Plant growth promoting rhizobacteria enhances germination and bioactive compound in cucumber seedlings under saline stress

Rizobacterias promotoras del crecimiento vegetal mejoran la germinación y los compuestos bioactivos en plántulas de pepino sometidas a estrés salino

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ABSTRACT. Soil salinity is a major abiotic stressor that negatively impacts agricultural productivity worldwide. One potential strategy to alleviate its effects is the use of plant growth-promoting rhizobacteria (PGPR). This study evaluated the impact of PGPR (*Pseudomonas paralactis*, *Bacillus cereus*, *Sinorhizobium meliloti*, and *Acinetobacter radioresistens*) on cucumber seedling (*Cucumis sativus* L.) growth under saline stress conditions (0, 5, 10, and 15% of NaCl). The results showed that PGPR biopriming significantly enhanced germination rates, plumule and radicle lengths, fresh and dry weights compared to non-inoculated controls. Notably, the highest germination rates were observed with *P. paralactis* and *A. radioresistens* at 81.20% and 79.39%, respectively, under saline stress. Additionally, PGPR inoculation enhanced chlorophyll content, proline accumulation, and antioxidant activity, indicating improved photosynthetic efficiency and osmotic adjustment under saline conditions. These findings suggest that PGPR inoculation is an effective, sustainable strategy for mitigating the detrimental effects of salt stress, improving cucumber seedling development. In order to increase the benefits of PGPR, further evaluations are being pursued using bacterial consortia to maximize individual effects and further improve plant growth under these conditions.
Keywords: *Cucumis sativus* L., rhizobacterias, Salinity stress.

RESUMEN. La salinidad del suelo es un factor de estrés abiótico importante que impacta negativamente la productividad agrícola a nivel mundial. Una estrategia potencial para mitigar sus efectos es el uso de rizobacterias promotoras del crecimiento vegetal (PGPR). Este estudio evaluó el impacto de las PGPR (*Pseudomonas paralactis, Bacillus cereus, Sinorhizobium meliloti* y *Acinetobacter radioresistens*) en el crecimiento de plántulas de pepino (*Cucumis sativus* L.) bajo condiciones de estrés salino (0, 5, 10 y 15% de NaCl). Los resultados mostraron que el biocebado con PGPR mejoró significativamente las tasas de germinación, las longitudes de plúmula y radícula, y los pesos frescos y secos en comparación con los controles no inoculados. Específicamente, se observaron las tasas de germinación más altas con *P. paralactis* y *A.* radioresistens con 81.20% y 79.39%, respectivamente, bajo estrés salino. Además, la inoculación con PGPR incrementó el contenido de clorofila, la acumulación de prolina y la actividad antioxidante, lo que indica una mejora en la eficiencia fotosintética y el ajuste osmótico bajo condiciones salinas. Estos hallazgos sugieren que la inoculación con PGPR es una estrategia efectiva y sostenible para mitigar los efectos perjudiciales del estrés salino, mejorando el desarrollo de las plántulas de pepino. Con el fin de aumentar los beneficios de las PGPR, se están llevando a cabo evaluaciones adicionales utilizando consorcios bacterianos para maximizar los efectos individuales y mejorar aún más el crecimiento de las plantas bajo estas condiciones.
Palabras clave: *Cucumis sativus* L., rizobacterias, estrés salino.

