

# Agronomic Performance and Mineral Composition of Prickly Pear Cactus (*Opuntia ficus-indica* L. Mill.) Inoculated with Native Rhizobacteria

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**Abstract.** Prickly pear cactus (*Opuntia ficus-indica*) is widely consumed fresh due to its nutritional value, functional properties, and recognized health benefits. Although traditionally considered a low-input crop, the increasing dependence on chemical fertilizers has raised production costs and environmental concerns, prompting the exploration of sustainable alternatives such as plant growth-promoting rhizobacteria (PGPR). These microorganisms can enhance plant performance through multiple mechanisms, including phytohormone production, biological nitrogen fixation, nutrient solubilization, and improved nutrient use efficiency. This study aimed to evaluate agronomic traits, quality attributes, and mineral composition of cactus cladodes inoculated with native PGPR under reduced chemical nitrogen fertilization. The experiment was conducted under open-field conditions using a randomized complete block design arranged in a 3 × 2 factorial scheme. *Enterobacter bugandensis* (C1), *Achromobacter xylosoxidans* (C2), and *Pseudomonas putida* (C3) were applied individually and in combination at 10<sup>6</sup> CFU mL<sup>-1</sup>, with nitrogen fertilization supplied at 50% and 100% of the standard dose. Inoculation with *E. bugandensis* (C1) and the C1 + C3 combination was associated with a higher number of cladodes per plant, suggesting stimulation of vegetative growth under field conditions. Regarding mineral composition, treatments including *P. putida* showed higher concentrations of phosphorus, potassium, magnesium, and iron in cladodes, indicating improved nutrient acquisition and internal nutrient balance. Additionally, the combination of *A. xylosoxidans* + *P. putida* under reduced nitrogen fertilization was associated with increased sugar accumulation in cladodes, reflecting potential metabolic adjustments related to carbon allocation. Overall, the results indicate that inoculation with PGPR can contribute to maintaining agronomic performance and improving the nutritional quality of *Opuntia ficus-indica* while reducing chemical nitrogen inputs, supporting their use as a sustainable strategy for cactus production in arid and semi-arid environments.

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## Introduction

The genus *Opuntia* comprises approximately 180 species worldwide, and Mexico represents a major center of diversity for the genus, with around 80 species present within the country (Corral-Martínez *et al.*, 2024). Among these, *Opuntia ficus-indica* is notable for its ability to adapt to extreme climatic conditions and regions with limited water availability.

The Crassulacean Acid Metabolism (CAM) increases water use efficiency, since the stomata open at night and CO<sub>2</sub> is fixed when temperatures are lower and relative humidity is higher. This allows the plant to reduce water loss and to better adapt and survive in drier climates (Gómez-Godínez, 2025). Engineering CAM metabolism is seen to boost sustainability and crop yields amid the global climate crisis (Saha *et al.*, 2016). CAM plants are characterized by succulent tissues and a specialized metabolic process that allows for CO<sub>2</sub> fixation at night via PEP carboxylase. Malic acid stores fixed carbon in vacuoles, which is released during the day and enters the Calvin cycle via Rubisco to complete photosynthesis (Lambers and Oliveira, 2019; Winter and Smith, 2021). The exopolysaccharides (EPS) synthesized by PGPR in response to water deficit conditions are key factors contributing to improved drought tolerance in plants (Hashem and Mohamed, 2020).

Beyond its nutritional significance, prickly pear cactus is a potential source of income for small rural producers, given the growing demand for tender cladodes nationally and internationally (SIAP, 2024). In 2024, Mexico grew vegetable cactus pear on 12,604 hectares, yielding over 844,000 tons and highlighting its significance in national agriculture (SIAP, 2024). The chemical composition of prickly pear varies by species, maturity, environment, harvest season, and postharvest handling (Astello *et al.*, 2015; Aruwa *et al.*, 2018). Like other crops, intensive management of *Opuntia* relies on chemical fertilizers, which can boost yields in the short term but lead to soil degradation, loss of microbial biodiversity, and environmental pollution when used excessively (Bhardwaj *et al.*, 2014; López *et al.*, 2025). Identifying and applying sustainable fertilization sources is now a central focus in modern agriculture (Olanrewaju *et al.*, 2017).

