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RESEARCH

Increased Survival and Prolonged Longevity Mainly Contribute to the Temperature-Adaptive Evolutionary Strategy in Invasive *Bemisia tabaci* (Hemiptera: Aleyrodidae) Middle East Asia Minor 1

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ABSTRACT. With increasing global climate change, analyses of stress-inducing conditions have important significance in ecological adaptation and the biological distribution of species. To reveal the difference in temperature-adaptive strategy between Turpan and Beijing populations of *Bemisia tabaci* (Gennadius) Middle East Asia Minor 1 (MEAM1) under high-temperature stress conditions, we compared thermal tolerance and life history traits between Beijing and Turpan populations of MEAM1 after exposure to different heat shock treatments for different times. The experimental design reflected the nature of heat stress conditions suffered by MEAM1. The results showed that eggs, red-eyed pupae, and adults of the Turpan population were more heat tolerant than those of the Beijing population under the same stress conditions. Additionally, it was found that longevity and F1 adult survival rate were significantly higher in the Turpan population than in the Beijing population after heat shock stress, but egg number and F1 female ratio were not significantly different between Turpan population and Beijing population. Overall, it was suggested that heat tolerance and longevity traits were the most relevant for climate characteristics and not reproductive traits, and improved heat tolerance and prolonged longevity were important adaptive strategies that helped MEAM1 to survive in harsh high-temperature conditions such as Turpan arid desert climate. The present results provided further insight into the modes of heat tolerance and the ways in which survival and longevity traits respond to environmental selection pressures.

Key Words: geographical population analysis, heat tolerance, longevity, survival, temperature-adaptive evolution

With increasing global climate change, analyses of stress-inducing conditions are a major focus of studies that relate to ecological adaptation and the biological distribution of species (Bale et al. 2002). The adaptive genetic changes that occur during stress tolerance mainly depend on the environmental conditions faced by organisms (Sisodia and Singh 2010). High temperatures are one of main selection pressures encountered by organisms; this is especially the case for ectothermic insects. Insects can suffer thermal damages at a wide range of nonlethal elevated temperatures. These damages may manifest during later developmental stages, which results in reduced survival and fitness (Denlinger and Yocum 1998).

A comparison of geographically distinct populations of the same species is one of the leading strategies for studying an insect's thermal adaptation ability (Griffiths et al. 2005, Sørensen et al. 2005, Arthur et al. 2008, Sgrò et al. 2010). Different populations may have different geographic origins or other habitat properties; they also often experience different selection pressures and exhibit large differences in resistance to thermal stress (Endler 1977, Krebs and Loeschcke 1995). *Drosophila* species show latitudinal clines in heat resistance (reviewed in Hoffmann et al. 2004, Hoffmann and Week 2007), and they can be used to examine the action of climate selection on heat tolerance (Sisodia and Singh 2010). Geographical variations in heat tolerance are at least partly due to the result of genetic variation (De Barro et al. 2011). Our present results showed that heat tolerance variation occurred in the sweetpotato whitefly *Bemisia tabaci* (Gennadius) from the two different geographical regions of Turpan and Beijing. The results at least contributed to the genetic variation because *B. tabaci* from

different geographical regions had complex genetic variation (Boykin et al. 2007; Chu et al. 2007, 2011).

Studies regarding geographical variations in heat tolerance have mainly focused on the model species, *Drosophila*. It remains unknown whether geographical variations in thermal tolerance caused by adaptive evolution occur in smaller insects like whiteflies. Small insects have a limited ability to buffer thermal changes due to their large surface area-to-volume ratio, which prevents the utilization of evaporation as a cooling mechanism (Prange 1996). Additionally, small insects have limited mobility during their immature developmental stages (Grill 1990). Therefore, a comparison of heat tolerance among geographically distinct populations of small insects was necessary to further our understanding of ecological adaptation and the biological distribution of species.

The sweetpotato whitefly, *B. tabaci* (Hemiptera: Aleyrodidae) Middle East Asia Minor 1 (MEAM1), has emerged as one of the most serious agricultural pests in the world. For example, in Beijing and Turpan Xinjiang province, China, MEAM1 had caused great losses to vegetables and cottons, respectively, and the damage was up to 70% losses (Lu and Zhang 2000). MEAM1 has incited one of the major global invasion events and has a wide distribution range (De Barro et al. 2011). Although the heat resistance of *B. tabaci* may be one of the potential mechanisms underlying its invasive traits (Cui et al. 2008, Lü and Wan 2008, Wan et al. 2009, Yu et al. 2012), it is not clear whether differential heat tolerance occurs as different populations adapt to different geographic environments or how it evolves. A small body size, high heat resistance, a large number of invasive traits, and a wide

