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Source: Florida Entomologist, 97(2) : 504-510

Published By: Florida Entomological Society

URL: <https://doi.org/10.1653/024.097.0222>

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EFFECTS OF EXPOSURE TO HIGH TEMPERATURE ON *FRANKLINIELLA OCCIDENTALIS* (THYSANOPTERA: THRIPIDAE), UNDER ARRHENOTOKY AND SEXUAL REPRODUCTION CONDITIONS

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ABSTRACT

Temperature plays a critical role in the population dynamics of insects. This study was designed to estimate the effect of exposure of *Frankliniella occidentalis* (Pergande) in the parental generation to 41 °C for various durations (2, 6, 12, 24, and 36 h) on their reproduction and on the first generation progeny. The data indicated that, under both the arrhenotoky and the sexual reproduction pattern, the longevity of adult females and the numbers of larvae and adults in the first generation decreased significantly as the period of exposure to heat increased. When adults were exposed at least 24 hours under arrhenotoky and at least 6 hours under sexual reproduction, the total survival rate from larva to adult in the first progeny generation was significantly lower compared with control groups whose parents had not been exposed to heat treatments. Furthermore, high-temperature exposure of sexually reproducing adults significantly decreased the proportion of females in the first progeny generation: The sex ratio (♀:♂) changed from 2.69:1 in the control to 2.31:1 after 2 h to 2.14:1 after 36 h of heat treatment. These results support the hypothesis that heat stress could be of use in the control of the western flower thrips.

Key Words: heat shock, longevity, offspring, population, western flower thrips

RESUMEN

La temperatura juega un papel crítico en la dinámica poblacional de los insectos. Este estudio fue diseñado para estimar el efecto sobre la reproducción de la generación parental de *Frankliniella occidentalis* (Pergande) expuesta a 41 °C para varias horas de duración (2, 6, 12, 24, y 36 h) y sobre la primera generación de su progenie. Los datos indicaron que, tanto en el patrón de arrhenotoquia y el patrón de reproducción sexual, la longevidad de las hembras adultas y el número de larvas y adultos de la primera generación se redujo significativamente con el incremento en el período de exposición al calor. Cuando los adultos fueron expuestos por lo menos 24 horas bajo el patrón de arrhenotoquia y por lo menos 6 horas bajo el patrón la reproducción sexual, la tasa de sobrevivencia total de larva a adulto en la primera generación de la progenie fue significativamente menor en comparación con los grupos de control, cuyos parientes no fueron expuestos a tratamientos térmicos. Además, se disminuyó significativamente la proporción de hembras en la primera generación de descendientes en los adultos que se reproducen sexualmente expuestos a altas temperaturas: La proporción de sexos (♀:♂) cambió de 2.69:1 en el control de 2.31:1 después de 2 horas y 2.14:1 después de 36 horas del tratamiento térmico. Estos resultados apoyan la hipótesis de que el estrés por calor puede ser útil en el control del trips occidental de las flores.

Palabras Clave: golpe de calor, longevidad, descendencia, población, trips occidental de las flores

Temperature is one of the most important abiotic factors that can strongly influence survival, development, behavior, life history, fitness, distribution, and species richness of insects (Rogers & Randolph 2000). In the favorable range of temperatures, insect growth, development, foraging, courtship, mating, and reproduction will be

accelerated by increased environmental temperatures (Coyne et al. 1983; Porter et al. 1991). Currently, many believe that global climate warming will result in the exposure of insects to higher-temperature environments. Higher environmental temperatures may increasingly impact pests in glasshouses and in the field with respect to

survival rate, growth rate, reproductive capacity, etc. (Musolin 2007). Exposure of insects to high or extremely high temperatures for various periods can result in thermal damage and mortality. Thus, pest managers can use heat stress, which in some instances is considered an environmentally friendly method, to control insect pests (Fields 1992; Mourier & Poulsen 2000). However, the individuals of the pests' population that survive through periods of exposure to sublethal high temperatures may produce offspring with increased thermotolerance. The success and failure of high-temperature pest control would depend largely on the reproductive adaptation to exposure to sublethal high temperatures.

Induction of thermotolerance may also induce tolerance to other forms of stress, and vice versa; for example, Patil et al. (1996) showed that the development of resistance to insecticides in *Anopheles stephensi* Liston (Diptera: Culicidae) and *Aedes aegypti* L. (Diptera: Culicidae) induced thermotolerance and that insecticide resistance could also be induced by the development of thermotolerance. Knowledge of the relationship between high temperature and pest performance may contribute to understanding how pests adapt to temperature and to identifying ways to postpone the development of thermotolerance in pest populations.

