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Effects of large temperature fluctuations on hatching and subsequent development of the diamondback moth (Lepidoptera: Plutellidae)

Kun Xing[1,2], *Chun-Sen Ma*[3], *Fei Zhao*[2,*], *and Jv-Cai Han*[1*]

Abstract

Temperature in habitats of organisms generally is not constant but changes spatially and temporally. When eggs of ectotherms are exposed to large temperature fluctuations, egg phenotypes and post-hatching traits may be altered, but little relevant information is available on insects. Hence, we simulated a set of natural diurnal temperature fluctuations each with the same mean temperature (25 ± 0, 25 ± 2, 25 ± 4, 25 ± 6, 25 ± 8, 25 ± 10 °C), to which we exposed the eggs of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), and assessed subsequent egg development, survival and post-hatching traits. Our results showed that there were no significant differences in these phenomena between the constant temperature treatment and the treatments with moderate temperature fluctuations. However, large temperature fluctuations slowed development and lowered hatching rate during the egg stage. In addition the effects of these large temperature fluctuations extended to the larval stage, but not to the pupal and adult stages. No apparent costs of compensatory responses, which occurred in the larval stage, were detected in the later stages. These findings indicate that fluctuating temperature effects are potentially important in predicting insect phenology and population dynamics. As an independent factor, the effects of temperature fluctuations on a stage in the life history must be factored into models for predicting insect development that are based on mean temperatures. The larger of the temperature fluctuations to which eggs of diamondback moth were exposed, affected development time, hatching rate, larval growth and pre-pupal mass.

Key Words: egg stage; diurnal temperature fluctuations; compensatory growth; *Plutella xylostella*

Resumen

La temperatura en los hábitats de organismos generalmente no es constante, pero cambia espacialmente y temporalmente. Cuando los huevos de ectotermos están expuestos a grandes fluctuaciones de temperatura, los fenotipos de los huevos y sus caracteristicas pos-eclosión puede ser alterados, pero poca información pertinente en los insectos está disponible. Por lo tanto, se simuló un conjunto de fluctuaciones naturales de temperatura diurnas cada uno con el promedio de temperatura (25 ± 0, 25 ± 2, 25 ± 4, 25 ± 6, 25 ± 8, 25 ± 10 °C), a la que los huevos de la polilla dorso de diamante, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) fueron expuestos, y se evaluó el desarrollo de los huevos, la sobrevivencia y sus caracteristicas pos-eclosión. Nuestros resultados mostraron que no hubo una diferencia significativa en estos fenómenos entre el tratamiento temperatura constante y los tratamientos temperaturas moderadas fluctuantes. Sin embargo, las temperaturas más ampliamente fluctuantes alargaron el desarrollo y bajaron la tasa de eclosión durante el estadio de huevo. Además, el efecto de estos grandes fluctuaciones de temperatura extendio el estadio larval, pero no a los estadios de pupa y adulto. No se detectaron costos aparentes de estas respuestas compensatorias, que se produjo en el estadio larval, pero no fueron detectados durante los estadios de la pupa y el adulto. Estos hallazgos indican que la fluctuación de efectos de la temperatura son potencialmente valiosos en la predicción de la fenología del insecto y la dinámica de la población. Como un factor independiente, las temperaturas fluctuantes durante un estadio en la historia de la vida deben ser considerados en el modelo de predicción de la desarrollo de insectos basados en el promedio de la temperatura. La mayor de las fluctuaciones de la temperatura a la que se expusieron los huevos de polilla dorso de diamante, el tiempo de desarrollo afectados, tasa de eclosión, el crecimiento de las larvas y la masa pre-pupal.

Palabras Clave: estadio de huevo; fluctuaciones de la temperatura diurna; crecimiento compensatorio; *Plutella xylostella*

Despite the shortness of the egg period, egg temperature plays a crucial role in egg traits of ectotherms, such as egg development (Du et al. 2009) and hatchling morphology (Booth 2006). An extreme egg temperature may induce the change of post-hatching traits (Metcalfe & Monaghan 2001), including locomotor performance (Mickelson & Downie 2010), muscle phenotype (Macqueen et al. 2008), immune function (Ardia et al. 2010) and fecundity (Callebaut 1991). It may also change the subsequent growth rate (Orizaola et al. 2010) or even give rise to compensatory growth responses later in life (Dmitriew & Rowe 2007).

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Diurnal temperature fluctuations impose different effects on ectotherms compared with constant temperatures due to the effects of daily maximum or/and minimum temperatures. Thus, diurnal fluctuating temperatures generate changes in gene expression (Podrabsky & Somero 2004), development (Niederegger et al. 2010), reproduction (David et al. 2005), and survival (Lalouette et al. 2011), behavior (Miyazaki et al. 2011). Eggs are frequently exposed to diurnal temperature fluctuations in nature, rather than to constant temperatures. Short-term exposure is often used to explore the impact of daily maximum or minimum temperatures on the egg stage (Roux et al. 2010). However, these experiments cannot show the real effects of diurnal temperature fluctuations, because they ignore the repair of the potential heat injury from adverse daytime high temperatures that may subsequently occur during favorable lower nighttime temperatures (Rohmer et al. 2004). Therefore, short-term exposure under high and/or low temperatures is not sufficient to elaborate the effects of temperature fluctuations on egg development.

