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EFFECTS OF HEAT SHOCK ON LIFE PARAMETERS OF *FRANKLINIELLA OCCIDENTALIS* (THYSANOPTERA: THRIPIDAE) F1 OFFSPRING

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ABSTRACT

The western flower thrips (WFT), *Frankliniella occidentali*s (Pergande) (Thysanoptera: Thripidae), an invasive insect pest in China, causes great economic losses worldwide. To understand the effects of heat shock on WFT population dynamics, we constructed life tables to quantify the effects of heat shock on the growth rate, survival, and fecundity of WFT offspring. WFT adults and 2nd instars were heat shocked at 45 °C, and the treatment was repeated after a 24-h recovery period. Heat-shocked and control insects were reared on the leaves of purple cabbage (*Brassica oleracea* L.; Brassicales: Brassicaceae), and various life-table and development parameters of their F1 offspring were evaluated. The duration of the immature period of the offspring of heat-shocked adults was not significantly shorter than that of the control, whereas the duration of the immature period of the offspring of the heat-shocked 2nd instars was longer than that of the other treatments, indicating that heat-shock of second instars slowed the development of their offspring. The preoviposition period during the adult stage and the total oviposition period of the F1 offspring of the heat-shocked adults were significantly longer than those of the control. The fecundities of the F1 offspring of the heat-shocked 2nd instars and adults were 81.8 and 70.6 eggs/female, respectively, both of which were significantly less than that of the control (149.1). The use of heated tents might be effective for the prevention and control of WFT infestations in greenhouses. Our life-table analysis of the effects of heat shock on F1 survival and reproduction provides a strong basis for future studies of thermal treatments for the control of WFT.

Key Words: age-stage reproductive value, finite rate of increase, intrinsic rate of increase, net reproduction rate, mean generation time, high temperature, two-sex life table analysis

RESUMEN

El trips occidental de flores (TOF), *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), es una plaga invasor insectil que causa grandes pérdidas económicas en todo el mundo. Para comprender el efecto de las altas temperaturas sobre la dinámica de poblaciones de TOF, hemos construido una tabla de vida para demostrar el efecto del choque térmico sobre la tasa de crecimiento, la supervivencia y fecundidad de la progenie de TOF. Los adultos y larvas de segundo estadio de TOF fueron sometidos al choque térmico a 45 °C por 2 horas y el tratamiento fue repetido después de un período de recuperación de 24 horas. Los insectos sometidos al choque y para control fueron criados sobre hojas de *Brassica oleracea* y se les evaluó el desarrollo y varios parámetros de tabla de vida de su cría F1. La duración del período de inmaduros (11.74 días) de la progenie de los adultos sometidos al choque térmico fue menor que la del grupo de control (11.86 días), mientras que la duración del período de los inmaduros de la progenie de las larvas sometidos al choque térmico fue de 12.36 días, lo que indica que choque térmico disminuyó el desarrollo de la progenie. El período de la preoviposición y de la oviposición total de la progenie de los adultos sometidos al choque térmico (3.70 y 15.67 días, respectivamente) fue significativamente más largo que los del grupo de control. La fecundidad de la progenie de las larvas y adultos sometidos al choque térmico fueron 81.76 y 70.59, respectivamente, ambos significativamente menor que la del grupo de control (149.14). El uso de tiendas de campaña con calefacción podría ser un tratamiento eficaz para la prevención y el control de las infestaciones de TOF en invernaderos. Nuestro análisis de tablas de vida con efectos del choque térmico sobre la sobrevivencia y reproducción de las progenie F1 ofrece una sólida base teórica para estudios de tratamientos térmicos para el control de TOF en el futuro.

Palabras Clave: *Frankliniella occidentalis*; alta temperatura; fluctuación de temperatura; tabla de vida; progenie

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The western flower thrips (WFT), *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), is a destructive pest of vegetables, flowers, and various crops worldwide. This pest causes direct damage by feeding and oviposition, and indirect damage by transmitting several species of destructive plant viruses, especially *Tomato spotted wilt* virus and *Impatiens necrotic spot virus* (Kirk & Terry 2003; German et al. 1992). Certain biological characteristics, such as small size, short generation time, high reproductive capacity, wide distribution range, and increasing insecticide resistance, confound efforts to control the WFT (Childers & Achor 1995). In china, the first report of WFT was in Beijing by an outbreak in 2003(Zhang et al. 2003), and then hundreds of WFT could be found in vegetables and flowers. So far, western flower thrips has been reported in some provinces in China (Zheng et al. 2007; Wu et al. 2007; Yuan et al. 2008; Liu et al. 2010; Yan et al. 2010).

