Shahid Bahonar University of Kerman

Journal of Advances in Plant Protection

JAPP 2023

Association of Iranian Plant Protection Societies

Effects of climate change on overwintering survival of *Eurytoma amygdali* Enderlein (Hymenoptera: Eurytomidae) larvae

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Article Info.

Article type:
Original article

Article history:
Received 02 May 2026
Received in revised form 08 Jun. 2026
Accepted 15 Jun. 2026
Available Online 15 Jun. 2026

Keywords:
Almond seed wasp,
Eurytoma amygdali,
Larval microhabitat,
Low temperature exposure,
Overwintering survival,
Temperature fluctuations.

Abstract

The almond seed wasp (*Eurytoma amygdali*) is a serious pest of almond orchards, causing significant yield losses through larval feeding inside kernels. This study examined the effects of low-temperature exposure duration, larval microhabitat position, and temperature fluctuations on overwintering larval survival under field and laboratory conditions in an almond orchard in Kerman Province, Iran. In the first experiment, infested fruits were exposed to −18 °C for 12 days under different placement conditions (air suspension, soil surface, dry soil, and moist soil). In the second experiment, larvae were subjected to fluctuating temperature regimes for 27 days to simulate winter conditions. Results showed that prolonged exposure to severe cold significantly reduced larval survival, with strong effects of microhabitat. Larvae in fruits placed on the soil surface exhibited the highest survival under freezing conditions. In contrast, those buried in dry soil showed the highest mortality, with survival declining more rapidly over time. In the temperature fluctuation experiment, the highest survival rate was observed under natural orchard conditions (90.00 ± 3.02%), whereas the lowest was in the alternating freezer–orchard treatment (58.00 ± 4.90%). Significant differences were observed among treatments, indicating strong effects of thermal regime on survival. Overall, the findings demonstrate that both microhabitat characteristics and temperature stability are key determinants of overwintering survival in *E. amygdali*, providing valuable insights for predicting population dynamics and improving integrated pest management strategies under changing climatic conditions.

Cite this article: Nikooei, S., Ahmadi, K., & Asadi, M. (2026). Effects of climate change on overwintering survival of *Eurytoma amygdali* Enderlein (Hymenoptera: Eurytomidae) larvae. *Journal of Advances in Plant Protection*, *3*(1), 9–18.

Publisher: Shahid Bahonar University of Kerman

Introduction

Eurytoma amygdali Enderlein (Hymenoptera, Eurytomidae) (the almond seed wasp) is a significant pest affecting almond crops in several regions, including the Middle East and Central Asia (Abdul-Rassoul & Mohammed, 2017; Ibrahim et al., 2008; Khanmohamadi et al., 2016; Zerova & Fursov, 1991), Southeastern Europe (Skendžić et al., 2021; Haltrich & Viktor, 1998), Mediterranean countries (Arambourg et al., 1983), as well as Azerbaijan, Armenia, Georgia (Zerova & Fursov, 1991), and Romania (Cioaca et al., 2022). It also poses a potential invasion risk to almond-growing areas where it has not yet been detected, including the United States (California), Australia (PHA, 2013), and northern Africa. Recently, *Eurytoma tomentosae* sp. nov., a newly described species belonging to the *Eurytoma amygdali* species group, has been identified in South Korea (Park & Lee, 2021). Females use their long ovipositors to lay eggs in green, unripe almonds (Kouloussis & Katsoyannos, 1991). The newly hatched larvae feed on the kernel and embryo sac of the almond, completing their development by mid-summer before entering diapause (Duval & Millan, 2010; Margaritopoulos & Tzanakakis, 2006). This species can destroy up to 90% of the almond crop (Mohamadi Khoramabadi & Arzani, 2009). The larvae remain inside the damaged almond shell, which often becomes mummified on the trees (Kouloussis, 2008). Pupation occurs from late winter to early spring, and adults emerge by creating an exit hole in the almond shell (Rodrigo et al., 2024). Prolonged exposure to cold or heat, temperature variations, and sudden cold shocks can negatively affect multiple biological and physiological functions in ectothermic animals like insects (Teets & Denlinger, 2013; Daly et al., 2024). In insect ecology, cold hardiness is categorized into two strategies: freeze tolerance and freeze avoidance through supercooling (Sinclair et al., 2015). However, applying this concept to insect overwintering survival remains challenging due to variations in climatic conditions and complexities in accurately measuring cold hardiness (Bale, 1996). Insect species are protected against cold by physiological mechanisms, the intensity of which varies depending on the climatic conditions and the duration of exposure to low temperatures (Turnock & Fields, 2005). The overwintering site significantly affects survival rates under extreme cold conditions (Lombardero et al., 2000). Also, temperature changes during acclimation, especially mild and fluctuating temperatures, can significantly improve insect survival when exposed to cold stress (Khodayari et al., 2025). These temperature variations help insects better adapt to cold conditions and increase their chances of surviving severe or prolonged cold (Khodayari et al., 2025). The effect of temperature during winter conditions on the survival rate of larvae of the genus *Eurytoma* has been studied by various experts (Damanabi et al., 1980; Roshandel & Noorbakhsh, 2005; Khanmohamadi et al., 2016; Mohammadzadeh et al., 2017; Nguyen & Hong, 2023; Ahmadi & Nikooei, 2025).These studies have shown that the environmental temperature and its fluctuations throughout the winter play an important role in larval survival and can either increase or decrease their survival rates (Ahmadi & Nikooei, 2025). Cold temperatures can significantly influence the distribution and impact of pest insects by reducing outbreak sizes or even ending them, although accurately assessing their effects is challenging since insect mortality estimates are usually made at the end of winter (MacQuarrie et al., 2024).