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INTRODUCTION

Cucumber (*Cucumis sativus* L.) is an economically and nutritionally important crop worldwide, valued for its culinary versatility and high content of bioactive compounds such as flavonoids, vitamins, and antioxidants (Huerta-Reyes *et al.* 2022). However, its production is often constrained by both biotic and abiotic factors that negatively affect crop yield and quality. Among these, soil salinity is one of the most significant challenges, disrupting plant growth, nutrient uptake, and essential physiological functions (Aslam *et al.* 2020). Soil salinity has been exacerbated by excessive fertilization and irrigation practices in arid and semi-arid regions, resulting in a progressive decline in agricultural productivity (Shao *et al.* 2016). It is estimated that approximately 1.125 million hectares of agricultural land worldwide are affected by salinity, representing 6% of global agricultural land. In Mexico, salinity is particularly problematic in arid and coastal regions, where salt accumulation in the soil has occurred over time (Ojeda-Barrios *et al.* 2021). Saline stress particularly affects cucumber seedlings, compromising their germination and early growth, which in turn reduces both the quality and quantity of the harvest. Cucumber seedlings are highly sensitive to salinity stress because their root systems are still immature and have limited capacity to absorb water and nutrients under high salt concentrations. This results not only in reduced seedling viability but also in negative impacts on the subsequent fruit production, posing a significant challenge for farmers (Kaur y Sharma 2022). In this context, plant growth-promoting rhizobacteria (PGPR) have emerged as a sustainable strategy to mitigate the adverse effects of saline stress and improve cucumber seedling production PGPR are beneficial microorganisms that colonize the rhizosphere and promote plant growth through various direct and indirect mechanisms, such as nitrogen fixation, phosphate solubilization, siderophore production, and the synthesis of phytohormones like indole-3-acetic acid (IAA) (Vocciante *et al*. 2022). Additionally, some PGPR strains can induce systemic resistance (ISR), enhancing plant defense mechanisms against abiotic stress (Tirry *et al.* 2021). Recent studies have shown that specific PGPR species can mitigate the adverse effects of salt stress by stimulating root growth, improving nutrient uptake, and increasing the accumulation of key metabolites such as proline and antioxidants (Abbas *et al*. 2019, Ilyas *et al*. 2020). However, the effects of different PGPR strains on specific crops, such as cucumber, require further investigation. This study aimed to evaluate the effect of inoculating cucumber seeds with four PGPR strains (*Pseudomonas paralactis*, *Bacillus cereus*, *Sinorhizobium meliloti*, and *Acinetobacter radioresistens*) on germination and bioactive compound production under salt stress conditions. We hypothesized that PGPR biopriming would enhance germination rate, chlorophyll content, and antioxidant accumulation, providing a viable alternative for agricultural production in saline-affected soils.

MATERIALS AND METHODS

Halotolerance

The salt stress resistance of four PGPR strains - *Bacillus cereus*, *Sinorhizobium meliloti*, *Acinetobacter radioresistens*, and *Pseudomonas paralactis* - was evaluated. These strains, provided by the Microbial Ecology Laboratory of the Universidad Juárez del Estado de Durango, were isolated from the

rhizosphere of plants in the Chihuahua Desert. They were cultured on LB medium supplemented with various NaCl concentrations (0, 5, 10, 15, and 20%) in Petri dishes, with four replicates per treatment. The cell concentration used was 1×10^8 UFC mL^{-1}.

Plant Material and Inoculation

Cucumber (*Cucumis sativus* L.) seeds of the Poinsett 76 variety (Southern Star Seeds, S.A. de C.V.) were used. Before sowing, the seeds were disinfected with a 10% (v/v) sodium hypochlorite solution for 5 minutes and then rinsed with sterile distilled water. Subsequently, they were inoculated for 1 h in a suspension of each rhizobacterium in 50 mL beakers. After the inoculation period, 10 seeds per treatment were placed in a germination tray containing sterile peat moss as a substrate. The trays were then transferred to a germination chamber and placed in an artificial growth incubator (Yamato Scientific America®, IC403) under a 12:12 photoperiod at 25 ± 2 °C and 60% relative humidity, measured with a Bosh Digital Multi-Scanner GMS120G. Irrigation began after the emergence of the first true leaf and was applied daily for five days using NaCl solutions at concentrations of 0, 5, 10, and 15%. Fifteen days after sowing, the rhizobacteria were re-inoculated (1×10^8 CFU mL^{-1}) at the base of each seedling stem.

Treatments and Experimental Design

The halotolerance bioassay included the four previously described bacterial strains, a control without bacteria, and five different NaCl concentrations (0, 5, 10, 15, and 20%) with 3 replications, using Petri dishes as the experimental unit. The bioassay included the four previously described bacterial strains, a control without bacteria, and four different NaCl concentrations (0, 5, 10, and 15%) with 10 replications. The experimental design followed a completely randomized design with 5 × 4 factorial arrangements, where the first factor corresponded to rhizobacteria inoculation and the second factor to NaCl concentration.

Evaluated Parameters

The parameters assessed in each treatment for relevant comparisons were as follows. Germination Percentage (G). Determined by counting the number of germinated seeds at the end of the evaluation period using the following equation: G = (Number of germinated seeds/Total number of seeds) × 100. Plumule Length (PL). Measured from the junction of the radicle and hypocotyl to the base of the cotyledon. Radicle Length (RL). Measured from the base of the hypocotyl to the radicle apex. Measurements were taken using a digital caliper (Generic® DMC0144, Mexico), and the results were expressed in cm. Biomass. Fresh weight and dry weight were recorded, and Fresh weight was measured by placing the samples on a watch glass and weighing them using an analytical balance. To determine dry weight, samples were placed in kraft paper bags and then dried in an oven (Novatech S.A. de C.V.; Ohaus® 547A, Jalisco, Mexico) at 72 °C for 24 h.