In China, WFT begins to appear in the field at the end of spring, and the insect peak numbers occur from June to July. Consequently, at this stage, heat shock in glasshouses is more appropriate. High-temperatures are widely employed in glasshouses in Shandong province for preventing plant diseases and insect pests, and the temperature is usually set at 45-46 °C for 2h. Also the vents are opened slowly to ensure that the greenhouse temperature decreases slowly. In addition, previous experiments have shown that such manipulation of the temperature had little effect on the plants (Zhang et al. 2009).

The life history and occurrence regularity of WFT were affected by environmental factors, especially temperature. Temperature is an important abiotic factor that affects the distribution and abundance of organisms. In addition, temperature plays an important role in the biological functions of organisms from the molecular to ecosystem level (Hochachka & Somero 2002), and can determine the niche of a species. Sensitivity to fluctuations in temperature can cause changes in physiological, biochemical, and ecological responses. Suitable temperature ranges are necessary for insect growth and development, with excessively high or low temperatures adversely affecting the growth and development of insects. Gaum et al. (1994) found highest population growth and net reproductive rate of WFT was on 30 °C, and host plant was English cucumbers. McDonald et al. (1998) studied the development of the WFT at 6 temperatures between 10 and 35 °C, and found that the developmental rate increased linearly as rearing temperature increased.

Adaptability to temperature, especially extreme temperatures, has an important influence on the prevalence and distribution of insect populations, and is a critical factor for the reproduction and survival of insects. Heat shock stress has been shown to adversely affect the growth of insects, and induce dysplasia and other defects, which lead to diminished health, including decreased reproductive adaptation and fecundity of the subsequent generation (Yocum & Denlinger 1992). Detailed studies of *Trialeurodes vaporariorum* (Westwood), *Bemisia tabaci* (Gennadius), *Helicoverpa armigera* (Hubner), and *Liriomyza sativae* Blanchard have shown that heat shock had a significant impact on longevity, reproduction, and the sex ratio of the offspring (Cui et al. 2008; Liu et al. 2006; Hiroshi et al. 2000). A previous study of *B. tabaci* showed that heat shock reduced the prevalence of the Q biotype, altered the sex ratio, reduced the survival, delayed reproduction, and shorten the duration of the reproductive period of the F1 offspring (Zhu et al. 2010). Previous studies of *Helicoverpa armigera* have shown that heat shock reduces the longevity of both sexes, and causes male sterility (Guo et al. 2000). Although tolerance to heat shock also has been reported for WFT (McDonald et al. 1997a; McDonald et al. 1997b; Tsumuki et al. 2007), previous, the work mainly concentrated on constant temperature effects, and failed to reflect the effects of fluctuating temperatures on the population dynamics of WFT. In this study, we simulated the high temperature applied in greenhouse conditions to study the response of WFT to heat shock.

The purpose of the current study was to investigate the effects of a 45 °C heat shock applied to the WFT parental generation on the life table parameters of the F1 generation. Also, we sought to determine whether the various life stages of WFT are differentially sensitive to heat shock. Therefore, we constructed an age-stage, two-sex life table (Chi & Liu 1985; Chi 1988) of the WFT adults and 2nd instars that were heat shocked at 45 °C to demonstrate how heat shocking the parental generation affects the growth rate and fecundity of the F1 generation. Our results were expected to provide a scientific basis for the application of heat shock to control the WFT in greenhouses.

Materials and Methods

Insect Rearing and Host Plants

The WFT used in our current study were derived from specimens collected from clover plants (*Trifolium repens* L.; Fabales: Fabaceae) at the Experimental Station of Qingdao Agricultural University. The WFT colony was maintained in MGC-250BP-2 incubators (Shanghai Yiheng Instruments, China) at 55% to 60% RH and 16:8 h L:D. All of the insects were reared on purple cabbage (*Brassica oleracea* L.; Brassicales: Brassicaceae) because the heat-shock treatment caused minimal dehydration of the leaves of the plant, compared to that observed for various other host

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plants. The baseline experimental conditions were designed to simulate natural greenhouse conditions by cycling the temperature as follows: 22 °C for 4 h, 25 °C for 8 h, 28 °C for 4 h, and 25 °C for 8 h.

Effects of Heat Shock of Adults on Their F1 Offspring

To evaluate the development and survival of heat shocked WFT, we placed a number of female and male adult WFT into rearing bottles containing purple cabbages leaves. The insects were heat shocked by placing them in an incubator at 45°C for 2 h, and the treatment was repeated after a 24-h recovery period. Using a suction sampler, the surviving adults were placed into rearing bottles containing purple cabbage leaves for 24 h to allow oviposition to produce the F1 generation.

After hatching, a fine camel-hair brush was used to place each F1 larva in a 1.5-mL microcentrifuge tube (Shanghai Sangon Biotech, China) containing a 1-cm disc of purple cabbage leaf. A total of 60 first instars were studied. A hole was punched in the lid of each tube to ensure that the temperature and humidity were consistent in each tube. The opening of the tube was covered with 200 mesh nylon gauze. The lid was closed, and sealed with plastic wrap to prevent the escape of larvae. The larvae were reared under the baseline experimental conditions. Observations were recorded every 24 h, and the development and survival were calculated. Fresh cabbage discs were provided every 2 to 3 days until the adults emerged.