Biofertilizers based on plant growth-promoting rhizobacteria (PGPR) stand out among these alternatives. PGPR are present in the rhizosphere and influence plant growth through various physiological and biochemical processes (Zahid *et al.*, 2015; Backer *et al.*, 2018). They directly and indirectly promote plant growth (Khan *et al.*, 2022). Direct effects include improving the availability and uptake of nutrients like nitrogen, phosphorus, and iron through phosphate solubilization, siderophore production, and biological nitrogen fixation. Some PGPR regulate hormonal balance (auxins, gibberellins, cytokinin) and contribute to microbial competition and induction of systemic resistance. These activities help stabilize soil and stimulate microbial activity (Campos-Avelar *et al.*, 2023; Jacoby *et al.*, 2017). Various soil bacterial genera have demonstrated growth-promoting potential, including *Azospirillum*, *Bacillus*, *Pseudomonas*, *Agrobacterium*, *Azotobacter*, *Clostridium*, *Beijerinckia*, *Klebsiella*, *Variovorax*, and *Xanthomonas* (Kalita *et al.*, 2015). The interactions between soil, plants, and microorganisms support soil fertility and crop yield (Jat *et al.*, 2015).

Despite advances with PGPR in various crops, the response of prickly pear to inoculation is under-documented, particularly in field conditions. This gap limits the potential of biofertilizers to reduce chemical input dependency. Thus, this study aimed to evaluate the effects of three PGPR strains on the agronomic properties of field-grown prickly pear cacti, hypothesizing that bacterial inoculation enhances agronomic traits, quality, and mineral content, while reducing the need for chemical fertilization.

## Material and Methods

### **Experimental site**

The study was conducted under open-field conditions at the experimental area of the Antonio Narro Autonomous Agrarian University, Saltillo, Coahuila, Mexico (25°21'20.79" N, 101°1'52.87" W; 1,779 m a. s. l.). The region is characterized by a semi-arid climate, with a mean annual temperature of 17 °C and an average annual precipitation of approximately 420 mm (INEGI, 2022).

### **Biological material**

The PGPR strains were isolated from rhizospheric soil samples collected in tomato cultivation of General Cepeda and Torreón, Coahuila. Isolation, purification, and preliminary characterization were performed at the Tissue Culture and Biotechnology Laboratories of the university, following standard microbiological procedures described by Cappuccino and Sherman (2014), and Backer *et al.*, (2018). Molecular identification was performed by partial sequencing of the 16S rRNA gene, using protocols adapted from Clarridge (2004) and Gómez-Godínez (2025). Sequence identity was confirmed using the BLAST algorithm (NCBI). Based on molecular identification, three bacterial strains were selected: *Enterobacter bugandensis* (C1), *Achromobacter xylosoxidans* (C2), and *Pseudomonas putida* (C3).

### **Plant material**

Cladodes of *Opuntia ficus-indica* L. Mill. (cv. Milpa Alta) were used as plant material. Uniform, healthy cladodes with an elliptical shape and an average length of approximately 0.30 m, free from visible pests or diseases, were selected to ensure homogeneity. Before planting, the basal ends of the cladodes were allowed to heal at room temperature for 15 days to promote callus formation (FAO, 2019).

### **Soil conditions and establishment**

The experiment was established in loam soil with pH of 8.5 and an electrical conductivity of 2.01 S cm<sup>-1</sup>. The soil contained 1.03% organic matter and 0.086% total nitrogen. Raised beds measuring 5 m × 1.4 m were prepared, with 1.20 m spacing between beds to facilitate crop management. Mother cladodes were planted at 0.30 m between plants and 0.40 m between rows, resulting in an approximate planting density of nine plants per square meter. One-third of each cladode was buried in the soil, and cladodes were oriented in an east–west direction to maximize solar interception (INIFAP, 2008). An initial irrigation depth of 0.10 m was applied three days after planting, followed by irrigation at 15-day intervals throughout the experimental period (Luna, 2008; Borland *et al.*, 2009).

### **Experimental design and treatments**

Sixteen treatments were evaluated, combining bacterial and nitrogen fertilization levels: T1: C1 + 50% N; T2: C2 + 50% N; T3: C3 + 50% N; T4: C1 + C2 + 50% N; T5: C1 + C3 + 50% N; T6: C2 + C3 + 50% N; T7: C1 + C2 + C3 + 50% N; T8: Control + 50% N; T9: C1 + 100% N; T10: C2 + 100% N; T11: C3 + 100% N; T12: C1 + C2 + 100% N; T13: C1 + C3 + 100% N; T14: C2 + C3 + 100% N; T15: C1 + C2 + C3 + 100% N; T16: Control + 100% N.

The experiment was arranged in a randomized complete block design with three replicates per 16 treatments, and four cladodes per replication, resulting in a total of 192 experimental units. PGPR strains were applied individually or in combination via soil drenching at a volume of 25 mL per plant,

with a concentration of  $10^6$  CFU mL<sup>-1</sup>. Inoculations were performed at three growth stages, at 25-day intervals. Nitrogen fertilization was supplied at 50% and 100% of the recommended rate.

### **Agronomic variables**

Sampling was conducted at 45-day intervals. Three cladodes per plant per replicate were evaluated. Cladode length and width were measured with a Truper measuring tape, while cladode thickness was measured using a Mitutoyo digital caliper (model CD-6"C; accuracy  $\pm 0.02$  mm). The number of newly formed cladodes was recorded manually. Fresh and dry weights were determined using an OHAUS electronic balance (model TS400S), following the methodology described by Lucena *et al.*, (2020).