Chlorophyll Extraction and Measurement

Chlorophyll quantification was performed on the leaves of plants from each treatment, following the protocol of Zhang and Huang (2013). Total chlorophyll was extracted from 0.1 g of fresh leaves, which were submerged in Eppendorf tubes containing N,N-9 dimethylformamide (DMF) for 24 h at 4 °C in darkness. The concentrations of chlorophyll A and chlorophyll B were determined by

spectrophotometry, measuring absorbance at 664 nm and 647 nm, respectively. The content of chlorophyll A, chlorophyll B, and total chlorophyll (A+B) was calculated by substituting the absorbance values into the following equations:

$$Chlorophyll\ A = 12.7 \times A664 - 2.79 \times A647$$

$$Chlorophyll\ B = 20.7 \times A647 - 4.62 \times A664$$

$$Chlorophyll\ A + B = 17.90 \times A647 + 8.08 \times A664$$

Proline Extraction and Measurement

Proline extraction was performed following the methodology of Bates *et al*. (1973). The samples were collected from 30-day-old plants. For each treatment, 10 leaf samples were used, and the experiment was conducted in triplicate. The aerial plant parts (100 mg) were weighed using an analytical balance and placed into an Eppendorf tube containing a 140 mM sulfosalicylic acid solution. The plant material was then macerated with a pestle, and the resulting solution was filtered using a 0.20 µm filter. The liquid extract was mixed with a 140 mM acid ninhydrin solution and glacial acetic acid in a 1:1:1 ratio. The tubes were heated at 100 °C for 1 h and subsequently cooled on ice. Toluene was then added in a 1:1 ratio, and the mixture was vigorously vortexed to facilitate phase separation. The organic fraction was extracted and transferred to a quartz cell for absorbance measurement of the ninhydrin-proline complex at 520 nm using spectrophotometry. A proline calibration curve was prepared using commercial proline concentrations of 10, 20, 40, 50, 75, and 100 µg.

Phytochemical Compounds

For phytochemical extraction, 2 g of leaves were mixed with 10 mL of 80% ethanol and kept under constant agitation at 120 RPM for 24 h. The extracts were then centrifuged at 11 000 RPM for 10 minutes, and the supernatant was collected for further analyses. Total antioxidant capacity was measured using the in vitro 2,2-diphenyl-1-picrylhydrazyl-hydrate (DPPH+) method. A DPPH+ solution (Sigma-Aldrich, St. Louis, MO, USA) was prepared in ethanol at a concentration of 0.025 mg mL^{-1}. Then, 50 µL of ethanolic extract was mixed with 1950 µL of the DPPH+ solution. After 30 minutes, the samples were quantified using a UV-Vis spectrophotometer (Thermo Scientific™, Genesys 20) at 517 nm. The results were expressed in Mequiv TROLOX/100 g^{-1} fresh weight.

Statistical Analysis

The data were analyzed using analysis of variance (ANOVA) and Tukey's multiple comparison test ($p \leq 0.05$) with SAS v9.4. The normality of percentage data (germination percentage) was verified using the Kolmogorov-Smirnov test, and percentage data were transformed using the arcsine square root transformation before performing ANOVA. The experiment was conducted in the Microbial Ecology Laboratory at the Faculty of Biological Sciences, Juárez University of the State of Durango.

RESULTS

Halotolerance Test

Four rhizobacterial strains exhibited growth in LB medium supplemented with 0, 5, 10, and 15% NaCl; however, none of them grew at 20% NaCl after 48 h (Table 1). For this reason, this concentration was not used in subsequent experiments due to the absence of bacterial growth. This threshold suggests an adaptive limitation to extreme salinity levels.

Table 1. Halotolerance of the strains at different concentrations of NaCl. "+" symbols indicate bacterial growth.

Rizobacteria	NaCl				
	0 %	5 %	10 %	15 %	20 %
Sinorhizobium meliloti	+	+	+	+	
Acinetobacter radioresistens	+	+	+	+	
Pseudomonas paralactis	+	+	+	+	
Bacillus cereus	+	+	+	+	

Morphological Parameters of the Seedlings

The strains *Pseudomonas paralactis* and *Acinetobacter radiorresistens* exhibited the highest germination rates (81.20 and 79.39%, respectively) under salt stress (0-15% NaCl), outperforming the other strains and the uninoculated control. Overall, rhizobacteria promoted greater seedling development compared to the control treatment (Table 2). The interaction between PGPR and NaCl was significant for germination, plumule and radicle length, as well as biomass production.

Table 2. Effect of PGPR inoculation, NaCl concentration, and their interaction (PGPR × NaCl) on plumule length, radicle length, and fresh and dry weight.

