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The combined effects of temperature and insecticide on the fecundity of adult males and adult females of the brown planthopper *Nilaparvata lugens* Stål (Hemiptera: Delphacidae)

Yan-Li Yu, Liu-Juan Huang, Li-Ping Wang, Jin-Cai Wu*

School of Plant Protection, Yangzhou University, Yangzhou 225009, China

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ABSTRACT

Extreme temperatures are thought to be one of the main factors suppressing natural population growth of the brown planthopper *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae). In contrast, sublethal doses of some pesticides (such as triazophos) stimulate reproduction of adult males and adult females of *N. lugens*. However, the combined effects of high or low temperature and sublethal doses of pesticides on the reproduction of adult males or adult females have not been investigated. This study examined the effects of high (34 °C), typical (26 °C) and low (20 °C) temperature and the insecticide triazophos on the protein content of male accessory glands (MAGs) and adult female ovaries and on the fecundity of adult females. The study demonstrated that temperature and triazophos concentration significantly influence the protein content of MAGs and of adult female ovaries before and after mating. The protein content in MAGs before mating attained a maximum value at 26 °C (45.1 μg per adult male, grand mean of all concentrations), followed by an intermediate value of 38.0 μg at 20 °C and a minimum value of 10.4 μg at 34 °C. These results indicate that the reproduction of males is more sensitive to high temperature compared to adult females. Protein content in MAGs after mating at 26 °C remained at a maximum value (25.6 μg per adult male, grand mean of all concentrations), followed by 21.9 μg at 20 °C and a minimum value of 8.3 μg at 34 °C. The protein content of MAGs after mating decreased with increasing triazophos concentration at the three temperatures. This result indicates that treated males transferred more MAG protein to adult females through mating. For example, MAG protein after mating at 26 °C for 0, 10, 20, 40 and 80 ppm triazophos treatments decreased by 16.5, 39.2, 42.8, 53.5 and 58.2%, respectively, compared with the corresponding values before mating. The protein content of adult female ovaries both before and after mating at three temperatures for all concentrations was significantly higher than in the control. However, the increase of ovary protein (percent) both before and after mating for all concentrations attained its maximum value at 34 °C, an intermediate value at 26 °C, and its minimum value at 20 °C, compared with the control. Similarly, percent increases in the number of eggs laid for 10, 20, 40 and 80 ppm triazophos treatments at 34 °C and 20 °C (except for 80 ppm) were greater than those at 26 °C.

1. Introduction

The brown planthopper, *Nilaparvata lugens* Stål (Hemiptera: Delphacidae), belongs to a category of insect pests whose resurgence has been induced by pesticides (Ressig et al., 1982; Wang et al., 1994; Gu et al., 1996; Yin et al., 2008). The pesticide-induced resurgence of *N. lugens* has been attributed to the destruction of natural enemies (Fabellar and Heinrichs, 1986; Gao et al., 1988) and the stimulation of reproduction (Gu et al., 1984; Wang et al., 1994; Zhuang et al., 1999; Yin et al., 2008). Pesticide-induced stimulation of reproduction of pests is attributed to the hormesis effect of sublethal doses or concentrations of pesticides (Cohen, 2006). Hormesis is a dose-response phenomenon that is characterized by low-dose stimulation and high-dose inhibition (Calabrese and Baldwin, 1997). A sublethal dose/concentration is defined as inducing no apparent mortality in the experimental population, while sublethal effects are defined as effects (either physiological or behavioral) on individuals that survive exposure to a pesticide (Desneux et al., 2007). Past research on resurgence mechanisms has focused on the role of insecticides in stimulating the reproduction of adult females. Recently, we demonstrated that insecticides such as

* Corresponding author. Department of Plant Protection, Agricultural College, Yangzhou University, Yangzhou 225009, PR China. Tel.: +86 0514 7979246; fax: +86 0514 7349817.
E-mail address: jc.wu@public.yz.js.cn (J.-C. Wu).

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triazophos and deltamethrin stimulate increases in the protein content of the male accessory glands (MAGs) of *N. lugens*. These increases result in a transference effect by which the fecundity of the adult females is stimulated through mating (Wang et al., 2010; Ge et al., 2010a, 2010b). This finding represents an innovative contribution to theories concerning *N. lugens* resurgence. However, we lack information on the combined effects of temperature, especially high or low temperature, and insecticide on the protein content of MAGs and on the mating effect of insecticide-treated males on the fecundity of females at high or low temperatures. Further research is needed to address these issues.

