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Research Article

Thermal tolerance of adult greenbug, *Schizaphis graminum*: Different role of sugars and polyols

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Abstract: The Greenbug *Schizaphis graminum* (Rondani), one of the major pests of cereals, overwinter as adults and nymphs in temperate regions. The aphid population increases in early spring as the weather conditions become favorable, but it gradually decreases in mid-June as air temperature rises. Adult aphid colonies were acclimated to measure cold tolerance at 20, 15, 10, 5, and 0 °C for one week. In contrast, other colonies were acclimated to measure heat tolerance at 20, 25, and 30 °C for one week and 35 °C for two days. Then, the lowest temperature resulting in 50% mortality (LLT_{50}) and the highest temperature resulting in 50% mortality (ULT_{50}) of tested populations were defined. Moreover, changes of sugars and polyols were studied at the end of each thermal regime. The lowest LLT_{50} was -13.2 °C at 0 °C and the highest ULT_{50} was 40.1 °C at 35 °C. In the cold acclimation condition, glucose was the highest at 0 °C and reached to 80.9 µmol/g f.w. However, in the heat acclimation condition, the mannitol was the highest at 35 °C and reached to 43.7 µmol/g f.w. Findings indicate that high temperatures due to climate change could be a threat to aphid population size and distribution.

Keywords: *Schizaphis graminum*, cold tolerance, heat tolerance, glucose, mannitol

Introduction

Greenbug *Schizaphis graminum* (Rondani) is one of the major pests of cereals worldwide. The aphid causes significant damages to cereals especially wheat and barley by feeding on plant sap and transferring viral particles (Blackman and Eastop, 2000; Pendelton *et al*., 2009). Greenbug overwinters as egg in cold regions with sever winters, while spends winter as adults and nymphs in temperate climates (Blackman and Eastop, 2000; Jones *et al*., 2008). According to our observations in Tehran and Karaj, this aphid is anholocyclic and overwinters as adults and nymphs on winter wheat, barley and other Gramineae. Overwintering adults and nymphs are active during cold season, continue to feed and reproduce. The aphid's population increases in early spring as the weather conditions become favorable, but it decreases in mid-June as temperature increases. Seasonal activity of insects including aphids is affected by several biotic and abiotic factors. Among these factors, temperature is the most dominant abiotic factor that affects insects' development, survival, and abundance (Wallner, 1987; Harrington *et al*., 1995; Dixon and Hopkins, 2010). The ability to withstand extremes of low and high temperature plays important role in dynamics of aphids' population (Leather, 1992). Therefore, the thermal tolerance studies may help to

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explain the role of temperature in the seasonal aphid population dynamics.

Previous studies have shown that aphids have supercooling point (SCP) ranging from -19 to -23 °C but die at 7 °C to 10 °C beyond their SCP. Therefore, measurement of SCP is not a good indicator to detect aphids' tolerance to cold (Bale *et al*., 1988; Butts, 1992; Asai *et al*., 2002; Saeidi *et al*., 2012). The lowest temperature causing 50% mortality of tested population (LLT_{50}) is usually used in studies of aphids' thermal tolerance (Bale, 2002; Saeidi *et al*., 2012). Despite the studies of cold tolerance in some aphids, little information is available about aphids' heat tolerance. Considering the increase in global warming, significance of knowing about the heat tolerance and its role in the abundance and distribution of aphids is increasing day by day. In this study, the highest temperature causing 50% mortality of tested population (ULT_{50}) was used as an indicator of heat tolerance.

Similar to other insects, aphids adopt a variety of behavioral and physiological mechanisms to cope with low and high temperature stresses. Synthesis of low molecular weight sugars and polyols including glycerol, trehalose, myo-inositol, mannitol, etc. is one of the most important physiological mechanisms underlying cold and heat tolerance in insects (Storey and Storey, 1991; Košťál *et al*., 2001; Košťál *et al*., 2007; Teets, 2013; Toxopeus *et al*., 2019). Despite many studies on insect species, only a limited number of studies have focused on the relationship between these compounds and aphids thermal tolerance (Saeidi *et al*., 2012; Ghaedi and Andrew, 2016). The objectives of this research were: 1) to study cold and heat tolerance of *S. graminum*, 2) to investigate the major low molecular weight sugars and polyols associated with thermal tolerance.

