

Article

Plant Growth Promoting Rhizobacteria Favor Vegetative Development and Optimize Nutrient Uptake in Lisianthus

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Abstract

Lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] is among the 10 most produced and marketed cut flowers in the world. However, its slow growth represents a challenge for its production. This study evaluated the efficiency of rhizobacterial strains in vegetative growth and nutrient acquisition in lisianthus plants. Freshly germinated seeds of lisianthus cv. Mariachi Blue Double were used. Seven rhizobacterial strains and two controls (sterile distilled water and nutrient broth) were evaluated in a completely randomized design. Replication varied among treatments and variables: shoot growth traits were assessed on 10–12 plants per treatment, root biomass on a destructive subsample of six plants per treatment and shoot nutrient contents on four composite samples per treatment. Measurements taken 149 days after sowing showed that plants inoculated with the strains *Acinetobacter vivianii* C48, *Achromobacter xylosoxidans* C56, and *Arthrobacter pokkali* JLB4 had greater height, leaf area, leaf number, and fresh and dry biomass, both aerial and in the root. These strains also enhanced N and P uptake in shoot tissues. In contrast, the *Bacillus pumilus* strain R44 significantly decreased height and leaf number. The results suggest that strains C48, C56 and JLB4 can stimulate nutrition, accelerate plant growth, and shorten the vegetative phase in lisianthus.

Keywords: Gentianaceae; *Eustoma grandiflorum*; rhizobacteria; growth parameters; mineral nutrition



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1. Introduction

Global trade in ornamental plants and floriculture products involves more than 100 countries [1,2]. Within this sector, cut flowers represent the most important group due to their high economic value, increasing production and commercial demand [1]. The main players in this industry are the Netherlands, Colombia, Ecuador, Kenya and Ethiopia, which control about 85% of the industry [3–5]. Cut flowers play a prominent role in the economy, society and culture, with global impacts ranging from the emotional to the commercial spectra [6]. In 2023, cut flower production was valued at USD 105 billion according to estimates based on exported amounts [7]. Supported by air transport and cold chain logistics, the international cut flower trade allows for an efficient and dynamic balancing of supply and demand [5,8]. However, the large growth of this industry has generated

adverse impacts, primarily of environmental nature [9], significantly affecting developing countries [10].

Currently, the floriculture industry faces numerous criticisms due to its intensive use of inputs in its efforts to achieve high-quality and yield standards [11,12]. This sector uses large amounts of mainly nitrogen-based fertilizers, which acidify and alter the beneficial microbiota of soils over time [13–15]. In addition, intensive floriculture relies on large volumes of pesticides [1,16], with applications reaching more than 22.4 kg ha^{-1} , a figure 33 times higher than that used in wheat cultivation and nine times higher than in maize [2,17]. Furthermore, continuous monoculture, a common production system in ornamental crops, has contributed to the deterioration of soil physicochemical properties, increased incidence of pests and diseases, allelopathic effects, and imbalances in soil microbial communities with reduced diversity [18].

In particular, lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] is an elegant cut flower, boasting a variety of striking colors and excellent post-harvest life [19]. Royal FloraHolland [20] lists it among the 10 most marketed and produced cut flowers. Lisianthus is a slow-growing plant [21,22], which represents one of the main challenges in its production. It can require 50 to 140 days from seed germination to obtaining seedlings ready for transplanting, and an additional 154 to 168 days to reach the flowering stage [23,24]. Furthermore, during the early stages of development, there are problems such as poor development of the root system, leaf chlorosis as a result of the conditions of the growing medium or pH, and incidence of root diseases caused mainly by species of destructive soil-borne pathogenic fungi (e.g., *Rhizoctonia* and *Pythium*) or oomycete (e.g., *Fusarium*) [23,25]. Therefore, the incorporation of biotechnological tools that allow improving and accelerating the growth of lisianthus plants is needed, especially in the initial stages, thereby facilitating early and high-quality flower production.