In this study, the effects of severe cold, duration of exposure to low temperatures, larval position within the almond orchard, and temperature fluctuations on the overwintering survival of almond seed wasp (ASW) larvae were investigated. The aim was to gain a better understanding of how these factors influence larval survival, to explore their implications for improving pest management strategies under changing climatic conditions.

Material and Methods

The experiments were conducted in an almond orchard located in Farrokh Dasht Village, 2 km south of Bardsir, Kerman Province, Iran (29°55′N, 56°34′E), at an elevation of 2000 m above sea level. The climate in this area is moderate, characterized by cool and mild summers and cold winters. The almond cultivar in this orchard was “Kaghazi” or “Yalda almond,” and the soil texture was sandy. The orchard was irrigated by flooding. This study was carried out in the form of two experiments as described below.

First experiment: evaluation of the effect of the location of infested almond fruits containing larvae of the almond seed wasp on larval survival under severe frost conditions

To investigate the impact of the location of infested almond fruits on the survival of the pest larvae, on December 23, 2024, infested fruits containing the larvae were collected from the above-mentioned orchard. The infested fruits were placed in mesh bags (each containing 12 fruits). Before starting the experiment, the percentage of live larvae in the almond fruits was recorded. These mesh bags had proper ventilation and were considered experimental units, with ten replicates. A temperature of -18 °C in a freezer was used to simulate artificial severe frost conditions, and the experiment included the following treatments:

1- Mesh bags containing the infested almonds suspended in the air (SIA): From December 23, 2024 to January 3, 2025, for a duration of 12 days (288 hours), the mesh bags containing the infested almond fruits were hung in the freezer at a temperature of -18 °C.

2- Mesh bags containing the infested almonds placed on the soil surface (POSS): In this treatment, cylindrical plastic containers with a diameter of 12 cm and a height of 9 cm were filled with soil. Then, the infested almonds were placed on the soil surface of these containers and kept in the freezer at -18 °C for 12 days.

3- Infested almonds buried in dry soil (BDS): In this treatment, the infested almonds were buried inside the dry soil of the same plastic containers mentioned in the second treatment and stored in the freezer at -18 °C for 12 days.

4- Infested almonds buried in moist soil (BMS): This treatment was conducted in the same way as the previous treatment, except that the containers were filled with moist soil. The soil moisture content was maintained between 20 and 30%.

