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Role of natural day-length and temperature in determination of summer and winter diapause in *Pieris melete* (Lepidoptera: Pieridae)

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Abstract

Under field conditions, the cabbage butterfly, *Pieris melete*, displays a pupal summer diapause in response to relatively low daily temperatures and gradually increasing day-length during spring and a pupal winter diapause in response to the progressively shorter day-length. To determine whether photoperiod is 'more' important than temperature in the determination of summer and winter diapause, or vice versa, the effects of naturally changing day-length and temperature on the initiation of summer and winter diapause were systematically investigated under field conditions for five successive years. Field results showed that the incidence of summer diapause significantly declined with the naturally increasing temperature in spring and summer generations. Path coefficient analysis showed that the effect of temperature was much greater than photoperiod in the determination of summer diapause. In autumn, the incidence of diapause was extremely low when larvae developed under gradually shortening day-length and high temperatures. The incidence of winter diapause increased to 60–90% or higher with gradually shortening day-length combined with temperatures between 20.0°C and 22.0°C. Decreasing day-length played a more important role in the determination of winter diapause induction than temperature. The eco-adaptive significance of changing day-length and temperature in the determination of summer and winter diapause was discussed.

Keywords: *Pieris melete*, day-length, temperature, summer diapause, winter diapauses

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Introduction

In the temperate zone, photoperiod is considered the most predominant stimulus in the determination of diapause in many insects, because it is the most reliable signal for long-term predictor of environmental change (Tauber *et al.*, 1986; Saunders, 2002; Bradshaw & Holzapfel, 2010). Other physical factors such as temperature generally fluctuate more vastly than photoperiod and, thus, tend to be used in the stimulation or inhibition of insect growth on a short-term basis

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(Roff, 1983). Even so, insects are responsive to temperature in the process of diapause determination in several different ways (Tauber *et al.*, 1986; Danks, 1987; Xue *et al.*, 2002).

The cabbage butterfly, *Pieris melete* Ménétriés, is a serious pest of crucifers in the mountainous areas in China, displays both summer and winter diapause in the pupal stage. Besides its agricultural significance, this insect can also serve as an excellent experimental animal for diapause study because it has a multi-voltine life cycle with both summer and winter diapause in the pupal stage, which were mainly induced by relatively long and short day lengths, respectively. Furthermore, the cabbage butterflies can be easily mass-reared within an outdoor nested insectary (Xue *et al.*, 1996, 1997). The effects of temperature and photoperiod on diapause induction and termination have been evaluated in detail in this butterfly under laboratory conditions (Xue *et al.*, 1997; Xiao *et al.*, 2006, 2008a,b, 2009). These studies revealed that high temperatures strongly weakened the diapause-inducing effects of long day-length and significantly reduced the incidence of summer diapause; whereas winter diapause can be induced under short day-length at relatively high temperatures, and a diapause-inducing short day-length has a stronger diapause-inducing effect than a long day-length at higher temperatures (Xue *et al.*, 1997; Xiao *et al.*, 2008a,b, 2009). Thus, we suggest a hypothesis that temperature may exhibit a much greater effect in the determination of summer diapause induction than photoperiod, whereas photoperiod may play a more important role in the initiation of winter diapause than temperature under field conditions. However, it was not verified in the aforementioned studies. In the present study, we conducted an analysis based on the field investigation for five successive years to clarify the role of naturally changing day-length and temperature in the determination of summer and winter diapause in the cabbage butterfly.

Material and methods

The cabbage butterfly, *P. melete*, used in the experiments originated from a wild population in the suburbs of Nanchang (28°46′N, 115°50′E; at an altitude of 120–200 m above sea level), Jiangxi Province, P.R. China. Full-grown larvae prior to pupation were collected from crucifers in late November in 2002, 2003, 2004, 2005 and 2006 and were transferred to wooden cages (30 × 30 × 35 cm) for pupation and overwintering under natural conditions. To examine the effect of seasonal variation on summer and winter diapause, adults from the overwintering pupae were released to an outdoor web-screened insectary equipped with potted Chinese cabbage, *Brassica chinensis*, for mating and oviposition. Under natural conditions, almost all individuals in the first spring generation entered summer diapause. Therefore, some larvae were kept under natural conditions to observe the diapause incidence, whereas some of the rest larvae of the first generation were reared under an intermediate artificial photoperiod of LD 12.5:11.5 under otherwise natural conditions to obtain more non-diapausing individuals for further mass-rearing. Adults emerging from non-diapauing pupae were released into an outdoor web-screened insectary to mate and produce the second generation. Full-grown larvae were collected every few days from the insectary and were transferred to wooden cages for pupation under natural photoperiods and temperatures. When adults emerged, they were released into an outdoor screened insectary to start another generation. The same rearing process was repeated in the following generations until the last generation of the year in which all pupae entered winter diapause in late November. In each generation, the dates of hatching, pupation and the incidence of diapause were recorded in detail.

