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Desiccation resistance and water balance in populations of the maize weevil *Sitophilus zeamais*



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ABSTRACT

Water balance is a challenge for insects due to their small size and body with high surface area-to-volume ratios, and it is particularly important for insects that inhabit dry environments, such as stored grains, and warm climates. This subject has been curiously neglected in stored product insects, including the maize weevil *Sitophilus zeamais* Motschulsky, where broad population differences have been reported with management consequences. Here, we assessed variation in desiccation resistance and water balance among three strains of the maize weevil exhibiting differences in body mass. The survival of male and female weevils from three strains was therefore assessed at relative humidities ranging from 0 to 100%, in which their water content and water loss were also assessed. The effect of insect aggregation (1–25 insects per group) on water balance was also assessed, as was the water gain by the drinking of free water and drinking preference when exposed to insecticide-contaminated water. The median survival time (LT₅₀) of individual insects increased with relative humidity and varied significantly among the weevil strains. The larger strain exhibited 60–80% higher LT₅₀ at 50% relative humidity (r.h.) and above, with little difference between strains at 0% r.h. Heavier weevils exhibited higher water content and lower overall rates of water loss; these qualities made heavier weevils more resistant to dehydration. Larger groups of weevils facilitate water retention in individual insects. Weevils actively drink water to achieve favorable water balance when dehydrated, which is a major source of water intake. Under dehydration, weevils in general were not able to discriminate between insecticide-contaminated and uncontaminated water. However, females of the insecticide-susceptible strain avoided contaminated water.

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1. Introduction

Water availability along with temperature suitability are major determinants of animal abundance and distribution in terrestrial environments (Hadley, 1994; Chown and Gaston, 1999; Willmer et al., 2005). Water balance is particularly important for arthropods in general, and insects in particular, because of their vulnerability to water loss due to their small size and their body with high surface area-to-volume ratios (Edney, 1977; Hadley, 1994; Addo-Bediako et al., 2001; Chown et al., 2011). Small size is disadvantageous in terrestrial environments because smaller organisms have smaller water storage capacities and larger surface areas available for losing water (Chown and Nicolson, 2004).

The ability of an insect to obtain water depends on the availability of water in its environment. Dry environments pose challenges for water balance and organism homeostasis; stored grain

environments are prime examples of such conditions because water is scarce and food sources tend to have low water content (Hadley, 1994; Hagstrum et al., 1996; Chown and Nicolson, 2004; Yocum et al., 2012). Stored grain environments in warmer climates pose even more challenging conditions for water balance and insect homeostasis due to the interplay between temperature and water availability (Hagstrum et al., 1996; Chown and Nicolson, 2004). However, stored product insects appear to be well-adapted to these conditions, as revealed by comparative studies of water balance in some species studied (Hadley, 1994; Benoit et al., 2005; Yoder et al., 2010). Curiously, little is known about variation in water balance among populations within a species; only a single study in a stored grain insect, the cowpea beetle *Callosobruchus maculatus*, has been conducted exploring potential strain differences in larval competition leading to higher adult body mass and consequent high tolerance to water stress (Hadley and Massion, 1985; Yoder et al., 2010; Weldon et al., 2013).

Changes in an insect's water content are consequences of differences in water gain and loss, which delimit the concept of water

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balance (Wharton, 1985; Hadley, 1994). Mechanisms of gaining water include drinking free water, extracting water from food, absorbing water from the atmosphere, and producing water metabolically (Hadley, 1994; Chown and Nicolson, 2004). In contrast, water is lost by cuticular and respiratory transpiration, oral and anal secretions, and excretion (Addo-Bediako et al., 2001; Chown et al., 2011). Aggregation of conspecific individuals may also influence water balance by creating and maintaining local microclimates that enhance thermal mass and lead to more stable body temperatures (Yoder and Grojean, 1997; Yoder and Smith, 1997; Chown and Nicolson, 2004). Stable temperatures are achieved because metabolic heat is conserved and convective cooling is reduced within aggregations, while water loss through evaporation or excretion generates a micro-environment with higher vapor pressure (Chown and Nicolson, 2004).

Animal species, including insect species, often differ in their level of resistance to desiccation (or dehydration) in their native environments (and its water availability) and their response to habitat alterations, climate change, biological invasions, pollution and overexploitation (Kleynhans and Terblanche, 2009; Chown et al., 2011; Zheng et al., 2013; Kleynhans et al., 2014). Desiccation resistance in insects can be accomplished through increasing body water content, reducing the rate of water loss, or tolerating greater losses of water (Chown and Nicolson, 2004). The first two strategies aim primarily at minimizing water loss, while the latter is based on increasing tolerance to water loss, also referred to as desiccation or dehydration tolerance (Edney, 1977; Addo-Bediako et al., 2001). Although such strategies have been recognized among different insect species (Addo-Bediako et al., 2001; Kleynhans and Terblanche, 2009; Parkash et al., 2011; Kleynhans et al., 2014), studies assessing population variation in desiccation resistance have been restricted to very few insect species – the grasshopper *Aeropedellus clavatus*, the cowpea beetle *C. maculatus*, and the Queensland fruit fly *Bactrocera tryoni* (Hadley and Massion, 1985; Yoder et al., 2010; Weldon et al., 2013).