The western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), is a polyphagous and globally distributed thrips species that has caused significant damage to crops by feeding and oviposition, as well as by vectoring plant viruses (such as tomato spotted wilt virus, etc.), especially during the past 30 years. The chlorophyll and nutrients in the leaves of *Phaseolus vulgaris* L. decreased with the western flower thrips feeding on (Cong et al. 2013). TSWV (Tomato spotted wilt virus) has already been detected in Beijing diffused by western flower thrips, it has caused serious damage to the vegetables and flowers with the virus continue spreading (Li 2013). This species is difficult to control because of its rapid reproduction, small size, and resistance to major insecticides. In addition, the western flower thrips have 2 reproductive modes: arrhenotoky and sexual reproduction, which are thought to contribute to its rapid establishment, development of insecticide resistance, and adaptation to other unfavorable conditions.

Previous studies revealed that temperature can impact developmental time, sex ratio, and population growth of western flower thrips (Li et al. 2007). Nevertheless, few studies have investigated the reproductive adaptability of western flower thrips to high temperature. Our preliminary experiments showed that adults were able to survive under high temperatures, with a 90% survival rate when they were exposed to 41 °C for 12 h (unpublished data), and no significantly

negative impact of temperatures below 41 °C was observed.

The purpose of this study was to explore the relationship between fecundity of western flower thrips and high temperature and to determine the longevity of parental female adults as well as the survival rate from larva to adult and the sex ratio in the first progeny generation after high-temperature treatment of the parents. Results were expected to elucidate the mechanism of adaptation of western flower thrips to a high-temperature environment and to help forecast spread and outbreaks as well as further develop integrated control of western flower thrips.

MATERIALS AND METHODS

Insects and Host Plants

Western flower thrips used in this study were originally collected from clover (*Trifolium repens* L.) at the Experimental Station of Qingdao Agricultural University. The colony was maintained on purple cabbage (*Brassica oleracea* L.) plants in separate greenhouses under constant conditions (25 ± 2 °C, 50-60% RH, and a photoperiod of 16:8 h L:D).

Effects of Exposure to High Temperature on the Female Adult under Arrhenotoky Conditions

Frequently, 41 °C is a high temperature that is observed in our greenhouses. During the summer, this high temperature may occur for 2 to 6 h on any given day and it is harmless to the crop. Hence, we selected exposure times of 2 and 6 h, as well as 12, 24, and 36 h 1) examine how long thrips can resist an exposure to 41 °C; 2) determine whether a dynamic change in thermotolerance occurs within one day; and 3) generate reference data for future experiments that will investigate heat stress responses induced by 36 h exposures to 41 °C.

Female adults within one day of emergence were collected in rearing bottles, which were placed in an incubator (RXZ, Jiangnan Instrument Factory, Ningbo, China) at 41 °C for 2, 6, 12, 24, and 36 h, respectively. Subsequently, these female adults were divided into groups of 20. Each group was placed in a 100 mL centrifuge tube and held in another incubator at 25 °C, 50-60% RH, and a photoperiod of 16:8 h L:D. Every day, a fresh piece of purple cabbage leaf was inserted into each centrifuge tube, and the old leaf with thrips eggs was transferred to a Petri dish. The number of hatched larvae was recorded every day, and these larvae were then held in a rearing bottle. The parental females were held until all had died, and the first generation progeny was monitored until no larvae hatched and no adult emergence occurred for 3 days. Each treatment

was replicated 3 times with 3 groups of 20 females per replicate. The thrips in the control were held at 25 °C, 50-60% RH, and a photoperiod of 16:8 h L:D.

Effects of Exposure to High Temperature on the Female Adult under Sexual Reproduction Conditions

The methods used in this experiment were essentially the same as in the above experiment, but they differed in that (i) both female and male adults within one day of emergence were exposed to the high temperature and (ii) 20 females and 20 males were assembled in each 100 mL centrifuge tube. Furthermore, (iii) when the adults of the first generation progeny emerged, the sex ratio (♀:♂) was determined.

Statistical Analysis

Longevity, numbers of larvae and adults produced to form the first progeny generation, and the survival rate (from larva to adult) and the sex ratio (♀:♂) of the first progeny generation were recorded and calculated with EXCEL (Microsoft Office Excel 2003). The data from the treatments and the control were analyzed by one-way ANOVA and Duncan's new multiple range method (DPS v7.05).

