International Journal of Horticultural Science and Technology (2026) Vol. 13, No. 3, pp. 549-562 doi.org/10.22059/ijhst.2025.390321.1029

International Journal of Horticultural Science and Technology

Journal homepage: https://ijhst.ut.ac.ir

Potassium Silicate and Jasmonic Acid Increase Defense of Pistachio Trees by Operating Flavonoid Status and Physiological Properties of *Agonoscena pistaciae*

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ARTICLE INFO

Article history:

Received: 23 February 2025,
Received in revised form: 19 April 2025,
Accepted: 28 April 2025,

Article type:

Research paper

Keywords:

Antioxidant enzymes,
Energy sources,
Jasmonic acid,
Potassium silicate,
Psyllid

ABSTRACT

The pistachio psylla, *Agonoscena pistaciae* Burckhardt and Lauterer (Hemiptera, Psyllidae), is a significant pest that has caused considerable damage to pistachio trees worldwide. In this study, the effects of jasmonic acid (JA), potassium silicate (PS), and the combination of these compounds on the resistance of pistachio trees to *A. pistaciae* were investigated in 2020 and 2021. This that the treatments had a significant impact on the nymphal period of the psyllid in both years. Additionally, the content of flavonoids was found to be considerably higher in the treated trees compared to the control. The highest nymphal period and the lowest survival rate of the psyllid were observed in trees treated with a combined application of JA and PS in both years. Furthermore, the study revealed that the levels of lipid and glycogen in *A. pistaciae* were the lowest when the psyllid was fed on trees treated with JA integrated with PS. In addition, the activity of peroxidase and esterase enzymes was found to be lowest in the JA+PS treatment. These findings suggest that the exogenous application of JA integrated with PS on pistachio trees can successfully suppress *A. pistaciae* population and can be considered in integrated management programs against psyllids.

Abbreviation: *Agonoscena pistaciae* (*A. pistaciae*), catalase (CAT), Esterase (EST), Glutathione S-transferase (GST), Gram Liter^{-1} (gr L^{-1}), Induced systemic resistance (ISR), Jasmonic acid (JA), Methyl jasmonate (MeJA), microgram (µg), milligram (mg), milliMolar (mM), Peroxidase (POX), Potassium silicate (PS), Revolutions Per Minute (rpm), Salicylic acid (SA), Silicon (Si), Ultraviolet Visible (UV/Visible), United States of America (USA)

Introduction

As an important export product, pistachio (*Pistacia vera* L.), has a special position among agricultural products (Esmailpor et al., 2011). The pistachio psylla, *Agonoscena pistaciae* Burckhardt and Lauterer (Hemiptera: Psyllidae), is one of the key pests of pistachio trees (Mehrnejad, 2001; Shahabinejad et al., 2014; Dilmen et al., 2022). It is also distributed in Turkey, Greece, Iran, Armenia, and Tajikistan (Burckhardt and Lauterer, 1989, 1993; Lababidi and Zebitz, 1995; Lauterer et al., 1998; Dilmen et al., 2022). In adult and nymphal periods, it directly damages trees by absorbing plant sap (Mehrnejad, 2001; Shahabinejad et al., 2014; Dilmen et al., 2022). Moreover, some psyllid species are involved in transmitting pathogens and cause significant losses to the host (Burckhardt and Ouvrard, 2012).

In recent years, researchers have focused on identifying efficient and environmentally friendly methods to prevent biotic agents that damage plants. Potential Induced systemic Resistance (ISR) elicitors have been a subject of particular interest (Sattari Nasab et al., 2018; Ziaaddini et al., 2022). ISRs can be induced by natural or synthetic elicitors (Kuc, 2001; Vallard and Goodman, 2004) and mediated by the jasmonic acid (JA) or ethylene pathways (Pieterse et al., 1998; Knoester et al., 1999). The stimulation of analogous plant defense mechanisms by specific elicitors can serve as a protective measure against pests (Ziaaddini et al., 2022; Mirza Hosseinii Zarandi et al., 2022).

Jasmonates are one group of potential plant growth regulators that participate in many physiological processes and play a defensive role in the plant (Bari and Jones, 2009; Sirhindi et al., 2020). They are produced from lipid peroxide by increasing lipoxygenase activity (Maksymiec and Krupa, 2002). The lipid-derived signal jasmonate coordinates various inducible defense responses (Koo, 2018). JA can be used in narrow amounts for increasing plant growth, gene expression, carotenoids, osmolytes, and antioxidant enzymes (Sofy et al., 2020; Keshtkar et al., 2022). JA significantly increases the activity of peroxidase and polyphenol oxidase enzymes, and amounts of total phenol and protein. As a result, it could be involved in the induced resistance of plants (War et al., 2011). The researchers recommend that pretreatment with inducers such as JA provides more opportunity for plant defense against pests (War et al., 2011; Mondego et al., 2019). In fact, using JA in some plants could be a possible and effective alternative for pesticide application (Awang at al., 2015). On the other hand, the exogenous application of JAs enhanced photosynthetic pigments and improved photosynthetic efficiency (Sirhindi et al., 2020).

