J. Crop Prot. 2021, 10 (1): 75-84

Research Article

Rapid cold hardiness response and its ecological costs in Cabbage aphid *Brevicoryne brassicae* (Hemiptera: Aphididae)

Fatemeh Saeidi and Saeid Moharramipour*

Department of Entomology, Faculty of Agriculture, Tarbiat Modares University, Tehran, Iran.

Abstract: Rapid cold hardiness in response to sudden decline in air temperature plays an important role in the aphid survival. Rapid cold hardiness is a phenomenon that increases insect's survival at sub-zero temperatures following a brief exposure to low temperatures above 0 °C. In this regard, the cabbage aphid *Brevicoryne brassicae* (L.) is able to increase its cold hardiness gradually during cold season and produce large population on host plants in Brassicaceae family. In this research, rapid cold hardiness of *B. brassicae*, and its effects on development time, longevity and fecundity were investigated. Direct transfer of aphids from 20 °C to a series of sub-zero temperatures for 2 h, resulted in a LT_{80} (estimated temperature required to kill 80% of tested population) of -7.3 °C. Preconditioning of first instar nymphs for 3 h and adults for 2 h at 0 °C resulted in the highest survival rates of 63% and 71%, respectively. Acclimation of aphids, by a cooling rate of 0.05 °C/min form 20 to 0 °C, prior the exposure to LT_{80} (-7.3 °C) resulted in the highest survival. No detrimental effects of rapid cold hardiness were observed on development time, longevity and fecundity. Results of the present study showed that rapid cold hardiness is induced in *B. brassicae* and increases the aphid survival in response to unexpected changes of temperature.

Keywords: *Brevicoryne brassicae*, rapid cold hardiness, overwintering, cold acclimation

Introduction

The cabbage aphid *Brevicoryne brassicae* (L.) (Hemiptera: Aphididae) is considered as a serious pest of Brassicaceae crops that causes severe damages to these plants throughout the year by feeding and transmitting various plant viruses (Gabrys *et al*., 1997; Ellis *et al*., 1998; Satar *et al*., 2005; Pal and Singh, 2013). *Brevicoryne brassicae* spend the winter as egg in cold regions with severe winters (Gabrys *et al*., 1997; Pal and Singh, 2013), however, in temperate regions with milder winters like Tehran, the aphid overwinters as nymphs and adults on a number of hosts especially ornamental cabbages where the average daily temperature fluctuates from about 22 to 4 °C over the season (Saeidi *et al*., 2012). This strategy of overwintering enables the aphid to make large colonies on winter hosts. Our previous studies showed that this aphid has high capacity to tolerate cold temperatures in Tehran winters. More than 70% of aphids can tolerate -5 °C for 24 h during cold season, but aphid survival at -10 °C showed significant difference during studied months, so that survival at -10 °C/24 h increased from 55% in October and November to 87% in December, remaining steady until March, then decreased

Handling Editor: Azam Mikani

* **Corresponding author:** moharami@modares.ac.ir
Received: 15 August 2020, Accepted: 11 October 2020
Published online: 19 October 2020

in April and May. These results indicated that *B. brassicae* has the ability to develop its cold hardiness gradually by decreasing air temperature during cold seasons (Saeidi *et al*., 2012). However, the ability of the aphid to rapid response to sudden decrease in air temperature plays an important role in its population survival. Studies of rapid cold hardiness are important especially in spring when seasonal cold hardiness is reduced by warming air temperature (Lee and Denlinger, 2010). Rapid cold hardiness is generally acquired by chilling at temperatures between 0 and 10 °C for hours or even minutes, compared to seasonal cold hardiness which can be achieved within weeks or months (Czajka and Lee, 1990; Overgaard *et al*., 2007; Teets and Denlinger, 2013). Studies have shown that cooling at ecologically relevant rates to moderately low temperatures also induces rapid cold hardiness (Lee and Denlinger, 2010). The phenomenon of rapid cold hardening was first described by Lee *et al*. (1987) with the flesh fly, *Sarcophaga crassipalpis* Macquart and has since been described in a wide variety of insect species (Coulson and Bale, 1991; Kelty and Lee, 2001; Powell and Bale, 2004; Yi *et al*., 2007; Ju *et al*., 2011; Overgaard *et al*., 2014; Yang *et al*., 2018).