Diapause in *P. melete* was recognized in the pupal stage. Non-diapause pupae generally emerged within 7–10 days in spring-summer generations and 12–14 days at the end of autumn. The longest period for pupal development in non-diapausing individuals did not exceed 30 days. Thus, pupae that did not emerge within 30 days were considered to be in diapause (Xue *et al.*, 1997).

During the entire experimental period, temperatures were recorded by an auto thermograph. The daily mean temperature was calculated by averaging the temperatures recorded at 2 am, 8 am, 2 pm and 8 pm. The day-length from larvae hatching to pupation (including twilight) was calculated according to the civil twilight table (Danilevski, 1965).

Statistical analyses were conducted using the STATA package Version 9.0. The percentage of diapause (arcsin-square root transformed) was modeled as a function of photoperiod and temperature associated interaction terms. Stepwise regression was used to analyze the correlation between the incidence of diapause and environmental factors. Path coefficient analysis was useful in that it revealed the true nature of cause-and-effect relationships of photoperiod and temperature with the incidence of diapause (Bhatt, 1973). Therefore, regression analysis and path coefficient analysis were used together to determine whether the variance in the incidence of diapause in different spring-summer and autumn generations were mainly caused by day-length or temperature.

Results

Incidence of summer diapause in successive spring-summer generations

The incidences of summer diapause in successive spring-summer generations were observed under the natural conditions for five successive years. As seen in table 1, the incidence of summer diapause in different spring-summer generations (SG) was strongly affected by natural environment stimuli. In the first generation (SG1), almost all individuals were induced to enter diapause (>96%) when larvae growing from late March to early May experienced relatively low mean daily temperatures (<20.2°C) and gradually increasing day-length from 13 h 0 min to 14 h 5 min. However, in 2004 and 2006, 33.33% and 34.04% individuals in the first generation developed without diapause when the larval period was from March 6 to April 12 and from March 15 to April 13, respectively. The mean daily temperature experienced by these caterpillars was 13.7 and 16.4°C, respectively, combined with an intermediate to relatively long day-length (12 h 30 min ~ 13 h 36 min).

The incidence of summer diapause in the second generation (SG2) during spring-summer differed in different years, depending on the mean daily temperatures. More than 94% pupae were induced to enter diapause in 2004, 2006 and 2007, when the larvae experienced a mean daily temperature below 22°C and a gradually increasing day-length from 13 h 49 min to14 h 42 min. The incidence of diapause dropped to 50.93% and 47.22% when larvae experienced the mean daily temperature of 22.3°C and long day-length from 14 h 16 min to 14 h 44 min in 2003 and 2005, respectively. The diapause incidence

Table 1. Incidence of summer diapause for successive generations in *P. melete* reared under natural spring and summer conditions.

