



Effects of developmental acclimation on fitness costs differ between two aphid species

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ABSTRACT

Most ectotherms are able to increase their tolerance to heat stress via the acclimation response. However, there is ongoing debate about whether the acclimation response is associated with fitness costs, and what factors can affect the consequences of acclimation are still unclear. To elucidate this, we sought to determine whether fitness costs varied with acclimation conditions in two cereal aphids, *Sitobion avenae* and *Rhopalosiphum padi*. Thus, the basal and inducible thermal tolerances (maximum critical temperature [CT_{max}]) and fitness traits (proportion of adult emergence, adult longevity, fecundity, and population parameters) of adult aphids were measured under three conditions of developmental acclimation: 1) 22 °C constant temperature (no acclimation), 2) 22 °C + 34 °C for 2 h per day (low daytime temperature), and 3) 22 °C + 38 °C for 2 h per day (high daytime temperature). We found that the thermal tolerances of both species were significantly higher following developmental acclimations, where higher basal and inducible thermal tolerances were observed in *R. padi* than in *S. avenae*. Low daytime temperature acclimation conditions (34 °C) resulted in negligible reproductive costs and improved the intrinsic rates of population increase in both species. In contrast, substantial fitness costs were detected in both species in response to high daytime temperature acclimation (38 °C), especially for *S. avenae*. Our results indicate that the effects of acclimation conditions on fitness costs differ between the two aphid species. These findings will not only enhance our understanding of species dynamics in the context of climate change but could also potentially improve pest control efforts.

1. Introduction

Global climate change has not only led to continually increasing in average atmospheric temperatures (Lin and Franzke, 2015), but has also increased the frequency and intensity of extreme heat events (Easterling et al., 2000; IPCC, 2013). Climate change has already brought about several ecological consequences, such as changes in population dynamics (Welbergen et al., 2008), community composition (Lomeli-Flores et al., 2010), and the diversity and thermal boundaries of species (Deutsch et al., 2008; Kellermann et al., 2012). In comparison to moderate increases in mean temperatures, frequent high-temperature events that have been directly linked to survival in species may be particularly challenging for organisms to cope with (Fischer et al., 2014), and are considered to be important agents of selection (Hoffmann et al., 2003).

Organisms can increase their thermal tolerance by evolutionary and plastic responses (Chevin et al., 2010; Overgaard et al., 2011; MacLean

et al., 2017), which both play an important role in coping with variations in environmental conditions (Fischer and Karl, 2010; Esperk et al., 2016; Kingsolver and Buckley, 2017). Plastic responses to fluctuations in environmental conditions have been reported in a multitude of species, including arthropods (Lachenicht et al., 2010; Chidawanyika and Terblanche, 2011; Xing et al., 2014, 2015), mollusks (Littlewood, 1989; Scheil et al., 2011), reptiles (Kosh and Hutchison, 1972; Guderley and Seebacher, 2011), birds (McKechnie et al., 2007; Hepp and Kenamer, 2012), and even mammals (Hansen and Boonstra, 2000; Nespolo et al., 2001). Two main forms of plastic responses to thermal stress—hardening and acclimation—have been frequently discussed in previous studies (Fischer et al., 2010; Fischer and Karl, 2010). Hardening is defined as a mechanism by which thermal tolerance is increased under extreme temperatures following a brief pre-exposure (typically for a few hours) to a sub-lethal temperature (Bowler, 2005), whereas acclimation may involve longer periods of pre-exposure, typically for a few days or even weeks (Esperk et al., 2016).

Abbreviations: NA, No acclimation; LA, Low daytime temperature acclimation; HA, High daytime temperature acclimation

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Despite the benefits of heat acclimation on thermal tolerance, heat acclimation is often accompanied by deleterious fitness costs (Hoffmann, 1995; MacLean et al., 2017). These costs, which have been most thoroughly explored in insects, include delayed development (Vladimír and Michaela, 2009; Wang et al., 2015), decreased larval viability and fecundity in *Drosophila* (Loeschcke et al., 1994; Krebs and Feder, 1998), and reduced rates of parasitism in the pest *Trichogramma carverae* (Scott et al., 1997). However, in some studies, acclimation has been reported to occur with low costs (Huey et al., 1995; Minois, 2000), or without any fitness costs at all (Hoffmann and Hewa-Kapuge, 2010). It has been well established that benefits of acclimation vary across exposed conditions (Allen et al., 2012; Alemu et al., 2017) and species (Hazell et al., 2010; Overgaard et al., 2011). And this raises the question of whether fitness costs also associate with the two factors?

Here, we tested whether the fitness costs of plastic responses may vary with acclimation conditions in two cereal aphids—*Sitobion avenae* and *Rhopalosiphum padi*—both of which are important global pests, usually coexist in many cereal-growing regions (Vickerman and Wratten, 1979; Lu et al., 2016), and differ in their temperature preferences. These two species occupy different temporal niches, where *S. avenae* appears earlier in the cereal-growing season, and *R. padi* becomes dominant at the season's end (Asin and Pons, 2001). *Sitobion avenae* is relatively dominant in most temperate regions (e.g., Spokane [47°39' N; Clement et al., 2004], Göttingen [51°32' N; Thies et al., 2005], and Prague [50°05' N; Leslie et al., 2009]), whereas *R. padi* is relatively dominant in higher-temperature regions (e.g. as Yibin [28°46' N; Huang et al., 1996], Santa Maria [29°41' S; Parizoto et al., 2013], and Luxor [25°41' N; Slman, 2006]).