Plant growth is closely associated with soil physical properties (Gliñski, 2011). Silicon (Si) is the second-most plentiful element in the soil. Most sources of Si are insoluble and in plant-unavailable form (Balakhnina, 2013). Potassium silicate (PS, K_2SiO_3) is used as a plant stimulant and a source of available potassium and highly soluble Si (Rodrigues et al., 2009; Hafez et al., 2021). Several functions have been attributed to Si: improvement of nutrient imbalance, reduction of mineral toxicities, improvement of the mechanical properties of plant tissues, and enhancement of resistance to various abiotic and biotic stresses (Epstein, 1999; Ma and Yamaji, 2006). There is evidence that Si is effectively induces resistance to pests by causing physically- or chemically-based negative interference on development (Assis et al., 2015), biology (Correa et al., 2005), feeding behavior (Assis et al., 2012), and reproduction (Pereira et al., 2010). In addition, Si could help increase nutrient and water uptake, photosynthesis, plant pigments (Ma, 2004), and reinforce plant cell walls (Ma, 2004; Liang et al., 2005). Biel et al. (2008) demonstrated that the defensive role of Si in plants may be related to the accumulation of polysilicic acids inside cells. On the other hand, potassium nutrition can improve yield, ascorbic acid concentrations, soluble solids, fruit color and size, shelf life, and shipping quality in some crops (Kanai et al., 2007, Abdou et al., 2022). Various studies have revealed the role of PS in alleviating different stress reasons (Chen et al., 2016; Gomaa et al., 2021; Abdou et al. 2022). PS does not contain any volatile organic compounds, so its application does not lead to the release of risky or environmentally persistent by-products (Romero-Aranda et al., 2006). Some reports have suggested that PS improves plant growth, production, and quality (Liang et al., 2007; Gomaa et al., 2021; Hafez et al., 2021). Consequently, enhancing the activities of enzymatic antioxidants during salinity stress retains plasma-membrane functions (Ahmad et al. 2019; Salim et al., 2019; Hafez et al., 2021).

Elicitors can influence the secondary metabolite contents in plants in response to herbivores and induce defense mechanisms, thereby increasing the resistance of plants against pests (Sattari Nasab et al., 2020; Khoshfarman-Borji et al., 2020). Insects detoxify some plant allelochemicals and toxic secondary metabolites by different detoxifying enzymes (Francis et al., 2005; Cai et al., 2009). Further, secondary metabolites can affect oxidative stress through producing free radicals and modifying the antioxidant enzyme systems (Zhang and Feng, 2018). Glutathione S-transferases (GST), esterases (EST), catalases (CAT), and peroxidases (POX) are important detoxification enzymes in the defense systems of insects (Francis et al., 2001; Francis et al., 2005; Scott et al., 2010; War et al., 2013, Ziaaddini et al., 2022). The activity levels of detoxifying enzymes in insects are assumed to be significant factors in determining their resistance to an extensive range of toxic chemicals (Despres et al., 2007).

Information about elicitor impacts on interactions between insects and plants is useful for the induction of resistance. Methyl jasmonate (MeJA) and Salicylic acid (SA) have been studied on pistachio micro-propagating (Dulcet-Sanjuan and Claveria, 1995). Also, Bastam et al. (2012) reported that treating pistachio trees with SA enhanced the salt tolerance in plant roots. Mohit Rabari et al. (2023) demonstrated that exogenous calcium could improve the growth of pistachio trees under salinity by reducing excess boron symptoms. Shojaaddini (2022) suggested that the integrated use of Si with each of the MeJA or SA can elicit the pistachio's defense against *A. pistaciae*. Shahabinejad (2014) showed the effects of MeJA and SA were concentration-dependent, such that SA with the higher concentration failed to induce a more active response. Some studies have shown that JAs improve plant stress tolerance via JA signaling pathways under various adverse environmental conditions (Wang et al., 2021). MeJA and JA cause a wide range of direct and indirect chemical defenses, including secondary metabolites (Mohamed et al., 2021). JAs as elicitors can potentiate plant defense responses via modulating the metabolism of flavonoids and phenolic, as well as detoxification enzyme systems of reactive oxygen species (Nafie et al., 2011). Gharibiyan et al. (2023) showed that applying elicitors such as SA at 1.0 mM can better the growth and physiological parameters of pistachio plants and also reduce the negative effects of salinity.