Materials and Methods

Aphid colony

S. graminum was originally hand-collected from wheat fields in Karaj (35° 48' N, 51° 00' E), Iran, in the spring of 2016, and transferred to the laboratory of Tarbiat Modares University. The aphids were reared on wheat seedlings cultivar 'Pishtaz' grown in plastic pots (10.5 cm in diameter and 9.5 cm in height) and covered with transparent cylindrical plastic containers in a growth chamber set at 20 ± 1 °C, 65 ± 5% RH, and a photoperiod of LD 12:12 h.

Experimental design

In this study, the aphid colonies were cold and heat acclimated to measure cold and heat tolerance. Experiments were run in two series: A) cold acclimation: In this experiment, some plastic pots (10.5 cm in diameter and 9.5 cm in height) of wheat plant cultivar 'Pishtaz' infested with high population of adult aphids of different ages covered with transparent cylindrical plastic were kept at 20 °C and 60 ± 5% RH for one week. The same colony was then transferred successively to temperatures of 15, 10, and 5 °C each for one week, and finally the experiment ended with the transfer of adults to zero °C for one week. The cold acclimation process was done in growth chamber set at LD 8:16h in order to induce winter-like condition (Fig. 1. A). When cold acclimation process was completed, a number of adult aphids (≥ 24 h old) were randomly sampled and survival at subzero temperatures (-7, -10, -13, and -15 °C) was determined (Fig. 1. Aa-Ae). Then, LLT_{50} values were estimated. B) Heat acclimation: In this experiment, adult aphid colonies were transferred from 20 °C (one week) to 25 °C and then 30 °C for one week and subsequently kept at 35 °C for 2 days. The colony was kept at 35 °C for 2 days because a longer period caused more deaths. The acclimation process was done in growth chamber at 60 ± 5% RH and LD 16:8 h in order to induce summer-like condition (Fig. 2. B). Then, a number of adult aphids were randomly sampled from the colony and survival at high temperatures (37, 39, 40, 41, and 42 °C) was determined (Fig. 2. Ba - Bd).

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ULT_{50} values were then estimated. In addition, a number of aphid specimens were weighed and stored at -20 °C to measure sugars and polyols. The thermal regimes as well as duration of acclimation used in this study were designed based on pretested experiments as well as Terblanche *et al.* (2007) and Jumbam *et al.* (2008) works that were appropriate for induction of cold and heat acclimation.

