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Research Article

Linking PGPR-boosted cucumber defensive compounds to disrupted growth rate of *Tetranychus urticae* in pest management

Elahe Darini [1], Hamidreza Alizadeh[1], Mostafa Khanamani[1] &Amin Sedaratian-Jahromi[2]

1. *Department of Plant Protection, Faculty of Agriculture, University of Jiroft, Jiroft, Iran*
2- Department of Plant Protection, Faculty of Agriculture, Yasouj University, Yasouj, Iran

Abstract. Beneficial rhizobacteria inhabiting the rhizosphere may suppress aboveground herbivores by enhancing plant defensive traits, including the production of secondary metabolites. This study investigated whether three plant growth-promoting rhizobacteria (*Bacillus subtilis*, *Pseudomonas fluorescens*, and *Azospirillum brasilense*) could enhance cucumber resistance to *Tetranychus urticae* Koch modulation of secondary metabolite production and subsequent effects on mite population dynamics. Life table parameters of *T. urticae* were assessed using the age-stage, two-sex life table approach. In addition, leaf samples were analyzed for phenolic, flavonoid, and anthocyanin content at 0, 24, and 72 h following mite infestation. All three bacterial treatments significantly reduced the population growth potential of *T. urticae* compared with the untreated control, with *B. subtilis* exhibiting the strongest suppressive effect, followed by *P. fluorescens* and *A. brasilense*. For the *B. subtilis* treatment, the intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), gross reproductive rate (*GRR*), and mean generation time (T) were 0.169 day^{-1}, 1.184 day^{-1}, 18.35 eggs/individual, 22.19 eggs/individual, and 17.08 days, respectively, compared with 0.217 day^{-1}, 1.243 day^{-1}, 28.76 eggs/individual, 33.25 eggs/individual, and 15.38 days in the control treatment. Furthermore, under mite-free conditions, bacterial inoculation significantly increased the concentrations of total phenolics, flavonoids, and anthocyanins in cucumber plants. However, this increase was greater in treatments infested with *T. urticae*, suggesting that the tested rhizobacterial species contribute to the activation of plant defense mechanisms and stimulate the accumulation of defensive secondary metabolites in response to herbivore attack. These findings demonstrate the potential of beneficial rhizobacteria to induce resistance in cucumber through the enhancement of defensive secondary metabolites and highlight their potential application in sustainable pest management strategies.

Keywords: Plant growth-promoting rhizobacteria (PGPR), *Bacillus subtilis*, *Pseudomonas fluorescens*, *Azospirillum brasilense*, Induce resistance

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Corresponding authors: Mostafa Khanamani

E-mail: m.khanamani@ujiroft.ac.ir

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Introduction

Plants are central mediators between belowground microbial communities and aboveground herbivores in terrestrial ecosystems (Hosseini *et al.,* 2022). Processes between these subsystems are likely to entail sophisticated signaling and biochemical cascades, leading to effects cascading upwards and downwards through the ecological hierarchy (Friman *et al.,* 2021). Among soil microbiota, plant growth-promoting rhizobacteria (PGPR) are a group of free-living free-motile bacteria with the capacity to enhance plant growth, nutrient uptake, and defense against biotic stress factors like pathogens and herbivores (Pieterse *et al.*, 2014). The potentiality of PGPR offers an attractive way to replace the use of chemical fertilizers, pesticides and other supplements. More commonly known

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PGPR genera such as *Bacillus*, *Pseudomonas*, and *Azospirillum* can colonize the rhizosphere, fix atmospheric nitrogen, solubilize soil nutrients, and trigger systemic resistance responses in the host plant (El-Akhal *et al.*, 2013).

PGPR serve many functions for plant growth and development. They fix the atmospheric nitrogen, involved in the formation of several growth-promoting phytohormones. Moreover, the PGPR also contain enzymes that solubilize minerals which regulate plant growth (Oves *et al.*, 2013). Induced systemic resistance (ISR) triggered by PGPR colonization activates a defense response gene set and biochemical pathways, leading to increased production of secondary metabolites like phenolic compounds, flavonoids, and anthocyanins (Mithöfer & Boland, 2012; Pieterse *et al.*, 2014; Mierziak *et al.*, 2014). These compounds not only serve as antioxidants but also involve the vital task of plant defense through repelling the herbivores and suppressing the pathogens' growth (War *et al.*, 2012; Salunke & Koche, 2023). Plant secondary metabolism regulation by PGPR thus is a viable area for adopting the sustainable strategies for pest control practices. Currently, PGPR are sold commercially for seed formulations, seedling root dip, soil application, and drip irrigation. The two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), is a cosmopolitan and extremely polyphagous pest infesting numerous economically important crops such as cucumber (Farazmand, 2020; Hashemi *et al.*, 2021). Feeding damages inflicted by *T. urticae* reduce photosynthesis capacity, induce chlorosis and leaf desiccation, and ultimately lead to severe yield loss (Van Leeuwen *et al.*, 2010). Traditionally, chemical acaricides dominate control, but their extensive use has resulted in the emergence of resistance on a broad scale additional environmental and health problem (Riahi *et al.*, 2011; Gould *et al.*, 2018; Dalir *et al.*, 2024, 2025). Such problems highlight the necessity for alternative and environmentally safe control measures.

There have been recent studies examining the feasibility of PGPR in spider mite injury control and have concluded that inoculation with certain PGPR strains can reduce the population density of mites and decline their reproductive efficiency by enhancing plant resistance (Tomczyk, 2006; Hosseini *et al.*, 2022). These effects are also often linked with elevated levels of defensive secondary metabolites and altered plant physiology, which are detrimental to mite growth and fertility (Fahimi *et al.*, 2014; Salunke & Koche, 2023). For instance, exposure to *Azotobacter chroococcum* has been found to increase generation time and reduce intrinsic rates of increase (r) in *T. urticae* by increasing defense of the plant (Hosseini *et al.*, 2022). Despite this mounting evidence, little is known about how PGPR and *T. urticae* interact with cucumber plants because the majority of studies have concentrated on other crops like tomatoes, peppers, or strawberries. Examining how PGPR can affect the physiology of the pest and host plant in this system is essential given the economic significance of cucumbers and their vulnerability to spider mite infestations. Thus, the purpose of this study is to assess how three PGPR species, *Bacillus subtilis*, *Pseudomonas fluorescens*, and *Azospirillum brasilense*, affect the life history and demographic parameters of *T. urticae* on cucumbers. Furthermore, as indicators of induced plant defense responses, we evaluate alterations in important secondary metabolites of plants, such as anthocyanins, flavonoids, and total phenols. By explaining these interactions, our work seeks to contribute to the development of integrated pest management strategies that leverage beneficial microbes for sustainable cucumber production.