In the present study we addressed the following questions: (1) Does thermal tolerance and acclimation capacity vary with acclimation conditions between the two aphid species? (2) If so, do the fitness costs of plastic responses to temperature exposure vary with acclimation conditions? In order to assess plastic responses in the two aphid species, we investigated adult basal and inducible tolerances by observing CT_{max} (maximum critical temperature [CT_{max}]) and examining fitness traits (proportion of adult emergence, longevity, fecundity, and population parameters) after exposure to three developmental acclimation conditions (22 °C constant temperature, 22 °C + 34 °C for 2 h per day, and 22 °C + 38 °C for 2 h per day).

2. Material and methods

2.1. Insects and rearing

S. avenae and *R. padi* were collected from a wheat field near Linfen, China (35°55'N, 111°16'E) in May of 2016. The two species were sent to the laboratory, where one clone per species was established via parthenogenesis. All aphids were maintained in rearing rooms for more than one year prior to the beginning of experiments, which were performed on 10–20 cm tall wheat seedlings. Pots with seedlings were placed in screened cages (60 × 60 × 60 cm) in controlled rearing rooms (22 ± 0.5 °C, 50–60% relative humidity, with a 16:8 h L:D photoperiod). New seedlings were provided every week.

2.2. Conditions of developmental acclimation

Three climate chambers (RXZ-280B; Jiangnan Ltd., Ningbo, China) were used to program three developmental acclimation conditions during the nymphal period: (1) 22 °C constant temperature (no acclimation: NA), (2) 22 °C + 34 °C for 2 h per day (low daytime temperature acclimation: LA), and (3) 22 °C + 38 °C for 2 h per day (high daytime temperature acclimation: HA) (Fig. 1).

In the NA treatment, the temperature was kept constant at 22 °C throughout the experiment. In the temperature-ramping phase of the LA and HA treatments, temperature was increased linearly from 8:00 h to reach a maximum (34 or 38 °C) at 12:00 h, maintained for 2 h, and

subsequently decreased to 22 °C by 16:00 h. For the remainder of the day, temperature was kept constant at 22 °C. The relative humidity in each chamber was set at approximately 50%. The photoperiod was set to 16 h L: 8 h D, where the light period was from 06:00 to 22:00 h. The temperature in each chamber was recorded at 20 min intervals using data loggers (U23-001; Onset Ltd. Bourne, USA). Differences in the average daily temperatures were small among the three developmental acclimation conditions (22, 24.25, and 25 °C, respectively), where the averages were lower than the optimum temperatures for both species (28.5 °C for *R. padi* and 26.5 °C for *S. avenae*) (Asin and Pons, 2001). Changes in survival and reproductive traits for the two aphids have been shown to be minimal in this temperature range (Asin and Pons, 2001).

2.3. Experimental manipulation

2.3.1. Experiment 1: Effects of developmental acclimation on the CT_{max} of adults

Preliminary experiments were performed in both species to determine the length of time necessary for newly born aphids (< 6 h old) to develop into adults following exposure to the three conditions of developmental acclimation. For all treatments, newly emerged nymphs that had developed into adults were observed beginning on the 7th day, and all nymphs in all treatments had developed into adults by the 9th day.

To test basal and inducible thermal tolerances after exposure to different acclimation conditions, the two species were treated separately to eliminate any possible interspecific competition. For both species, one group of 100 newborn aphids (< 6 h old) was placed in each of the three acclimation chambers at 7:00 h. Aphids in each acclimation chamber were reared on wheat seedlings (height 2–3 cm) in a rearing pot (approximately 50 seedlings per pot) placed inside a screen cage. The seedlings were watered every 2–3 days to maintain freshness. To prevent the aphids from escaping, host plants were not replaced during the experiment.

On the ninth day of the acclimation treatment, 30 adults per acclimation condition were randomly selected, and their CT_{max} was tested as described by Zhao et al. (2017). Briefly, the aphids were placed individually in the holes (diameter 5 mm, depth 5 mm) of a honey comb plate (80 × 80 mm) attached to nylon gauze (200 mesh size) on one side and a transparent plastic board on the other side. The honeycomb plate was placed vertically within a double-glazed container (diameter 100 mm, height 100 mm) heated by a glycol bath (Ministat 230-cc-NR; Huber Ltd., Germany; accuracy ± 0.01 °C). Temperatures in the container were monitored using a thermocouple (Pt100) connected to the bath equipment. After 5 min of equilibration at 22 °C, the temperature was increased at a rate of 0.5 °C min⁻¹ from 22 to 30 °C and then from 30 to 45 °C at 0.1 °C min⁻¹. Aphids were observed for movement using a SONY® video camera (HDR-PJ50E; Sony Corporation, Shanghai, China). The CT_{max} was defined as the temperature at which each aphid last moved its legs or antenna.

2.3.2. Experiment 2: Effects of developmental acclimation on fitness traits

To assess how conditions of developmental acclimation affected fitness traits, 48 newborn nymphs (< 6 h old) from each species were held individually in rearing units until adulthood under the respective acclimation regimes, and subsequently moved to 22 °C (constant temperature conditions) as follows. Rearing units were constructed from hollow plastic tubes (15 mm diameter, 70 mm length), which were sealed by a sponge plug (17 mm diameter, 20 mm length) on the upper end. A single aphid was placed on a newly excised wheat leaf (50 mm length) that was held firmly by a 10 mm slit in another sponge plug (17 mm diameter, 20 mm length) at the bottom of the rearing unit. Twenty-four rearing units were placed separately in the 24 holes (17 mm diameter) of a multiporous lucite plate (200 mm length, 135 mm width) held in a tray containing water deep enough to wet the

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