To determine the longevity and fecundity of the offspring of heat shocked adult WFT, pairs of newly emerged F1 male and female WFT were placed in 15-mL plastic tubes (Shanghai Sangon Biotech) containing a 1.5-cm disc of purple cabbage leaf. The tubes were placed in a light incubator under baseline conditions to allow oviposition. The cabbage discs were removed to collect the eggs, and replaced with a fresh disc daily. Dead males were replaced with new males. Fecundity and survival were calculated daily, until the death of each female, and the longevity of the male and female adults was measured. Cabbage discs with eggs were placed in a 1.5-mL microcentrifuge tube, and the tube was placed in light incubator to allow hatching. The number of nymphs was used to represent the number of F2 offspring.

Effects of Heat Shock of Second Instars on Their F1 Offspring

The parental generation larvae, prepupae, and pupae were heat shocked in an identical manner to that used for the parental generation adults. One hundred surviving 2nd instars were selected for further analysis because they exhibited lower mortality following the heat-shock treatment than the other developmental stages. The mortality of the first instar larvae was 95%, and that of the prepupae and pupae reached 100%. Surviving second instar larvae were collected, and placed in rearing bottles containing purple cabbage leaves. Sixty newly emerged adults were mated, and the development and fecundity of their F1 offspring were evaluated, as described in the above section.

Data Analysis

The data were analyzed using an age-stage, two-sex life table analysis. A one-way analysis of variance and the LSD method were performed using the SPSS, version 19.0, software (IBM, Armonk, NY, USA). Moreover, the figures were analyzed and plotted using SigmaPlot, version 12.0, software. The mean of the developmental period for each stage, the longevities of the adult males and females, the adult pre-oviposition period (APOP), the total pre-oviposition period (TPOP), and the fecundity of were calculated. The TPOP was the interval between hatching of a female and the first oviposition. The APOP was the interval between the emergence of an adult female insect and the start of its egg laying. The age-stage-specific survival rate (S_{xj}), the age-stage-specific fecundity (f_{xj}), age-specific survival rate (l_x), age-specific fecundity (m_x), age-specific maternity ($l_x m_x$), age-stage specific life expectancy (e_{xj}), and the age-stage reproductive value (v_{xj}) were calculated based on the daily observations of survival and fecundity.

The bootstrap was used to analyze the data for the population parameters of the F1 offspring of heat-shocked adult and second instars. The life table parameters that were examined included the intrinsic rate of increase (r_m), net reproduction rate (R_0), finite rate of increase (λ), and mean generation time (T). The value of r was estimated using the iterative bisection method as $\Sigma_x^{\infty} = {}_0 l_x m_x e^{-r(x+1)} = 1$, with age indexed from 0. The net reproductive rate to age x was calculated as $R0 = \Sigma_x^{\infty} = {}_0 l_x m_x$. The value of T was calculated as $T = lnRr^{-1}$, and λ was calculated as $\lambda = e^r$.

Results

Effects of Heat Shock of Adults and 2nd Instars on Developmental Stages of Their F1 Offspring

As shown in Table 1, the mean duration of egg stage of the F1 offspring of the heat shocked adults (3.18 days) was significantly longer than the control (3.02 days) but not longer than the heat shocked 2nd instars (3.12 days) ($F_{2, 177} = 3.71$, $P < 0.05$). Moreover, the mean duration of the first instars of the F1 offspring of the heat shocked 2nd instars (2.62 days) was significantly longer than both the control (2.08 days) and the F1 offspring

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TABLE 1. DURATIONS OF DEVELOPMENT OF THE IMMATURE LIFE STAGES OF THE F1 OFFSPRING OF HEAT-SHOCKED ADULT AND SECOND INSTAR LARVAE OF *FRANKLINIELLA OCCIDENTALIS*. THE INSECTS WERE HEAT SHOCKED BY PLACING THEM IN AN INCUBATOR AT 45 °C FOR 2 H, AND THE TREATMENT WAS REPEATED AFTER A 24-H RECOVERY PERIOD.