Recent studies have revealed that not only temperature means but also temperature fluctuations have great influence in egg development and hatchling phenotypes in ectotherms (Du & Shine 2010; Micheli-Campbell et al. 2012). Nevertheless, effects of temperature fluctuations on hatching traits and subsequent life history traits have not been completely understood and they remain largely unknown in insects. First, there often are conflicting reports on the effects of temperature fluctuations on egg development rates. For example, temperature fluctuations fluctuating temperatures enhanced the rate of egg development in some species (Shine & Harlow 1996), and yet inhibited it in other species (Du et al. 2009). Second, there is still controversy over long-term effects of egg temperature on ectotherms' performance. For example, egg temperature induced long-term shifts in form and function through adulthood in some studies (Macqueen et al. 2008), but in several studies, egg temperature caused only short-term shifts that appeared in the larval stages (Geister et al. 2009; Orizaola et al. 2010), or egg temperatures affected only the egg stage, having no long-term or short-term effects (Warner et al. 2012). Third, effects of temperature fluctuations on hatchling phenotypes, such as hatchling size (Booth 2006) and locomotor performance (Mickelson & Downie 2010), have been studied extensively, but post-hatchling survival, growth, fecundity and population growth are less reported. Therefore, more comprehensive studies are needed to elucidate both the developmental and ecological effects of fluctuating egg temperatures.

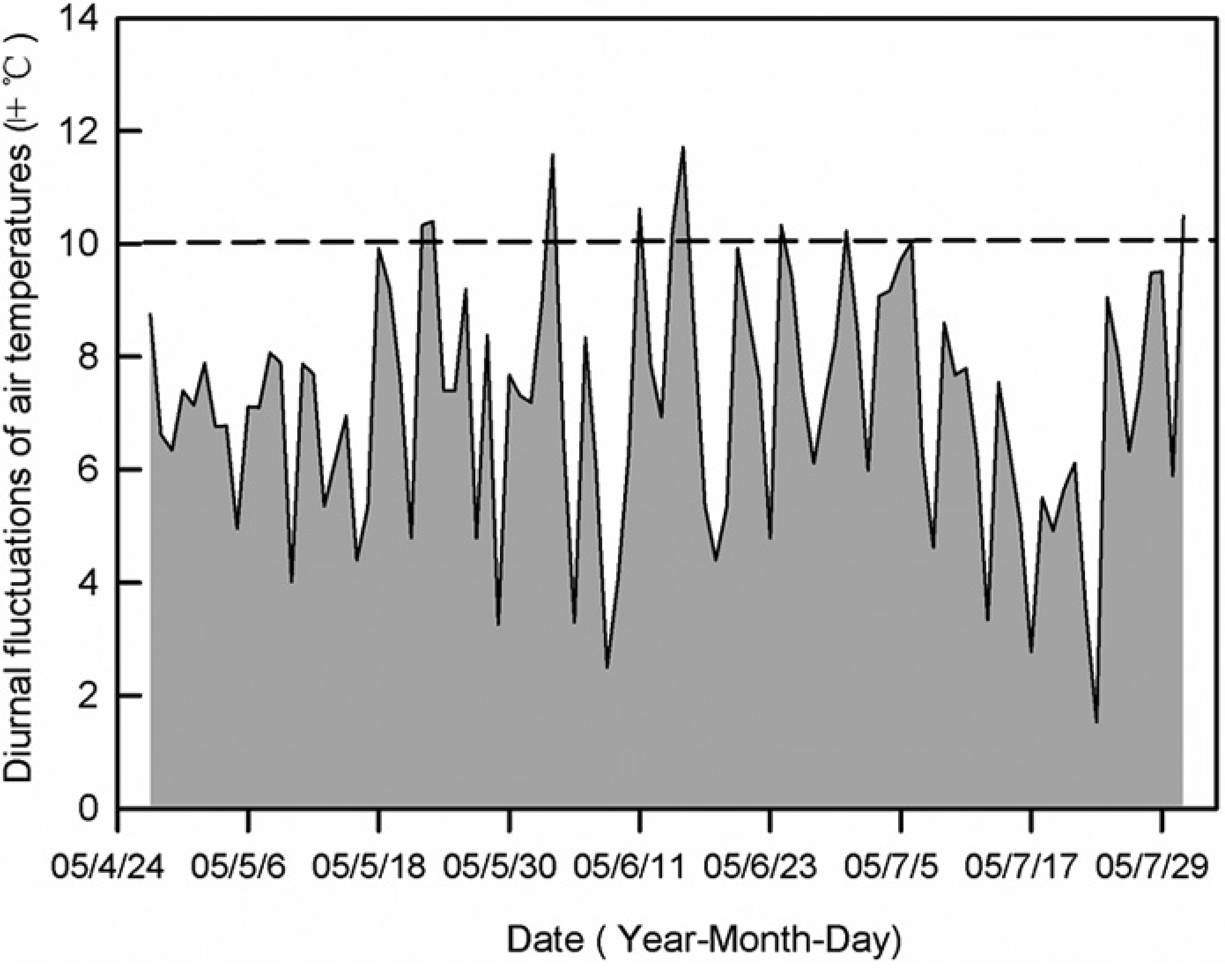

Fig. 1. Diurnal air temperature fluctuations in a cabbage field in the summer in Beijing. Temperature was recorded with a data logger placed close to the underside of leaves and placed 30–35 cm above the ground in the middle of a 2 ha cabbage field.