distribution range make MEAM1 a promising model system to aid our understanding of the thermal tolerance evolution mechanisms of geographically distinct populations of nonmodel species. Turpan (Xinjiang, China) has a unique temperate continental arid desert climate with bright sunshine, high temperatures, large difference in temperature between day and night, low level of precipitation, and powerful winds. According to unpublished data, the maximum temperature of Turpan reached 49.6°C in the summer, and the average maximum temperature was above 38°C from June to August. There were more than 100 d in which the daily maximum temperature was above 35°C and 35–40 d in which the daily maximum temperature was above 40°C. However, Beijing has a typical warm-temperate semihumid continental monsoon climate. Beijing is strictly according with the lunar calendar of solar terms transform, with four climate distinct seasons such as winter cold and summer heat. According to unpublished data, the average maximum temperature was ~26°C from June to August, with a small difference in temperature between day and night and high level of precipitation. Therefore, a study of the Turpan area, with its specific climate characteristics, will help us to understand the mechanism of temperature-adaptive evolution in MEAM1. To achieve this understanding, we will compare the thermal tolerance of Turpan population to Beijing population.

In the present study, it is hypothesized that Turpan MEAM1 is better adapted to deal with heat stress compared with Beijing MEAM1. We compared survival, longevity, and reproduction between Beijing and Turpan populations of MEAM1 eggs, pupae, and adults under heat shock conditions over a wide range of elevated temperatures. The aim was to reveal the difference in temperature-adaptive strategy between Turpan and Beijing populations of MEAM1 under high-temperature stress conditions.

Materials and Methods

Insects and Host Plants

Populations of MEAM1 of ~200 red-eyed nymphs were collected from Beijing and Turpan in the Xinjiang province of China in September 2009. The MEAM1 colonies were reared on cotton plants, *Gossypium hirsutum* (L.) (var. Simian No. 3), in the greenhouse at 22–28°C, 50–60% relative humidity (RH), and a photoperiod of 14:10 (L:D) h. The plants were individually grown in pots (9 cm in diameter) under the same conditions as whiteflies. Both populations of whiteflies were maintained under greenhouse culture for six generations before being used to measure the following traits.

Effects of Heat Shock on Egg Hatch Rate, Nymph Emergence, and Adult Survival of Beijing and Turpan Populations of MEAM1

1 Egg Hatch Rate. The temperature tolerance test was conducted using Materials and Methods described previously (Cui et al. 2008). Cotton plants that were ~30 cm in height were selected, and one group comprised four cotton plants in one cage with ~200 whiteflies. The whiteflies were removed after 24 h, and the eggs were counted under a stereomicroscope. The cotton plants with eggs were heat shocked at each of the five temperatures (37, 39, 41, 43, and 45 ± 0.2°C) in climatic incubators (MHT350, Sanyo Electric Co., Ltd., Osaka, Japan) for 1, 2, 4, and 6 h. The temperature and treatment durations were selected based on our preliminary experiments (Cui et al. 2008), which showed that these treatments were sufficient to cause changes in the whiteflies. After the treatments, the plants were placed at 26 ± 0.5°C, 60% RH, and a photoperiod of 14:10 (L:D) h. The hatched eggs were counted after 4 d. The eggs were continuously examined every 2 d until no eggs had hatched for four successive days. Plants with eggs maintained at 26°C were used as untreated controls. Five replicates were performed for each treatment.

Nymph Pupation Rate. We placed ~200 whiteflies on cotton plants in one cage for 24 h, and then put the plants at 26 ± 0.5°C, 60% RH, and a photoperiod of 14:10 (L:D) h conditions until the collection of

nymphs. Leaves with at least 50 red-eyed nymphs were collected, and the other instars (including eggs and larvae) were removed under a stereomicroscope. The red-eyed nymphs on every leaf were then counted, and the nymph-containing leaves were placed in 9-cm-diameter Petri dishes containing filter paper to provide moisture. They were then heat shocked at each of the five temperatures and treatments as described in Egg Hatch Rate. After the treatments, the leaves were placed at 26 ± 0.5°C, 60% RH, and a photoperiod of 14:10 (L:D) h. The pupated nymphs were counted after 24 h. The nymphs were continuously examined every 24 h until no adults emerged. Leaves with red-eyed nymphs maintained at 26°C were used as untreated controls. Five replicates were performed for each treatment.

