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Effect of Temperature on the Development, Survival, and Fecundity of *Heliothis viriplaca* (Lepidoptera: Noctuidae)

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Abstract

Heliothis viriplaca (Hüfnagel) (Lepidoptera: Noctuidae) is worldwide an important economic pest of major agricultural crops. The effect of temperature on the biology, in particular the duration of the different developmental stages, of this insect pest was examined. The development, survival, and fecundity of *H. viriplaca* at five different temperatures (22, 25, 28, 31, and 34°C) were investigated, and experimental population life tables calculated. The results show that the developmental time of larvae, pupae, pre-oviposition, adults, and the entire generation decreases with increasing temperature. Larvae emerged fastest from the eggs at 28°C. The percentage of larvae that reached the seventh instar stage was 32.69, 38.60, 19.67, 3.61, and 20.88% at 22, 25, 28, 31, and 34°C, respectively. The developmental threshold temperature of the eggs, larvae, pupae, pre-oviposition and total pre-oviposition period was 10.53, 12.34, 5.60, 11.47, and 10.01°C, respectively. The effective accumulative temperature was 42.90, 239.68, 309.19, 77.72, and 767.64 degree-days, respectively. The population trend index (*I*) and the intrinsic rate of increase (*r*) of *H. viriplaca* were the highest at 31°C (133.97 and 0.12 d⁻¹, respectively). The results of this study may be useful for predicting the population dynamics of *H. viriplaca* and thus provides information on this important insect pest that may assist in its management.

Key words: ecdysis, effective accumulative temperature, developmental threshold temperature, pod borer, population life table

Heliothis viriplaca (Hüfnagel) (Lepidoptera: Noctuidae) is an important economic pest of major crops in West Palaearctic Europe, North Africa, Near Middle East, Central Asia, and North India (Mu et al. 2004, Alexei et al. 2008, Zhao et al. 2016). In China, H. viriplaca is an occasional pest, widely distributed in more than 30 provinces (Mu et al. 2004, Zhao et al. 2016). It is an important pest in northern China. Adults undertake long-distance migration on the prevailing winds of the East Asian monsoon (Zhao et al. 2016). H. viriplaca larvae are polyphagous, feed on about 70 herbaceous plant species belonging to 22 botanical families (Alexei et al. 2008) and are mainly harmful to cotton, soybean, chickpea, maize, alfalfa, sugar beet, scutellariae, and cornflower (Cui et al. 1997, Liu et al. 2010). In China, it has emerged in recent years as a serious pest on soybean, cotton, and beets. Severe infestations commonly reduce yields by 40-90% (Mu et al. 2004, Zhao et al. 2016). In the Middle East, H. viriplaca can cause severe damage to chickpea. In some years, the yield of chickpea was reduced by about 90% (Kahrarian 2009, 2012; Kahrarian et al. 2010). In China, there are two generations of this noctuid species each year (Cui et al. 1997). In Syria, Turkey (Kahrarian 2012), and Israel (Alexei et al. 2008) only one generation per year has been reported.

Temperature is one of the most important environmental factors affecting insect growth and development such as generation time, body size, and voltinism (Huffaker 1944, Shi et al. 2014, Kobori

and Hanboosong 2017). Important aspects of the biology of insect populations such as developmental threshold temperatures and thermal requirements to complete development usually adapt to local temperatures (Kobori and Hanboosong 2017). Knowledge of environmental factors that can affect the increase in insect populations is crucial for predicting potential changes in population dynamics and developing sustainable and environment-friendly pest control strategies (Kroschel et al. 2013). The influence of temperature on the biology of H. viriplaca has not been studied well so far. Therefore, it was the objective of this study to examine the effects of different temperatures on the life cycle duration, reproduction, and longevity of H. viriplaca. The developmental threshold temperature and the effective accumulative temperature were also investigated. Experimental population life tables of *H. viriplaca* are presented. The data obtained in this study could be useful for assisting in the development of pest forecasting programs and the improvement of current management strategies for this important insect pest.