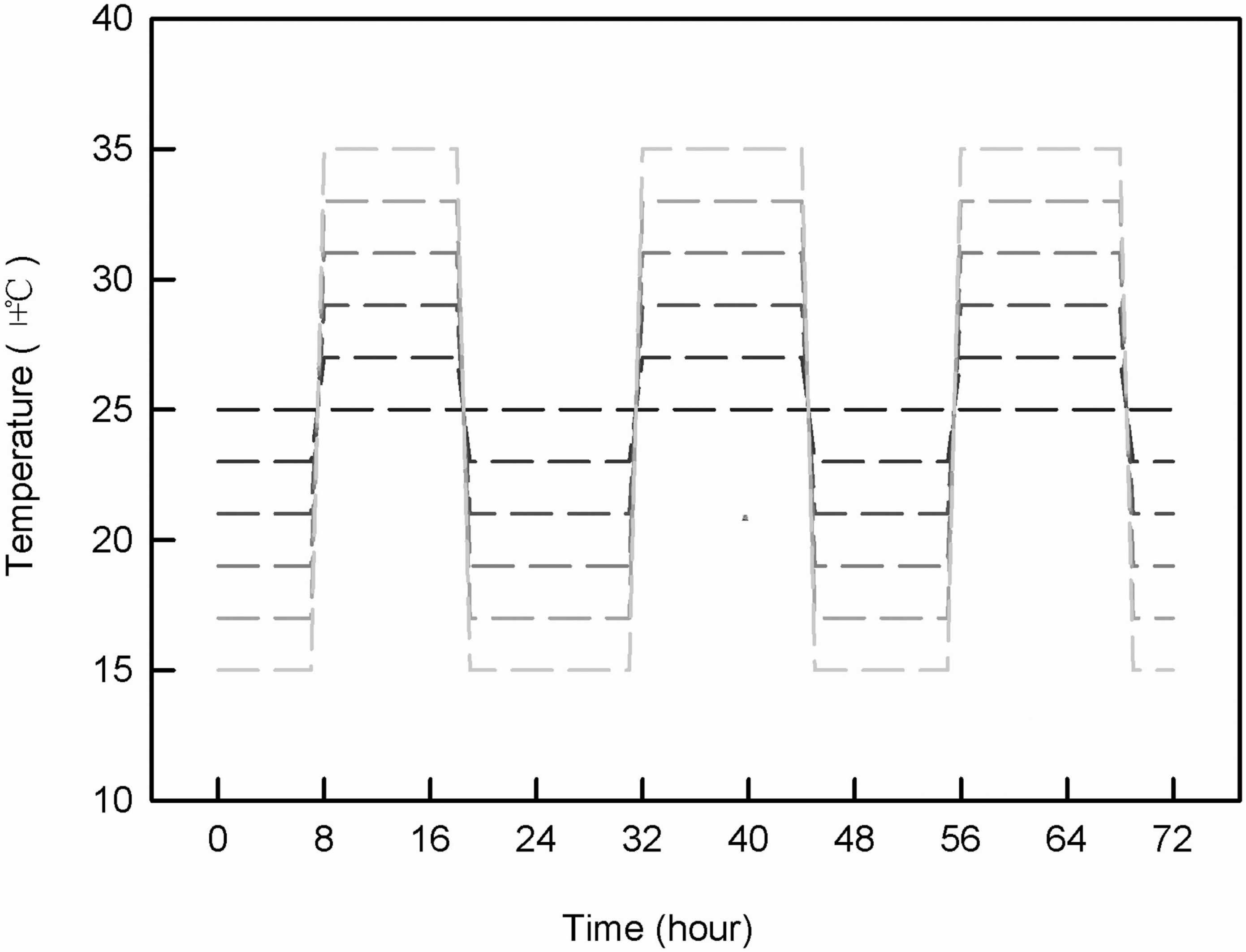

Fig. 2. Target temperatures in experiments. Target temperatures with different ranges of temperature fluctuations around 25 °C in climate chambers for 3 consecutive days.

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), the most destructive pest of cruciferous vegetables, is widely distributed throughout the world, from the tropical to the cool temperate regions with temperature fluctuations of greatly divergent magnitudes around suitable mean temperatures (Furlong et al. 2013). Effects of constant temperatures on life history traits such as growth, development, survival, reproduction (Liu et al. 2002; Golizadeh et al. 2009) and migration (Xing et al. 2013) have been well documented. Thus, the elucidation of the effects on eggs of fluctuating temperature fluctuations subsequently on life history traits of the diamondback moth, is not only important in biological research but also in population prediction and decision making for integrated pest management.

We questioned: 1) Do temperature fluctuations during the egg stage affect hatching traits in the diamondback moth? 2) Can the effects of temperature fluctuations be carried over to the larval, pupal or even the adult stage? Here, we incubated eggs of diamondback moth at one constant temperature of 25 °C and at 5 fluctuating temperatures (25 ± 2, 25 ± 4, 25 ± 6, 25 ± 8 and 25 ± 10 °C) to focus their effects on life history traits such as development time of the egg, larva and pupa stage, growth rate of larvae, survival of the egg, larval and pupal stages, mean lifetime reproduction, reproduction duration and adult longevity.

Materials and Methods

INSECT REARING

Diamondback mothlate-instar larvae and pupae were collected from *Brassica* fields in May 2010, with the permission of the Experiment Station of Hubei Academy of Agricultural Sciences, in Wuhan, Hubei Province, China, and were reared in an insect rearing room with artificial diets (Southland Products Incorporated, USA). The rearing room was kept at the constant 25 °C, 50-70% RH and a photoperiod of 10:14 h L:D. The diamondback moth was reared in more than 10 generations before this study. After pupation, 200 pupae (1 male: 1 female) (Chen et al. 2011) were transferred to a screen cage (35 × 20 × 35cm) for adult emergence. Once adults emerged, a cotton ball immersed in 10% honey water solution was supplied for adult feeding. Two pieces of laboratory film (7 × 5cm) were immersed in fresh juice of cabbage leaves for 3-5 s and then hung from the top of screen cage at 3:00-4:00 p.m. for overnight egg laying. The film strips with eggs were collected at 7:00-8:00 a.m. the next day. About 300 eggs on the film were counted and placed on the surface of artificial diet (120 g) in a plastic rearing box (10 × 10 × 9cm). The rearing box was kept in the rearing room until pupation and then subjected to the same procedures that were described above for pupae and adults rearing.

