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Wide diurnal temperature variation inhibits larval development and adult reproduction in the diamondback moth

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ABSTRACT

Although thermal variability is known to influence the performance of ectotherms, there is limited information on the influence of variation in diurnal temperature range (DTR) during early developmental stages. Here we test variation in DTR (± 0 °C, ± 4 °C, ± 6 °C, ± 8 °C, ± 10 °C and ± 12 °C) with a constant mean temperature (25 °C) on the larval stage of diamondback moth (DBM), *Plutella xylostella* (L.), and assess immediate effects on larval development and survival, and delayed effects on pupal development and survival and adult longevity and reproductive performance. Wide amplitudes (± 10 °C and ± 12 °C) inhibited larval development and adult performance, but increased the proportion of eggs laid early, while moderate amplitudes (± 4 °C, ± 6 °C and ± 8 °C) resulted in only minor effects. Larval development rate under wide amplitudes (± 10 °C and ± 12 °C) was faster than predicted by a degree-hour model. Overall, the intrinsic rate of increase of the population was lowered with increasing DTR, despite mean temperatures being the same. These findings highlight marked cross-stage effects of DTR when temperatures fluctuate substantially, likely linked to maximum temperature, and they emphasize the importance of considering DTR when assessing effects of climate warming.

1. Introduction

In nature, environmental temperatures vary diurnally, which can result in variation in diurnal temperature range (DTR) at different latitudes and across different seasons even though mean temperature remains relatively constant (Lambrechts et al., 2011; Paaijmans et al., 2013). For example, during June at Wuhan (30.62°N) and Beijing (39.80°N), two major agricultural regions in China, organisms experience similar average temperatures (about 25 °C) but marked differences in DTR (Fig. 1). Theoretical approaches (Colinet et al., 2015; Vázquez et al., 2017) and empirical observations (Easterling, 2000; Paaijmans et al., 2010) indicate that global warming is increasing not only mean temperature but also temperature variation. In this context, the effect of DTR on organisms has been attracting increasing attention in recent years (Folguera et al., 2011; Estay et al., 2011, 2014; Bozinovic et al., 2013, 2016), although most studies on biological impacts of global warming have focused on changes in mean temperature (Morris et al., 2008; Ju et al., 2015).

Diurnal temperature fluctuations have different effects on ectotherm performance compared with constant temperatures (Joshi, 1996; Lalouette et al., 2007; Arias et al., 2011; Bozinovic et al., 2011; Foray et al., 2013; Thompson et al., 2013). Moderate amplitudes of DTR can improve the development rate and survival rate of many ectotherms such as frogs (Arrighi et al., 2013), fish (Sadati et al., 2011), lizards (Du and Shine, 2010) and insects (Folguera et al., 2009). On the other hand, wide DTRs can lead to death and even population extinction (Uvarov, 2003; Estay et al., 2011).

Insects and other small invertebrates exchange heat rapidly with the environment, and thus are thought particularly susceptible to fluctuating ambient temperatures (Huey and Bennett, 1990). For insects with complex life cycles, the larval stage usually has a longer duration and is thought to be particularly sensitive to thermal variability (McMillan et al., 2005; Atapour et al., 2007; Cui et al., 2011; Zhang et al., 2015). Temperature fluctuations at an early developmental stage can influence performance of immediate and later stages (Potter et al., 2011; Xing et al., 2014), and even the next generation (unpublished data).

Abbreviations: Diurnal temperature range, (DTR); Diamondback moth, (DBM); Intrinsic rate of increase, (r_m); Net reproductive rate, (R_o); Mean generation time, (T)

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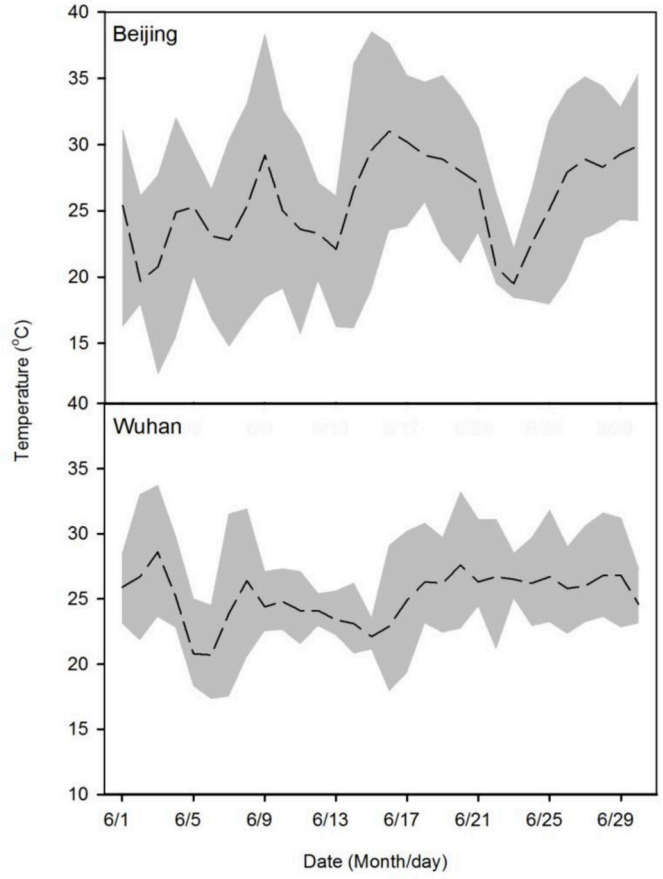