Year	Generation	Date of hatching–pupation	Day length	Temperature (°C)	Diapause (%) (no. of individuals)
2003	SG1	Apr 2–Apr 28	13 h 17 min ~ 14 h 2 min	17.3	99.56 (2066)
	SG2	May 11–May 31	14 h 23 min ~ 14 h 44 min	22.3	50.93 (108)
	SG3	Jun 11–Jun 28	14 h 52 min ~ 14 h 53 min	25.6	21.25 (80)
	SG4	Jul 11–Jul 25	14 h 15 min ~ 14 h 30 min	31.7	0.00 (37)
2004	SG1	Mar 6–Apr 12	12 h 30 min ~ 13 h 33 min	13.7	66.67 (60)
	SG1	Mar 12–Apr 15	12 h 39 min ~ 13 h 40 min	14.3	86.01 (143)
	SG1	Mar 15–Apr 19	12 h 45 min ~ 13 h 47 min	15.3	94.31 (211)
	SG1	Mar 26–Apr 22	13 h 5 min ~ 13 h 50 min	18.4	98.64 (516)
	SG1	Apr 1–Apr 25	13 h 15 min ~ 13 h 57 min	19.2	100.00 (912)
	SG2	Apr 20–May 10	13 h 49 min ~ 14 h 21 min	21.1	97.01 (603)
2005	SG1	Apr 5–Apr 28	13 h 22 min ~ 14 h 2 min	20.2	99.71 (3079)
	SG2	May 7–May 26	14 h 16 min ~ 14 h 39 min	22.3	47.22 (108)
2006	SG1	Mar 15–Apr 13	12 h 46 min ~ 13 h 36 min	16.4	65.96 (658)
	SG1	Mar 17–Apr 14	12 h 50 min ~ 13 h 38 min	16.7	87.82 (936)
	SG1	Mar 22–Apr 16	12 h 59 min ~ 13 h 41 min	17.1	96.07 (936)
	SG1	Mar 24–Apr 18	13 h 2 min ~ 13 h 46 min	17.3	99.05 (734)
	SG1	Mar 28–Apr 22	13 h 9 min ~ 13 h 50 min	18.1	99.29 (4375)
	SG2	Apr 30–May 21	14 h 5 min ~ 14 h 35 min	20.5	95.56 (180)
	SG2	May 2–May 24	14 h 8 min ~ 14 h 38 min	20.9	94.18 (292)
	SG2	May 5–May 26	14 h 13 min ~ 14 h 39 min	20.9	93.50 (446)
	SG2	May 8–May 29	14 h 18 min ~ 14 h 42 min	21.1	95.90 (293)
	SG3	Jun 1–Jun 18	14 h 45 min ~ 14 h 55 min	24.4	10.39 (154)
2007	SG1	Mar 20–Apr 18	12 h 55 min ~ 13 h 45 min	17.1	99.85 (1980)
	SG2	Apr 23–May 13	13 h 54 min ~ 14 h 24 min	21.7	96.69 (1177)
	SG3	May 27–Jun 12	14 h 41 min ~ 14 h 53 min	25.8	13.68 (117)
	SG4	Jun 20–Jul 4	14 h 56 min ~ 14 h 50 min	29.0	0.00 (59)

SG, spring-summer generation.

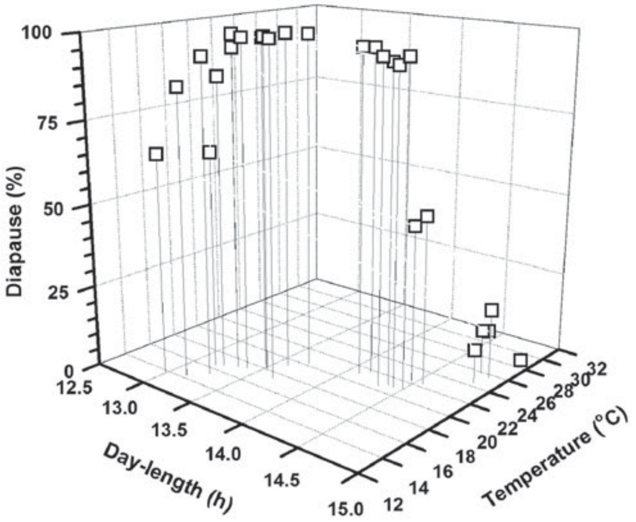

Fig. 1. Influence of day-length and temperature on the incidence of summer diapause in *P. melete*.

in SG3 was 21.25% in 2003, 10.39% in 2006 and 13.68% in 2007. Summer diapause disappeared in SG4 in July in both 2003 and 2007.

Role of day-length and temperature in the determination of summer diapause

Regression analysis was carried out based on the data from table 1 (fig. 1). It was clear that relatively low mean daily temperatures (<22°C) combined with long day-length from 13 h 0 min to 14 h 30 min induced almost all individuals to enter diapauses, whereas high temperatures (>22°C) combined with long day-length (>14.5 h) caused most individuals to develop without diapause. Regression analysis indicated that the incidence of summer diapause correlated negatively with the increasing day-length and temperature. Both day-length and temperature had significant impacts on the incidence of summer diapause in different spring-summer

Table 2. Incidence of winter diapause for successive generations in *P. melete* reared under natural autumn and winter conditions.