Materials and methods

Bacteria Preparation

Three bacterial isolates, *Bacillus subtilis*, *Pseudomonas fluorescens*, and *Azospirillum brasilense*, were obtained from the bacterial culture collection of the University of Jiroft. These isolates were originally derived from the Soil and Water Research Institute (SWRI) in Tehran, Iran, where they had been characterized and preserved as reference strains. Initially, the bacterial species were cultured on Nutrient Agar (NA) plates and incubated for 24 hours at 28 °C. Following incubation, the bacterial cells were harvested and suspended in sterile 0.01 M magnesium sulfate ($MgSO_4$) solution in Falcon tubes. The suspensions were centrifuged twice at 4,000 rpm for 10 min and the supernatant was discarded after each centrifugation step. To obtain homogeneous bacterial suspensions, each of the resulting pellets was individually resuspended in an appropriate volume of sterile distilled water and thoroughly mixed using a vortex mixer. The optical density (OD) of each bacterial suspension was measured at 600 nm a spectrophotometer. The concentration of each bacterial suspension was adjusted to 10^8 CFU//mL^{-1} (OD_{600}=0.8), following the method described by Park *et al.* (2013). The prepared bacterial

suspensions were then applied separately to the soil of pots containing cucumber seedlings at the two-true-leaf stage. The amount of suspension added was calculated to achieve a final concentration of approximately 10^7 CFU/g^{-1} soil. Sterile distilled water was used for the control treatment (plants).

Plant Material

Seeds of cucumber (*Cucumis sativus* cv. Soorna) were used in this study. Prior to sowing, the seeds were surface-sterilized by soaking in 1% sodium hypochlorite solution for 30 s and rinsed three times with sterile distilled water to remove residual chemicals. The seeds were then incubated between sterile moist filter papers at 28°C for 24 hours to promote germination. Seedlings were grown in the research greenhouse at the University of Jiroft under natural light conditions, with a temperature of 25 ± 1°C and relative humidity of 60±5%. At the two-true-leaf growth stage, the seedlings were transplanted into sterile plastic pots (8 cm in diameter, 10 cm in height) containing an autoclaved mixture of peat, perlite, and farm soil at a 1:1:2 ratio. Plants were irrigated every three days. To prevent infestation by unwanted pests typical of greenhouse environments, the plants were kept inside insect-proof mesh cages (with a pore size of approximately 74 µm (200 mesh), which effectively prevents the entry of thrips, aphids, whiteflies, and spider mites while allowing adequate airflow and light transmission).

Establishment and maintenance of *Tetranychus urticae* colony

To establish a laboratory colony of *T. urticae*, infested cucumber plants were collected from greenhouses in Jiroft, Iran. The mite species was identified using standard taxonomic keys (Seeman & Beard, 2011) and confirmed by Dr. Sayed Mosayeb Mahdavi. A separate colony was then maintained on untreated cucumber plants within mesh cages under controlled laboratory conditions. Prior to the initiation of the main experiments, the mite population was reared for two generations on cucumber plants treated with the bacterial species used in the study. To maintain the colony and ensure a sufficient food supply, the plants in each cage were regularly replaced with fresh ones.

Experiment 1. Life Table Analysis of *Tetranychus urticae*

To evaluate PGPR-induced resistance in rhizosphere-treated cucumber plants against *T. urticae*, demographic and population growth parameters were studied on plants treated with *B. subtilis*, *P. fluorescens*, and *A. brasilense*, as well as on control plants treated with sterile distilled water. Bacterial suspensions were applied to the soil of each pot 7 days before the initiation of demographic experiments (at the two-true-leaf stage). This 7-day interval was selected based on previous studies demonstrating that this period is sufficient for bacterial colonization of the cucumber rhizosphere and the subsequent activation of induced systemic resistance (ISR) and defense-related enzymes (Van Wees *et al.*, 2008; Pieterse *et al.*, 2014). On the 7th day after bacterial application, leaf discs were excised from treated cucumber leaves and used for the life table experiments. It should be noted that the bacterial inoculation was performed twice during the experimental period. the second inoculation was performed 14 days after the first application (i.e., 7 days after mite release) to maintain bacterial population density in the rhizosphere and ensure sustained induction of plant defense responses. This two-step inoculation strategy is consistent with the protocol recommended by Kloepper *et al.* (2004) and Ryu *et al.* (2007) for maintaining effective rhizobacterial populations throughout the experimental period.

Each experimental unit consisted of two Petri dishes. The smaller one, 6 cm in diameter and 1.5 cm in height, contained a centrally positioned aperture created using a heated metal rod. A 1-mm-thick layer of cotton was placed at the bottom of the small dish, onto which circular leaf discs, each measuring 3 cm in diameter, were cut from the leaves of cucumbers from each treatment and placed with the abaxial (lower) surface facing upward. To prevent mite escape, the margin of each disc was surrounded by a thin layer of cotton. This setup was then placed inside a larger Petri dish, 8 cm in diameter, containing approximately 1 cm of water. The water reached the smaller dish through the central aperture, thus moistening the cotton both below and around the leaf disc to maintain leaf freshness. The water level in the 8 cm Petri dish was checked daily and water was added if necessary. For each treatment, 50 age-synchronized eggs (<12 h old) laid by females reared on the respective treated plants were transferred individually onto the leaf discs (2.5 cm diameter) from treated cucumber leaves. These experimental units were checked daily and developmental duration and mortality of different immature stages were recorded using a stereomicroscope. Upon adult emergence, females were paired with males of the same

treatment group. The pairs were transferred to new rearing discs, and daily observations were conducted to record the fecundity of females and longevity of both sexes until death. The obtained data were used to calculate *T. urticae* population growth parameters. Experiments were carried out in a growth chamber at 25±1°C, 60±5% relative humidity, and a 16:8 (L:D) h photoperiod. Leaf discs were changed every three days, and the mites were transferred carefully to fresh discs. A camel hair brush was used to transfer the mites from old leaf discs to new ones. The age-stage, two-sex life table theory developed by Chi & Liu (1985) and the methodology outlined by Chi (1988) were used to analyze the demographic parameters of *T. urticae* under the various bacterial treatments. The TWOSEX-MSChart software was used to process the data (Chi, 2024). Variances and standard errors (SE) of the life table parameters were estimated using the bootstrap procedure with 100,000 iterations. Paired bootstrap tests were used to compare the life table parameters among treatments based on their 95% confidence intervals.

Experiment 2. Assessment of Secondary Metabolites in Plants

The impact of three species of bacteria, *B. subtilis*, *P. fluorescens*, and *A. brasilense*, on the plant biochemical parameters of the treated cucumber, especially the contents of total phenol, anthocyanin, and flavonoid was assessed during interaction with *T. urticae* at different time intervals (0, 24, and 72 h after mite infestation) that received one of eight treatments: C, control plants without bacteria and without mites (negative control); M, plants without bacteria but infested with mites (positive control); B, plants treated with *B. subtilis* without mite infestation; BM, plants treated with *B. subtilis* and infested with mites; P, plants treated with *P. fluorescens* without mite infestation; PM, plants treated with *P. fluorescens* and infested with mites; A, plants treated with *A. brasilense* without mite infestation; and AM, plants treated with *A. brasilense* and infested with mites. The experiment was conducted using a completely randomized design with four biological replications per treatment, each replication consisting of one pot (one cucumber plant). Bacterial suspensions were applied to the soil of each pot 7 days before the initiation of mite infestation (at the two-true-leaf stage). For treatments with mites, the cucumber plants at four-leaf stage were initially infested with 20 mated adult females (< 48 h old) per plant, with 5 specimens per leaf. At each sampling time (0, 24, and 72 h), leaves were harvested from cucumber plants, in mite-infested treatments, mites were gently brushed off the sampled leaf areas prior to collection. The leaf samples were wrapped immediately in aluminum foil, flash-frozen in liquid nitrogen, and stored at −80°C for subsequent biochemical analyses.

