

Synergistic application of plant growth-promoting rhizobacteria and iron oxide nanoparticles enhances agro-physiological traits, antioxidant properties, and essential oil production in *Satureja khuzistanica* Jamzad: A sustainable biofortification approach

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ARTICLE INFO

Keywords:

Phenylalanine ammonia lyase
Flavonoids
Fe₂O₃
Antioxidant enzymes
Carvacrol

ABSTRACT

Satureja khuzistanica Jamzad, a medicinal plant endemic to Iran, struggles with micronutrient deficiencies, especially iron, in alkaline soils, limiting its growth and essential oil production. This study aimed to investigate the interaction impact of plant growth-promoting rhizobacteria (PGPR) (*Curtobacterium plantarum* and *Pseudomonas brassicacearum*) and Fe₂O₃ in both nano and bulk forms, applied at concentrations of 0, 100, and 200 mg L⁻¹, on the yield, photosynthetic pigments, antioxidant activity, and essential oil of *S. khuzistanica*. The experiment was arranged as a factorial combination in a completely randomized design under greenhouse conditions. PGPR inoculation significantly improved root growth, absolute growth rate, leaf dry weight, relative water content, chlorophyll, flavonoid, essential oil content, yield, and iron content. Foliar application of Fe₂O₃ enhanced the activity of phenylalanine ammonia lyase in the non-inoculated plants. Additionally, antioxidant activity was increased with the foliar spray of 200 mg L⁻¹ Fe₂O₃, with notable improvements observed in the activities of catalase and ascorbate peroxidase. However, the combination of PGPR inoculation and Fe₂O₃ significantly enhanced yield-related traits, relative water content, chlorophyll content, essential oil content, and Fe levels. Notably, the carvacrol percentage was markedly higher in non-inoculated plants treated with Fe₂O₃. The highest yield of essential oil was recorded with PGPR inoculation and 100 mg L⁻¹ Fe₂O₃NPs. These findings provide the first evidence that integrating PGPR with Fe₂O₃NPs can sustainably enhance essential oil biosynthesis and agronomic traits in *S. khuzistanica*. This integrated biofortification strategy offers a promising, eco-friendly approach to improve growth and phytochemical quality in nutrient-deficient soils, with significant implications for the sustainable cultivation of high-value medicinal plants.

1. Introduction

The genus *Satureja* (Lamiaceae) encompasses approximately 30 species worldwide (Nooshkam et al., 2017). *Satureja khuzistanica* Jamzad, an aromatic species endemic to Iran, thrives naturally in the calcareous soils of the mountainous slopes of southwestern Iran (Sefidkon et al., 2022; Jahanshahi et al., 2024). Renowned for its high phenolic content—particularly carvacrol and free phenolic acids such as rosmarinic acid—the essential oils and extracts of *S. khuzistanica* are

highly regarded in the pharmaceutical and food industries for their notable pharmacological properties (Mumivand et al., 2021a). Carvacrol, a monoterpene comprising over 80 % of the essential oil in this species, exhibits potent antimicrobial and antioxidant activities (Shams et al., 2023). Carvacrol microcapsules, known for their controlled-release applications in food and nutraceuticals, have shown promising efficacy; at a concentration of 0.5 %, they fully inactivated norovirus surrogates, while at 1 %, they achieved a 1-log reduction in hepatitis A virus (Sanchez et al., 2015). These findings underscore the

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<https://doi.org/10.1016/j.indcrop.2025.121543>

Received 22 May 2025; Received in revised form 10 July 2025; Accepted 15 July 2025

Available online 24 July 2025

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considerable potential of carvacrol for diverse applications in food processing, medical treatments, and polymer production, owing to its economic viability and functional benefits. Given the rising pharmaceutical demand and the ecological vulnerability of this endemic species, there is an urgent need for sustainable cultivation practices to ensure the species' conservation while meeting commercial demands.

Iron, the fourth most abundant element in the Earth's crust, primarily exists as Fe^{3+} , an insoluble form that restricts its availability for plant absorption (Ahmed et al., 2023). This essential nutrient serves as a cofactor for around 140 enzymes critical to various processes such as photosynthesis, gas exchange, nitrogen fixation, and nucleic acid synthesis (El-Sonbaty et al., 2022). Iron is indispensable for multiple plant functions, including respiration, hormone synthesis, and DNA replication (Khan et al., 2023). Additionally, it plays a pivotal role in regulating the enzymatic antioxidant system, supporting plant growth and enhancing environmental adaptability (Rui et al., 2016). However, iron availability in soils is often limited due to its low solubility, particularly in calcareous, arid soils like those found in Iran (Khanizadeh et al., 2024). Iron deficiency in plants leads to chlorosis and diminishes the activity of heme-containing enzymes, such as catalase (CAT) and peroxidase (POD), which are essential for metabolic functions (Anwar et al., 2018). For example, in iron-deficient conditions, soybean and sunflower show reduced POD activity, impairing hydrogen peroxide (H_2O_2) scavenging, as enzymes like CAT, POD, and ascorbate peroxidase (APX) depend heavily on iron to neutralize H_2O_2 effectively (Moradbeygi et al., 2020).

Recent advancements in nanotechnology have paved the way for the development of smart, slow-release nano fertilizers, which offer a promising strategy to improve nutrient use efficiency (NUE) in plants (Ostadi et al., 2020). Nanoparticles (NPs), with dimensions under 100 nm, exhibit varying sizes, shapes, and properties, making them highly applicable across agriculture, biotechnology, and pharmaceuticals (Khan et al., 2023; Ahmadi et al., 2024). Among these, metal-based NPs, particularly Fe_2O_3 , have garnered increasing attention for their ability to serve as Fe-enriching micronutrient fertilizers, which can significantly enhance crop yields (Munir et al., 2018). The successful application of these NPs in agriculture hinges on a thorough understanding of their mechanisms of uptake and accumulation in plant tissues (Haydar et al., 2021). Studies have shown that low doses of NPK nano-fertilizers (10 %) can improve agro-physiological traits, bioactive compound production, and both crop yield and quality more effectively than higher doses of either nano or chemical fertilizers (Elshamy et al., 2019; Abdel-Aziz et al., 2021). Martínez-Fernández and Komárek (2016) observed that iron oxide nanoparticles (Fe_2O_3 NPs) uniquely influence the nutritional status of *Solanum lycopersicum* by enhancing root function. Furthermore, foliar applications of humic acid combined with iron supplementation have been shown to improve iron fortification in crops such as rice, soybean, and lettuce (Sharma et al., 2023). Fe_2O_3 NPs have also been demonstrated to significantly increase phenolic compound production in *Dracocephalum kotschy* Boiss. hairy roots at concentration of 75 mg L^{-1} (Nourozi et al., 2019), and to boost scopolamine and hyoscyamine levels five-fold in *Hyoscyamus reticulatus* when Fe NPs were used at concentrations of 450 and 900 mg L^{-1} (Moharrami et al., 2017). Additionally, the application of 50 mg L^{-1} of Fe_2O_3 NPs has been shown to substantially enhance growth, biomass, flavonoid, antioxidant activity, essential oil production, and geranial content in *D. kotschy* (Khanizadeh et al., 2024). These nano-enabled solutions not only improve nutrient uptake efficiency but also reduce dependence on chemical fertilizers, aligning with the principles of sustainable agriculture.

However, despite these promising benefits, concerns remain regarding the environmental fate, bioaccumulation, and potential toxicity of Fe_2O_3 NPs. Recent investigations suggest that foliar application of Fe_2O_3 NPs does not significantly impact soil microbial communities or plant physiological functions (Pontes et al., 2023). Furthermore, no detectable bioaccumulation in edible plant tissues was

reported following foliar spraying (Adil et al., 2022). Nonetheless, comprehensive long-term and field-based studies are still necessary to fully evaluate the environmental safety and regulatory implications of using nano-enabled fertilizers in agriculture.

Sustainable agriculture aims to meet the growing demand for food and medicinal resources while minimizing environmental degradation and preserving natural ecosystems. It focuses on practices that maintain soil fertility, reduce chemical inputs, and support biodiversity, thus aligning agricultural productivity with long-term ecological health (Gliessman, 2022; FAO, 2021). Effective nutrient management in medicinal crop cultivation is crucial for achieving high yields and enhancing the quality of bioactive compounds. Proper soil fertility and plant nutrition not only promote robust plant growth but also contribute to environmental sustainability by improving water quality, reducing soil erosion, and preserving biodiversity (Aghamirzaei et al., 2024). While chemical fertilizers are widely used around the world, their high costs, inefficiency, and negative environmental impact have led to a growing interest in biofertilizers. These offer a sustainable solution for supplying essential nutrients such as nitrogen, phosphorus, and potassium (Kafi et al., 2022). Among biofertilizers, plant growth-promoting rhizobacteria (PGPR) are particularly recognized for their eco-friendly and cost-effective properties. PGPRs enhance crop production through various mechanisms, including the production of phytohormones, phosphorus solubilization, iron sequestration, and nitrogen fixation (Kudan et al., 2015; Mondal and Kaur, 2017; Helaly et al., 2018; Arora et al., 2019). Furthermore, PGPRs act as biotic elicitors, stimulating the production of pharmaceutically active metabolites in medicinal plants. For instance, *Melissa officinalis* L. exhibited improved growth, physiological traits, and antioxidant activity in response to PGPRs (Hatami et al., 2021); *Origanum onites* L. showed enhanced essential oil production, including carvacrol, thymol, and linalool (Çakmakçı et al., 2023); *D. kotschy* displayed improved growth and biochemical traits (Gasemi et al., 2023); and *Myrtus communis* showed an increase in essential oil yield (Azizi et al., 2021). These traits make PGPRs integral to sustainable crop management by reducing reliance on synthetic fertilizers while boosting metabolite production.

The synergistic interaction between Fe_2O_3 NPs and PGPR can significantly enhance nutrient availability and plant tolerance to abiotic stress through a set of complementary mechanisms. Fe_2O_3 NPs act as a readily bioavailable iron source, supporting essential physiological functions in plants (Guardiola-Márquez et al., 2023). Simultaneously, PGPR strains such as *C. plantarum* and *P. brassicacearum* facilitate nutrient acquisition by solubilizing phosphate, fixing atmospheric nitrogen, and producing siderophores—iron-chelating compounds that mobilize iron in the rhizosphere. The presence of Fe_2O_3 NPs can further amplify these microbial activities by ensuring a consistent iron supply, thereby promoting bacterial growth, metabolism, and effective colonization of the rhizosphere (Basit et al., 2023). In addition to enhancing nutrient dynamics, both Fe_2O_3 NPs and PGPR contribute to the mitigation of abiotic stresses such as salinity and drought. Together, this integrated approach supports cellular homeostasis, enhances nutrient uptake, and improves overall plant resilience under adverse conditions (Singh, Roychoudhury, 2025; Shukla et al., 2018).