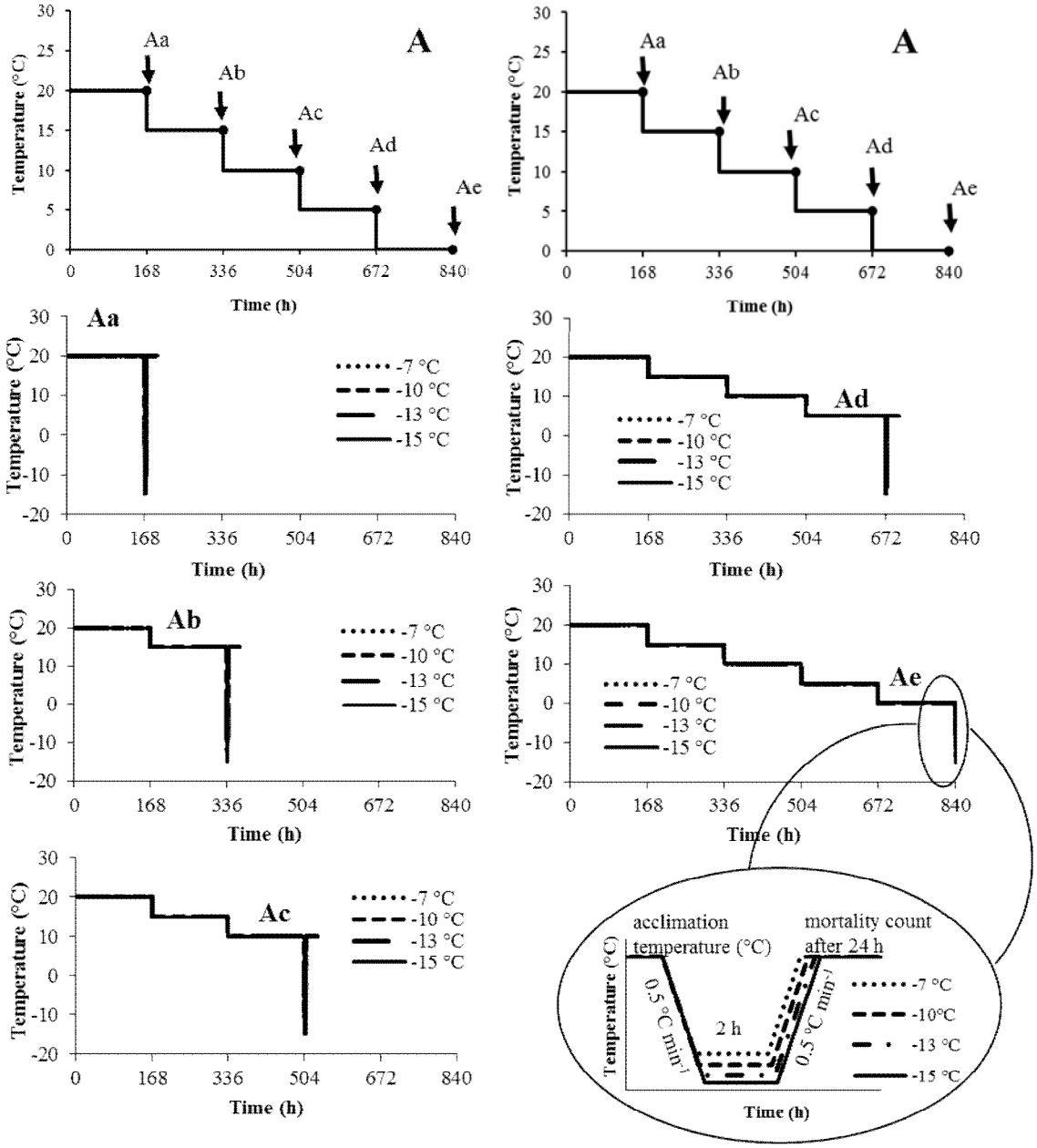

Figure 1 Graphical representation of cold acclimation for measuring the cold tolerance in *Schizaphis graminum*adults. A number of colonies of the aphids were acclimated for one week at low temperatures of 20, 15, 10, 5 and 0 °C (A). Following each cold treatment, survival at subzero temperatures was determined (Aa, Ab, Ac, Ad, Ae) and a number of samples were kept frozen for measurement of sugars and polyols content.