Stored grain insects are generally regarded as xerophilic because they exhibit a water loss reduction profile suitable for xeric (i.e., dry) environments (Hadley, 1994; Appel et al., 1999; Benoit et al., 2005; Yoder et al., 2010). Longevity, size (and mass), respiration rate, and behavior are traits that may affect water balance (Hadley, 1994; Yoder et al., 2010), and such traits may vary among insect populations (e.g., Guedes et al., 2003, 2006, 2007; Guedes and Smith, 2008). Populations of the maize weevil *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae) exhibit variation in body mass (and size) and respiration rate, which have been linked with insecticide resistance and the mitigation of physiological costs usually associated with this phenomenon (Guedes et al., 2006, 2009a, b, 2010; Oliveira et al., 2007; Ribeiro et al., 2007). Therefore, such traits may also affect water balance and desiccation resistance of maize weevil populations, a species for which these traits have not been studied, with potential implications for their management. This was the objective of the present study, in which we assessed the water balance and desiccation resistance of three maize weevil populations.

2. Materials and methods

2.1. Insect strains

Three strains of the maize weevil were used in the study. One strain is the standard susceptible laboratory population originally collected in the mid-1980s from Sete Lagoas county (state of Minas Gerais, Brazil). The other two strains are resistant to pyrethroid insecticides (ca. 100-fold resistant, as periodically checked), one collected in 1999 from Juiz de Fora (state of Minas Gerais, Brazil) and the other collected in the late 1980s from Jacarezinho (state of

Paraná, Brazil) (Guedes et al., 1994, 1995; Ribeiro et al., 2003; Oliveira et al., 2007; Corrêa et al., 2011). The Juiz de Fora strain bears a fitness disadvantage for insecticide resistance: individuals reared in the absence of pyrethroids develop slowly and have reduced progeny production, in contrast with the Jacarezinho strain (Fragoso et al., 2005; Oliveira et al., 2007). Furthermore, insects from Jacarezinho are larger, heavier, and have higher energy reserves than the other two strains, which may allow the Jacarezinho strain to mitigate the costs associated with pyrethroid resistance (Guedes et al., 2006; Oliveira et al., 2007; Araújo et al., 2008; Lopes et al., 2010). The overall body mass of the Jacarezinho weevils used in the present study was 3.40 ± 0.03 mg, while the body mass of the insects from Juiz de Fora and Sete Lagoas was 2.62 ± 0.03 mg and 2.69 ± 0.04 mg, respectively. Both resistant strains exhibited the same major pyrethroid resistance mechanism: altered target site sensitivity, with secondary involvement of enhanced insecticide detoxification (Guedes et al., 1995; Fragoso et al., 2003, 2007; Araújo et al., 2011). Insects from all strains exhibited substantial intrastrain and interstrain behavioral variation, as previously reported (Guedes et al., 2009a, b; Morales et al., 2013). All three weevil strains were maintained in whole maize grains (13% moisture content) free of insecticide residues under controlled temperature (25 ± 2 °C), relative humidity ($70 \pm 5\%$) and photoperiod (12:12 L:D).

2.2. Overall experimental conditions

Newly emerged adult weevils were sexed using their patterns of rostrum texture and punctuation (Tolpo and Morrison, 1965) and individually weighed on an electronic scale (model XS3DU, Mettler Toledo, Columbus, OH, EUA). Each insect was isolated in a perforated Eppendorf tube and placed for 24 h within glass desiccators (3000 cm^3) at 33% relative humidity (r.h.) until 4–6% of its body mass was lost, as determined through preliminary assessments. Insect feeding was prevented with procedures that minimized the effects of digestion, reproduction and excretion on body mass, which were measured. This pre-treatment standardizes the individual weevils, allowing us to follow the changes in body mass, which are due to the loss of water content from the insect body (Arlian and Ekstrand, 1975). All of the experiments were performed with 25–30 weevils of each sex, for each strain and relative humidity value.

Temperature and relative humidity were controlled in environmental chambers (maintained at 25 ± 2 °C) within sealed glass desiccators (3000 cm^3). A range of relative humidities (0, 8, 33, 50, 75, and 100%) was established with drierite (anhydrous calcium sulfate), saturated saline solutions and glycerol-distilled water mixtures and used in the experiments following the methods of Winston and Bates (1960) and Benoit et al. (2005). These relative humidities were selected based on previous studies of water balance in insects (Wharton, 1985; Hadley, 1994). Relative humidity was recorded using digital thermohygrometers (IP-747RH, Impac, São Paulo, SP, Brazil).

The pre-treated insects individually maintained in perforated Eppendorf tubes were removed only for daily measures of body mass, which lasted for less than 1 min, and were returned to the container with controlled conditions of temperature and relative humidity until their eventual death. Insect dry mass was determined after insect death by drying them at 70 °C in an oven containing calcium sulfate (CaSO_4) until a constant mass was obtained. Each dead insect was weighed three consecutive times at the end of each experiment, as described by Wharton (1985) and Hadley (1994).

2.3. Time-mortality (survival) bioassays

The length of survival of each adult weevil was determined as the time from their placement under the desired conditions of

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