After 24 hours from the start of each treatment, one infested almond fruit from each mesh bag was randomly selected and transferred to the laboratory. The infested fruit was carefully dissected using a scalpel to expose the larvae, which were then gently extracted from the tissue without causing any damage using a fine soft brush or delicate forceps. The larvae from each treatment were subsequently transferred intact into separate Petri dishes and maintained at room temperature. Once the larvae became active and started moving, their survival rates were recorded. The daily survival rate was determined in the same way as previously described. In this experiment, because larval survival had to be assessed outside the fruit and it was not possible to continue keeping the larvae alive in the experiment, all live and dead larvae were removed from the study after the initial survival evaluation.

Second experiment: Investigation of the effect of temperature fluctuations on the survival rate of the almond seed wasp

To examine the impact of temperature changes on the pest's survival, on December 23, 2024, infested almond fruits containing larvae were collected from the aforementioned orchard and placed in mesh bags, each containing ten fruits. During the experiment, regional meteorological data for the area where the orchard is located were obtained from the local weather station (Table 1). These mesh bags had adequate ventilation and were considered as experimental units with ten replicates. Based on the climatic conditions of the region and to simulate different temperature variations (Table 2), the experiment included the following treatments:

1- Treatment of orchard conditions (T_1): From December 23, 2024, to January 18, 2025, for a period of 27 days, mesh bags containing infested almond fruits were randomly hung suspended on the branches of almond trees in the orchard mentioned above.

Table 1. Regional meteorological data recorded during the experimental period at the orchard site (Data obtained from the local meteorological station, 2024 & 2025).

Date	Max Temperature (°C)	Average Temperature (°C)	Min Temperature (°C)	Average Relative Humidity (%)	Average Wind Speed (m/s)	Precipitation (mm)	Weather Condition
22 Dec 2024	7	-1.3	-8	52	2.4	1.1	Clear
23 Dec 2024	11	1.0	-11	50	2.6	0.0	Partly Cloudy
24 Dec 2024	14	1.6	-10	48	2.5	0.0	Partly Cloudy
25 Dec 2024	10	1.2	-9	46	2.7	0.0	Clear
26 Dec 2024	8	0.1	-9	44	2.8	0.0	Clear
27 Dec 2024	11	0.8	-10	42	3.0	0.0	Clear
28 Dec 2024	15	4.9	-11	40	3.1	0.0	Partly Cloudy
29 Dec 2024	14	12.0	4	41	2.9	0.0	Partly Cloudy
30 Dec 2024	13	11.5	5	43	2.7	0.0	Clear
31 Dec 2024	8	8.5	6	45	2.6	0.0	Clear
1 Jan 2025	2	3.9	0	47	2.5	0.0	Partly Cloudy
2 Jan 2025	0	-4.8	-7	49	2.4	0.0	Partly Cloudy
3 Jan 2025	1	-3.7	-9	51	2.3	0.0	Clear
4 Jan 2025	1	-5.2	-12	53	2.2	0.0	Clear
5 Jan 2025	6	-2.1	-7	55	2.1	0.0	Clear
6 Jan 2025	13	2.4	-5	54	2.2	0.0	Partly Cloudy
7 Jan 2025	11	2.5	0	52	2.3	0.0	Partly Cloudy
8 Jan 2025	5	-1.3	-3	50	2.4	0.0	Clear
9 Jan 2025	2	-2.8	-4	48	2.5	0.0	Clear
10 Jan 2025	7	-1.9	-4	46	2.6	0.0	Clear
11 Jan 2025	12	1.4	-4	44	2.7	0.0	Partly Cloudy
12 Jan 2025	11	2.5	-2	42	2.8	0.0	Partly Cloudy
13 Jan 2025	7	1.4	-1	40	2.9	0.0	Clear
14 Jan 2025	6	-1.9	-4	41	2.8	0.0	Clear
15 Jan 2025	9	0.1	-4	43	2.7	0.0	Partly Cloudy
16 Jan 2025	12	4.5	-6	45	2.6	0.0	Partly Cloudy
17 Jan 2025	9	2.9	0	47	2.5	0.0	Clear