Year	Generation	Date of hatching–pupation	Day length	Temperature (°C)	Diapause (%) (no. of individuals)
2003	AG1	Aug 1–Aug 15	14 h 22 min ∼ 14 h 0 min	31.2	3.85 (182)
	AG2	Aug 23– Sep 7	13 h 47 min ∼ 13 h 22 min	30.2	8.33 (132)
	AG3	Sep 16–Oct 4	13 h 6 min ∼ 12 h 38 min	22.8	1.04 (193)
	AG4	Oct 17–Nov 15	12 h 15 min ∼ 11 h 31 min	16.7	95.52 (1340)
2004	AG1	Aug 16–Sep 2	14 h 20 min ∼ 13 h 31 min	27.8	4.65 (43)
	AG2	Sep 15–Oct 4	13 h 4 min ∼ 12 h 38 min	23.5	10.27 (146)
	AG2	Sep 19–Oct 10	13 h 7 min ∼ 12 h 25 min	22.3	60.71 (168)
	AG2	Sep 25–Oct 15	13 h 2 min ∼ 12 h 18 min	21.8	85.35 (157)
	AG2	Sep 29–Oct 22	12 h 45 min ∼ 12 h 7 min	20.9	100.00 (265)
	AG3	Oct 23–Nov 20	12 h 6 min ∼ 11 h 28 min	17.5	99.73 (1461)
2005	AG1	Aug 25–Sep 10	13 h 44 min ∼ 13 h 17 min	26.4	6.78 (59)
	AG2	Sep 22–Oct 11	12 h 56 min ∼ 12 h 25 min	23.7	43.35 (173)
	AG2	Oct 4–Oct 27	12 h 38 min ∼ 11 h 59 min	19.9	64.43 (194)
	AG2	Oct 7–Oct 31	12 h 31 min ∼ 11 h 51 min	19.3	91.13 (406)
	AG2	Oct 12–Nov 6	12 h 23 min ∼ 11 h 43 min	19.1	95.59 (612)
	AG2	Oct 20–Nov 15	12 h 11 min ∼ 11 h 30 min	17.9	100.00 (238)
	AG3	Nov 2–Dec 8	11 h 50 min ∼ 11 h 13 min	13.7	100.00 (433)
2006	AG1	Sep 10–Sep 27	13 h 17 min ∼ 12 h 48 min	23.1	1.59 (757)
	AG2	Oct 6–Oct 26	12 h 27 min ∼ 11 h 58 min	21.9	89.60 (721)
	AG2	Oct 10–Nov 1	12 h 26 min ∼ 11 h 50 min	21.6	86.76 (68)
	AG3	Nov 3–Dec 9	11 h 48 min ∼ 11 h 17 min	13.2	100.00 (738)
2007	AG1	Sep 21–Oct 10	12 h 55 min ∼ 12 h 26 min	25.5	3.58 (1507)
	AG2	Oct 21–Nov 18	11 h 53 min ∼ 11 h 30 min	16.8	100.00 (1153)

AG, autumn generation.

Table 3. Statistics table for the effects of day-length and temperature on the incidence of summer and winter diapause (arcsin-square root transformed) in *P. melete*.

Source of variance	df	SS	MS	F	*P*	R^2	Path coefficient	
							direct	indirect
Summer diapause								
Day-length	1,24	1.3396	1.3396	14.010	0.0010	0.3686	0.2513	0.8584
Temperature	1,24	2.2215	2.2215	37.730	0.0000	0.6112	0.9979	0.2161
Day-length × Temperature	2,23	2.2811	1.1406	19.380	0.0000	0.6276		
Cohorts = residuals		1.3534	0.0588					
Winter diapause								
Day-length	1,21	3.2298	3.2298	54.880	0.0000	0.7233	0.6921	0.1583
Temperature	1,21	3.0206	3.0206	43.900	0.0000	0.6764	0.1672	0.6552
Day-length × Temperature	2,20	3.2427	1.6214	26.520	0.0000	0.7262		
Cohorts = residuals		1.2229	0.0611					

generations (table 3). However, path coefficient analysis showed that temperature played a more significant role in regulating summer diapause, while increasing day-length had minor influence. The direct path coefficient of temperature in the determination of summer diapause was 0.9979, and indirect effect path coefficient (i.e. influence via day-length) was 0.2161. For the increasing day-length, however, the direct path coefficient in the determination of summer diapause was 0.2513, and the indirect effect path coefficient was 0.8584 (table 3).