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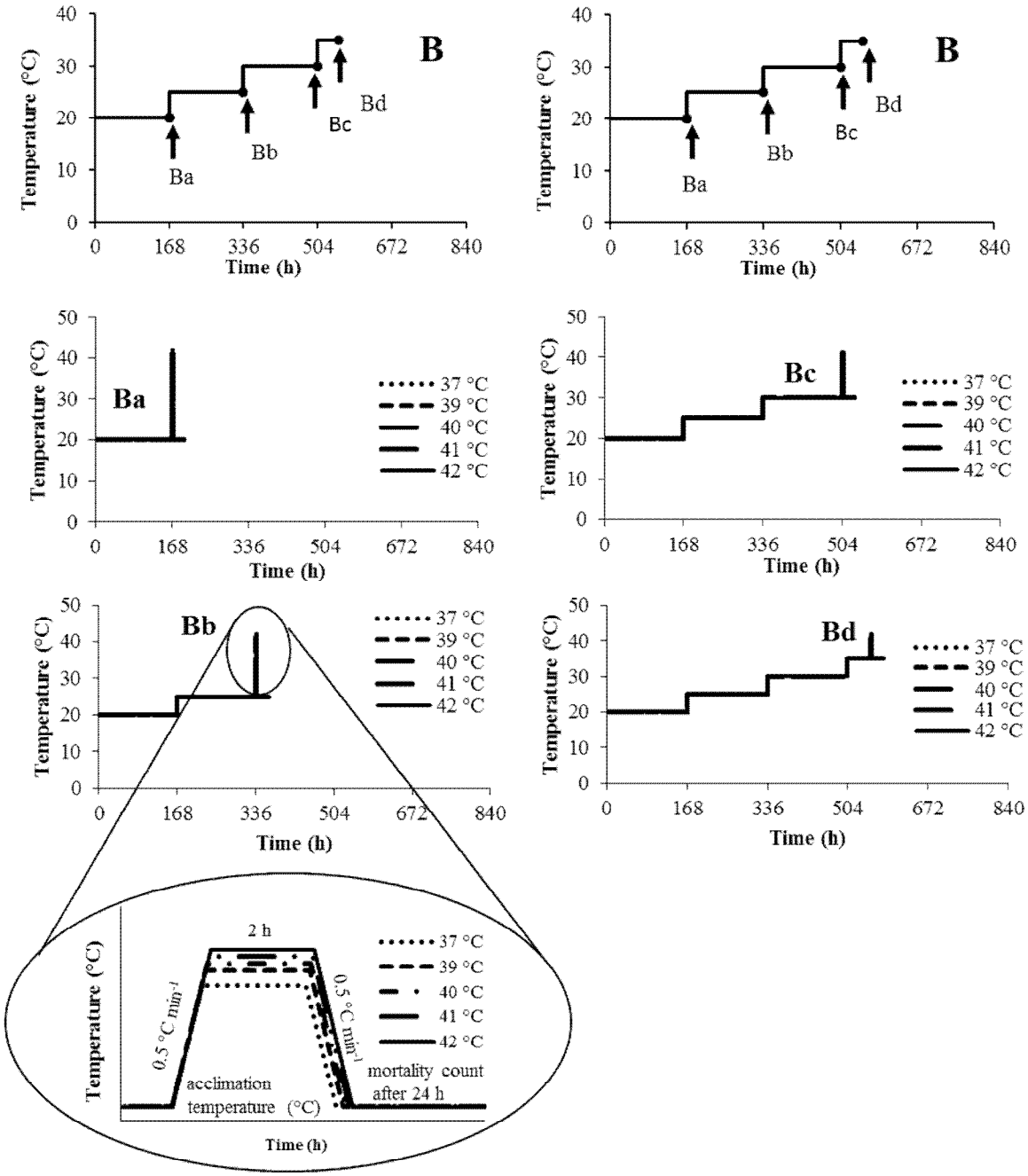

Figure 2 Graphical representation of heat acclimation for measuring the heat tolerance in adult aphids *Schizaphis graminum*. A number of colonies of the aphids were acclimated for one week at high temperatures of 20, 25, 30, and 35 °C for 2 days (B). Following each heat treatment, survival at extreme high temperatures was detemined (Ba, Bb, Bc, Bd) and a number of samples were kept frozen for measurment of sugars and polyols content.

Thermal tolerance assays

Survival at subzero temperatures was determined by exposing adult aphids to -7, -10, -13 and -15 °C for 2 h. Also, survival at high temperatures was determined by exposing adult aphids to 37, 39, 40, 41 and 42 °C for 2 h. Each experiment was performed in 10 replications by placing 10 aphids in each glass tube as 1

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replication, plugged with medical cotton. Samples were transferred to a programmable refrigerated test chamber model MK53 (Binder, Tuttlingen, Germany) in which temperature was lowered or raised at a constant rate of 0.5 °C/min. After 2 h exposure, aphids were returned to the acclimation temperature at the same rate. The mortality count was done 24 h after treatment. Aphids were considered dead when they did not show any movement in the antenna and legs in response to brush stimulation. This data set was used to determine LLT_{50} and ULT_{50} values by the logistic regression method:

$$P(x) = \frac{e^{a+bx}}{1+e^{a+bx}}$$

Where, a is the constant of the equation, b characterizes the coefficient of the predictor variable, x describes the temperature, and P is mortality percent (Saeidi *et al*., 2012).