In ornamental crops such as lisianthus, nutrient acquisition is closely associated with plant growth and traits that determine commercial quality. Adequate mineral nutrition plays a fundamental role in plant growth and development and directly influences morphological attributes such as plant height, shape and overall visual quality of ornamental plants [26–28]. Plant growth-promoting rhizobacteria (PGPR) are known to enhance plant performance partly through improving plant nutritional status via mechanisms such as nutrient solubilization, mobilization and stimulation of root development [29–31]. Therefore, evaluating macro- and micronutrient accumulation can provide valuable insight into how PGPR influence plant development and physiological performance in ornamental crops.

Plant growth-promoting rhizobacteria (PGPR) represent a promising alternative to optimize growth and improve crop quality [12,32]. In addition, they have gained special relevance as a sustainable option that can contribute to reducing dependence on chemical fertilizers [33,34]. PGPR are beneficial, soil-borne bacteria that colonize the rhizosphere—the soil region surrounding plant roots [35,36]—and the root surface, enhancing soil and plant health [37]. Consequently, these bacteria can live as ectophytes or endophytes and are organized in colonies [38,39]. Through the activation of different physiological, biochemical and molecular mechanisms, PGPR enhance plant growth and development, facilitate the acquisition of essential elements, and improve plant resistance or tolerance to various types of biotic and abiotic stresses [37,40]. Several genera, such as *Acinetobacter*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Chromobacterium*, *Enterobacter*, *Flavobacterium*, *Rhizobium*, *Rhodococcus*, *Pseudomonas*, *Serratia*, *Streptomyces* and *Micrococcus*, have been shown to prompt beneficial traits, thus promoting plant growth [32,41].

There are significant advances in research on the use of PGPR in agricultural crops. For example, in corn (*Zea mays* L.), inoculation with *Pseudomonas koreensis* A20 and *Pseudomonas mandelii* A36 favors root development by increasing the length and surface area of roots. In

addition, these strains raise the levels of total nitrogen, phosphorus and potassium in the soil through processes such as nitrogen fixation, phosphate solubilization, siderophore synthesis and indole-3-acetic acid (IAA) production [42]. In tomato (*Solanum lycopersicum* L.) plants grown under salt stress conditions, colonization of *Pseudomonas aeruginosa* HG28-5 improves growth parameters (height, diameter, shoot and root fresh and dry biomass) and stimulates abscisic acid (ABA) biosynthesis and signaling [43]. Inoculation of bell pepper (*Capsicum annuum* L.) with *Bacillus pumilus* R44 increases the photosynthetic efficiency of photosystem II (Fv/Fo) [44]. Other species of the genera *Mucilaginibacter* and *Pseudomonas* increase the production of secondary metabolites [mainly tetrahydrocannabinol (THC) and cannabidiol (CBD)] in *Cannabis sativa* L. [45]. Likewise, an increase in the production of plant hormones (ABA and IAA) has been reported after inoculation with *Bacillus methylothrophicus*, which favored the growth of tobacco (*Nicotiana tabacum* L.) under drought stress conditions [46]. However, knowledge about its use in cut flowers, particularly lisianthus, remains limited. Based on previous reports of plant growth-promoting activity in different crops, seven PGPR strains from the Soil Microbiology Laboratory collection of the Colegio de Postgraduados Montecillo Campus were selected for evaluation in lisianthus. These strains included isolates belonging to the genera *Bacillus*, *Acinetobacter*, *Achromobacter*, *Arthrobacter* and *Pseudomonas*, which had been previously characterized for indole production and phosphate solubilization [44,47,48]. Therefore, this study aimed to evaluate the efficiency of individual rhizobacterial strains in vegetative growth and nutrient acquisition in lisianthus plants and to identify the most promising strains for subsequent evaluation in combined formulations and intensive crop production systems.