Rapid cold hardiness studies in aphids have been reported on *Sitobion avenae* (F.) and *Diuraphis noxia* (Kurjomove) (Powell and Bale, 2004, 2005; Saeidi *et al*., 2017). In aphids, population size depends not only on the ability to survive at low temperatures, but also on the ability of survivors to continue feeding and reproducing (Parish and Bale, 1993; Lee and Denlinger, 2010). Therefore, it is necessary to consider the sub-lethal effects of rapid cold hardiness on the size of the population.

Although the cabbage aphid is active in winter with a low population, its population rises sharply early in the spring, but the rapid cold hardiness status of this aphid is still unclear. Therefore, the aim of the present study is to investigate rapid cold hardiness of *B. brassicae* in nymphs and adults and evaluate its impact on development time, longevity and fecundity.

Materials and Methods

Aphid colony

Aphids were collected in the spring of 2010 from ornamental cabbages planted in Tehran and transferred to the laboratory. The aphid population was reared on rapeseed leaf disks (8 cm diameter) (Var. Okapi) in a growth chamber set at 20 ± 1 °C, 50% ± 10% RH, and photoperiod of 16L: 8D h for two generations prior to experiments. Only 24-h-old nymphs (first instar) and prereproductive adults were used for the experiments. Previous studies have shown that cold hardiness of aphids reared at 20 °C was not affected by ageing (Powell and Bale, 2008).

Determination of the LT_{80} value

Lethal temperature to cause 80% mortality (LT_{80}) was used as a discriminating temperature to evaluate rapid cold hardiness response. According to preliminary experiments, rapid cold hardiness response was tested by direct transfer of first instar nymphs and adults from rearing temperature to a range of sub-zero temperatures including -5, -6, -7, -8, and -9 °C for 2 h. Then samples were rewarmed to 20 °C at a rate of 1 °C/min. Aphids were then held at rearing temperature on rapeseed leaf disks (3 cm diameter). The mortality was determined after 24 h, and the LT_{80} value was calculated by binary logistic model. The ability to move was defined as surviving index. The experiment was performed in 10 repetitions each with 10 insects.

Impact of rapid and gradual cold acclimation on rapid cold hardiness response

Experiments were run in two series: 1) rapid cold acclimation experiment was conducted by direct transfer of aphids from 20 °C to 0 °C for varying periods of 0.5, 1, 2, 3, 4, 5 and 6 h prior exposure to LT_{80} level for 2 h (Fig. 1. A), 2) gradual cold acclimation experiment was conducted by cooling aphids from 20 °C to 0 °C at a ramping rate of 1, 0.5, 0.1 and 0.05 °C/min, and then transferred to LT_{80} level for 2

h (Fig. 1. B). Following each treatment, aphids were rewarmed at 1 °C/min and transferred to rearing condition (Powell and Bale, 2004). Each aphid was placed on an individual leaf disk and survival was determined after 24 h and monitored daily for the following experiments. The experiments were carried out in a programmable refrigerated test chamber (Binder, Model MK 53, Germany) which was scheduled to the desired treatment.

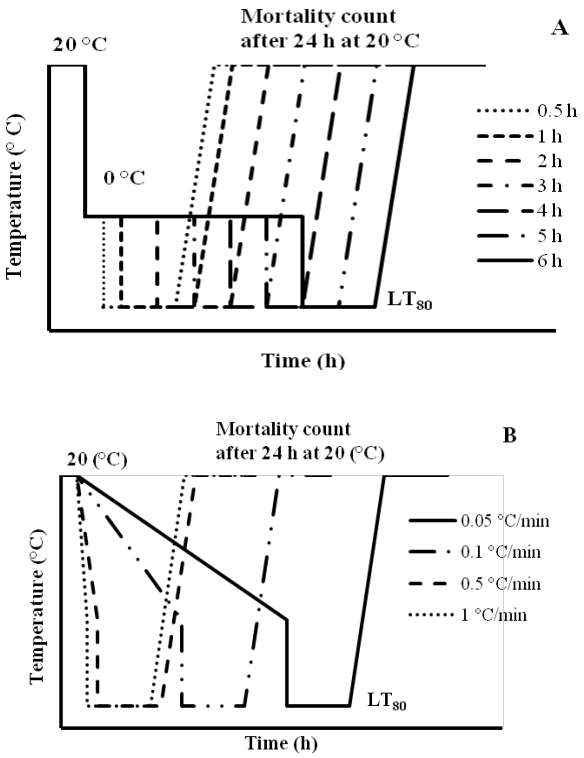

Figure 1 Experimental protocol for impact of rapid and gradual acclimation on rapid cold hardiness of first instar nymphs and adults of *Brevicoryne brassicae* starting from 20 °C. (A) Acclimation at 0 °C for different durations prior transferring to LT_{80} (rapid cold acclimation). (B) Cooling to 0 °C at different cooling rates prior to transferring to LT_{80} (gradual cold acclimation).