Measurement of sugars and polyols

Three replicates were used for each treatment in order to measure sugars and polyols. Each sample contained 200 to 250 adult aphids weighing ca. 100 mg. Samples were homogenized in 1.5 ml of 80% ethanol. After centrifugation at 12000 g for 15 min, the supernatant was removed. The extract (ethanol 80%) was evaporated at 30 ºC in a vacuum drying oven (Memmert, VO, 400) and then the residue was dissolved in 300 µl of HPLC grade water. Just before injection, the samples were cleaned by cellulose acetate filter syringe. Sugars and polyols were analyzed using high performance liquid chromatography (HPLC) (Waters, Milford, USA) equipped with Supelco carbohydrate column (300 × 7.8 mm, Supelco, USA). The eluent was HPLC grade water and elution speed was 0.5 ml/min. Sugar and polyols were detected by RI (refractive index) detector (Saeidi *et al*., 2012).

Statistical analysis

Statistical analysis of data was performed by one-way analysis of variance (ANOVA) with a post-hoc Tukey's test at $P < 0.05$ using SPSS version 16.00. The results were expressed as mean ± SE.

Results

Thermal tolerance assays

Survival at: -7 °C ($F = 85.728$; df = 4, 45; $P < 0.0001$), -10 °C ($F = 95.118$; df = 4, 45; $P < 0.0001$),-13 °C ($F = 34.843$; df = 4, 45; $P < 0.0001$), and -15 °C ($F = 29.864$; df = 4, 45; $P < 0.0001$) increased significantly by lowering cold acclimation temperature. The highest survival at subzero temperatures was observed under acclimation at 0 °C for one week (Fig. 3). No significant difference was observed in survival of adult aphids at 37 °C ($F = 0.536$; df = 3, 36; $P = 0.661$), 39 °C ($F = 2.092$; df = 3, 36; $P = 0.118$), and 40 °C ($F = 1.017$; df = 3, 36; $P = 0.359$) between heat acclimation temperature treatments. 50% to 80% of adults could survive high temperatures in all heat acclimation temperatures. Survival at 41 °C showed significant difference between heat acclimation temperatures ($F = 8.08$; df = 3, 36; $P < 0.0001$). Survival at 41 °C was 21% at acclimation temperature of 20 °C but increased significantly to 45% at acclimation temperature of 35 °C. There was no survival at 42 °C for any of the acclimation temperatures (Fig. 4).

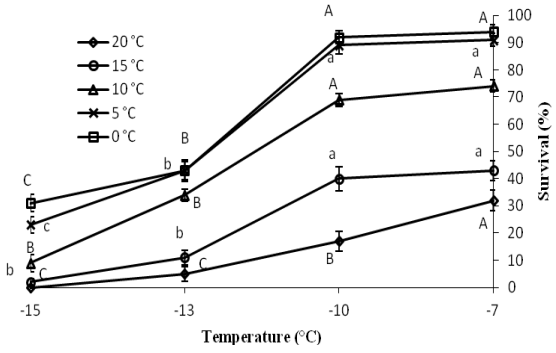

Figure 3 Mean (± SE) percent survival at sub-zero temperatures in adult aphids *Schizaphis graminum* under cold acclimation. For the method refer to Fig. 1. A. Means with the same letters are not significantly different (Tukey's test after ANOVA, $P < 0.05$).

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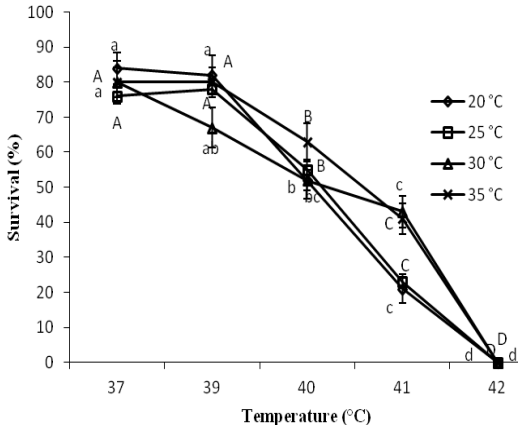

Figure 4 Mean (± SE) percent survival at high temperatures in adult aphids *Schizaphis graminum* under heat acclimation. For the method refer to Fig. 1. B. Means with the same letters are not significantly different (Tukey's test after ANOVA, $P < 0.05$).