Fig. 1. The high latitude (Beijing) and the low latitude (Wuhan) locations have different diurnal temperature amplitudes with the same mean temperature of 25 °C in June 2017. The dashed line is the daily mean temperature, the gray area is the daily temperature amplitude.

Previous studies have considered the effect of larval/nymphal temperatures through short-term (several hours) heat exposure (Chavadi et al., 2006; Zhao et al., 2017) or different constant temperatures (Zhang et al., 2015a,b; Arambourou et al., 2017) which ignore the mitigation of thermal injury by favorable nighttime temperatures (Cui et al., 2011; Zhao et al., 2014) and don't reflect diurnal fluctuations in nature (Kingsolver et al., 2016). Other studies have considered the effect of daily fluctuating or alternating temperatures, involving a single daily fluctuation in a laboratory (Zhao et al., 2019) or field (Atapour et al., 2007; Zhang et al., 2015) context, or changes in both mean temperature and fluctuating temperature range simultaneously (Cao et al., 2018). These experiments do not allow the relative impact of changing DTR to be evaluated. Studies have generally not considered cross-stage effects of larval temperature fluctuations on life history performance, although larval temperature fluctuations can affect adult emergence, maturation success (Zhang et al., 2015), adult body size and coloration (Knapp and Nedved, 2013) and wing pattern (Kooi and Brakefield, 1999). On the other hand, modular life cycles may help metamorphosing insects reduce effects of environmental stress at the larval stage, as has been observed for chemical pollutants, food and pesticides (Servia et al., 2002; Campero et al., 2008), and more studies are needed to evaluate the impact of DTR across life stages.

The diamondback moth (DBM), *Plutella xylostella*, is widely distributed and the most destructive pest of cruciferous vegetables (Furlong et al., 2013). Temperature has a significant influence on growth (Golizadeh et al., 2007), survival (Marchioro and Foerster, 2011), reproduction (Ma and Chen, 1993; Golizadeh et al., 2009) and migration (Chapman et al., 2002; Xing et al., 2013) of DBM. Most of studies on DBM have focused on constant temperature conditions except for alternating temperatures (Liu et al., 2002; Ahmad et al., 2008), whereas we have previously tested the effects of temperature fluctuations at the egg stage on the performance of DBM and found effects of diurnal temperature fluctuations on later developmental stages (Xing et al., 2014, 2015). Compared with the egg stage, the larval stage of DBM lasts much longer and is particularly important from a control perspective. Therefore, we examined immediate and cross-stage effects of larval temperature fluctuations in DBM.

Here, we incubated larvae at one constant temperature (25 °C) and six symmetric temperature amplitudes (± 0 °C, ± 4 °C, ± 6 °C, ± 8 °C, ± 10 °C and ± 12 °C) and tested the effect on life history traits including development and survival of larvae and pupae, as well as longevity and fecundity of adults. We addressed the following questions. 1) What is the immediate effect of different temperature amplitudes on larval traits? 2) Do the larvae exposed to different temperature amplitudes show a cross-stage effect on pupal and adult traits? 3) How do these findings translate into overall fitness effects at the population level?

2. Materials and methods

2.1. Insect rearing

A stock population of DBM was established in the laboratory from larvae collected originally from *brassica* fields at Wuhan (30.62°N 114.13°E) in China in May 2010. This population was reared on an artificial diet (Southland Products Incorporated, USA) at a constant 25 ± 1 °C, 50%–70% RH and a photoperiod of 15L : 9D, as described elsewhere (Xing et al., 2014), and DBM had been reared under these conditions for at least 8 years before this study.

2.2. Experimental protocol

We investigated the effect of temperature amplitudes during the larval stage on immediate development and survival, subsequent development and survival of pupae, and longevity/fecundity of adults. We simulated temperature amplitudes in cabbage fields in summer in Beijing (39.80°N 116.47°E), as reported by Xing et al. (2014). We included a 25 °C constant treatment and five temperature amplitudes across a 24 h cycle: ± 4 °C, ± 6 °C, ± 8 °C, ± 10 °C and ± 12 °C (Fig. 2A) by using climate chambers. Temperatures in the chambers were recorded every 20 min by data loggers (U23-001, Hobo Ltd., USA), and showed that mean temperatures in chambers were around 25 °C (Table 1, Fig. 2B). Relative humidity in the chambers was 50%–70% and photoperiod was set to 15L : 9D during the experiment.