Outbreaks of *N. lugens* have occurred in China and other countries in Asia in recent years (Gao et al., 2006; Liu and Liao, 2006). These outbreaks have been associated primarily with pesticide overuse and the resistance of the planthopper to imidacloprid. However, the life cycles and the population growth of *N. lugens* are also known to be associated with temperature (Li, 1984; Yin et al., 1984; Chen et al., 1986; Zhu et al., 1994). High temperature (above 34 °C) and low temperature (below 20 °C) have been shown to significantly reduce survival and fecundity (Zhu et al., 1994; Dai et al., 1997a). These findings suggest that further research on the combined effects of temperature and insecticide on the reproduction of adult males and adult females will be valuable for understanding the physiological and ecological mechanisms of the *N. lugens* resurgence.

The aim of the present investigation was to examine the effect of sublethal doses of triazophos (one of the insecticides that typically induce resurgence) under different temperatures, i.e., high (34 °C), low (20 °C) and suitable temperatures (26 °C), on the protein content of MAGs and of adult female ovaries and on the MAG protein transference effect on the fecundity of adult females through mating.

2. Materials and methods

2.1. Rice variety, insects and insecticides

The rice (*Oryza sativa* L.) variety Shengyou 1 (japonica rice) was used in the trials. This variety of rice was selected because it is commonly planted in Jiangsu province, China. Seeds were sown outdoors in standard rice-growing soil in cement tanks (height 60 cm, width 100 cm and length 200 cm). When seedlings reached the 6-leaf stage, they were transplanted into 16 cm diameter plastic pots, with 4 hills per pot and two plants per hill. The rice plants used in the experiments were at the tillering stage.

A laboratory strain of *N. lugens*, originally obtained from the China National Rice Research Institute (CNRRI, Hangzhou, China), was reared using susceptible variety shengyou 1 for ten generations at 26 ± 1 °C, with 70–80% humidity and a 16-h light/8-h dark photoperiod in a greenhouse at Yangzhou University.

The insecticide used in the trials was the organophosphate 20% triazophos EC (Changqin Pesticide Co. Ltd., Jiangdu, Jiangsu, China), which the insecticide was commonly used to control rice borers in China. However, its use has recently been banned due to cause the resurgence of *N. lugens*.

2.2. Experiments

2.2.1. Effect of temperature on the protein content of triazophos-treated MAGs and female ovaries

To examine the effects of a series of triazophos concentrations and temperatures on the protein content of MAGs and on the fecundity of adult females, rice plants were sprayed with 10, 20, 40 or 80 ppm of triazophos based on our previous toxicity test (Azzam et al., 2009). A total of 300 third-instar nymphs were released per pot. Foliar sprays were applied at the tillering stage using a Jacto sprayer (Maquinas Agricolas Jacto S.A., Brazil) equipped with a cone nozzle (1-mm diameter orifice, pressure 45 psi, flow rate 300 ml/min) 24 h after the insects were infested. Control plants at the same stages were sprayed with tap water and inactive compositions (emulsifier and solvent, provided by Nanjing Huiyu Agrichemistry Co. Ltd., Nanjing, Jiangsu, China) lacking insecticide. Each treatment and control was replicated five times. The treated and control plants were covered with cages (screen size: 60-mesh). The nymphs on the treated and control plants were collected when nymphs reached the fifth instar (last instar), and a single nymph was placed in a glass jar (diameter 10 cm, height 12 cm) with untreated rice plants. Emerged adult females and males were transferred to biological culture boxes at three temperatures, 20 ± 1 °C, 26 ± 1 °C and 34 ± 1 °C, representing low, suitable and high temperatures, respectively, with the same photoperiods (16L:8D) and relative humidity (75% r.h.). One adult female and one adult male were placed in a jar (diameter 6 cm, height 15 cm) containing a rice plant. The plant was changed daily. The protein contents of the MAGs and of adult female ovaries of 20 specimens per sex per replicate prior to mating and 48 h after mating was measured. Mated female is close to the male on rice plants, while unmated female is far from the male according to our observation. It has been reported that both adult females and males could mate 1 day after emergence, and mated repeatedly, the mating course of the experimental population lasted (70.38 ± 41.77) s, the percentage of successful mating was relatively higher (Dai et al., 1997b).