Total Phenolic Content

In a mortar, 0.1 g of leaf tissue and 1 ml of 96% ethanol were thoroughly ground. After centrifugation of the homogenate for 10 minutes at 10,000 rpm, the supernatant was transferred to a sterile tube and kept at -20 °C until further analysis. 100 µl of ethanolic extract, 400 µl of 95% ethanol, and 125 µl of 50% Folin–Ciocalteu reagent were combined to determine the total phenolic content. The mixture was incubated for 15 minutes at 40°C in a water bath after 250 µl of 5% sodium carbonate had been added after 5 minutes. A spectrophotometer was used to measure the absorbance at 760 nm after the solution was centrifuged for three minutes at 4000 rpm.

Total Flavonoid Content

100 µl of ethanolic extract, 400 µl of 95% ethanol, 20 µl of 10% aluminum chloride, 20 µl of 1 M potassium acetate, and 560 µl of sterile distilled water were mixed to measure the total flavonoids. After 30 minutes at room temperature, the mixture's absorbance was measured with a spectrophotometer set to 415 nm. 95% ethanol was used in place of the extract to create a blank. The calibration curve's standard was quercetin (Chang *et al.,* 2002).

Anthocyanin Content

About 0.02 g of leaf tissue was ground in 2 ml of acidified methanol and incubated in darkness for 24 h in order to measure the anthocyanin content. At 550 nm, absorbance was measured with a spectrophotometer. Methanol that had been acidified served as a blank. The following formula was used to determine the anthocyanin concentration in µmol per gram of fresh weight (Wagner, 1979):

$$A=\varepsilon bc$$

where b is the path length of the sample (cm), c is the concentration of the compound in solution (mol/L), and ε is the extinction coefficient (33,000 L/mol·cm).

Results

Population Demographic Parameters

Table 1 shows the effects of plant growth-promoting rhizobacteria (PGPR) on the population growth parameters of the two-spotted spider mite, *T. urticae*. The demographic characteristics of *T. urticae* were significantly affected by feeding on cucumber plants inoculated with PGPR. The species that demonstrated the strongest suppressive effect on important population growth parameters, such as intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), and gross reproductive rate (*GRR*), was *B. subtilis*. Net and gross reproductive rates of this mite on *B. subtilis* treatments were significantly lower than those observed in the *A. brasilense* treatment, while there were no significant differences among other treatments. The growth rate of *T. urticae* on the plants treated with *B. subtilis* was significantly lower than that on plants treated with *P. fluorescens*, as well as untreated plants (control). The mean generation time (T) in the *B. subtilis* treatment was significantly longer than observed in the other bacterial treatments (Table 1).

Age-stage specific survival rate (s_{xj}) curves of *T. urticae* showed that only mites feeding on cucumber plants treated with *B. subtilis* experienced mortality during the egg stage (Fig. 1). Additionally, mites on these treated plants *had* the highest mortality rates during the larval-nymph and pre-adult stages. PGPR treatments affected the two-spotted spider mite's age-specific survivorship (l_x), age-specific fecundity (m_x), and age-stage specific fecundity (f_{xj}) in cucumbers (Fig. 2). The l_x curves indicated that mites reared on cucumber plants treated with *B. subtilis* showed the highest pre-adult mortality. Age-specific fecundity (m_x) refers to the average number of eggs laid by individual mites at each age (x), while age-stage specific fecundity (f_{xj}) indicates the average egg production at a specific age (x) and developmental stage (j). Since only adult female mites can reproduce, the f_{xj} curve specifically reflects the egg-laying behavior of females under each treatment. Mites feeding on untreated cucumber plants (control) had the highest peak in egg production. In addition, the longest oviposition period was observed in this treatment. By contrast, a significant decline in both the peak number of eggs laid and the duration of reproduction was seen in all three other treatments.

Plant biochemical content (secondary metabolites)

Total Phenol

The total phenol content in cucumber plants treated with the selected bacterial species is shown in Fig. 3. This parameter varied significantly among the rhizobacterial treatments compared with both mite-infested and untreated plants. There was no significant difference in phenol levels in the negative control treatment (C) across all three sampling times. At time 0, the phenol content was not significantly different from that of the negative control; however, a significant increase was recorded at 24 and 72 hours after mite infestation, reaching 1.67 and 2.4 mg/g FW, respectively.

Table 1. The mean (±SE) population demographic parameters of *Tetranychus urticae* reared on leaves of cucumber plants treated with plant growth-promoting rhizobacteria (PGPR)

Parameter	Control	*Azospirillum brasilense*	*Bacillus subtilis*	*Pseudomonas fluorescens*
Intrinsic rate of increase (r)	0.217±0.013^{a}	0.193±0.010^{ab}	0.169±0.014^{b}	0.199±0.011^{a}
Finite rate of increase (λ)	1.243±0.013^{a}	1.213±0.012^{ab}	1.184±0.015^{b}	1.220±0.013^{a}
Gross reproductive rate (*GRR*)	33.25±3.92^{a}	27.08±5.82^{ab}	22.19±3.96^{b}	27.49±4.19^{ab}
Net reproductive rate (R_0)	28.76±4.84^{a}	24.46±3.63^{ab}	18.35±3.65^{b}	24.29±3.58^{ab}
Mean generation time (T)	15.38±0.40^{b}	16.46±0.30^{b}	17.08±0.27^{a}	15.95±0.38^{b}

Different superscript letters within rows show significant differences ($P < 0.05$) among treatments based on paired bootstrap tests.