Impact of rapid cold hardiness on aphid performance

Survived aphids from previous experiments were monitored daily and development time for nymphs, longevity and fecundity for adults were recorded. The leaf disks (3 cm diameter) containing aphids were placed in a plastic petri dishes and in order to maintain wet and fresh, water was added to the box every day and leaf disks were renewed once a week throughout the study. There were two control groups in this experiment: 1) aphids reared at 20 °C which had never been exposed to cold; 2) cold-shocked aphids (Direct transfer from 20 °C to temperature at LT_{80} level for 2 h) (Powell and Bale, 2004).

Statistical analysis

Statistical analysis of data was performed by one-way analysis of variance (ANOVA) with a post-hoc Tukey's test using SPSS version 16.00. The results were expressed as mean ± SE, and considered significantly different at $P < 0.05$. The parameter LT_{80} was calculated from binary logistic model using the equation:

$$y = \frac{e^{a+bx}}{1+e^{a+bx}}$$

In this equation, *y* is percent survival, *a* and *b* are intercept and slope of the line respectively, *x* indicates the temperature (Vittinghoff, 2005; Rodríguez, 2007).

Results

Aphid cold hardiness at LT_{80} level

The percent mortality of first instar nymphs ($F = 23.773$; df = 3, 36; $p < 0.0001$) and adults ($F = 14.317$; df = 4, 45; $p < 0.0001$) when transferred directly from 20 °C to sub-zero temperatures was significantly different (Fig. 2). The lowest mortality was 58% at -6 °C for nymphs and 42% at -5 °C for adults. The highest mortality was 100% and 96% at -9 °C for nymphs and adults, respectively. According to these results, LT_{80} value for nymphs (-7.28 °C) and adults (-7.26 °C) was rounded to -7.3 °C.

Impact of rapid cold acclimation on rapid cold hardiness

Percent survival of first instar nymphs ($F = 11.967$; df = 7, 72; $P < 0.0001$) and adults ($F = 14.275$; df = 7, 72; $P < 0.0001$) in preconditioned aphids at 0 °C before introduction to -7.3 °C was

significantly different (Fig. 3.). Brief exposure to 0 °C increased survival at -7.3 °C, so that preconditioning of nymphs at 0 °C for 2 h increased survival to 45% and the highest percent survival (63%) was attained as a result of acclimation at 0 °C for 3 h. A similar trend was observed in adults. However, acclimation for 2 h resulted in the highest survival (71%) of adults.

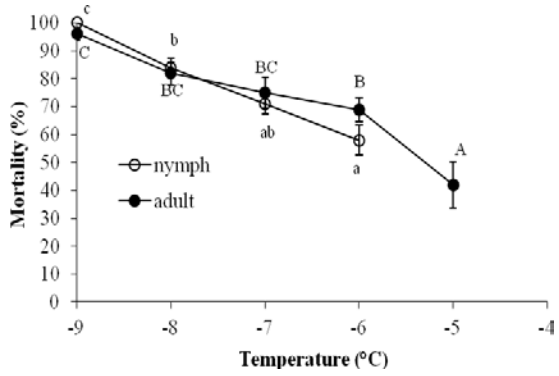

Figure 2 Mean (± SE) percent mortality of first instar nymphs and adults of *Brevicoryne brassicae* directly transferred from 20 °C to a range of subzero temperatures for 2 h to determine LT_{80} value. Means with the same letters (capital letters for adult and lower case letters for nymph) are not significantly different (One-way ANOVA followed by Tukey's test, $P < 0.05$).

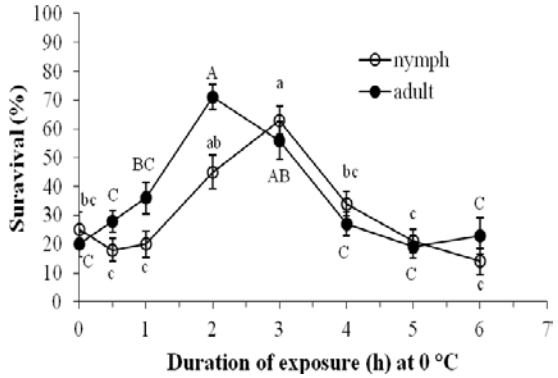

Figure 3 Mean (± SE) percent survival of first instar nymphs and adults of *Brevicoryne brassicae* treated for rapid cold acclimation. For the method refer to Fig. 1. A. Means with the same letters (capital letters for adult and lower case letters for nymph) are not significantly different (One-way ANOVA followed by Tukey's test, $P < 0.05$).