Although *S. khuzistanica* is primarily an endemic wild species native to Iran, it is increasingly recognized as a valuable medicinal and aromatic plant with significant industrial potential. Due to overharvesting from natural habitats and increasing demand for its essential oils and extracts in pharmaceutical and food industries, domestication and cultivation efforts have been initiated in Iran (Nooshkam et al., 2017; Mumivand et al., 2021; Shams et al., 2023). A key aspect of these efforts is optimizing the plant's nutrient and fertilizer requirements. Despite numerous studies investigating the individual effects of PGPR and Fe_2O_3 NPs on medicinal plants, there remains a critical lack of integrated research exploring their combined synergistic impact on *S. khuzistanica*. Therefore, in Fig. 5 this study, we explored the impact of PGPRs and Fe_2O_3 (both nano and bulk forms) application on the growth, yield,

photosynthetic pigments, enzymatic and non-enzymatic antioxidants, and essential oil production of *S. khuzestanica*. This approach aims to develop a low-input, sustainable, and resource-efficient cultivation strategy for this endangered medicinal species. Top of Form

2. Materials and methods

2.1. Characterization of Fe₂O₃ nanoparticles (NPs)

(Fe₂O₃NPs) sourced from Nanosany Company, Ltd., Iran, were characterized using Transmission Electron Microscopy (TEM) (LEO 906E, Zeiss, Germany) and Scanning Electron Microscopy (SEM) (Hitachi S-4160, Japan) (Fig. 1). The size distribution and zeta potential of the NPs were measured using the Zetasizer Nano ZS (Malvern Instruments, Worcestershire, UK) (S1).

2.2. Plant material and greenhouse experiment

For the greenhouse experiments, *Satureja khuzestanica* cuttings were obtained from the Academic Center for Education, Culture, and Research in Lorestan, Khorramabad, Iran. These cuttings were transplanted into 5 kg plastic pots located in the greenhouses of the Faculty of Agriculture, Lorestan University, Khorramabad, Iran. The potting substrate was prepared by mixing sand, agricultural soil, and manure in a 1:1:1 ratio (Table S2). The experimental design followed a factorial arrangement based on a completely randomized design with three replications (five pots per replication), comprising 15 pots per treatment combination, bringing the total number of 150 pots, each containing a

single plant. The study was carried out under controlled greenhouse conditions.

Foliar treatments of Fe₂O₃ included: control (distilled water spray), 100 mg L⁻¹ bulk Fe₂O₃, 200 mg L⁻¹ bulk Fe₂O₃, 100 mg L⁻¹ Fe₂O₃NPs, and 200 mg L⁻¹ Fe₂O₃NPs. Tween 20 was used as a surfactant to facilitate foliar application of Fe₂O₃. Plant Growth-Promoting Rhizobacteria (PGPR) inoculation was conducted at two levels: no inoculation and inoculation with both *Curtobacterium plantarum* and *Pseudomonas brassicacearum*. The inoculation involved three soil drench applications targeted at the root zone, administered at 20-day intervals (see Table S3). The bacterial suspension was prepared at a concentration of 1 × 10⁷ CFU/mL. The concentration range for Fe₂O₃ foliar spray was determined through literature review and preliminary studies (Moradbeygi et al., 2020; Hassanpouraghdam et al., 2022; Rizwan et al., 2018). Foliar applications were carried out biweekly until the harvest, resulting in a total of six spray applications. The first application occurred on March 7, 2023, with the final spray on May 16, 2023. Throughout the five-month growth period, the greenhouse environment was carefully monitored for weed, pest, and disease control. The average temperature in the greenhouse was approximately 20°C at night and 30°C during the day, with relative humidity ranging from 55 % to 85 %. The photosynthetically active photon flux density inside the greenhouse was approximately 700 ± 100 μmol quanta m⁻² s⁻¹.

2.3. Growth parameters

At the full flowering stage, several growth parameters were assessed, including leaf length (mm), leaf width (mm), stem diameter (mm), and

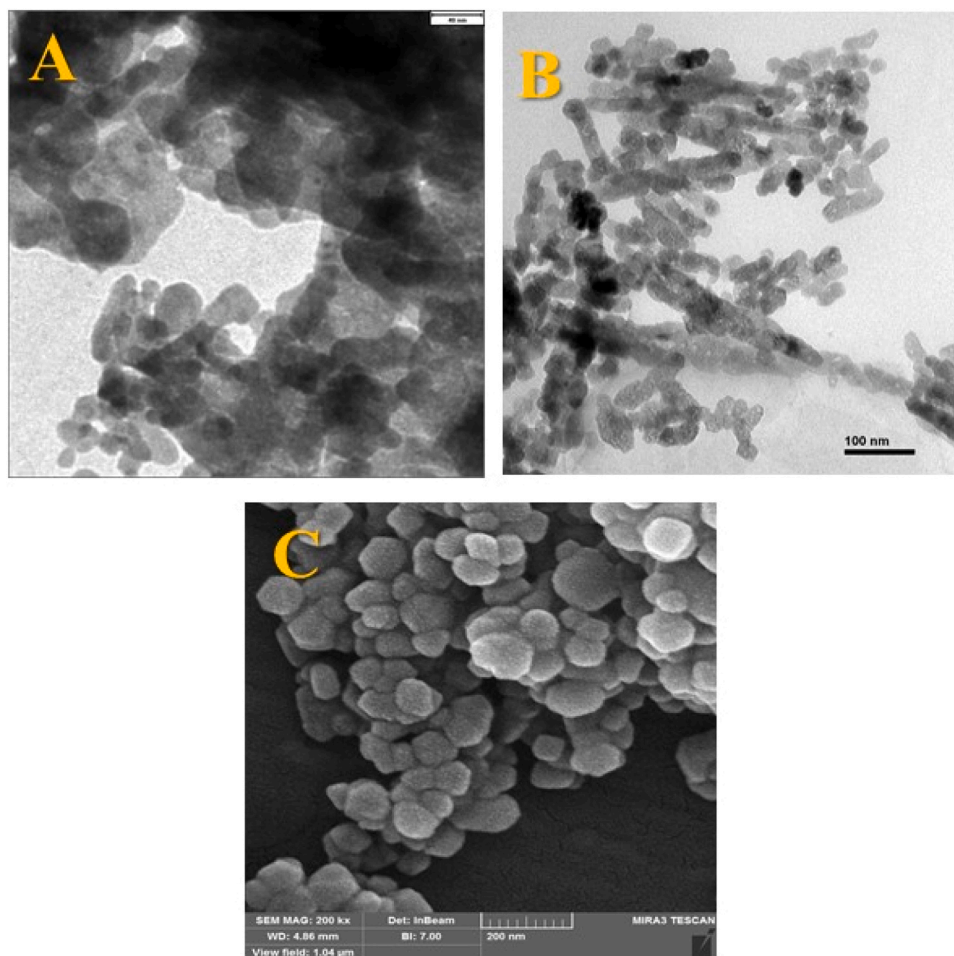


Fig. 1. The TEM (A and B) and SEM (C) of Fe₂O₃ NPs used in this study.

internode length (mm). To calculate the absolute growth rate (AGR), the final plant height at the end of the experiment and the initial plant height at transplanting stage were recorded. The AGR was then determined using the following formula:

$$\text{AGR} = \frac{\text{Height2} - \text{Height1}}{\text{Time2} - \text{Time1}} \quad (1)$$

Following this, plants were harvested, and the fresh weights of both aerial and root parts were recorded, along with root length (cm). Aerial and root parts were oven-dried at 50°C to determine dry weights. Leaves were separated from stems, and the dry weights of both stems and leaves were recorded, from which the leaf-to-stem ratio was calculated.

2.4. Relative water content (RWC) and photosynthetic pigments

The RWC was measured following the method of Ferrat and Lova (1999). Ten fully expanded leaves were immediately weighed to acquire the fresh weight (FW), and then dipped in distilled water at 25°C for 24 h to ascertain the saturated weight (SW). After this, the leaves were oven-dried at 80°C for 48 h to measure the dry weight (DW). RWC was computed with the standard formula, with measurements taken in triplicate.

Carotenoid, chlorophyll a, and chlorophyll b levels were measured using the method of Lichtenthaler (1987). Freshly frozen leaf samples (0.25 g) were processed in 10 mL of 80 % acetone and centrifuged at 10,000 rpm for 15 min. The absorbance of the supernatant was recorded at 663, 645, and 470 nm to obtain the concentrations of chlorophyll a, chlorophyll b, and carotenoids, respectively. The level of photosynthetic pigments was calculated using the appropriate formulas.

2.5. Non-enzymatic antioxidant-related parameters

A 100 mg of sample from every experimental group was combined with 2 mL of 80 % methanol and incubated in the dark at room temperature for 16 h. The extract was then centrifuged for 20 min at 14,000 × g, and after filtration, the liquid phase was separated and stored at 4°C (Jadidi et al., 2023). Total phenol content was measured using the Folin-Ciocalteu method (McDonald et al., 2001). A 0.4 mL aliquot of the diluted extract was combined with 1.6 mL of sodium carbonate solution and 2 mL of Folin-Ciocalteu reagent. After incubating the mixture for 30 min at room temperature, the absorbance was recorded at 760 nm. A standard curve was constructed using various concentrations of gallic acid (0–500 mg L⁻¹), and the total phenolic level was reported as milligram of gallic acid equivalent per gram of leaf dry weight (mg GAE g⁻¹ DW).

For total flavonoid concentration, a 2 mL aliquot of the diluted extract was blended with 2 mL of 2 % AlCl₃ solution and incubated for 15 min at room temperature. Absorbance was measured at 415 nm using a spectrophotometer (SHIMADZU, model UV-1700, Japan). A standard curve was prepared with various rutin concentrations (0–500 mg L⁻¹), and the total flavonoid level was reported as milligram of rutin equivalent per gram of leaf dry weight (mg RE g⁻¹ DW) (Hang et al., 2002).

Antioxidant capacity was assessed using the FRAP assay (Benzie, Strain, 1996). The FRAP reagent was prepared as a fresh solution, combining 300 mM acetate buffer (pH 3.6), 10 mM TPTZ, and 20 mM ferric chloride in a 10:1:1 ratio. For each test, 0.18 mL of FRAP reagent and 0.02 mL of sample solution were incubated at 30°C for 30 min, and the absorbance was measured at 593 nm using a spectrophotometer (SHIMADZU, model UV-1700, Japan).