Materials and Methods

Insects

H. viriplaca larvae were collected from a soybean field in Changchun (125°41′08″ E longitude, 43°80′15″ N latitude), Jilin province,

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China, during June 2016, and reared in the laboratory at $25 \pm 1^{\circ}$ C, 60-70% relative humidity (RH) and a 12:12 (L:D) h photoperiod. Larvae were fed with fresh soybean leaves. The freshly-emerged adults were kept separate in insect rearing cages (50 cm diameter \times 50 cm high). Each cage contained 20 moths which were provided with 5% honeyed water as a source of water and carbohydrates. Eggs deposited on the soybean leaves were collected and placed individually into glass tubes.

Experimental Setup

Soybean leaves with more than 70 freshly-laid eggs (<24 h old) were collected and placed in a controlled climate chamber at 22, 25, 28, 31, and 34 \pm 1°C, with 60 \pm 5% RH and a 12:12 (L:D) h photoperiod. Egg survival was daily recorded for each temperature. The freshly-hatched larvae were placed individually in Petri dishes (10 cm diameter × 2 cm high) and every day fed with fresh soybean leaves. The duration of each instar stage and the number of surviving larvae were recorded. The mature larvae were not fed soybean leaves anymore and moist sterile soil was prepared to produce cocoons. Pre-pupal and pupal periods were recorded when the larvae moved into the soil. Pupae were weighted 2 d after pupation. Pre-pupal and pupal survival was calculated based on the number of emerging adults. Gender of the adults was recorded for each temperature. The females and males that had freshly emerged (<24 h old) at a given temperature were paired and each pair was placed in an insect rearing pot (10 cm diameter × 15 cm high). Soybean seedlings were placed in the rearing pots to fed the adults and as a substrate for egg deposition. The adults were provided with 5% honeyed water. Soybean seedlings and the honeyed water were replaced daily. The number of eggs laid per female, the duration of the pre-oviposition period and the longevity of the adults were recorded.

Statistical Analysis

For comparisons of developmental duration, longevity, pupa weight, and fecundity H. viriplaca at the different temperatures, means, and standard errors were determined using SAS software version 9.4 (SAS Institute Inc., Cary, NC). Significant differences (P < 0.05) between different temperatures were determined by single-factor analysis (one-way ANOVA), Tukey's multiple range test (P < 0.05). The developmental threshold temperature (C) and thermal constant (K) of each insect developmental stage were calculated using the following formulae (Li and Wang 1986):

$$C = \frac{\sum_{i=1}^{n} T_{i} D_{i}^{2} - \bar{D} \sum_{i=1}^{n} T_{i} D_{i}}{\sum_{i=1}^{n} D_{i}^{2} - n \bar{D}^{2}}$$
$$K = \frac{1}{n} \sum_{i=1}^{1} K_{i}$$

Where T_i = treatment temperature; D_i = developmental duration at T_i ; K_i = effective accumulative temperature at the developmental threshold temperature C.

The experimental population life tables were calculated based on the effect of temperature on *H. viriplaca* development, growth, reproduction, and survival. The index of the population trend was calculated using the data of the life tables (Li et al. 2013).

The population parameters intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0) and the mean generation time (T) were calculated using the equations described by Birch (1948).

$$R_0 = \sum l_x m_x$$

$$T = \sum l_x m_x x / R_0$$

$$r = \ln R_0 / T$$

$$\lambda = \exp(r)$$

Where l_x = number of individuals life at time x (age-specific survival), m_x = number of offspring per female at time x (age-specific fertility).