For larval rearing, we used 24 well plates sterilized for 30min by ultraviolet light, with each well containing 1.7 ml artificial diet. One new hatched larva (hatched within the last 4 h from the second day of egg production) was transferred into a well with a fine camel hair brush. To allow for ventilation, the plates were covered with fine nylon mesh (200 mesh nylon gauze). Over 72 larvae (1 larva × 24 wells × 3 plates/replications = 72 larvae) were set up for each temperature treatment. During daily routine checking, we transferred larvae to fresh diet to avoid larvae being exposed to diet that had dried out.

After larvae pupated, all tested insects were moved to a 25 °C rearing room. Once adults emerged, new male and female adults from the same replicate under the same temperature treatment were paired and transferred into a glass tube (3 × 12 cm) for mating and egg-laying. Two sides of the tube were covered with the fine nylon mesh for ventilation. A piece of cotton immersed with honey water solution (10%) was placed in the tubes for adult feeding. A piece of fresh cabbage leaf (4 × 2 cm) was inserted into the tube for egg laying. The adults were transferred into a new tube with fresh cabbage leaf at 07:00–08:00am every day until adults died.

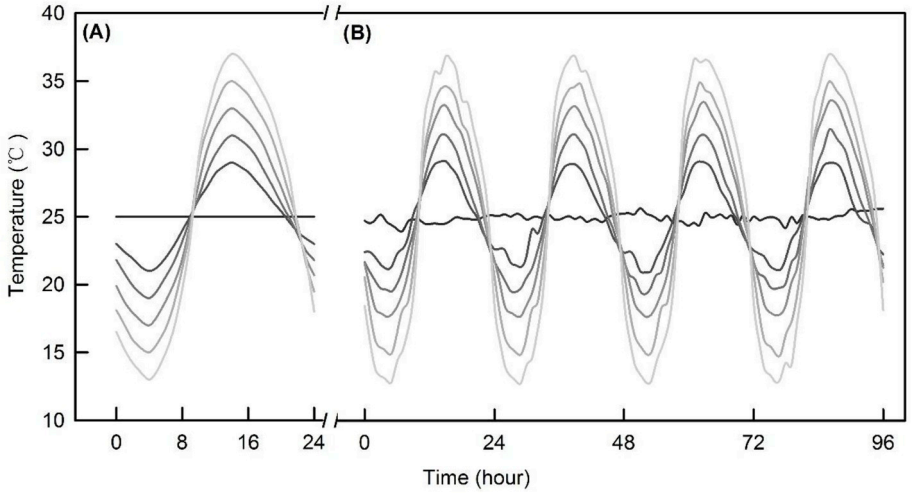

Fig. 2. Target (A) and recorded temperatures with different temperature amplitudes in different climate chambers for four consecutive days (B).

Table 1
Target and actual recorded temperatures with different temperature amplitudes around 25 °C in climate chambers.

Target temperature range (+/−°C)	Recorded temperature (mean ± SD)	
	Average (°C)	Temperature amplitudes (°C)
0	25.14 ± 0.32	0.59 ± 0.26
4	24.91 ± 0.10	3.89 ± 0.12
6	24.94 ± 0.08	6.03 ± 0.28
8	25.18 ± 0.32	7.92 ± 0.13
10	24.90 ± 0.21	10.21 ± 0.31
12	25.21 ± 0.29	11.98 ± 0.08

2.3. Measurements

In the experiment, development and survival of larvae was checked daily at 08:00 a.m., within a period of 1.5 h. When larvae became spindle-shaped and formed a white thin silk cocoon, they were recorded as having entered the pupal stage and weighed (Golizadeh et al., 2009) and kept at 25 °C. Pupae continued to be observed at 08:00am until all adults emerged or pupae died (based on lack of adult emergence). Survival and development time were recorded for the pupal stage. After female and male moths were paired, adult survival was checked daily at 08:00am and all eggs laid on the leaf and inner surface of the tube were counted daily.

