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Halotolerant Plant Growth-Promoting Rhizobacteria Enhance Growth, Antioxidant Defense and Salinity Tolerance in *Vitis vinifera* Cultivars

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Abstract

Salinity stress is one of the major constraints on plant growth and productivity, especially in arid and semi-arid regions. A promising strategy to improve plant tolerance is the use of Salt-Tolerant Plant Growth-Promoting Rhizobacteria (ST-PGPR), which are naturally adapted to saline environments. In this study, we tested two halophilic bacterial strains, Bacillus subtilis POE26 and *Oceanobacillus sp*. 76, isolated from halophytic plants, for their ability to enhance salinity tolerance in three grapevine cultivars: Fakhri, Bidaneh Sefid (syn. Thompson Seedless) and Gaznehei. Plant responses were evaluated by measuring growth traits, osmoprotectant accumulation, antioxidant enzyme activity and K^+/Na^+ balance. Salinity stress markedly reduced all growth parameters, although inoculation partially mitigated this reduction. Inoculation with *Oceanobacillus sp*. 76 significantly increased root length and root biomass, while *B. subtilis* POE26 improved stem fresh and dry weights. Both strains enhanced antioxidant defense, as shown by higher Ascorbate Peroxidase (APX), Superoxide Dismutase (SOD) and Catalase (CAT) activities and promoted proline accumulation under salinity stress (35.12% and 16.58% increase over control for *B. subtilis* and *Oceanobacillus*, respectively). They also increased glycine betaine levels under saline conditions and reduced malondialdehyde. The K^+/Na^+ ratio was higher in treatments without bacterial inoculation. These results indicate that halophilic bacteria can improve growth and stress physiology in grapevine seedlings exposed to salinity. Further studies are needed to validate these findings under field conditions and to better understand the underlying mechanisms.

Keywords: Grapevine cultivars; Halophilic bacteria; Osmoprotectants; Plant Growth-Promoting Rhizobacteria (PGPR); Salinity stress

Introduction

Salinity stress, intensified by climate change and unsustainable farming practices, is one of the major challenges facing global agriculture. High salt levels in soil disturb water uptake, disrupt ion balance and damage plant metabolism, leading to lower growth, reduced yield and poor fruit quality in many crops [1,2,3,4]. In grape production, salinity is often worsened by poor irrigation management. Excessive salts in the soil limit water absorption, restrict nutrient availability and disturb Na^+/K^+ balance, resulting in stunted growth, yield losses and reduced berry quality [5]. With salinity becoming more frequent and severe, understanding how crops respond at physiological, biochemical and molecular levels is essential for developing effective tolerance strategies [6].

Grapevine (*Vitis vinifera L.*) is one of the most important fruit crops worldwide, valued for both fresh consumption and wine production. However, it is highly sensitive to abiotic stresses, including salinity, which can greatly reduce its productivity and profitability [7]. Various approaches have been explored to improve tolerance, such as biostimulants

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[8], beneficial microbes [9,10], natural metabolites [11], phytochemicals and antimicrobial peptides [12,13]. Among these, the use of plant-associated halophilic and Halotolerant Plant Growth-Promoting Bacteria (H-PGPB) has received special attention as a sustainable and eco-friendly strategy.

Halophilic and halotolerant bacteria, naturally adapted to saline soils and halophyte environments, can enhance plant growth and stress tolerance through diverse mechanisms. They support plant growth by regulating hormones and improving nutrient uptake [9,14]. They also enhance osmoprotection by stimulating the accumulation of compatible solutes such as proline and soluble sugars [15], help maintain ion balance by reducing Na^+ uptake and sustaining a favorable Na^+/K^+ ratio [16] and strengthen antioxidant defenses by boosting enzymes such as Superoxide Dismutase (SOD), Peroxidase (POD) and Catalase (CAT) [17,18]. Additional benefits include stimulation of photosynthesis and root development, improved nutrient acquisition through siderophore production, nitrogen fixation and phosphate solubilization and the release of volatile organic compounds and secondary metabolites [10,11]. Through these combined actions, H-PGPB can reduce the harmful effects of salinity and support sustainable crop production. Still, challenges remain, particularly in understanding strain–host specificity, testing microbial consortia under field conditions and evaluating their effectiveness in different cultivars and environments [19].

Despite the global importance of grapevine, relatively few studies have investigated the role of halophilic PGPR in improving its salinity tolerance. Given the sensitivity of *V. vinifera* and the adaptability of halophilic microbes, these bacteria represent promising candidates for use in viticulture. In this study, we evaluated the effects of two halophilic bacterial strains *Bacillus subtilis* POE26 and *Oceanobacillus sp*. 76 isolated from halophytic plants, on three grapevine cultivars: Fakhri, Bidaneh Sefid (syn. Thompson Seedless) and Gaznehei. The study focused on morphological traits, osmoprotectant accumulation, antioxidant enzyme activity and nutrient balance under NaCl stress. By exploring these responses, our work aims to advance sustainable strategies for grapevine cultivation in salt-affected regions.

