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Effects of alternating temperatures on development and reproduction of the armyworm, *Mythimna separata* (Walker)

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Abstract— Effects of cycling and constant temperature on development and reproduction of the armyworm, *Mythimna separata* (Walker) were investigated by rearing the insects on the artificial diet under temperatures covering low(16–24 ℃ vs. 20 ℃), medial(20–28 ℃ vs. 24 ℃) and high(24–32 ℃ vs. 28 ℃) regions. In the low region, all the immature stages of the insect developed significantly faster under alternating temperatures than at corresponding constant temperatures. For the medial region, their development was little affected by variable temperatures. For the high region, developmental durations tended to be longer under cycling temperatures except egg stage.

Mean fecundities of the adult moths markedly increased under cycling temperatures as compared with those at respective constant temperature in all regions.

Possible reasons for effect of alternating temperatures on insect development are discussed in some details.

Keywords: alternating temperature; armyworm (*Mythimna separata*); development duration; population parameters; fecundity.

INTRODUCTION

Insects are essentially ectothermic organisms with their physiological processes displaying a high sensitivity to environmental temperature. The global climate worming mainly resulting from greenhouse effect will certainly produce a substantial influence on their occurring dynamics and damage caused by them to crops. In any attempt to estimate by means of laboratory experiments, the effect of temperature on an insect species in the field, consideration must be given to the fact that in most natural situations ambient temperature is variable instead of constant, showing diurnal and seasonal cycles.

The effects of temperature on insect growth, behaviour, general physiology and ecology have been much studied. But most of such works have been done at various constant temperatures. A little attention has been given to the effect of variable temperature on insect population dynamics.

The present paper focuses on the effects of alternating temperature on development and fecundity of the armyworm, *Mythimna separata*, a key species of insects pest, mainly infesting the crops in grass family.

MATERIALS AND METHODS

Insect stock

The armyworm, *Mythimna separata* (Walker) used in present study was progenies from a stock that was originally collected as moths in Beijing suburbs and had been reared on the artificial diet (Li, 1990) for several generations. The eggs laid within 12 hours were taken to initiate the experiment.

Temperature treatment

Five constant temperature chambers (0.5×0.5×0.5 m in content) were employed to establish 3 constant and 3 alternating temperatures, covering low, medial and high temperature regions, as shown in Table 1.

Table 1 Establishment of constant and alternating temperature

Temp. region, ℃	Temp., ℃ × exposure time, .h	Temp. amplitude
Low constant	20×24	–
Alternating	16×12–24×12	8
Medial constant	24×24	–
Alternating	20×12–28×12	8
High constant	28×24	–
Alternating	24×12–32×12	8

Temperatures in these chambers varied ±1.0 ℃. Because the chambers in this study could maintain only constant temperatures, alternation of the temperature was made by transferring the insects in the containers from one chamber to another at fixed time every day.

Insect rearing

The larvae, soon after hatching, were transferred by a fine brush on the artificial diet in breakers of 25 ml, 10 individuals per container. Beginning from the 3rd instar, they were separately reared on the diet in each of glass tubes (2.0 cm in dia. × 8.0 cm high). Mature larvae were removed into the identical tubes with some moist soil for pupation. Fresh weight of the two-day-old pupae was taken. Couples of adult moths with the same age were separately confined in each of lamb chimneys (10 cm in dia. × 10 cm high) which were covered on both sides by plastic screen and put on jars containing some water. A 10% bee honey solution was supplied as their additional nutrients.

The eggs, adults and pupae with some moist soil in the containers were directly exposed to designed temperatures. All the rearing experiments were conducted with a 12 L:12 D photoperiod.

Collection and analysis of data

Development and survivalship during egg, larval and pupal stages, and performance of adult moths were monitored daily. These data were used to calculate population parameters of the insect, namely, net reproduction rate (R_0), intrinsic rate of increase (r_m), finite rate of increase (λ) and mean generation length (T), according to the procedures described by Birch (Birch, 1984) and Wu *et al.* (Wu, 1980).

RESULTS AND ANALYSES

Effect on developmental duration

The times required for eggs, larvae and pupae to complete their development under regions of temperatures tested are presented in Fig. 1. In the low temperature region all these immature stages developed significantly faster under variable temperatures than at constant temperatures. For the medial region, however, no marked differences of developmental durations in any stage were detected between treatments of variable and constant temperatures, although they developed a little faster in the latter case. For the high region, developmental times of larvae and pupae tended to be shorter at the constant temperature. These results indicate that acceleration of *M. separata* development under alternating temperatures only occurred in the low temperature region.