Table 2. Daily temperature profiles for each treatment during the larval survival study from December 22, 2024 to January 17, 2025

Date	Treatments (°C)			
	T_1	T_2	T_3	T_4
22 Dec 2024	-1.3	-8	-8	-8
23 Dec 2024	1.0	-8	-8	-8
24 Dec 2024	1.6	-8	-8	-8
25 Dec 2024	1.2	-8	-8	-8
26 Dec 2024	0.1	-8	-8	-8
27 Dec2024	0.8	-8	-8	-8
28 Dec 2024	4.9	-8	-8	-8
29 Dec 2024	12.0	-8	-8	-8
30 Dec 2024	11.5	-8	-8	-8
31 Dec 2024	8.5	8.5	24	8.5
1 Jan 2025	3.9	3.9	24	3.9
2 Jan 2025	-4.8	-4.8	24	-4.8
3 Jan 2025	-3.7	-3.7	24	-3.7
4 Jan 2025	-5.2	-5.2	24	-5.2
5 Jan 2025	-2.1	-2.1	24	-2.1
6 Jan 2025	2.4	2.4	24	2.4
7 Jan 2025	2.5	2.5	24	2.5
8 Jan 2025	-1.3	-1.3	24	-1.3
9 Jan 2025	-2.8	-8	-2.8	24
10 Jan 2025	-1.9	-8	-1.9	24
11 Jan 2025	1.4	-8	1.4	24
12 Jan 2025	2.5	-8	2.5	24
13 Jan 2025	1.4	-8	1.4	24
14 Jan 2025	-1.9	-8	-1.9	24
15 Jan 2025	0.1	-8	0.1	24
16 Jan 2025	4.5	-8	4.5	24
17 Jan 2025	2.9	-8	2.9	24
Mean	1.41	-5.33	5.56	5.34

2- Treatment of 9 days freezer – 9 days orchard temperature – 9 days freezer (T_2): In this treatment, mesh bags containing infested fruits were suspended in a freezer at -8 °C for 9 days starting December 23, 2024. Then, from January 1, 2025, for 9 days, they were randomly hung suspended on the branches of almond trees in the orchard. Finally, from January 10, 2025, for 9 days, the bags were again suspended in the freezer at.-8 °C.

3- Treatment of 9 days freezer – 9 days room temperature – 9 days orchard temperature (T_3): In this treatment, mesh bags with infested fruits were suspended in a freezer at -8 °C for 9 days from December 23, 2024. Then, from January 1, 2025, for 9 days, they were suspended at room temperature (average 24 °C). Finally, from January 10, 2025, for 9 days, the bags were randomly hung suspended on almond tree branches in the orchard.

4- Treatment of 9 days freezer – 9 days orchard temperature – 9 days room temperature (T_4): In this treatment, mesh bags with infested fruits were suspended in a freezer at -8 °C for 9 days from December 23, 2024. Then, from January 1, 2025, for 9 days, they were randomly hung suspended on almond tree branches in the orchard. Finally, from January 10, 2025, for 9 days, the bags were suspended at room temperature.

After the completion of each treatment period, the infested fruits were transferred to the laboratory, and the larvae inside them were carefully removed without damage. The larvae from each treatment were separately placed in individual Petri dishes at room temperature. Once they became active and started moving, the survival rate of each treatment was calculated.

Data analysis

Statistical analyses of the experiments conducted in this study were performed using Stat Plus software (2009 version). In the first experiment, the means and standard errors of the survival percentages were calculated. Subsequently, a linear regression analysis was conducted to evaluate the relationship between larval survival rate and the duration of exposure to cold conditions. In the second experiment, initial calculations of means were followed by assessment of differences between these means. Statistically significant differences among means were determined at the 5% significance level. For laboratory investigations, comparison of means was carried out using one-way analysis of variance (One-Way ANOVA) followed by Fisher's Least Significant Difference (LSD) test, with significance assessed at $P \leq 0.05$.

