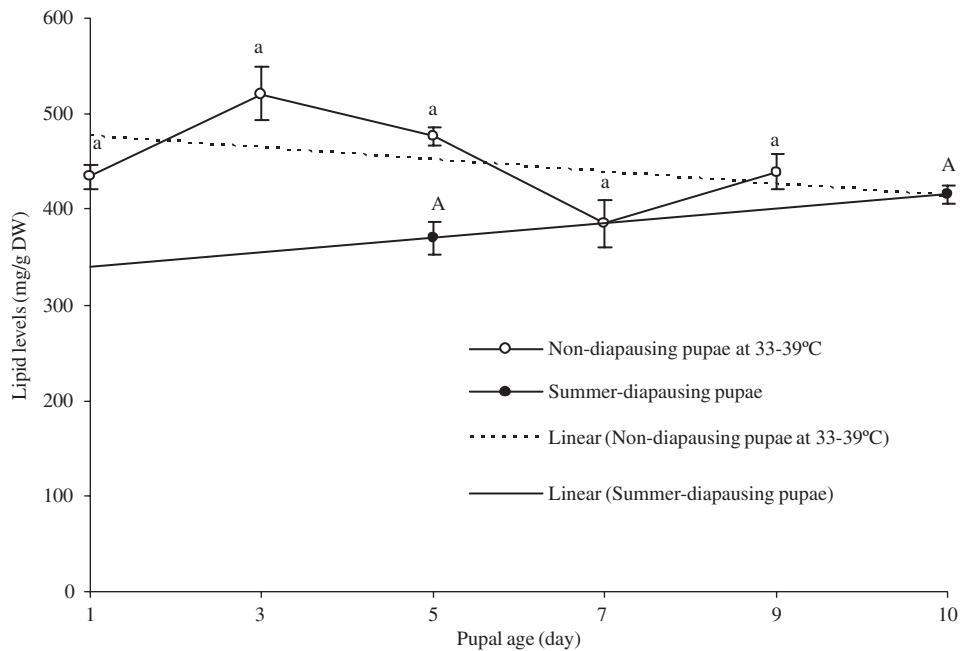


Fig. 2. Changes in lipid levels of summer-diapausing and non-diapausing pupae under high temperatures (33–39 °C). The bar indicates Mean \pm SE and the same letter above the bar indicates the absence of significant differences by Duncan's multiple range test ($P > 0.05$).

3.4. Energy storage and the metabolic dynamics of lipid and glycogen contents

Comparisons of lipid and glycogen levels are shown in Table 2. There were no differences in terms of mg/g DW among lipid and glycogen levels. However, with regard to absolute amounts, mg/pupa, diapausing pupae contained significantly more lipid and glycogen levels than did non-diapausing pupae (lipids: 27.2 and 33.8 mg/pupa for non-diapausing pupae at 33–39 °C and summer-diapausing pupae, respectively

($F = 9.143$; $df = 1, 38$; $p = 0.04$); glycogen: 9.0 and 7.1 mg/pupa for summer-diapausing pupae and non-diapausing pupae at 33–39 °C, respectively [$F = 18.860$; $df = 1, 20$; $p < 0.001$]).

The dynamics of lipid and glycogen levels are shown in Figs. 2 and 3. Levels of lipids did not differ much between both summer-diapausing and non-diapausing pupae at 33–39 °C. Glycogen levels decreased significantly ($y = -18.92x + 120.78$; $R^2 = 0.9585$) in non-diapausing pupae, whereas in summer-diapausing pupae, they remained almost the same.