Moreover, Si may act directly on insect herbivores by reducing insect growth and reproduction or indirectly through lower plant penetration, allowing natural enemies easier access to the crop (Reynolds et al., 2009; Züst and Agrawal, 2016). Although the exogenous application of jasmonates and PS may induce resistance to pests, studies on their utility of them as elicitors in insect management programs are limited (Shahabinejad et al., 2014; Awang et al., 2015; Melo et al., 2015; War et al., 2015; Cooper and Horton, 2017; Shojaaddini, 2022). Thus, the present research aimed to evaluate the effects of PS and JA on the contents of secondary metabolites in pistachio leaves and the resultant effects on development parameters and detoxifying enzymes of *A. pistaciae*, which could help to reduce pest populations.

Materials and Methods

Field experiments were conducted during two years (2020 and 2021) on 25 to 30-year-old pistachio trees (cv: Fandoghi) in a 2.5 ha orchard located in Zarand, Kerman, Iran (latitude 33.57276 and longitude 49.9937) based on a completely randomized design. Induction treatments were PS (1 gr L^{-1}) (Merck, Germany), JA (1 mM) (84210 Sigma-Aldrich > 99%), and PS+JA, according to the product label. Also, an aqueous solution of distilled water was applied as a control. Foliar spraying time was based on common regional practices for PS at the end of spring when the population of psyllid eggs and nymphs increased in the orchard.

In PS+JA, sprayings were carried out during the day, with one of the compounds in the early morning and the other in the evening. The total sample size for the life table study was 100 eggs at the beginning of this experiment (4 treatments × 25 samples) and then 80 nymphs (4 treatments × 20 samples) in the continuation of the study. Further, the total sample size for the preadult survival rate was 40 (4 treatments × 10 samples), and for biochemical analysis was 12 (4 treatments × 3 samples).

Life table study

To determine the effect of the studied inducers on the development time of *A. pistaciae*, 25 trees that were almost identical in size and pistachio psyllid population were selected. Then five trees were considered for each treatment. There was one untreated tree among the trees studied. Five branches were considered in north, south, east, west, and center directions of each tree and were distinguished by tying the ribbon. The assessment of the development time of *A. pistaciae* started 48 h after the spraying of treatments. For this purpose, leaves containing two to three eggs of the same age of psylla were considered, and the surface of the leaves was cleaned with wet cotton so that there was nothing else on the surface of the leaf other than *A. pistaciae* eggs. Fine mesh gauze coverings to prevent the occurrence of parasitism and the migration of psyllids enclosed the branches. Daily observations were made until adult emergence to determine the development time and preadult survival of this pest.

Measurement of total phenol and flavonoid contents by spectrophotometer

Total phenol and flavonoid contents in the young psylla-infested leaves of pistachio trees under the studied treatments and control (48 h after spraying) were evaluated in three replicates. The leaves washed with distilled water and dried at ambient temperature in the shade. The dried leaves crushed with a mortar and soaked with n-hexane (2:1) as a solvent. The resulting mixture was put in the shaker for 48 h and was stirred occasionally. Then, the mixture was centrifuged at 10,000 rpm for 5 min. The obtained extract was used to measure secondary compounds.

Total phenols were estimated using the Folin Ciocalteu reagent, based on the method defined by Soland and Laima (1999) with brief variations. 0.2 mL of the extract was added to 1 mL of Folin–Ciocalteau's phenol reagent (diluted 1:10 with water). Then the solution remixed and allowed to remain for 5 min at room temperature. Subsequently, 0.8 mL sodium carbonate (5%) was added to the reaction, and the mixture was reserved in the dark. The level of absorbance of the reaction was determined at 765 nm using a spectrophotometer. Total phenolic content was calculated as mg gallic acid equivalents per gram of sample (mg g^{-1}). This estimation was carried out in three replicates.

The flavonoid contents were determined by the aluminum chloride colorimetric technique (Chang et al., 2002). Each plant extract (0.5 mL of 1:10 g mL^{-1}) in methanol was individually mixed with 0.1 mL of 10% aluminum chloride, 0.1 mL of 1 M potassium acetate, 1.5 mL of methanol, and 2.8 mL of distilled water. It remained at room temperature for 30 min, and the absorbance of the reaction mixture was calculated 510 nm with a double beam Perkin Elmer UV/Visible spectrophotometer (USA). The calibration curve was obtained by preparing quercetin solutions at concentrations of 12.5 to 100 µg mL $^{-1}$ in methanol.