Adult Survival Rate. Bowler and Terblanche (2008) observed that adults of different ages respond differently to temperature exposure; thus, we standardized the ages of the flies by using only newly emerged whitefly adults that were less than 3 h old. At least 50 adults were assayed. A single adult was placed in a 0.2-ml polymerase chain reaction (PCR) tube and heat shocked at each of the five temperatures and treatments as described in Egg Hatch Rate, and the analysis was conducted on unsexed batches of adults. After the treatments, the whiteflies were placed at 26°C for 1 h to allow the adults to recover, and the number of whiteflies that had recovered was recorded. The adults were considered dead if all the appendages did not move after probing with a brush. Adults maintained at 26°C were used as untreated controls. Five replicates were performed for each treatment.

Effects of Heat Shock on Reproduction of Beijing and Turpan Populations of MEAM1

Egg Number. The egg deposition test was conducted using Materials and Methods described previously (Cui et al. 2008). Newly emerged adults of the Beijing and Turpan populations of MEAM1 were collected and sexed under a stereomicroscope. A single female and male adult were placed in a 0.2-ml PCR tube and were heat shocked at each of the five temperatures (37, 39, 41, 43, and 45 ± 0.2°C) in climatic incubators for 1 h. The egg deposition of the surviving adults was further examined in constant environment chambers at 26°C, 60% RH, and a photoperiod of 14:10 (L:D) h. Each pair of adult female and male whiteflies was confined on the lower leaf surface of a cotton plant using a leaf clip-on cage (Zang et al. 2005). Live whiteflies inside the clip-on cages were transferred to another new leaf every 2 d. The leaves with whitefly eggs were cut from the plant after the whiteflies were transferred to a new leaf, and the whitefly eggs were counted under a stereomicroscope. The process was repeated until the females died. A new male was added if the previous one died during the experiment. Females that died within 24 h or produced no eggs were excluded from the analysis. Adults maintained at 26°C were used as untreated controls. Five replicates were performed for each treatment.

F1 Female Ratio and Survival Rate of F1 Adults. Newly emerged adults of the Beijing and Turpan populations of MEAM1 were collected, and at least 50 adults were assayed. The temperature treatments were performed as described in Egg Number. After the treatments, the whitefly adults were placed in one cage with cotton plants and allowed to lay eggs for 24 h at 26°C, 60% RH, and a photoperiod of 14:10 (L:D) h; after this period, the adults were removed. The plants with eggs were placed in constant environment chambers. After the F1 adults emerged, the F1 female adults were counted. After heat shock at 37, 39, 41, 43, and 45 ± 0.2°C for 1 h with a 1-h recovery period, the F1 adult survival rate was examined. Samples maintained at 26°C were used as untreated controls. Five replicates were performed for each treatment.

Lifespan. Newly emerged adults of the Beijing and Turpan populations of MEAM1 were collected and sexed under a stereomicroscope following separation into female and male groups. A single adult was placed in a 0.2-ml PCR tube. The temperature treatments were performed as described in Egg Number. The surviving adults

of each sex were further examined in constant environment chambers. During each treatment, each adult female and adult male whitefly was confined on the lower leaf surface of a cotton plant using a leaf clip-on cage (Zang et al. 2005). Each clip-on cage contained of 10 whiteflies of the same sex. Survival was checked every 2 d until all the whiteflies were dead. Adults maintained at 26°C were used as untreated controls. Five replicates were performed for each treatment and each gender.

Statistical Analysis

Statistical analyses were conducted using the SPSS package (version 13). Before all statistical analyses, the data were examined for assumptions of normality using the Kolmogorov–Smirnov test, and the data of survival rate and female ratio were log transformed for statistics. Data on the egg hatch rate, nymph pupation rate, and adult survival rate with different temperature and time treatments were analyzed by the least significant difference (LSD) test after one-way analysis of variance (ANOVA), with temperature and time as a factor. The egg number, F1 female ratio, survival rate of F1 adult, and lifespan were analyzed by the LSD test after one-way ANOVA, with a 1-h temperature exposure as a factor. Comparisons of the data between Beijing and Turpan population were made using an independent t-test, and the data were egg hatch rate, nymph pupation rate, adult survival rate, egg number, and F1 female ratio after a same temperature and time treatment. The generalized linear model (GLM) for the F1 female ratio and survival was done on Excel. The results were expressed as the means \pm standard errors (mean \pm SEM). The differences were considered significant when the P values were < 0.05 .