Treatment	Durations of Development of Various Stages (days)					
	Egg	First instar	Second instar	Prepupa	Pupa	Immature
Control	3.02 ± 0.13 b	2.08 ± 0.27 b	2.86 ± 0.45 ab	1.42 ± 0.54 ab	2.48 ± 0.50 a	11.86 ± 0.73 b
Heat shocked Adults	3.18 ± 0.43 a	2.04 ± 0.28 b	2.82 ± 0.48 b	1.48 ± 0.79 a	2.46 ± 0.50 a	11.74 ± 0.85 b
Heat shocked 2nd Instars	3.12 ± 0.37 ab	2.62 ± 0.49 a	3.02 ± 0.38 a	1.24 ± 0.43 b	2.38 ± 0.49 a	12.36 ± 0.72 a

Values followed by the same letter within a column are not significantly different, $P < 0.05$.

of the heat shocked adults (2.04 days) ($F_{2, 147}$ = 39.80, $P < 0.05$). Moreover, for this trend of the first instars was also the same of the overall immature stage ($F_{2, 147} = 9.12$, $P < 0.05$); thus, among the 3 treatment groups, the duration of development of the immature stage was the longest for the F1 offspring of the heat shocked 2nd instars (12.36 days).

Effects of Heat Shock of Adults and 2nd Instars on Reproduction-Related Development of Their F1 Offspring

APOP, TPOP, fecundity, and female longevity are listed in Table 2. The period between the emergence of the adult female and the first oviposition (APOP), and the period between egg hatch and the first oviposition (TPOP) of the F1 offspring of the heat shocked adults were significantly longer (3.70 and 15.67 days, respectively) than those of the control group. The APOP and TPOP of control group were not significantly different from those of F1 offspring of heat shocked 2nd instars. The fecundities of the F1 offspring of the heat shocked 2nd instars and adults (81.76 and 70.59 eggs per female, respectively) was significantly less than that of the control (149.14 eggs) ($F_{2, 88} = 129.527$, $P < 0.05$). The female longevities of the F1 offspring of the heat shocked 2nd instars and adults (24.52 and 23.04 days, respectively) were significantly shorter than that of the control (35.6 days) ($F_{2, 83}$ = 106.680, $P < 0.05$).

Effects of Heat Shock of Adults and 2nd Instars on the Population Dynamics of the F1

The population-related parameters, R_0, r_m, T and λ, were calculated for the age-stage, two-sex life table analysis, and are listed in Table 3. The mean and standard error of the various population parameters were estimated using the bootstrap method. The R_0 of the control (74.59) was significantly higher than that of the F1 offspring of the heat shocked 2nd instars (39.62) and heat shocked adults (31.77). The r_m was greater than zero for all of the groups, indicating positive growth for the 3 populations. The r_m of the control group (0.1806 day^{-1}) was larger than those of the F1 offspring of heat-shocked adults and 2nd instars, but the r_m was not significantly different between the F1 offspring of the heat-shocked 2nd instars (0.1551 day^{-1}) and heat-shocked adults (0.1443 day^{-1}). The value of T was not significantly different between the control, F1 offspring of the heat-shocked adults, and the F1 offspring of the heat-shocked 2nd instars (23.82, 23.88, 23.66 days). The λ of the control (1.1985 day^{-1}) was significantly greater than those of the F1 offspring of the heat-shocked adults and the F1 offspring of the heat-shocked 2nd instars, and the differ-

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TABLE 2. FEMALE REPRODUCTION PARAMETERS OF THE F1 OFFSPRING OF HEAT-SHOCKED ADULTS AND SECOND INSTARS OF *FRANKLINIELLA OCCIDENTALIS*. THE INSECTS WERE HEAT SHOCKED BY PLACING THEM IN AN INCUBATOR AT 45 °C FOR 2 H, AND THE TREATMENT WAS REPEATED AFTER A 24-H RECOVERY PERIOD.

	Reproduction Parameters			
Treatment	Adult pre-oviposition period (days)	Total pre-oviposition period (days)	Fecundity (F) (eggs/female)	Female longevity (days)
Control	2.47 ± 0.57 b	14.37 ± 0.96 b	149.13 ± 27.85 a	35.60 ± 4.90 a
Heat shocked Adults	3.70 ± 1.44 a	15.67 ± 1.59 a	70.59 ± 21.91 b	23.04 ± 2.30 b
Heat shocked 2nd Instars	2.55 ± 1.27 b	14.86 ± 1.60 b	81.76 ± 19.83 b	24.52 ± 2.91 b

APOP, Adult pre-oviposition period; TPOP, Total pre-oviposition period
Values followed by the same letter within a column are not significantly different, $P < 0.05$.

ence in λ between of the F1 offspring of the heat-shocked adults and the F1 offspring of the heat-shocked 2nd instars was not significant.

Effects of Heat Shock of Adults and 2nd Instars on the Survival of Their F1 Offspring

The value of S_{xj} represents the probability that a newly laid egg will survive to age x and stage j. For the purpose of our analysis, the survival rate of eggs was considered as 100% because of the difficulty in assessing the mortality of embryos in eggs. The survival rates of the F1 larvae (l1 and l2) of the heat-shocked adults (Fig. 1, middle panel) and heat-shocked 2nd instars (Fig. 1, lower panel) were less than that of F1 control larvae (upper panel). The survival rates of females in the F1 offspring of the control, heat-shocked adults, and heat-shocked 2nd instars were 50%, 45%, and 48.3%, respectively, and the survival rates of the F1 male offspring were 33%, 25%, and 20%, respectively. Because of the variability in the development rates of the egg, first instar, second instar, pre-pupa, and pupa stages, significant overlaps among the survival curves of the various stages were observed (Fig. 1).