2.4. Statistical analysis

We analyzed effects of different temperature amplitudes during the larval stage on development time and pupation rate of larvae, development time and emergence rate of pupae, and pupal mass. We assessed adult longevity and fecundity as well as the proportion of adults ovipositing in the first two days, and we used these data to estimate life table parameters. Development time of the different stages was estimated for individuals still alive when entering the next stage. Pupation rate and emergence rate were estimated as the percentage of individuals still alive when entering the pupal stage or adult stage. Longevity was measured as the number of days between the emergence of an adult and its death, and fecundity was computed as the total number of offspring per adult female. Development, pupal mass and longevity were analyzed with ANOVAs in which larval temperature and adult sex were treated as fixed factors, and replicate plates as a random factor (nested within larval temperatures). Life table parameters, consisting of the intrinsic rate of increase (r_m), net reproductive rate (R_0) and mean generation time (T) were calculated through POP TOOLS 3.2.5 (Hood, 2011), and were analyzed with ANOVAs. Means were compared using Duncan's multiple range tests. All indices and variables were compared among treatment groups with SPSS 20.0.

To consider the effect of temperature amplitudes during the larval stage on development rate of larvae, we compared our results to different models (degree-hour linear model, logistic model and Wang model) used in previous studies on the same species (Liu et al., 2002). We found that the degree-hour linear model provided the best fit to our data, and we therefore compared our results to predictions based on this model using the parameters given in Liu et al. (2002), but adjusting for the longer development rate across instars found in our study at constant 25 °C (0.123 1/d) compared to the time noted in that study at constant 24 °C (0.120 1/d). In the degree-hour model, we set the upper threshold for development at 32 °C and the threshold was not reached even in the widest amplitude treatment (Liu et al., 2002). We predicted development every hour based on the constant degree day model and development was denoted as zero when hourly temperature exceeded 32 °C. The mean development rates of different temperature amplitudes can be evaluated by calculating the average development rates across 24 h.

3. Results

3.1. Immediate effects of larval temperature amplitudes on larval stage

Development rate of larvae was impacted significantly by larval temperature amplitudes ($F_{5,247} = 7.76$, $P < 0.01$), but was not affected by either sex ($F_{1,247} = 1.46$, $P = 0.35$) or replicate plates ($F_{2,247} = 4.01$, $P = 0.27$) (Table 2). Larvae reared at 25 °C constant temperature (0.123/d) or under moderate amplitudes (0.123/d, 0.121/d, under ± 4 °C and 6 °C respectively) developed significantly faster than those incubated at the widest amplitude (0.111/d under ± 12 °C). When we compared the data to expectations based on the degree-hour linear model through computing observed and expected development rates, we found that development rate was faster than expected particularly when temperature fluctuated ± 10 °C and ± 12 °C (Fig. 3A).

There were no marked effects of larval temperature amplitudes on larval survival, and pupation rate did not differ significantly between larval treatments ($F_{5,17} = 1.80$, $P = 0.20$), although there was a suggestion of a decrease in pupation rate at wide amplitudes (Fig. 3B).

3.2. Cross stage effects of larval temperature amplitudes on pupa and adult stages

Neither the development rate of pupae ($F_{5,247} = 0.65$, $P = 0.67$)

Table 2
Results of ANOVAs for effects of larval temperatures, sex, and replicate plates (as a random factor, nested within larval temperatures) on development rate of larva, pupation rate, development rate of pupa, emergence rate, longevity, fecundity and proportional of females ovipositing in the first two days.

Trait	Source	*df*	*F*	*P*
Development rate of larva	Larval treatment (LT)	5,247	7.76	< **0.01**
	Replicate plates	2,247	4.01	0.27
	Sex (S)	1,247	1.46	0.35
	LT x S	5,247	1.16	0.39
Pupation rate	Larval treatment	5,18	1.80	0.20
	Replicate plates	2,18	4.58	0.04
Development rate of pupa	Larval treatment (LT)	5,247	0.65	0.67
	Replicate plates	2,247	0.28	0.78
	Sex (S)	1,247	66.12	0.67
	LT x S	5,247	0.61	0.69
Emergence rate	Larval treatment	5,18	1.06	0.44
	Replicate plates	2,18	0.53	0.61
Longevity	Larval treatment (LT)	5,247	0.65	0.67
	Replicate plates	2,247	0.28	0.78
	Sex (S)	1,247	66.12	**0.02**
	LT x S	5,247	0.61	0.69
Fecundity	Larval treatment	5,90	5.11	**0.01**
	Replicate plates	2,90	2.09	0.17
Proportion females laying in first two days of oviposition	Larval treatment	5,90	8.66	< **0.01**
	Replicate plates	2,90	0.03	0.97

Note: Significant *P*-values are given in bold.

(Fig. 4A) nor the emergence rate of adults ($F_{1,247} = 1.06$, $P = 0.44$) (Fig. 4B) was influenced by larval temperature amplitudes (Table 2).