Results

Effects of Heat Shock on Egg Hatch Rate, Nymph Emergence, and Adult Survival of the Beijing and Turpan Populations of MEAM1

Egg hatch rate, nymph pupation ratio, and adult survival ratio of MEAM1 from Beijing and Turpan population were significantly affected after different temperature and time treatments (egg hatch

rate: Beijing, $F_{(20, 104)} = 157.046$, $P < 0.001$; Turpan, $F_{(20, 104)} = 231.213$, $P < 0.001$; nymph pupation ratio: Beijing, $F_{(20, 104)} = 85.611$, $P < 0.001$; Turpan, $F_{(20, 104)} = 260.163$, $P < 0.001$; survival ratio: Beijing, $F_{(20, 104)} = 306.578$, $P < 0.001$; Turpan, $F_{(20, 104)} = 129.462$, $P < 0.001$; Table 1). The Turpan population had a higher egg hatch rate, nymph pupation ratio, and adult survival ratio than those of Beijing after certain temperature and time treatments (egg hatch rate: 43°C 4–6 h and 45°C 1–2, 6 h; nymph pupation ratio: 41°C 4–6 h; 43°C 1–6 h; 45°C 2, 6 h; adult survival ratio: 37°C 6 h, 39°C 6 h, 41°C 4 h, 43°C 2–4 h, 45°C 1–6 h; $P < 0.05$), respectively (Table 1).

Effects of Heat Shock on Reproduction in Beijing and Turpan Populations of MEAM1

There was a significant difference in the F1 female ratio at different exposure temperatures in both the Beijing and Turpan populations (Beijing: $F_{(5, 29)} = 36.766$, $P < 0.001$; Turpan: $F_{(5, 29)} = 38.675$, $P < 0.001$). Additionally, we did not detect a difference between the Beijing and Turpan populations at any certain temperature ($P > 0.05$; Table 2). Temperatures and populations had a significant interaction on F1 adult survival rate ($F_{(5, 59)} = 122.655$, $P < 0.001$). At 41–45°C, F1 adults of the Turpan population had a higher survival rate than that of the Beijing population ($P < 0.001$; Table 2). The Turpan population had a longer longevity than the Beijing population at 39–43°C for 1 h ($P < 0.05$; Table 2). In addition, the GLMs for F1 female ratio and adult survival rate from Beijing population and Turpan population was $Y = 4.55x - 160.1$ ($R^2 = 0.940$) and $Y = 4.617x - 166.6$ ($R^2 = 0.977$), respectively (Fig. 1).

Discussion

In the present study, we compared the thermal tolerance and life history traits of Beijing and Turpan populations of MEAM1 after different heat shock treatments for different exposure times. The experimental design reflected the natural heat stress conditions encountered by MEAM1, and the present results revealed the different temperature adaptive strategy between Beijing and Turpan populations under increasing global climate change conditions. We found an increased

Table 1. Mean (\pm SEM) egg hatching rate, nymph pupation, rate and adult survival rate of Beijing and Turpan *B. tabaci* MEAM1 under different treatment temperatures and times