2. Materials and Methods

2.1. Plant Material and Experimental Conditions

The experiment was carried out in a greenhouse at the Colegio de Posgraduados Montecillo Campus, Texcoco, State of Mexico, located at geographic coordinates 19.52° N and 98.88° W, at an elevation of 2250 m. Freshly germinated seeds of lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double from the Sakata company (Zapopan, Mexico) were sown on December 16, 2023, in 200-cavity black plastic trays, with one seed per cavity. A mixture of peat and perlite (70/30, v/v) was used as substrate. Chemical properties of this substrate mixture are presented in Table 1. Irrigation was supplied manually according to water demand and by misting using a hand-held pressure sprayer.

Table 1. Chemical properties of the substrate used for germination of lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double.

Parameter	Value
pH	6.35
Electrical conductivity (dS m ⁻¹)	0.881
Organic matter (%)	8.629
Bulk density (g cm ⁻³)	0.267
NO ₃ ⁻ (mg kg ⁻¹)	12.25
NH ₄ ⁺ (mg kg ⁻¹)	19.25
P (mg kg ⁻¹)	11.24
Ca (cmol kg ⁻¹)	30.65
K (cmol kg ⁻¹)	1.088
Mg (cmol kg ⁻¹)	6.368
Na (cmol kg ⁻¹)	0.692
Cu (mg kg ⁻¹)	4.462
Fe (mg kg ⁻¹)	21.277
Mn (mg kg ⁻¹)	52.2755
Zn (mg kg ⁻¹)	11.273

Fertilization was carried out with 10% Steiner nutrient solution [49], which contained the following concentrations (g L^{-1}): $0.1063 \text{ Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$, $0.0493 \text{ MgSO}_4 \cdot 7\text{H}_2\text{O}$, $0.0136 \text{ KH}_2\text{PO}_4$, 0.0303 KNO_3 and $0.0261 \text{ K}_2\text{SO}_4$ (J.T. Baker; Phillipsburg, NJ, USA). In addition, the nutrient solution was provided with 0.0133 g L^{-1} of a commercial mixture of micronutrients as follows (mg L^{-1}): 0.998 Fe , 0.466 Mn , 0.094 Zn , 0.038 Cu , 0.086 B and 0.034 Mo . The pH of the nutrient solution was adjusted to 5.5 with $\text{H}_2\text{SO}_4 \text{ 1 N}$ (J.T. Baker; Phillipsburg, NJ, USA). Application frequency was once per week at a dose of 1 mL per plant. At 106 days after sowing (das), the application frequency was three times per week at a dose of 1.5 mL per plant. At 130 das, the seedlings were transplanted into 0.40 L pots, using the same substrate mix to ensure optimal growth conditions.

2.2. Microbiological Material

Seven strains of plant growth-promoting rhizobacteria (PGPR) from the microbial collection of the Soil Microbiology Laboratory of the Department of Soil Science at the Colegio de Postgraduados Montecillo Campus were used. These strains have already undergone biochemical characterization of indole production and phosphate solubilization, as well as morphological tests and molecular identification. The strains used were *Bacillus pumilus* C22, *Acinetobacter vivianii* C48 isolated from filter cake compost, and *Achromobacter xylosoxidans* C56 from filter cake compost and chicken manure [47]; *Arthrobacter pokkali* JLB4 and *Arthrobacter enclensis* JN24 isolated from the rhizosphere of a tomato crop [48]; and *Pseudomonas tolaasii* P61 and *Bacillus pumilus* R44 from the potato rhizosphere [44]. These strains were selected based on their previously reported plant growth-promoting effects in other crops, including increases in plant height, leaf area, root development and biomass production, as well as improved N, P and K content. Their documented functional traits, together with their diverse ecological origins, justified their evaluation in lisianthus.