Incidence of winter diapause in successive autumn generations

The incidences of winter diapause for successive generations in *P. melete* were observed under natural autumn and winter conditions for five successive years (table 2). The incidence of winter diapause was very low (<10.27%), when the gradually shortening day-length combined with the high mean daily temperatures (>23.1°C) in the first and second autumn generations (AG1 and AG2). With the gradually shortening day-length during mid-September and early October, the incidence of winter diapause increased from 60% to 90% in AG2. The day-length shorter than 12 h induced nearly all individuals to enter winter diapause in AG2, AG3 and AG4.

Role of day-length and temperature on the determination of winter diapause

Regression analysis was used to interpret the data from table 2 (fig. 2). Obviously, the influence of day-length and temperature on the incidence of diapause showed a negative correlation (table 3). Path coefficient analysis indicated that temperature and day-length showed an opposite role to that in

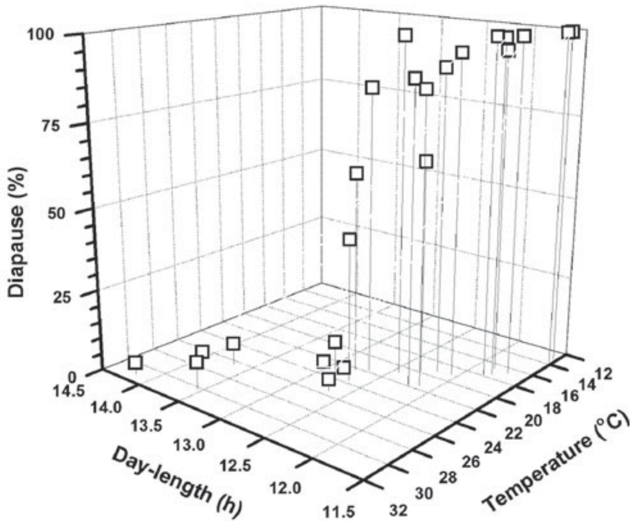

Fig. 2. Influence of day-length and temperature on the incidence of winter diapause in *P. melete*.

the induction of summer diapause. The direct path coefficient of day-length in the induction of winter diapause was 0.6921, and indirect effect path coefficient (i.e. influence via temperature) was 0.1583. For the decreasing temperature, however, the direct and indirect path coefficient in determination of winter diapause was 0.1672 and 0.6552, respectively (table 3).

Discussion

In many organisms, photoperiod and temperature are thought to be the most significant cues for seasonally timed events, including diapause in the life history of arthropods. Temperature is known to influence the photoperiodic control of summer as well as winter diapause. In many aestivating insects, it is generally accepted that long photoperiod and high temperature tend to induce or maintain summer diapause, and low temperatures tends to prohibit it (Masaki, 1980; Tauber *et al.*, 1986; Danks, 1987). This is shown, for example, by Masaki & Sakai (1965) in the cabbage moth, *Mamestra brassicae*; Sullivan & Wallace (1967) in the European pine sawfly, *Neodiprion sertifer*; Khoo (1968) in the stonefly, *Capnia bifrons*; Sáringer & Deseö (1966) in the alfalfa weevil, *Hypera variablis*; Paarmann (1976) in the carabid, *Orthomus barbarus atlanticus*; Butler *et al.* (1985) in the tobacco budworm, *Heliothis virescens*; Finch & Collier (1985) in the cabbage root fly, *Delia radicum*; and Xue *et al.* (2001) in the leaf-mining fly, *Pegomyia bicolor*. In contrast to the above species, high temperatures strongly weakened the diapause-inducing effects of long day-length and significantly reduced the incidence of summer diapause in *P. melete* under laboratory conditions; whereas relatively low temperatures combined with long day-length induced nearly all individuals to enter summer diapause (Xue *et al.*, 1997; Xiao *et al.*, 2008a, 2009). The present study for five successive years of field observations further confirmed that summer diapause was induced by relatively low temperatures rather than high temperatures, as suggested by the fact that almost all individuals were induced to enter diapause (>95%) when larvae growing from late March to early May experienced relatively low mean daily temperatures (<22°C) (table 1). Undoubtedly, the gradually increasing day-length during spring also played an important role in the induction of summer diapause. However, path coefficient analysis showed that the effect of temperature was much greater than photoperiod in the determination of summer diapause in the cabbage butterfly (table 3). Similar results were also found in the cabbage beetle, *Colaphellus bowringi*, in which high temperatures obviously inhibited the incidence of summer diapause (Xue *et al.*, 2002).