Temperature (°C)	Time (h)	Egg hatch rate (%)		Nymph pupation rate (%)		Adult survival rate (%)	
		Beijing	Turpan	Beijing	Turpan	Beijing	Turpan
37	1	93.78 \pm 1.24abA	92.06 \pm 2.25bA	93.43 \pm 0.47aA	94.11 \pm 0.80bA	97.21 \pm 1.50aA	98.94 \pm 0.43aA
	2	93.19 \pm 0.87bA	90.30 \pm 0.59bA	92.18 \pm 0.60aA	93.76 \pm 0.90bA	96.47 \pm 1.00aA	96.77 \pm 1.24aA
	4	71.90 \pm 2.12dA	78.21 \pm 1.77dA	75.58 \pm 1.60bA	77.73 \pm 1.11dA	51.86 \pm 3.47cA	57.02 \pm 3.51cA
39	6	61.35 \pm 1.80eA	63.98 \pm 1.19eA	52.81 \pm 7.40cA	65.41 \pm 0.83gA	10.65 \pm 1.33eB	18.60 \pm 3.00fA
	1	92.22 \pm 1.00bA	93.02 \pm 0.72bA	91.86 \pm 1.00aA	92.81 \pm 0.49bA	95.95 \pm 1.50aA	96.34 \pm 0.67aA
	2	86.62 \pm 2.10cA	85.38 \pm 1.15cA	84.44 \pm 0.93bA	85.03 \pm 1.06cA	76.96 \pm 1.88bA	86.17 \pm 3.71aA
41	4	72.88 \pm 1.48dA	76.12 \pm 1.37dA	67.00 \pm 1.04bA	70.12 \pm 1.97fA	19.24 \pm 1.46eA	29.01 \pm 7.34eA
	6	65.78 \pm 1.22eA	65.25 \pm 1.29deA	54.52 \pm 1.49cA	52.80 \pm 2.14iA	4.41 \pm 0.34eB	14.03 \pm 1.71fA
	1	85.93 \pm 0.86cA	83.80 \pm 1.36cA	80.35 \pm 0.82bA	82.09 \pm 0.66cA	91.40 \pm 4.42aA	94.23 \pm 1.57aA
43	2	73.804 \pm 0.83dA	77.17 \pm 1.51dA	71.10 \pm 0.40bA	73.87 \pm 1.20eA	50.91 \pm 4.71cA	67.89 \pm 7.32bA
	4	65.64 \pm 1.12eA	64.32 \pm 1.23deA	56.34 \pm 1.68cB	61.87 \pm 1.26hA	9.23 \pm 0.55eB	15.43 \pm 0.85fA
	6	55.12 \pm 1.60fA	55.62 \pm 1.25eA	45.83 \pm 1.15cB	53.20 \pm 1.01iA	1.74 \pm 0.11eA	5.43 \pm 1.70fA
45	1	81.95 \pm 1.55cA	84.17 \pm 1.19cA	72.23 \pm 1.46bB	82.36 \pm 0.75cA	74.96 \pm 3.49bA	85.25 \pm 6.12aA
	2	75.51 \pm 1.44dA	77.00 \pm 1.17dA	65.46 \pm 0.58bB	73.52 \pm 1.37eA	15.14 \pm 1.30eB	45.65 \pm 4.68dA
	4	55.21 \pm 1.43fB	60.53 \pm 1.48dA	48.33 \pm 0.54cB	53.37 \pm 1.38iA	5.44 \pm 0.20eB	13.56 \pm 0.60fA
45	6	37.07 \pm 1.10gB	42.66 \pm 1.27fA	38.12 \pm 0.28cB	43.37 \pm 1.21jA	0eB	3.61 \pm 0.15fA
	1	68.06 \pm 4.30eB	80.46 \pm 0.45dA	58.40 \pm 3.87cA	65.36 \pm 1.15gA	27.97 \pm 5.25dB	56.61 \pm 6.12cA
	2	54.80 \pm 1.53fB	61.57 \pm 0.75deA	43.68 \pm 1.40cB	55.44 \pm 1.31iA	2.51 \pm 0.40eB	18.74 \pm 0.82fA
Control	4	38.17 \pm 1.70gA	42.86 \pm 1.76fA	37.54 \pm 3.89cA	43.74 \pm 1.23jA	0.33 \pm 0.33eB	6.53 \pm 0.51fA
	6	16.52 \pm 1.60hB	21.31 \pm 0.70gA	27.31 \pm 1.21dB	32.83 \pm 0.26kA	0eB	1.48 \pm 0.38fA
		98.34 \pm 0.82aA	98.79 \pm 0.70aA	98.07 \pm 0.67aA	98.75 \pm 0.57aA	100aA	100aA
F		157.046	231.213	85.661	260.163	306.578	129.462
P		0.000	0.000	0.000	0.000	0.000	0.000

Different lowercases indicated significant differences under different temperatures and times of a certain population by LSD tests at $P < 0.05$. Different uppercases indicated significant differences between Beijing and Turpan populations by t-tests at $P < 0.05$.

Table 2. Mean (\pm SEM) egg number, F1 female ratio, survival rate of F1 adults, and female and male longevity of Beijing and Turpan *B. tabaci* MEAM1 following 1-h treatment at the temperature indicated