2.3. Bacterial Culture Preparation

Each bacterial strain was streaked onto nutrient agar plates and incubated at 28°C for 72 h. A loopful of pure colonies was transferred into 50 mL sterile nutrient broth (8 g L^{-1} ; DB Bioxon™, Bioxon Laboratories; Oaxaca, Mexico) and incubated at 28°C for 72 h on a rotary shaker at 180 rpm.

Bacterial cultures were harvested at the stationary growth phase. Cell concentration was determined using a Neubauer chamber (Marienfeld-Superior, Lauda-Königshofen, Germany) after serial dilution with sterile distilled water and expressed as cells mL^{-1} . Final inoculum concentrations ranged between 6.4×10^7 and 2.4×10^8 cells mL^{-1} , depending on the strain and inoculation event.

No adjustment of inoculum density was performed prior to application, and cultures were used directly at their final growth concentration. The same nutrient broth medium was used for all strains, as commonly reported for the cultivation of heterotrophic PGPR strains evaluated under similar conditions.

2.4. Treatments and Experimental Design

A completely randomized experimental design was used. Nine treatments were evaluated, including the seven rhizobacterial strains, an absolute control with sterile distilled water, and a nutrient broth control. The experimental unit was one seedling per cavity within the tray. Twelve seedlings were initially established for most bacterial strains. However, the final number of plants available for shoot measurements varied slightly among treatments: C48, C56, JLB4, JN24 and R44 included 12 plants; AC and P61 included 11 plants due to the loss or exclusion of one plant; C22 included 10 plants; and the nutrient broth control (NBC) included six plants due to limited plant availability.

Root traits were evaluated on a destructive subsample (six plants per treatment) because complete substrate removal without root damage was not feasible for all plants.

2.5. Application of the Treatments

Two inoculations with PGPR were performed throughout the experiment. The first was conducted at 46 das using 2 mL of bacterial inoculum in nutrient broth, applied to the base of the stem of each seedling. Bacterial suspensions were added at their final growth concentration (ranging between 6.4×10^7 and 2.4×10^8 cells mL⁻¹, as indicated in Section 2.3). The second inoculation was performed at 88 das (42 days after the first inoculation) to ensure effective establishment of the microorganisms, when seedlings were at the stage of formation of the third and fourth true leaves, considered a critical vegetative stage in *lisianthus* preceding transplanting. The same inoculum volume was used in both applications.

2.6. Measurements of Growth Parameters and Nutrient Analysis

Growth and nutrient analysis variables were measured at the end of the experiment (149 das), when plants were at the final stage of the vegetative phase and the beginning of stem elongation. This timing allowed a reliable assessment of the impact of PGPR on plant biometric parameters.

Plant height was determined from the base of the stem to the terminal apex using a graduated ruler. Leaf area per plant was determined with an area meter (LI-CORLI-3000A; Lincoln, NE, USA). The number of leaves was counted manually. Stem diameter was measured with a digital caliper (Truper 14388; Shanghai, China). To determine the weight of fresh matter, the plants were divided into aerial and root parts and weighed on an analytical balance (Adventurer Ohaus Pro AV213C; Parsippany, NJ, USA). The plant tissue was subsequently dried in a forced-air oven (Riossa HCF-125D; Guadalajara, Mexico) at 70 °C for 72 h, and finally, the dry biomass weight was determined.

Nutrient concentrations in the aerial part were determined using the method described by Alcántar-González and Sandoval-Villa [50]. A mixture of acids (H₂SO₄: HClO₄; J.T. Baker, Phillipsburg, NJ, USA; 2:1; v:v) plus 30% H₂O₂ was added to 0.25 g of dry tissue for wet digestion. Once the digestion of the organic matter was completed, the samples were volumetrically calibrated to 25 mL with deionized water and then filtered. The resulting extracts were used to measure nutrient concentrations using an inductively coupled plasma optical emission spectroscopy system (Agilent, ICP-OES, 725-ES; Santa Barbara, CA, USA). Total N concentration was determined using the semi-micro Kjeldahl method. Nutrient content was estimated from the concentration results and the dry biomass weights of the aerial part.