Materials and Methods

Bacterial preparation and inoculation

The bacterial strains used in this study (*B. subtilis* POE26 and *Oceanobacillus sp*.76sp. 76) had been recovered and identified in Department of Plant Pathology, Bu-Ali Sina University [20] **(Table 1)**. Strains were initially cultured on Nutrient Agar (NA) petri plates at 30 °C for 24 hours. Colonies were then transferred to fresh media to obtain pure bacterial cultures and further grown in Nutrient Broth (NB) medium. For inoculation, 250 mL of the bacterial suspension (2×10^8 CFU mL^{-1}.) was applied directly to the rhizosphere of each plant after gentle agitation of the culture to ensure homogeneity [21]. Sterile distilled water was used to prepare the bacterial suspensions and as a control for un-inoculated plants.

Table 1: Characteristics of the studied bacterial strains.

Isolate strain code	Scientific name	Host plant genus	Plant tissue	Sampling location	Colony color	Gram	Biofilm	Sodium chloride (3 M)	GenBank accession number
76	Oceano bacillus	Cressa	Root	Desert areas of Yazd , Iran	Whitish	+	_	+	KX196282.1
POE26	B.subtilis	Thuja	Shoot	Shiraz, Iran	Whitish	+	_	+	KP241040.1

Experimental design and plant material

This experiment was conducted under controlled pot conditions using rooted cuttings of three grapevine (*Vitis vinifera L.*) cultivarie Fakhri, Bidaneh Sefid and Gaznehei, at the Faculty of Agriculture, Bu-Ali Sina University, Hamedan, Iran (34.79° N latitude, 48.51° E longitude).

The experiment followed a factorial design based on a Completely Randomized Design (CRD) with three replications. The experimental factors included cultivar (Fakhri, Bidaneh Sefid, Gaznehei), salinity stress (0, 80 and 100 mM NaCl) and bacterial inoculation (control or no inoculation, *B. subtilis* POE 26 and *Oceanobacillus sp*. 76).

In mid-February, healthy grapevine cuttings (~25 cm in length and 1 cm in diameter) containing four nodes from the one-year-old canes were collected from the Hamedan Agricultural Research Center. To promote rooting, the cuttings were treated with Indole-3-Butyric Acid (IBA) and placed in a rooting medium composed of cocopeat and perlite (1:1, v/v). After approximately two months, rooted cuttings with emerging shoots were transplanted into plastic pots (25 cm height × 18 cm diameter) containing a uniform

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growth medium consisting of peat moss, perlite and cocopeat (2:2:1, v/v/v). All pots were maintained under greenhouse conditions free from biotic and abiotic stress.

Growth conditions and nutrient management

Plants were grown in a greenhouse under controlled conditions with temperatures of 31 ± 2 °C during the day and 24 ± 2 °C at night and relative humidity maintained between 40% and 50%. Irrigation was carried out regularly according to plant water requirements and ambient temperature. A half-strength Hoagland nutrient solution [22] was applied every two weeks to support uniform nutrient availability.

Salinity stress application

Once the plants were well-established, salinity treatments were imposed using NaCl at concentrations of 0 (control), 80 and 100 mM, corresponding to Electrical Conductivity (EC) values of 1.34, 8.82 and 10 dS/m, respectively. To avoid osmotic shock and plasmolysis, salinity was introduced gradually over several weeks using lower concentrations (20, 40 and 60 mM NaCl, equivalent to EC values of 4.05, 6.55 and 8.22 dS/m, respectively). Urban tap water was used for irrigation of control plants. To prevent excessive salt accumulation in the root zone, solutions with lower EC were alternated periodically. Salinity treatment lasted for approximately two months, ending in late August, at which point physiological and morphological traits were evaluated.

Plant growth parameters and elemental analysis

Two months after initiating salinity treatments, plant height was measured in centimeters. Plants were then harvested and the roots and shoots were separated. After thoroughly rinsing the roots, fresh weights of roots and stems were recorded. Root length was also measured in centimeters. For dry weight determination, plant tissues were placed in an oven at 70 °C for 48 h and weighed using a digital analytical balance with a precision of 0.0001 g. Sodium (Na^+) and potassium (K^+) contents were determined according [23], using the flame emission spectrometry method (Model JENWAY, PFP7, UK), with standard solutions prepared for calibration.

Antioxidant enzyme activity assays

Antioxidant enzymes were extracted following the method of [24], with slight modifications. One gram of fresh leaf tissue was rapidly frozen in liquid nitrogen and homogenized in 5 mL of cold extraction buffer containing 0.1 M phosphate buffer (pH 7.0), 1% Polyvinylpyrrolidone (PVP) and 1 mM EDTA. The homogenate was centrifuged at 15,000 rpm for 20 min at 4 °C and the resulting supernatant was used for enzymatic assays.

Peroxidase (POD) activity was determined using guaiacol as a substrate. The enzymatic reaction was monitored by measuring the increase in absorbance at 470 nm using a spectrophotometer (UV-1280, Shimadzu, Japan), as described by [25]. Ascorbate Peroxidase (APX) activity was assayed by following the decrease in absorbance at 290 nm due to ascorbic acid oxidation in the presence of H_2O_2, based on the method of [26]. Catalase (CAT) activity was measured by the rate of decomposition of hydrogen peroxide, with absorbance recorded at 240 nm, according to [27]. Superoxide Dismutase (SOD) activity was quantified by its capacity to inhibit the photochemical reduction of nitroblue tetrazolium. Absorbance was measured at 560 nm, following the method of [28].