Results

Effect of Temperature on Developmental Duration, Longevity, and Fecundity

The duration of each developmental stage (eggs, instars, pupae), longevity, pre-oviposition period, generation time, and female fecundity is shown in Table 1. At 22 to 34°C, the duration of the egg stage, instars, pupae and pre-oviposition period was significantly affected by temperature: the duration decreased as the temperature increased. The duration of the egg stage was the shortest at 28°C. At temperatures higher than 28°C, larval development took longer. At 28, 31, and 34°C, pupal developmental duration was 13.33, 11.24, and 11.81 d, respectively, but the differences were not significant. At 22 and 25°C, pupal developmental duration was 157.33 and 121.00 d, respectively, which is longer compared to all other temperatures because of diapause. Females lived longer than males and female longevity was the longest at 22 and 25°C. Male longevity was not influenced by temperature. Female fecundity was the highest at 31°C and significantly the lowest at 34°C. Temperature had a significant effect on the number of instars (Table 2). Larvae had five to seven instars before pupation. Temperature also had an effect on the percentage of larvae that formed pupae at the fifth, sixth, or seventh instar. For example, 5.26-7.69% of the fifth instar, 50.88-53.85% of the sixth instar and 34.62-43.86% of the seventh instar at 22-25°C. The highest percentage of larvae that formed pupae was 85.54% (sixth instar) and the lowest percentage was 3.61% (seventh instar), both observed at 31°C. The percentage of the larvae that reached seventh instar was higher at 34°C than at 31°C. The population did not develop without feathering when kept more than 3 mo at temperatures below 25°C. At a temperature of 28°C or higher, the larvae emerged from the eggs in less than 13 d (Table 1). Temperature also had a significant effect on pupal weight (Fig. 1). Pupal weight was significantly lowest at 34°C.

Effect of Temperature on Survival

No significant effect of temperature on egg hatching was observed. Larvae at the first and sixth instar stages were more affected by temperature (Table 3). At 31 and 34°C, the survival rate of the first instars was 88.78 and 90.29%, respectively, which is significantly lower compared with 22°C (98%). At 28 and 31°C, the survival rate of the sixth instars was higher compared with the other temperatures. The highest rates of larval survival were observed at 28°C. The emergence rate of the adults from the pupae was positively correlated with the 22–31°C temperature range. In contrast, 34°C had a significant negative effect on the emergence rate of the adults.

Developmental Threshold Temperature and Effective Accumulative Temperature

Based on the observed duration of each developmental stage and the whole generation at 28, 31, and 34°C, the developmental threshold

Table 1. Effect of temperature on the duration of the different developmental stages of Heliothis viriplaca

Developmental stage		Develop	omental duration (da	iys)		F	df	P
	22°C	25°C	28°C	31°C	34°C			
Egg	3.69 ± 0.09a	2.92 ± 0.12b	1.99 ± 0.07d	$2.30 \pm 0.05c$	2.05 ± 0.03cd	98.13	4,379	<0.0001
First instar	$3.48 \pm 0.07a$	$2.73 \pm 0.07b$	2.17 ± 0.06 d	2.32 ± 0.03 cd	$2.50 \pm 0.01c$	96.71	4,362	< 0.0001
Second instar	$2.88 \pm 0.11a$	$3.06 \pm 0.07a$	2.05 ± 0.05 b	$1.18 \pm 0.03c$	$1.05 \pm 0.04c$	267.83	4,357	< 0.0001
Third instar	$3.04 \pm 0.10a$	$2.50 \pm 0.13b$	$2.19 \pm 0.06c$	$1.86 \pm 0.03d$	$0.60 \pm 0.03e$	188.54	4,351	< 0.0001
Fourth instar	$3.13 \pm 0.15a$	$2.77 \pm 0.10a$	$1.92 \pm 0.10b$	$1.80 \pm 0.08b$	1.90 ± 0.06 b	37.04	4,342	< 0.0001
Fifth instar	3.22 ± 0.15 ab	$3.38 \pm 0.18a$	$2.83 \pm 0.08b$	$2.16 \pm 0.07c$	$2.13 \pm 0.09c$	27.92	4,324	< 0.0001
Sixth instar	$5.24 \pm 0.39a$	$4.55 \pm 0.28ab$	$3.91 \pm 0.18b$	$2.95 \pm 0.06c$	$2.89 \pm 0.09c$	28.89	4,285	< 0.0001
Seventh instar	$5.83 \pm 0.51a$	5.43 ± 0.43 ab	$3.27 \pm 0.23ab$	$3.00 \pm 0.00b$	$3.13 \pm 0.64b$	6.81	4,68	< 0.0001
Larva	$22.82 \pm 0.42a$	20.80 ± 0.40 b	$15.41 \pm 0.15c$	$12.17 \pm 0.13d$	11.36 ± 0.16d	425.28	4,306	< 0.0001
Pre-pupa + pupa	157.33 ± 8.21a	121.00 ± 11.87b	$13.33 \pm 0.27c$	$11.24 \pm 0.10c$	11.81 ± 0.46c	667.90	4,178	< 0.0001
Pre-oviposition	$5.40 \pm 0.87a$	$6.33 \pm 2.03a$	$5.23 \pm 0.67a$	$4.13 \pm 0.29a$	$3.50 \pm 0.50a$	1.64	4,39	0.187
Female adult	$20 \pm 4.51a$	$18.00 \pm 6.43ab$	$8.65 \pm 0.84c$	9.47 ± 0.97 bc	$6.75 \pm 0.25c$	12.30	4,39	<.0001
Male adult	$7.40 \pm 2.48a$	$9.33 \pm 3.84a$	$8.23 \pm 1.06a$	$6.77 \pm 0.73a$	$6.25 \pm 0.75a$	0.545	4,39	0.704
Generation (egg to oviposition)	185.40 ± 11.18a	169.33 ± 22.17a	35.17 ± 0.84 b	28.81 ± 0.50 b	$26.88 \pm 0.72b$	221.28	4,39	<0.0001
Ratios of ovoposited females (%)	62.5	50	65	75	33.33	-	-	-
Fecundity (F) (eggs/ female)	179.6 ± 65.85ab	300.67 ± 152.86ab	173.54 ± 32.14ab	449.80 ± 62.06a	94.50 ± 26.97b	5.55	4,39	0.001