For nutrient analysis, four composite samples of shoot tissue were obtained per treatment from the available plants. Each composite sample consisted of pooled aerial biomass to obtain sufficient material for chemical determination. These composite samples were considered the experimental units for nutrient variables.

2.7. Statistical Analysis

Data were analyzed using linear mixed models (PROC MIXED, SAS version 9.4; SAS Institute Inc.; Cary, NC, USA [51]) to accommodate unequal replication among treatments and variables. Treatment was included as a fixed effect.

Least square means were estimated and compared with the absolute control and the nutrient broth control using Dunnett-adjusted comparisons ($p \leq 0.05$).

Principal component analysis (PCA) was performed using PROC PRINCOMP in the previously mentioned software to explore multivariate relationships among treatments based on plant growth parameters and shoot nutrient contents. Prior to analysis, variables

were standardized to unit variance. PCA was conducted separately for growth variables and nutrient variables to identify patterns of association among bacterial treatments and plant responses.

3. Results

3.1. Growth Parameters

The greatest plant height was recorded with strains C56, JLB4, C48 and C22, which increased plant height by approximately 69.9, 69.5, 61 and 49.8%, respectively, compared to the absolute control according to Dunnett's test (Figure 1). In contrast, plants inoculated with strain R44 showed the lowest height, with reductions of 9% and 35% compared to the absolute and nutrient broth controls, respectively (Figure 1).

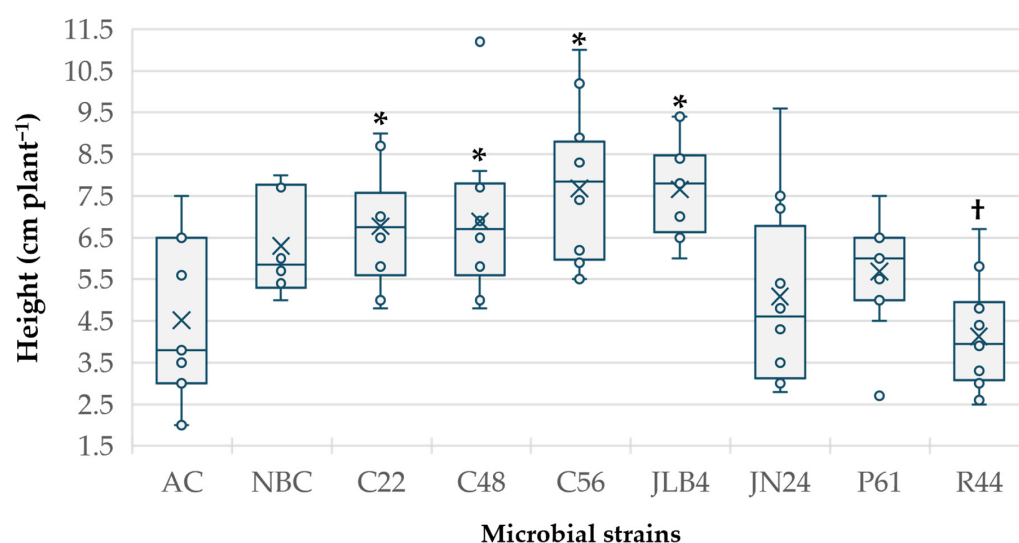


Figure 1. Effect of plant growth-promoting rhizobacteria on height of lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double plants 149 days after sowing. Box-and-whisker plots represent individual plant values ($n = 6$ – 12 per treatment), shown as circles. Boxes indicate the interquartile range (25–75%), the horizontal line within the box represents the median, the “x” indicates the mean, and whiskers indicate the minimum and maximum values. Symbols denote significant differences according to Dunnett's test ($p \leq 0.05$): * vs absolute control (AC) and † vs nutrient broth control (NBC). AC: Absolute control, NBC: Nutrient broth control, C22: *Bacillus pumilus*, C48: *Acinetobacter vivianii*, C56: *Achromobacter xylosoxidans*, JLB4: *Arthrobacter pokkali*, JN24: *Arthrobacter enclensis*, P61: *Pseudomonas tolaasii* and R44: *Bacillus pumilus*.