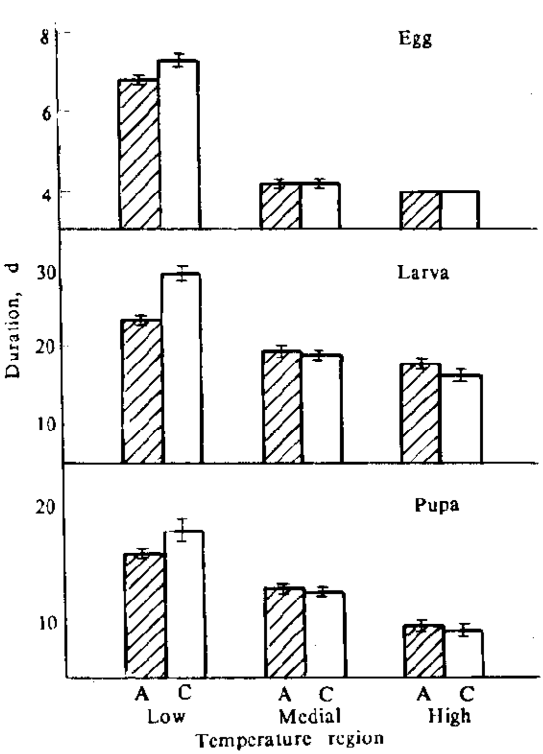

Fig. 1 Developmental durations of immature stages of the armyworm under constant and alternating temperatures
A —Alternating temperature; C —Constant temperature

Effect on survivalship of immature stages

In 3 temperature regions tested, egg-hatching percentages were higher at constant temperatures than under respective alternating temperature while survival rates of larvae were nearly the same under both constant and variable temperatures(Table 2). In low and medial regions, alternating temperatures were beneficial to pupal survivalship, and in the former case its survival rate increased by some 30% relative to that under the constant temperature.

Table 2 Survival rates of the armyworm under constant and alternating temperatures

Temp. region	Low		Medial		High	
	20	16–24	24	20–28	28	24–32
No. eggs tested[1]	350	129	295	195	239	70
Hatching, %	87.4	72.9	99.0	77.4	88.7	71.4
	80	80	100	80	100	104
No. larvae tested						
survival, %						
Larval stage	71.3	70.0	78.0	76.3	68.0	67.3
Pupal stage	40.4	69.6	83.3	93.4	64.7	58.6

[1] Eggs that had been identified as unfertilized at the end of experiment had been excluded

Effect on pupal size

Fresh weights of the two-day-old pupae from the larvae reared under different constant and variable temperatures are shown in Fig. 2. In all temperature regions tested, both female and male pupae weighed significantly heavier when their larvae were kept under alternating temperatures than at corresponding constant temperatures. Fig. 2 also shows that pupae size for alternating temperature treatments increased with increasing temperature while the biggest pupae for constant temperature treatment occurred at 24 ℃ .

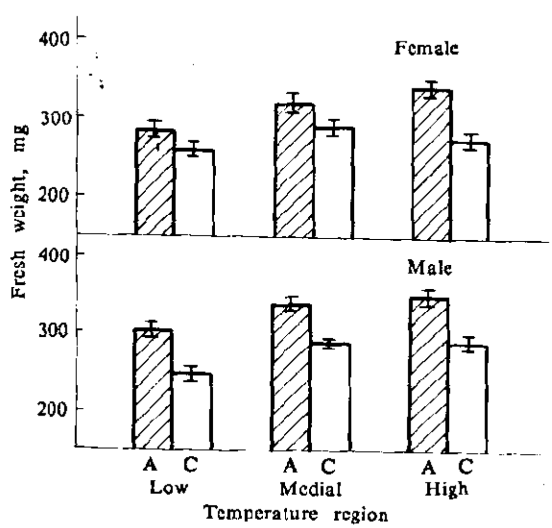

Fig. 2 Fresh weights of *M. separata* pupae from the larvae kept under constant and alternating temperatures
A –Alternating temperature; C –Constant temperature

Effect on adult performance

Table 3 shows the performances of *M. separata* adults under different alternating and constant temperatures. Mean numbers of eggs laid per female moth increased by 68%, 38% and 61%, under variable temperatures in low, medial and high temperature regions, respectively, as compared with that at the corresponding constant temperatures. Generally, alternating temperatures prolonged longevity of the female moths to different extent, but shortened life-span of the male moths, especially in high temperature region. A comparison of adult fecundities and longevities in 3 temperature regions indicates that 32 ℃ may be too high for their normal life activity.