Osmoprotectant quantification

Proline content was determined following the method of [29]. Briefly, 0.5 g of fresh leaf tissue was homogenized in 10 mL of 3% sulfosalicylic acid and centrifuged at 6000 rpm for 10 min. Two milliliters of the supernatant were mixed with 2 mL each of glacial acetic acid and acid ninhydrin reagent. The mixture was incubated at 100 °C for 1 h, cooled in an ice bath and extracted with 4 mL of toluene. Absorbance of the colored upper phase was measured at 520 nm.

Glycine betaine content was measured according to the method of [30]. A total of 0.25 g of dried leaf powder (ground in liquid nitrogen) was mixed with 10 mL of distilled water and shaken at 25 °C for 24 h. The extract was filtered (Whatman No. 1) and an equal volume of 2 N H_2SO_4 was added. After chilling the mixture in an ice bath for 60 min, 0.2 mL of potassium iodide–iodine solution (7.5 g I_2 and 20 g KI in 100 mL water) was added and gently vortexed. Samples were incubated at 0–4 °C for 16 h, then centrifuged at 10,000 rpm for 15 min. The resulting crystalline layer was dissolved in 9 mL of dichloroethane and left at room temperature for 2 h. Absorbance was read at 365 nm and concentrations were calculated using a standard curve.

Lipid peroxidation measurement

Lipid peroxidation, as indicated by Malondialdehyde (MDA) content, was assessed using the Thiobarbituric Acid (TBA) method [31]. Fresh leaf tissue (0.2 g) was homogenized in 5 mL of 1% Trichloroacetic Acid (TCA) and centrifuged at 13,000 rpm for 15 min.

One milliliter of the supernatant was added to 4 mL of 20% TCA containing 0.5% TBA and the mixture was incubated in a water bath at 95 °C for 30 min. After rapid cooling in an ice bath, the samples were centrifuged at

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12,000 rpm for 5 min. Absorbance of the supernatant was measured at 532 nm and 600 nm and MDA concentration was calculated using the following formula:

MDA (μmol g^{-1} FW) = (OD532 – OD600) /155 × 1000

where 155 $mmol^{-1}$ cm^{-1} is the extinction coefficient of MDA.

Statistical analyses

All data were subjected to Analysis of Variance (ANOVA) using SAS software (version 9.4). Mean comparisons were performed using Duncan's multiple range test at a significance level of $p < 0.05$.

Results

Plant growth parameters

The effects of cultivar, salinity levels and bacterial inoculation on root and stem growth of grapevine seedlings are summarized in **Table 2**. Interaction effects of cultivar, salinity and bacterial strain on growth parameters significantly influenced all traits ($p < 0.05$).

Table 2: Interaction effects of cultivar, salinity and bacterial strain on growth parameters in grapevines.

Cultivar	Salinity (mM)	Bacterial strain	Root fresh weight (g)	Root dry weight (g)	Root dry mater (%)	Shoot length (cm)	Shoot fresh weight (g)	Shoot dry weight (g)	Shoot dry mater (%)
Fakhri	0	Control	52.03^{b}	11.46^{bc}	22.14^{b-d}	110.33^{a}	60.67^{a}	21.06^{a}	34.72^{c-h}
	80	Control	28.37^{e-g}	5.98^{g-i}	21.11^{b-d}	70.66^{cd}	30.84^{cd}	11.62^{c-e}	38.58^{b-d}
	100	Control	29.70^{ef}	5.85^{g-i}	19.70^{b-d}	43.66^{g-i}	28.60^{c-g}	8.42^{e-g}	29.48^{f-i}
	0	*Oceanobacillus*	51.13^{bc}	12.52^{b}	24.48^{b-d}	68.66^{c-e}	36.40^{bc}	8.54^{e-g}	23.21^{i}
	80	*Oceanobacillus*	29.17^{ef}	5.73^{g-i}	19.70^{b-d}	75^{bc}	25.30^{d-h}	8.36^{e-g}	33.66^{d-h}
	100	*Oceanobacillus*	27.36^{e-g}	5.15^{g-j}	18.75^{c-d}	32.66^{h-k}	16.66^{hi}	4.62^{gh}	27.71^{hi}
	0	*B.subtilis*	42.23^{cd}	9.07^{c-e}	21.55^{b-d}	88^{b}	28.66^{c-g}	9.52^{d-e}	33.18^{d-h}
	80	*B.subtilis*	23.70^{e-h}	4.80^{h-j}	20.22^{b-d}	41.66^{g-j}	29.54^{c-e}	8.66^{e-g}	29.30^{f-i}
	100	*B.subtilis*	16.84^{h}	3.37^{j}	19.97^{b-d}	29.66^{h-k}	16.36^{hi}	4.50^{h}	27.78^{g-i}
Gaznehei	0	Control	48.40^{b-d}	11^{bc}	22.76^{b-d}	75.66^{bc}	29.72^{c-e}	10.40^{d-e}	34.86^{c-g}
	80	Control	28.60^{e-g}	7.16^{e-g}	25.06^{bc}	51^{e-g}	19.56^{g-i}	7.16^{f-h}	36.69^{b-f}
	100	Control	24.39^{e-h}	5.69^{g-j}	23.23^{b-d}	24^{jk}	15.89^{hi}	5.86^{f-h}	37^{b-f}
	0	*Oceanobacillus*	54.05^{b}	12.29^{b}	22.73^{b-d}	78.33^{bc}	42.09^{b}	21.01^{a}	49.65^{a}
	80	*Oceanobacillus*	27.90^{e-g}	6.66^{f-h}	23.98^{b-d}	38^{g-k}	19.88^{f-i}	7.66^{e-h}	37.52^{b-e}
	100	*Oceanobacillus*	20.92^{f-h}	5.51^{g-j}	25.50^{bc}	54.50^{d-g}	19.62^{f-i}	8.83^{d-g}	44.12^{ab}
	0	*B.subtilis*	73.52^{a}	19.15^{a}	25.92^{b}	51^{e-g}	29^{c-f}	14.22^{bc}	49.49^{a}
	80	*B.subtilis*	40.44^{d}	9.62^{cd}	23.80^{b-d}	63.33^{c-f}	40.74^{b}	17.38^{ab}	42.58^{a-c}
	100	*B.subtilis*	20.75^{gh}	4.48^{h-j}	21.46^{b-d}	46.66^{gh}	25.30^{d-h}	11.14^{c-e}	43.92^{ab}
Bidaneh sefid	0	Control	41.29^{d}	9.06^{c-f}	21.85^{b-d}	43.66^{g-i}	41.87^{b}	13.22^{b-d}	31.51^{d-h}
	80	Control	19.30^{h}	3.38^{j}	17.61^{d}	26^{i-k}	23.18^{d-h}	7.04^{f-h}	29.87^{e-i}
	100	Control	29.30^{ef}	5.30^{g-j}	17.99^{d}	20.25^{k}	17.04^{hi}	7.28^{f-h}	41.34^{bc}
	0	*Oceanobacillus*	41.27^{d}	8.62^{d-f}	20.88^{b-d}	47^{f-h}	21.96^{e-i}	7.82^{e-h}	35.03^{c-f}
	80	*Oceanobacillus*	31.45e	6.57^{f-h}	20.83^{b-d}	20.50^{k}	22.26^{d-i}	6.64^{f-h}	30.08^{e-i}
	100	*Oceanobacillus*	28.17^{e-g}	6.15^{g-i}	21.83^{b-d}	32.33^{h-k}	14.32^{i}	5.42^{gh}	38.40^{b-d}
	0	*B.subtilis*	52.75^{b}	11.01^{bc}	20.71^{b-d}	52^{e-g}	28.72^{c-g}	10.47^{c-f}	36.54^{b-f}
	80	*B.subtilis*	21.52^{f-h}	4.07^{ij}	18.91^{b-d}	37.33^{g-k}	23.92^{d-h}	8.20^{e-h}	34.11^{d-h}
	100	*B.subtilis*	17.88^{h}	5.97^{g-i}	34.98^{a}	21.66^{k}	17.58^{hi}	5.28^{gh}	29.94^{e-i}
Significance	level		P=0.025	p<0.001	P=0.023	p<0.001	p<0.001	p<0.001	P=0.014