Impact of gradual cold acclimation on rapid cold hardiness

Survival of first instar nymphs ($F = 23.257$; df = 4, 45; $P < 0.0001$) and adults ($F = 42.064$; df = 4, 45; $P < 0.0001$) cooled at various rates from 20 to 0 °C before exposing to -7.3 °C was significantly different (Fig. 4.). Survival of nymphs increased significantly from 17% to 55% by lowering cooling rate from 1 °C/min to 0.1 °C/min and the highest survival rate (82%) was reached at cooling rate of 0.05 °C/min. Similar trend was observed in survival rate of adults. Cooling to 0 °C at 0.05 °C/min showed significant difference with other treatments in adults.

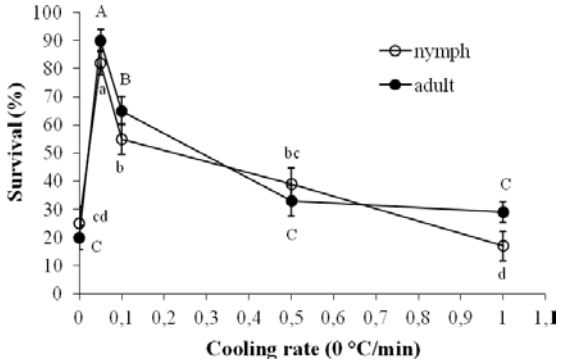

Figure 4 Mean (± SE) percent survival of first instar nymphs and adults of *Brevicoryne brassicae* treated for gradual cold acclimation. For the method refer to Fig. 1. B. Means with the same letters (capital letters for adult and lower case letters for nymph) are not significantly different (One-way ANOVA followed by Tukey's test, $P < 0.05$).

Impact of rapid cold acclimation on aphid performance

No significant difference was observed between development time of nymphs preconditioned at 0 °C during different time periods before transfer to -7.3 °C ($F = 0.835$; df = 8, 212; $P = 0.975$) (Table 1). However, the longevity ($F = 4.973$; df = 8, 317; $P < 0.0001$) and the total fecundity ($F = 2.796$; df = 8, 321; $P = 0.005$) were significantly different (Table 1). The longevity and total fecundity of adult aphids reared at 20 °C were not significantly different

from those treatments induced by rapid cold hardiness.

Table 1 Mean (± SE) development time of first instar nymphs, longevity, and total fecundity of adults of *Brevicoryne brassicae* treated for rapid cold acclimation. For the method refer to Fig. 1. A.

Duration of exposure (h) at 0 °C	Development time (Day)	Longevity (Day)	Fecundity (Nymphs / adult)
C1[1]	9.8 ± 0.3 a	13.4 ± 1.1 a	40.0 ± 3.9a
C2[2]	9.8 ± 0.4 a	6.7 ± 0.1b	20.6 ± 4.6ab
0.5	9.8 ± 0.5 a	7.2 ± 1.0b	21.5 ± 4.6ab
1	9.9 ± 0.4 a	9.2 ± 1.0ab	28.4 ± 4.2ab
2	9.9 ± 3.3a	9.3 ± 1.0ab	27.4 ± 3.0ab
3	10.1 ± 0.3a	8.9 ± 0.9 ab	26.3 ± 3.5ab
4	9.9 ± 0.3a	7.6 ± 1.1 b	23.4 ± 4.7ab
5	10.2 ± 0.4a	6.1 ± 1.0 b	17.5 ± 5.1b
6	10.6 ± 0.7a	6.3 ± 1.0 b	18.4 ± 4.6b

[1] C1: Aphids reared at 20 °C, [2]C2: Cold-shocked aphids. Means with the same letters are not significantly different (One-way ANOVA followed by Tukey's test, $P < 0.05$).

Impact of gradual cold acclimation on aphid performance

Development time of nymphs cooled to 0 °C at various rates (°C/min) before exposure to -7.3 °C was not significantly different (F = 0.027; df = 5, 194; P = 1). The longevity and total fecundity (F = 3.535; df = 5, 273; P = 0.004) of adults cooled to 0 °C at various rates were significantly different (Table 2). The longevity (F = 5.894; df = 5, 271; P < 0.0001) and the total fecundity (F = 3.535; df = 5, 273; P = 0.004) increased by lowering cooling rate. There was no significant difference between longevity and fecundity of adults cooled at 0.1 °C/min and 0.05 °C/min with aphids reared at 20 °C. However, they were significantly different when aphids were treated with cold shocked regimes (Table 2).