Table 3 Performance of *M. separata* moths exposed to constant and alternating temperatures

Temp. region,	Low		Medial		High	
℃	20	16－24	24	20 28	28	24－32
Mean fecundity						
egg production	404.4	678.5	873.5	1201.8	735.0	1181.2
	±68.9	±88.1[1]	±58.5	±71.1[1]	±89.4	±97.1[1]
No. egg unladid	14.4	44.3	17.8	24.7	16.6	30.0
	±8.3	±14.7	±3.6	±4.1	±5.8	±9.7
Total	418.8	722.8	891.3	1226.5	751.6	1211.5
	±69.3	±78.4[1]	±57.9	±69.9[1]	±90.0	±95.1[1]
Longevity						
Femal	16.8	18.4	15.2	16.4	11.4	11.9
	±1.7	±1.5[1]	±1.0	±0.8	±0.7	±0.5
Male	25.7	24.9	20.5	18.6	17.7	13.2
	±3.7	±3.7	±1.0	±1.1[1]	±1.2	±1.2[1]

[1] Indicates significant difference from that at the corresponding constant temperature

Effect on population growth

The population parameters presents in Table 4 are common indices for assessing potential of insect population growth, which integrate effects of environmental factors on insect development, survivalship and age-specific fecundity. Clearly, capability of *M. separata* population growth increased a lot with a shorter mean generation time under the alternating temperature as compared with that at the constant temperature in the low temperature region. For the medial region, variable temperature also accelerated population growth of the insect, but not as much as that in the low region. For the high region, most of the population parameters are nearly the same under both alternating and constant temperatures.

Table 4 Population parameters of the armyworm exposed to constant and alternating temperatures

Temp. region,	Low		Medial		High	
℃	20	16 – 24	24	20 – 28	28	24 – 32
Net reproduction rate, R_0	49.03	108.48	249.77	324.47	153.20	162.11
Intrinsic rate of increase, r_m	0.0615	0.0882	0.1104	0.1244	0.1331	0.1376
Finite rate of increase, λ	1.0634	1.0922	1.1168	1.1325	1.1424	1.1475
Mean generation length, T, day	63.3	53.1	50.0	46.5	37.8	37.0

DISCUSSION

Ambient temperature controls insect development and has substantial influence on their survival and fecundity, because they are ectothermic animals. Effect of temperature on insect development are most often estimated with experiments conducted at constant temperatures. However, under natural conditions they are exposed to daily cycles of temperature whose influence on development may be different from that of constant temperature.

Out of lepidopterous insects examined, most species showed faster development under cycling temperatures than at corresponding constant temperatures (Miyashita, 1971; Eubank, 1973; Foley, 1981; Kaster, 1984; Rock, 1985; Roltsch, 1990; Taylor, 1990). But no special effect of alternating temperature on development of the armyworm, *pseudaletia unipuncta* was found (Guppy, 1969). On the contrary, Siddiqui *et al.* (Siddiqui, 1973) observed slower development of the mediterranean flour moth, *Anagasta kuehniella* under variable temperature than at corresponding constant temperature. They presumed this would be an adaptation to the relative constant environment found in the insect habitat. Rock (Rock, 1985) described a more complex case where the tufted apple bud moth, *Platynota idaeusalis*, developed faster under alternating temperature in low temperature region, and did even below the reported threshold, and large amplitudes of temperature gave faster development than small ones. When variable region was within the range of 20 – 33℃, the amplitude generally had no effect on development. When alternating regions included the temperature higher than 33 ℃, slower development occurred. Responses of the armyworm, *Mythimna separata*, to cycling and constant temperatures are quite similar to the tufted apple bud moth. In addition, alternating temperatures obviously benefited adult fecundity.

In his review, Beck (Beck, 1983) supposed that disparity of responses among insect species to alternating temperature might depend on how the development was measured or on the nature of the temperature regions employed as well as on the particular species being studied.

The relationship between temperature and insect developmental rate which equals the reciprocal of development duration usually shows sigmoidal curvelineal forms within temperatures effective for development. Such curves suggest that the apparent acceleration or deceleration of insect development under alternating temperatures might be due to a slight concavity or convex in the true curve. As a matter of fact, insect development rates should be comparable under constant and the equivalant mean of alternating temperatures in medial temperature region since this portion of the curve appears to be a straight line. However, the situation might be different within upper or lower non-linear portion of the curve. In the higher temperatures region or convex portion of the curve, average of developmental rates at any two given temperatures would be less than that under corresponding constant temperature. The opposite result would be obtained in lower temperature region or concavity of the curve.

Another possible explanation for effect of variable temperatures on insect development involves kinetics of enzymic reaction (Sharpe, 1977; Wang, 1989). Generally, organism development is considered as the results of a series of individual physiological and biochemical processes in which different enzymes are involved. Each of these enzymes is presumed to have its own optimal temperature. At constant temperature, some enzymes can display their maximal activities while others can not and become limitary factors for development. Variable tempertures provide all the enzymes with an opportunity to alternatively exhibit their full activities, resulting in faster development of the organism.

This hypothesis seems to be reasonable, however, more valid experimental evidences are in great need.

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