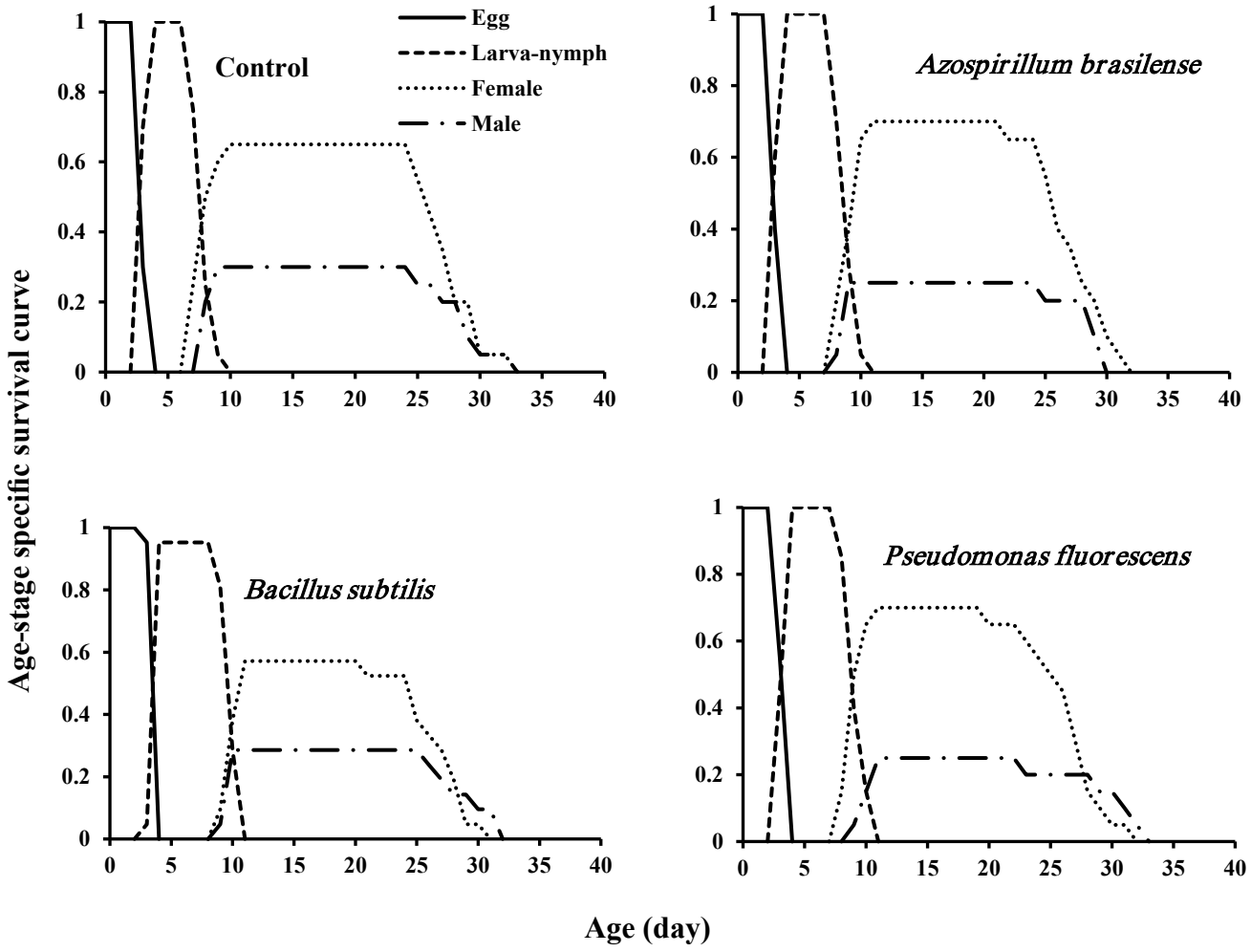


Fig. 1. Age-stage specific survival rate (s_{xj}) of *Tetranychus urticae* reared on leaves of cucumber plants treated with plant growth-promoting rhizobacteria (PGPR)

The total phenol content in B, A, and P treatments was significantly higher than in the C treatment at all times (0, 24, and 72 hours). At all times tested, the phenol content in BM, PM, and AM treatments was significantly higher than in both the negative and positive controls. Among all treatments, the highest phenol content was recorded in the BM treatment at 24 hours, reaching 3.89 mg/g FW. This was followed by PM at 72 hours (3.53 mg/g FW) and AM at 24 hours (3.12 mg/g FW).

Anthocyanin

Fig. 4 depicts the anthocyanin content in cucumber plants treated with the selected bacterial species. Anthocyanin levels did not vary significantly among the three sampling times within the negative control treatment. The anthocyanin content in the M treatment was not significantly different from that of the C treatment at time zero; however, a significant increase was observed at 24 and 72 hours after mite infestation, reaching 65.66 µg/g and 98.43 µg/g, respectively. A, B, and P treatments showed significantly higher anthocyanin levels compared to the negative control (C) at all three time points. In addition, BM, AM, and PM treatments exhibited significantly higher levels of anthocyanin compared to C and M treatments at 24 and 72 hours after mite infestation. Among the three bacterial treatments, the highest anthocyanin accumulation was recorded at 72 hours post-infestation, with the PM treatment reaching 136.36 µg/g, followed by AM with 105.85 µg/g.