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Fresh and dry weight of roots and stem, dry biomass and root and stem length of plants decreased with increasing salinity level in all three grape cultivars. Bacterial inoculation produced variable effects. *Oceanobacillus sp*.76 was the most effective bacterial inoculant in root development, showing a 65.7% increase compared with the uninoculated control **(Figure 1)**.

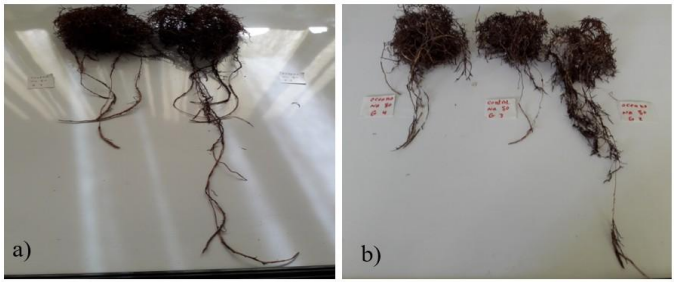

Figure 1: Effect of bacterial inoculation on root length. (a) Comparison between *Oceanobacillus sp*. 76 inoculation and the uninoculated control; (b) Comparison among *Oceanobacillus sp*. 76, B. subtilis and the uninoculated control, with the central root representing the control. Inoculation with *Oceanobacillus sp*. 76 resulted in a noticeable increase in root length compared with the control.

Among cultivars, 'Fakhri' recorded the greatest root length (37.79 cm). Both bacterial strains improved root fresh and dry weight, especially in 'Bidaneh Sefid' and 'Gaznehei' compared to the uninoculated control. Root fresh weight increased by 12.50% with the *Oceanobacillus sp*.76 strain and 52% with the *B. subtilis* POE26 strain in 'Gaznehei' compared to the uninoculated control and under 0 mM conditions. Root fresh weight in 'Gaznehei' and under moderate salinity (80 mM) improved by 42.85% with the *B. subtilis* POE26 strain compared to the control. In 'Bidaneh Sefid', root fresh weight increased by 63.15% with the *Oceanobacillus sp*.76 strain and 10.52% with the *B. subtilis* POE26 strain compared to the control and under 80 mM salinity conditions. Similarly, root dry weight and root dry biomass also increased with the inoculation of both bacterial strains and under the influence of salinity in some treatments.

The fresh and dry weight of the stem increased, especially in 'Gaznehei' under the influence of bacterial strains. The fresh weight of the stem in 'Gaznehei' increased by 110.52% and 66.66% with inoculation of the *B. subtilis* POE26 strain and under salinity conditions of 80 and 100 mM, respectively. The dry weight of the stem also increased in 'Gaznehei' with both bacterial strains and under salinity stress, although the *B. subtilis* POE26 strain was more effective.