Table 1. Results of ANOVAs for the effects of egg temperature treatments, sex, and replicate plates (as a random factor, nested within egg temperatures) on development times of eggs, larvae or pupae, pre-pupal mass, growth rate of larvae, adult longevity, fecundity, hatching rate, pupation rate and emergence rate in *Plutella xylostella.*

Phenotype	Source	df	MS	*F*	*P*
Egg development time	Egg treatment (ET)	5,169	3.055	11.570	<0.001
	Replicate plates (RP)	3,169	0.661	6.958	0.584
	Sex (S)	1,169	0.010	0.044	0.844
	ET x S	5,169	0.177	0.469	0.792
Hatching rate	Egg treatment (ET)	5,24	1675.556	21.340	<0.001
	Replicate plate (RP)	3,24	111.111	1.415	0.277
Pre-pupal mass	Egg treatment (ET)	5,169	919.488	14.569	<0.001
	Replicate plate (RP)	3,169	117.944	3.994	0.250
	Sex (S)	1,169	1.569	0.112	0.752
	ET x S	5,169	67.183	1.500	0.267
Growth rate of larvae	Egg treatment (ET)	5,169	17.774	6.011	0.006
	Replicate plate (RP)	3,169	2.534	1.828	0.374
	Sex (S)	1,169	0.656	2.572	0.136
	ET x S	5,169	3.300	1.993	0.158
Larval development time	Egg treatment (ET)	5,169	0.359	0.179	0.965
	Replicate plate (RP)	3,169	0.661	0.345	0.793
	Sex (S)	1,169	0.642	2.306	0.203
	ET x S	5,169	0.398	1.358	0.311
Pupation rate	Egg treatment (ET)	5,24	25.761	0.244	0.937
	Replicate plate (RP)	3,24	220.608	2.086	0.145
Pupal development time	Egg treatment (ET)	5,169	1.014	0.752	0.601
	Replicate plate (RP)	3,169	3.668	4.037	0.085
	Sex (S)	1,169	1.106	13.358	0.001
	ET x S	5,169	1.021	2.345	0.110
Emergence rate	Egg treatment (ET)	5,24	18.231	0.220	0.948
	Replicate plate (RP)	3,24	321.176	3.879	0.051
Adults longevity	Egg treatment (ET)	5,169	6.864	1.338	0.318
	Replicate plate (RP)	3,169	11.374	2.159	0.189
	Sex (S)	1,169	170.182	72.307	0.002
	ET x S	5,169	0.962	0.463	0.796
Female fecundity	Egg treatment (ET)	5,24	203.909	0.183	0.965
	Replicate plate (RP)	3,24	603.585	0.594	0.627

DESIGN AND MANIPULATION OF FLUCTUATING TEMPERATURES

A 24-h temperature cycle was designed to simulate the temperature fluctuations occurring in the cabbage field during the summer (Fig. 1). In this cycle, the daytime temperature (DT) lasted for 10 h (8:00 a.m. to 6:00 p.m.) and the nighttime temperature (NT) lasted for 14 h (6:00 p.m. to 8:00 a.m.). One constant temperature (25 °C) and 5 temperature fluctuations of progressively greater magnitudes (25 ± 2, 25 ± 4, 25 ± 6, 25 ± 8 and 25 ± 10 °C) were set to mimic the diurnal temperature fluctuations (Fig. 2). We selected 25 ± 10 °C as the widest diurnal range, because most daily temperature fluctuations in the microhabitat which diamondback moth would experience in the cabbage field were within ± 10 °C in the summer in Beijing (39° 54' N, 116° 23' E). Relative humidity in different chambers was 50-70% and the photoperiod was set to 10:14 h L: D during the experiment.

GROWTH, SURVIVAL AND REPRODUCTION

Plates were sterilized for 30 min by ultraviolet light, and each well was filled with 1.7 mL prepared artificial diet for diamondback moth feeding. One new egg (laid within the last 12 h by 1- to 2-day-old females) was transferred into each well with a fine camel's hair brush. To facilitate ventilation, the plates were covered with fine nylon mesh. Four plates were placed in each climate chamber. Forty (1 egg × 10 wells × 4 plates) eggs were observed in each temperature regimen. Hatching status of eggs was checked (with a stereo microscope) twice daily, at 8:00 a.m. and 8:00 p.m., because temperatures in climate chambers at these times were similar to room temperature (about 25 °C).