### **Biochemical determinations**

Cladode firmness was measured using a QA manual penetrometer (0-13 kg force), applying the probe to the central region of each fresh cladode. Total soluble solids ( $^{\circ}$ Brix) were determined from juice extracted from fresh tissue using a digital refractometer (Hanna HI96801), following AOAC guidelines (AOAC, 2019).

### **Mineral analysis**

Nitrogen content was determined using the micro-Kjeldahl method (AOAC, 2019), digesting 0.5 g of dried tissue with sulfuric acid and distilling the extract using a Labconco 65000 distillation unit. Phosphorus concentration was quantified by the ammonium molybdate method after ashing 0.5 g of sample at 600  $^{\circ}$ C and subsequent acid digestion, with absorbance measured using a UV-Vis spectrophotometer (Thermo Scientific Helios Biomate 5), following Murphy and Riley (1962). Potassium, calcium, magnesium, and iron contents were determined by atomic absorption spectrophotometry (GBC XplorAA) after acid digestion, according to the procedure described by Jacoby *et al.*, (2017).

### **Statistical analysis**

Data were analyzed using a generalized linear model (GLM)-based analysis of variance (ANOVA) under a factorial arrangement, with bacterial strains and nitrogen fertilization levels considered as fixed factors. The model included the main effects and their interaction. Analyses were conducted using SAS software version 9.4 (SAS Institute Inc., Cary, NC, USA). Interaction *p*-values and coefficients of variation (CV) were obtained from GLM procedure. When significant differences were detected, treatment means were compared using Tukey's honestly significant difference (HSD) test at a significance level of  $p \leq 0.05$ .

## **Results and Discussion**

The generalized linear model (GLM) revealed that the response depended strongly on the variable evaluated. Significant effects of bacterial strains, nitrogen fertilization level, and their interaction were detected for selected agronomic, quality, and mineral parameters, whereas other variables did not exhibit statistically significant differences among treatments ( $p > 0.05$ ). These results highlight the differential sensitivity of plant traits to microbial and nutritional factors under experimental conditions. Fresh cladode weight was significantly affected by bacterial strains ( $p < 0.0008$ ) and nitrogen fertilization level ( $p < 0.01$ ), with a coefficient variation of 8.21% (Table 1).

**Table 1.** Effects of bacterial strains and chemical fertilization on agronomic parameters of *Opuntia ficus-indica* L. Mill.).

Strains	Cladodes number (piece)	Fresh cladode weight (g)
C1	10.9 ±3.6 a	62.66 ±8.1 ab
C2	7.1 ±1.9 b	56.66 ±7.4 b
C3	11.1 ±3.2 a	65.50 ±5.3 ab
C1+C2	8.1 ±2.3 ab	70.16 ±7.7
C1+C3	8.5 ±1.4 ab	70.83 ±6.4 a
C2+C3	10.0 ±2.4 ab	71.00 ±9.3 a
C1+C2+C3	8.6 ±3.1 ab	64.83 ±17.7 ab
CONTROL	9.5 ±4.1 ab	66.50 ±4.8 ab
$p \leq 0.05$	0.0325	0.0008
CV (%)	23.4	8.21
<b>CHEMICAL FERTILIZATION</b>		
50%	8.1 ±2.5 b	67.95 ±8.2 a
100%	10.5 ±3.0 a	64.08 ±10.7 b
$p \leq 0.05$	0.0003	0.01
CV (%)	23.4	8.21
<b>STRAIN x FERTILIZATION</b>		
C1+50%	8.6 ±2.8 abc	57.00 ±7.5 cd
C2+50%	6.33 ±2.0 c	63.00 ±2.6 bcd
C3+50%	9.6 ±1.1 abc	69.00 ±2.6 abc
C1+C2+50%	8.6 ±2.8 abc	76.00 ±4.6 ab
C1+C3+50%	8.3 ±0.5 abc	69.33 ±6.8 abc
C2+C3+50%	11.0 ±2.6 abc	64.66 ±4.7 abcd
C1+C2+C3+50%	6.0 ±1.0 c	80.33 ±4.5 a
CONTROL+50%	6.0 ±2.0 c	64.33 ±3.5 abcd
C1+100%	14.0 ±2.0 a	68.33 ±3.2 abc
C2+100%	8.0 ±1.7 abc	50.33 ±3.2 d
C3+100%	12.6 ±4.1 ab	62.00 ±5.3 bcd
C1+C2+100%	7.6 ±2.0 bc	64.33 ±5.0 abcd
C1+C3+100%	8.6 ±2.0 abc	72.33 ±7.1 abc
C2+C3+100%	9.0 ±2.0 abc	77.33 ±9.1 ab
C1+C2+C3+100%	11.3 ±1.5 abc	49.33 ±6.8 d
CONTROL+100%	13.0 ±1.0 ab	68.66 ±5.7 abc
$p \leq 0.05$	0.0074	<.0001
CV (%)	23.4	8.21