Stem length was improved by the use of both strains of bacteria studied in some treatments. In 'Gaznehei' at 100 mM salinity, stem length increased by 125% and 91.66% with inoculation of *Oceanobacillus sp*.76 and *B. subtilis* POE26 strains, respectively, compared to the control. In 'Bidaneh Sefid', stem length also increased under different salinity levels and under the influence of both bacterial strains compared with the uninoculated control. The highest fresh (60.67 g) and dry (21.06 g) weight of the stem and the stem length (110 cm) were observed in 'Fakhri' under conditions without bacterial inoculation and 0 mM salinity, but the highest fresh (73.52 g) and dry (19.15 g) weight of the root was observed in the Gaznehei cultivar inoculated with *B. subtilis* POE26 and under 0 mM conditions.

Antioxidant enzyme activity

The activities of POD, SOD, APX and CAT were significantly influenced by cultivar, salinity and bacterial inoculation **(Table 3)**. In general, salinity increased antioxidant enzyme activity, though responses varied by cultivar and bacterial treatment.

Table 3: Interaction effects of cultivar, salinity and bacterial strain on leaf antioxidant enzyme activities in grapevines.

Cultivar	Salinity (mM)	Bacterial strain	CAT (U/ mg protein)	APX (U/ mg protein)	SOD (U/ mg protein)	POD (U/ mg protein)
Fakhri	0	Control	2.81^{d-f}	1.80^{a}	69^{b-g}	5.63^{e-g}
	80	Control	2.98^{b-f}	0.89^{h}	88^{b-e}	6.26^{d-g}
	100	Control	3.88^{a}	1.09^{e-h}	53.33^{b-g}	3.70^{fg}
	0	*Oceanobacillus*	2.46^{f}	1.30^{b-h}	99^{bc}	5.02^{e-g}
	80	*Oceanobacillus*	2.65^{d-f}	1.57^{a-e}	26.66^{fg}	10.07^{a-c}
	100	*Oceanobacillus*	2.51^{ef}	1.28^{c-h}	91.33^{b-d}	12.42^{a}
	0	*B.subtilis*	2.57^{ef}	0.89^{h}	34^{fg}	6.61^{c-g}
	80	*B.subtilis*	2.85^{c-f}	1.18^{d-h}	89.33^{b-e}	8.33^{b-e}
	100	*B.subtilis*	2.95^{c-f}	1.30^{b-h}	111^{ab}	6.73^{c-f}

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Gaznehei	0	Control	2.49^{f}	1.23^{c-h}	40^{d-g}	4.01^{fg}
	80	Control	2.51^{ef}	1.09^{e-h}	47^{b-g}	4.22^{fg}
	100	Control	2.41^{f}	1.09^{e-h}	44.66^{c-g}	3.68^{fg}
	0	*Oceanobacillus*	3.36^{bc}	0.90^{gh}	77.33^{b-f}	3.80^{fg}
	80	*Oceanobacillus*	2.55^{ef}	1.26^{c-h}	36.66^{e-g}	3.75^{fg}
	100	*Oceanobacillus*	3.16^{b-d}	1.75^{ab}	158.66^{a}	3.66^{fg}
	0	*B.subtilis*	2.52^{ef}	1.01^{f-h}	69.33^{b-f}	3.63^{g}
	80	*B.subtilis*	2.62^{ef}	1.66^{a-c}	26^{fg}	3.70^{fg}
	100	*B.subtilis*	2.51^{ef}	1.26^{c-h}	57^{b-g}	3.66^{fg}
Bidaneh sefid	0	Control	3.55^{ab}	1.64^{a-d}	34^{fg}	3.59^{g}
	80	Control	2.71^{d-f}	1.44^{a-f}	61.33^{b-g}	12.25^{ab}
	100	Control	2.68^{d-f}	1.37^{a-g}	14.66^{g}	4.29^{fg}
	0	*Oceanobacillus*	3.08^{b-e}	1.64^{a-d}	28^{fg}	3.73^{fg}
	80	*Oceanobacillus*	2.48^{f}	1.50^{a-f}	88^{b-e}	8.80^{b-d}
	100	*Oceanobacillus*	2.56^{ef}	1.41^{a-f}	68.66^{b-g}	4.08^{fg}
	0	*B.subtilis*	2.41^{f}	0.89^{h}	72^{b-f}	8.41^{b-e}
	80	*B.subtilis*	2.65^{d-f}	1.67^{a-c}	30.66^{fg}	5.60^{e-g}
	100	*B.subtilis*	2.46^{f}	1.45^{a-f}	50.66^{b-g}	3.68^{fg}
Significance level			P=0.024	P=0.048	p<0.001	p<0.001

Bacterial inoculation under 80 and 100 mM salinity conditions increased APX enzyme activity in all three grape cultivars. In 'Bidaneh Sefid' and 'Fakhri', enzyme activity increased with increasing salinity levels in the treatment with *B. subtilis* POE26 bacteria and in 'Gaznehei', enzyme activity increased with increasing salinity levels in the treatment with both strains of bacteria. SOD activity was generally enhanced by bacterial inoculation, with the highest values typically under severe salinity Inoculation with *Oceanobacillus sp*.76 and *B. subtilis* POE26 strains increased by 71.25% and 108.14% In 'Fakhri', by 253.78% and 27.63% in 'Gaznehei' and by 368.35% and 245.57% In 'Bidaneh Sefid', respectively, compared to the control. As salinity levels increased, the activity of this enzyme increased in some bacterial treatments.

