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Effects of high-temperature stress and heat shock on two root maggots, *Bradysia odoriphaga* and *Bradysia difformis* (Diptera: Sciaridae)

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ABSTRACT

Bradysia odoriphaga and *B. difformis* (Diptera: Sciaridae) are devastating pests of vegetables, ornamentals and edible mushrooms. In Chinese chive fields, the two *Bradysia* species occur with similar regularities: outbreaks in spring and autumn, and population decreases in summer. Temperature may be an important factor restricting their population abundance in summer. Here, we performed a life-table study under constant high temperatures and assessed the tolerance of two *Bradysia* species to heat shock. Life parameters of the *Bradysia* species indicated slow developmental rates, and low survival rates and fecundity, when the temperature was higher than 30 °C. At 34 °C, individuals were unable to reach the adult stages from eggs. Moreover, temperatures above 36 °C showed lethal effects, decreasing their survival rates. The median lethal time (LT50) values of 4th instar *B. odoriphaga* and *B. difformis* larvae were 46.82 and 32.97 h, respectively, while the values at 38 °C were 2.12 and 1.51 h, respectively. The 4th instar larvae and pupae possessed higher thermotolerance levels than adults and eggs, indicating sensitivities to heat stress. Moreover, *B. odoriphaga* was more thermotolerant than *B. difformis*. Thus, weak thermotolerance levels may restrict their occurrences during the period of summer heat, and the difference in thermotolerance levels between the two species may be related to their regional distributions.

Introduction

Bradysia odoriphaga Yang et Zhang (Diptera: Sciaridae) and *B. difformis* Frey, two main root maggot flies, are devastating pests of liliaceous crops and edible fungi (Yang and Zhang, 1985; Xue et al., 2005; Jagdale et al., 2007; Liu et al., 2015). Their larvae tend to aggregate to attack and damage roots and corm tissues, resulting in weak or withered plants; the two species may coexist on the same host plant in protected cultivation or open fields (Xue et al., 2005; Gou et al., 2015; Zhang et al., 2015). In addition to reducing yields directly, they transmit viral and fungal diseases. Because the larvae primarily damage the underground portions of plants, they are difficult to prevent or control. One prevalent management practice against *B. odoriphaga* is the application of insecticides, including organophosphates, carbamates and neonicotinoids (Li et al., 2014). However, insecticide use has become increasingly restricted owing to the concern regarding environmental pollution and human health as well as the development of pesticide resistance (Xue et al., 2005; Zhang et al., 2015). Reducing insecticide applications will require a better understanding of *B. odoriphaga* population dynamics under various environmental conditions.

Temperature is regarded as a critical abiotic factor that affects the behavior, survival, distribution, colonization, abundance and life history of an insect (Hoffmann et al., 2003; Chown and Terblanche, 2007; Hoffmann, 2010). Insects are typical small-bodied poikilotherms, which have a poor ability to adjust and maintain body temperature under capricious environmental conditions. Their body temperatures fluctuate closely with the environmental temperature, which directly affects their metabolisms, phenotypes and adaptations (Kontodimas et al., 2004; Forster et al., 2011). temperatures lead to rapid increase in insect populations, while temperatures over or below the optimal temperature result in diverse negative effects, such as restricting movement and suppressing development, survival and fecundity (Hallman and Denlinger, 1998; Olson et al., 2013). For example, the optimum temperature range for *Megacopta cribraria* (Heteroptera: Plataspidae) is from 20 °C to 28 °C. Its survival and fecundity decline when the temperature is over 29 °C or below 17 °C, and no individuals survive above 33 °C (Shi et al., 2014). *Phenacoccus solenopsis* (Hemiptera: Pseudococcidae) survives at 15 °C–40 °C, but the survival rate declines at over 35 °C or below 25 °C, and adult longevity is shortened at higher temperatures (Prasad et al., 2012). Clarifying the effects of temperature on insects is important for better understanding their ecology and will aid in predicting the occurrence of insects in different seasons and regions.

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Global warming has increased over the past 30 years, and the frequency and extent of extreme heat events have increased in summer (Fischer and Schar, 2009; Hansen et al., 2011), which may be particularly important for temperate species, with thermal anomalies occurring more drastically at higher latitudes (Kätterer and Andrén, 2009; Tantowijoyo and Hoffmann, 2010; Overgaard et al., 2014). In particular, with the increase in the average temperature, high-temperature stress may easily decrease individual fitness levels and ultimately cause death (Fischer et al., 2010; Overgaard et al., 2011). Species with high thermal tolerance will have an advantage in terms of range expansion and will perform better during severe and frequent extreme temperature events (Bürgi and Mills, 2010).

In outdoor Chinese chive fields, the two *Bradysia* species occur with similar regularities, with outbreaks in spring and autumn, and population decreases in summer (Dang et al., 2001). In addition, the population of two species increases severely in winter in Chinese chive greenhouses. Temperature is an important factor affecting their population dynamics during different seasons. Previous research had confirmed that the optimum temperature ranges for development was 13 °C–28 °C for *B. odoriphaga* and 10 °C–25 °C for *B. difformis*, and the lower threshold temperatures of eggs, larvae and pupae were 8.20, 6.29, 7.39 °C, respectively, for *B. odoriphaga*, and 4.04, 5.79, 4.97 °C, respectively, for *B. difformis* (Mei et al., 2004; Liu et al., 2015). *B. difformis* with a lower threshold temperature had a greater cold tolerance than *B. odoriphaga*. However, thermal tolerance of the two *Bradysia* flies against heat stress has been scarecely reported. In their distribution region, the temperature frequently fluctuates, often exceeding 30 °C, and the temperature in summer can reach 39 °C, for several hours in the daytime, resulting in a soil temperature (0–5-cm underground) of 35–38 °C (Chen et al., 2012). *B. odoriphaga* adults are sensitive to heat-shock stress (Cheng et al., 2017), and no individuals are able to complete development from larva to pupa at 35 °C (Mei et al., 2004; Jiao, 2014). Thus, high temperature is thought to be an important factor restricting their occurrences in summer (Dang et al., 2001; Hu et al., 2016; Cheng et al., 2017).