Table 2 Mean (± SE) development time of first instar nymphs, longevity, and total fecundity of adults of *Brevicoryne brassicae* treated for gradual cold acclimation. For the method refer to Fig. 1. B.

Cooling rate to 0 (°C / min)	Development time (Day)	Longevity (Day)	Fecundity (Nymph / adult)
C1[1]	9.8 ± 0.3a	13.4 ± 1.1a	40.0 ± 3.9a
C2[2]	9.8 ± 0.4 a	6.7 ± 0.1 c	20.6 ± 4.6a
0.05	9.9 ± 0.2a	11.6 ± 0.7ab	34.5 ± 2.7a
0.1	9.9 ± 0.3a	10.1 ± 0.7abc	32.4 ± 3.2a
0.5	10.0 ± 0.3a	8.7 ± 1.1bc	25.3 ± 4.5a
1.0	10.0 ± 0.5a	7.0 ± 1.1c	19.1 ± 4.6a

[1] C1: Aphids reared at 20 °C, [2]C2: Cold-shocked aphids. Means with the same letters are not significantly different (One-way ANOVA followed by Tukey's test, $P < 0.05$).

Discussion

In this research, LT_{80} value was used as an indicator of rapid cold hardiness response. This value has been used as discriminating temperature for cold shock experiments and different pretreatment temperatures (Powell and Bale, 2004; Wang *et al*., 2011; Saeidi *et al*., 2017; Yang *et al*., 2018). Rapid cold hardiness can be induced by different acclimation temperatures in insect species. In this study, 20% of aphids could survive direct exposure to -7.3 °C/2 h (LT_{80} = -7.3 °C) showing aphids suffer from cold shock injuries. However, rapid acclimation at 0 °C for a short time before exposure to -7.3 °C increased survival. In many insect species, induction of rapid cold hardiness could be accomplished in a period as short as 0.5 h at 0 and 5 °C. In the current study, significant increase in survival of first instar nymphs and adults of *B. brassicae* required at least 2 h exposure at 0 °C. The highest survival was induced by preconditioning of first instar nymphs and adults at 0 °C for 3 h and 2 h, respectively. Acclimation at these thermal regimes increased survival 2.5 fold compared to that of cold shocked aphids. These results show that nymphs and adults have the capacity to

rapidly increase their cold hardiness. Apart from rapid cold acclimation, gradual cooling to 0 °C at rates of 0.1 and 0.05 °C/min increased survival at -7.3 °C. In most studies, rapid cold hardiness was achieved at cooling rate of 0.5 °C/min (Lee and Denlinger, 2010). In our study, lower cooling rates of 0.1 and 0.05 °C/min which usually occur under natural conditions resulted in considerable increase of survival. Our results correspond with the studies of rapid cold hardiness on *D. noxia* and *S. avenae* (Powell and Bale, 2004, 2005; Saeidi *et al*., 2017).

The increased cold tolerance through 2-3 h acclimation at 0 °C or lower cooling rates is likely due to more opportunity the aphids have to activate physiological mechanisms underlying rapid cold hardiness at these thermal regimes. However, acclimation more than 3 h caused reduction in survival which can be related to disadvantages of the additional time spent for inducing rapid cold hardiness. Results suggest that certain periods of exposure to low temperatures are required to induce maximum increase in cold tolerance and extended exposure to low temperatures increases mortality (Wang *et al*., 2011).

Here, we address the question of how long the acquired rapid cold hardiness can last. Additional research is needed to determine if rapid cold hardiness is lost by returning rapid cold hardened aphids to rearing temperature. The physiological and biochemical mechanism underlying rapid cold hardiness response in insects have been well reviewed by Lee and Denlinger (2010), Teets and Denlinger, (2013) and Teets *et al*. (2019). In summary, the elevation of low molecular weight sugars and polyols, increase in two amino acids including alanine and glutamine, increase in cell membrane fluidity, and inhibiting cold-induced apoptosis are important mechanisms that have been documented during rapid cold hardiness response. Pyruvate also increases during rapid cold hardiness, suggesting that this response may favor the glycolytic pathway (Michaud and Denlinger, 2006). There is also an argument over up-regulation of stress related genes (e. g. heat shock proteins) in rapid cold hardiness response (Teets and Denlinger, 2013; Teets *et al*., 2019). However, there is a gap in the study of physiological adjustments of rapid cold hardiness in aphids.