According to our field observations for nine years (1988, 1989, 1994, 1995, 2003, 2004, 2005, 2006 and 2007), if the overwintered pupae eclosed into adults between mid-March and early April (1988, 1989, 1994, 1995, 2003, 2005 and 2007), almost all their progenies would enter summer diapause because larvae of the first generation experienced relatively low temperatures (<20°C) and relatively long day-length (>13 h). However, if adults emerged between late February and late March, some progenies produced by the early emerged adults would develop without diapauses; as shown in 2004 and 2006, 33.33% and 34.04% individuals developed without diapauses because they experienced the intermediate to relatively long day-length (12 h 30 min ~ 13 h 31 min) (table 1). These individuals emerged as adults in late April and produced the second generation. These results suggest that the butterfly has the potential ability to reproduce in summer, although this is usually not expressed under local climatic conditions.

In winter diapause with long-day photoperiodic response, the effect of temperature on diapause induction can also be expressed as that diapause incidence varies with temperature when the combined photoperiod is inductive at certain temperatures only. Photoperiodic cues may be effective in diapause induction only when the temperature is above or below particular thresholds, i.e. diapause cannot be induced at any photoperiod when the temperature is above a particular level in some insects. For example, in the swallowtail *Sericinus montelus*, although diapause induction in the pupa was regulated by photoperiod, high temperature could reverse the effect of short day-length on diapause induction (Wang *et al.*, 2009). However, in the grape berry moth, *Lobesia botrana*, under the photoperiod of L:D 12:12 combined with various temperatures (from 12 to 30°C), almost 100% of individuals were induced to enter winter diapause, indicating that in the range of field temperatures occurring in Crete in August, the temperature probably had no effect on diapause induction (Roditakis & Karandinos, 2001). In the bean blister beetle *Epicauta gorhami*, lower temperatures (20 and 22.5°C) induced all larvae to enter pseudopupae diapause. By contrast, at higher temperatures (27.5 and 30°C), almost all larvae pupated without diapause, regardless of the photoperiod (Shintani *et al.*, 2011). In natural lines of *Drosophila melanogaster* from both Florida and Maine, temperature was the primary determinant of dormancy; however, photoperiod had no significant effect either between populations or among lines within populations (Emerson *et al.*, 2009).

In autumn, adults of *P. melete* from the aestivating pupae emerge over a long period, usually from the end of August to early November. The aestivating individuals which emerge at the end of August and develop without diapause, produce three generations; those emerging before mid-October and then developing without diapause, produce two generation; and, finally, those emerging after mid-October produce only one generation (Xue *et al.*, 1996, 1997). The present study also showed that there are three generations under autumnal conditions (table 2). However, there are always some individuals entering winter diapause regardless of temperature, as suggested by the fact that 3.85% in 2003, 4.65% in 2004 and 6.78% of individuals in 2005 that hatched in August entered winter diapause even under high temperatures from 26.4 to 31.2°C (table 2). This result suggests that gradually shortening summer-fall day-length may play an important role in inducing these individuals to enter diapause. With shortening day-length and decreasing mean daily temperature, the incidence of winter diapause increased (fig. 2). Path coefficient analysis indicated that the decreasing day-length has more importance in the determination of winter diapause than temperature.

All these results revealed that in *P. melete*, the roles of photoperiod and temperature in the determination of summer and winter diapause were quite different. This photoperiod-temperature response mechanism in the induction of summer and winter diapause in *P. melete* was important in ecological adaptations. Temperature had a stronger effect in the induction of summer diapause. In nature, such a thermal mechanism for diapause induction ensures that almost all larvae that grow in spring enter pupal diapause, thus avoiding reproduction during adverse summer conditions, e.g. drought and food shortage. In the field, all cruciferous vegetables are harvested in May, and are generally not cultivated until autumn. Winter diapause induction mainly depended on the daily shortening day-length. Such a response pattern allows individuals pupating in late autumn under warm conditions to enter diapause in time, thus ensuring the population to overwinter in a safe stage, and avoiding adult emergence in winter when the conditions are unfavorable for continuous reproduction and growth.

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