LLT_{50} values showed significant difference at cold acclimation temperatures (Table 1). LLT_{50} value was -5.4 °C for 20 °C which dropped significantly to -10.8 °C when acclimated at 10 °C. LLT_{50} value dropped gradually by lowering cold acclimation temperature and reached the lowest value of -13.2 °C when acclimated at 0 °C. ULT_{50} values did not change significantly by increase in heat acclimation temperatures (Table 2). So that, ULT_{50} value was 39.5 °C for acclimation temperature of 20 °C, while it slightly rose to 40.1 °C when acclimated at 35 °C.

Table 1 Changes of LLT_{50} in adult aphid *Schizaphis graminum* under cold acclimation.

Treatments (°C)	95% CI (°C)		
	LLT_{50} (°C)	Lower	Upper
20	-5.4a	-6.3	-3.7
15	-7.1a	-7.7	-6.0
10	-10.8b	-11.0	-10.7
5	-12.7c	-12.8	-12.7
0	-13.2d	-13.2	-13.1

LLT_{50s} followed by the same letters in a column are not significantly different if their 95% confidence intervals (CI) overlap. For the method refer to Fig. 1. A.

Table 2 Changes of ULT_{50} in adult aphid *Schizaphis graminum* under heat acclimation.

Treatments (°C)	ULT_{50} (°C)	95% CI (°C)	
		Lower	Upper
20	39.5a	27.3	57.3
25	39.6a	27.3	57.6
30	39.7a	26.7	59.1
35	40.1a	27.4	58.7

ULT_{50s} followed by the same letters in a column are not significantly different if their 95% confidence intervals (CI) overlap. For the method refer to Fig. 1. B.

Measurement of sugars and polyols

Glucose, trehalose, and mannitol were the major identified sugar and polyols in this research. Glucose content was 36.8 ± 8.6 µmol/g f.w.at 20 °C, which increased under cold acclimation and reached to the highest amount of 80.9 ± 19 µmol/g f.w.at 0 °C, however the changes were not significant ($F = 2.41$; df = 4, 10; $P = 0.118$). Trehalose content was 5.9 ± 5.9 µmol/g f.w.at 20 °C which increased significantly ($F = 37.637$; df = 4, 7; $P < 0.0001$) under cold acclimation and reached to the highest amount of 49.1 ± 4.8 µmol/g f.w at 0 °C. Mannitol content was 3 ± 0.6 µmol/g f.w.at 20 °C, but did not show significant changes($F = 2.85$; df = 4, 10; $P = 0.082$) under cold acclimation (Fig. 5).

Changes of glucose content was not significant ($F = 2.23$; df = 3, 8; $P = 0.162$) under heat acclimation treatment, however, it increased from 36.8 ± 8.6 µmol/g f.w.at 20 °C to 53.07 µmol/g f.w.at 30 °C and then decreased to 26.36 µmol/g f.w.at 35 °C. Changes of trehalose content were significant ($F = 111.84$; df = 3, 8; $P < 0.0001$) and showed a similar trend with changes to glucose. Mannitol content differed significantly under heat acclimation ($F = 392.08$; df = 3, 8; $P < 0.0001$). It was 3 ± 0.6 µmol/g f.w.at 20 °C and reached to the highest amount (43 ± 0.8 µmol/g f.w.) at 35 °C (Fig. 6).

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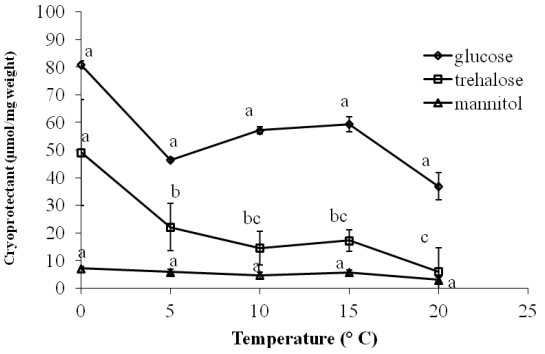

Figure 5 Changes of sugars and polyols as a result of cold acclimation in adult aphids *Schizaphis graminum*. Means with the same letters are not significantly different (Tukey's test after ANOVA, $P < 0.05$).