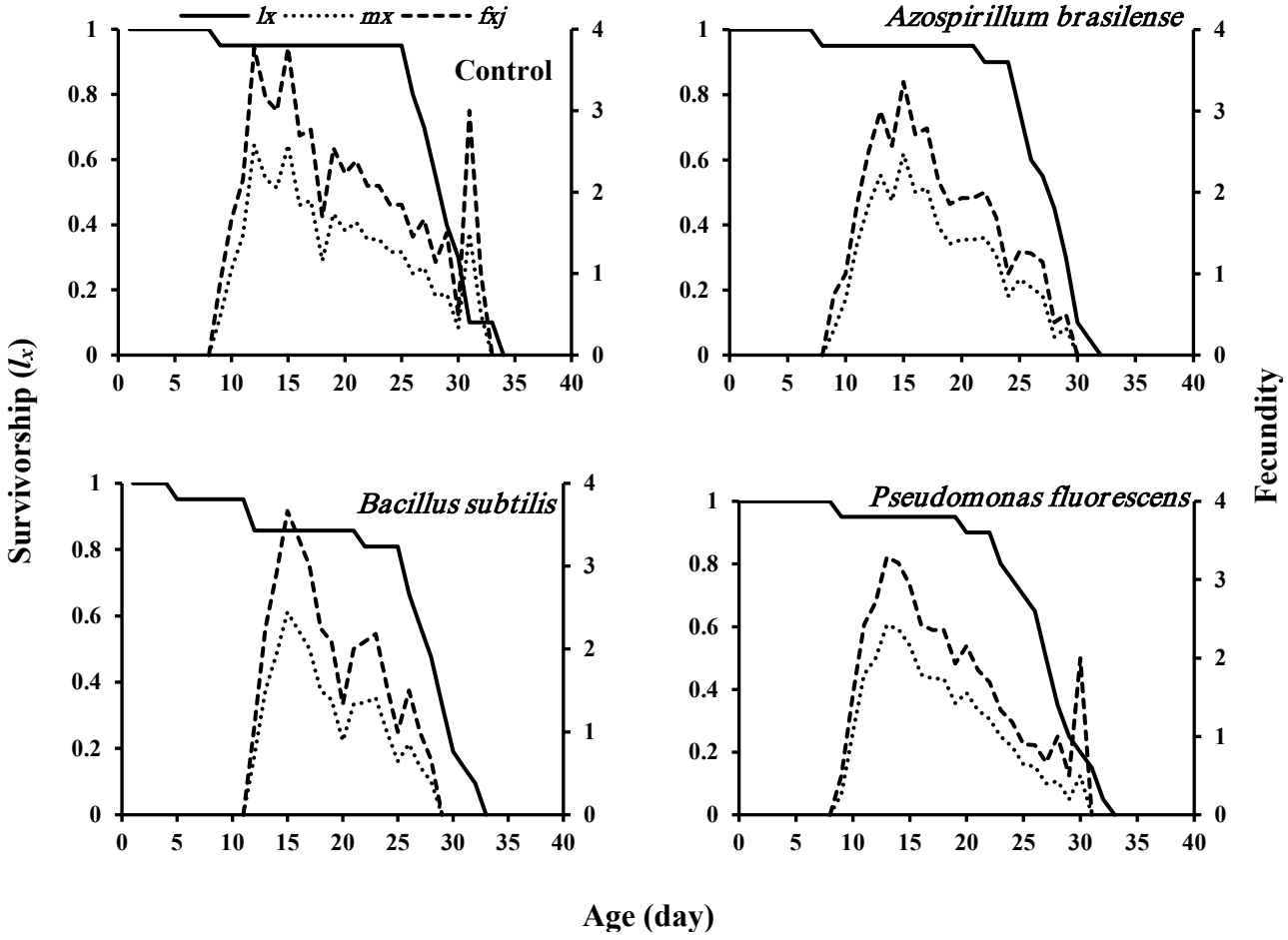


Fig. 2. Age-specific survivorship (l_x), age-stage fecundity of female (f_{xj}), and age-specific fecundity (m_x) of *Tetranychus urticae* reared on leaves of cucumber plants treated with plant growth promoting rhizobacteria (PGPR).

Flavonoid

Different PGPR, in the presence and absence of spider mites, affected the flavonoid content of cucumber plants (Fig. 5). Flavonoid content remained relatively stable across all three time points in the C treatment. Flavonoid levels increased significantly in the M treatment compared to the C treatment at 24 and 72 hours after mite infestation. Treatments A, B, and P exhibited significantly higher flavonoid content compared to the C treatment at all three time points. The flavonoid content in these treatments remained statistically unchanged over time. Flavonoid content in the BM, AM, and PM treatments increased significantly at 24 and 72 hours after mite infestation compared to the C and M treatments. The highest and lowest flavonoid contents were observed in the BM treatment at 72 h post-infestation (0.567 mg/g FW) and the AM treatment (0.531 mg/g FW) at the same time point.

Discussion

Plant growth-promoting rhizobacteria (PGPR) are naturally occurring soil bacteria that colonize plant roots, an important site for plant microbe interactions. PGPR can trigger or enhance biosynthesis of defense-related chemical compounds in plants and, thereby, decrease life history performance and population growth of herbivores attacking aboveground plant tissue (Pourya *et al.*, 2020). According to the results of the current study, PGPR, specifically *B. subtilis*, enhanced the resistance and changed the biochemical content of cucumber plants when infested with *T. urticae*. The treatment with *B. subtilis* increased secondary metabolites including total phenols, anthocyanins and flavonoids. As mentioned by Salunke & Koche (2023), these compounds are known for their antioxidant activity and ability to protect against herbivorous pests. They alter plant defense mechanisms by

strengthening cellular structures, eliminating reactive oxygen species, and preventing pest growth (War *et al.*, 2012).

Spider mite populations were found to be adversely affected by rhizobacteria, suggesting that mite activity on infested plants is either directly or indirectly inhibited (Hosseini *et al.*, 2022). It is possible that the microbes are altering the parameters of plant growth, thereby reducing the host plant's suitability for mites. Plant-microbe interactions and the composition of the microbial community mediate the seemingly complex interactions between beneficial microbes and plant defenses. Our study demonstrated that plants treated with *B. subtilis* significantly influenced *T. urticae* life history parameters by suppressing the species' population growth rate and reproductive potential. Additionally, the extended generation time observed in the aforementioned treatment suggests delayed development, most likely resulting from a combination of induced biochemical defenses and altered plant nutritional quality. Similarly, a decreased oviposition rate of *T. urticae* was noted on rhizobacteria-treated strawberry plants compared to those fed untreated plants (Hosseini *et al.*, 2022). Additionally, spider mites fed on strawberry plants treated with *Azotobacter chroococcum* and *A. brasilense* exhibited the lowest intrinsic rate of increase. Smaller and slower development of mite populations has been reported in various PGPR-treated plants. A study by Tomczyk & Kielkiewicz (2000) indicated that in cucumbers and tomatoes treated with PGPR, *Tetranychus* population growth decreased by approximately 34–43%, with a more severe impact on younger leaves. In another study, cucumber plants infected with *P. fluorescens* had a lower population density of *T. urticae* and experienced a 35% decrease in fecundity after six weeks (Tomczyk, 2006).