2.2.2. Effect of temperature on fecundity of triazophos-treated females

Other emerging adults from the above treatments and controls were used for examining the fecundity of females at three temperatures. One adult female and one adult male were placed in a glass jar (diameter 10 cm, height 12 cm) with untreated rice plants for oviposition. The number of eggs laid per female was counted under a microscope. Eggs were scraped from the leaf sheath and leaf blade using a pin. Each treatment and control was replicated twenty times (20 mating pairs).

2.3. Extraction of total protein

Protein content was measured using the method described by Li and Yu (1997) and Wang et al. (2010). The MAGs from each of the males and the ovaries from each of the females within a replicate were removed, placed in ice-cold physiological saline solution under a microscope, and washed with phosphate-buffered saline (PBS; 8 g NaCl, 0.2 g KCl, 1.44 g Na_2HPO_4 and 0.24 g KH_2PO_4 were dissolved in 800 ml distilled water, adjusted with HCl to pH 7.4 and fixed with distilled water to 1000 ml). The MAGs and ovaries were homogenized on ice, placed in iced centrifuge tubes and centrifuged at 12,000 rpm at 4 °C for 25 min. The supernatant was collected after removing the upper fat layer. Sediment in the tubes was washed with distilled water three times and centrifuged again, and the supernatant was put into the tubes.

2.4. Measurement of protein content

The procedure described in Li and Yu (1997) was followed to measure protein content with Coomassie Brilliant Blue R 250 (Shanghai Chemical Agent Co., Ltd., Shanghai, China). A standard curve was established based on a standard protein (bovine serum albumin, made at Shanghai Biochemistry Research Institute, Shanghai, China). The absorbance at 670 nm was determined using a UV755 B spectrometer (Shanghai Precision Instrument Co., Ltd., Shanghai, China). Protein content in the sample solution was calculated according to the standard curve.

2.5. Statistical analysis

Data were tested for normality and homogeneity of variance prior to statistical analysis. The data on protein content in MAGs and in female ovaries were analyzed using 3-way analysis of variance (ANOVA) (insecticide concentration, temperature and mating status). The number of eggs laid was analyzed using 2-way ANOVA (triazophos concentration and temperature). Multiple comparisons of means were performed using Fisher's Protected Least Significant Difference (PLSD) test. All analyses were conducted using the GLM procedure (SPSS Inc., 2002). The relationship between the insecticide concentration and protein content of MAGs and female ovaries was analyzed using a regression method. Likewise, a regression method was used to analyze the relationship between insecticide concentration and the number of eggs laid.