Factor	Germination (%)	Plumule length (cm)	Radicle length (cm)	Fresh weight (mg)	Dry weight (mg)
		Strains			
Control	56.02 e	6.42 c	4.68 c	204.8 e	6.9 e
Sinorhizobium meliloti	76.22 d	8.14 b	7.70 b	266.7 a	15.1 c
Acinetobacter radioresistens	81.20 a	8.95 a	9.02 a	256.5 c	16.7 a
Pseudomonas paralactis	79.39 b	8.49 ab	7.72 b	250.2 d	15.5 b
Bacillus cereus	76.73 c	8.02 b	7.15 b	265.5 b	13.9 d
		NaCl			
NaCl 0%	80.91 a	7.49 c	6.84 b	285.9 a	16.1 a
NaCl 5%	80.51 b	8.81 a	7.34 b	257.5 b	18.0 b
NaCl 10%	69.79 c	8.38 b	7.02 b	248.8 c	12.3 c
NaCl 15%	64.45 d	7.34 c	7.82 a	202.8 d	7.9 d
		Strain x NaCl			
	*	*	**	*	*

Different letters in the same column indicate significant differences according to Tukey's HSD test ($P \leq 0.05$). ns = not significant, * = significant at $P \leq 0.05$, ** = significant at $P \leq 0.01$

The interaction between PGPR and NaCl was significant for plumule length (Figure 1). At 5% NaCl, the rhizobacteria *Acinetobacter radioresistens* and *Pseudomonas paralactis* improved plumule length by 25% compared to the control. Similarly, at 10 and 15% NaCl concentrations, increases of 22 and 32%, respectively, were observed relative to the control. These rhizobacteria exhibited the greatest plumule length across all analyzed NaCl concentrations.

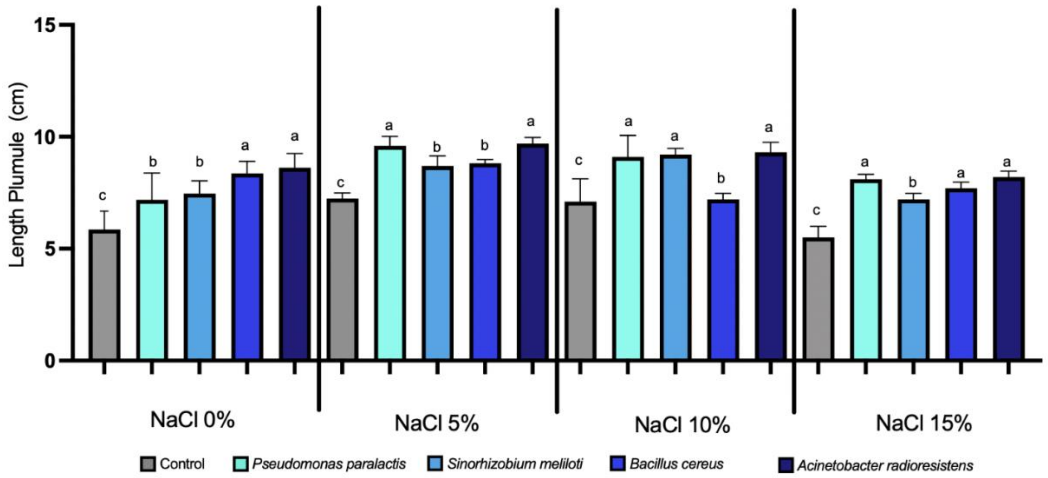

Figure 1. Effect of the interactions between PGPR inoculation and NaCl concentration on the plumule length. *Columns with different letters are statistically different (Tukey, $p < 0.05$).

The interaction between PGPR and NaCl was significant for radicle length (Figure 2). The strain *Acinetobacter radioresistens* showed a 46 and 48% increase in radicle length at 5 and 10% NaCl, respectively. At 15% NaCl, *Pseudomonas paralactis* outperformed the control by 25%. Notably, PGPR inoculation, regardless of NaCl concentration, resulted in an overall increase in radicle length compared to the control, suggesting a positive effect of rhizobacteria in enhancing salt stress tolerance.