2.6. Fe content

The Fe concentration was determined following the method of (Bao et al., 2000), with minor modifications. Approximately 1 g of the sample was ashed at 500°C for 3 h in a muffle furnace. After cooling, the ash was dissolved in 10 mL of 2 N hydrochloric acid and transferred to a 50 mL

volumetric flask. Fe concentration was measured using Atomic Absorption Spectrometry (Agilent 240FS AA, USA) and expressed as mg g⁻¹ dry weight (DW).

2.7. Phenylalanine ammonia-lyase (PAL) activity

Fresh leaf samples (0.5 g) were homogenized in 5 mL of phosphate buffer (0.05 M, pH 7.8) containing 1 mM EDTA and 1 % PVP. The homogenate was centrifuged at 12,000 × g for 20 min at 4°C, and the supernatant was collected for the PAL and ascorbate peroxidase (APX) activity assays. PAL activity was measured using a modified version of the method described by Whetten and Sederoff (1992). The reaction mixture (1.2 mL) composed of 50 mM Tris-HCl (pH 8.8), 1 mM L-phenylalanine, and enzyme extract. After incubating the mixture at 30°C for 30–60 min, the reaction was suspended by adding 0.5 mL of 4 N HCl. The mixture was then vortexed with 2 mL of toluene and centrifuged at 750 × g for 5 min. The absorbance was noted at 290 nm.

2.8. Enzymatic antioxidant activity

The activity of APX was measured using the method described by Nakano and Asada (1981). The enzyme extract was blended with a reaction solution containing 50 mM phosphate-potassium buffer (pH 7.0), 0.1 mM EDTA, 0.1 mM H₂O₂, and 0.5 mM ascorbic acid, with absorbance recorded at 290 nm via a spectrophotometer (SHIMADZU, model UV-1700, Japan).

For activity of catalase (CAT), 0.5 g of fresh leaf tissue was ground in liquid nitrogen and homogenized with 2 mL of 0.1 M Tris buffer (pH 8.0) consisting of 1 mM EDTA and 0.05 g of polyvinylpyrrolidone (PVP). The homogenate was centrifuged at 13,000 × g for 15 min at 4°C. The experimental mixture for CAT activity contained 0.05 mL of the supernatant and 0.4 mL of 50 mM buffer (pH 7.0) with 12.5 mM H₂O₂. Absorbance was measured for 2 min at 240 nm every 10 s (Gallego et al., 1996). Peroxidase (POD) activity was assessed by guaiacol oxidation (Zhang et al., 1995). The solution mixture consisting of 50 µL of crude extract, 50 µL of 30 % H₂O₂, and 50 µL of 0.05 M guaiacol in 1.2 mL of 50 mM phosphate buffer (pH 7.0). The absorbance was noted every 10 s at 470 nm.

2.9. Hydrogen peroxide (H₂O₂) measurement

H₂O₂ level was measured according to the method of Velikova et al. (2000). Fresh leaf tissue (0.5 g) was ground in 5 mL of 0.1 % (w/v) trichloroacetic acid (TCA). The resulting mixture was centrifuged at 10,000 × g for 15 min. To quantify H₂O₂, 0.5 mL of the liquid phase was mixed with 2 mL of potassium iodide (KI) and 0.5 mL of potassium phosphate buffer (pH 7.0). The absorbance was noted at 390 nm.

2.10. Essential oil isolation

For essential oil isolation, a 25 g of dried leaf tissue was hydro-distilled using a Clevenger apparatus for 3 h. The essential oil was collected, stored at 4°C, and quantified in triplicate, expressed as milligrams per 100 g of dry weight (w/w). The essential oil yield per plant was calculated by multiplying the essential oil content by the dry weight of the aerial parts (g plant⁻¹) (Mumivand et al., 2023).

2.11. Essential oil analysis

Essential oil components were separated using gas chromatography/mass spectrometry (GC-MS) with a BP-5 fused-silica capillary column, using helium as the carrier gas. The injector and interface temperatures were set to 280°C and 260°C, respectively, with electron impact ionization at 70 eV and a split ratio of 1:20. Mass spectra were recorded in the 35–450 amu range. The oven temperature was programmed to rise from 55°C to 285°C at a rate of 4 °C/min, with a 15-minute isothermal

hold at 285°C (Beiranvandi et al., 2022).

For gas chromatography with flame ionization detector (GC-FID) analysis, a Thermoquest Finnigan system with a BP-5 column was used, following the same temperature program. Detector and injector temperatures were maintained at 300°C and 250°C, respectively, with helium at a flow rate of 1 mL/min. Retention indices (RI) were calculated using an *n*-alkane series (C6-C40) on the BP-5 column. Constituents were identified by comparing mass spectra with the WILEY 275 and NIST 17 libraries, retention indices with Adams standards, and retention times with available standards (Mumivand et al., 2021).

2.12. Data analysis

The data were processed via SAS software in accordance with the experimental design. Duncan's multiple range test was used for comparison of means between treatments, with statistical significance determined at $p \leq 0.05$.

3. Results

3.1. Fe₂O₃NPs characteristics

The morphological characteristics of Fe₂O₃ NPs synthesized for present study are systematically presented in Fig. 1 and Supplementary Table S1. Detailed TEM analyses, as illustrated in Figs. 1A and 1B, along with SEM observations in Fig. 1C, reveal that these NPs mainly exhibit a spherical shape. The selection of these NPs for the present investigation was based on their high stability, nanoscale dimensions, and exceptional purity. Subsequent experiments focused on examining the interaction of Fe₂O₃NPs with *S. khuzistanica*, particularly their uptake and movement within leaf tissues. As depicted in Fig. 2, SEM analyses provide clear evidence of nanoparticle absorption and systemic distribution within the leaves treated with Fe₂O₃NPs at a concentration of 200 mg L⁻¹. This figure presents a comparative assessment of leaf tissues from treated plants and the control group. Notably, segments D, E, and F of Fig. 2 illustrate nanoparticle deposition on the surface of stomatal cells, offering valuable insights into the dynamic interactions between NPs and plant structures.

3.2. Biomass and yield attributes

The findings indicated that the AGR, leaf length, root length, and leaf-to-stem ratio were significantly influenced by the inoculation of PGPR. The foliar spray of Fe₂O₃ also had a notable effect on the AGR, leaf length, root fresh weight, root dry weight, and stem dry weight. Furthermore, the interaction between PGPR inoculation and Fe₂O₃ treatment significantly affected the AGR, plant dry weight, root length, fresh and dry weight of root, dry weight of leaf, dry weight of stem, and leaf-to-stem ratio (Table S4). PGPR inoculation led to an 8.68 % increase in leaf length compared to the non-inoculated plants (Fig. 3.A). Among the various Fe treatments, the highest leaf length was obtained with foliar applications of 100 mg L⁻¹ Fe₂O₃NPs (15.91 mm) and 100 mg L⁻¹ bulk Fe₂O₃ (15.026 mm). In contrast, plants treated with 200 mg L⁻¹ bulk Fe₂O₃ exhibited no statistically significant difference when compared to the control group (Fig. 3.B).

Fig. 3

The maximum AGR of 0.165 was achieved by combining PGPR inoculation with a 100 mg L⁻¹ bulk Fe₂O₃ foliar spray, which represented a 79.34 % increase over the control. This result did not significantly differ from the plants treated with 200 mg L⁻¹ bulk Fe₂O₃ or 200 mg L⁻¹ Fe₂O₃NPs, both in PGPR-inoculated and non-inoculated plants. The highest root fresh weight (11.8 g) was observed in non-inoculated plants treated with 100 mg L⁻¹ bulk Fe₂O₃, showing a 95.68 % increase compared to the control. No significant differences were found when comparing this treatment with PGPR-inoculated plants treated with 200 mg L⁻¹ Fe₂O₃NPs or 100 mg L⁻¹ bulk Fe₂O₃. The highest root dry weight (7.03 g) was recorded in the interaction of PGPR inoculation with 100 mg L⁻¹ Fe₂O₃NPs, representing a 2.008-fold increase over the control. The longest root length (28.75 cm) was achieved with PGPR inoculation combined with 100 mg L⁻¹ Fe₂O₃NPs, with no significant differences observed when compared with 200 mg L⁻¹ bulk Fe₂O₃ combined with PGPR inoculation as well as with 200 mg L⁻¹ Fe₂O₃NPs combined with no PGPR inoculation. Regarding the dry weight of the plants and leaves, the foliar spray of 100 and 200 mg L⁻¹ Fe₂O₃NPs, as well as 200 mg L⁻¹ bulk Fe₂O₃, resulted in the highest values, regardless of PGPR inoculation. The highest stem dry weight (1.28 g) was observed in PGPR-inoculated plants treated with