Our previous studies have shown that *B. brassicae* like other aphids such as *S. avenae*, *Myzus persicae* (Sulzer), *D. noxia* is a chill-susceptible insect that dies from cold-shock injuries above their supercooling point (SCP) (Hazell *et al*., 2010; Saeidi *et al*., 2012, 2017; Alford *et al*., 2014). Results obtained from this study showed that nymphs and adults of *B. brassicae* are capable of rapid cold hardening and brief exposure to low temperatures reduces the effects of cold shock injuries occurring at temperatures above SCP. Moreover, there was no significant difference in rapid cold hardiness capacity between nymphs and adults. Despite insect species having diapause during cold season, anholocylic aphids are active over winter and continue feeding and reproduction. Their short life span, make them to pass several generations throughout winter. So, aphids may have a limited ability to cold harden seasonally. It could therefore be argued that rapid cold hardiness is likely more important in aphids including *B. brassicae* (Powell and Bale, 2004). Under natural conditions, environmental temperatures undergo daily fluctuations with higher daytime temperatures than nighttime temperatures. Rapid cold hardiness helps *B. brassicae* to respond to daily fluctuations of ambient temperature, while seasonal cold hardiness is the major response in longer-lived overwintering insects. This research was conducted on laboratory reared aphids at 20 °C. It is suggested that overwintering aphids with natural cold acclimation be investigated during cold season to understand if rapid cold hardiness could be induced in these aphids and to what extent might increase survival. In this study, survived aphids from rapid cold hardiness treatments were maintained to determine if there would be a trade-off between rapid cold hardening capacity and parameters related to population size increase. Longevity and fecundity of adults in rapid and gradual

acclimation treatments showed no significant difference with control aphids reared at 20 °C, indicating that rapid cold hardiness had no deleterious effects on life span and that the survived aphids through rapid cold hardiness have the ability to reproduce and increase their population. Our results are similar with those of Powell and Bale (2004, 2005) and Saeidi *et al*. (2017) who reported no ecological costs of rapid cold hardiness on *S. avenae* and *D. noxia*. Shreve *et al*. (2004) showed positive effects of rapid cold hardiness on fecundity of *Drosophila melanogaster* Meigen. However, our findings are in contrast with Coulson and Bale (1990) which showed reduction of fecundity and life span of housefly *Musca domestica* (L.) in response to rapid cold hardiness. These studies suggest that ecological costs of rapid cold hardiness vary among species (Powell and Bale, 2005), however, the cabbage aphid benefit from severe cold conditions.

It is believed that large amount of insect population dies because of sudden decline in air temperature which occurs especially in late winter or early spring and subsequently, their damages to crops will decrease. Results showed that *B. brassicae* has potential to increase rapidly their cold tolerance, so survival at subzero temperatures increases and survived individuals resettle in conditions where food and air temperature is suitable for activity and reproduction. Therefore, this phenomenon should be considered in aphid population forecasting and pest management particularly in the recent years that global climate warming has caused unexpected temperature fluctuations (Bale, 2002).

Conclusion

B. brassicae has a rapid cold hardening response, which could be induced by a short exposure to 0 °C or through gradual cooling at rates between 0.1 and 0.05 °C/min. There was no trade-off between rapid cold hardiness response and aphids development and reproduction parameters. Rapid cold hardiness is an adaptive response that allows *B. brassicae* to enhance survival in response to unexpected diurnal and possibly seasonal decreases in air temperature.

Conflict of interest

The Authors state that there is no conflict of interest.

Acknowledgements

This work was supported by the Tarbiat Modares University "[82D/2292]" which is greatly appreciated.

References

Alford, L., Andrade, T. H., Georges, R., Burel, F. and Baaren, J. V. 2014. Could behaviour and not physiological thermal tolerance determine winter survival of aphids in cereal fields? Plos One, 9(12): e114982.

Bale, J. S. 2002. Insects and low temperatures: from molecular biology to distributions and abundance. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 357: 849-862.

Coulson, S. J. and Bale, J. S. 1990. Characterisation and limitations of the rapid cold-hardening response in the housefly *Musca domestica* (Diptera: Muscidae). Journal of Insect Physiology, 36: 207-211.

Coulson, S. J. and Bale, J. S. 1991. Anoxia induces rapid cold hardening in the housefly *Musca domestica* (Diptera: Muscidae). Journal of Insect Physiology, 37(7): 497-501.

Czajka, M. C. and Lee, R. E. 1990. A rapid cold hardening response protecting against cold shock injury in *Drosophila melanogaster*. Journal of Experimental Biology, 148: 245-254.