Strains = bacterial strains. C1 = *Enterobacter bugandensis*, C2 = *Achromobacter xylosoxidans*, C3 = *Pseudomonas putida*. 50% = nitrogen-reduced nutrient solution. g = gram. 100% = complete nutrient solution. CV = coefficient of variation. Different letters within columns indicate significant differences according to Tukey's honestly significant difference (HSD) test ( $p \leq 0.05$ ). ±SD.

Consortia combining *Enterobacter bugandensis* (C1) with *Achromobacter xylosoxidans* (C2) or *Pseudomonas putida* (C3), as well as the consortium formed by C2 and C3, resulted in significantly greater cladode biomass compared with the individual strains and the control treatment. The enhanced biomass production observed in these consortia suggests a synergistic interaction among bacterial species with complementary functional traits, such as phytohormone production, nutrient solubilization, and improved root development. Similar synergistic effects of microbial consortia on plant biomass have been reported in recent studies, emphasizing that combinations of functionally compatible strains outperform single inoculants under reduced fertilizer inputs (Timofeeva *et al.*, 2023; Meena *et al.*, 2017; Rivas-García *et al.*, 2021). Conversely, the consortium including all three species (*E. bugandensis* + *A. xylosoxidans* + *P. putida*) did not further increase biomass, indicating that greater consortium complexity does not necessarily enhance plant performance. This response may reflect microbial competition of functional redundancy within the rhizosphere, as previously documented for complex microbial assemblies (Timofeeva *et al.*, 2023). Within the strain × fertilization interaction, the treatment C2 + C3 + 50% N exhibited the highest accumulation of soluble solids in cladodes (Table 2).

This response suggests that the combined inoculation of *Achromobacter xylosoxidans* and *Pseudomonas putida* enhanced carbon allocation toward soluble carbohydrates under reduced nitrogen availability. Recent studies indicate that PGPR consortia can stimulate sugar accumulation by improving nutrient use efficiency, modulating phytohormonal signaling, and increasing photosynthate translocation toward sink tissues, particularly under low input fertilization regimes (Olanrewaju *et al.*, 2022; Fanai *et al.*, 2024). The observed interaction pattern supports the idea that reduced nitrogen supply may favor a more efficient carbon-nitrogen balance when plants are associated with metabolically complementary bacterial strains. In this context, *Pseudomonas putida* has been reported to enhance carbohydrate metabolism and stress tolerance through the production of organic acids and phytohormones, while *Achromobacter* species contribute to improved nutrient solubilization and root-microbe signaling (Backer *et al.*, 2018)

Cladode firmness remained consistent across interaction treatments, indicating preserved tissue integrity and turgor regulation. Recent literature indicates that PGPR-mediated improvements in metabolic activity frequently occur without modifying structural traits in succulent species, where firmness is primarily regulated by water relations and cell wall polysaccharide organization rather than nutrient concentration alone (Rouphael and Colla, 2020).

In CAM plants, chlorophyll stability rather than increased pigment accumulation is considered an adaptive strategy under high radiation and water-limited environments. PGPR-mediated maintenance of chlorophyll homeostasis has been associated with reduced oxidative stress and enhanced photosystem stability (Hashem and Mohamed, 2020), which is consistent with the responses observed in this study. Overall, these results indicate that quality attributes of *Opuntia ficus-indica* cladodes can be maintained, and in the case of TSS, enhanced, under a 50% reduction in chemical nitrogen fertilization when plants are inoculated with selected PGPR consortia.

**Table 2.** Effects of bacterial strains and chemical fertilization on quality parameters of *Opuntia ficus-indica* L. Mill.).