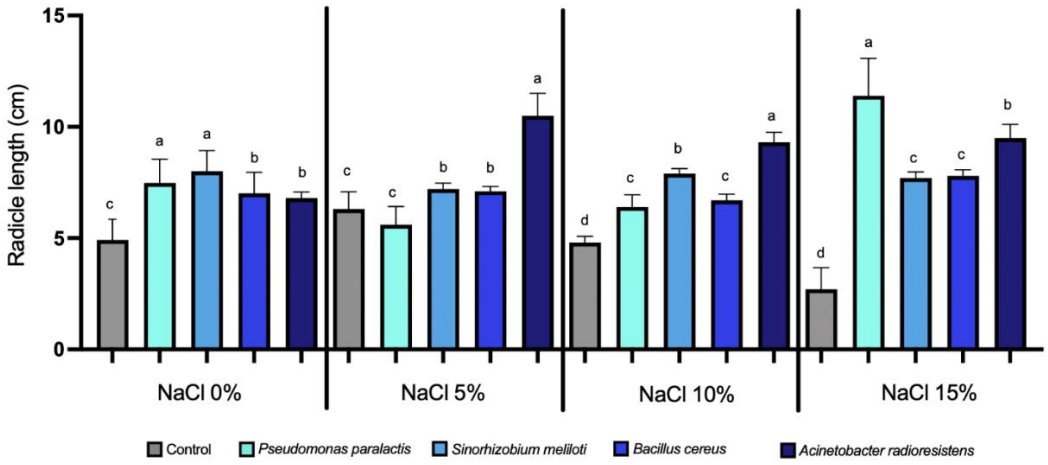

Figure 2. Effect of the interactions between PGPR inoculation and NaCl concentration on the radicle length. *Columns with different letters are statistically different (Tukey, $p < 0.05$).

The interaction between PGPR and NaCl showed that *Bacillus cereus* increased fresh weight at all evaluated salinity levels, with increases of 14, 26, and 55%, respectively, compared to the control (Figure 3a). For dry weight, *Acinetobacter radioresistens* demonstrated the highest increase at 0 and 15% NaCl, with increments of 67 and 51%, respectively, relative to the control (Figure 3b). *Pseudomonas paralactis* improved dry weight by 59% under 5% NaCl, while *Sinorhizobium meliloti* exhibited the greatest increase at 10% NaCl, with a 54% improvement over the control.