After larvae hatched, they were moved to a 25 °C rearing room. Newly hatched larvae from different treatments were randomly assigned to wells (1 larva per well). The pupation status was checked daily at 8:00 a.m. until all larvae had died or developed to pupae. When larvae developed into the pre-pupa (Sarfraz et al. 2011), they were weighed. Plates were renewed every three days to keep artificial diets fresh. When larvae became spindle shaped and had a thin white silk cocoon, they were recorded as having entered the pupa stage (Golizadeh et al. 2009). Pupae were observed daily at 8:00 a.m. until all adults emerged or pupae died (based on lack of adult emergence). Survival and development time were recorded for all immature stages. Newly emerged male and female adults which were from the same replicate under the same egg temperature treatment were paired and transferred into a glass tube (3 × 12 cm) for mating and egg-laying. The ends of the tube were covered with fine stainless steel mesh for ven-

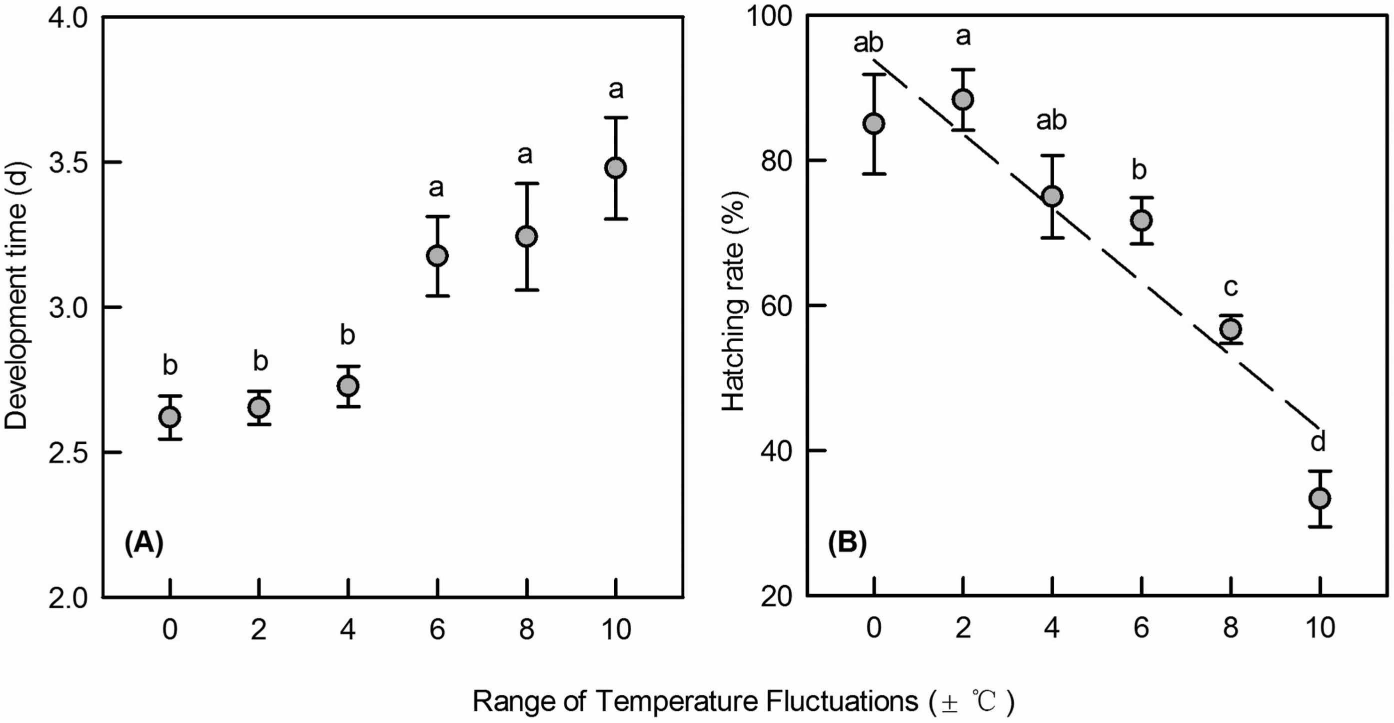

Fig. 3. Egg traits (mean ± SE) after different treatments. (A) Development time of eggs and (B) hatching rate of diamondback moth under 6 different temperature regimens with the same mean temperature but different ranges of temperature fluctuations (25 ± 0, 25 ± 2, 25 ± 4, 25 ± 6, 25 ± 8 and 25 ± 10 °C). Different letters at the tops of the columns indicate significant differences at *P* = 0.05.

tilation. A piece of cotton immersed with honey water solution (10%) was placed in the tubes for adult feeding. At 3:00-4:00 p.m., a piece of laboratory film was inserted to the tube for egg laying. The adults were transferred into a new tube with new film at 7:00-8:00 a.m. every day until females died. All eggs laid on the film and inner surface of the tube were counted.

STATISTICAL ANALYSIS

Effects of different temperature treatments during egg stage on all indices of growth, survival and reproduction were analyzed with ANOVA in which egg temperatures and adult sex were treated as fixed factors, and replicate plates as a random factor (nested within egg temperatures). Means were compared using Duncan's multiple range tests in SAS V8 (SAS Institute, Cary, North Carolina, USA). We analyzed effects of different temperature treatments during the egg stage on development time of eggs/larvae/pupae, growth rate of larvae, percent hatching rate (number of larvae per number of eggs × 100%), percent pupation rate (number of pupae per number of larvae × 100%), percent emergence rate (number of adults per number of pupae × 100%), adult fecundity and longevity. Growth rate of larvae was expressed as mg/day (pre-pupal mass per development duration of larvae).

Results

Egg development was not affected by sexual gender (*F* = 0.044; df = 1,169; *P* = 0.844) or replicate plates (*F* = 6.958; df = 3,169; *P* = 0.584), but was significantly affected by the temperature fluctuations to which the eggs were exposed (*F* = 11.570; df = 5,169; *P* < 0.001) (Table 1). Eggs incubated at a constant temperature of 25 °C or to moderate temperature fluctuations around 25 °C temperatures (25 ± 0, 25 ± 2, 25 ± 4 and 25 ± 6 °C) developed significantly faster than those incubated at the same mean temperature but with fluctuations of greater magnitude, i.e., 25 ± 8 and 25 ± 10 °C (Fig. 3A). Hatching rate differed significantly between egg temperature treatments (*F* = 21.340; df = 5,24; *P* < 0.001) (Fig. 3B) and replicate plates (*F* = 1.415; df = 3,24; *P* = 0.277) (Table 1).