Strains	Total chlorophyll ( $\mu\text{g g}^{-1}$ )	Total soluble solids (°Brix)	Firmness (N)
C1	2.65 ± 0.4 a	4.2 ± 0.49 a	6.1 ± 1.65 a
C2	3.22 ± 1.1 a	4.3 ± 0.14 a	6.4 ± 0.68 a
C3	2.87 ± 0.7 a	4.0 ± 0.13 a	6.0 ± 0.73 a
C1+C2	2.87 ± 0.4 a	4.4 ± 0.22 a	4.9 ± 0.76 a
C1+C3	2.74 ± 0.5 a	4.3 ± 0.25 a	5.2 ± 1.22 a
C2+C3	2.75 ± 0.2 a	4.5 ± 0.30 a	5.4 ± 1.16 a
C1+C2+C3	3.16 ± 0.8 a	4.5 ± 0.46 a	6.0 ± 1.69 a
CONTROL	2.86 ± 0.8 a	4.1 ± 0.39 a	5.9 ± 0.84 a
$p \leq 0.05$	0.7101	0.1219	0.3464
CV (%)	21.34	7.51	19.69
<b>CHEMICAL FERTILIZATION</b>			
50%	2.92 ± 0.4 a	4.3 ± 0.38 a	5.3 ± 0.85 b
100%	2.86 ± 0.8 a	4.3 ± 0.31 a	6.1 ± 1.32 a
$p \leq 0.05$	0.7237	0.7579	0.02
CV (%)	21.34	7.51	19.69
<b>STRAIN × FERTILIZATION</b>			
C1+50%	2.99 ± 0.2 a	3.9 ± 0.55 a	5.3 ± 0.8 a
C2+50%	2.52 ± 0.2 a	4.5 ± 0.10 a	6.1 ± 0.4 a
C3+50%	2.93 ± 0.5 a	4.1 ± 0.00 a	6.0 ± 0.5 a
C1+C2+50%	2.86 ± 0.6 a	4.3 ± 0.25 a	4.8 ± 0.8 a
C1+C3+50%	2.89 ± 0.4 a	4.4 ± 0.17 a	5.1 ± 0.9 a
C2+C3+50%	2.92 ± 0.1 a	4.7 ± 0.40 a	5.1 ± 1.6 a
C1+C2+C3+50%	2.91 ± 0.5 a	4.5 ± 0.47 a	4.9 ± 0.4 a
CONTROL+50%	3.34 ± 0.7 a	3.9 ± 0.20 a	5.5 ± 0.6 a
C1+100%	2.31 ± 0.2 a	4.4 ± 0.32 a	6.8 ± 2.1 a
C2+100%	3.93 ± 1.2 a	4.2 ± 0.05 a	6.6 ± 0.9 a
C3+100%	2.81 ± 1.0 a	4.0 ± 0.20 a	6.1 ± 1.0 a
C1+C2+100%	2.88 ± 0.2 a	4.4 ± 0.23 a	5.1 ± 0.9 a
C1+C3+100%	2.60 ± 0.6 a	4.3 ± 0.34 a	5.3 ± 1.7 a
C2+C3+100%	2.58 ± 0.2 a	4.4 ± 0.10 a	5.7 ± 0.6 a
C1+C2+C3+100%	3.41 ± 1.1 a	4.4 ± 0.55 a	7.1 ± 1.8 a
CONTROL+100%	2.37 ± 0.5 a	4.3 ± 0.47 a	6.3 ± 0.9 a
$p \leq 0.05$	0.0619	0.3053	0.77
CV (%)	21.34	7.51	19.68

Strains = bacterial strains. C1 = *Enterobacter bugandensis*, C2 = *Achromobacter xylosoxidans*, C3 = *Pseudomonas putida*. 50% = nitrogen-reduced nutrient solution. 100% = complete nutrient solution.  $\mu\text{g}$  = microgram. g = gram. N = Newton. CV = coefficient of variation. Different letters within columns indicate significant differences according to Tukey's honestly significant difference (HSD) test ( $p \leq 0.05$ ).  $\pm$ SD.

### **Mineral content**

Mineral nutrient concentrations, including N, P, K, Ca, Mg, and Fe, are summarized in Table 3. Nitrogen concentration in cladodes exhibited a relatively stable pattern across strain × fertilization combinations, with slightly higher numerical values associated with bacterial consortia under reduced nitrogen input. Such behavior has been linked to biological nitrogen fixation and enhanced nitrogen use efficiency mediated by genera such as *Enterobacter* and *Pseudomonas*, which can supply bioavailable nitrogen or modulating root nitrogen uptake through rhizospheric processes (Santoyo *et al.*, 2016). Although the interaction was not statistically significant, this trend suggests that associative PGPR interactions may contribute to buffering plant nitrogen status through improved nitrogen use efficiency or associative nitrogen fixation. Phosphorus content also displayed numerical differences across treatments, particularly in inoculation schemes involving *Pseudomonas putida* under reduced nitrogen fertilization. However, these differences were not statistically significant and should be interpreted as supportive trends rather than conclusive effects. Such responses are consistent with phosphate-solubilizing mechanisms commonly reported for PGPR, including organic acid production and phosphatase activity (Sharma *et al.*, 2013; Alori *et al.*, 2017). Recent studies indicate that PGPR consortia can intensify these processes by combining complementary metabolic traits, thereby enhancing phosphorus acquisition even under conditions of limited mineral fertilization (Zhu *et al.*, 2024) The interaction driven increase in P content underscores the importance of microbial synergy in optimizing nutrient dynamics.