RESULTS

Effects of Different Hours of Exposure to 41 °C on the Longevity of Adult Females

Under arrhenotoky conditions, the longevity of adult females of the parental generation exposed to 41 °C was shortened significantly from 34.65 days in the control to 17.67 days after a 36 h heat shock ($F_{(5, 12)} = 117.34$, $P = 0.0001$) (Fig. 1). Similarly, under sexual reproduction conditions, the longevity of adult females was shortened significantly from 30.28 days in the control to 18.40 days after a 36 h heat shock ($F_{(5, 12)} = 26.32$, $P = 0.0001$). Under both conditions, there was no significant difference between longevity in the 2 h treatment and the control.

The longevity of parental adult females differed between the 2 reproductive modes under control conditions and after short heat shock treatments (Fig. 1). At 25 °C (control) and after an exposure to 41 °C for 2 h, the longevity of adult females under arrhenotoky was significantly longer than that under sexual reproduction (control: $F_{(1, 4)} = 25.3$, $P < 0.01$; 2 h exposure: $F_{(1, 4)} = 7.74$, $P < 0.05$). When the exposure to 41 °C was 6 h or longer, the longevity of adult females did not differ between the 2 reproductive modes.

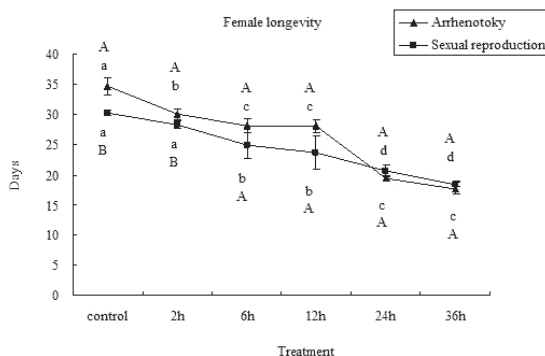


Fig. 1. Effects of different hours of exposure to 41 °C on the longevity of western flower thrips adult females (parent generation) under arrhenotoky and sexual reproduction conditions. Temperature in the control was 25 °C. DPS v7.05 program was used to analyze the data. The different lower case letters next to the broken line represent significant differences between various durations of exposure to 41 °C under the same reproductive modes at $P = 0.05$; the different upper case letters next to the lower case letters represent significant differences between asexual and sexual reproductive modes at the same exposure durations at $P = 0.05$.

Effects of Different Hours of Exposure of Parents to 41 °C on the Numbers of Larvae and Adults in the First Progeny Generation

Exposure to 41 °C for increasing numbers of hours progressively reduced the numbers of larvae (Fig. 2) and adults (Fig. 3) in the first progeny generation. With an increasing duration of exposure to 41 °C, the numbers of larvae in the first progeny generation declined significantly compared with the control (arrhenotoky: $F_{(5, 12)} = 116.70$, $P = 0.0001$; sexual reproduction: $F_{(5, 12)} = 38.64$, $P = 0.0001$). However, under the arrhenotoky condition, these numbers were not significantly different between 2, 6, and 12 h or between 24 and 36 h of exposure. Under the sexual reproduction condition, the changes in numbers of progeny larvae in response to increasing durations of heat exposure were similar to those under the arrhenotoky condition.

The numbers of first progeny generation larvae differed between the 2 reproductive modes (Fig. 2). At the control temperature of 25 °C ($F_{(1, 4)} = 292.42$, $P < 0.01$) and after exposure to 41 °C for up to 12 h, the quantity of first progeny generation larvae was significantly higher under arrhenotoky than under sexual reproduction (2 h: $F_{(1, 4)} = 35.15$, $P < 0.01$; 6 h: $F_{(1, 4)} = 38.31$, $P < 0.01$; 12 h: $F_{(1, 4)} = 49.72$, $P < 0.01$). In contrast, when the exposure time was 24 h or longer, no difference between the 2 reproductive modes was observed.