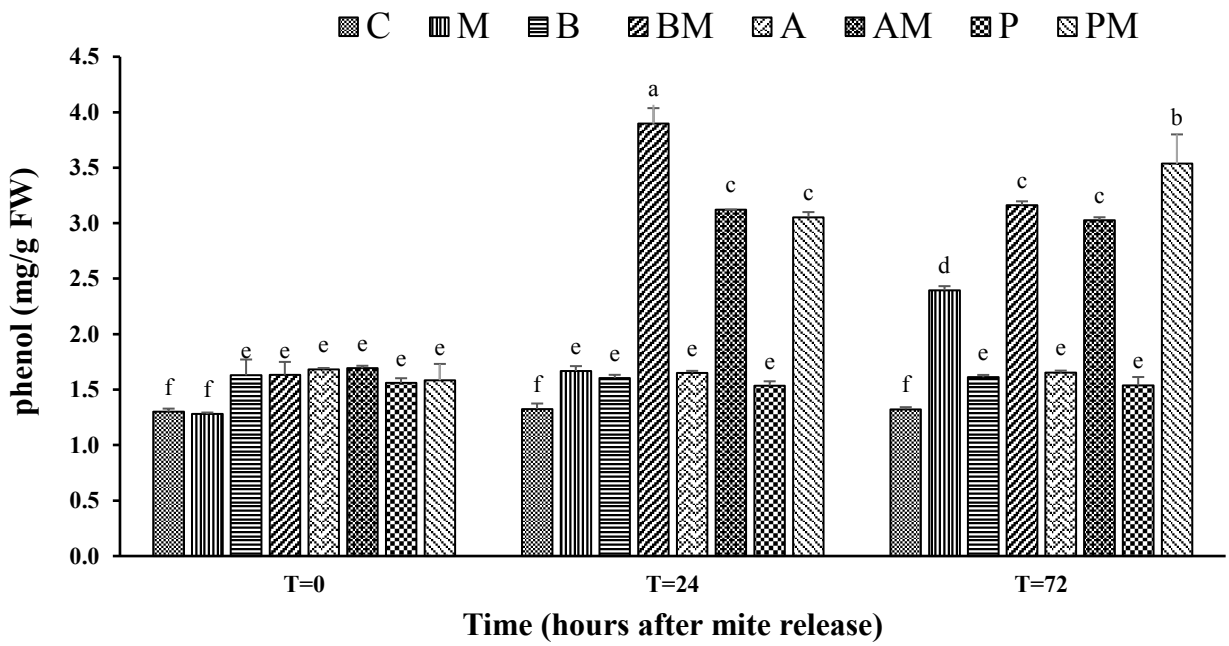


Fig. 3. Phenol content of cucumber plant at different time intervals (0, 24 and 72 hours) that received one of eight treatments: C, control plants without bacteria and without mites (negative control); M, plants without bacteria but infested with mites (positive control); B, plants treated with *B. subtilis* without mites; BM, plants treated with *B. subtilis* and infested with mites; P, plants treated with *P. fluorescens* without mites; PM, plants treated with *P. fluorescens* and infested with mites; A, plants treated with *A. brasilense* without mites; and AM, plants treated with *A. brasilense* and infested with mites. Different superscript letters within columns indicate significant differences among treatments (Duncan's test, P<0.05).

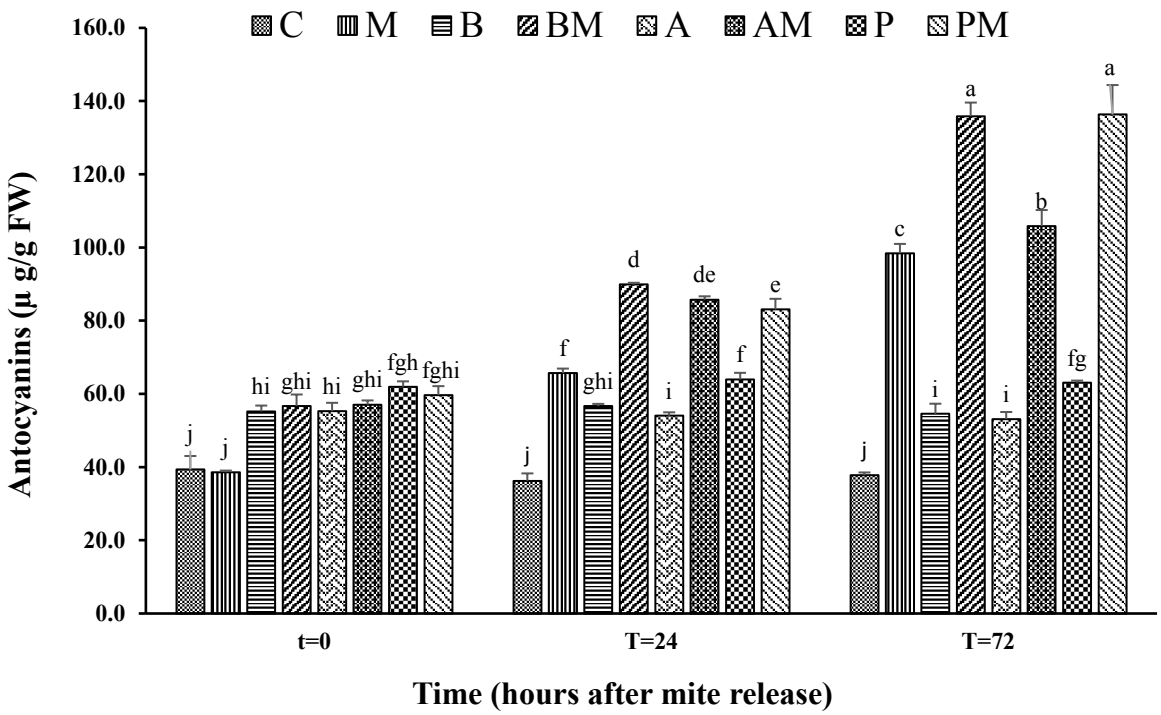


Fig. 4. Anthocyanins content of cucumber plants at different time intervals (0, 24 and 72 hours) that received one of eight treatments: C, control plants without bacteria and without mites (negative control); M, plants without bacteria but infested with mites (positive control); B, plants treated with *B. subtilis* without mites; BM, plants treated with *B. subtilis* and infested with mites; P, plants treated with *P. fluorescens* without mites; PM, plants treated with *P. fluorescens* and infested with mites; A, plants treated with *A. brasilense* without mites; and AM, plants treated with *A. brasilense* and infested with mites. Different superscript letters within columns indicate significant differences among treatments (Duncan's test, P<0.05).

All three bacterial species exerted adverse effects on population growth parameters of *T. urticae* and positive effects on the plant biochemical content of the treated cucumber. In addition, in our previous study (Darini *et al.*, 2025), the results showed that treatment of cucumber plants with plant growth-promoting rhizobacteria (PGPR) caused an increase in developmental time and immature mortality rate, as well as a decrease in adult longevity, oviposition period, and fecundity of *T. urticae*. These results demonstrate that beneficial rhizobacteria can induce resistance in cucumber by enhancing defensive secondary metabolites, thereby limiting *T. urticae* performance. We argue that the three studied PGPR systemically strengthened and/or induced resistance in above-ground plant parts and enhanced the level of biochemical anti-herbivore defense. This was probably achieved by inducing or upregulating the production of secondary plant metabolites, such as phenolics, flavonoids and anthocyanins. Phenolic compounds play a major role in how plants interact with their environment, particularly with microorganisms (Kisiel *et al.*, 2024). Due to their high biological activity and capacity to be liberated from root tissues, they serve as the first line of defense against infections. This pathway is essential for insect feeding, UV exposure, high temperatures, and plant disease resistance (Ren *et al.*, 2019). Furthermore, phenolic compound production could be a sign that systemic immunity has been induced (Gholami *et al.*, 2014). The increase in total phenol content, especially notable in the *B. subtilis* treatment at 24 h post-infestation, suggests activation of phenylpropanoid pathways commonly associated with plant defense responses (Mithöfer & Boland, 2012). Plant PGPR were found to increase the synthesis of phenolic compounds in plants such as chickpea plants, raspberry plants, and *Medicago truncatula*, which is consistent with our findings (Singh *et al.*, 2003; Kisiel *et al.*, 2024). In the present investigation, rhizobacteria and mite infestation interacted to produce an additive effect, whereby rhizobacteria bolstered the plant defense mechanisms triggered by mite infestation. In a similar study, mite infestation has been shown to raise the concentration of specific phenolic compounds in strawberry plants and *Tilia platyphyllos* (Mouden *et al.*, 2021). Additionally, compared to uninoculated control plants, the total phenolic content of plants

inoculated with PGPR bacteria (*B. subtilis*, *P. fluorescens*) increased both before and after infestation by the green peach aphid (*Myzus persicae*) (Sulzer) (Mardani-Talaee *et al.*, 2016). The effects of rhizobacteria vary depending on the type of rhizobacteria and the plant species, even though they caused defense compounds to accumulate in plants. Moreover, rhizobacteria treatment can raise the phenolic content, which mite infestation can alter on its own. This demonstrates the intricate relationships that exist between herbivore pressure, plant defense systems, and rhizobacteria.