3. Results

3.1. Changes in the protein content of MAGs for triazophos-treated adults at three temperatures

ANOVA (data, Fig. 1) showed that the protein content of MAGs was significantly influenced by temperature, triazophos concentration and mating status (Table 1). Interaction effects between temperature, triazophos concentration and mating status also significantly influenced the protein content of MAGs. Before mating, the protein content of MAGs attained its maximum value at 26 °C (45.1 μg per adult male, grand mean of all concentrations), followed by an intermediate value of 38.0 μg per adult male at 20 °C and a minimum value of 10.4 μg per adult male at 34 °C. The values at 34 and 20 °C decreased by 76.9 and 15.7%, respectively, compared with the value at 26 °C. This result indicated that the reproduction of males is more sensitive to high temperature. Multiple comparisons showed that the protein content of MAGs for the 10, 20 and 40 ppm treatments at 26 °C were significantly higher than in the control and increased with triazophos concentration (Fig. 1). However, a decrease in protein content occurred at the 80 ppm treatment. The relationship between protein content and triazophos concentration was therefore described by a quadratic (parabolic) equation (Table 2). However, protein content at 20 °C decreased with triazophos concentration. Protein content for the 20 ppm treatment was significantly higher than that for the 40 and 80 ppm treatments. The value for the 80 ppm treatment was significantly lower than for the control. No significant differences were found among the 10 and 20 ppm treatments and the control. Similarly, the relationship between protein content and triazophos concentration at 20 °C was described by a parabolic equation (Table 2). The protein content of MAGs at 34 °C showed an irregular response to triazophos concentration. After mating, the protein content of MAGs at 26 °C remained the maximum value (25.6 μg per adult male, grand mean of all concentrations), followed by a value of 21.9 μg per adult male at 20 °C and a minimum value of 8.3 μg per adult male at 34 °C. The values at 34 and 20 °C decreased by 67.5 and 14.4%, respectively, compared to the value at 26 °C. The protein content of MAGs decreased with increasing triazophos concentration at three temperatures. Multiple comparisons showed that the values of protein content after mating for the 20, 40 and 80 ppm treatments at 20 and 26 °C and for the 40 and 80 ppm triazophos treatments at 34 °C were significantly lower than in the control. These results indicate that treated adult males transferred more MAG protein to adult females through mating with increasing insecticide concentration (a significant decrease after mating, compared with control males). For example, the decreases in MAG protein (percent) after mating at 26 °C for the 0, 10, 20, 40 and 80 ppm treatments were 16.5, 39.2, 42.8, 53.5 and 58.2%; these at 20 °C for the 0, 10, 20, 40 and 80 ppm treatments were 21.7, 40.4, 72.1, 37.7 and 28.4%; these at 34 °C for the 0, 10, 20, 40 and 80 ppm treatments were 15.4, 41.8, 19.8, 47.8 and 28.6%, respectively, compared with MAG protein before mating.

3.2. Changes in the protein content of adult female ovaries for triazophos-treated adults at three temperatures

ANOVA (data, Fig. 1) showed that the protein content of female ovaries was significantly influenced by temperature, triazophos concentration and mating status (Table 1). Interactions among temperature, triazophos concentration and mating status also significantly influenced the protein content of female ovaries with the exception of the interaction among triazophos and mating status. The protein contents of adult female ovaries of most treatment combinations both before and after mating at three temperatures were significantly higher than in the control. Protein content of adult females attained the maximum value at 26 °C, an intermediate value at 20 °C, and the minimum value at 34 °C. Generally, however, the maximum percent increases of ovary protein before and after mating for various triazophos concentrations were attained at 34 °C, followed by intermediate values at 26 °C and minimum values at 20 °C, compared to control. For example, the values for the 10, 20, 40 and 80 ppm treatments at 34 °C were 85.9, 107.4, 137.7 and 215.8% before mating and 53.4, 62.9, 131.2 and 186.8% after mating, respectively. Furthermore, the values obtained for these treatments at 26 °C were 30.0, 6.3, 62.4 and 79.3% before mating and 15.2, 31.3, 30.5 and 38.9% after mating, respectively. These results indicate that the rate of change of ovary protein content at a high temperature (34 °C) was greater than the corresponding rate at a suitable temperature (26 °C) or else that the insecticide treatment enhanced the resistance of the insect to high-temperature stress and amplified the beneficial effect. These results show that triazophos treatments reduced the effect of high temperature on the reproduction of females through mating. In addition, regression models provided an excellent fit to the relationships between protein content, both before and after mating, and triazophos concentration (Fig. 1) (Table 2).

3.3. Combined effects of temperature and triazophos on the fecundity of adult females

ANOVA (data, Fig. 2) showed that temperature and triazophos concentration significantly influenced the number of eggs laid ($F = 43.2$, df = 2, 210, $P = 0.0001$ for temperature; $F = 10.9$, df = 4, 210, $P = 0.0001$ for triazophos concentration). Multiple comparisons showed that the grand mean of the number of eggs laid at 26 °C was significantly higher than that observed at 34 or 20 °C. The value of the grand mean increased by 56.3 and 77.6% compared with the values observed at 34 and 20 °C, respectively, but no significant difference was found between 34 and 20 °C. The values of percentage change in ovary protein before mating for 0, 10, 20, 40 and 80 ppm triazophos at 34 °C were −67.7, −53.9, −37.0, −52.8 and −43.1%, respectively, compared with values at the same concentrations at 26 °C, these after mating were −37.9, −17.0, −23.0, +9.8 and +28.1%, respectively, indicating that treated males stimulated reproduction of adult females via mating under high temperature (34 °C). The grand means of the number of eggs laid for triazophos concentrations (except 80 ppm) at 34 and 20 °C were significantly higher than in the control. Similarly, the variation in percentages (when compared to untreated control) of the number of eggs laid for the 10, 20, 40 and 80 ppm treatments at 34 and 20 °C (except for 80 ppm at 20 °C) were greater than those at 26 °C. For example, the values at 34 and 20 °C were 52.6, 76.0, 122.2 and 31.1% and 66.8, 117.5, 137.6 and −5.3%, respectively. The values at 26 °C were 7.9, 2.9, 19.9 and 10.3% compared with the control.