The numbers of adult progeny in the first progeny generation (Fig. 3) in response to heat treatments showed similar trends to those of the

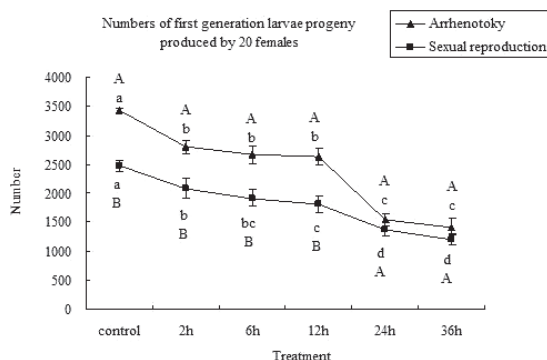


Fig. 2. Effects of different hours of exposure to 41 °C on the numbers of larvae in the first progeny generation of western flower thrips produced by 20 females under arrhenotoky and sexual reproduction conditions. Temperature in the control was 25 °C. DPS v7.05 program was used to analyze the data. The different lower case letters next to the broken line represent significant differences between various durations of exposure to 41 °C under the same reproductive modes at $P = 0.05$; the different upper case letters next to the lower case letters represent significant differences between asexual and sexual reproductive modes at the same exposure durations at $P = 0.05$.

larvae. Under the arrhenotoky condition, the numbers of adults in the first progeny generation were reduced from 2,483 in the control to 929 in the 36 h treatment, and the difference between treatments and the control was highly significant

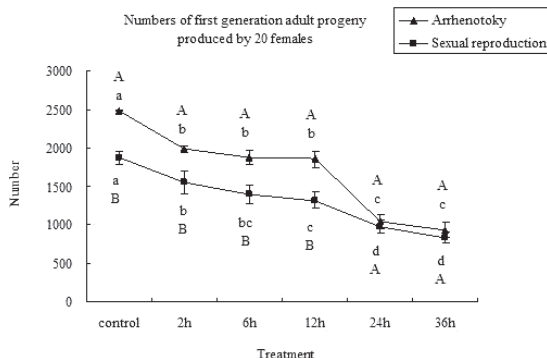


Fig. 3. Effects of different hours of exposure to 41 °C on the numbers of adults in the first generation of western flower thrips progeny produced by 20 females under arrhenotoky and sexual reproduction conditions. Temperature in the control was 25 °C. DPS v7.05 program was used to analyze the data. The different lower case letters next to the broken line represent significant differences between various durations of exposure to 41 °C under the same reproductive modes at $P = 0.05$; the different upper case letters next to the lower case letters represent significant differences between asexual and sexual reproductive modes at the same exposure durations at $P = 0.05$.

($F_{(5, 12)} = 160.26, P = 0.0001$). Under the sexual reproduction condition, the numbers of adults in the first progeny generation were reduced from 1,877 in the control to 835 in the 36 h treatment, and the difference between treatments and the control was highly significant ($F_{(5, 12)} = 38.70, P = 0.0001$).

The numbers of first progeny generation adults in the controls and in response to heat shock treatments differed between the 2 reproductive modes (Fig. 3). At 25 °C and after exposure to 41 °C for up to 12 h, the quantity of first progeny generation adults under arrhenotoky was significantly higher than that under sexual reproduction (25 °C: $F_{(1, 4)} = 163.6, P < 0.01$; 2 h: $F_{(1, 4)} = 22.73, P < 0.01$; 6 h: $F_{(1, 4)} = 33.94, P < 0.01$; 12 h: $F_{(1, 4)} = 40.92, P < 0.01$). After heat exposure for 24 and 36 h, however, no difference in numbers of progeny was seen between arrhenotoky and sexual reproduction.

Effects of Different Hours of Exposure of Parents to 41 °C on Survival Rates in the First Progeny Generation

Compared with the control, the female adults exposed to high temperature produced first progeny generations with slightly lower survival rates (from larvae to adults) (Fig. 4). Under the arrhenotoky condition, no significant decline in the survival rate of the progeny occurred after exposure of the parental generation to 41 °C for up to 12 h, but after exposure for 24 and 36 h, the decline was

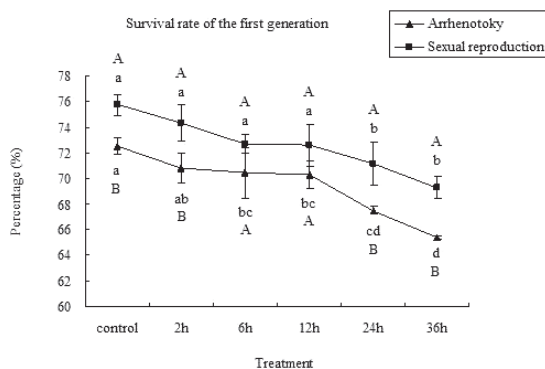


Fig. 4. Effects of different hours of exposure to 41 °C on the survival rates from larva to adult in the first progeny generation of western flower thrips produced by 20 females under arrhenotoky and sexual reproduction conditions. Temperature in the control was 25 °C. DPS v7.05 program was used to analyze the data. The different lower case letters next to the broken line represent significant differences between various durations of exposure to 41 °C under the same reproductive modes at $P = 0.05$; the different upper case letters next to the lower case letters represent significant differences between asexual and sexual reproductive modes at the same exposure durations at $P = 0.05$.

significant ($F_{(5,12)} = 12.50, P = 0.0002$). Under the sexual reproduction condition, a significant decline in the survival rate of the progeny was found after at least 6 h of exposure ($F_{(5,12)} = 13.05, P = 0.0002$).