The data in the table are the means \pm SE. Different letters in the same row indicate significant differences at P < 0.05.

Table 2. Effect of temperature on pupation of H. viriplaca

Temperatures (°C)	Individuals of fifth instar	Percentage that formed pupa at fifth instar (%) ^a	Percentage that formed pupa at sixth instar (%) ^a	Percentage that formed pupa at seventh instar $(\%)^a$	Ratio of diapause pupae (%)
22	52	7.69 (n = 4)	53.85 (n = 28)	34.62 (n = 18)	100 (14)
25	57	5.26 (n = 3)	50.88 (n = 29)	43.86 (n = 25)	100 (18)
28	61	11.48 $(n = 7)$	62.30 (n = 38)	19.67 (n = 12)	_
31	83	4.82 (n = 4)	85.54 (n = 71)	3.61 (n = 3)	_
34	91	2.20 (n = 2)	64.84 (n = 59)	28.57 (n = 26)	_

^aSome individuals did not pupate.

temperature (C) and effective accumulative temperature (K) values of these developmental stages and the whole generation were calculated (Table 4). The values of C and K differed among the different developmental stages. Of the larval instar stages, C was the highest for the third instar. For all developmental stages, the value of C for eggs, larvae, pupae and the pre-oviposition period was 10.53, 12.34, 5.60, and 11.47°C, respectively. For the entire generation, C was 10.01°C, and K was 767.64 degree days.

Experimental Population Life Tables

Calculation of the experimental population life tables was based on the actual data of the duration and survival rates of the different developmental stages, and female fecundity. The initial number of eggs was assumed to be 100 (Table 5). A temperature of 28°C was most suitable for survival. At this temperature, the larval survival rate, pupation rate, and adult emergence rate were higher than at the other temperatures. The population trend index (I) was higher than 1 at 22 to 34°C. At 31°C, the next generation increased 133.97 times. The intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0) and mean generation time (T) are shown in Table 6. The population parameters could not be calculated at 22 and 25°C, due to the diapause of T0. The longest generation time observed was 41.60 d at 28°C and the shortest 30.44 d at 34°C. T1 was greater than 1 at each temperature. The population had a

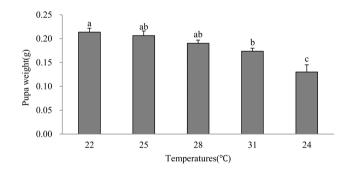


Fig. 1. Pupal weight of H. viriplaca at different temperatures. Mean \pm SE. Bars with different letters indicate significant differences at P < 0.05.

geometric base growth from 28 to 34°C. R_0 and r reached the greatest values at 31°C (49.59 and 0.12 d⁻¹, respectively).