Ellis, P. R., Pink, D. A. C., Phelps, k., Jukes, P. L., Breeds, S. E. and Pinnegar, A. E. 1998. Evaluation of a core collection of brassicae accessions for resistance to *Brevicoryne brassicae*. Euphytica, 103: 149-160.

Gabrys, B. J., Gadomski, H. J., Klukowski, Z., Pickett, J. A., Sobota, G. T., Wadhams, L. J. and Woodcock, C. M. 1997. Sex pheromone of cabbage aphid *Brevicoryne brassicae*:

identification and field trapping of male aphids and parasitoids. Journal of Chemical Ecology, 23: 1881-1890.

Ju, R. T., Xiao, Y. Y. and Li, B. 2011. Rapid cold hardening increases cold and chilling tolerances more than acclimation in the adults of the sycamore lace bug, *Corythucha ciliata* (Say) (Hemiptera: Tingidae). Journal of Insect Physiology, 57: 1577-1582.

Kelty, J. D. and Lee, R. E. 2001. Rapid cold-hardening of *Drosophila melanogaster* (Diptera: Drosophilidae) during ecologically based thermoperiodic cycles. Journal of Experimental Biology, 204: 1659-1666.

Lee, R. E. and Denlinger, D. L. 2010. Rapid cold-hardening: ecological significance and underpinning mechanisms. In: Denlinger, D. L. and Lee, R. E. (Eds.), Low Temperature Biology of Insects. Cambridge, UK: Cambridge University Press. pp. 35-58. doi: 10.1017/CB09780511675997.003.

Lee, R. E., Chen, C. P. and Denlinger, D. L. 1987. A rapid cold-hardening process in insects. Science, 238: 1415-1417.

Michaud, M. R. and Denlinger, D. L. 2006. Oleic acid is elevated in cell membranes during rapid cold-hardening and pupal diapause in the flesh fly, *Sarcophaga crassipalpis*. Journal of Insect Physiology, 52: 1073-1082.

Overgaard, J., Malmendal, A., Sorensen, J. G., Bundy, J. G., Loeschcke, V., Nielsen, N. C. and Holmstrup, M. 2007. Metabolomic profiling of rapid cold hardening and cold shock in *Drosophila melanogaster*. Journal of Insect Physiology, 53: 1218-1232.

Overgaard, J., Sorensen, J. G., Comc, E. and Colinet, H. 2014. The rapid cold hardening response of *Drosophila melanogaster*: Complex regulation across different levels of biological organization Journal of Insect Physiology, 62: 46-53.

Pal, M. and Singh, R. 2013. Biology and Ecology of the cabbage aphid, *Brevicoryne brassicae* (L.) (Homoptera: Aphididae): A review. Journal of Aphidology, 27: 59-78.

Parish, W. E. G. and Bale, J. S. 1993. Effects of brief exposures to low temperature on the development, longevity and fecundity of the grain aphid *Sitobion avenae* (Hemiptera: Aphididae). Annals of Applied Biology, 122: 009-021.

Powell, S. and Bale, J. S. 2004. Rapid cold hardening increases the survival and fecundity of overwintering aphids. Outlooks on Pest Management, 15: 165-166.

Powell, S. J. and Bale, J. S. 2005. Low temperature acclimated populations of the grain aphid *Sitobion avenae* retain ability to rapidly cold harden with enhanced fitness. Journal of Experimental Biology, 208: 2615-2620.

Powell, S. J. and Bale, J. S. 2008. Intergenerational acclimation in aphid overwintering. Ecological Entomology, 33: 95-100.

Rodríguez, G. 2007. Lecture notes on generalized linear models. Available from: http://data.princeton.edu/wws509/notes/.

Saeidi, F., Moharramipour, S. and Barzegar, M. 2012. Seasonal patterns of cold hardiness and cryoprotectant profiles in *Brevicoryne brassicae* (Hemiptera: Aphididae). Environmental Entomology, 41: 1638-1643.

Saeidi, F., Moharramipour, S. and Mikani. A. 2017. Rapid cold Hardening capacity and its impact on Performance of Russian Wheat Aphid (Hemiptera: Aphididae). Environmental Entomology, 46(4): 954-959.

Satar, S., Kersting, U. and Ulusoy, M. R. 2005. Temperature dependent life history traits of *Brevicoryne brassicae* (L.) (Hom., Aphididae) on white cabbage. Turkish Journal of Agriculture and Forestry, 29: 341-346.