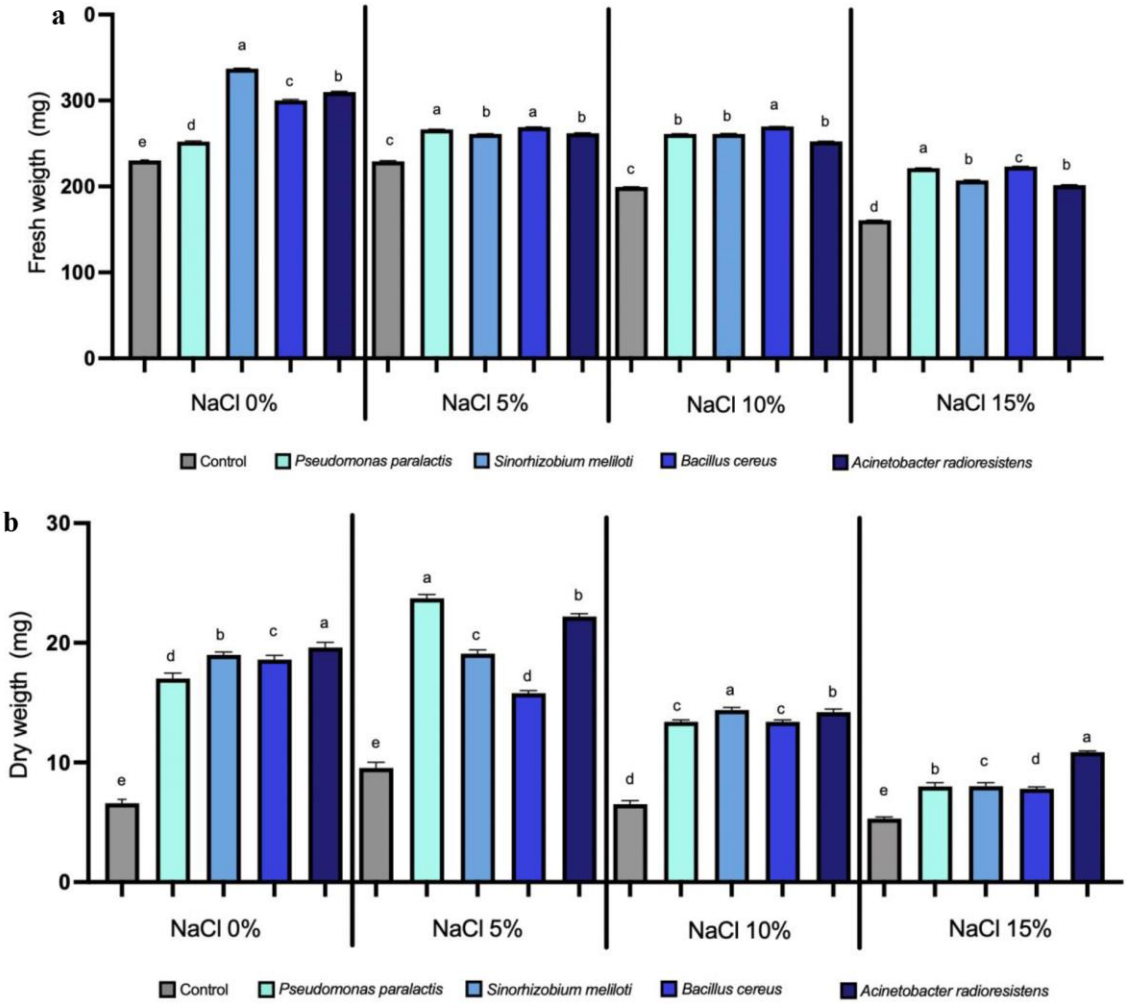

Figure 3. Effect of the interactions between PGPR inoculation and NaCl concentration a) fresh weight and b) dry weight. *Columns with different letters are statistically different (Tukey, $p < 0.05$).

Phytochemical Compounds

Total chlorophyll content increased by 10-25% with rhizobacteria inoculation compared to the control (Table 3), highlighting their ability to maintain photosynthetic function under salt stress conditions. The proline content increased by 15-30% above the control, indicating an adaptive response to osmotic stress induced by salinity. Regarding antioxidants, rhizobacteria inoculation increased their content by 10-20% compared to the control treatment, reflecting a higher level of protection against oxidative damage.

Table 3. Effect of PGPR inoculation, NaCl concentration, and their interaction (PGPR × NaCl) on total chlorophyll, proline, and antioxidant content.

Factor	Total chlorophyll (µg mg $^{-1}$FW)	Proline (µmol g $^{-1}$FW)	Antioxidant (Mequiv TROLOX/ 100 g^{-1}FW)
		Strains	
Control	58.4 d	56.25 e	96.51 d
Sinorhizobium meliloti	59.2 c	60.37 a	103.6 a
Acinetobacter radioresistens	60.9 b	71.97 c	98.73 c
Pseudomonas paralactis	85.1 a	64.27 d	99.67 b
Bacillus cereus	56.1 e	80.76 b	103.7 a
		NaCl	
NaCl 0%	671 b	89.9 a	94.70 a
NaCl 5%	59.9 c	70.3 b	98.60 b
NaCl 10%	75.8 a	59.8 c	107.6 c
NaCl 15%	53.0 d	46.7 d	100.8 d
		Strain x NaCl	
	**	**	*

Different letters in the same column indicate significant differences according to Tukey's HSD test (P ≤ 0.05). ns = not significant, * = significant at P ≤ 0.05, ** = significant at P ≤ 0.01.

The PGPR × NaCl interactions were significant for chlorophyll and proline content (Table 3). At 0% NaCl, *Pseudomonas paralactis* exhibited the highest chlorophyll content, surpassing the control by 65%. As salinity increased (5 and 10% NaCl), *Bacillus cereus* stood out with increases exceeding 5 0% compared to the control. Finally, at 15% NaCl, *Pseudomonas paralactis* showed the highest increase, surpassing the control by 200%. These results indicate that rhizobacteria differentially affect chlorophyll synthesis depending on salinity concentration, with *Bacillus cereus* being more effective under moderate salinity (5 and 10%) and *Pseudomonas paralactis* maintaining outstanding performance in both non-saline and highly saline conditions (Figure 4).

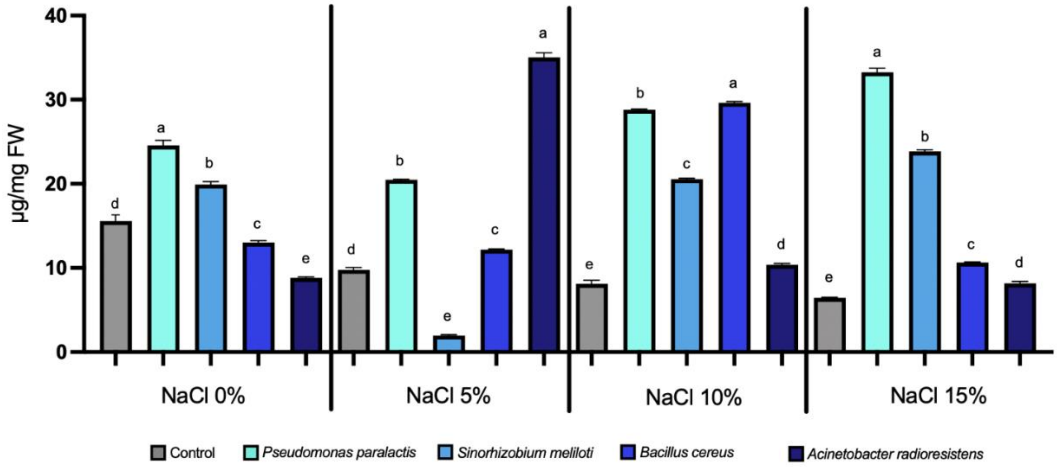

Figure 4. Effect of the interactions between PGPR inoculation and NaCl concentration and total chlorophyll content. *Columns with different letters are statistically different (Tukey, p < 0.05).