The pre-pupal mass was affected significantly by egg temperature treatments (*F* = 14.569; df = 5,169; *P* < 0.001) (Fig. 4C) but not by replicate plates (*F* = 3.994; df = 5,169; *P* = 0.250) or sexual gender (*F* = 0.112; df = 5,169; *P* = 0.752) (Table 1). Growth rates of larvae followed a similar pattern as the pre-pupal mass (*F* = 6.011; df = 5,169; *P* = 0.006) (Fig. 4D). Larvae that hatched from eggs that had been incubated at 25 ± 8 and 25 ± 10 °C grew significantly faster (ca.1.3 mg/day) than those from eggs that had been incubated at the same mean temperature but with smaller temperature fluctuations. There were no differences in growth rates of larvae from eggs that had been held at 25 ± 8 and 25 ± 10 °C, or between those from eggs held at the same mean temperature but with smaller temperature fluctuations. Larval development was not significantly influenced by egg treatments (*F* = 0.179; df = 5,169; *P* = 0.965) (Fig. 4A), replicate plates (*F* = 0.345; df = 2,169; *P* = 0.793) or sexual gender (*F* = 2.306; df = 1,169; *P* = 0.203). The pupation rate was not affected by the egg treatments (*F* = 0.244; df = 5,24; *P* = 0.937) (Fig. 4B) or replicate plates (*F* = 2.086; df = 3,24; *P* = 0.145).

No pupal or adult traits were influenced by the egg treatments (Table 1). There were no differences in pupal development time (*F* = 0.752; df = 5,169; *P* = 0.601) (Fig. 5A), emergence rate (*F* = 0.220; df = 5, 24; *P* = 0.948) (Fig. 5B), adult longevity (*F* = 1.338; df = 5, 169; *P* = 0.318) (Fig. 5C) or fecundity (*F* = 0.183; df = 5,24; *P* = 0.965) (Fig. 5D). Adult longevity differed significantly between sexes (*F* = 72.307; df = 1,169; *P* = 0.002).

Discussion

In our results, the magnitudes of temperature fluctuations around the same mean temperature significantly affected development time