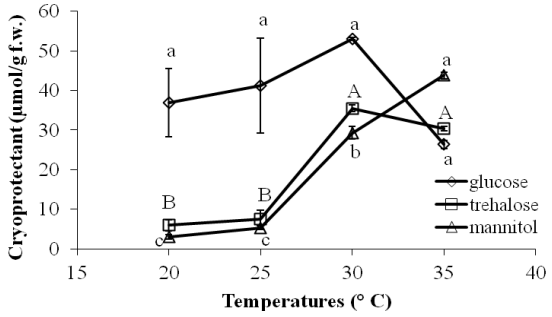

Figure 6 Changes of sugars and polyols as a result of heat acclimation in adult aphids *Schizaphis graminum*. Means with the same letters are not significantly different (Tukey's test after ANOVA, $P < 0.05$).

Discussion

In the present study, cold tolerance of *S. graminum* increased by cold acclimation at low but nonlethal temperatures. The lowest LLT_{50} was -13.2 °C showing that *S. graminum* has a high capacity to tolerate cold temperatures. Due to the global warming and increase in winter temperature, this species can easily survive subzero temperatures at temperate regions like Tehran and Karaj and it can be a source of outbreaks in spring. Findings showed that 42 °C is lethal for *S. graminum*, but 50% of aphids could tolerate temperatures between 39.5 °C to 40.1 °C for 2 h. Based on our observations, the size of aphid population decreases from mid-June when maximum daily temperature exceed 39 °C. Reduction in population size from mid-June can be attributed to the fact that high temperatures experienced in the environment cause a reproduction decrease. Study of Tofangsazi *et al*. (2010) showed that temperatures above 31 °C cause reduction in reproduction.

In this study, glucose and trehalose content decreased at 35 °C. Reduction in reproduction at high temperatures may be related to reduction in nutritional reserves such as carbohydrate contents of the body which needs further investigations. The aphids were exposed to extreme high temperatures just for 2 h in this study, while the duration and frequency of exposure at high temperature is higher in nature. For instance, Rose grain aphid *Methopolophium dirhodum* (Walker) who co-exists with *S. graminum* in wheat fields, 100% death is caused when they were exposed to 34 °C for 8 h (Ma *et al*., 2004). Findings of this study indicated that high temperatures are more threating to *S. graminum* than low temperatures. Therefore, aphids migrate to the lower parts of the plant to avoid high temperatures especially at noon (Ma and Ma, 2012) which should be paid more attention in sampling programs. It is suggested that comprehensive laboratory and field researches are necessary to investigate the effects of high temperatures on *S. graminum* and other aphids.

Glucose, trehalose, and mannitol were the major identified sugars and polyol. Glucose and trehalose content increased by cold acclimation and reached to the highest level at 0 °C, showing the importance role of these compounds in greenbug cold tolerance. In previous studies, glucose was found to be the major cryoprotectant in adults of *B. brassicae* collected in winter (Saeidi *et al*., 2012). The amount of glucose and trehalose initially showed an increasing trend due to heat acclimation, but then decreased considerably at 35 °C. While, the amount of mannitol increased by heat acclimation and reached to the highest amount at 35 °C. It seems that there is a

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negative relationship between mannitol with glucose and trehalose changes at 35 °C. The changes of mannitol due to heat acclimation were much higher than its changes due to cold acclimation. Hendrix and Salvucci (1998) showed that high temperatures (> 35 °C) stimulate mannitol synthesis in *Aphis gossypii* Glover. Mannitol content in aphids collected at noon (temperatures between 38- 42 °C) was considerably higher than morning aphids (Hendrix and Salvucci, 1998). The increase in mannitol at high temperatures may enhance aphid's heat tolerance (Hendrix and Salvucci, 1998).It was reported that polyols like mannitol stabilize the native conformation of proteins, protecting them from thermal denaturation (Wimmer *et al*., 1997). Aphids are phloem-feeding insects that ingest diets rich in sugars. So they tolerate osmotic stress from their diet of concentrated sugar solution and both thermal and water stress in their environment(Hendrix and Salvucci, 1998).This may be suggest that mannitol accumulation at high temperatures may provide a mechanism for thermoprotection and osmoregulation in *S. graminum*. There may be possibility of two pathways for mannitol synthesis: 1) Salvucci (2000), and Hendrix and Salvucci (1998) supposed that sucrose in the gut is converted to glucose and fructose, and then the fructose is used for mannitol synthesis. Therefore, it has been proved that fructose is used as substrate for polyols biosynthesis such as mannitol in many organisms. 2) According to our findings, it may be supposed that reduction in glucose and trehalose content at 35 °C may leads to synthesis of mannitol. Trehalose is a disaccharide composed of two molecules of glucose. Trehalose can be used for synthesis of other sugars and polyols such as mannitol in aphids (Wyatt, 1967) or sorbitol in whiteflies which have thermo-osmoprotective role in these insects (Hendrix and Salvucci, 1998; Wolfe *et al*., 1998).