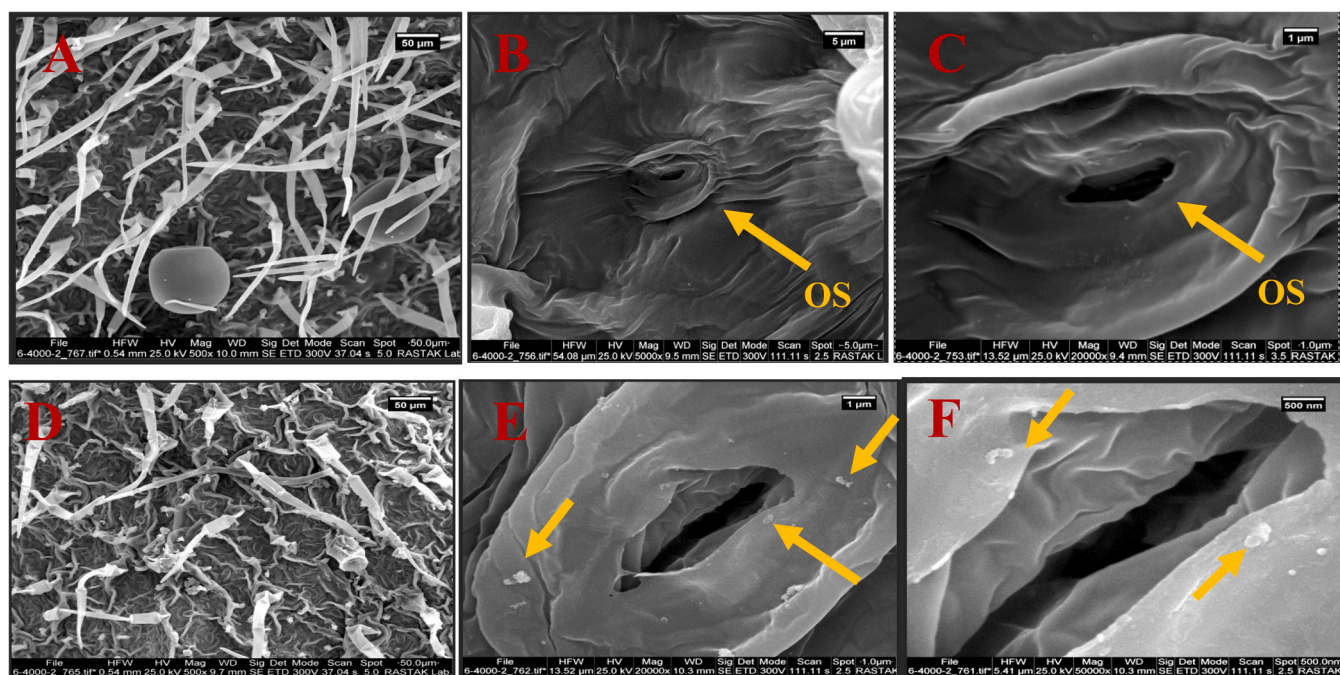


Fig. 2. SEM images of leaf surfaces: (A) trichomes on the control leaf, (B, C) stomata on the control leaf, (D) trichomes on the leaf treated with Fe₂O₃ nanoparticles (NPs), and (E, F) stomata on the leaf treated with Fe₂O₃ NPs. Arrows in (E) and (F) show the internalization of Fe₂O₃ NPs within the leaf tissues.

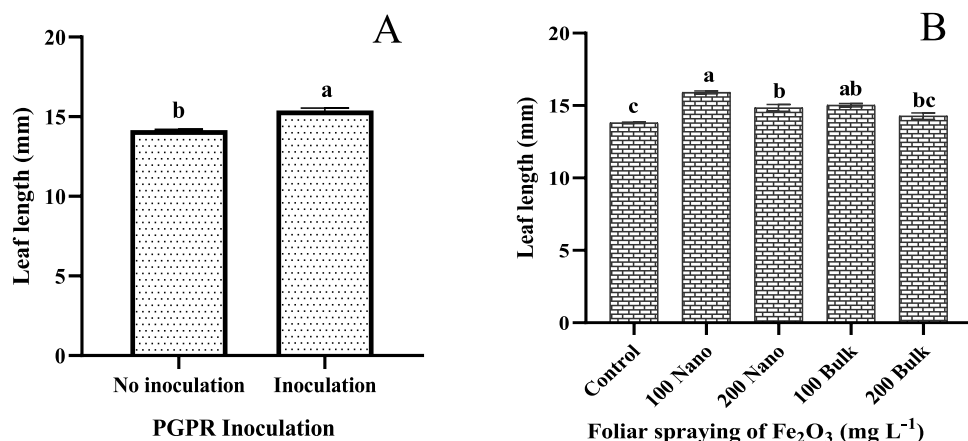


Fig. 3. The effects of inoculation with plant growth-promoting rhizobacteria (PGPR) (A) and foliar application of Fe₂O₃ (nano and bulk) (B) on the leaf length of *S. khuzistanica*; Values are presented as means \pm standard error of the mean (S.E.M.), based on three biological replicates (n = 3), each consisting of five subsamples.

200 mg L⁻¹ Fe₂O₃NPs, showing a 51.83 % increase over the control, with no significant difference in compare to non-inoculated plants treated with 100 mg L⁻¹ Fe₂O₃NPs. Additionally, the highest leaf-to-stem ratio was found in PGPR-inoculated plants with foliar applications of either 100 or 200 mg L⁻¹ bulk Fe₂O₃, as well as in non-inoculated plants with 200 mg L⁻¹ Fe₂O₃NPs (Table 1).

3.3. RWC and photosynthetic pigments

The ANOVA results indicated that PGPR inoculation, foliar application of Fe₂O₃, and their interaction had a significant impact on RWC, as well as the levels of chlorophyll a, total chlorophyll, and carotenoids ($p \leq 0.01$). However, no significant changes were detected in chlorophyll *b* level due to PGPR inoculation, Fe₂O₃ foliar application, or their interaction (Table S5). The highest RWC was recorded in plants treated with both 100 or 200 mg L⁻¹ Fe₂O₃NPs in combination with PGPR inoculation, with values of 87.62 % and 84.47 %, respectively. The highest chlorophyll a content was obtained in PGPR-inoculated plants sprayed with 200 mg L⁻¹ Fe₂O₃NPs (0.34 mg g⁻¹ FW) or 100 mg L⁻¹ bulk Fe₂O₃ (0.33 mg g⁻¹ FW), which represented a 2.26- and 2.22-fold increase over the control, respectively. The greatest total chlorophyll level was observed in PGPR-inoculated plants sprayed with 100 mg L⁻¹ bulk Fe₂O₃ (0.75 mg g⁻¹ FW), with no significant difference from PGPR-inoculated plants treated with either 100 or 200 mg L⁻¹ Fe₂O₃NPs. The lowest carotenoid level (9.16 mg g⁻¹ FW) was recorded in the control plants, which received no PGPR inoculation or Fe₂O₃ foliar application (Table 2).

3.4. Total phenol and flavonoid content, and antioxidant activity

No significant changes in phenolic levels were observed among the treatments. In contrast, total flavonoid content was notably influenced by PGPR inoculation, Fe₂O₃ foliar application, and their interaction ($p \leq 0.01$). Antioxidant activity was significantly impacted by Fe₂O₃ foliar application ($p \leq 0.05$), while PGPR inoculation and its interaction with Fe₂O₃ did not have a significant effect (Table S5). The highest total flavonoid level (1.83 mg RE g⁻¹ DW) was achieved with PGPR inoculation and the application of Fe₂O₃NPs at 200 mg L⁻¹, reflecting a 14.37 % increase over the control (Table 2). Furthermore, the highest antioxidant activity was observed following the foliar spraying of Fe₂O₃ at 200 mg L⁻¹, both in NP and bulk forms (12.36 and 13.77 $\mu\text{mol Fe}^{2+}$ g⁻¹ DW, respectively), representing increases of 9.28 % and 21.83 % compared to the control (Fig. 4).

3.5. Fe content

The ANOVA results revealed that iron concentration was significantly influenced by Fe₂O₃ foliar application, PGPR inoculation, and their interaction ($p \leq 0.01$; Table S5). The highest iron concentration in *S. khuzistanica* leaves was observed with the combined treatment of PGPR inoculation and bulk Fe₂O₃ foliar application at 200 mg L⁻¹ (204.301 mg g⁻¹ DW), representing a 6.23-fold increase over the control. A high iron concentration (182.26 mg g⁻¹ DW) was also recorded in PGPR-inoculated plants treated with 200 mg L⁻¹ Fe₂O₃NPs (Table 2).

3.6. PAL activity

The analysis of variance indicated that Fe₂O₃ foliar application, PGPR inoculation, and their interaction significantly affected PAL enzyme activity ($p \leq 0.01$; Table S6). The highest PAL activity was observed in non-inoculated plants treated with Fe₂O₃ application at 100 mg L⁻¹, both in NPs and bulk forms, yielding 8.56 and 88.8 $\mu\text{g Cin min}^{-1}$ g⁻¹ FW, respectively—representing a 2.26- and 2.34-fold increase compared to the control (5A).

3.7. Antioxidant enzymes activity and H₂O₂ content

The variance analysis results for APX, POD, and CAT enzyme activities revealed significant differences due to Fe₂O₃ application, PGPR inoculation, and their interaction ($p \leq 0.01$). Significant change in H₂O₂ levels was also observed in response to Fe₂O₃ application and its interaction with PGPR inoculation ($p \leq 0.01$) (Table S6). The highest APX activity was recorded in non-inoculated plants sprayed with Fe₂O₃NPs at 200 mg L⁻¹ (2.186 $\mu\text{mol min}^{-1}$ g⁻¹ FW), showing a 7.97-fold increase over the control. This was followed by PGPR inoculation combined with bulk Fe₂O₃ at 100 mg L⁻¹ (1.628 $\mu\text{mol min}^{-1}$ g⁻¹ FW) (5B Fig. 5). The highest POD activity was observed in non-inoculated plants treated with bulk Fe₂O₃ at 200 mg L⁻¹ (0.065 $\mu\text{mol min}^{-1}$ g⁻¹ FW), representing a 2.24-fold increase over the control, followed by no PGPR inoculation and bulk Fe₂O₃ application at 100 mg L⁻¹ (5C). For CAT activity, the highest levels were noted with the application of 200 mg L⁻¹ Fe₂O₃NPs, both in the absence of PGPR inoculation (0.079 $\mu\text{mol min}^{-1}$ g⁻¹ FW) and with PGPR inoculation (0.072 $\mu\text{mol min}^{-1}$ g⁻¹ FW). These treatments showed a 2.79-fold increase and a 2.48-fold increase over the control, respectively (5D). The highest H₂O₂ level was recorded in plants with PGPR inoculation and treated with 100 mg L⁻¹ Fe₂O₃NPs (13.11 $\mu\text{g g}^{-1}$ FW), which did not differ significantly from the non-inoculated plants treated with 200 mg L⁻¹ bulk Fe₂O₃ (12.48 $\mu\text{g g}^{-1}$ FW) (5E).

Table 1
Mean comparison of the interaction effects of Fe₂O₃ (nano and bulk) foliar application and inoculation with plant growth promoting rhizobacteria (PGPR) on biomass and yield attributes of *S. khuzistanica*.