Among several phytoalexins, flavonoids are polyphenolic secondary metabolites that are essential to plant defense systems (Taulavuori *et al.*, 2016). According to Mierziak *et al.* (2014) they play a role in plants' defense against biotic and abiotic stresses. The crop's developmental stage, the type of plant, and the type of stress experienced are some of the variables that greatly influence their biosynthesis (Schijlen *et al.*, 2004). Host plant flavonoid content can be modified as a treatment with rhizobacteria. In legumes, the production of certain isoflavones such as genistein and daidzein was induced following rhizobial infection (Kumar *et al.*, 2024). PGPR are capable of inducing genes associated with flavonoid production and secretion in the rhizosphere (Vacheron *et al.*, 2013). Root treatment of raspberry plants with *P. fluorescens* was found to trigger the expression of some flavonoid biosynthetic genes and flavonoid levels in the fruits (García-Seco *et al.*, 2015). Likewise, increased levels of flavonoids and flavonols were found in strawberries inoculated with *A. brasilense* (Pii *et al.*, 2017).

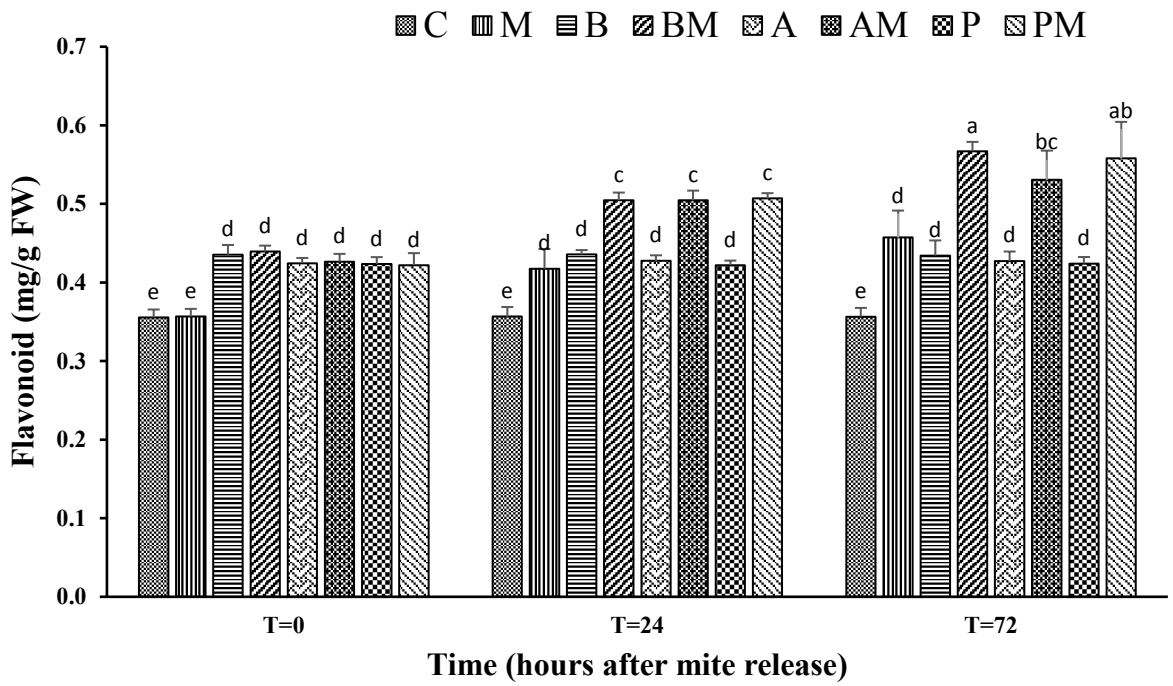


Fig. 5. Flavnoid content of cucumber plants at different time intervals (0, 24 and 72 hours) that received one of eight treatments: C, control plants without bacteria and without mites (negative control); M, plants without bacteria but infested with mites (positive control); B, plants treated with *B. subtilis* without mites; BM, plants treated with *B. subtilis* and infested with mites; P, plants treated with *P. fluorescens* without mites; PM, plants treated with *P. fluorescens* and infested with mites; A, plants treated with *A. brasilense* without mites; and AM, plants treated with *A. brasilense* and infested with mites. Different superscript letters within columns indicate significant differences among treatments (Duncan's test, P<0.05)

Inoculation of sweet pepper plants with *B. subtilis* and *P. fluorescens* led to a rise in flavonoid content in the leaves prior to and following the infestation by the green peach aphid, as compared to the control plants (Mardani-Talaee *et al.*, 2016). In agreement with these results, the current study proved that treatment with *A. brasilense*, *B. subtilis*, and *P. fluorescens* significantly boosted flavonoid content in cucumber plants, especially after the infestation by *T. urticae*.

Anthocyanins are water-soluble pigments of the phenolic compound group, usually occurring in glycosylated forms (Khoo *et al.*, 2017). The pigments are important in plant tolerance to a wide range of stress factors including defense against pathogens and herbivores (Gould *et al.,* 2004). The current study revealed that treatment with *B. subtilis*, *P. fluorescens*, and *A. brasilense* greatly increased anthocyanin content in cucumber plants. The increase was higher following *T. urticae* feeding and differed significantly from the positive control, revealing the potential of the bacteria in enhancing accumulation of anthocyanin. Consistent with our results, Trinh *et al.*, (2018) demonstrated that application of *Paenibacillus pabuli* P7S greatly enhanced total anthocyanin content in Arabidopsis. Also, the application of PGPR bacteria (*B. subtilis* and *P. fluorescens*) in sweet pepper against *M. persicae* resulted in the elevation of anthocyanin content in the leaves prior to and after aphid infestation in plants treated with *B. subtilis*, and prior to infestation in those treated with *P. fluorescens* (Mardani-Talaee *et al.*, 2016).

While both *P. fluorescens* and *A. brasilense* had some positive impacts on secondary metabolite accumulation and mite population suppression, the impacts were less consistent and statistically less significant than those achieved with *B. subtilis*. These variations could be due to differences in induced systemic resistance mechanisms, along with differences in root colonization efficiency and the level or type of bioactive metabolite production by the different bacterial species (Fourneau *et al.*, 2024). The observed inverse relationship between the accumulation of secondary metabolites and the population growth parameters of *T. urticae* provides compelling evidence for the role of PGPR-induced biochemical defenses in suppressing mite performance. Specifically, the *B. subtilis* treatment, which consistently induced the highest levels of total phenols, flavonoids, and anthocyanins, concurrently resulted in the lowest intrinsic rate of increase (r), the lowest net reproductive rate (R_0), and the longest mean generation time (T). This strong correlation suggests that elevated phenolic, flavonoid and anthocyanin compounds directly contribute to reduced mite fitness by impairing fecundity, increasing pre-adult mortality, and prolonging developmental duration, as evidenced by the age-stage specific survival (s_{xj}) curves and decreased oviposition peaks observed in treated plants.