Preparation of samples for evaluation of detoxifying enzyme activities in pistachio psylla tissues

In 2020, 48 h after the spraying, last instar nymphs of *A. pistaciae* were prepared randomly from plants under each treatment. To evaluate the esterase enzyme activity, psyllid samples were homogenized in 0.1 M phosphate buffer (200 µL) comprising 0.1% triton® X-100 (Sigma Aldrich). The centrifuge of homogenated of samples was completed at 10,000 rpm for 15 min at 4 °C. To assess the peroxidase enzyme activity, psyllid samples homogenized in 20 mM phosphate buffer (200 µL) and then centrifuged at 2,600 rpm for 5 min at 4 °C. To measure the activity of CAT, and GST, the *A. pistaciae* specimens were homogenized in 200 µL cold phosphate buffer (10 mM), and afterwards the homogenates were centrifuged for 15 min at 4 °C at 13,000 rpm. The top layer was collected and kept at -20 °C before beginning biochemical analyses. All enzymes evaluates were done in three replications.

Esterase

A solution comprising 10 µL of prepared enzyme sample, 10 µL of β -naphthyl (10 mM in acetone), 40 µL of phosphate buffer, and 50 µL of fast blue RR salt solution (Sigma Aldrich) was applied for calculation of the esterase activity by the spectrophotometer at 405 nm (Van Asperen, 1983).

Peroxidase

The reaction was done in 0.5 mL volume, including 225 µL of 45 mM Guaiacol and 225 µL of 225 mM H_2O_2 (Merck Germany). In addition, 50 mM potassium phosphate buffer (50 µL) was considered a blank. The guaiacol reaction was determined at 470 nm by spectrophotometer (Bergmeyer, 1974).

Catalase

The Aebi method (1984) was employed to assess CAT activity. In this method, 50 µL of the sample, 225 µL of H_2O_2, and 225 µL of 70 mM potassium phosphate buffer solution (pH = 7) were mixed. The mixture was then analyzed using a spectrophotometer, with the measurement conducted at 240 nm.

Glutathione S-transferase

In this experiment, 200 µL of the reaction mixture was utilized, comprising 100 µL of 1-chloro-2,4-dinitrobenzene (CDNB) (1.2 mM), 100 µL of reduced glutathione (10 mM), and 15 µL of enzyme sample. The mixture was subsequently transferred into a cuvette for analysis. The spectrophotometer (Habig et al., 1974) was employed to measure the optical density at 340 nm.

Determination of energy sources

The amount of protein was determined using Bradford reagent according to the Greenfield method (Greenfield, 2018), and its absorption was read at 595 nm.

Sugar, lipid, and glycogen content was quantified following the method described by Foray et al. (2012). The homogenized psyllids (last instar nymphs) centrifuged at 2600 rpm for 5 min at 4 °C. Then homogenized samples of *A. pistaciae* were poured into Falcon tubes, and then 1.875 mL of the methanol-chloroform mixture (2:1 v/v) and 22.5 µL of 20% sodium sulfate were added and vortexed. The Supernatant containing sugar and lipids was separated using distilled water. The upper part containing sugar was measured using an antron reagent at a wavelength of 625 nm in the spectrophotometer (UV-2100). The lower part contained lipid, which was measured after adding 98% sulfuric acid (50 µL) and vanillin reagent in a spectrophotometer at a wavelength of 525 nm. Glucose (German Merck) and cholesterol (German Merck) were used to plot the standard curves of sugar and lipid, respectively.

The determination of glycogen content was achieved through the following series of steps. Initially, homogenized samples were prepared according to the established protocol. The separation of the upper layer from the lower layer was facilitated by micropipette usage. Subsequently, 1 mL of antron reagent and 1 mL of 80% methanol were added to the pellet. The spectrophotometer was then utilized to ascertain the sample's absorbancy at 625 nm, with glucose serving as the standard.

Statistical analysis

The normality test with Kolmogorov-Smirnov was performed on all data, and the variables were evaluated using the one-way analysis of variance in SPSS. Subsequently, the Tukey test was conducted for multiple comparisons (SPSS, 2022).

Results

Life table study

There was no significant difference in the egg-hatching time of *A. pistaciae* among the studied treatments during 2020 (F = 1.88; df = 3, 96; P = 0.137) and 2021 (F = 0.84; df = 3, 96; P = 0.474) (Tables 1 and 2). However, tested treatments significantly influenced the nymphal period of this psyllid in both years (F = 338.08; df = 3, 76; P < 0.001 and F = 257.82; df = 3, 76; P < 0.001 respectively) (Tables 1 and 2).

In both years, the shortest and longest nymphal periods of *A. pistaciae* were observed in the control and PS+JA, respectively (Tables 1 and 2). In addition, the nymphal period of psylla was significantly longer on trees treated with JA compared to PS In 2020, but no significant difference was observed between JA and PS In 2021.