CAT enzyme activity in Gaznehei cultivars increased with bacterial inoculation at all salinity levels, although inoculation with *Oceanobacillus sp*.76 strain was more effective. In 'Fakhri', enzyme activity increased with increasing salinity levels in all treatments. In 'Bidaneh Sefid', with increasing salinity stress, only in the treatment with *B. subtilis* POE26, the activity of this enzyme increased. In 'Gaznehei', with all three salinity levels and with the activity of bacterial strains, POD enzyme activity decreased compared with the uninoculated control. In the Bidaneh Sefid variety, enzyme activity decreased at two salinity levels of 80 and 100 mM with inoculation of the two bacterial strains, although bacterial inoculation increased the enzyme in 'Fakhri'. With increasing salinity levels, especially at 80 mM, enzyme activity increased in 'Bidaneh Sefid' and 'Fakhri'.

Overall, PGPR treatments, particularly *Oceanobacillus sp*.76, enhanced antioxidant enzyme activities under salinity stress, indicating their role in alleviating oxidative damage and supporting stress tolerance.

Sodium and potassium contents

Salinity and bacterial inoculation significantly affected sodium (Na^+) and potassium (K^+) levels in grapevine leaves **(Table 4)**. The potassium content in grapevine leaves either increased or remained relatively constant with increasing salinity levels. *Oceanobacillus sp*.76 enhanced K^+ retention, particularly in 'Gaznehei' and 'Bidaneh Sefid', maintaining levels above 4.0 mg/g at 80 mM NaCl. These findings suggest a role for *Oceanobacillus sp*.76 in maintaining ionic balance under salt stress.In 'Gaznehei', inoculation with *Oceanobacillus sp*. 76 and *B. subtilis* POE26 strains increased by 20.49% and 3.76%, respectively, compared to the control and at 80 mM salinity. The highest potassium content was observed in 'Fakhri' and at 100 mM salinity and without bacterial inoculation (7.54 mg/g DW).

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Table 4: Interaction effects of cultivar, salinity and bacterial strain on sodium and potassium contents and osmoprotectant characteristics of grapevines.

Cultivar	Salinity (mM)	Bacterial strain	K+ (mg/g)	Na+ (mg/g)	MDA (µmol/g-1FW)	GB (mg/g-1DW)
Fakhri	0	Control	6.02^{c-h}	1.02^{j}	0.746^{a}	0.531^{ab}
	80	Control	7.34^{ab}	4.39^{e-g}	0.621^{a-c}	0.147^{h-k}
	100	Control	7.54^{a}	3.63^{g-i}	0.510^{a-f}	0.346^{c-f}
	0	*Oceanobacillus*	5.62^{e-j}	1.50^{j}	0.441^{d-f}	0.582^{a}
	80	*Oceanobacillus*	5.22^{h-l}	3.59^{g-i}	0.577^{a-e}	0.277^{d-h}
	100	*Oceanobacillus*	6.25^{c-f}	4.16^{e-g}	0.477^{b-f}	0.253^{e-i}
	0	*B.subtilis*	6.21^{c-f}	1.24^{j}	0.656^{ab}	0.304^{d-g}
	80	*B.subtilis*	5.72^{d-i}	6.36^{a}	0.374^{fg}	0.389^{b-e}
	100	*B.subtilis*	6.84^{a-c}	5.34^{b-d}	0.333^{fg}	0.124^{i-k}
Gaznehei	0	Control	5.12^{i-l}	1.24^{j}	0.555^{a-f}	0.181^{g-k}
	80	Control	5.32^{g-k}	3.91^{f-h}	0.394^{e-g}	0.285^{d-h}
	100	Control	4.37^{l-n}	4.96^{c-e}	0.397^{e-g}	0.068^{k}
	0	*Oceanobacillus*	4.53^{k-n}	1.43^{j}	0.542^{a-f}	0.202^{g-k}
	80	*Oceanobacillus*	6.41^{c-e}	4.39^{e-g}	0.380^{e-g}	0.111^{jk}
	100	*Oceanobacillus*	4.23^{mn}	4.55^{d-f}	0.307^{fg}	0.093^{k}
	0	*B.subtilis*	4.93^{i-n}	1.43^{j}	0.500^{b-f}	0.195^{g-k}
	80	*B.subtilis*	5.52^{f-j}	3.05^{hi}	0.361^{fg}	0.085^{k}
	100	*B.subtilis*	4.86^{j-n}	6.26^{ab}	0.255^{g}	0.180^{g-k}
Bidaneh sefid	0	Control	4.76^{j-n}	1.88^{j}	0.559^{a-e}	0.413^{b-d}
	80	Control	5.09^{i-m}	6.07^{ab}	0.641^{ab}	0.190^{g-k}
	100	Control	6.15^{c-g}	5.79^{a-c}	0.460^{c-f}	0.243^{e-j}
	0	*Oceanobacillus*	4.46^{k-n}	1.69^{j}	0.445^{c-f}	0.464^{a-c}
	80	*Oceanobacillus*	6.54^{b-d}	2.86^{i}	0.342^{fg}	0.324^{c-g}
	100	*Oceanobacillus*	4.13^{n}	4.58^{d-f}	0.305^{fg}	0.150^{h-k}
	0	*B.subtilis*	4.93^{i-n}	1.78^{j}	0.578^{a-d}	0.133^{i-k}
	80	*B.subtilis*	5.12^{i-l}	4.17^{e-g}	0.352^{fg}	0.218^{f-k}
	100	*B.subtilis*	5.42^{f-j}	5.59^{a-c}	0.711^{a}	0.213^{f-k}
Significance level	-	-	p<0.001	p<0.001	p<0.001	p<0.001