Longevity (Fig. 4C) was also not affected by larval temperature amplitudes ($F_{5,247} = 0.65$, $P = 0.67$) or replicate plates ($F_{2,247} = 0.28$, $P = 0.78$), but differed significantly between sexes ($F_{1,247} = 66.12$, $P = 0.02$) (Table 2). Fecundity was impacted significantly by larva temperature amplitudes ($F_{5,90} = 5.11$, $P = 0.01$) (Table 2) due to a lower total fecundity at wide amplitudes (± 10 °C and ± 12 °C) (Fig. 5A), and was not affected by replicate plate ($F_{2,247} = 2.09$, $P = 0.17$). Compared with a mean fecundity of 175 eggs/adult for the constant temperature (25 °C) treatment, there was a decrease of at least 19 eggs/adult for wider DTR (± 10 °C and ± 12 °C). The proportion of adults ovipositing in the first two days was also influenced significantly by larval temperature amplitudes ($F_{5,90} = 8.66$, $P < 0.01$) (Table 2) reflecting a higher initial rate of egg laying for the ± 10 °C and ± 12 °C treatments (Fig. 5B). Compared with the 55% of females ovipositing in the first two days for the constant temperature (25 °C), there was an increase of at least 13% for wide amplitudes (± 10 °C and ± 12 °C). Total egg production and early fecundity were not affected when larvae were held under moderate amplitudes.

The summary life table parameters (Table 3) showed that the intrinsic rate of population increase (r_m) differed among treatments ($F_{5,17} = 4.23$, $P = 0.02$) and was higher at the constant temperature (25 °C) or moderate amplitudes (± 4 °C, ± 6 °C and ± 8 °C) compared to wide amplitudes (± 10 °C and ± 12 °C) (Fig. 6), and a similar difference was apparent for the net reproductive rate (R_0) ($F_{5,17} = 4.30$, $P = 0.02$) with increasing temperature amplitudes decreasing this measure. But the mean generation time (T) was not significantly different among different temperature amplitudes ($F_{5,17} = 1.82$, $P = 0.18$).

4. Discussion

Development rates of larvae under wide temperature amplitudes (± 10 °C and ± 12 °C) were slower than those under a constant temperature (25 °C) or moderate amplitudes (± 4 °C, ± 6°Cand ± 8 °C). Within the optimum temperature range, development in DBM was accelerated in an approximately linear pattern with temperature increasing (c.f. Chen and Liu, 2003; Colinet et al., 2015). Daytime temperatures above the mean temperature can accelerate development, but nighttime temperatures below the mean can retard it (Xing et al., 2014). With regular sinusoidal fluctuating temperatures as in our experiments, the development increments are equal to the decrements under moderate amplitudes, with no significantly effects on

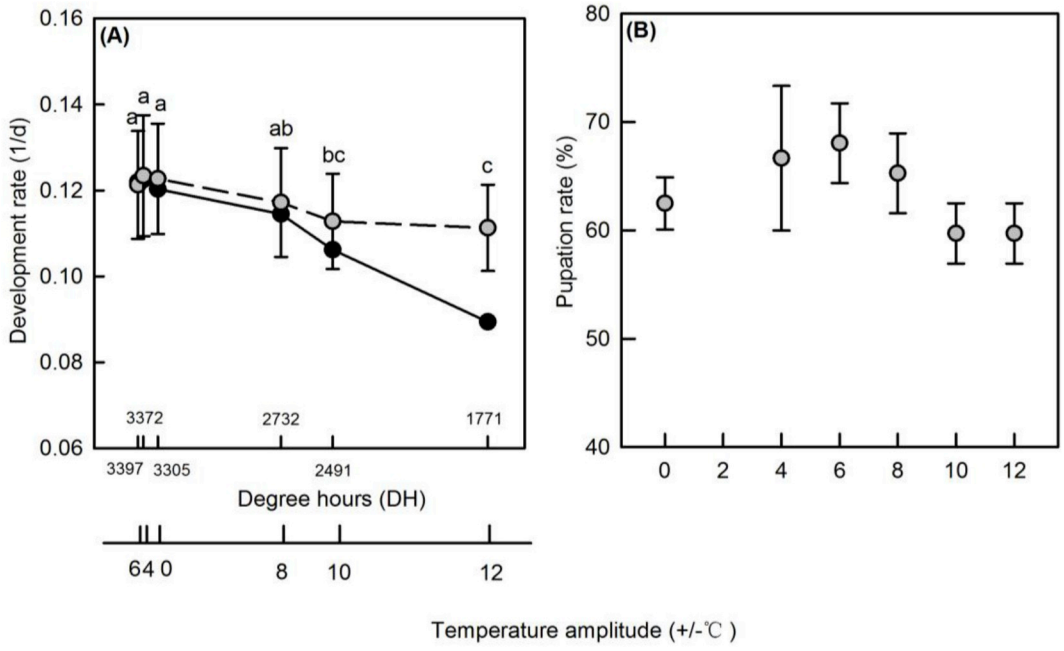

Fig. 3. (A) Development rate of different temperature treatments (bottom bar indicates amplitudes) and constant temperature models (x axis in degree hours). The dotted line and shaded symbols indicate means from the experimental data, the solid line and symbols are the degree-hour linear model describing development rates in DBM based on data from Liu et al. (2002). Different letters at the top of columns indicate significant differences among treatments at $P = 0.05$. (B) Pupation rate under the six different temperature amplitudes (± 0 °C, ± 4 °C, ± 6 °C, ± 8 °C, ± 10 °C and ± 12 °C). Vertical bars indicate ± SE. Pupation rates are not significantly different among temperature amplitudes.