Shreve, S. M., Kelty, J. D. and Lee, R. E. 2004. Preservation of reproductive behaviors during modest cooling: rapid cold-hardening fine-tunes organismal response. Journal of Experimental Biology, 207(11): 1797-1802.

Teets, N. M. and Denlinger, D. L. 2013. Physiological mechanisms of seasonal and rapid cold-hardening in insects. Physiological Entomology, 38: 105-116.

Teets, N. M., Kawarasaki, Y., Potts, L. J., Philip, B. N., Gantz, J. D., Denlinger, D. L. and Lee Jr, R. E. 2019. Rapid cold hardening protects against sublethal freezing

injury in an Antarctic insect. Journal of Experimental Biology, 222: jeb206011. doi:10.1242/jeb.206011.

Vittinghoff, E., Glidden, D., Shiboski, S. and McCulloch, C. 2005. Regression methods in biostatistics: linear, logistic, survival and repeated measures models. Springer Science Business Media, New York.

Wang, H., Lei, Z., Li, X. and Oetting, R. D. 2011. Rapid cold hardening and expression of heat shock protein genes in the b-biotype *Bemisia tabaci*. Environmental Entomology, 40: 132-139.

Yang, G., Wen, J., Han, Y. and Hou, M. 2018. Rapid Cold Hardening Confers a Transient Increase in Low Temperature Survival in Diapausing *Chilo suppressalis* Larvae. Insects. 53(9): 1-8.

Yi, S.-X., Moore, C. W. and Lee, R. E. 2007. Rapid cold-hardening protects *Drosophila melanogaster* from cold-induced apoptosis. Apoptosis,12: 1183-1193.

واکنش سریع به دماهای پایین و اهمیت اکولوژیکی آن در شته مومی کلم *Brevicoryne brassicae* (L.)

فاطمه سعیدی و سعید محرمی‌پور*

گروه حشره‌شناسی کشاورزی، دانشکده کشاورزی، دانشگاه تربیت مدرس، تهران، ایران.
پست الکترونیکی نویسنده مسئول مکاتبه: moharami@modares.ac.ir
دریافت: ۲۵ مرداد ۱۳۹۹؛ پذیرش: ۲۰ مهر ۱۳۹۹

چکیده: توانایی سرماسختی سریع نقش مهمی در بقای شته‌ها ایفا می‌کند. سرماسختی سریع پدیده‌ای است که بقای حشرات در دماهای زیر صفر را پس از قرار گرفتن به‌مدت کوتاه در دماهای پایین افزایش می‌دهد. با توجه به این موضوع، شته مومی کلم، *Brevicoryne brassicae* (L.) قادر است سرماسختی خود را طی فصل سرما به‌تدریج بالا برده و جمعیت انبوهی روی گیاهان خانواده کلمیان ایجاد کند. در این تحقیق، سرماسختی سریع در شته مومی کلم و اثرات آن روی طول دوره رشد، طول عمر و باروری مورد بررسی قرار گرفت. زمانی‌که شته‌های پرورش داده شده در دمای ۲۰ درجه سلسیوس به‌طور مستقیم در معرض یک‌سری از دماهای زیرصفر قرار گرفتند، مقدار LT_{80} (دمای لازم برای مرگ‌ومیر ۸۰ درصد افراد جمعیت مور آزمایش) برابر با ۷/۳- درجه سلسیوس به‌دست آمد. اما قرار دادن پوره‌ها به‌مدت ۳ ساعت و افراد بالغ به‌مدت ۲ ساعت در دمای صفر درجه سلسیوس، قبل از انتقال به ۷/۳- درجه سلسیوس منجر به افزایش بقا به بیش‌ترین مقدار به‌ترتیب برابر با ۶۳ و ۷۱ درصد شد. سرمادهی شته‌ها از دمای ۲۰ به صفر درجه سلسیوس با سرعت ۰/۰۵ °C/min قبل از انتقال به ۷/۳- درجه سلسیوس نیز سبب به‌دست آمدن بالاترین میزان بقا شد. هیچ‌گونه اثرات زیان‌باری از سرماسختی سریع روی طول دوره رشد، طول عمر و باروری افراد بالغ مشاهده نشد. نتایج مطالعه حاضر نشان داد که شته مومی کلم ظرفیت سرماسختی سریع را داشته و می‌تواند در واکنش به تغییرات ناگهانی و غیرقابل پیش‌بینی دمای محیط بقا را افزایش دهد.

واژگان کلیدی: شته مومی کلم، سرماسختی سریع، زمستان‌گذرانی، سازش سرمایی