The studied treatments showed a significant difference in terms of survival of the immature stage of *A. pistaciae* during 2020 (F = 4.19; df = 3, 36; $P < 0.05$) and 2021 (F = 3.33; df = 3, 36; $P < 0.05$; Fig. 1). The highest survival rate was on control (80% in 2020 and 77.5% in 2021), and the lowest on PS+JA (55% in 2020 and 57.5% in 2021). In both years, there was no significant difference in the survival rate of this pest between treatments of JA and PS compared to control and PS+JA (Fig. 1).

Table 1. Mean ± Standard error of the embryonic and nymph periods of *Agonoscena pistaciae* fed on pistachio trees treated with jasmonic acid (JA) and potassium silicate (PS) in 2020.

Treatments	**Embryonic period (d)**	**Nymph period (d)**
Control	3.56±0.16^{a}	18.06±0.33^{d}
PS	2.00±96.21^{a}	21.00±80.32^{c}
JA	3.00±0.22^{a}	27.00±30.34^{b}
JA+PS	3.00±0.22^{a}	31.00±35.22^{a}

PS: Potassium silicate, JA: Jasmonic acid; Different letters in each column indicate the existence of a significant difference at the probability level of $P < 0.05$ using Tukey's test.

Table 2. Mean ± Standard error of the embryonic and nymph periods of *Agonoscena pistaciae* fed on pistachio trees treated with jasmonic acid (JA) and potassium silicate (PS) in 2021.

Treatments	**Embryonic period (d)**	**Nymph period (d)**
Control	4.00±44.15^{a}	22.00±5.36^{c}
PS	4.00±20.20^{a}	25.00±65.23^{b}
JA	4.00±12.29^{a}	26.00±65.41^{b}
JA+PS	4.00±56.20^{a}	34.00±90.31^{a}

PS: Potassium silicate, JA: Jasmonic acid; Different letters in each column indicate the existence of a significant difference at the probability level of $P < 0.05$ using Tukey's test.

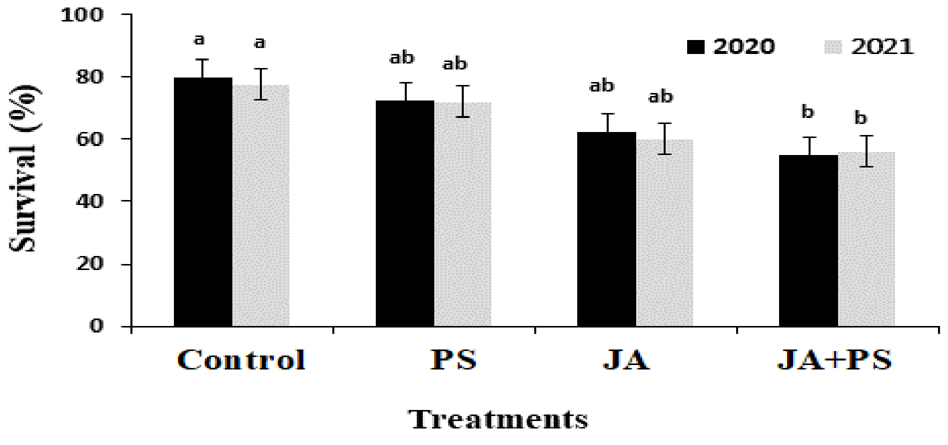

Fig. 1. Mean survival rate, from egg to adult, of *Agonoscena pistaciae* fed on pistachio trees treated with jasmonic acid (JA) and potassium silicate (PS) in 2020 and 2021.

Determination of some secondary metabolites

Total phenol and flavonoid contents

There was no significant difference in the amount of total phenol in pistachio leaves under different treatments (F = 1.64; df = 3, 8; $P = 0.255$; Table 3), while the flavonoid content was significantly higher in treatments of JA, PS, and PS+JA compared to control (F = 8.63; df = 3, 8; $P < 0.007$; Table 3).

Antioxidant enzyme activities

There were significant differences in the activity levels of peroxidase (F = 21.77; df = 3, 8; $P < 0.001$), and esterase enzymes (F = 11.98; df = 3, 8; $P < 0.001$) in psyllids reared on pistachio trees under the studied treatments (Table 4). The activity of peroxidase enzyme was highest on control, which showed a significant difference compared to other treatments. The esterase activity on PS and control was significantly higher than that on JA and PS+JA (Table 4). No significant differences were observed in activity levels of GST and CAT enzymes among tested treatments (F = 0.74; df = 3, 8; P = 0. 554 and F = 2.35; df = 3, 8; $P = 0.148$; respectively) (Table 4).

Table 3. Mean ± Standard error of total phenolic and flavonoid levels in leaves of pistachio trees treated with jasmonic acid (JA) and potassium silicate (PS).