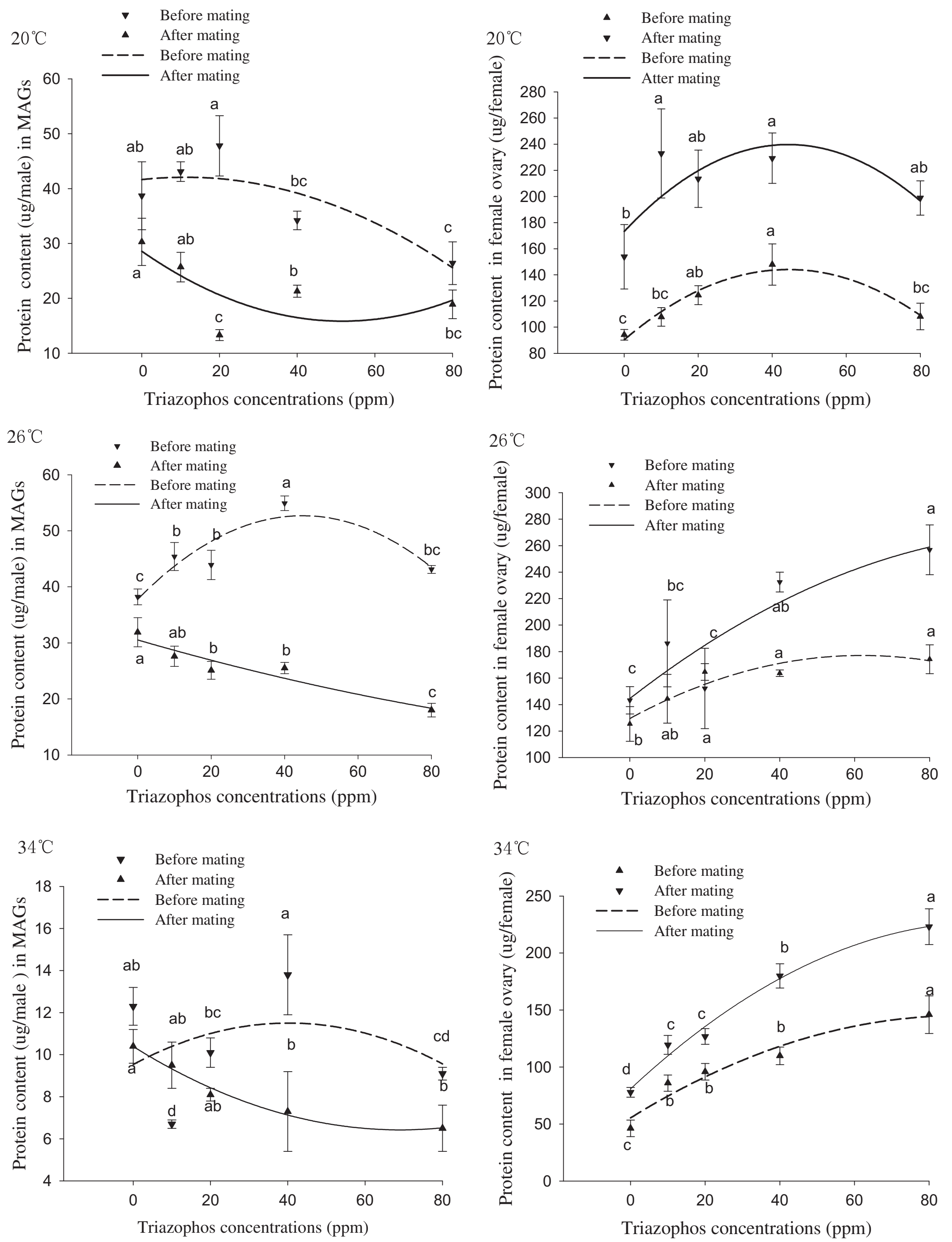

Fig. 1. Changes of protein contents in both MAGs and female ovaries of *Nilaparvata lugens* following triazophos treatment under the three temperatures conditions.