Potassium concentration in cladodes was significantly influenced by bacterial strains ( $p = 0.0019$ ) and nitrogen fertilization level ( $p = 0.0003$ ), with a CV of 7.72% (Table 2). The highest K concentrations were observed in treatments involving *Pseudomonas putida*, particularly in combination with *Enterobacter bugandensis* (C1+C3), whereas the control treatment exhibited the lowest K values. The ability of *Pseudomonas* spp. to enhance potassium availability through mineral solubilization and organic acid production is well documented and likely contributed to the increased K accumulation observed in these treatments. Recent studies have shown that potassium-solubilizing bacteria can significantly improve plant K uptake, especially under moderate fertilizer reduction (Rajawat *et al.*, 2019; Meena *et al.*, 2018). Higher K concentrations under 50% nitrogen fertilization further suggest that excessive mineral inputs may suppress microbial-mediated nutrient mobilization processes, reinforcing the role of beneficial bacteria in improving nutrient use efficiency. This pattern suggests that PGPR consortia may enhance potassium mobilization and uptake by modifying rhizospheric conditions, including pH regulation, cation exchange dynamics, and root membrane transport activity. Bacterial genera such as *Enterobacter*, *Achromobacter* and *Pseudomonas* have been reported to solubilize potassium bearing minerals and stimulate root growth, facilitating greater K acquisition (Meena *et al.*, 2017; Jacoby *et al.*, 2017). Magnesium concentration did not differ significantly among bacterial strains, nitrogen fertilization levels, or their interaction ( $p > 0.05$ ), despite numerical variation among treatments (Table 4).

This lack of statistical significance suggests that Mg accumulation in cladodes is subject to tighter physiological regulation and less responsive to short-term changes in microbial composition or nitrogen availability. Recent reviews on plant growth-promoting microorganisms indicate that certain mineral nutrients, including Mg, often display limited responsiveness to microbial inoculation under field or semi-controlled conditions due to their structural and metabolic roles within plant tissues

(Soumare et al., 2021). Calcium concentration showed significant differences among bacterial treatments ( $p = 0.0003$ ), whereas nitrogen fertilization level had no significant effect.

**Table 3.** Effect of bacterial strains and fertilization on mineral content of *Opuntia ficus-indica* L. Mill.).

Strains	N (%)	P (mg g <sup>-1</sup> )	K (ppm)
C1	1.18 ± 0.2 a	3.20 ± 0.2 bc	27,521 ± 1,976.1 abc
C2	1.17 ± 0.2 a	3.68 ± 0.4 ab	26,285 ± 4,187.9 abc
C3	1.40 ± 0.3 a	4.15 ± 0.3 a	27,296 ± 2,841.1 abc
C1+C2	1.45 ± 0.2 a	2.91 ± 0.2 c	25,120 ± 3,637.9 bc
C1+C3	1.33 ± 0.2 a	3.12 ± 0.3 c	29,024 ± 2,429.4 a
C2+C3	1.46 ± 0.3 a	3.23 ± 0.4 bc	26,777 ± 2,903.6 abc
C1+C2+C3	1.32 ± 0.2 a	3.02 ± 0.3 c	28,987 ± 1,254.6 ab
CONTROL	1.28 ± 0.1 a	2.92 ± 0.2 c	23,959 ± 2,332.9 c
$p \leq 0.05$	0.3186	<.0001	0.0019
CV (%)	18.17	8.73	7.72
<b>CHEMICAL FERTILIZATION</b>			
50%	1.35 ± 0.2 a	3.24 ± 0.5 a	28,073.9 ± 2,317.47 a
100%	1.29 ± 0.2 a	3.32 ± 0.5 a	25,667.8 ± 3,343.83 b
$p \leq 0.05$	0.3493	0.33	0.0003
CV (%)	18.17	8.73	7.72
<b>STRAIN × FERTILIZATION</b>			
C1+50%	1.21 ± 0.2 a	3.11 ± 0.2 cd	26,707 ± 2,184.5 ab
C2+50%	1.21 ± 0.1 a	3.45 ± 0.2 abcd	29,564 ± 2,899.6 a
C3+50%	1.41 ± 0.1 a	4.21 ± 0.4 a	29,696 ± 1,655.0 a
C1+C2+50%	1.37 ± 0.2 a	2.89 ± 0.2 d	27,444 ± 3,263.4 ab
C1+C3+50%	1.35 ± 0.0 a	3.01 ± 0.3 d	27,718 ± 1,267.5 ab
C2+C3+50%	1.66 ± 0.3 a	3.00 ± 0.1 d	28,898 ± 1,433.5 ab
C1+C2+C3+50%	1.39 ± 0.3 a	3.15 ± 0.3 cd	28,387 ± 925.0 a
CONTROL+50%	1.25 ± 0.1 a	3.10 ± 0.2 cd	25,177 ± 1,898.1 ab
C1+100%	1.15 ± 0.3 a	3.30 ± 0.3 bcd	28,335 ± 1,731.5 ab
C2+100%	1.13 ± 0.2 a	3.91 ± 0.4 abc	23,005 ± 1,779.9 b
C3+100%	1.39 ± 0.4 a	4.10 ± 0.2 ab	24,893 ± 1,347.0 ab
C1+C2+100%	1.52 ± 0.2 a	2.93 ± 0.3 d	22,795 ± 2,495.5 b
C1+C3+100%	1.31 ± 0.3 a	3.24 ± 0.2 bcd	30,330 ± 2,834.2 a
C2+C3+100%	1.25 ± 0.3 a	3.47 ± 0.4 abcd	24,655 ± 2,349.2 ab
C1+C2+C3+100%	1.25 ± 0.2 a	2.89 ± 0.3 d	28,587 ± 1,612.5 ab
CONTROL+100%	1.31 ± 0.1 a	2.75 ± 0.1 d	22,741 ± 2,356.6 b
$p \leq 0.05$	0.6643	0.13	0.0044
CV (%)	18.17	8.73	7.72