Treatments	Total phenolic level (µg g^{-1} DW plant)	Total flavonoid level (µg g^{-1} DW plant)
Control	24.00±36.63^{a}	14.2±83.36^{b}
PS	21.00±89.25^{a}	54.20±8.46^{a}
JA	24.1±10.04^{a}	49.10±22.79^{a}
JA+PS	19.20±65.95^{a}	56.50±10.78^{a}

PS: Potassium silicate, JA: Jasmonic acid; Different letters in each column indicate the existence of a significant difference at the probability level of $P < 0.05$ using Tukey's test.

Table 4. Mean ± Standard error of detoxification enzymes activities in *Agonoscena pistaciae* fed on pistachio trees treated with jasmonic acid (JA) and potassium silicate (PS).

Treatments	Catalase (units mg^{-1} protein)	Peroxidase (units mg^{-1} protein)	Glutathione S-transferase (units mg^{-1} protein)	Total esterase (units mg^{-1} protein)
Control	0.178±0.005^{a}	0.416±0.003^{a}	0.355±0.012^{a}	0.102±0.008^{a}
PS	0.096±0.031^{a}	0.098±0.011^{c}	0.419±0.080^{a}	0.102±0.005^{a}
JA	0.246±0.076^{a}	0.283±.027^{b}	0.329±0.022^{a}	0.069±0.001^{b}
JA+PS	0.133±0.014^{a}	0.153±0.052^{c}	0.405±0.048^{a}	0.071±0.003^{b}

PS: Potassium silicate, JA: Jasmonic acid; Different letters in each column indicate the existence of a significant difference at the probability level of P < 0.05 using Tukey's test.

Energy sources

In this study, the analysis of energy sources of *A. pistaciae* feeding on plants under studied treatments showed significant differences in contents of sugar ($F = 52.82$; df = 3, 8; $P < 0.001$), lipid ($F = 1423$; df = 3, 8; $P < 0.001$), and glycogen ($F = 5.68$; df = 3, 8; $P < 0.05$) (Table 5). No significant differences were observed in protein contents among tested treatments (F = 1.30; df = 3, 8; $P = 0.338$; Table 5).

The highest sugar contents were in PS, and JA treatments, and the lowest was in the control (Table 5). The greatest and least contents of lipid were on PS and PS+JA, respectively. The glycogen contents were significantly lower on PS+JA compared to other treatments (Table 5).

Table 5. Mean ± Standard error of energy resources in *Agonoscena pistaciae* fed on pistachio trees treated with jasmonic acid (JA) and potassium silicate (PS).

Treatments	Sugar (mg g^{-1} body weight)	Lipid (mg g^{-1} body weight)	Glycogen (mg g^{-1} body weight)	Protein (mg g^{-1} body weight)
Control	0.05±0.002^{c}	21.82±0.31^{b}	0.3±0.05^{a}	1.89±0.01^{a}
PS	0.163±0.012^{a}	24.32±0.23^{a}	0.28±0.05^{a}	1.78±0.1^{a}
JA	0.20±0.010^{a}	9.45±0.03^{c}	0.3±0.04^{a}	1.82±0.07^{a}
JA+PS	0.102±0.006^{b}	7.04±0.23^{d}	0.09±0.01^{b}	1.87±0.02^{a}

PS: Potassium silicate, JA: Jasmonic acid; Different letters in each column indicate the existence of a significant difference at the probability level of $P < 0.05$ using Tukey's test.

Discussion

In the current research, pistachio trees treated with the studied inducers negatively affected the nymph development time of *A. pistaciae* compared with the control. Our results provided strong evidence that combined treatment had the highest effect on the nymph development time and survival rate of this pest. Among individual treatments, JA was more effective on nymph development time than PS. Using JA elicitor to promote plant-induced resistance has shown satisfactory results in insect pest control (War et al., 2011). The octadecanoid pathway is used to produce JA from linolenic acid. This plant hormone regulates an assortment of physiological processes in higher plants, including defensive responses, flowering and also senescence (Cheong and Choi, 2003). JA plays a crucial role in plant defense reactions against insect damage (Wasternack, 2007; Awang et al., 2015). Several studies have demonstrated that exogenous application of JA enhances resistance to herbivore challenges and induces the expression of defense-related genes (Lorenzo and Solano, 2005; Howe and Jander, 2008). The positive effect of MeJA and SA on the defensive response of pistachio trees to this psyllid was reported (Shahabinejad et al., 2014). Some previous studies have also proved the effects of JA in induced resistance against various insects in soybean (Creelman et al., 1992), tomato (Thaler, 1999; Iverson et al,. 2001), celery (Black et al., 2003), wheat (Jayaraj et al., 2004), tobacco (von Dahl and Baldwin, 2004), cotton (Barbosa et al., 2008), groundnut (War et al., 2011), and chilli (Awang et al., 2015). No negative effect on the environment was reported for the JA application (Thaler, 1999; Awang et al., 2015). Our study achieved a discovery concerning the applications of integrated JA and PS, leading to lower survival and a longer development time for this pest. Similarly, Shojaaddini (2022) suggested the integrated use of sodium silicate with each phyto-hormone of the MeJA or SA could elicit defense reactions in pistachio trees against *A. pistaciae*. Si accumulation can act directly, leading to a reduction in insect performance and plant damage, whereas indirect effects delay herbivore establishment (Reynolds et al., 2009). In our study, the population density of *A. pistaciae* was not estimated. Results of Shojaaddini (2022) indicated the population density of *A. pistaciae* was significantly lower (1.82 ± 0.45 to 4.32 ± 1.0 nymphs/leaflet) when pistachio trees treated with MeJA, SA, and Si compounds individually or in combination (MeJA+Si, and SA+Si) compared with those untreated (124.7 ± 8.17 nymphs/leaflet).