The PGPR × NaCl interaction was significant for proline content. The strain *Bacillus cereus* enhanced proline production by 39 at 5% NaCl and by 67 at 10% NaCl compared to the control. Additionally, *Acinetobacter radioresistens* showed an 85% increase at 15% NaCl in comparison to the control (Figure 5).

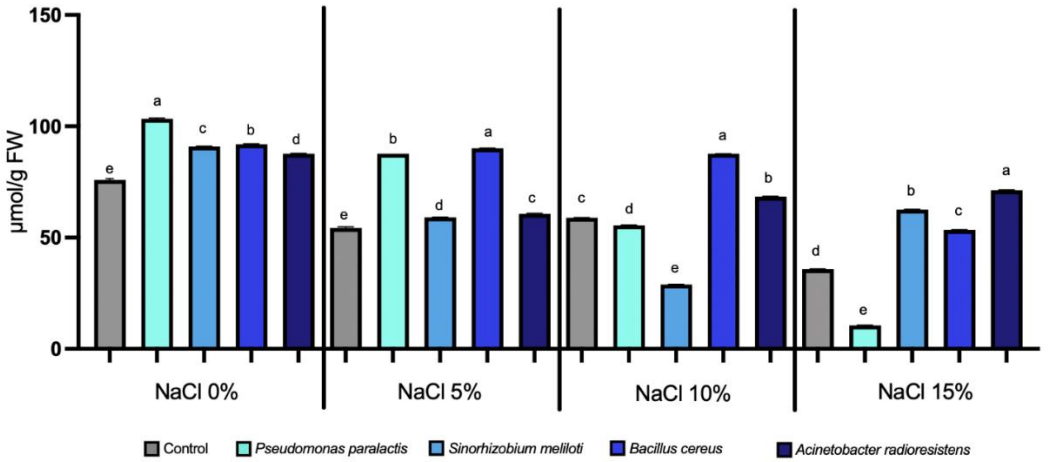

Figure 5. Effect of the interactions between PGPR inoculation and NaCl concentration proline. *Columns with different letters are statistically different (Tukey, $p < 0.05$).

The production of antioxidant compounds in seedlings due to the PGPR × NaCl interaction showed that *Bacillus cereus* exhibited a 15% increase at 5% NaCl compared to non-inoculated seedlings. Finally, *Sinorhizobium meliloti* achieved increases of 14 and 11% at 10 % and 15% NaCl, respectively, as shown in Figure 6.

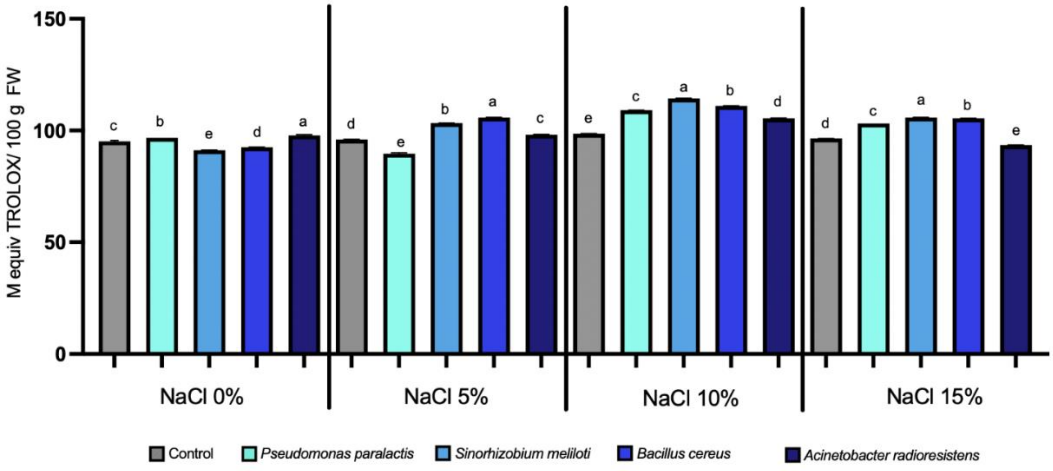

Figure 6. Effect of the interactions between PGPR inoculation and NaCl concentration antioxidant content. *Columns with different letters are statistically different (Tukey, $p < 0.05$).