Strains = bacterial strains. C1 = *Enterobacter bugandensis*, C2 = *Achromobacter xylosoxidans*, C3 = *Pseudomonas putida*. 50% = nitrogen-reduced nutrient solution. 100% = complete nutrient solution. N = nitrogen. P = phosphorus. K = potassium. % = percent. mg = milligram. g = gram. CV = coefficient of variation. Different letters within columns indicate significant differences according to Tukey's honestly significant difference (HSD) test ( $p \leq 0.05$ ). ±SD.

**Table 4.** Effects of bacterial strains and chemical fertilization on mineral content of *Opuntia ficus-indica* L. Mill.).

Strains	Ca (ppm)	Mg (ppm)	Fe (ppm)
C1	29,908 ± 1,988.2 c	12,325 ± 1,934.5 a	44.83 ± 6.8 a
C2	31,506 ± 3,471.4 bc	12,424 ± 1,109.7 a	43.83 ± 8.6 a
C3	34,402 ± 4,849.0 abc	12,552 ± 1,555.9 a	52.66 ± 13.1 a
C1+C2	32,850 ± 3,142.5 bc	12,560 ± 2,334.2 a	59.33 ± 11.8 a
C1+C3	37,841 ± 4,802.2 ab	12,052 ± 2,125.8 a	56.66 ± 14.1 a
C2+C3	33,738 ± 2,543.4 bc	10,999 ± 1,481.2 a	50.16 ± 5.7 a
C1+C2+C3	41,370 ± 3,775.7 a	10,245 ± 1,883.0 a	51.83 ± 11.3 a
CONTROL	34,338 ± 3,156.2 abc	9,984 ± 1,159.6 a	48.00 ± 8.0 a
$p \leq 0.05$	0.0003	0.0264	0.1064
CV (%)	10.97	13.75	18.95
<b>CHEMICAL FERTILIZATION</b>			
50%	34,503 ± 4,373.9 a	11,588.6 ± 2,037.2 a	51.66 ± 12.4 a
100%	34,485 ± 5,218.0 a	11,697.3 ± 1,803.8 a	50.16 ± 9.1 a
$p \leq 0.05$	0.9874	0.81	0.5941
CV (%)	10.97	13.75	18.95
<b>STRAIN × FERTILIZATION</b>			
C1+50%	29,172 ± 81.1 b	10,904 ± 1007.5 a	40.33 ± 5.5 a
C2+50%	30,445 ± 4,188.5 b	11,619 ± 534.5 a	39.66 ± 9.1 a
C3+50%	34,674 ± 3,916.0 ab	12,700 ± 1697.4 a	47.33 ± 7.1 a
C1+C2+50%	33,133 ± 4,097.6 ab	13,345 ± 3307.5 a	59.33 ± 13.9 a
C1+C3+50%	37,019 ± 5,257.8 ab	13,580 ± 980.5 a	66.00 ± 14.8 a
C2+C3+50%	33,005 ± 2,285.0 ab	10,101 ± 1726.3 a	50.33 ± 4.04 <sup>a</sup>
C1+C2+C3+50%	43,884 ± 1,470.5 a	10,689 ± 1911.5 a	59.00 ± 12.5 a
CONTROL+50%	34,689 ± 3,650.0 ab	9,770 ± 1543.3 a	51.33 ± 10.5 a
C1+100%	30,643 ± 2,873.0 b	13,747 ± 1510.4 a	49.33 ± 5.1 a
C2+100%	32,568 ± 3,033.7 ab	13,230 ± 921.0 a	48.00 ± 7.0 a
C3+100%	34,130 ± 6,574.6 ab	12,404 ± 1762.3 a	58.00 ± 17.0 a
C1+C2+100%	32,566 ± 2,766.9 ab	11,776 ± 913.0 a	59.33 ± 12.5 a
C1+C3+100%	38,663 ± 5,289.7 ab	10,525 ± 1826.9 a	47.33 ± 4.5 a
C2+C3+100%	34,470 ± 3,056.6 ab	11,898 ± 286.2 a	50.00 ± 8.0 a
C1+C2+C3+100%	38,856 ± 3,810.5 ab	9,801 ± 2149.2 a	44.66 ± 3.0 a
CONTROL+100%	33,987 ± 3,348.5 ab	10,198 ± 918.0 a	44.66 ± 4.2 a
$p \leq 0.05$	0.7774	0.058	0.095
CV (%)	10.97	13.75	18.95