Results

First experiment: Impact of the location of almond fruits containing larvae on the survival rate of almond seed wasp larvae under severe frost conditions

The results concerning the impact of the placement method of almond fruits containing larvae (SIA: Suspended in the Air; POSS: Placed on Soil Surface; BDS: Buried in Dry Soil; BMS: Buried in Moist Soil), which were exposed to a temperature of -18 °C for 12 days, are presented in Fig. 1. The overall results indicate that increasing the duration of exposure of almond fruits containing larvae to -18°C significantly reduced the larval survival rate of the almond seed wasp. This decline in survival varied among treatments. The treatment where fruits were placed on the soil surface (POSS) showed the least negative slope in the regression, indicating a slower decrease in larval survival and thus higher survival rates compared to other treatments. In contrast, the treatment with fruits buried in dry soil (BDS) exhibited the steepest negative slope, reflecting the fastest decrease in survival and the greatest larval mortality. The suspended in air (SIA) and buried in moist soil (BMS) treatments showed intermediate decreases in survival rates.

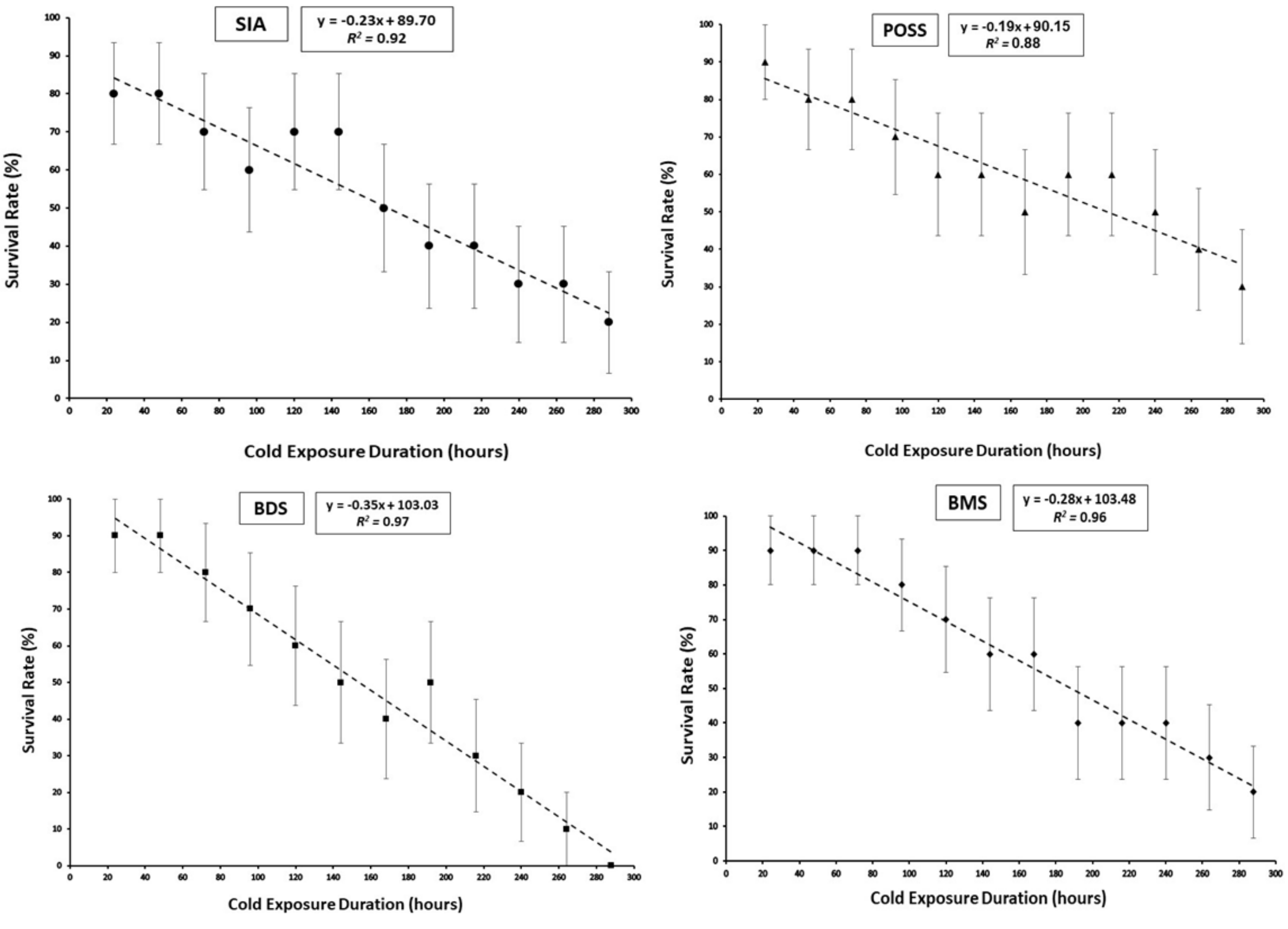