The l_x curve represents the age-specific survival of all of the individuals in each treatment, irrespective of the stage of development (Fig. 2), and, therefore the l_x curve is a simplified version of the S_{xj} curve (Fig. 1). Age-stage specific life expectancy, e_{xj}, is an estimate of the time that an individual of age x and stage j is expected to live. Thus, the life expectancy of a newly laid WFT egg in the control group is 36.01 days with life expectancy decreasing with age. The e_{xj} values of the F1 offspring of the heat-shocked adults and heat-shocked 2nd instars were 22.27 and 24.41 days, respectively, both of which were less than that of the control group (36.01 days) (Fig. 3). The e_{xj} of females was longer than that of males in all of the treatment groups.

Effects of Heat Shock of Adults and 2nd Instars on the Reproduction of Their F1 Offspring

The value of f_x represents the mean number of fertile eggs produced by a female adult at age x. The value of m_x represents the fecundity of the total population at age x. When only a portion of the population has reached the adult stage, the value of f_x is higher than that of m_x. When all of the individuals in the population have emerged as adults, the f_x value is equal to that of m_x, and the graphs of f_x and m_x, will overlap as shown in Fig. 2. The peaks of f_x, m_x, and $l_x m_x$ were higher in the control than in F1 offspring of either the heat shocked adults or the heat shocked 2nd instars.

TABLE 3. POPULATION PARAMETERS OF THE F1 OFFSPRING OF HEAT-SHOCKED ADULTS AND SECOND INSTARS OF *FRANKLINIELLA OCCIDENTALIS*. THE INSECTS WERE HEAT SHOCKED BY PLACING THEM IN AN INCUBATOR AT 45 °C FOR 2 H, AND THE TREATMENT WAS REPEATED AFTER A 24-H RECOVERY PERIOD.

	Population Parameters			
Treatment	Net reproduction rate (R_0) (daughters/female)	Intrinsic rate of increase (r_m) (progeny/day)	Average generation period (T) (days)	Finite rate of natural increase (λ)
Control	74.59 ± 9.9667 a	0.1806 ± 0.0067 a	23.82 ± 0.2551 a	1.1985 ± 0.0080 a
Heat shocked Adults	31.77 ± 4.9298 b	0.1443 ± 0.0072 b	23.88 ± 0.2262 a	1.1553 ± 0.0083 b
Heat shocked 2nd Instars	39.62 ± 5.5205 b	0.1551 ± 0.0068 b	23.66 ± 0.2827 a	1.1678 ± 0.0079 b

Values followed by the same letter within a column are not significantly different, $P < 0.05$.

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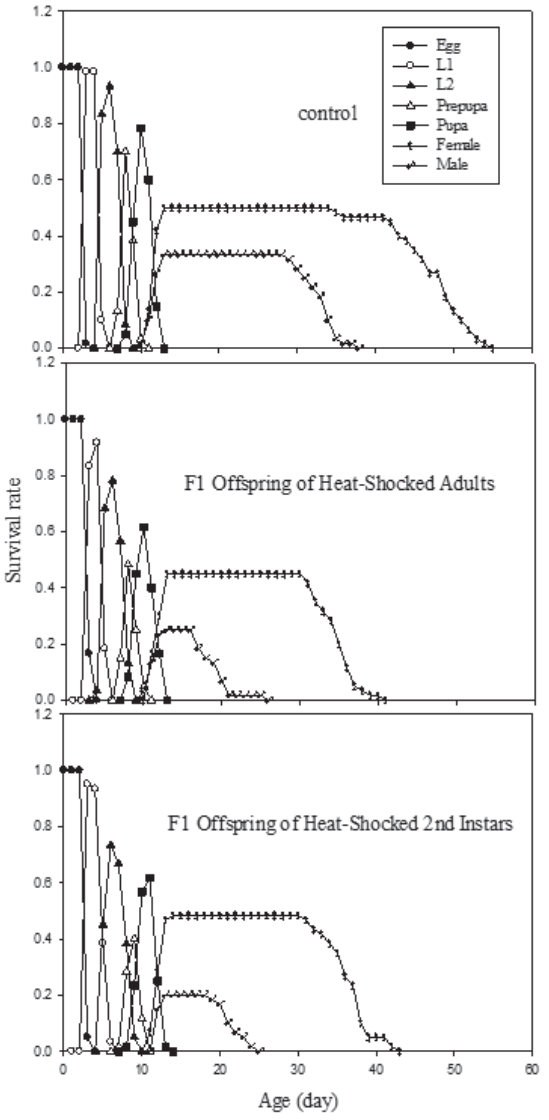


Fig. 1. Age-stage specific survival rate (S_{xj}) of the F1 offspring of *Frankliniella occidentalis* heat shocked twice at 45 °C for 2 h.