DISCUSSION

This study demonstrates that inoculation with *Pseudomonas paralactis* and *Acinetobacter radiorresistens* significantly improved the germination rate and seedling growth of cucumber under salt stress conditions. These results are consistent with previous research attributing PGPR the ability to enhance germination by modulating the production of phytohormones such as indoleacetic acid (IAA), gibberellin, and abscisic acid, thereby regulating the activation of stress tolerance-related genes (Qi *et al*. 2021, Bartucca *et al*. 2022). Additionally, some rhizobacteria can reduce osmotic stress, promoting water imbibition in the seed and uniform seedling emergence (Cardarelli *et al.* 2022, Mouradi *et al.* 2023). The salt stress negatively affects the growth and development of cucumber seedlings, with a reduction in morphological parameters observed in the control as NaCl concentration increases. However, inoculation with the rhizobacteria *Pseudomonas paralactis*, *Bacillus cereus*, *Sinorhizobium meliloti*, and *Acinetobacter radioresistens* effectively mitigates the negative effects of salt stress, promoting seedling development and increasing plumule and radicle length (Qi *et al*. 2021, Bartucca *et al*. 2022, Patel *et al*. 2022). This increased root system growth under salinity conditions is essential for water and nutrient absorption (Karnwal *et al*. 2020, Kadam *et al*. 2024). Some previous studies have shown that PGPR can optimize root architecture, contributing to enhanced tolerance by improving water and nutrient uptake (Sabkia *et al*. 2021, Ibrahim 2022). The negative impact of salinity on plant development is a consequence of osmotic or ionic components that induce water stress, toxicity, and nutritional imbalance (Ha-Tran *et al*. 2021). Nevertheless, PGPR inoculation proves effective in the overall improvement of seedlings, suggesting that these microorganisms can partially counteract the negative effects of salinity (Sapre *et al.* 2022). The chlorophyll content significantly increased in seedlings inoculated with PGPR, especially at NaCl concentrations of 5 and 15%, indicating that these bacteria can contribute to the stability of the photosynthetic apparatus under stress conditions (Peng *et al*. 2023). The PGPR have been reported to enhance chlorophyll production by improving nutrient uptake and reducing oxidative damage in plant cells (Sapre *et al*. 2022). The most significant increases in chlorophyll content were observed with *Acinetobacter radioresistens* and *Pseudomonas paralactis*, aligning with previous studies demonstrating the ability of these bacterial genera to enhance photosynthesis under adverse conditions (Bai *et al*. 2023). The proline accumulation is a key mechanism in plant responses to salt stress, acting as an osmoprotectant and stabilizer of cellular structures (El-Moukhtari *et al*. 2020). In this study, proline synthesis increased in PGPR-inoculated seedlings, particularly in the presence of 10 and 15% NaCl. The *Acinetobacter radioresistens* strain promoted an 85% increase in proline content under 15% NaCl, suggesting an important role in plant adaptation to high salinity conditions. Furthermore, the PGPR inoculation stimulated antioxidant mechanisms, increasing the synthesis of enzymes such as peroxidase and superoxide dismutase, which reduce oxidative stress by eliminating reactive oxygen species (Velasco-Jiménez *et al*. 2020, Ha-Tran *et al*. 2021, Gupta *et al*. 2022). In this study, *Bacillus cereus* and *Sinorhizobium meliloti* improved antioxidant capacity under salt stress, in line with previous research highlighting the role of PGPR in mitigating oxidative damage (Shultana *et al*. 2022, Gowtham *et al.* 2022).

CONCLUSIONS

The salt stress inhibits cucumber seedling growth, but inoculation with rhizobacteria can mitigate salinity effects. The inoculated seedlings exhibited higher germination rates, increased plumule and radicle elongation, greater biomass, and an increase in chlorophyll and proline content, suggesting improved photosynthetic stability and osmoprotective response. Additionally, an activation of antioxidant mechanisms was observed, reducing oxidative stress. Each strain demonstrated specific effects: *Pseudomonas paralactis* promoted plumule and radicle growth as well as photosynthesis; *Bacillus cereus* increased biomass and antioxidant capacity; *Sinorhizobium meliloti* enhanced antioxidant capacity and improved elongation; *Acinetobacter radioresistens* promoted proline accumulation and osmotic tolerance. PGPR inoculation is a sustainable strategy to enhance plant growth under saline conditions. However, the use of bacterial consortia is necessary to maximize individual beneficial effects and further improve plant growth under these conditions.

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CONFLICT OF INTEREST

The authors have no competing interests to declare that are relevant to the content of this article.

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