The results of current research could potentially be associated with environmental factors. For instance, Mehrnejad and Copland (2005) demonstrated a close inverse correlation between increased temperature and pre-oviposition period. Both winter and summer forms of *A. pistaciae* are adapted for reproduction at temperature ranges of 20–30 ºC. Based on the linear model, the lower temperature thresholds for egg, nymph, and total preadult stages were 8.06, 10.38, and 9.97 °C, respectively (Hassani et al., 2011).

PS plays a crucial role in alleviating different stress factors (Chen et al., 2016; Gomaa et al., 2021) using the increased activity of antioxidant enzymes and the root's ability to obtain the necessary nutrients (Salim et al., 2019; Hafez et al., 2021). Si can generally enhance plant resistance against insects through two main mechanisms. Physical resistance (constitutive) is associated with silica deposition on leaves, which reduces digestibility and/or increases the hardness and abrasiveness of plant tissues. Conversely, soluble Si can induce chemical defenses against insect herbivory by increasing the production of defensive enzymes (Reynolds et al., 2009).

Research reports have described the effectiveness of Si in inducing resistance to pests by causing physically- or chemically-based negative interference on the biology of *Bemisia tabaci* biotype B on cucumber (Correa et al., 2005) and chrysanthemum (Melo et al., 2015), on the feeding behavior of *Diabrotica speciosa* on potato (Assis et al., 2012), on the reproduction of *Schizaphis graminum* (Rondani) on wheat (Pereira et al., 2010), and the induction of resistance against *C. lacinia* saundersii in sunflower (Assis et al., 2015).

On the other hand, potassium fertilization improves the nut yield and quality in pistachio trees (Mimoun et al., 2004). In another study, foliar application of K and Zn fertilizers led to better fruit yield and quality in pistachio (Norozi et al., 2019). The beneficial effects of Si application have been widely suggested on crop growth and yield (Marschner, 2012). Moreover, MeJA has proven to be a main natural compound that inhibits post-harvest fungal diseases and extends the shelf life of fruits. The production of secondary metabolites, including flavonoids and other antioxidant molecules, can enhance the fruit quality (Reyes-Díaz et al., 2016).

Our results suggest the minor suitability of pistachio trees treated with inducers, particularly, the combined treatment (JA+PS), compared with the control for this psyllid. Elicitors can trigger new genes so that enzymes and diverse biosynthetic routes of secondary metabolites are formed and modified (Zhang et al., 2006; Howlett, 2006). Moreover, plants respond to the invasion of herbivores by activating defense mechanisms, including the induction of secondary metabolites (Vasconsuelo and Boland, 2007). In this research, the studied inducers influenced the flavonoid contents of pistachio leaves. The lower suitability of plants treated with inducers for this psyllid in the current study was related to the higher levels of flavonoids in pistachio leaves. The shikimic acid pathway is a basic route in the biosynthesis of phenolic compounds, including flavonoids in plants (Díaz-Rivas et al., 2018). The amino acid phenylalanine is one of the products of the shikimate pathway (Divekar et al., 2022). Díaz-Rivas et al. (2018) have shown that the elicitors could enhance the phenylalanine ammonia-lyase activity in plants, which promotes the phenolic synthesis associated with the enhancement of the defense resistance of the plants. On the other hand, the defensive proteins could be induced by JAs. For example, exogenous JA or MeJA, which effectively protects plants from herbivores (Divekar et al., 2022), can induce the important defensive enzyme polyphenol oxidase. Flavonoids as feeding deterrents are involved in the inhibition of key digestive enzymes in insect midguts, which are amylases, glycosidases, lipases, and proteases (Pereira et al., 2024). In addition to their antifeeding and phagostimulatory effects, flavonoids have been reported to delay development and growth, induce malformations, and affect the reproductive cycle of adult insects by increasing the pre-reproductive period and decreasing fecundity (Pereira et al., 2024).