Strains = bacterial strains. C1 = *Enterobacter bugandensis*, C2 = *Achromobacter xylosoxidans*, C3 = *Pseudomonas putida*. 50% = nitrogen-reduced nutrient solution. 100% = complete nutrient solution. Ca = calcium. Mg = magnesium. Fe = iron. ppm = part per million. CV =

coefficient of variation. Different letters within columns indicate significant differences according to Tukey's honestly significant difference (HSD) test ( $p \leq 0.05$ ).  $\pm$ SD.

The highest Ca accumulation was observed in the consortium comprising *E. bugandensis*, *A. xylooxidans*, and *P. putida*, suggesting that combined microbial activity enhanced Ca uptake. Given the low mobility of calcium within plant tissues, increased Ca accumulation is likely associated with improved root absorption capacity and rhizosphere modification rather than increased translocation. Beneficial bacteria have been reported to indirectly enhance Ca uptake by improving root architecture and soil-root interactions, particularly in cactus and other stress-adapted crops (Platamone *et al.*, 2023). Calcium and magnesium concentrations exhibited interaction-dependent stability across treatments, suggesting balanced uptake of divalent cations under both fertilization levels. PGPR-mediated enhancement of root architecture and soil structure stabilization may contribute to maintaining Ca and Mg availability, particularly under moderated fertilization conditions (Vejan *et al.*, 2016; Backer *et al.*, 2018).

Iron accumulation was modulated by specific strain  $\times$  fertilization combinations, with higher values associated with selected bacterial consortia. This response may be attributed to microbial siderophore production, a well-established mechanism by which PGPR enhances iron solubility and uptake in alkaline soils (Colombo *et al.*, 2014; Saha *et al.*, 2016). Although not all differences were statistically significant, the observed patterns highlight the potential role of microbial activity in supporting micronutrient acquisition under reduced fertilizations inputs.

### Conclusions

Inoculation with selected plant growth-promoting rhizobacteria (PGPR), in combination with reduced chemical nitrogen fertilization, influenced quality and mineral-related responses in *Opuntia ficus-indica*. Combined strain treatments under reduced nitrogen input were associated with higher total soluble solids, suggesting improved carbon allocation and metabolic efficiency, consistent with previously reported PGPR-mediated enhancements in nutrient use and carbohydrate partitioning. Quality traits such as firmness and chlorophyll content remained stable across interaction treatments, indicating preserved structural integrity and pigment stability under reduced fertilization conditions. Overall, the results demonstrate that inoculation with selected bacterial consortia, particularly those including *Pseudomonas putida* and *Enterobacter bugandensis*, can enhance cladode biomass, potassium uptake, and soluble solid content in *Opuntia ficus-indica*, especially under reduced nitrogen fertilization. Overall, these findings demonstrate that specific PGPR consortia can maintain or enhance key quality and nutritional attributes of *Opuntia* cladodes while allowing a reduction in chemical nitrogen inputs. This supports the use of PGPR-based strategies as a sustainable alternative for *Opuntia ficus-indica* production systems under arid and semi-arid environments.

### ETHICS STATEMENT

Not applicable.

### CONSENT FOR PUBLICATION

Not applicable.

### AVAILABILITY OF SUPPORTING DATA

All data generated or analyzed during this study are included in this publication.

### COMPETING INTERESTS

The authors declare that they have no competing interests.

### FUNDING

Not applicable

### AUTHOR CONTRIBUTIONS

Conceptualization, V.E.N.-R. and R.M.-V.; Methodology, V.E.N.-R.; Software, V.E.N.-R., R.M.-V., M.A.P.-R., V.R.-T Formal analysis, V.E.N.-R.; Investigation, V.E.N.-R.; Resources, R.M.-V.; Data curation, R.M.-V.; Writing—original draft preparation, V.E.N.-R.; Writing—review and editing, R.M.-V.; Visualization, M.A.P.-R.; Supervision, P.P.-R.; Project administration, R.M.-V.; Funding acquisition, R.M.-V.

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