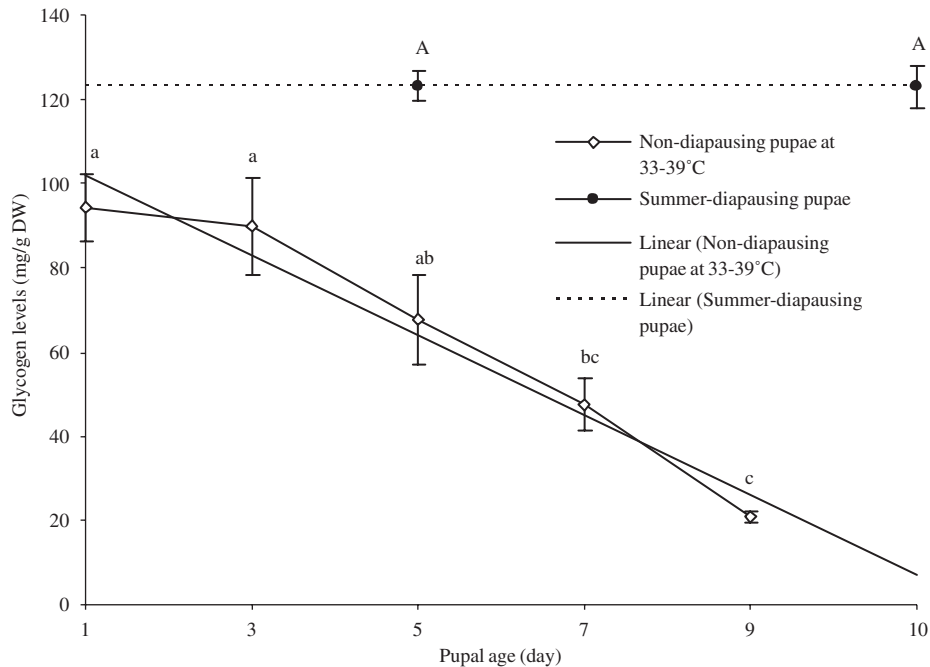


Fig. 3. Changes in glycogen levels of diapausing and non-diapausing pupae at high temperatures (33–39 °C). The bar indicates Mean \pm SE and the different letter above the bar indicates significant differences by Duncan's multiple range test ($P < 0.05$).

4. Discussion

Summer diapause may be defined as a diapause that is induced before the height of summer, which is terminated and followed by reproductive, developmental, or feeding activities in autumn or winter (Masaki, 1980). Wu and Gong (2000) reported that summer diapause in the pupal stage of *H. armigera* was induced by exposure to high temperatures (> 33 °C); photoperiod had no significant effect. Wu and Gong (2000) also found that many summer-diapausing pupae survived for a month at 35 °C, and 20% of the diapausing pupae could survive up to two months at this temperature. No other details have been reported. Some scholars have wondered if summer diapause is simply a period of “hot quiescence” or, as Nibouche (1998) referred to it, a “hot thermal diapause.” We provide evidence for the occurrence of a true summer diapause in *H. armigera*.

We found that summer-diapausing pupae need to experience diapause development before they can resume development. But the time pupae required to restart development when exposed to favorable temperatures depended on whether or not they had been kept at high temperatures (> 33 °C) (see Table 1). If they did not experience the high temperatures needed to maintain the induced summer diapause, they needed to spend about 10 days at 30 °C recovering from diapause; individuals varied from 2 to 23 days. However, they spent only 3 days at 30 °C recovering from diapause if they had been kept for a few days at high temperatures (> 33 °C); then individuals varied only from 2 to 4 days. Therefore, diapausing pupae should be understood as having a refractory phase, or as

experiencing diapause development. Moreover, this kind of diapause can be maintained at high temperatures for at least one month (Figs. 4 and 5). We know that in the cotton bollworm diapause induction by high temperatures must occur during the prepupal stage, whereas diapause is noticeable at the pupal stage. The perception and response to stimuli that occur before the diapause stage indicate that the arrest in development is diapause, not quiescence (Mansingh, 1971).

Nibouche (1998) induced pupal dormancy of *H. armigera* by exposing individuals from the third-instar to the pupal stage to high temperatures (37 °C). Males were more sensitive than females. But when diapausing pupae were transferred from high to moderate temperatures, the dormancy terminated immediately, so he referred to the stage as a “hot thermal diapause.” The results in our lab differed from Nibouche's in several ways: First, in our study third instars did not survive to the pupal stage if they were exposed to the high temperature at an early age. This difference in response to temperatures is most likely related to the different populations that we tested: the population used in Nibouche's experiment was from Burkina Faso, a tropical area, and the population in our experiment was from Beijing, a temperate zone. Second, unlike Nibouche, we observed diapause development (i.e. a delay in resuming development after pupae were transferred to moderate temperatures). Thus, we conclude that the dormancy described here is a true summer diapause, neither “hot quiescence” nor “hot thermal diapause.”