Temperature (°C)	Egg number		F1 female ratio (%)		F1 adult survival rate (%)		Female longevity (d)		Male longevity (d)	
	Beijing	Turpan	Beijing	Turpan	Beijing	Turpan	Beijing	Turpan	Beijing	Turpan
26	92 \pm 2.43aA	90.8 \pm 2.00aA	54.19 \pm 1.35abA	56.57 \pm 1.37aA	95.21 \pm 0.10aA	97.61 \pm 0.81aA	18.58 \pm 1.61bcA	22.24 \pm 1.36abA	14.88 \pm 1.27aB	18.38 \pm 0.58aA
37	89.4 \pm 3.83aA	91 \pm 3.63aA	56.48 \pm 1.37aA	57.00 \pm 1.21aA	94.86 \pm 1.78aA	98.26 \pm 0.55aA	21.48 \pm 1.68abA	24.3 \pm 1.78aA	15.66 \pm 1.41aA	19.36 \pm 1.27aA
39	95 \pm 3.42aA	92.4 \pm 3.66aA	52.54 \pm 1.84abA	54.15 \pm 1.38abA	94.68 \pm 0.55aA	97.13 \pm 0.89abA	17.08 \pm 1.23cdB	24.4 \pm 1.37aA	15.76 \pm 0.49aB	18.42 \pm 0.32aA
41	96.6 \pm 3.97aA	99.4 \pm 5.80aA	50.43 \pm 1.88ba	51.70 \pm 1.8ba	86.69 \pm 2.02bB	93.35 \pm 0.43bcA	15.96 \pm 0.74cdB	23.46 \pm 0.85aA	13.22 \pm 1.07aB	18.06 \pm 0.22aA
43	88.6 \pm 3.88aA	93.8 \pm 2.01aA	37.87 \pm 1.53cA	42.07 \pm 1.35cA	24.24 \pm 2.23cB	45.32 \pm 2.63dA	14.94 \pm 1.79cdB	22.38 \pm 0.36abA	14.46 \pm 0.41aB	18.02 \pm 0.43aA
45	97.6 \pm 4.23aA	96 \pm 4.30aA	33.88 \pm 1.14cA	37.58 \pm 1.33dA	2.01 \pm 0.30dB	14.20 \pm 0.72eA	16.86 \pm 1.31cdA	19.42 \pm 0.89bcA	14.68 \pm 0.81aA	14.48 \pm 0.20aA

Different lowercases indicate significant differences under different temperatures of a certain population by LSD tests at $P < 0.05$. Different uppercases indicate significant differences between Beijing and Turpan populations by t-tests at $P < 0.05$.

level of heat tolerance in the Turpan population compared with the Beijing population for eggs, pupae, and adults under the same stress conditions (Table 1). Given that Turpan has a specific climate characterized by extreme high temperatures that last for long periods of time, a generally higher heat tolerance could be expected to be selected in the Turpan population compared with the Beijing population. Studies showed that heat tolerance varied depending on the geographic location and the environmental conditions; for example, temperate populations have lower levels of heat tolerance compared with tropical populations (Sgrò et al. 2010). Sørensen et al. (2001) reported that populations of *Drosophila buzzatii* Patterson & Wheeler from mountain areas were less resistant to heat stress than populations in other areas. There could be multiple mechanisms underlying the difference in heat tolerance between the Beijing and Turpan populations. First, it is possible that circadian rhythms genes or heat shock genes determine this difference in heat tolerance (Sørensen and Loeschke 2002, Lü and Wan 2011, Yu et al. 2012). Second, genetic variation may be one of the factors leading to the heat tolerance difference between Beijing and Turpan populations since *B. tabaci* has complex genetic variation among different geographical populations (Boykin et al. 2007; Chu et al. 2007, 2011). Thus, further experiments are needed to examine the different mechanisms behind the ecologically important heat-tolerance trait in MEAM1.

Interestingly, the study showed that egg number and F1 female ratio were not significantly different between Turpan population and Beijing population after heat shock stress, but longevity and the F1 adult survival rate were significantly higher in the Turpan population compared with the Beijing population (Table 2). These results indicated that the maternal effects of heat shock only manifested in the offspring survival rate, and the transgenerational effect of temperature on heat tolerance was first reported in MEAM1. Elbaz et al. (2011) found that the development rate of MEAM1 progeny increased after maternal heat shock at 42°C. Some research has shown that resistance to thermal stress was correlated with longevity (Norry and Loeschke 2002, 2003). Norry et al. (2006) reported that there was geographic variation in the longevity and fecundity of *D. buzzatii*, with both reduced longevity and increased early fecundity occurring in highland populations. Highland areas were always harsher environments with scarce, low-quality food, a high risk of desiccation due to low levels of precipitation, strong winds, and unpredictable extreme temperatures (Mani 1962; Lencioni 2004), all of which create an environment with a strong selective pressure. In contrast, the present study showed that the Turpan population exhibited a longer longevity and a higher heat tolerance compared with the Beijing population after heat shock. It might be that a higher heat tolerance and an extended lifespan may keep the MEAM1 population size stable during extended exposure to extreme high temperatures and harsh environmental conditions. Thus, it was suggested that improved heat tolerance and prolonged longevity were important adaptive strategies that allowed MEAM1 to survive harsh high-temperature conditions.