These results indicate that low (10, 20 and 40 ppm) insecticide doses enhanced the resistance of the insect to high-temperature (34 °C) or low-temperature (20 °C) stress and amplified the beneficial effects on fecundity. These findings are consistent with those found for ovary protein.

4. Discussion

In China, *N. lugens* outbreaks are associated with the number of immigration planthoppers, the planting of susceptible rice varieties, pesticide overuse and temperature (Cheng et al., 2003). In rice-producing regions of southern China, as well as the middle and lower reaches of the Yangtze River, natural population growth after immigration is suppressed by high temperatures at the middle stage (booting stage) or by low temperatures at the late stage (grain-filling stage) of rice growth (Cheng et al., 1992; Chen and Wang, 1996). In addition, *N. lugens* is a classic example of an insecticide-induced resurgent pest (Chelliah and Heinrichs, 1980; Gao et al., 1988). Therefore, the study of the combined effects of temperature and insecticide on the reproduction of *N. lugens* has

Table 1
ANOVA of data in Fig. 1.

Variance source	Df	F-value for protein content in MAGs	P-value	Df	F-value for protein content in female ovaries	P-value
Temperature (A)	2	1000.6	0.0001	2	87.3	0.0001
Triazophos concentration (B)	4	24.2	0.0001	4	64.9	0.0001
Mating status (C)	1	613.9	0.0001	1	91.1	0.0001
A × B	8	8.9	0.0001	8	10.3	0.0001
A × C	2	116.4	0.0001	2	123.8	0.0001
B × C	4	20.2	0.0001	4	1.2	0.32
A × B × C	8	17.4	0.0001	8	6.6	0.0001

Df is degree of freedom.

great significance for the understanding of outbreaks or resurgence. The present investigation demonstrated that high temperatures significantly decreased the protein content of MAGs and of female ovaries. Adult males were particularly sensitive to high temperature. However, triazophos treatment enhanced the resistance of female reproduction to high-temperature stress. This effect was a result of mating. The physiological mechanism for the enhancement may be associated with the accumulation of energy in the body of the insect following insecticide treatment. For example, triazophos and deltamethrin treatments have been shown to increase soluble sugar and fat content in third- and fifth-instar nymphs and in adults that developed from nymphs feeding on insecticide-treated rice plants (Yin et al., 2008). Physiologically, lipids and sugars are not only necessary substances for growth, development and movement of insects, they are also important elements in the composition of insect yolk (Wang, 2004). Therefore, substance or energy base of the insecticide-induced stimulation of reproduction of adult males and adult females is provided by an increase of soluble sugar and fat contents in adult body of treated *N. lugens*. In addition, it has been demonstrated that the flight capacity of insecticide-treated *N. lugens* adults is significantly enhanced, especially in adult females (Zhao et al., 2011).

More interestingly, female fecundity after the mating of triazophos-treated males and females was significantly higher than was observed after the mating of untreated males with treated females (Wang et al., 2010). These findings indicate that the reproductive effects of insecticide on males can be transferred to females through mating. Thus, triazophos-treated males may contribute to the enhancement of fecundity of treated females through mating to a greater extent than do untreated males in high temperatures. Many studies found that the number of eggs laid by

Table 2
Regression equations and R-squared values of the relationship between triazophos concentrations (X) and protein content (Y_1) in male accessory glands (MAGs) or ovarian protein content (Y_2) in adult female.