PGPR	Fe ₂ O ₃ (mg L ⁻¹)	Absolut growth rate	Root fresh weight (g)	Root dry weight (g)	Root length (cm)	Plant dry weight (g)	Leaf dry weight (g)	Stem dry weight (g)	Leaf/Stem ratio
No inoculation	Control	0.092 ± 0.16 ^e	6.03 ± 0.26 ^e	3.50 ± 0.54 ^b	19.50 ± 0.67 ^d	1.38 ± 0.25 ^c	0.64 ± 0.06 ^{bc}	1.092 ± 0.06 ^b	0.616 ± 0.02 ^{cd}
	Nano 100	0.134 ± 0.2 ^{bc}	7.77 ± 0.30 ^{de}	4.69 ± 0.11 ^b	20 ± 0.19 ^d	1.896 ± 0.14 ^{ab}	0.736 ± 0.05 ^{ab}	1.16 ± 0.06 ^{ab}	0.68 ± 0.05 ^{bc}
	Nano 200	0.148 ± 0.01 ^{abc}	8.59 ± 1.52 ^{cd}	3.60 ± 0.86 ^b	26.16 ± 0.15 ^{ab}	1.822 ± 0.02 ^{ab}	0.74 ± 0.04 ^e	0.74 ± 0.04 ^e	0.86 ± 0.04 ^a
	Bulk 100	0.098 ± 0.08 ^{de}	11.80 ± 0.16 ^a	5.09 ± 0.56 ^b	22.16 ± 0.64 ^{bcd}	1.58 ± 0.17 ^{bc}	0.92 ± 0.02 ^{cd}	0.568 ± 0.17 ^c	0.71 ± 0.09 ^{bc}
Inoculation	Bulk 200	0.146 ± 1.7 ^{abc}	9.83 ± 0.24 ^{bc}	4.22 ± 0.25 ^b	22.66 ± 0.73 ^{bcd}	1.736 ± 0.05 ^{ab}	0.71 ± 0.04 ^{ab}	1.068 ± 0.12 ^{bc}	0.48 ± 0.09 ^d
	Control	0.132 ± 0.13 ^{bc}	7.81 ± 0.55 ^{de}	3.73 ± 0.24 ^b	24 ± 0.75 ^{bcd}	1.403 ± 0.04 ^c	0.56 ± 0.12 ^c	0.843 ± 0.06 ^{de}	0.66 ± 0.10 ^{bc}
	Nano 100	0.121 ± 0.28 ^{cd}	8.90 ± 0.24 ^{bcd}	7.03 ± 0.72 ^a	28.75 ± 0.14 ^a	1.932 ± 0.03 ^{ab}	0.80 ± 0.08 ^{ab}	1.132 ± 0.06 ^b	0.71 ± 0.05 ^{bc}
	Nano 200	0.155 ± 0.16 ^{ab}	10.69 ± 0.46 ^{ab}	3.26 ± 0.38 ^b	21.83 ± 0.33 ^{bcd}	2.036 ± 0.27 ^a	0.756 ± 0.11 ^{ab}	1.28 ± 0.03 ^a	0.58 ± 0.15 ^{cd}
Bulk 100	Control	0.165 ± 0.74 ^a	10.07 ± 0.20 ^{abc}	4.48 ± 0.28 ^b	21.5 ± 0.28 ^{cd}	1.61 ± 0.04 ^b	0.67 ± 0.01 ^{bc}	0.94 ± 0.05 ^{cd}	0.79 ± 0.06 ^{ab}
	Bulk 200	0.161 ± 0.69 ^{ab}	9.18 ± 0.05 ^{bcd}	5.17 ± 0.18 ^b	25.5 ± 0.38 ^{abc}	1.907 ± 0.18 ^{ab}	0.858 ± 0.13 ^a	1.049 ± 0.12 ^{bc}	0.899 ± 0.06 ^a

Values are presented as means ± standard error of the mean (S.E.M.), based on three biological replicates (n = 3), each consisting of five subsamples. Means followed by the same letter within each column are not significantly different according to Duncan's multiple range test at p < 0.05.

Table 2
Mean comparison of the interaction effects of Fe₂O₃ (nano and bulk) foliar application and inoculation with plant growth promoting rhizobacteria (PGPR) on biochemical traits and Fe concentration of *S. khuzistanica*.

PGPR	Fe ₂ O ₃ (mg L ⁻¹)	Relative water content (%)	Chlorophyll a (mg g ⁻¹ FW)	Total chlorophyll (mg g ⁻¹ FW)	Carotenoid (mg g ⁻¹ FW)	Flavonoids (mg RE g ⁻¹ DW)	Fe concentration (mg g ⁻¹ DW)
No inoculation	Control	71.71 ± 0.12 ^c	0.15 ± 0.02 ^c	0.47 ± 0.01 ^d	9.16 ± 0.14 ^c	1.60 ± 0.05 ^b	32.79 ± 0.33 ^c
	Nano 100	72.61 ± 0.25 ^c	0.25 ± 0.03 ^b	0.39 ± 0.04 ^e	13.23 ± 0.16 ^b	1.28 ± 0.04 ^c	45.16 ± 0.29 ^{de}
	Nano 200	74.07 ± 0.41 ^c	0.14 ± 0.01 ^e	0.63 ± 0.03 ^{bc}	14.49 ± 0.17 ^a	1.06 ± 0.10 ^d	165.58 ± 1.42 ^{bc}
	Bulk 100	54.92 ± 0.14 ^e	0.14 ± 0.04 ^e	0.63 ± 0.04 ^{bc}	14.59 ± 0.09 ^a	0.93 ± 0.06 ^d	55.108 ± 0.52 ^{cd}
Inoculation	Bulk 200	70.29 ± 0.03 ^c	0.21 ± 0.03 ^c	0.57 ± 0.03 ^c	13.55 ± 0.31 ^{ab}	1.34 ± 0.05 ^c	154.839 ± 0.77 ^c
	Control	80.37 ± 0.20 ^b	0.193 ± 0.01 ^d	0.54 ± 0.07 ^{cd}	14.69 ± 0.07 ^a	1.51 ± 0.12 ^b	38.17 ± 1.14 ^{de}
	Nano 100	84.48 ± 0.70 ^{ab}	0.169 ± 0.06 ^{de}	0.67 ± 0.03 ^{ab}	14.01 ± 0.16 ^{ab}	1.83 ± 0.03 ^a	144.89 ± 0.42 ^c
	Nano 200	87.62 ± 0.13 ^a	0.34 ± 0.05 ^a	0.67 ± 0.12 ^{ab}	13.92 ± 0.19 ^{ab}	1.28 ± 0.09 ^c	182.26 ± 1.64 ^b
Bulk 100	Control	65.26 ± 0.60 ^d	0.33 ± 0.02 ^a	0.75 ± 0.02 ^a	14.64 ± 0.11 ^a	1.62 ± 0.17 ^b	171.23 ± 0.74 ^{bc}
	Bulk 200	75.37 ± 0.04 ^c	0.114 ± 0.02 ^f	0.48 ± 0.06 ^d	14.07 ± 0.17 ^{ab}	1.54 ± 0.01 ^b	204.301 ± 0.68 ^a

Values are presented as means ± standard error of the mean (S.E.M.), based on three biological replicates (n = 3), each consisting of five subsamples. Means followed by the same letter within each column are not significantly different according to Duncan's multiple range test at p < 0.05.

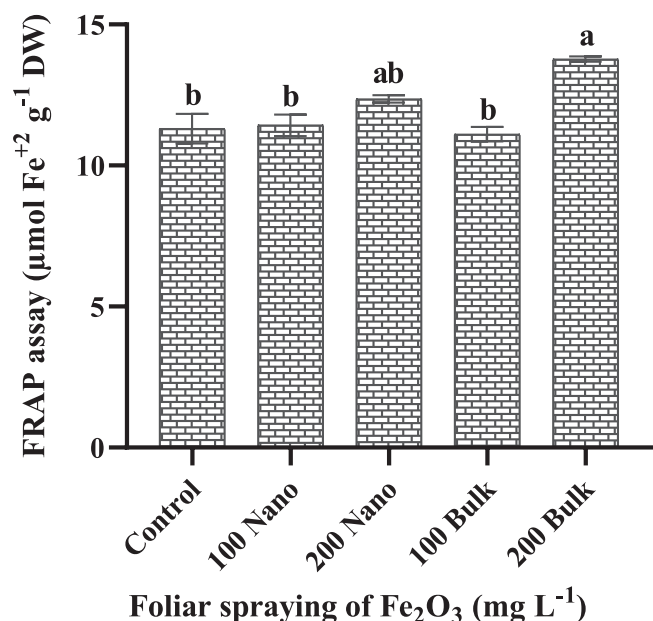


Fig. 4. The effect of foliar application of Fe₂O₃ (nano and bulk) on the anti-oxidant activity of *S. khuzistanica*; Values are presented as means ± standard error of the mean (S.E.M.), based on three biological replicates (n = 3), each consisting of five subsamples.

3.8. Essential oil content and yield

Both PGPR inoculation and foliar application of Fe₂O₃, as well as their interaction, significantly affected essential oil content and yield (Table S6). The highest essential oil percentage (3.29 %) was recorded in plants inoculated with PGPR and sprayed with 100 mg L⁻¹ of Fe₂O₃NPs, representing increases of 2.043-fold compared to the control. This was not significantly different from the treatment of PGPR inoculation combined with 100 mg L⁻¹ of bulk Fe₂O₃ (3.02 %), representing increases of 1.87 times compared to the control (Fig. 6A). Similarly, the highest yield of essential oil (0.11 g plant⁻¹) was observed in plants inoculated with PGPR and treated with 100 mg L⁻¹ of Fe₂O₃NPs, a 4.07-fold increase over the control. This was followed by the PGPR inoculation treatment combined with 100 mg L⁻¹ of bulk Fe₂O₃ foliar application (0.091 g plant⁻¹) (Fig. 6B).

3.9. Essential oil composition

GC-MS and GC-FID analyses of *S. khuzistanica* essential oil identified 17 constituents, with carvacrol as the predominant component (up to 90.96 %), followed by *p*-cymene (2.85 %), *Z*-sabinene hydrate (1.47 %), terpinolene (1.13 %), β -bisabolene (1.48 %), and caryophyllene oxide (1.08 %). Variance analysis revealed that PGPR inoculation significantly influenced the levels of α -thujene, β -myrcene, α -terpinene, *p*-cymene, γ -terpinene, *Z*-sabinene hydrate, terpinolene, thymol, carvacrol, *E*-caryophyllene, and β -bisabolene. Foliar application of Fe₂O₃ significantly affected the levels of α -thujene, β -myrcene, α -phellandrene, α -terpinene, *p*-cymene, limonene, γ -terpinene, *Z*-sabinene hydrate, terpinen-4-ol, thymol, carvacrol, thymol acetate, *E*-caryophyllene, and β -bisabolene. The interaction between PGPR inoculation and Fe₂O₃ foliar application was significant for the following essential oil constituents: α -thujene, β -myrcene, α -Phellandrene, α -terpinene, *p*-cymene, limonene, γ -terpinene, *Z*-sabinene hydrate, terpinolene, thymol, carvacrol, thymol acetate, *E*-caryophyllene, β -bisabolene, and caryophyllene oxide (Table S7).