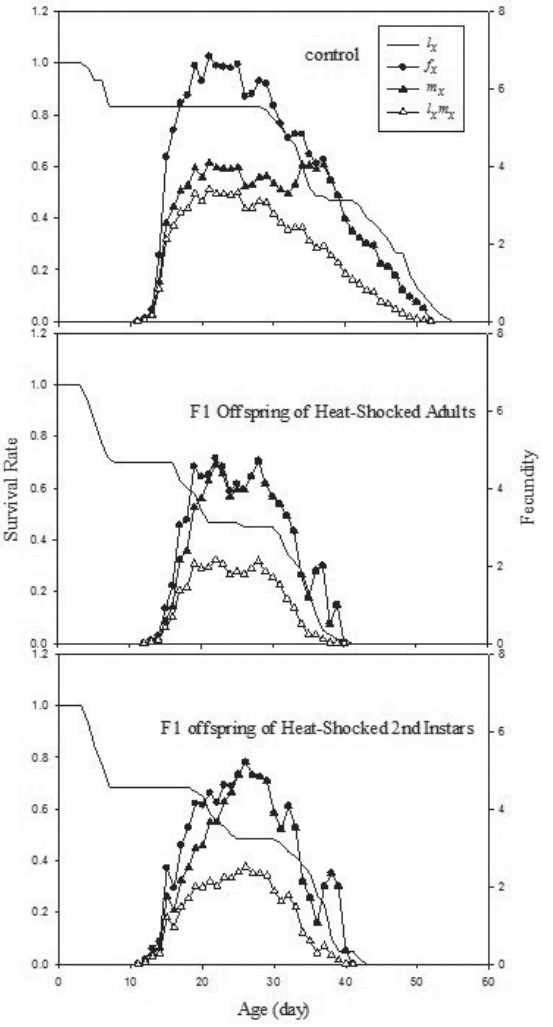


Fig. 2. Age specific survival rate (l_x), age-stage specific fecundity (f_x), age-specific fecundity (m_x), and age specific maternity ($l_x m_x$) of the F1 offspring of *Frankliniella occidentalis* heat shocked twice at 45 °C for 2 h.

The value of v_{xj} represents the contribution of an individual at age x and stage j to the growth of the population. The reproductive value significantly increases when female adults emerge. In the control, the peak v_{xj} value occurred at age 19 days (Fig. 4). This result implies that, compared to those at other ages, 19-day-old females made the highest contribution to the population (37.1). The peak v_{xj} values for the F1 female offspring of the heat-shocked adults and 2nd instars were 17 and 20 days, respectively. When older adult females cease to produce offspring, the value of v_{xj} becomes zero. In our study, the v_{xj} reached zero on day 52, day 40, and day 42 for the control, F1 female offspring of heat-shocked adults, and F1 female offspring of heat-shocked 2nd instars, respectively.

Discussion

Temperature is a very important factor that affects the population growth of WFT. In nature, insects experience fluctuating daily temperatures; therefore, data measured at a constant temperature cannot precisely reflect the changes that occur in populations exposed to variations in temperature under natural conditions, as in the field (Lamb 1961; Hagstrum & Hagstrum 1970). Moreover, Michels & Behle (1989) and Davis et

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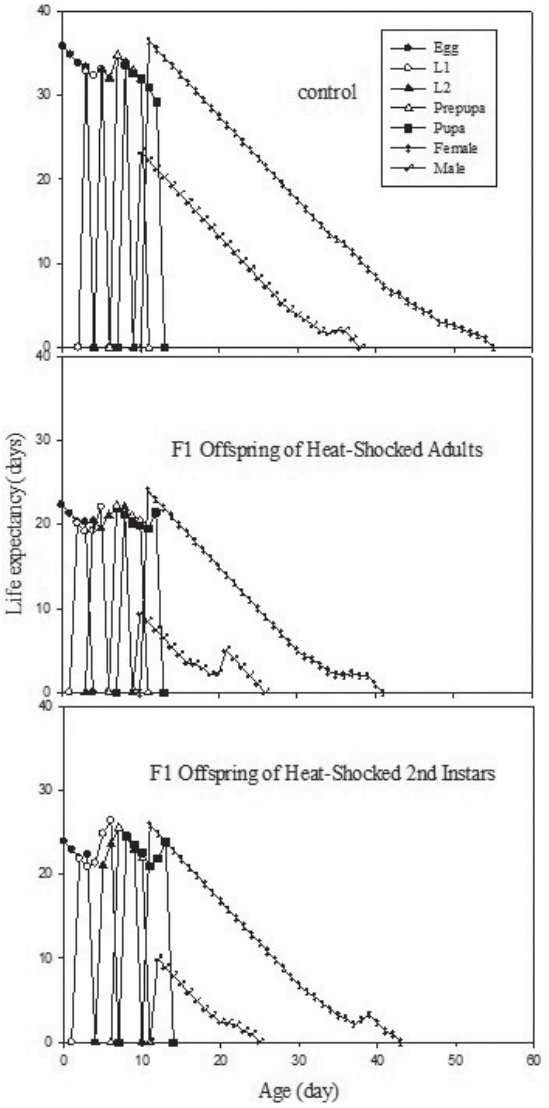