Fig. 1. Linear regression analysis of the effect of different placement methods of almond fruits containing larvae (SIA: Suspended in the Air; POSS: Placed on Soil Surface; BDS: Buried in Dry Soil; BMS: Buried in Moist Soil) on the survival rate of almond seed wasp larvae (*Eurytoma amygdali*) after 12 days at -18°C.

Second experiment: Influence of temperature fluctuations on the survival rate of almond seed wasp larvae

The results of this experiment (Fig. 2) demonstrated that the highest larval survival rate of the almond seed wasp was observed in treatment T_1 (90.00 ± 3.02%), while the lowest survival rate was recorded in treatment T_2 (58.00 ± 4.90%). Comparison of the means indicated that there was a significant difference between treatments T_1 and T_2 ($P \leq 0.401$). Additionally, significant differences were found between treatments T_1 and T_3 ($P \leq 0.0001$), treatments T_2 and T_4 ($P \leq 0.0001$), and treatments T_3 and T_4 ($P \leq 0.0128$).

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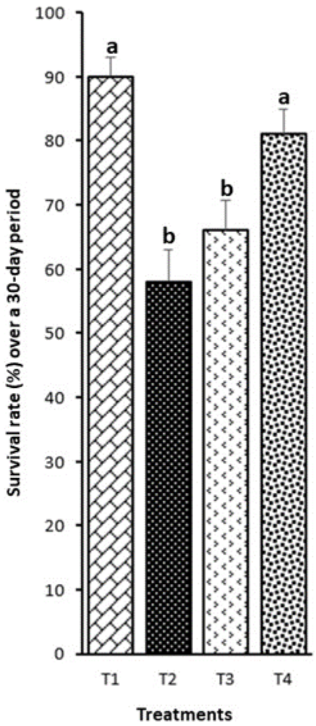

Fig. 2. Comparison of larval survival rates of the almond seed wasp (*Eurytoma amygdali*) under different temperature fluctuation treatments (T_1, T_2, T_3, and T_4).