Temperature (°C)	Mating status	Regression equations	R^2 value
20	Before mating	$Y_1 = -0.035X^2 + 0.0787X + 41.62$	0.731
		$Y_2 = -0.027X^2 + 2.4286X + 90.3$	0.963
	After mating	$Y_1 = 0.0048X^2 - 0.4939X + 28.61$	0.502
		$Y_2 = -0.0338X^2 + 22.9987X + 173.29$	0.607
26	Before mating	$Y_1 = -0.0074X^2 + 0.6646X + 37.77$	0.819
		$Y_2 = -0.0123X^2 + 1.529X + 129.4$	0.898
	After mating	$Y_1 = 0.0005X^2 - 0.1914X + 30.54$	0.904
		$Y_2 = -0.0097X^2 + 2.2202X + 144.54$	0.824
34	Before mating	$Y_1 = -0.0012X^2 + 0.099X + 9.517$	0.104
		$Y_2 = -0.0115X^2 + 2.0287X + 55.379$	0.941
	After mating	$Y_1 = 0.0008X^2 - 0.116X + 10.413$	0.988
		$Y_2 = -0.0159X^2 + 3.5046X + 80.83$	0.986

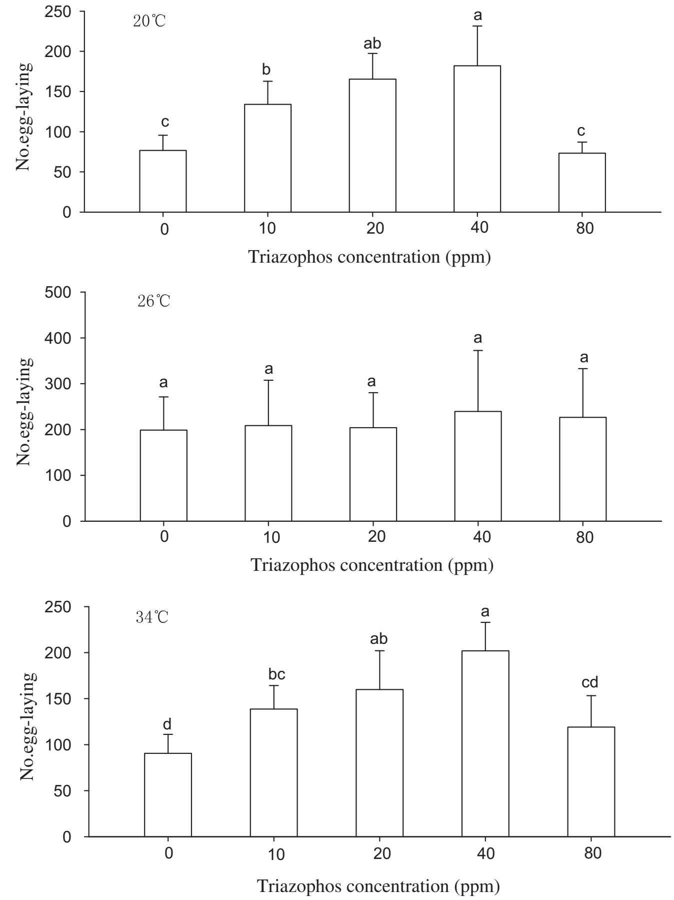

Fig. 2. The relationship between the number of eggs laid and triazophos concentrations under three temperatures.

untreated *N. lugens* females at high temperatures (over 32 °C)was significantly lower than that observed at low temperatures (20 °C) (Li, 1984; Chen et al., 1986; Zhu et al., 1994). For example, the number of eggs laid by females at 19 °C was 8.2 times greater (from 23 to 212 per female) than that observed at 34 °C (Zhu et al., 1994). Changes in resistance to stress in insecticide-treated *N. lugens* at temperatures over 34 °C, as well as changes in resistance to other stress factors, will require further investigation.

Insects are poikilothermal and their growth, development and fecundity are significantly influenced by temperature. In the middle and lower reaches of the Yangtze River in China, chemical control of *N. lugens* in rice field is mainly in the summer (high temperature reason) and the autumn (relative to low temperature). Thus the combination effects of temperature and insecticides have a significant significance for understanding of *N. lugens* resurgence and IPM. The present findings showed that percent increases in ovary protein after mating and fecundity (the number of egg laid) for triazophos-treated at 20 and 34 °C are greater than those at 26 °C, indicating that triazophos treatment enhanced the resistance of adult males or females to temperature stresses. Physiological mechanism of the enhancement may be hormesis and pesticide-mediated homeostatic modulation of sublethal doses of insecticides (Cohen, 2006). Hormesis is a dose-response phenomenon that is characterized by low-dose stimulation and high-dose inhibition (Calabrese and Baldwin, 1997). Similarly, substance or energy base of the hormesis is from an increase of soluble sugar or fat in adult body following insecticide treatment (Yin et al., 2008).

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