The highest percentages of *p*-cymene, limonene, and γ -terpinene were observed in plants that did not receive PGPR inoculation or Fe₂O₃ application, as well as in plants without PGPR inoculation but sprayed with 100 mg L⁻¹ Fe₂O₃NPs. *Z*-sabinene hydrate reached its highest level

in plants inoculated with PGPR and treated with 100 mg L⁻¹ bulk Fe₂O₃. The highest terpinolene percentage was obtained in non-inoculated plants treated with 100 mg L⁻¹ Fe₂O₃NPs, with no significant changes compared to plants sprayed with 100 mg L⁻¹ bulk Fe₂O₃, regardless of inoculation status. The highest carvacrol percentage was noted in non-inoculated plants sprayed with 200 mg L⁻¹ Fe₂O₃NPs or 200 mg L⁻¹ bulk Fe₂O₃, as well as in inoculated plants without Fe₂O₃ application. The maximum β -bisabolene percentage was recorded in non-inoculated plants treated with 200 mg L⁻¹ bulk Fe₂O₃. The highest caryophyllene oxide level was noted in PGPR-inoculated plants sprayed with 200 mg L⁻¹ bulk Fe₂O₃, although no significant difference was found when compared to plants without inoculation and either untreated or treated with 100 mg L⁻¹ Fe₂O₃NPs (Table 3).

4. Discussion

The results of the present study demonstrated the beneficial effects of PGPR inoculation on root growth, yield-related traits, RWC, chlorophyll levels, flavonoid content, essential oil content and yield, and leaf Fe content. Notably, combining PGPR with Fe₂O₃ application resulted in a marked improvement in these parameters, including enhanced yield, RWC, chlorophyll content, essential oil yield, and increased leaf Fe levels in *S. khuzistanica*. These findings suggest a synergistic interaction between PGPR inoculation and Fe₂O₃ foliar application, supporting the hypothesis that combining PGPR with nano-enhanced nutrient delivery systems can significantly promote plant growth and yield under optimal conditions (Ullah et al., 2024). Previous studies have highlighted the positive impacts of PGPR on plant growth through enhanced nutrient uptake, improved root development, and increased resilience to environmental stresses (Parmar, Kumar, 2024; Ranjan et al., 2024). For instance, inoculating plants with PGPR such as *Bacillus subtilis* and *P. fluorescens*, coupled with the application of zinNPs, resulted in substantial improvements in growth, dry matter accumulation, and seed yield in *Triticum aestivum* (Jalal et al., 2023). This aligns with the results of our study, where the highest plant growth and yield were achieved with the combination of Fe₂O₃ foliar application and PGPR inoculation. This combination likely improved iron availability and enhanced root function, facilitating better water and nutrient absorption (Ullah et al., 2024; Basit et al., 2023). Similarly, foliar application of Fe₂O₃NPs at concentrations of 100 and 200 mg L⁻¹ significantly increased leaf length, dry weight, and the leaf-to-stem ratio in *D. kotschyti*, contributing to higher biomass and improved yield attributes (Khanizadeh et al., 2024). Maintaining iron homeostasis is essential for preventing the harmful Fenton reaction, which generates toxic hydroxyl radicals (Venkataramani, 2021). The Fe₂O₃ application helps to sustain this balance, which is critical for several key physiological processes in plants, ultimately leading to improved growth and yield (Berger et al., 2023).

The observed increase in RWC, particularly with the combined application of PGPR and Fe₂O₃NPs, suggests that the synergistic effects of these treatments enhance the plant's ability to retain water under various conditions (Thabet, Alqudah, 2024). This improvement is likely attributable to enhanced root function driven by PGPR, which boosts water uptake, along with Fe₂O₃NPs' role in supplementing iron, thereby increasing water content in plant tissues (Basit et al., 2023). Such improvements in water status are critical for maintaining cellular turgor, optimizing photosynthetic efficiency, and supporting overall plant growth and development (Sodhi et al., 2025). Furthermore, the positive impact of these treatments on photosynthetic pigments, particularly chlorophyll, underscores the importance of PGPR inoculation and Fe supplementation in enhancing plant physiological functions. The increased chlorophyll content observed in PGPR-inoculated plants treated with Fe₂O₃ suggests that this combination promotes higher chlorophyll synthesis, likely due to improved iron availability, which plays a vital role in chlorophyll biosynthesis (Yousaf et al., 2024). These results support previous findings that PGPR inoculants and

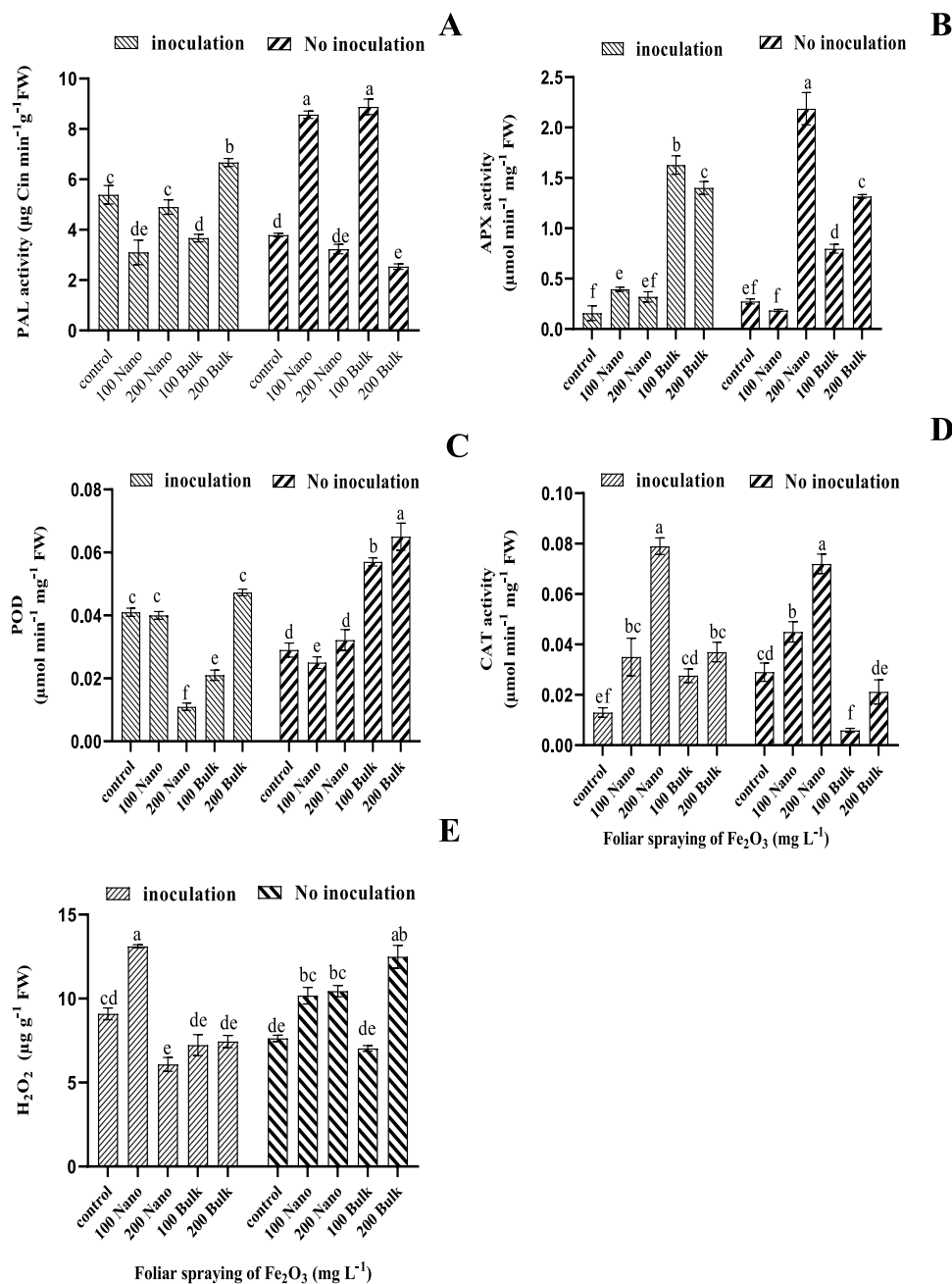


Fig. 5. The interaction effects of inoculation with growth-promoting rhizobacteria and foliar application of Fe_2O_3 (nano and bulk) on the activity of PAL (A), APX (B), POD (C), CAT (D) and H_2O_2 content (E) in *S. khuzistanica*; Values are presented as means \pm standard error of the mean (S.E.M.), based on three biological replicates ($n = 3$), each consisting of five subsamples.

nanomaterials can work synergistically to enhance photosynthetic activity by increasing pigment concentration and optimizing nutrient uptake (González-García et al., 2025; Yousaf et al., 2024).

Flavonoids are well known for their ability to mitigate oxidative stress and improve plant resilience in response to environmental challenges (Tariq et al., 2024). The observed increase in total flavonoid content following PGPR inoculation, regardless of Fe_2O_3 foliar application, can be attributed to the capacity of these beneficial bacteria to influence plant metabolic pathways through multiple mechanisms. Specifically, PGPR, particularly endophytic strains, enhance flavonoid biosynthesis by activating critical enzymatic pathways, most notably the phenylpropanoid pathway (Kisiel et al., 2024). Additionally, PGPR stimulate the generation of signaling compounds like reactive oxygen species (ROS) and nitric oxide (NO), which act as secondary messengers,

triggering the expression of flavonoid biosynthetic genes (Han, 2024). Furthermore, PGPR promote the secretion of phytohormones like salicylic acid and indole-3-acetic acid (IAA), both of which further boost flavonoid accumulation by upregulating the associated biosynthetic pathways (Vega-Celedón et al., 2024).