The climate varies between the Turpan and Beijing areas, especially with respect to temperature, and the selection pressures in the field as well as the mechanisms used for adaptation are complex. Each population is faced with a unique environment and temperature condition. Survival rate and longevity were found to be higher in the Turpan population than in the Beijing population in the present study, and egg number and F1 female ratio were not significantly different between the two populations. It is possible that the measured heat tolerance and longevity traits, but not the reproductive traits, were most relevant for the climate traits. Overall, the present results suggested that improved heat tolerance and prolonged longevity were part of an important adaptive strategy that allowed MEAM1 to survive harsh high-temperature conditions such as Turpan arid desert climate. The present study mainly contribute to our understanding of how heat tolerance and longevity traits respond to environmental selection pressures and partly highlight the ecological importance of adaptation to environmental stress.

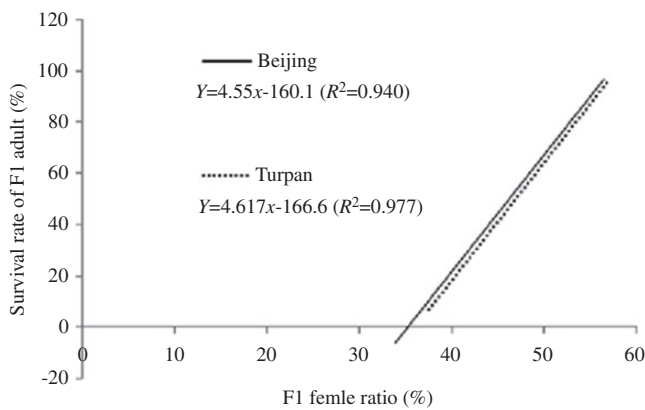


Fig. 1. The GLM for F1 female ratio and adult survival rate of *B. tabaci* MEAM1, where Y is survival rate of F1 adult (%), and x is F1 female ratio (%).