Overall, root inoculation of cucumber plants with PGPR, particularly *B. subtilis*, was able to promote growth and to generate an induced systemic resistance (ISR) response against *T. urticae*. The current body of evidence indicates that PGPR can enhance cucumber resistance against *T. urticae*, potentially through mechanisms involving the alteration of plant secondary metabolites, volatile emissions, and overall plant health. These not only suppress mite populations but also improve crop yield and reduce chemical inputs, highlighting their potential as valuable components of sustainable pest management programs. Therefore, integrating such beneficial microbes into pest management programs can reduce reliance on chemical acaricides and mitigate associated environmental risks.

Author's Contributions

Hamidreza Alizadeh & **Mostafa Khanamani**; Conceptualization, methodology: **Hamidreza Alizadeh**, **Mostafa Khanamani** & **Amin Sedaratian**; formal analysis: **Elahe Darini**, **Mostafa Khanamani** & **Amin Sedaratian**; investigation: **Elahe Darini** & **Mostafa Khanamani**; draft preparation: **Elahe Darini** & **Mostafa Khanamani**; final review and edit: **Mostafa Khanamani**; visualization: **Hamidreza Alizadeh**, **Mostafa Khanamani** & **Amin Sedaratian**; supervision: **Hamidreza Alizadeh** & **Mostafa Khanamani**; project administration: **Hamidreza Alizadeh** & **Mostafa Khanamani**; **Hamidreza Alizadeh**. funding acquisition.

Author's Information

Elahe Darini	✉ elahedarinii@gmail.com	https://orcid.org/0009-0001-7553-1047
Hamidreza Alizadeh	✉ hamidalizadeh@ujiroft.ac.ir	https://orcid.org/0000-0002-4529-0158
Mostafa Khanamani	✉ m.khanamani@ujiroft.ac.ir	https://orcid.org/0000-0003-2164-9565
Amin Sedaratian-Jahromi	✉ Sedaratian@yu.ac.ir	https://orcid.org/0000-0002-2588-2359

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Data Availability Statement

All data generated or analyzed during this study, including detailed methodology, are available from the corresponding author upon reasonable request.

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Ethics Approval and Consent to Participate

Mites were used in this study. All applicable international, national, and institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by the authors.

Conflict of Interest

The authors declare that there is no conflict of interest regarding the publication of this paper.

Consent for Publication

Not applicable

Generative AI statement

The authors declare that they used AI-assisted tools for language editing and grammatical improvement of this manuscript.

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Research Article

ارتباط ترکیبات دفاعی تقویت‌شده خیار توسط ریزوباکتری‌های محرک رشد گیاه (PGPR) با اختلال در نرخ رشد کنه تارتن دولکه‌ای (*Tetranychus urticae*) در مدیریت آفات

الهه درینی [۱]، حمیدرضا علیزاده [۱]، مصطفی خنامانی [۱] و امین صدارتیان جهرمی [۲]

۱. گروه گیاه‌پزشکی، دانشکده کشاورزی، دانشگاه جیرفت، جیرفت، ایران

۲. گروه گیاه‌پزشکی، دانشکده کشاورزی، دانشگاه یاسوج، یاسوج، ایران

چکیده: متابولیت‌های ثانویه گیاهی نقش مهمی در دفاع گیاه میزبان در برابر آفات گیاهخوار ایفا می‌کنند. ریزوباکتری‌های مفید ریشه ممکن است با بهبود متابولیت‌های ثانویه گیاه، عملکرد آفات روی گیاه را به‌صورت منفی تحت تأثیر قرار دهند. این مطالعه ارزیابی کرد که آیا سه نوع باکتری محرک رشد ریشه (PGPR) شامل *Bacillus subtilis*، *Pseudomonas fluorescens* و *Azospirillum brasilense* می‌توانند با تغییر متابولیت‌های ثانویه گیاه و تأثیر بر پویایی جمعیت کنه، دفاع خیار را در برابر کنه تارتن دولکه‌ای افزایش دهند. فراسنجه‌های جدول زندگی با استفاده از جدول زندگی دو جنسی ارزیابی شدند. همچنین، نمونه‌های برگی برای ارزیابی میزان ترکیبات فنلی، فلاونوئیدها و آنتوسیانین‌ها در زمان‌های ۰، ۲۴ و ۷۲ ساعت پس از آلودگی به کنه مورد تجزیه قرار گرفتند. هر سه تیمار باکتریایی، به ویژه *B. subtilis*، نرخ رشد *T. urticae* را در مقایسه با گیاهان شاهد کاهش دادند. در میان سویه‌های آزمایش‌شده، *B. subtilis* بیشترین مهار را در رشد جمعیت کنه ایجاد کرد و پس از آن به ترتیب *P. fluorescens* و *A. brasilense* قرار داشتند. مقادیر نرخ ذاتی افزایش جمعیت (r)، نرخ متناهی افزایش جمعیت (λ)، نرخ خالص تولیدمثل (R_0)، نرخ ناخالص تولیدمثل (GRR) و میانگین مدت زمان یک نسل (T) در تیمار *B. subtilis* در مقایسه با شاهد به ترتیب برابر بود با: ۰/۱۶۹ در مقابل ۰/۲۱۷ برروز؛ ۱/۱۸۴ در مقابل ۱/۲۴۳ برروز؛ ۱۸/۳۵ در مقابل ۲۸/۷۶ تخم/فرد؛ ۲۲/۱۹ در مقابل ۳۳/۲۵ تخم/فرد، و ۱۷/۰۸ در مقابل ۱۵/۳۸ روز. علاوه بر این، گیاهان تلقیح شده در شرایط عاری از کنه، افزایش قابل توجهی در میزان فنول کل، فلاونوئیدها و آنتوسیانین‌ها نشان دادند. با این حال، این افزایش در تیمارهای آلوده به کنه بیشتر بود، که نشان دهنده تأثیر باکتری‌های مورد مطالعه در فعال‌سازی واکنش‌های دفاعی گیاهان خیار و افزایش تولید متابولیت‌های ثانویه پس از حمله کنه می‌باشد. هر سه گونه باکتری، به ویژه *B. subtilis*، اثرات منفی بر فراسنجه‌های رشد جمعیت *T. urticae* و اثرات مثبت بر ترکیبات دفاعی خیارهای تیمارشده اعمال کردند. این نتایج نشان می‌دهد که ریزوباکتری‌های مفید می‌توانند با افزایش متابولیت‌های ثانویه دفاعی، مقاومت را در خیار القاء کنند.

کلمات کلیدی: ریزوباکتری محرک رشد گیاه (PGPR)، *Bacillus subtilis*، *Pseudomonas fluorescens*، *Azospirillum brasilense*، مقاومت القایی

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دبیر تخصصی: آزاده فرازمند

نویسنده مسئول: مصطفی خنامانی

ایمیل: m.khanamani@ujiroft.ac.ir

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