Furthermore, the chemicals can affect tritrophic interactions between the host plant, pest, and its natural enemy, leading to pest population suppression by natural enemies in the resistant plant (Pahlavan Yali and Sattari Nasab, 2020). In addition, the longer nymphal developmental time and lower survival rate of psyllids on plants treated with JA+PS in this study were correlated to minor energy reserves (glycogen and lipid content) in *A. pistaciae*. Alterations in biochemical indicators could be used as an appropriate indicator of toxicant tension under laboratory conditions, as was verified in invertebrates exposed to stressful conditions (Jemec et al., 2007). A reduction in the contents of energy reserves may be due to increased utilization of energy demand related to toxic stress (Sancho et al., 2009). The silicon mechanisms involved in plant resistance to insect attacks could be due to this nutrient, which can be deposited in a soluble form among leaf tissues, inhibiting sucking by the insect (Reynolds et al., 2009). That can also increase the energy expenditure of herbivores, which consequently influences the insect’s survival and population growth (Marschner, 2012). Reyhani Haghighi et al. (2021) reported that the glycogen levels of *A. pistaciae* nymphs feeding on plants treated with SA (with or without drought stress) were lower compared to untreated plants. Moreover, SA treatment decreased lipid contents in *A. pistaciae* feeding on plants without drought stress compared with plants under drought stress. Karban and Agrawal (2002) described an energetic trade-off between allocation to defensive mechanisms against other biological traits, such as growth and reproduction, which depends on environmental factors, and this could have been modified in pistachio by inducers.

The elicitor applications can activate the plant secondary metabolism, which provokes a sequence of mechanisms implicated in the synthesis of metabolites (Díaz-Rivas et al., 2018). Ziaaddini et al. (2022) reported that some elicitors could increase the production of secondary metabolites and antioxidant activity in pear trees against *Cacopsylla bidens*. Plant defense is associated with higher levels of plant secondary metabolites, inhibiting insect growth and development (Howe and Jander, 2008; War et al., 2012) and hindering detoxification enzyme systems (Yu, 1983; Nation, 2008). JAs induce some plant secondary compounds involved in plant defense. These compounds serve as antifeedants that cause feeding deterrents or act as a toxin to the herbivore (Senthil-Nathan et al., 2009; Mohamed et al., 2021). Therefore, plant metabolites can directly influence herbivore growth and development or even be lethal to insects. *Spodoptera litura* (Fabricius) exposed to phytochemicals showed reduced survival and prolonged development (Chen et al., 2023). In addition, phytochemicals have an indirect impact on feeding and insect weight. The pupal weights in *S. litura* were significantly lower when they were fed on the strong plant toxins (Chen et al., 2023).

In the present study, different inducers, especially JA+PS, significantly appeared to reduce the activity of detoxifying enzymes (peroxidase and esterase) in *A. pistaciae* compared to the control. It can be attributed to high levels of flavonoids in plants treated with studied compounds. The augmentation of secondary compounds in host plants effectively obstructing the activity of detoxifying enzymes in insects (Jing et al., 2005; Zhang et al., 2013). Detoxifying enzymes play an essential role in the detoxification and antioxidant defense of insects in response to natural and synthetic exogenous xenobiotics and are involved in the adaptation of insects against undesirable environmental conditions (Ziaaddini et al., 2022). The lower levels of detoxifying enzymes in *A. pistaciae* reared on plants treated with JA and PS suggest this insect has been unable to detoxify the plant allelochemicals effectively under these compounds compared to control.

Conclusion

This study showed that, pistachio trees treated with JA and PS, especially in combination, were more resistant to *A. pistaciae*. The survival percentage of psyllids on the studied treatments had a negative association with levels of flavonoids. Plant defense could be due to higher levels of plant secondary metabolites, which prevent insect survival and development and hinder detoxification enzyme systems. In this research, the detoxifying enzymes of the insect under studied treatments could not overcome the plant defense system. In general, JA and PS improve plant growth and defense systems, which subsequently reduce the energy resources of *A. pistaciae* and increase the nymph development period. These treatments may have an indirect effect by increasing the exposure of the insect to its natural enemies because of prolonged developmental time. Therefore, induced systemic resistance using these compounds may serve as a potential alternative that may be integrated with management schemes for psyllids to minimize the use of insecticides. In this study, we did not evaluate the effects of these compounds on the quantity and quality of the product, suggesting that complementary studies be conducted in the future. Additionally, further research is required to investigate the cost considerations, potential interactions with other agronomic practices, and long-term field validation in pest control programs.

Acknowledgements
We appreciate Shahid Bahonar University (Iran) for the financial support of this study.

Author Contributions
All authors read and approved the final manuscript.

Funding
This research received no external funding

Conflict of Interest
The authors indicate no conflict of interest in this work.

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