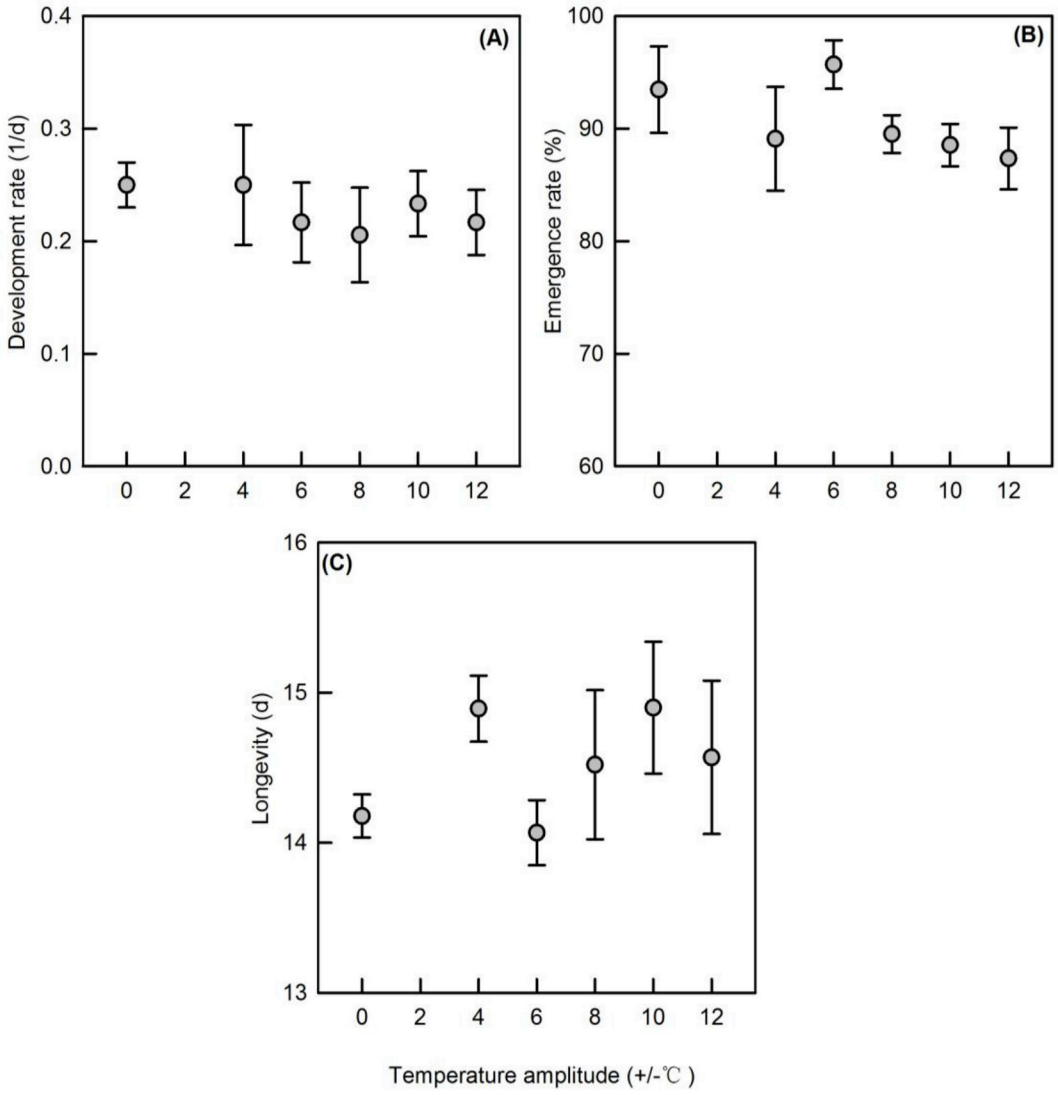

Fig. 4. (A) Mean development rate of pupa, (B) emergence rate and (C) mean longevity under six different temperature amplitudes (± 0 ℃, ± 4 ℃, ± 6 ℃, ± 8 ℃, ± 10 ℃ and ± 12 ℃). Vertical bars indicate ± SE. Development rate of pupa, emergence rate and mean longevity are not significantly different among temperature amplitudes.