Bacterial inoculation modified Na^+ uptake depending on cultivar and salinity. *B. subtilis* tended to increase Na^+ in 'Bidaneh Sefid' and 'Gaznehei' under high salinity, while *Oceanobacillus sp.*76 showed a more moderate Na^+ profile, especially under moderate salinity (80 mM). The highest K^+/Na^+ ratio was observed in 'Fakhri' under control conditions without inoculation. Although this ratio declined with salinity in all cultivars, it remained higher in 'Fakhri' compared with the other two. Bacterial inoculation reduced the K^+/Na^+ ratio, but did not appear to specifically limit K+ uptake or enhance Na+ uptake under salinity stress **(Table 5)**.

Table 5: Main effects of cultivar, salinity and bacterial strain on growth parameters in three grapevine cultivars.

Treatment	Root length (cm)	K^+/Na^+ ratio
Cultivar		
Fakhri	37.79^{a}	2.72^{a}
Gaznehei	30.94^{b}	2.06^{b}
Bidaneh sefid	34.96^{a}	1.76^{c}
Significance level	p<0.001	p<0.001
Salinity(mM)		
0	43.76^{a}	3.76^{a}

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80	33.16[b]	1.51[b]
100	26.31[c]	1.19[c]
Significance level	p<0.001	p<0.001
Bacterial strain		
Control	34.25[ab]	2.36[a]
Oceanobacillus	36.87[a]	2.02[b]
B.subtilis	32.59[b]	2.16[ab]
Significance level	P=0.023	P=0.075

Osmoprotectants

Salinity and bacterial inoculation significantly influenced Malondialdehyde (MDA) and Glycine Betaine (GB) contents in grapevine leaves ($p < 0.001$, **Table 5**). Cultivar, salinity and bacterial strain also significantly affected proline accumulation **(Figire 2)**. The highest and lowest leaf proline levels were recorded in 'Gaznehei' (0.271) and 'Bidaneh Sefid' (0.180), respectively. Proline accumulation increased with salinity and *B. subtilis* inoculation elevated proline by 35.12% compared with the uninoculated control. The interaction between cultivar and salinity was significant, with 'Gaznehei' at 100 mM showing the highest proline (0.510), while the same cultivar under control conditions exhibited the lowest (0.115).

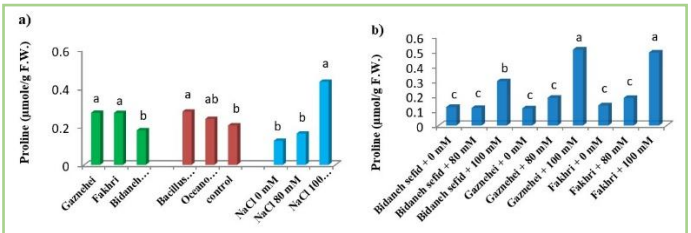

Figure 2: (a) The main effects of cultivar, salinity and bacterial strain on leaf proline content; (b) The interaction effects of cultivar and salinity on leaf proline content.

MDA, an indicator of lipid peroxidation, increased under salinity in all cultivars, especially in uninoculated plants. In 'Fakhri' and 'Gaznehei', with the activity of both PGPR strains and at all salinity levels, the amount of MDA showed a decreasing trend compared with the uninoculated control, underscoring the protective effect of bacterial inoculation. In 'Bidaneh Sefid' and in 80 mM conditions, the amount of MDA decreased compared with the uninoculated control and under the influence of the activity of both bacterial strains. Both PGPR strains generally reduced MDA levels, particularly under moderate and high salinity, suggesting improved membrane stability. GB levels varied across treatments and were significantly influenced by salinity and inoculation. The highest GB content (0.582 mg/g DW) was recorded in 'Fakhri' under control conditions, suggesting a strong intrinsic capacity for osmolyte production. The amount of amino acid glycine betaine increased in 'Fakhri' and 'Bidaneh Sefid', under moderate salinity (80 mM) and in 'Gaznehei' under 0 and 100 mM conditions compared with the uninoculated control. This increase in GB was due to the activity of both bacterial strains, especially *B. subtilis* POE26. Overall, bacterial inoculation, particularly with *B. subtilis*, reduced oxidative damage and enhanced osmoprotectant accumulation under salinity stress, with 'Gaznehei' and 'Fakhri' demonstrating stronger physiological resilience compared with 'Bidaneh Sefid'.

Discussion

High salinity is among the most detrimental abiotic stresses to plants, causing ionic imbalance, osmotic stress and oxidative damage. Excess sodium disrupts membrane integrity, impairs nutrient and water uptake and interferes with essential physiological and biochemical processes, ultimately reducing plant growth and productivity [7,32]. To counter these effects, plants activate defense strategies such as ion homeostasis, osmolyte accumulation and antioxidant defense systems. However, under prolonged or severe stress, these mechanisms are often insufficient. Recently, Plant Growth-Promoting Rhizobacteria (PGPR) have attracted attention as natural biostimulants that enhance salinity tolerance by regulating ion uptake, improving osmotic adjustment and stimulating antioxidant activity [33,34].