Discussion

The results of the first experiment indicate that the environmental conditions of the placement location of almond fruits infested with almond seed wasp larvae significantly influence larval survival under low-temperature stress (−18 °C for 12 days). Based on the different negative regression slopes across treatments, it is evident that harsher physical conditions (such as burial in dry soil) lead to a faster and more substantial decrease in larval survival. In contrast, placing the fruits on the soil surface (POSS) provided relatively milder conditions, resulting in the highest larval survival rates. The other two treatments—suspended in air (SIA) and buried in moist soil (BMS)—showed intermediate declines in survival compared to POSS and BDS. This pattern does not align with the findings of Lombardero et al. (2000), who demonstrated that *Ips pini* (Coleoptera: Scolytidae) beetles burrowing deeper into the soil beneath the litter had significantly higher winter survival rates (82%) compared to those overwintering within the litter layer itself (55%). Ahmadi & Nikooei (2025) showed that maintaining optimal soil moisture in orchards, rather than excessive wetness, can reduce the overwintering survival of almond seed wasp larvae, an almond pest, while dry soil creates even more unfavorable conditions for the survival of this pest. The larvae of the almond seed wasp are classified as freeze-avoidant insects because they cannot survive once their body fluids begin to crystallize after reaching the supercooling point (Khanmohammadi et al., 2016). Therefore, selecting an appropriate overwintering site that prevents freezing temperatures and reduces temperature fluctuations is crucial for enhancing larval survival. In particular, environments such as moist soil, which can provide more stable and relatively higher temperatures compared to air or dry soil, offer more favorable conditions for the larvae's survival (Ahmadi & Nikooei, 2025). Mohammadzadeh et al. (2017) demonstrated that another species of this genus, *Eurytoma plotnikovi*, increases cryoprotectant compounds such as sugars and lipids during diapause, which enhances cold tolerance. Their study showed that the last instar larvae exhibit a freeze-avoidance strategy to survive harsh winter conditions. Considering that the larvae of the almond seed wasp remain enclosed within the fruit throughout their development and do not exit (Kouloussis, 2008), the soil surface likely constitutes a more evolutionarily favorable overwintering habitat. This is consistent with the natural fate of infested fruits, which either remain attached to the host plant or abscise and accumulate on the soil surface. In contrast, some insect species exhibit subterranean overwintering strategies, actively seeking refuge within the soil where they may continue feeding and development during the diapause period (Vercher et al., 2023). These findings highlight the crucial role of soil conditions, particularly dry soil, in creating adverse environments for larval survival under extreme cold. Such results can be useful in designing integrated pest management strategies aimed at reducing almond seed wasp populations by manipulating the physical environment, including the placement of infested fruits under natural or artificial freezing conditions.

The results of the second experiment indicate that the highest larval survival rates occur under the typical winter conditions of the region, characterized by limited temperature fluctuations. Additionally, when the temperature gradually increases from cold to warm, larval survival remains significantly high. However, abrupt and alternating temperature changes—such as cycles of cold, then semi-cold, and back to cold, or cold, followed by warm, and then semi-cold—result in a significant decrease in larval survival rates. These findings highlight the larvae's sensitivity to temperature variation patterns and emphasize the importance of thermal stability for enhancing their overwinter survival. This aligns with previous research showing that cold acclimation and rapid cold hardening, especially under fluctuating thermal regimes, improve insect cold tolerance (Colinet et al., 2016; Teets & Denlinger, 2013). Moreover, metabolic adaptations, including the accumulation of amino acids and sugars during acclimation, play a crucial role in enhancing cold resistance (MacMillan et al., 2016). The present study demonstrated that both the physical placement of infested almond fruits and the pattern of winter temperature fluctuations significantly influence the overwintering survival of almond seed wasp larvae. Exposure to −18 °C reduced larval survival in all treatments, with the greatest mortality occurring when fruits were buried in dry soil, while fruits placed on the soil surface supported the highest survival rates. Furthermore, larvae survived best under stable winter temperatures or gradual warming conditions, whereas abrupt and alternating temperature changes markedly reduced survival. These findings indicate that the larvae rely on thermally stable microhabitats and are highly sensitive to both extreme cold and temperature instability. From a practical perspective, manipulating the overwintering environment of infested fruits, particularly through exposure to unfavorable soil conditions and freezing temperatures, may provide an effective component of integrated pest management programs aimed at reducing almond seed wasp populations.

Acknowledgments

Appreciation is extended to the management of the Agricultural Jihad Organization of Bardsir City for the provision of essential facilities.

Ethical Approval and Consent

This article does not contain any studies involving human participants or animals performed by any of the authors.

CRediT author statement

S. Nikooei: Conceptualization, Funding acquisition, Investigation, Methodology, Visualization, Validation, Data curation, Formal Analysis, Writing – original draft, Writing – review & editing. **K. Ahmadi:** Formal analysis, Investigation, Methodology, Validation, Writing – review & editing. **M. Asadi:** Conceptualization, Project administration, Resources, Supervision, Supervision, Validation, Writing – review & editing.

Funding

The author(s) received no financial support for the research.

Data Availability

All datasets generated during this study are available from the corresponding author upon request.

Conflict of interest

The authors declare no conflicts of interest.

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