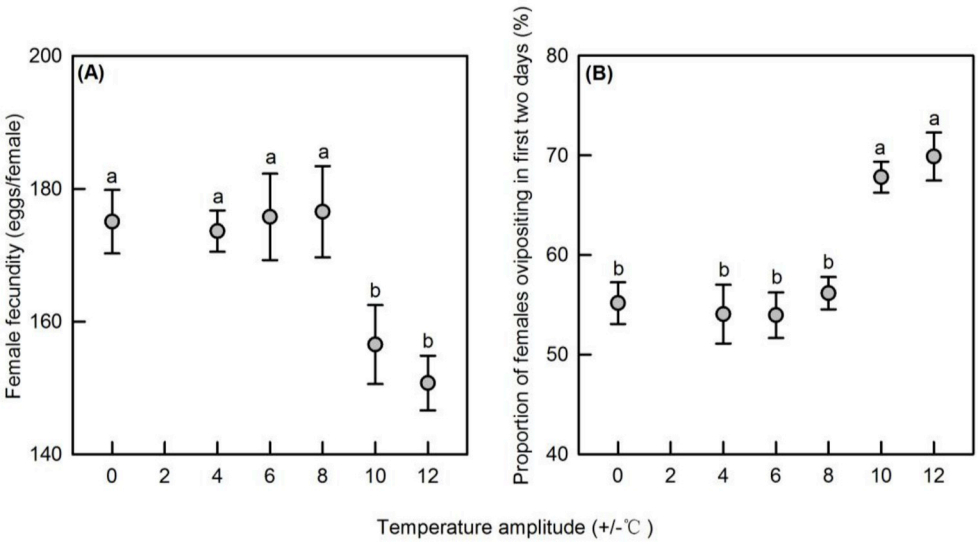

Fig. 5. (A) Mean fecundity and (B) proportion of females ovipositing in first two days under six different temperature amplitudes (± 0 ℃, ± 4 ℃, ± 6 ℃, ± 8 ℃, ± 10 ℃ and ± 12 ℃). Vertical bars indicate ± SE. Different letters at the top of columns indicate significant differences among treatments at $P = 0.05$.

Table 3
Life table parameters of *Plutella xylostella* under different larval temperature amplitudes with the same mean temperature of 25 °C.

Temperature treaments (+/− °C)	r_m	R_0	T
0	0.33 ± 0.01a	72.83 ± 5.05a	26.82 ± 0.65
4	0.31 ± 0.03 ab	67.10 ± 5.40 ab	27.24 ± 0.44
6	0.33 ± 0.02a	80.09 ± 7.56a	26.74 ± 0.69
8	0.30 ± 0.02abc	65.73 ± 6.34 ab	27.41 ± 0.21
10	0.26 ± 0.02c	45.99 ± 7.21c	28.14 ± 0.82
12	0.28 ± 0.02bc	51.85 ± 7.43bc	27.92 ± 1.08
df	5,17	5,17	5,17
F	4.23	4.30	1.82
P	**0.02**	**0.02**	0.18

Note: r_m, intrinsic rate of increase; R_o, net reproductive rate; T, mean generation time. X ± SE represent averages and their standard errors respectively. Different letters indicate significant differences among treatments at $P = 0.05$. Significant P-values are given in bold.

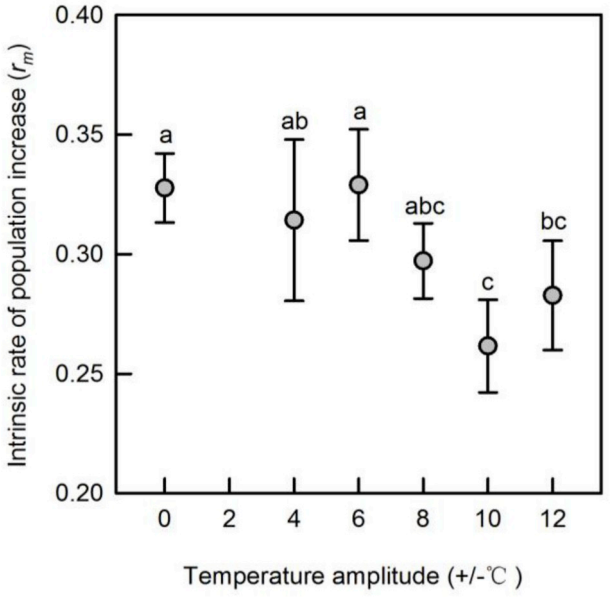

Fig. 6. Mean intrinsic rate of population increase (r_m) of *Plutella xylostella* at six different temperature amplitudes (± 0 °C, ± 4 °C, ± 6 °C, ± 8 °C, ± 10 °C and ± 12 °C). Vertical bars indicate ± SD. Different letters at the top of columns indicate significant differences among treatments at $P = 0.05$.