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References Cited

- Arthur, A. L., A. R. Weeks, and C. M. Sgrò. 2008. Investigating latitudinal clines for life history and stress resistance traits in *Drosophila simulans* from eastern Australia. *J. Evol. Biol.* 21: 1470–1479.
- Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Faraar, et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biol.* 8: 1–16.
- Boykin, L. M., R. G. Shatters, Jr., R. C. Rosell, C. L. McKenzie, R. A. Bagnall, P. De Barro, and D. R. Frohlich. 2007. Global relationships of *Bemisia tabaci* (Hemiptera: Aleyrodidae) revealed using Bayesian analysis of mitochondrial COI DNA sequences. *Mol. Phylogenet. Evol.* 44: 1306–1319.
- Bowler, K., and J. S. Terblanche. 2008. Insect thermal tolerance: what is the role of ontogeny, ageing and senescence. *Biol. Rev.* 83: 339–355.
- Chu, D., G. X. Liu, Z. X. Fan, Y. L. Tao, and Y. J. Zhang. 2007. Genetic differentiation of different geographical populations of *Bemisia tabaci* (Gennadius) complex. *Agric. Sci. China* 6: 696–705.
- Chu, D., C. S. Gao, P. J. De Barro, Y. J. Zhang, and F. H. Wan. 2011. Investigation of the genetic diversity of an invasive whitefly in China using both mitochondrial and nuclear DNA markers. *Bull. Entomol. Res.* 101: 477–486.
- Cui, X. H., F. H. Wan, M. Xie, and T. X. Liu. 2008. Effects of heat shock on survival and reproduction of two whitefly species, *Trialleurodes vaporariorum* and *Bemisia tabaci* biotype B. *J. Insect Sci.* 24: 1–10.
- De Barro, P. J., S. S. Liu, L. M. Boykin, and A. B. Dinsdale. 2011. *Bemisia tabaci*: a statement of species status. *Annu. Rev. Entomol.* 56: 1–19.
- Denlinger, D. L., and G. D. Yocum. 1998. Physiology of heat sensitivity, pp. 11–18. In G. J. Hallman and D. L. Denlinger (eds.), *Thermal sensitivity in insects and application in integrated pest management*. Westview Press, Boulder, CO.
- Elbaz, M., M. Weiser, and S. Morin. 2011. Asymmetry in thermal tolerance trade-offs between the B and Q sibling species of *Bemisia tabaci* (Hemiptera: Aleyrodidae). *J. Evol. Biol.* 21: 1099–1109.
- Endler, J. A. 1977. *Geographic variation, speciation and clines*. Princeton University Press, Princeton.
- Griffiths, J. A., M. Schiffer, and A. A. Hoffmann. 2005. Clinal variation and laboratory adaptation in the rainforest species *Drosophila birchii* for stress resistance, wing size, wing shape and development time. *J. Evol. Biol.* 18: 213–222.
- Grill, R. J. 1990. The morphology of whiteflies, pp. 13–46. In D. Gerling (ed.), *Whiteflies: their bionomics, pest status and management*. Atheneum Press, Andover, UK.
- Hoffmann, A. A., and A. Week. 2007. Climatic selection on genes and traits after a 100 year old invasion: a critical look at temperate-tropical clines in *Drosophila melanogaster* from eastern Australia. *Genetica* 129: 133–147.
- Hoffmann, A. A., C. M. Sgro, and A. Weeks. 2004. Chromosomal inversion polymorphisms and adaptation. *Trends Ecol. Evol.* 19: 482–488.
- Krebs, R. A., and V. Loeschke. 1995. Resistance to thermal stress in preadult *Drosophila buzzatii*: variation among populations and changes in relative resistance across life stages. *Biol. J. Linn. Soc.* 56: 517–531.
- Lencioni, V. 2004. Survival strategies of freshwater insects in cold environments. *J. Limnol.* 63(Suppl. 1): 45–55.
- Lu, C., and Z. L. Zhang. 2000. Thanking about *Bemisia tabaci* outbreaks. *Beijing Sci.* 18: 4–13.
- Lü, Z. C., and F. H. Wan. 2008. Differential gene expression in whitefly (*Bemisia tabaci*) B-biotype females and males under heat-shock condition. *Comp. Biochem. Physiol. D* 3: 257–262.
- Lü, Z. C., and F. H. Wan. 2011. Using double-stranded RNA to explore the role of heat shock protein genes in heat tolerance in *Bemisia tabaci* (Gennadius). *J. Exp. Biol.* 214: 764–789.
- Mani, M. S. 1962. Introduction to high altitude entomology-insect life above the timber-line in the north-west Himalaya. Methuen & Co., London.
- Norry, F. M., and V. Loeschke. 2002. Longevity and resistance to cold stress in cold-stress selected lines and their controls in *Drosophila melanogaster*. *J. Evol. Biol.* 15: 775–783.
- Norry, F. M., and V. Loeschke. 2003. Heat-induced expression of a molecular chaperone decreases by selecting for long-lived individuals. *Exp. Gerontol.* 38: 673–681.
- Norry, F. M., P. Sambucetti, A. C. Scannapieco, and V. Loeschke. 2006. Altitudinal patterns for longevity, fecundity and senescence in *Drosophila buzzatii*. *Genetica* 128: 81–93.
- Prange, H. D. 1996. Evaporative cooling in insects. *J. Insect Physiol.* 42: 493–499.
- Sgrò, C. M., J. Overgaard, T. N. Kristensen, K. A. Mitchell, F. E. Cockerell, and A. A. Hoffmann. 2010. A comprehensive assessment of geographic variation in heat tolerance and hardening capacity in populations of *Drosophila melanogaster* from eastern Australia. *J. Evol. Biol.* 23: 2484–2493.
- Sisodia, S., and B. N. Singh. 2010. Resistance to environmental stress in *Drosophila ananassae*: latitudinal variation and adaptation among populations. *J. Evol. Biol.* 23: 1979–1988.
- Sørensen, J. G., and V. Loeschke. 2002. Natural adaptation to environmental stress via physiological clock-regulation of stress resistance in *Drosophila*. *Ecol. Lett.* 5: 16–19.
- Sørensen, J. G., J. Dahlggaard, and V. Loeschke. 2001. Genetic variation in thermal tolerance among natural populations of *Drosophila buzzatii*: down regulation of Hsp70 expression and variation in heat stress resistance traits. *Funct. Ecol.* 15: 289–296.
- Sørensen, J. G., F. M. Norry, A. C. Scannapieco, and V. Loeschke. 2005. Altitudinal variation for stress resistance traits and thermal adaptation in adult *Drosophila buzzatii* from the New World. *J. Evol. Biol.* 18: 829–837.
- Wan, F. H., G. F. Zhang, S. S. Liu, C. Luo, D. Ch, Y. J. Zhang, L. S. Zang, M. Jiu, Z. C. Lü, X. H. Cui, et al. 2009. Invasive mechanism and management strategy of *Bemisia tabaci* (Gennadius) biotype B: Progress report of 973 Program on invasive alien species in China. *Chin. Sci. Ser. C* 52: 88–95.
- Yu, H., F. H. Wan, and J. Y. Guo. 2012. Different thermal tolerance and *hsp* gene expression in invasive and indigenous sibling species of *Bemisia tabaci*. *Biol. Invas.* 14: 1587–1595.
- Zang, L. S., Y. Q. Liu, and S. S. Liu. 2005. A new clip-cage for whitefly experimental studies. *Chin. Bull. Entomol.* 42: 329–331.

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