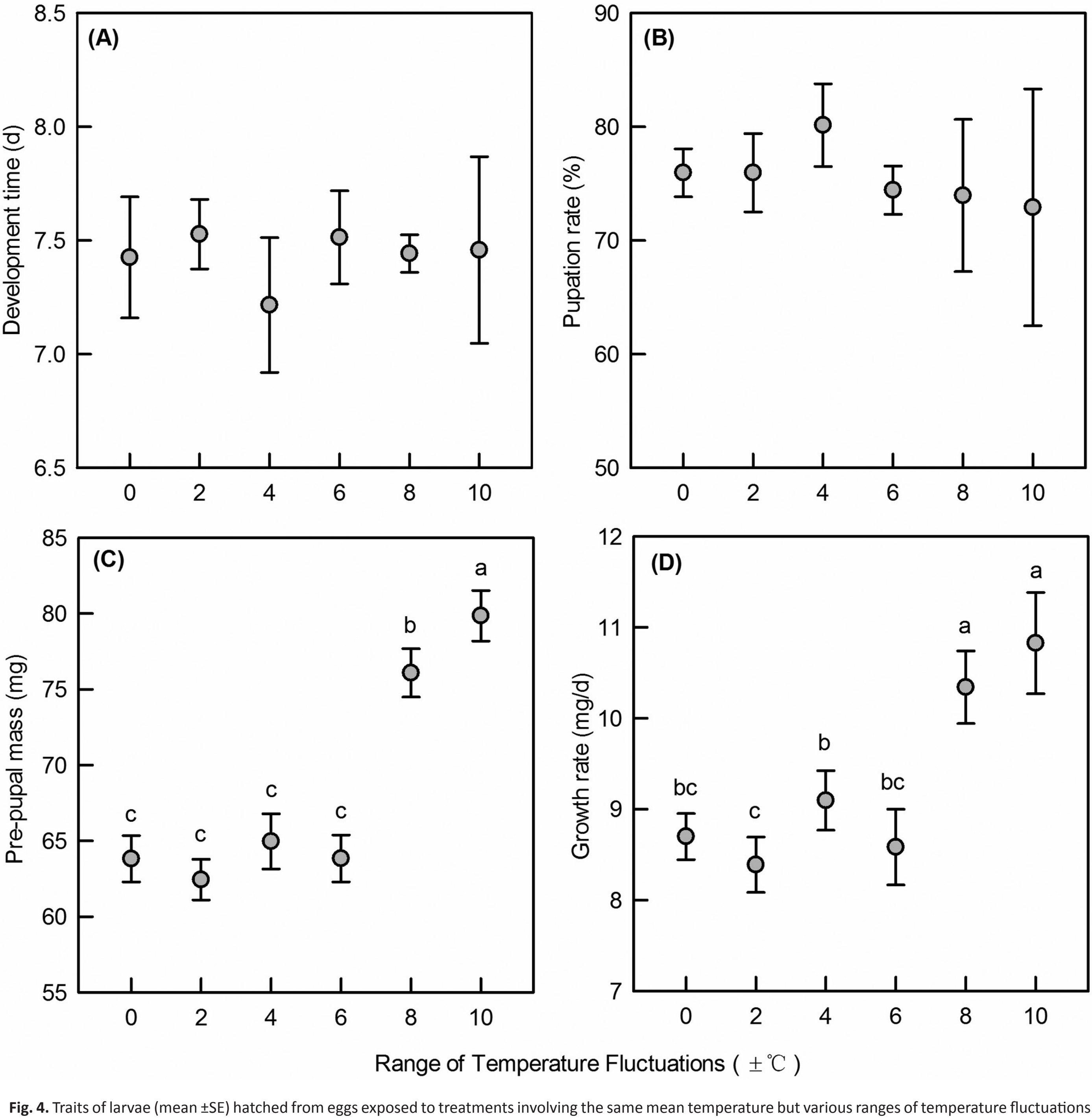

Fig. 4. Traits of larvae (mean ±SE) hatched from eggs exposed to treatments involving the same mean temperature but various ranges of temperature fluctuations. (A) Development times of larvae, (B) pupation rates, (C) pre-pupal masses and (D) growth rates of larvae following emergence from eggs exposed to different fluctuating temperature ranges (25 ± 0, 25 ± 2, 25 ± 4, 25 ± 6, 25 ± 8 and 25 ± 10 °C). Different letters at the tops of columns indicate significant differences at $P = 0.05$.

of the egg stage. Development time of the egg stage remained the same until the magnitudes of the temperature fluctuations exceeded ± 6 °C. When the magnitude of the temperature fluctuations reached ± 8 °C, development started to slow down. These results imply that the development time would not change significantly if temperatures fluctuated between 19-31 °C with a mean of 25 °C. However, if the temperature fluctuated between 17 and 33 °C or more with the same mean, development would be retarded. This is related to the upper and lower thermal limits for egg development (Andrews & Schwarzkopf 2012). Within an optimum range, development responds to temperature in an approximately linear manner (Escobar et al. 2012). Daytime temperatures are higher than the mean temperature and thus speed up egg development, but the nighttime temperatures are lower than the mean and slow down egg development. With regular sinusoidal temperature fluctuations as in our experiments, the development increments were equal to the decrements, which resulted in stable development of DBM eggs under the relatively narrow temperature fluctuations (≤25 ± 6 °C). Nevertheless, if the range of the fluctuation became very great, egg development should be inhibited if daytime temperatures rose to the upper thermal limit or nighttime temperatures decreased to the lower thermal limit of development. In our study, temperatures fluctuating in ranges of 25 ± 8 and 25 ± 10