Discussion

Insects are heterothermic poikilotherms, which are very sensitive to temperature changes. These changes may affect insect growth, development, reproduction, distribution, population dynamics, etc. (Messenger 1959, Li et al. 2017). The growth and development of insects tend to accelerate with a temperature increase in the favorable temperature range but are adversely affected when the temperature

Table 3. Effect of temperature on egg hatching and survival rate of the larval instar stages of H. viriplaca

Temperatures (°C)	Egg				Survival rate (%)	ate (%)				Emergence rate(%)
	hatchability (%)	First instar	First instar Second instar	Third instar	Third instar Fourth instar Fifth instar	Fifth instar	Sixth instar	Seventh instar	Total	
22	$81.43 \ (n = 70)$	98.25 $(n = 57)$ 100.00 $(n = 56)$	$100.00 \ (n = 56)$	98.21 (n = 56)	98.21 $(n = 56)$ 94.55 $(n = 55)$	96.15 (n = 52)	96.15 $(n = 52)$ 86.96 $(n = 46)$ 94.44 $(n = 18)$ 75.44 $(n = 43)$	94.44 (n = 18)	75.44 (<i>n</i> = 43)	32.56 $(n = 14)$
2.5	85.33 (n = 75)	98.44 (n = 64)	95.24 (n = 63)	98.33 (n = 60)	96.61 (n = 59)	100.00 (n = 57)	87.04 (n = 54)	88.00 (n = 25)	73.44 (n = 47)	38.30 (n = 18)
28	85.33 (n = 75)	98.44 (n = 64)	100.00 (n = 63)	98.41 (n = 63)	98.39 (n = 62)	93.44 (n = 61)	100.00 (n = 50)	100.00 (n = 12)	89.06 (n = 57)	87.72 (n = 50)
31	81.67 (n = 120)	88.78 (n = 98)	100.00 (n = 87)	97.70 (n = 87)	97.65 (n = 85)	93.98 (n = 83)	98.65 (n = 74)	100.00 (n = 3)	78.57 (n = 77)	98.70 (n = 76)
34	85.83 (n = 120)	90.29 (n = 103)	100.00 (n = 93)	100.00 (n = 93) $97.85 (n = 93)$	97.85 (n = 93)	95.60 (n = 91)	90.59 (n = 85)	$73.08 \ (n = 26) 69.90 \ (n = 72)$	69.90 (n = 72)	55.56 (n = 40)

range becomes unfavorable (Howe 1967, Lu et al. 2009). In this study, the developmental duration, survival rate, female fecundity, and population variables of H. viriplaca were determined at different temperatures. The results show that temperature had a significant effect on the growth and reproduction of H. viriplaca, which is consistent with the many studies on the effect of temperature on insect growth and development reporting a longer developmental duration at low temperatures and a shorter developmental duration at high temperatures (Xu et al. 2012, Oin et al. 2017). In northeastern China, H. viriplaca has two generations per year. In mid-September, the larvae inhabit the soil and overwinter as pupae. After the temperatures gradually rise during spring, the pupae continue to develop and enter the next developmental stage after termination of the diapause. In this study, the C value of the pupae was calculated as 5.6°C, and the developmental duration as 11.81-13.33 d at 28-34°C. However, at 22-25°C, which is a much higher temperature range than the developmental threshold temperature, development ceased and 100% of the larvae entered diapause. The cause of this observation is unclear. Diapause can be affected not only by the photoperiod but also by the ambient temperature. In a study of Papilio memnnon L. (Lepidoptera: Papilionidae), under the same daylength as used in our study, the percentage of diapaused larvae decreased with increasing temperature (Yi et al. 2007). At 30°C, no larvae went in diapause irrespective of daylength duration. Short daylength and low temperature benefitted diapause while long daylength and high temperature benefitted growth (Yi et al. 2007). The 12:12 (L:D) h photoperiod used in our experiment is shorter than the natural photoperiod in mid-September that the illumination time was 12 h 46 min to12 h 20 min. Therefore, the observation that pupae entered diapause at 22 and 25°C may be related to shortlength light conditions. In addition, we also observed that at each temperature female adults either deposited dozens of eggs or no eggs at all. This may be related to their migratory flight habit. Zhao et al. (2016) observed that the majority of H. viriplaca females trapped from August to September had little or no ovarian development, supporting the idea that the onset of migration is initiated by sexually immature individuals (Riley et al. 1995). The oviposition ratio of Spodoptera litura also varied greatly at different temperatures. The highest percentage of females which did not lay eggs was 41.34% at 15°C, followed by 15.39% at 34°C, indicating that both low and high temperature can have adverse effects on adult reproduction (Qin et al. 2002).