development. However, development should be inhibited when temperatures out of the optimum temperature range are experienced (Ruel and Ayres, 1999; Shi et al., 2011). In our study, the maximum temperature reached 37 °C and lasted for 6 h, higher than the upper threshold of 32 °C for larval development. Such high temperatures were expected to be unable to compensate slower development at lower temperatures (< 20 °C), and therefore development overall slowed. However, it is noteworthy that developmental rate under the wide amplitude treatment was faster than predicted by the degree-hour linear model; this might indicate that the insect is still developing slowly rather than stopping development completely above the upper threshold temperature. To understand the impact of environmental conditions on insect development, degree-day or degree-hour linear models are widely applied, and normally derived from a series of constant temperatures (Lin et al., 1959; Lischke et al., 1997; Park et al., 2014). Our results indicate that the traditional linear model for "constant temperature-development" can predict field development well if the mean temperature is optimal and the daily temperature amplitude is not particularly wide such as a mean of 25 °C and temperature amplitude less than 8 °C for DBM. However, these models may not predict development under wide temperature amplitudes exceeding this value.

Wide temperature amplitudes during the larval stage had little influence on the survival of larvae or pupae. Pupation rate of DBM at constant 14°C-30 °C did not change significantly from a value of around 80%, but decreased to ca. 50% at 32 °C, and no larvae survived 33 °C (Chen and Liu, 2003). However, our results showed that larval survivorship stayed relatively high (56%) under the widest amplitude (± 12 °C), in which the daily maximum reached 37 °C, far above the constant upper lethal limit of 32 °C. The difference may be related to heat injury repair during lower nighttime temperatures and highlight the importance of exposure period when considering impacts on fitness traits (Hoffmann, 2010). As in other studies (Yang and Stamp, 1995; Zhao et al., 2014), recovery from heat injury under nighttime temperatures of 13°C–25 °C may also buffer daytime heat stress effects. This is probably the result of increasing protective factors such as *hsp* proteins, mannitol or sorbitol produced under mild nighttime temperatures.

For adult reproduction, our results fail to support the hypothesis of "lifecycle modularity" reported in previous studies, in which it is suggested that modular life cycles may allow insects to mitigate the consequences of environmental stress by separating its ecological and physiological effects between life stages (Campero et al., 2008; Potter et al., 2011). This phenomenon has been documented in the laboratory; for example, high larval temperature in *Drosophila* (Huey et al., 1995), and egg heat exposure in *Manduca sexta* (Potter et al., 2011) and *Plutella xylostella* (Zhang et al., 2015a), did not influence female reproduction. However, we found that wide amplitudes (± 10 °C and ± 12 °C) could decrease lifetime fecundity of DBM. Moreover, temperature stress at the larval stage could alter adult performance without changing pupal traits. This could be linked to resource allocation shifts induced by larval thermal environments; when more resource is allocated to stress tolerance, less is available for reproduction (Pechenik et al., 1998; Metcalfe and Monaghan, 2001; Zhang et al., 2015a).

We found adult fecundity was decreased following wide amplitude (± 10 °C or ± 12 °C) of larval temperature. Under moderate amplitude environments, daytime temperatures may not have been high enough (< 32 °C) to cause injury and overcome the recovery of metamorphosis modularity (Huey et al., 1995; Zhang et al., 2015). The marked decrease in fecundity rather than longevity after larval exposure to a wide amplitude confirmed the conclusion of previous studies that reproduction is more sensitive to heat stress than the thermal tolerance of an individual (Zhao et al., 2017; Li et al., 2016). On the other hand, the early oviposition triggered by wide larval temperature amplitudes may reflect a stress response, with adverse conditions inducing accelerated oviposition which will maximize fitness before conditions further deteriorate. Stress conditions could cause adults to reproduce as early as possible to avoid more damage later (Javoiš and Tammaru, 2004).

Wide thermal amplitudes at the larval stage described here contrast with those during egg stage where there was little impact (Xing et al., 2014). Heat stress (at a daily peak of 40 °C for 3 h) at the egg stage also failed to impact adult reproduction in *Manduca sexta* (Potter et al., 2011). In *P. xylostella*, adult reproduction was affected more by heat stress (at constant 40°Cfor 8 h) at the 3rd-instar larval stage than at the egg stage (Zhang et al., 2015a). The most likely reason for this is that insects experiencing metamorphosis can recover and restructure morphology and physiological metabolism to diminish effects on subsequent life-stages (Seifert et al., 2012).

That wide diurnal temperature amplitudes have a significant effect on development, fecundity and population dynamics of insects suggests that predictions based on mean temperature may be tempered by effects of temperature amplitudes, with unexpected effects across life stages and even on the whole population. These changes need to be comprehensively understood through experimental analyses and though further work is required to assess influence of thermal amplitudes on insect traits and population dynamics under future climate change.

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