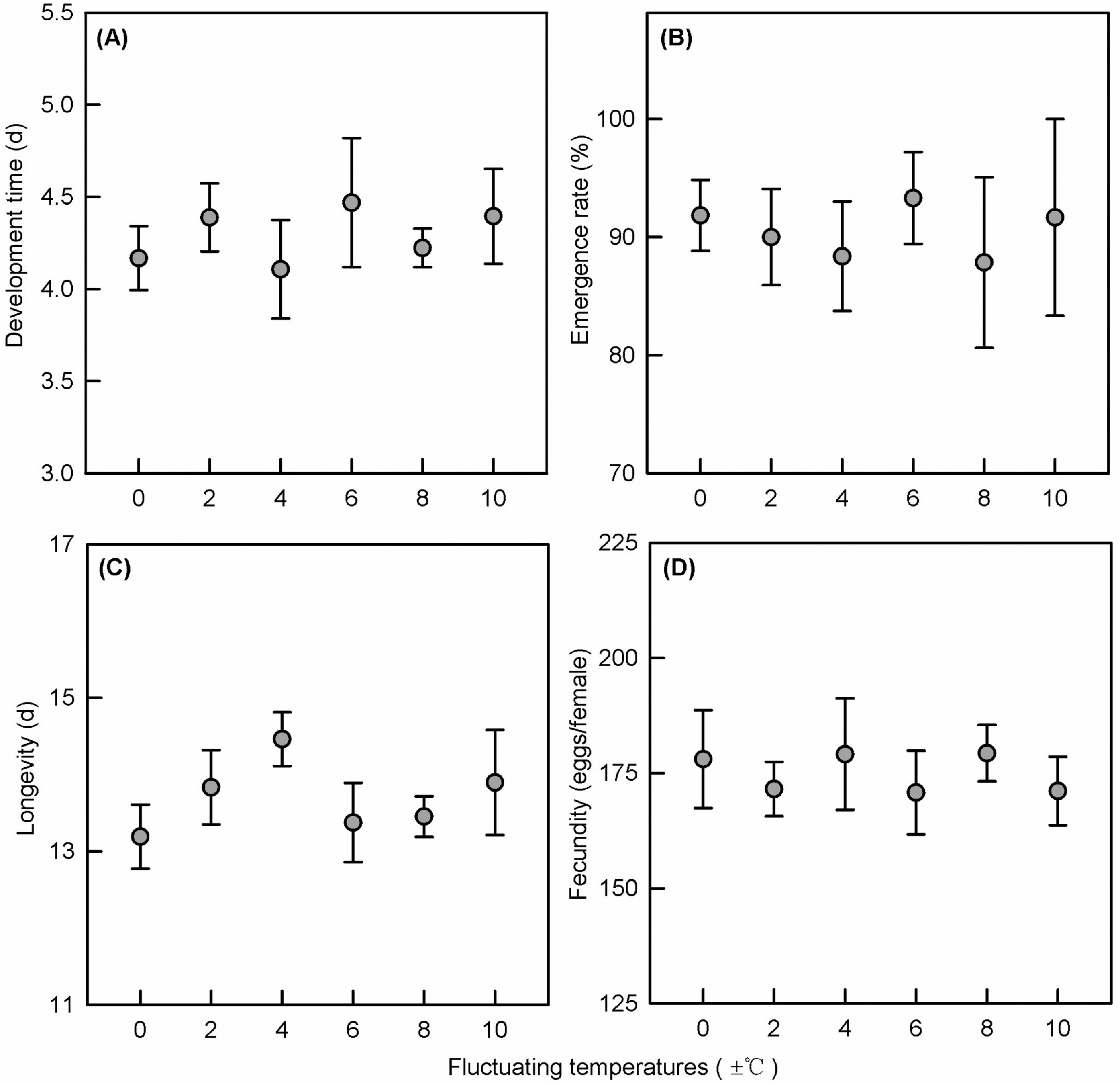

Fig. 5. Pupa and adult traits (mean ± SE) after different treatments. (A) Development time of pupae, (B) emergence rate, (C) adult longevity and (D) fecundity in the diamondback moth following emergence from eggs exposed to different fluctuating temperature ranges (25 ± 0, 25 ± 2, 25 ± 4, 25 ± 6, 25 ± 8 and 25 ± 10 °C). Different letters at the tops of columns indicate significant differences at *P* = 0.05.

°C implied that daytime temperatures reached 33-35 °C, which was close to or exceeded the upper threshold (34 °C) for development of the diamondback moth (Chen & Liu 2003). Such daytime temperatures do not compensate for the slow development at lower nighttime temperatures, such as 15-17 °C, and may depress development (Golizadeh et al. 2007). Therefore, widely fluctuating temperatures can delay egg development.

Temperature fluctuations around a suitable mean temperature improved egg survival. Previous work has shown that the hatching rate of diamondback moth eggs is not changed at constant temperatures ranging from 8–31 °C (Liu et al. 2002). When temperatures were close to or exceeded the upper thermal limit, survival rapidly declined with increasing temperature. Egg survival was virtually zero at a constant 35 °C (Dan et al. 1995). However, in our study, nearly half of the eggs survived (ca. 43%) wide temperature fluctuations (25 ± 10 °C) in which daytime temperature reached 35 °C. This substantial survival rate may relate to recovery from heat injury during optimum nighttime temperatures (Zhao et al. 2014). Under diurnal fluctuating temperatures, heat resistance substances, such as hsp70, mannitol and sorbitol (Wang et al. 2006; Colinet et al. 2011), are rapidly synthesized during periods of high daytime temperatures, whereas nighttime optimum temperatures provide an opportunity to reduce energy consumption and metabolism and increase energy reserves to repair heat-induced lesions.

In our study, the growth of larvae hatched from eggs exposed to substantial temperature fluctuations around a mean of 25 °C was significantly impacted. Their growth rates and body masses increased significantly in the larvae hatched from eggs that had experienced wide temperature fluctuations. Similar observations have been made with many other animals including turtles (Xie et al. 2012), lizards (Radder et al. 2007), frogs (Squires et al. 2010) and insects (Dmitriew & Rowe 2005). Compensatory growth can occur when the organisms suffer from stresses in nutrition (Dmitriew & Rowe 2005), salt (Squires et al. 2010), osmolality (Wu et al. 2012) and temperature (Potter et al. 2011) during early stages of development. We found that wide temperature fluctuations might cause harmful temperature stresses in the egg stage and impair compensatory growth in larvae. Gu et al. (2012) found that wide temperature fluctuations during the egg stage did not change significantly the number of cells but induced the synthesis of more JH and hsp. The production and function of JH and hsp would consume more energy (Robert Michaud et al. 2008; Tomanek & Zuzow 2010) and result in slower egg development. But these hatchlings would accelerate their food intake instead of increasing the need for more development time — they found that body mass was increased, but larval development time was not extended — to realize their normal reproduction (Ozanne & Hales 2002). So, compensatory growth occurred as a significant life history strategy in the diamondback moth to buffer the impact of unsuitable thermal conditions during the egg stage.

The effects of temperature fluctuations during the egg stage persisted only to the larval stage and disappeared at pupal and adult stages. Presumably, this lack of persistence into the pupal and adult stages is the result of complete metamorphosis (Potter et al. 2011). These insects experience major physiological and morphological changes during metamorphosis. Different stages have completely different morphs and behaviors, resulting in relative independence for each stage (Potter et al. 2011). The diamondback moth is a typical complete metamorphosis insect. Effects of temperature fluctuations during the egg stage can only be extended to the larva stage but not to the pupal and adult stages.

Any apparent costs for compensatory growth induced by the wider temperature fluctuations were not detected. It has been reported that costs of compensatory growth may be induced by predation risk, long-term effects or a stressful condition. Predation risk usually is connected with survival rate (Munch & Conover 2003) and activity rates (Lee et al. 2012). Long-term effects may occur in the next generation (Yearsley et al. 2004). And when individuals that underwent compensatory growth were exposed to stressful conditions once again, physiological costs have been detected (Dmitriew & Rowe 2007). However, this phenomenon was not tested in our experiment.

The time when insects occur in the environment is very important for population monitoring, forecasting and control strategies in resource management. Our results indicate that the traditional linear model for “constant temperature-development” can be applied widely if the mean temperature is optimal and the daily temperature fluctuation is not very wide (Worner 1992). However, this model may be not able to describe development or survival of insects in an area with non-optimal temperature or with wide temperature fluctuations, because we found that egg development and survival were decreased by the wide temperature fluctuations. To improve prediction accuracy and damage assessment, we should incorporate ranges of diurnal temperature fluctuations into phenology models (Georges et al. 2005; Paaijmans et al. 2010).

Acknowledgments

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