Insect ecdysis is affected by temperature. At unsuitable temperatures, the generation duration of insects will increase (Guppy 1969). At 15 and 19°C, some larvae molted six to seven times, reaching the seventh or eighth instar stage. At 29 to 34°C, only few larvae molted six times (Qin et al. 2002). In suitable habitats, larvae of the armyworm (Mythimna separate) usually reached the sixth instar stage, but when the temperature rose higher than 30°C the percentage of larvae that reached the seventh instar stage increased proportionally (Jiang et al. 1998). Cao et al. (2012) reported that at low temperatures only 18.18% of Athetis lepigone larvae reached the sixth instar stage while this number increased to 48.44% at 32°C. Kahrarian (2010) examined under laboratory conditions the larval development of H. viriplaca at 25°C. He distinguished five larval instar stages based on measurements of the head capsule width. He found that the larvae molted at least four times, up to the fifth instar stage, the majority of the larvae five to six times, reaching the sixth or seventh instar stage. The number of molts was related to temperature. At 22-25°C, the percentage of larvae that reached the sixth and seventh instar stages was less than 60% and higher than 30%, respectively. Most of the larvae molted 5 times at 31°C while more

Table 4. Effect of temperature on developmental threshold temperatures and effective accumulative temperatures of H. viriplaca

Parameters							Develo	pmental sta	ge			
	Egg	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar	Seventh instar	Larva	Pre-pupa + pupa	Pre- oviposition	Generation (egg to oviposition)
C (°C) K (degree- days)	10.53 42.9	6.59 57.48	18.41 16.3	19.66 13.67	9.75 39.99	7.85 53.26	9.51 68.45	13.57 54.95	12.34 239.68	5.6 309.19	11.47 77.72	10.01 767.64

Table 5. Effect of temperature on the experimental population life tables of H. viriplaca

Developmental stage	Number of individuals at the beginning of the different stages							
	22°C	25°C	28°C	31°C	34°C			
Egg	100.00	100.00	100.00	100.00	100.00			
First instar	81.43	85.33	85.33	81.67	85.83			
Second instar	80.00	84.00	84.00	72.50	77.50			
Third instar	80.00	80.00	84.00	72.50	77.50			
Fourth instar	78.57	78.67	82.67	70.83	77.50			
Fifth instar	74.29	76.00	81.33	69.17	75.83			
Sixth instar	71.43	76.00	76.00	65.00	72.50			
Seventh instar	27.95	40.81	18.24	2.64	23.03			
Pre-pupa + pupa	66.27	65.93	85.33	67.45	61.37			
Adult	21.58	25.25	74.85	66.58	34.10			
Female ratio	0.62	0.33	0.50	0.45	0.56			
Number of eggs laid per female	179.60	300.67	173.54	449.80	94.50			
Total eggs of next generation expected	2384.80	2530.43	6495.01	13397.43	1817.57			
Population trend index (I)	23.85	25.30	64.95	133.97	18.18			

than 90% of the larvae reached the sixth instar stage and 3.61% of the larvae reached the seventh instar stage. At 34°C, the percentage of larvae that reached the seventh instar stage increased to more than 20%. These results show that the frequency of insect molting and temperature are closely related (Cao et al. 2012). Qin et al. (2002) suggested that the increase in the number of larvae that molt at low or high temperatures might be a physiological response to adverse environmental conditions.