In this study, inoculation with two halotolerant bacterial strains *Bacillus subtilis* POE26 and *Oceanobacillus sp*. 76 improved growth and stress tolerance in three grape cultivars ('Fakhri', 'Bidaneh Sefid' and 'Gaznehei') subjected to salinity. Positive effects were evident in both morphological and physiological traits. *Oceanobacillus sp*. 76 particularly enhanced root biomass, while *B. subtilis* stimulated stem growth. Among cultivars, 'Gaznehei' accumulated the highest root biomass, whereas 'Fakhri' exhibited the longest roots and shoots, suggesting possible genotype–microbe specificity in stress responses. There are reports of *Oceanobacillus sp* bacteria significantly improving root growth and fresh and dry weight of wheat genotypes under salt stress [20,35,36].

Salinity stress typically induces excessive Na^+ accumulation, which competes with K^+ at enzyme binding sites and disrupts protein function. Thus, maintaining a high K^+/Na^+ ratio is widely regarded as a hallmark of salt tolerance. Previous studies have reported that PGPR can improve this ratio by enhancing K^+ uptake or limiting Na^+ influx [37,38]. For example, Bacillus inoculation increased K^+ uptake in peanut by over 30% under salinity [39]. However, in the present study, no consistent improvement in K^+/Na^+

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ratio was observed across cultivars and treatments, suggesting that bacterial effects on ionic homeostasis may depend on specific strain–host–environment interactions rather than representing a universal mechanism.

Besides ionic regulation, osmolyte accumulation is a central component of plant adaptation to salinity. Compatible solutes such as proline and Glycine Betaine (GB) contribute to osmotic adjustment, protect proteins and membranes and scavenge Reactive Oxygen Species (ROS) [40,41]. Previous studies have shown that PGPR enhance osmolyte accumulation under stress for instance, Halomonas sp. increased proline in tomato by more than 80% [42], while Pseudomonas sp. stimulated proline accumulation in citrus seedlings [21]. Consistently, in this study proline accumulation was particularly pronounced in 'Fakhri', especially under bacterial inoculation, reflecting improved osmotic adjustment. Glycine betaine also increased following inoculation, although the effect diminished at 100 mM NaCl in two cultivars, Fakhri and Bidanah Sefid, suggesting that osmolyte synthesis may be constrained beyond a certain stress threshold. Oxidative stress, a key secondary effect of salinity, was reflected in elevated Malondialdehyde (MDA) levels in uninoculated plants. Both PGPR strains reduced MDA accumulation, indicating improved membrane stability and protection against oxidative damage. Similar reductions in MDA have been reported in wheat, tomato and maize inoculated with PGPR under salinity [43,44].

Antioxidant enzymes provide a crucial defense against salinity-induced ROS. In the present study, bacterial inoculation altered enzyme activities in an enzyme-specific manner. APX activity was generally increased in inoculated plants, especially with Oceanobacillus and at 80 and 100 mM salinity levels, while CAT, POD and SOD responses varied depending on cultivar and salinity level.

SOD activity was increased in all three cultivars, especially at high salinity (100 mM), compared to the uninoculated control. Bacterial treatments in 'Gaznehei' induced stronger antioxidant responses in relation to CAT activity. A decrease in POD was observed in inoculated plants, especially in 'Gaznehei' and 'Bidanah Sefid'. These findings suggest that PGPR may selectively modulate specific antioxidant pathways, possibly enabling plants to optimize energy allocation under stress. Taken together, the findings suggest that in this system, PGPR-mediated salinity tolerance was primarily achieved through osmotic and oxidative stress regulation rather than consistent modulation of Na^+/K^+ balance. This aligns with reports from other crops, including wheat, maize, grapevine and tomato, where PGPR enhanced growth, osmotic adjustment and antioxidant capacity under saline conditions [45,46,47,48]. Although the two halotolerant strains tested here did not fully restore growth to control levels, they significantly improved multiple physiological and biochemical traits, underscoring their potential as biostimulants for sustainable viticulture in salt-affected regions. Future studies should explore underlying molecular mechanisms and validate these effects under long-term field conditions across diverse environments.

Conclusion

This study demonstrates that inoculation with halotolerant bacterial strains *Bacillus subtilis* POE26 and *Oceanobacillus sp*. 76 enhances salinity tolerance in grapevine cultivars by promoting growth, stimulating osmolyte accumulation and activating antioxidant defenses. While effects on ion homeostasis were limited, both strains effectively reduced oxidative damage and modulated key antioxidant enzymes, thereby improving stress resilience. The observed cultivar-specific responses emphasize the role of genotype–microbe interactions in determining the efficiency of microbial inoculation. Overall, these findings highlight the potential of halotolerant PGPR as sustainable biostimulants for mitigating salinity stress in viticulture, particularly in salt-affected regions. Future research should focus on unraveling the molecular mechanisms underlying these interactions and validating their effectiveness under field conditions to support long-term application.

Author Contribution Statement

F.H.Z.T: conceptualization, growth and physiological data and writing. M.S.: funding acquisition, methodology and review. HS: methodology, supervision, writing and review. J.S.: bacterial strain and methodology.

Conflict of interest statements

The authors declare no conflict of interest.

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Data availability

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

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