When parental adults were maintained at 25 °C (control) or exposed to 41 °C for 2 h, the survival rates of the first progeny generation under arrhenotoky were significantly lower than those under sexual reproduction (25 °C: $F_{(1,4)} = 27.93, P < 0.01$; 2 h: $F_{(1,4)} = 11.6, P < 0.05$). After 6 and 12 h of heat treatment, there were no significant differences between the 2 reproductive modes. When the heat treatment was extended to 24 and 36 h, the survival rates of the first progeny generation under arrhenotoky were significantly lower than those under sexual reproduction (24 h: $F_{(1,4)} = 13.37, P < 0.05$; 36 h: $F_{(1,4)} = 55.22, P < 0.01$).

Effects of Different Hours of Exposure to 41 °C of Females and Males on the Sex Ratio (♀:♂) of their First Progeny Generation

The sex ratio (under the sexual reproduction condition) proved to be significantly shifted in favor of males at all durations of exposure of the adults to 41 °C ($F_{(5,12)} = 104.67, P = 0.0001$) (Fig. 5). The percentage of females was reduced by about 13% at 2 h of exposure of the parents to about 20% at 36 h compared with the control.

DISCUSSION

When temperature exceeds the favorable temperature range of an insect species, it will cause death, and even if a species does survive expo-

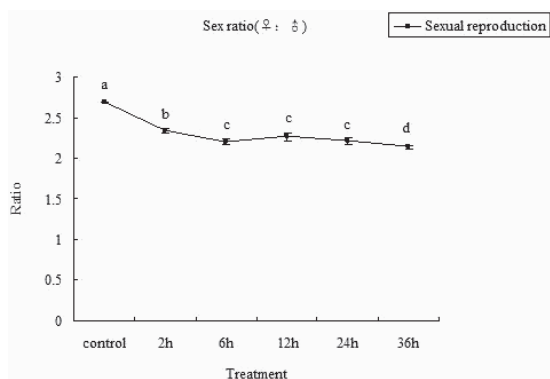


Fig. 5. Effects of different hours of exposure to 41 °C on the sex ratio (female: male) in the first progeny generation of western flower thrips produced by 20 females under sexual reproduction conditions. Temperature in the control was 25 °C. DPS v7.05 program was used to analyze the data. The different lower case letters next to the broken line represent significant differences between various durations of exposure to 41 °C under the sexual reproduction mode at $P = 0.05$.

sure to extremely high temperature, its fitness will be affected (Yocum & Denlinger 1992; Scott et al. 1997; Rinehart et al. 2000). Our results indicated that there was no immediate influence on the survival rate of female western flower thrips exposed to 41 °C for different durations. However, the longevity of surviving females exposed to 41 °C for various durations was significantly shorter than that of females maintained at the control temperature (25 °C). Our findings support several previous reports. For instance, the longevity of *Ophraella communa* LeSage (Coleoptera: Chrysomelidae) was significantly shortened by exposure to 44 °C (Chen 2012). Similarly, the longevity of Q-biotype adults of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), when exposed for 1 h to 44 °C, was 14.5 days, i.e., shorter than 20.4 days under the normal temperature of 26 °C (Zhu et al. 2010). The reason for this phenomenon might be that much energy was consumed to cope with the high-temperature stress and that unfavorable physiological changes took place in the insects under high temperature.

Our results showed that a high temperature also significantly impacts the fecundity of the western flower thrips, especially with exposures of at least 24 h. When adults were exposed to 41 °C for 24 and 36 h under arrhenotoky and sexual reproduction conditions, the numbers of the first progeny generation larvae and adults were reduced by more than one half. These results are consistent with findings involving other insect species. The mean number of eggs of a single female of *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) declined from 62.4 to 1.5 when she was exposed to the range of 37-43 °C for 1 h, and oviposition activity ceased after exposure to 45 °C for 1 h (Cui et al. 2008). *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) is incapable of oviposition after exposure to 50 °C for 39 min (Mahroof et al. 2005), and such exposure curtails the longevity of the female. So we summarize that most of the energy of exposed females was used to resist high-temperature stress, to survive, or to respond with stress-induced physiological changes. Therefore, oviposition was largely restricted, which, in turn, reduced the population. Another possibility is that the parental generation produced a high proportion of deformed eggs under high-temperature stress, which caused the hatching rate to decrease.