Insect growth and development not only require a specific temperature threshold, but also an accumulated quantity of heat to complete the life cycle (Wang et al. 2014). In this study, based upon the relationship between the developmental duration and the temperature of each developmental stage, the developmental threshold temperatures and effective accumulative temperatures were calculated. Our results show that the developmental threshold temperature and effective accumulative temperature for eggs to adult pre-oviposition of H. viriplaca were 21.76°C and 281.81 degreedays, respectively. This information could help predict and forecast the number of generations per year, the population dynamics and geographical distribution of this important insect pest in China (Cao et al. 2012). Based on the temperature data of 2014, 2015, 2016, and 2017 recorded in Changchun, north China, the effective accumulated temperatures above the developmental threshold temperatures for the second generation of H. viriplaca were 1485.55, 1535.88, 1504.22, and 1559.04 degree-days, respectively. There were 1.94, 2.00, 1.96, and 2.03 generations we could estimate by using lower thermal threshold and thermal constant in Changchun at different years. We also observed that it occurred two generations per year.

The stronger the reproductive ability of an insect species, the longer the life expectancy trend. In this study, female moths lived longer than male moths at each temperature examined. The fecundity

Table 6. Effect of temperature on the net reproductive rate (R_0) , generation time (T), intrinsic rate of increase (r), and finite rate of increase (λ) of H. viriplaca

Temperature (°C)	$R_{_{0}}$	T (d)	r (d-1)	λ (d-1)
22	-	-	-	-
25	-	-	-	-
28	21.79	41.60	0.08	1.08
31	49.59	33.82	0.12	1.12
34	4.73	30.44	0.05	1.05

of H. viriplaca females was the highest at 31°C and the longevity of the adults was the longest at 28-34°C. These results are consistent with the findings of Li et al. (2005). At different temperatures, the survival rate of H. viriplaca was different. Egg hatching ranged from 80 to 86%, irrespective of temperature. The survival rate of the larvae was the highest at 28°C, confirming that temperature has an impact on the survival rate of the larvae of H. viriplaca. The population trend index is not only an important index for forecasting population size but is also important for studying population suppression. The basic meaning of the population trend index (I) is that the size of the next generation population is a multiple of the current population size and is composed of the survival rates of each developmental stage and the fecundity of the females. When I is higher than 1, the size of the next generation is higher than that of the previous one. In contrast, when I is lower than 1, the size of the next generation will be lower than that of the previous one (Pang and Liang 1995). The intrinsic rate of increase (r) is a useful parameter describing population dynamics, which includes survival, development, and reproduction (Farhadia et al. 2011, Qin et al. 2017). In our experiment, the I value of H. viriplaca was exceeded at each temperature indicating that this insect species has a strong reproductive capacity and environmental adaptability. At the different temperatures, both I and r were the strongest at 31°C.

In this study, the developmental duration, survival rate, and population life tables of H. viriplaca at 22-34°C were studied to predict their population dynamics. Temperature changes can also have profound effects on many other aspects of the biology of insects such as body size (Atkinson 1994), immunity (Karl et al. 2011), feeding ability and feeding rate (Kingsolver and Woods 1997, Xiang et al. 2015), fitness (Berwaerts and Dyck. 2004), mating (Kuang et al. 2010), metabolism (Wang et al. 2016), and respiratory metabolism (Qian et al. 2017). In future studies, these factors should also be taken into account to more clearly compare the effects of temperature on insects. In addition to temperature there are many abiotic and biotic environmental factors that can affect the population dynamics of insects, such as host plant (Cao et al. 2012), and fertilizer (Tuan et al. 2014) and pesticide (Yu et al. 2012, Zuo et al. 2015) application. However, differences in the population dynamics of H. viriplaca exposed to these factors may differ when examined either under artificial laboratory conditions or under natural field conditions. In the future, it will be necessary to conduct more studies under field conditions to learn more about the population dynamics of H. viriplaca.

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