We also observed that only some individuals of this species enter summer diapause and that males were more

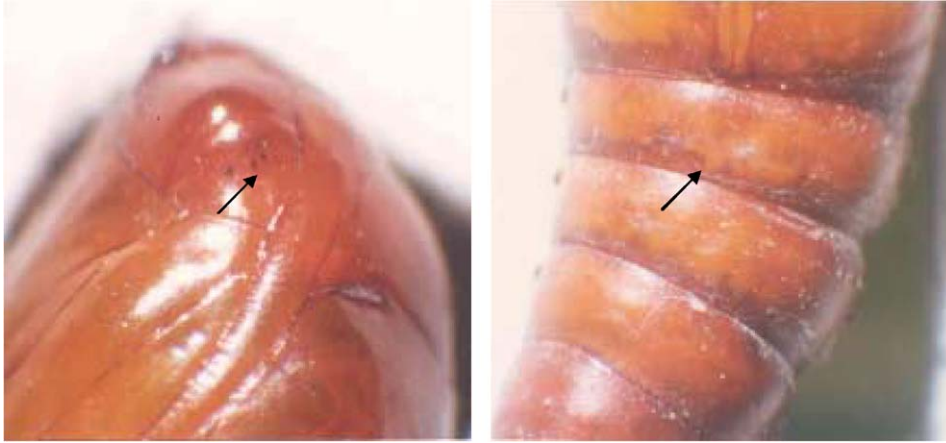


Fig. 4. Eye spots and fat body of summer-diapausing pupae kept at 35 °C for 30 days (Photograph by P.Y. Gong). The arrow shows the presence of eye spots and firm rounded fat body.

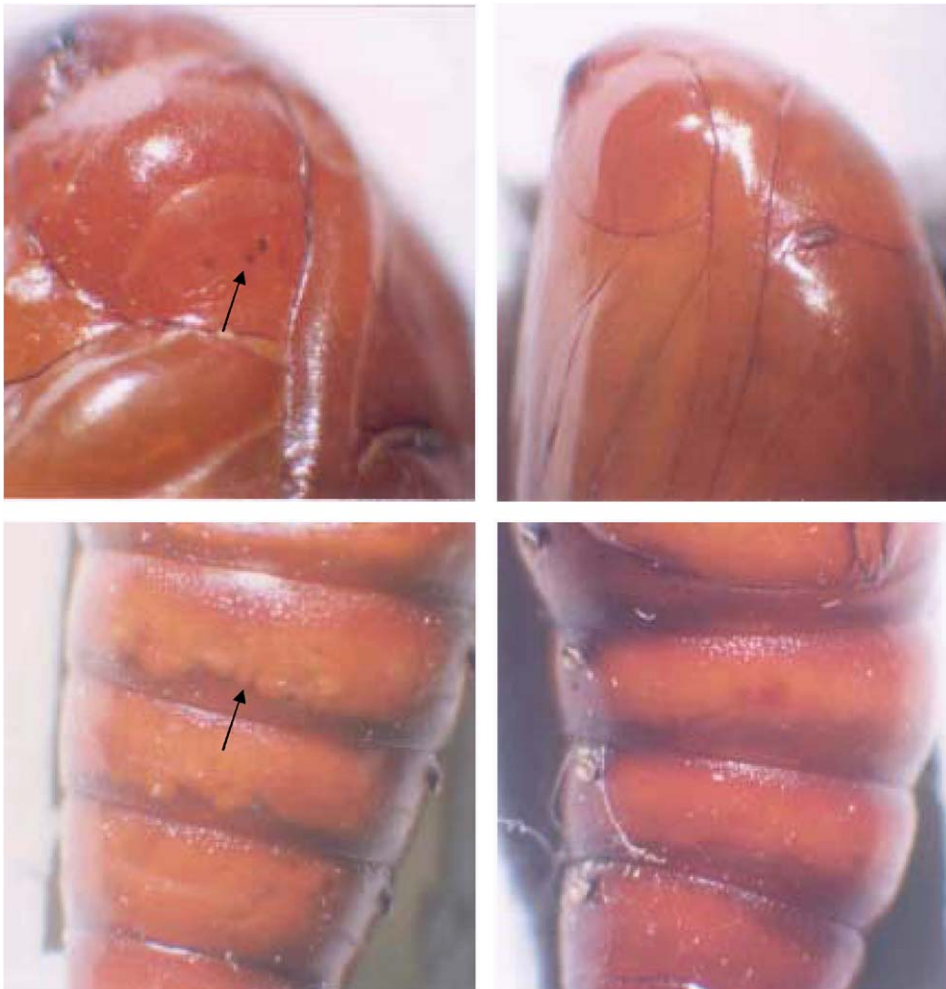


Fig. 5. Eye spots and fat body of developing pupae reared at 27 °C from first to third day (photograph by P.Y. Gong). The arrow shows the presence of eye spots and firm rounded fat body.

likely than females to enter diapause at high temperatures. This sexual discrepancy for entering summer diapause confirms what has been previously reported (Butler et al., 1985; Denlinger, 1981).