These differences are visually supported, as plants inoculated with C56, JLB4 and C48 exhibit greater overall vigor and shoot elongation compared to the controls, whereas R44-inoculated plants appear smaller and less developed (Figure 2).



Figure 2. Height of lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double plants 149 days after sowing, inoculated with different strains of plant growth-promoting rhizobacteria.

AC: Absolute control, NBC: Nutrient broth control, JLB4: *Arthrobacter pokkalii*, R44: *Bacillus pumilus*, JN24: *Arthrobacter enclensis*, C56: *Achromobacter xylosoxidans*, C22: *Bacillus pumilus*, P61: *Pseudomonas tolaasii* and C48: *Acinetobacter vivianii*.

The largest stem diameter was recorded in plants inoculated with strain C56, which increased stem thickness by approximately 24.4% relative to the absolute control, and 19.8% relative to the nutrient broth control (Figure 3). According to Dunnett's test, C56 was the only strain that significantly differed from both controls, whereas the remaining treatments showed intermediate responses.

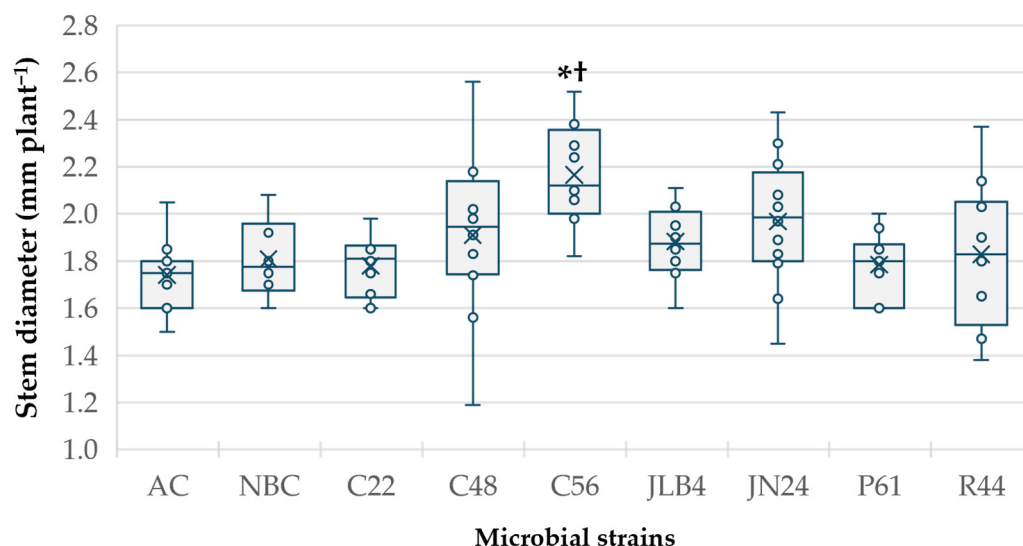


Figure 3. Effect of plant growth-promoting rhizobacteria on the stem diameter of lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double plants 149 days after sowing. Box-and-whisker plots represent individual plant values ($n = 6$ – 12 per treatment), shown as circles. Boxes indicate the interquartile range (25–75%), the horizontal line within the box represents the median, the “x” indicates the mean, and whiskers indicate the minimum and maximum values. Symbols denote significant differences according to Dunnett's test ($p \leq 0.05$): * vs. absolute control (AC) and † vs. nutrient broth control (NBC). AC: Absolute control, NBC: Nutrient broth control, C22: *Bacillus pumilus*, C48: *Acinetobacter vivianii*, C56: *Achromobacter xylosoxidans*, JLB4: *Arthrobacter pokkalii*, JN24: *Arthrobacter enclensis*, P61: *Pseudomonas tolaasii* and R44: *Bacillus pumilus*.