In this study, we performed life-table studies on the two *Bradysia* flies under constant high temperature using the age-stage, two-sex life table method, which could determine the actual population dynamics more accurately compared with a traditional life table (Chi and Su, 2006). Then, lethal effects of heat shock on the two *Bradysia* were tested. The objectives were to determine how the survival rates of the two *Bradysia* species at different developmental stages were affected by heat stress and to verify how high-temperature stress restricted their abundances in the summer heat.

Materials and methods

Insect materials

B. odoriphaga and *B. difformis* colonies were originally obtained from a Chinese chive greenhouse field in Tai'an, China, in April 2015. Insect colonies were maintained in the Shandong Provincial Key Laboratory of Applied Microbiology and reared on Chinese chives for more than five generations. Using the breeding method described by Xue et al. (2005) and Gou et al. (2015), eggs, larvae and pupae were reared in petri dishes (9 cm in diameter) lined with wet filter paper, and fresh Chinese chive was placed in a separate petri dish as the diets of larva. One pair of newly emerged adults was placed in oviposition containers (3-cm diameter × 1.5-cm height) lined with wet filter paper. To facilitate egg collection, fresh Chinese chive was cut into 2-cm-long pieces and placed in the rearing cages to allow females to oviposit. Insect colonies were maintained in growth chambers maintained at 25 ± 1 °C with 75 ± 5% relative humidity and a 12:12 h light:dark cycle.

Life table study at constant high temperature

The eggs newly spawned by adults were collected as the test insects. According to the method described by Li et al. (2015) and Zhang et al. (2015), a total of 150 eggs (15 eggs from each female) per species at every temperature were used in this study. All eggs per species were placed in growth chambers (MLR-352H-PC) at 25, 28, 30, and 32 °C, 80% RH, and a photoperiod of 14:10 (L:D) h. All 150 eggs were placed in a same petri dish and observed daily, and their hatching was recorded. Each day, the newly hatched larvae were separately transferred to a new petri dish. The number of larvae in every petri dish was between 10 and 50. The survival of the tested insects was recorded daily, and fresh Chinese chives were provided to avoid fungal growth. Deionized water was replenished daily to keep the filter paper moist. New pupae were moved to new petri dishes, and the number of newly emerged adults was recorded daily. After the emergence of adults, male and female insects were paired and placed in individual oviposition plastic containers for subsequent feeding according to the method mentioned above. Adults were checked daily, and the number of eggs produced by each pair was recorded until death.

Survival of two Bradysia species at 32 to 38 °C for 24 h

Eggs, 2nd and 4th instars, pupae and adults of the two *Bradysia* species were gathered at 34 h as the test subjects. Eggs, larvae and pupae were reared in petri dishes (9 cm in diameter) covered with wet filter paper, and adults were placed in 50-ml centrifuge tubes containing a piece of filter paper (2 cm in diameter) moistened with deionized water. All insects they were transferred and reared at target temperatures (32, 34, 36 and 38 °C) for 24 h. During the treatment, fresh Chinese chive and deionized water were replenished. The survival rates of larvae and adults under different treatment conditions were determined and recorded after each treatment. Eggs and pupae were transported to 25 °C, and the survival rates were determined daily until no eggs hatched or adults emerged. Every treatment had five replicates, and every replicate contained 20 individuals (larvae, pupae or adults). Every egg treatment had three replicates, using eggs gathered from 45 pairs of adults.

Survival rates of two Bradysia species after 36 °C and 38 °C heat shock

Eggs, 2nd and 4th instars, pupae and adults were chosen as the tested subjects. Eggs, larvae and pupae were put into 5-ml centrifuge tubes, while adults were put into 15-ml centrifuge tubes. Then, all of the subjects were exposed to 36 and 38 °C water baths. At 36 °C, the increased interval time was 6 h for eggs and pupae, 3 h for adults and 12 h for larvae, and the increased interval time was 0.5 h at 38 °C until all insects died. The larvae and adults were allowed to recover at 25 °C for 1 h, and the survival rates under different treatment conditions were determined and recorded. Eggs and pupae were then reared at 25 °C, and the survival rates were determined daily until no eggs hatched or adults emerged. The treatment maintained at 25 °C water bath was regarded as the control. The median lethal time (LT50) values were calculated according to the following Boltzmann regression Eq. (1): where the survival rates of the two *Bradysia* species after heat shock were regarded as the dependent variable (y), while the treatment times were regarded as the independent variable (x). $A1$ and $A2$ represent the original value and the end value, respectively. $x0$ represents the median value (LT50).

$$y = (A1 - A2)/\left\{1 + \exp\left[\frac{x - x0}{dx}\right]\right\} + A2 \quad (1)$$

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