High-temperature stress is disadvantageous to the parental generation, but can this damage be passed on to the offspring? In this study, we determined 2 indexes: survival rate (from larva to adult) and sex ratio of the first offspring of parents that were exposed to high temperatures. Our results indicated that there was no significant effect in the first progeny generation on the survival rate (from larva to adult), when the parental generation under arrhenotoky conditions was

exposed to 41 °C for 12 h or less. This is similar to findings involving *B. tabaci* Q-biotype by Zhu et al. (2010). However, when the western flower thrips were exposed to 41 °C for 24 h or longer, the survival rate in the first progeny generation decreased significantly. Also, under sexual reproduction conditions, the survival rate of this thrips species from larva to adult declined significantly when parents were exposed 6 h or more to 41 °C. In the cases of other species, high-temperature exposure had an adverse impact on the survival rate of the first progeny generation of *Agasicles hygrophila* Selman & Vogt (Coleoptera: Chrysomelidae) (Zhao et al. 2009). With increasing durations of parental exposure, the total survival rate from egg to adult of the first progeny generation of *B. tabaci* Q-biotype decreased from 71.3% to 31.3% (Cui et al. 2011). How many generations will be affected after the parental generation was exposed to high temperature? This question is a key point for pest control and needs to be further researched.

Another index that we determined is the effect on the sex ratio. Because the western flower thrips has 2 reproductive modes, arrhenotoky and sexual reproduction, the sex ratio of the first progeny generation was determined only for sexual reproduction. The impact of high-temperature exposure of the parents on the first progeny generation varies with different insect species. Short-term high-temperature exposure had no significant influence on the sex ratio of *B. tabaci* Q-biotype (Zhu et al. 2010). However, the results from the present study showed that the sex ratio of the first progeny generation of western flower thrips significantly decreased as the duration of the parents' exposure to 41 °C increased. Female offspring of western flower thrips only occurs under sexual reproduction, so reduction in fertilization causes the sex ratio to decrease. When adults were exposed to 41 °C for a sufficient time period, the reproductive systems of some adults possibility were damaged, which can cause infertility. In this case, under the sexual reproduction condition, the offspring was actually produced by arrhenotoky, which led to more male offspring. We can move forward a step to imagine what will happen in the second progeny generation. We predict that, with more male offspring in the first progeny generation, more mating opportunities will be available for females of the first progeny generation, and the sex ratio in the population will gradually stabilize in the coming generations.

Our results indicated that under different reproductive modes, female longevity and fecundity are affected differently by heat shock. At 25 °C, the longevity of female adults and the quantity of first progeny generation larvae and adults under arrhenotoky were significant higher than those under sexual reproduction, but the survival rates of the first progeny generation under arrhenotoky

were significantly lower than those under sexual reproduction. When thrips were exposed to 41 °C, with extension of the exposure duration, these differences gradually disappeared. Although arrhenotoky generated more offspring than sexual reproduction when the parental generation was exposed to no or relatively short (2 to 12 h) heat shock treatments, all of this offspring was male and only played the mating role in the population. Differently, the offspring under sexual reproduction consisted of many female individuals and exhibited higher survival rates than the offspring produced under arrhenotoky. When heat shock duration was extended to 24 and 36 h, western flower thrips favors to choose sexual reproduction to produce more female offsprings for population development of progeny.

Because the widespread insecticide resistance of the western flower thrips indirectly causes environmental pollution, high-temperature stress in glasshouses may offer an environmentally friendly way to control this insect. It is important, however, that control methods involving heat shock avoid 2 possible scenarios: (i) inducing the development of thermotolerance and (ii) causing harm to the vegetables being produced in glasshouses. Our data contribute insight into the effect of heat stress on the reproduction of western flower thrips. On the basis of these finding, we expect to test the effect of heat stress in practice, to investigate the physiological and molecular changes that occur under heat stress, and to determine how these changes affect thrips populations.

ACKNOWLEDGMENTS

This study was funded by the National Natural Science Foundation of China (NSFC) (31372003) and the Taishan Scholarship Construction Engineering Special Fund.

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