We compared some characteristics related to metabolism between summer-diapausing and non-diapausing pupae: body weight, weight loss per day, lipid and glycogen levels and their metabolism dynamics. The prepupa, a non-feeding

larval stage, is the stage sensitive to the programming of diapause, thus this insect does not accumulate additional food before entering diapause, yet the body weight of summer-diapausing pupae was heavier than that of non-diapausing pupae at 33–39 °C. Surprisingly, some prepupae moved around at high temperatures, thus consuming energy. Tombes (1964) pointed out that summer diapause existed in both males and females of *Hypera postica*, and that the summer-diapausing insects shared four characteristics: low water content, low respiratory rates, high lipid levels, and undeveloped reproductive organs. We also found that summer diapausing pupae had lower water and higher lipid levels compared to those of non-diapausing pupae at 33–39 °C. Weight loss per day in summer-diapausing pupae was very small, suggesting that metabolism was low (Fig. 1), as seen in summer diapause of *Eriogyna pyretorum* (Honek, 1980) and *Cymbalophora pudica* (Groeters and Dingle, 1987). Low metabolism is one of the indicators of diapause. In our experiment, lipid and glycogen levels in diapausing pupae remained nearly constant, indicating that metabolic activities were very low, while glycogen decreased quickly with pupal age in non-diapausing pupae at 33–39 °C.

Summer diapause is not as intense as winter diapause in *H. armigera*. Winter-diapausing pupae took 37 days, summer diapausing pupae only 10, to terminate diapause. Winter diapause in *H. armigera* is induced by low temperatures and short photoperiod during pre-winter (Wilson et al., 1979; Wu and Guo, 1995; Qureshi et al., 2000), which results in a very low metabolism during the long cold winter. Winter is long (about several months), while the hot summer is short (about ten days), which possibly is the reason why winter diapause is much longer than summer diapause. Summer diapause is maintained by high temperatures during summer and can be rapidly ended by moderate temperatures, making it difficult to observe in the field. In summer, the larvae develop mainly on agricultural crops, such as cotton, and are often subjected to hot, dry conditions, especially during the prepupal stage in the soil. Our experiments suggest that such conditions serve as a cue for induction of summer diapause. In North China, the temperatures in late July and early August are very high, sometimes reaching 40 °C; this is high enough to induce diapause. If temperatures are high and a substantial number of insects enter diapause during summer, adult

populations of the cotton bollworm may be relatively small during late July and early August. In late August after the end of summer diapause, which is synchronized so that nearly all the post-diapause adults emerge at the same time (see Table 1), a large population peak occurs. In the Xinjiang Autonomous Area, the emergence of the second generation is always delayed about 10 days compared with the first one (Guo, 1998), but temperatures are the hottest during July and August (Table 3). Thus, based on a thermal model, the peak of adult emergence should be earlier. Based on our results, we think the adult peak lags because of summer diapause, and in fact the moth peak has been known to increase abruptly at specific times in past summers, further confirming our assumption (pers. obs., Nü Zhaozhi, Institute of Geography, CAS).

The experience of summer diapause may confer benefits on the offspring. Butler et al. (1985) found some evidence for such benefits in the tobacco budworm. Our research has also confirmed that the offspring of parents which had experienced summer diapause had higher survival rates compared to those whose parents had not experienced summer diapause, and they weighed significantly more than those from non-summer-diapausing parents under normal rearing conditions (Liu et al., 2004).

We conclude that summer diapause of the cotton bollworm is a mechanism that confers advantages to the offspring. In addition, summer diapause has evolved its own adaptive characteristics. It is maintained by high temperatures during summer and rapidly ended by falling temperatures, and as a result the autumn emergence of adults is synchronized. This synchronization serves as a negative feedback system to stabilize the seasonal life cycle. In *H. armigera*, a portion of the population is dormant during the period of high temperature, but the rest continues to develop. Like other types of polymodal emergence strategies, which have been described as “bet hedging” (Waldbauer, 1978), this may protect the species from unpredictable risks due to a fluctuating environment.

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Table 3
Meteorological data records in Shanshan County, Xinjiang Autonomous Area, China

Year	Air temperature (°C)														
	May			June			July			August			September		
	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L
1999	23.6	23.9	23.7	28.8	25.8	29.0	28.7	32.5	32.3	29.3	27.0	28.9	25.7	22.3	18.4
2000	24.2	26.3	27.1	26.8	28.3	28.7	29.9	32.3	29.1	28.8	26.9	26.6	21.3	24.1	18.8
2001	23.1	25.5	24.9	27.5	29.6	30.3	29.7	31.1	29.6	30.2	28.9	27.4	26.0	20.8	18.1

*E, M, and L indicate early, medium, and late parts of the month, respectively.

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