Fig. 3. Age-stage specific life expectancy (e_{xj}) of the F1 offspring of *Frankliniella occidentalis* heat shocked twice at 45 °C for 2 h.

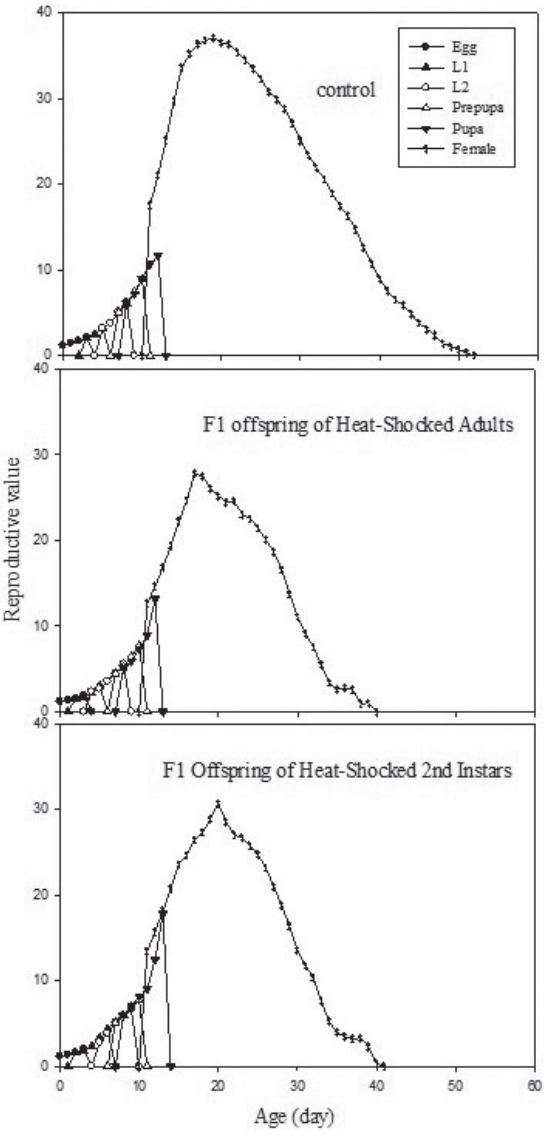


Fig. 4. Age-stage reproductive value (v_{xj}) of the F1 offspring of *Frankliniella occidentalis* heat shocked twice at 45 °C for 2 h.

al. (2006) found relative to the constant temperature, fluctuating temperatures can enhance the development and reproduction of aphids, and increase their longevity.

Therefore, we surmised that fluctuating temperature will not have the same effect on the western flower thrips? Our results indicated that under fluctuating temperatures with an average of 25 °C, the fecundity of per female was 149.1, which is higher than the fecundity of 125.2 per female reported by Wang et al. (2011) at a constant temperature of 25 °C. Similar phenomena were found in wheat aphids. For example, under naturally fluctuating temperatures with an average of 13.5 °C, the offspring number of *Rhopalosiphum padi* was 2.5 per female daily (Markkula & Mylymaki 1963), even more than the number of offspring (2.1) at a constant temperature of 15 °C (Tanaka 1957). Because simulated fluctuating temperatures more closely resemble the field environment, studies of the influence of fluctuating temperature might identify ecological and biological factors that contribute to the development, reproduction, survival, and longevity of WFT.

Insects are sensitive to high temperatures, because their bodies are small and their body tem-