The results of our study also demonstrate that Fe_2O_3 foliar spray in non-inoculated plants enhances PAL activity in *S. khuzistanica* leaves. PAL is a pivotal enzyme in the phenylpropanoid pathway, essential for synthesizing various secondary metabolites, including flavonoids, lignins, and phenolic acids. These compounds are integral to plant defense mechanisms against both abiotic and biotic stressors, as well as to boosting the plant's antioxidant capacity (Li et al., 2024). The marked increase in PAL activity suggests that Fe_2O_3 , particularly at a concentration of 100 mg L^{-1} in both nano and bulk forms, significantly

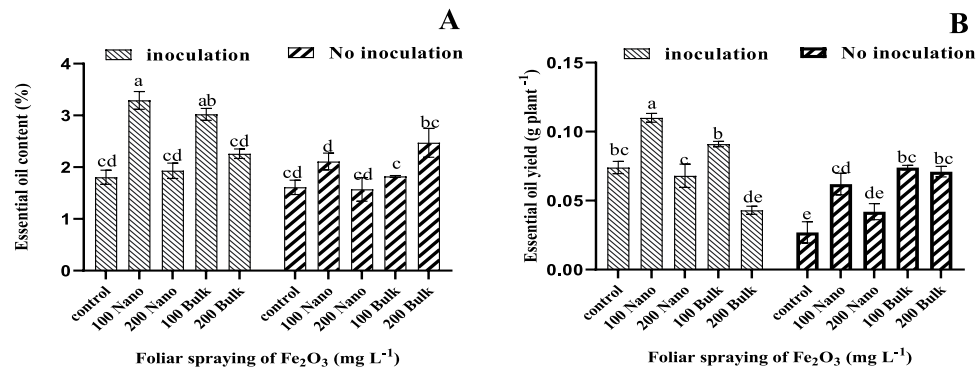


Fig. 6. The interaction effects of inoculation with growth-promoting rhizobacteria and foliar application of Fe₂O₃ (nano and bulk) on the essential oil content (A) and essential oil yield (B) of *S. khuzistanica*; Values are presented as means ± standard error of the mean (S.E.M.), based on three biological replicates (n = 3), each consisting of five subsamples.

Table 3

Mean comparison of the interaction effects of Fe₂O₃ (nano and Bulk) foliar application and plant growth-promoting rhizobacteria (PGPR) inoculation on *S. khuzistanica* essential oil composition.

Compounds	No inoculation					<i>Curtobacterium plantarum</i> * <i>pseudomonas brassicaearum</i>				
	Fe ₂ O ₃ (mg L ⁻¹)					Fe ₂ O ₃ (mg L ⁻¹)				
	Control	Nano 100	Nano 200	Bulk 100	Bulk 200	Control	Nano 100	Nano 200	Bulk 100	Bulk 200
α -thujene	0.2 ± 0.03 ^{ab}	0.28 ± 0.09 ^a	0 ± 0 ^d	0.21 ± 0.02 ^b	0 ± 0 ^d	0.04 ± 0.04 ^d	0.09 ± 0.04 ^c	0.27 ± 0.09 ^a	0.2 ± 0 ^{ab}	0.27 ± 0.05 ^a
β -Myrcene	0.14 ± 0.09 ^c	0.22 ± 0.08 ^a	0 ± 0 ^e	0.13 ± 0.01 ^c	0 ± 0.03 ^e	0.06 ± 0 ^d	0.06 ± 0.01 ^d	0.19 ± 0 ^{ab}	0.17 ± 0 ^b	0.18 ± 0.04 ^b
α -phellandrene	0.93 ± 1.01 ^a	0.87 ± 0.11 ^{ab}	0.11 ± 0.08 ^f	0.53 ± 0.10 ^c	0.17 ± 0.02 ^{ef}	0.45 ± 0.04 ^c	0.39 ± 0.07 ^{cd}	0.725 ± 0.06 ^b	0.287 ± 0.34 ^{de}	0.77 ± 0.06 ^{ab}
α -Terpinene	0.42 ± 0.19 ^a	0.33 ± 0.01 ^{abc}	0.07 ± 0.05 ^f	0.27 ± 0.05 ^{bcd}	0.11 ± 0.02 ^{ef}	0.25 ± 0.08 ^{cd}	0.2 ± 0.10 ^{de}	0.31 ± 0.03 ^{a-d}	0.38 ± 0.15 ^{ab}	0.38 ± 0.07 ^{ab}
<i>p</i> -Cymene	2.85 ± 0.22 ^a	2.85 ± 0.22 ^a	0.62 ± 0.16 ^f	1.68 ± 0.13 ^{bc}	0.74 ± 0.05 ^{ef}	1.30 ± 0.01 ^{cd}	1.47 ± 0.17 ^{bcd}	1.82 ± 0.06 ^b	1.43 ± 0.23 ^{bcd}	1.67 ± 0.16 ^{bc}
Limonene	0.14 ± 0.06 ^a	0.13 ± 0.05 ^a	0.04 ± 0 ^c	0.09 ± 0.03 ^b	0.09 ± 0.01 ^c	0.09 ± 0.04 ^b	0.09 ± 0.03 ^c	0.09 ± 0.05 ^b	0.117 ± 0.06 ^{ab}	0.114 ± 0.03 ^{ab}
γ -Terpinene	0.133 ± 0.08 ^a	0.142 ± 0.01 ^a	0.028 ± 0.01 ^d	0.072 ± 0.02 ^c	0.03 ± 0 ^d	0.07 ± 0.01 ^c	0.03 ± 0.01 ^d	0.11 ± 0.01 ^b	0.13 ± 0.01 ^{ab}	0.12 ± 0.01 ^{ab}
<i>cis</i> -sabinene hydrate	0.71 ± 0.13 ^e	1.01 ± 0.02 ^{bc}	0.25 ± 0.05 ^g	0.89 ± 0.06 ^{cd}	0.48 ± 0.05 ^f	0.98 ± 0.16 ^{cd}	0.79 ± 0.06 ^{de}	1.47 ± 0.05 ^e	1.47 ± 0.06 ^a	1.1 ± 0.11 ^b
Terpinolene	1.01 ± 0.03 ^{bc}	1.13 ± 0.07 ^a	0.97 ± 0.05 ^{cd}	1.07 ± 0.01 ^{abc}	1.01 ± 0.02 ^{bc}	1.01 ± 0.12 ^{bcd}	0.91 ± 0.05 ^d	0.97 ± 0.06 ^{cd}	1.05 ± 0.01 ^{abc}	0.97 ± 0.03 ^{cd}
Thymol	0.12 ± 0.15 ^{de}	0.1 ± 0.02 ^e	0.18 ± 0.10 ^{cd}	0.17 ± 0.13 ^{cd}	0.07 ± 0.02 ^e	0.22 ± 0.02 ^{bc}	0.57 ± 0.07 ^a	0.26 ± 0.06 ^b	0.18 ± 0.08 ^{cd}	0.14 ± 0.07 ^{de}
Carvacrol	85.7 ± 0.08 ^e	86.52 ± 0.15 ^{de}	90.96 ± 0.03 ^a	87.92 ± 0.03 ^{cd}	90.41 ± 0.01 ^a	90.5 ± 0.02 ^a	89.1 ± 0.05 ^b	88.4 ± 0.03 ^{bc}	88.5 ± 0.21 ^{bc}	87.85 ± 0.07 ^{cd}
thymol acetate	0.45 ± 0.02 ^{ef}	0.45 ± 0.03 ^{ef}	0.53 ± 0.02 ^{bcd}	0.66 ± 0.06 ^a	0.41 ± 0.05 ^f	0.46 ± 0.04 ^{def}	0.56 ± 0.73 ^{bc}	0.5 ± 0.11 ^{cde}	0.58 ± 0 ^b	0.52 ± 0.06 ^{bcd}
trans-Caryophyllene	0.21 ± 0.16 ^d	0.37 ± 0.11 ^c	0.49 ± 0.08 ^{bc}	0.47 ± 0.07 ^{bc}	0.69 ± 0.09 ^a	0.53 ± 0.02 ^b	0.48 ± 0.07 ^{bc}	0.47 ± 0.05 ^{bc}	0.76 ± 0.15 ^a	0.44 ± 0.08 ^{bc}
β -Bisabolene	0.88 ± 0.08 ^{cd}	1.01 ± 0.06 ^{bcd}	1.09 ± 0.08 ^b	0.87 ± 0.03 ^{cd}	1.48 ± 0.14 ^a	1.02 ± 0.11 ^{bc}	0.87 ± 0.05 ^{cd}	0.82 ± 0.08 ^d	0.99 ± 0.14 ^{bcd}	0.9 ± 0.05 ^{cd}
Caryophyllene oxide	0.88 ± 0.41 ^{abc}	0.99 ± 0.27 ^{ab}	0.72 ± 0.11 ^{bcd}	0.68 ± 0.13 ^{bcd}	0.55 ± 0.21 ^{cd}	0.56 ± 0.23 ^{cd}	0.54 ± 0.01 ^d	0.72 ± 0.18 ^{bcd}	0.39 ± 0.14 ^d	1.08 ± 0.13 ^a
Total	94.705	96.0372	95.576	95.249	95.547	97.017	95.641	95.904	95.939	96.074

Values are presented as means ± standard error of the mean (S.E.M.), based on three biological replicates (n = 3), each consisting of five subsamples. Means followed by the same letter within each column are not significantly different according to Duncan's multiple range test at p < 0.05.

enhances the plant's ability to produce secondary metabolites, likely through the activation of crucial enzymes in the phenylpropanoid pathway (Singh et al., 2021). This increase in PAL activity can be attributed to the role of Fe₂O₃ in plant metabolic processes. Iron acts as a vital cofactor for many enzymes involved in redox reactions and is directly contributing to the electron transport chain, influencing the synthesis of secondary metabolites. This enhancement emphasizes the important role of Fe₂O₃NPs in strengthening the plant's defense mechanisms, particularly by improving cellular processes that help prevent excessive ROS accumulation (Khanizadeh et al., 2024). The enhancement of PAL activity has considerable potential for improving the

therapeutic value of plants such as *S. khuzistanica*, where secondary metabolites play a key role in their medicinal properties. Our findings further indicate that Fe₂O₃ application enhances the antioxidant activity of plant extracts, further supporting its beneficial effects.

The positive impact of Fe₂O₃ foliar application on antioxidant enzyme activity, particularly CAT and APX, highlights the crucial role of iron in enhancing plant defense mechanisms, especially by improving cellular processes that prevent excessive ROS accumulation (Mishra et al., 2023). Notably, Fe₂O₃NPs exhibited a more significant effect on CAT activity compared to their bulk form, likely due to the greater surface area of NPs, which facilitates enhanced absorption and reactivity

(Majeed, Rasheed, 2022). These results are consistent with prior research demonstrating the ability of Fe₂O₃NPs to improve antioxidant enzyme efficiency in both medicinal and crop plants (Naseem et al., 2025; Haydar et al., 2021). This improvement is closely linked to the increased bioavailability of iron, a vital cofactor for antioxidant enzymes such as superoxide dismutase (SOD) and CAT (Trivedi et al., 2023). Previous studies have also shown that iron application can boost antioxidant enzyme activity in *Phaseolus vulgaris*, leading to reduced H₂O₂ levels and improved crop yield (Sida-Arreola et al., 2015, 2016). Additionally, Fe₂O₃NPs have been shown to elevate APX activity and decrease malondialdehyde levels in *T. aestivum* (Kreslavski et al., 2022). The application of Fe NPs optimizes the plant's ability to combat oxidative stress, especially under conditions of nutrient deficiency or environmental stress (Khan et al., 2023). The substantial reduction in POD activity when PGPR inoculation was combined with Fe₂O₃NPs at 200 mg L⁻¹ indicates that, under certain conditions, the interaction between NPs and PGPR may be inhibited, suggesting that further investigation into the underlying biological mechanisms is necessary.