In this study, sugars and polyols were synthesized under cold and heat acclimation but they played different role in enhancement of cold and heat tolerance. Glucose and trehalose increased under cold acclimation showing the cryoprotectant role of these compounds in *S. graminum*. Mannitol was the other identified polyol which increased considerably under heat acclimation playing important role in heat tolerance. However, further investigations are needed to study metabolisms and pathways of sugars and polyols synthesis under thermal stress in aphids.

Conclusion

Greenbug *S. graminum* showed high capacity to survive subzero temperatures. The high temperatures appear to threaten aphid population size in the future regarding the effects of climate change. Glucose, trehalose, and mannitol were the major identified sugars and together with polyols play important role in the aphid's thermal tolerance.

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تحمل دمایی در حشرات کامل شته معمولی گندم *Schizaphis graminum*: نقش متفاوت قندها و پلی‌ال‌ها

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چکیده: شته معمولی گندم (Rondani) *Schizaphis graminum* یکی از آفات مهم غلات می‌باشد که زمستان را در مناطق معتدل به‌صورت پوره و افراد بالغ سپری می‌کند. جمعیت این شته با مساعد شدن شرایط آب و هوایی در بهار افزایش می‌یابد اما به‌تدریج با گرم شدن هوا از اواسط خردادکاهش می‌یابد. جهت بررسی تحمل دمایی حشرات کامل، کلنی‌هایی از این شته به‌مدت یک هفته در دماهای ۲۰، ۱۵، ۱۰، ۵ و صفر درجه سلسیوس (تیمار سرما) و ۲۰، ۲۵ و ۳۰ درجه سلسیوس و دو روز در دمای ۳۵ درجه سلسیوس (تیمار گرما) قرار داده شدند. در پایان هر یک از تیمارهای سرما، میزان بقا در دماهای زیرصفر و در پایان هر یک از تیمارهای گرما، میزان بقا در دماهای بالا اندازه‌گیری و پایین‌ترین (LLT_{50}) و بالاترین (ULT_{50}) دمای کشنده ۵۰ درصد افراد جمعیت تعیین شد. هم‌چنین روند تغییرات قندها و پلی‌ال‌ها در هر یک از تیمارها مورد بررسی قرار گرفت. کم‌ترین دمای LLT_{50} برابر با ۱۳/۲- درجه سلسیوس در تیمار دمایی صفر درجه سلسیوس و بالاترین دمای ULT_{50} برابر با ۴۰/۱ درجه سلسیوس در تیمار دمایی ۳۵ درجه سلسیوس به‌دست آمد. بیش‌ترین مقدار گلوکز در تیمار دمایی صفر درجه سلسیوس برابر با ۸۰/۹ µmol/g f.w. و بیش‌ترین مقدار مانیتول در تیمار دمایی۳۵ درجه سلسیوس برابر با ۴۳/۷ µmol/g f.w به‌دست آمد. گلوکز مهم‌ترین ترکیب قندی مؤثر در تحمل سرما و مانیتول مهم‌ترین ترکیب قندی مؤثر در تحمل گرما شناسایی شدند. نتایج این مطالعه نشان داد که دماهای بالای ناشی از اثرات تغییرات اقلیمی می‌تواند در آینده به‌عنوان تهدیدی برای جمعیت این شته باشد.

واژگان کلیدی: شته معمولی گندم، تحمل سرما، تحمل گرما، گلوکز، مانیتول

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