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peratures vary with those of the environment. High temperature stress can result in water loss, disruption of membrane structure, and protein denaturation, and also restrict various enzyme-catalyzed reactions (Yoder et al. 2009). In addition, heat shock stress damages neurons, leading to the failure of nervous system functions. These injuries are reflected as reduced survival and reproductive capacity of insects (Yocum et al. 1994; Vollmer et al. 2004). Even if a species does survive heat shock stress, its fitness and adaptability will be affected (Yocum & Denlinger 1992; Scott et al. 1997; Rinehart et al. 2000). Our study showed that, the offspring of the heat-shocked 2nd instars and adults exhibited a prolonged adult and total pre-oviposition periods (adults: 3.70 and 15.67 days; 2nd instars: 2.55 and 14.86 days) than control (2.47 and 14.37 days) (Table 2), and their F1 offspring displayed significantly reduced longevity and fecundity, with the greatest reductions occurring in the offspring of heat-shocked adults. Our results also support several previous reports. When the Q-biotype of *B. tabaci* was exposed to 44 °C for 1 h, fecundity and longevity of both females and males were significantly reduced (77.2 eggs, 14.5 days, and 10.2 days, respectively) than those observed in the control at 26 °C *(100.1* eggs, 20.4 days, and 18.2 days, respectively) (Zhu et al. 2010). *Sarcophaga crassipalpi* (Macquarte) adults that were exposed to 45 °C for 1 h as pupa did not display a reduction in survival. However, although the males mated, they were unable to inseminate females, resulting in reduced fecundity (Denlinger & Yocum 1998). Neven et al. (2014) found that treatment of walnuts in air at > 45 °C for a short period of time (min) is effective in killing diapausing 5th instar codling moth [*Cydia pomonella* (L.); Tortricidae] larvae. So we surmised that most of the energy of parental females was used to resist heat shock stress, or stress induced physiological changes and heat shock proteins. Therefore, oviposition was largely restricted, and the pre-oviposition period of F1 progeny was prolonged, which affected the fecundity of the F1 offspring.

The two-sex life table has been widely applied to insects and mites, such as the aphid, *Therioaphis maculate* (Buckton; Hemiptera: Aphididae), the predatory gall midge *Feltiella acarisuga* (Vallot) (Diptera: Cecidomyiidae), *Tetranychus urticae* (Koch) (Acari: Tetranychidae), and *Chrysoperla externa* (Hagen) (Neuroptera: Chrysopidae) (Mo & Liu 2006; Kavousi et al. 2009; Schneider et al. 2009). The important life table parameters, r_m and R_0 measure population growth. The parameter, r_m, is primarily dependent on generation survival and fecundity, which involve the progress of development and other factors. Our data indicate that the r_m (0.1806 day^{-1}) and R_0 (74.59) of the control group were greater than those of the other treatment groups, demonstrating the rapid development of this pest under greenhouse conditions. However, the r_m and R_0 of the heat-shocked adults (0.1443 day^{-1} and 31.77, respectively) were smaller than those of the heat-shocked 2nd instars (0.1551 day^{-1} and 39.62, respectively). Based on the above phenomena, so we hypothesize that the heat shock directly caused physiological damage to the adult female's mature sexual organs, and then affected egg formation; or that the adult ovaries had been destroyed under the high temperature stress, and parental generation produces a high proportion of deformed eggs, which caused the hatching rate to decrease. However, during the larval stage in which energy accumulation occurs; much energy was consumed to cope with the high temperature stress, and when subjected to heat shock, the surviving larvae might develop resistance to it. Besides, the ovaries of heat-shocked 2nd instars have not developed, so heat shock has little effect on their sexual organs. In any case, the specific reasons for the observed reductions in the r_m and R_0 parameters need to be further researched.

Understanding the effects of heat shock stress on WFT survival and reproduction may provide insight into the effectiveness of brief heat shocks as a means of controlling WFT populations, and may indicate whether thermal treatments might be efficacious approaches for WFT control. Our data contribute insights into the effect of heat shock stress on the development and reproduction of WFT.

Because of widespread insecticide resistance, the western flower thrips indirectly causes environmental pollution. The application of high-temperature stress in glasshouses may be developed into an environmentally benign physical control method for the WFT. The results of some field experiments showed that heat-shock treatments of 42 °C to 46 °C for 2 h can decrease the population density of adult WFTs by 84.5% (Zhang et al. 2009). In greenhouses with 89%~ 100% RH, heat-shock treatments of 40 °C to 48 °C for 2 h have been used to effectively control whiteflies by inducing significant mortality in both adults (90.1% to 96.3%) and larvae (23.6% to 47.3%) (Wang & Fan 2003).

However, we need to pay attention to 2 points in the application of heat shock, i.e, (1) avoid the development of thermal tolerance by the WFT, and (2) make certain that the crop plants that must be protected from WFT are able to tolerate heat shock treatments. Our study was limited in its focus on the effects of heat shock on life table parameters; and, therefore, further research is needed to explore the heat tolerance mechanism of WFT, including the heat shock-induced changes at the physiological and molecular levels. For instance, heat shock can reduce the activity of AchE, and impede normal nerve transmission (Greenspan et al. 1980); also, thermal tolerance

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in insects is associated with stress-induced proteins, particularly heat-shock proteins (Guedes et al. 2008; Elekonich 2009; Kalosaka et al. 2009). Thus it would be helpful to gain an understanding of the mechanism of action of heat shock stress on WFT, and thereby provide an in-depth scientific basis for the prevention of WFT in glasshouses by this physical method.

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