Our study also demonstrated that both Fe₂O₃ foliar application and PGPR inoculation, as well as their interaction, significantly elevated iron concentration in *S. khuzistanica* leaves. The enhancement of iron content through PGPR and Fe₂O₃ application is a multifaceted process. PGPR secrete siderophores, which tightly bind to iron and increase its availability for plant uptake (Truong et al., 2024). This mechanism is particularly vital under iron-deficient conditions, as illustrated by growth stimulation in *Arabidopsis* treated with apo-siderophores (Truong et al., 2024). In addition, PGPR enhance root growth and architecture, increasing the root surface area for nutrient absorption (Gutierrez-Urrego, Johnston-Monje, 2024), and also produce phytohormones such as IAA, which stimulate root elongation (Han, 2024). Furthermore, PGPR reduce oxidative stress in roots, facilitating the remobilization of iron from root reserves to shoots (Truong et al., 2024). PGPR may also assist in converting Fe³⁺ to Fe²⁺, thereby further enhancing iron availability for the plants (Khan et al., 2023). Additionally, Fe₂O₃ foliar application serves as an external source of iron that can be readily absorbed by the plant's foliar tissues. Therefore, when combined with PGPR, the application of Fe₂O₃ likely creates an optimal environment for maximizing iron supply (Merinero et al., 2022), as observed in this study.

This study demonstrates that the combined application of PGPR and 100 mg L⁻¹ Fe₂O₃NPs significantly enhanced the content and yield of essential oil of *S. khuzistanica*, a medicinal plant known for its therapeutic properties. The observed interactions between PGPR inoculation and Fe₂O₃ application in terms of essential oil production underscore the synergistic potential of this approach, which aligns with previous research highlighting the positive effects of iron NPs and PGPR on secondary metabolite production (Verma et al., 2024; Weisany et al., 2023). Park et al., (2022) reported that combining Fe₂O₃NPs with PGPR promotes essential oil biosynthesis by upregulating the expression of key genes in the methylerythritol phosphate (MEP) and mevalonate (MVA) pathways, which are critical for terpenoid production. Additionally, PGPR stimulate the secretion of phytohormones such as gibberellins, auxins, and salicylic acid, all of which play essential roles in the biosynthesis of essential oil constituents (Hasan et al., 2024). Iron also plays a critical role in the function of cytochrome P450 enzymes, which are directly responsible for the biosynthesis of monoterpenes and sesquiterpenes, the primary components of essential oils (Cheng et al., 2024). In parallel, Fe₂O₃ enhances iron availability in plants, which consequently modulates the activity of key enzymes involved in secondary metabolite biosynthesis, including PAL and polyphenol oxidase (PPO), promoting the synthesis of essential oil precursors (Sun et al., 2024). Our findings corroborate previous studies indicating that Fe₂O₃NPs improve plant growth, yield, and secondary metabolite production in *D. kotschy* (Khanizadeh et al., 2024). Furthermore, Kasmaei et al., (2019) reported that PGPR enhance root development and nutrient uptake, thereby fostering an optimal environment for plant

growth and boosting essential oil production in *Rosmarinus officinalis* L. Similarly, previous studies have demonstrated that foliar application of Fe₂O₃NPs significantly increases essential oil yield in plants such as *Solidago virgaurea* (Abdulla Ahmed et al., 2023). Co-inoculation with PGPR and Fe₂O₃NPs has also been shown to improve seedling development and essential oil yield in plants like *Ocimum basilicum* and *Mentha × piperita* (Palermo et al., 2024; Chiappero et al., 2022). In line with our study, the application of 100 mg L⁻¹ Fe₂O₃NPs significantly boosted essential oil content and yield in *O. basilicum* (Al-Zyadi, 2022).

GC-MS and GC-FID analyses of *S. khuzistanica* essential oil revealed that the interaction between Fe₂O₃ and PGPR significantly altered the oil's composition. Notably, carvacrol, a dominant compound recognized for its antimicrobial and antioxidant properties, showed a marked increase in non-inoculated plants treated with Fe₂O₃. This suggests that Fe₂O₃ positively influences the metabolic pathways involved in carvacrol biosynthesis, potentially by enhancing iron uptake and utilization, which are crucial for enzyme activation in essential oil biosynthesis (Moradbeygi et al., 2020). It has been shown that iron can enhance the expression of genes associated with carvacrol biosynthesis, improving metabolic efficiency (Shams et al., 2023). Transcription factors such as CYP71D178, CYP71D180, MYC4, and bHLH are key regulators of pathways that promote carvacrol synthesis under Fe₂O₃'s influence (Hao et al., 2022; El Boukhari, Fatimi, 2025). The activation of these transcription factors enhances the metabolic pathways leading to carvacrol production (El Boukhari, Fatimi, 2025). Moreover, PGPR strains capable of producing siderophores facilitate iron chelation and mobilization in the rhizosphere, improving iron availability to the plant. This enhanced iron uptake can modulate the expression of biosynthetic genes and transcription factors, thereby strengthening secondary metabolite production—particularly carvacrol—in *S. khuzistanica* (Basit et al., 2023). While Fe₂O₃ and PGPR each independently promoted carvacrol accumulation, their combined application did not produce a synergistic effect. This unexpected outcome may result from non-additive interactions such as antagonistic signaling or competition for metabolic resources. One plausible explanation is that PGPR-enhanced antioxidant defenses mitigate oxidative signals induced by Fe₂O₃—signals typically required to activate ROS-mediated secondary metabolite pathways. Additionally, the combined treatment may shift metabolic allocation toward primary growth and structural development, reducing carvacrol biosynthesis (Verma et al., 2024). Previous studies have indicated that Fe₂O₃NPs changed essential oil composition of *Carum copticum*, particularly increasing carvacrol concentration (Kazemi, 2015). Furthermore, Fe₂O₃ application has been linked to an increase in the biosynthesis of key volatile constituents in essential oils (Yetukuri, Umashankar, 2024). In addition to carvacrol, other essential oil constituents were also significantly affected by Fe₂O₃ foliar application and PGPR inoculation. Although present in lower concentrations, these compounds are vital for the essential oil's overall bioactivity and fragrance profile. Their changes under the influence of Fe₂O₃ and PGPR highlight the potential of these treatments to modulate specific metabolic pathways involved in their biosynthesis (Kazemi, 2015; Abdossi, Kazemi, 2015). The observed effects of PGPR inoculation combined with Fe₂O₃NPs on plant growth, secondary metabolite biosynthesis, and essential oil yield in *S. khuzistanica* are likely mediated through enhanced iron bioavailability, regulation of growth hormones, and upregulation of key biosynthetic enzymes such as PAL and cytochrome P450 (Cheng et al., 2024). To confirm these mechanisms, future research should employ molecular and biochemical assays, including gene expression profiling and enzyme activity measurements, to elucidate the pathways underlying this biofortification strategy.

5. Conclusions

The study demonstrated that treatments with PGPR and foliar application of Fe₂O₃ independently improved plant growth, yield, and several physiological and biochemical traits. When combined, PGPR and

Fe₂O₃ application significantly enhanced key yield-related traits, RWC, chlorophyll levels, content and yield of essential oil, and leaf iron content in *S. khuzistanica*. The highest yield of essential oil was noted with the combined treatment of PGPR inoculation and Fe₂O₃NP spraying at 100 mg L⁻¹, followed by PGPR inoculation with bulk Fe₂O₃ at the same concentration. Overall, the combined application of PGPR inoculation and 100 mg L⁻¹ Fe₂O₃NPs emerged as the most effective treatment, demonstrating significant improvements across nearly all key study parameters. Given the prominence of *S. khuzistanica* for its essential oil production, these treatments appear to be the most effective for optimizing the species' cultivation. Overall, the use of PGPR in conjunction with Fe₂O₃, particularly in nano form, offers a promising strategy to enhance both plant yield and quality. This approach holds significant potential for advancing modern agricultural practices and plant nutrition management. The observed improvements can be attributed to enhanced nutrient uptake and increased stress tolerance resulting from the synergistic interaction between the biofertilizer and the nanomaterial. These findings present a sustainable alternative to conventional fertilization methods, offering the potential to reduce chemical inputs and improve crop value. However, future research should focus on field-scale trials and the long-term effects on soil health and microbial diversity to assess the environmental safety and agronomic viability of this approach. Such integrative strategies could pave the way for resource-efficient, climate-resilient cultivation of high-value medicinal plants within sustainable agricultural frameworks.

Abbreviations

PGPR	Plant Growth-Promoting Rhizobacteria
Fe ₂ O ₃ NPs	Iron Oxide Nanoparticles
NPs	Nanoparticles
AGR	absolute growth rate
FW	fresh weight
DW	Dry Weight
CAT	Catalase
APX	Ascorbate Peroxidase
SOD	Superoxide Dismutase
MDA	Malondialdehyde
H ₂ O ₂	Hydrogen Peroxide
RWC	Relative Water Content
PAL	Phenylalanine Ammonia Lyase
SEM	scanning electron microscopy
TEM	Transmission Electron Microscopy
(ROS)	Reactive Oxygen Species

CRediT authorship contribution statement

Mohamad Reza Morshedloo: Writing – review & editing, Conceptualization. **Ehsan Hasanvand:** Writing – review & editing, Resources. **Parisa Khanizadeh:** Writing – original draft, Visualization, Software, Investigation, Formal analysis. **Sergio Argento:** Writing – review & editing, Formal analysis. **Hasan Mumivand:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Data curation.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve language and readability, with caution. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Funding

No specific funding was allocated for this research.

Declaration of Competing Interest

The authors have nothing to declare.

Acknowledgment

This work was supported by Lorestan University as part of an institutional research project. The authors gratefully acknowledge the university for its financial and logistical support. Additionally, this research was financially supported by the PNRR project, Mission 4 project "Education and Research"- Investment Line 1.5, funded by the EU - "Next Generation EU", D.D. MUR No. 1059 of 23/06/2022 "Sicilian Micro-nanoTech Research" and Innovation Center - SAMOTHRACE (CUP: B63C22000620005). The authors extend their sincere gratitude to all contributors and funding bodies for making this study possible.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.indcrop.2025.121543](https://doi.org/10.1016/j.indcrop.2025.121543).

Data availability

Data will be made available on request.

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