Seedlings inoculated with strains C56 and JLB4 resulted in plants that had greater leaf area than the absolute control (Figure 4), with increases of 49.2% and 42.1%, respectively. Compared to the nutrient broth control, these strains showed increases of approximately 24.6% (C56) and 18.6% (JLB4); however, no statistically significant differences were detected relative to this control according to Dunnett's test.

Inoculation with strains C48, C56 and JLB4 resulted in an average increase in the number of leaves per plant compared to the absolute control (Figure 5), with increases of 38.3, 33.6 and 32.1%, respectively, according to Dunnett's test. In contrast, strain R44 reduced the number of leaves by 23.7% compared to the nutrient broth control.

The highest aerial fresh biomass was recorded in plants inoculated with strains C56 and JLB4, which increased shoot fresh weight by 53 and 48.9%, respectively, compared to the absolute control (Figure 6A). Regarding root fresh biomass, only strain C56 showed a significant increase, with an 81.9% rise relative to the absolute control (Figure 6B).

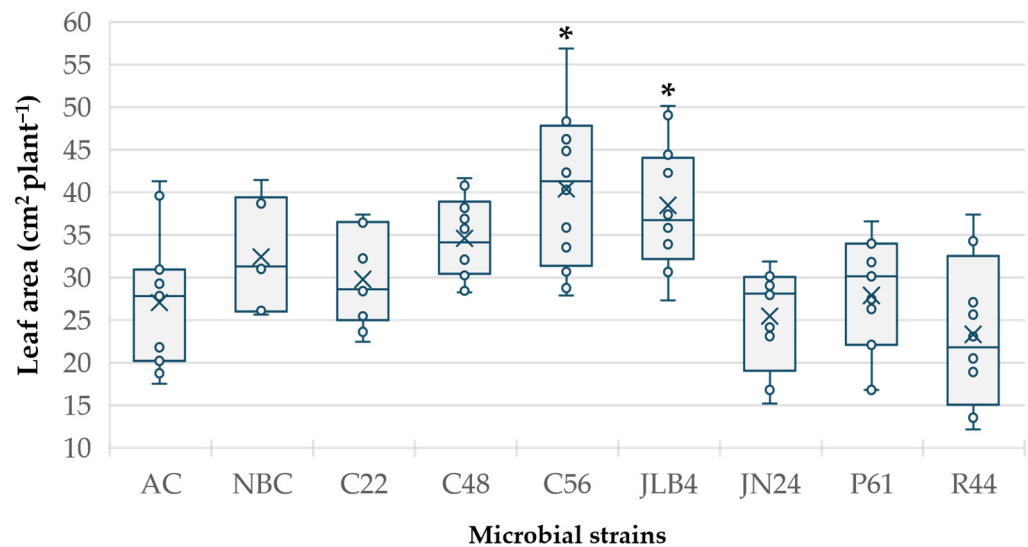


Figure 4. Effect of plant growth-promoting rhizobacteria on the leaf area of lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double plants 149 days after sowing. Box-and-whisker plots represent individual plant values ($n = 6\text{--}12$ per treatment), shown as circles. Boxes indicate the interquartile range (25–75%), the horizontal line within the box represents the median, the “x” indicates the mean, and whiskers indicate the minimum and maximum values. Symbols denote significant differences according to Dunnett’s test ($p \leq 0.05$): * vs. absolute control (AC). AC: Absolute control, NBC: Nutrient broth control, C22: *Bacillus pumilus*, C48: *Acinetobacter vivianii*, C56: *Achromobacter xylosoxidans*, JLB4: *Arthrobacter pokkali*, JN24: *Arthrobacter enclensis*, P61: *Pseudomonas tolaasii* and R44: *Bacillus pumilus*.

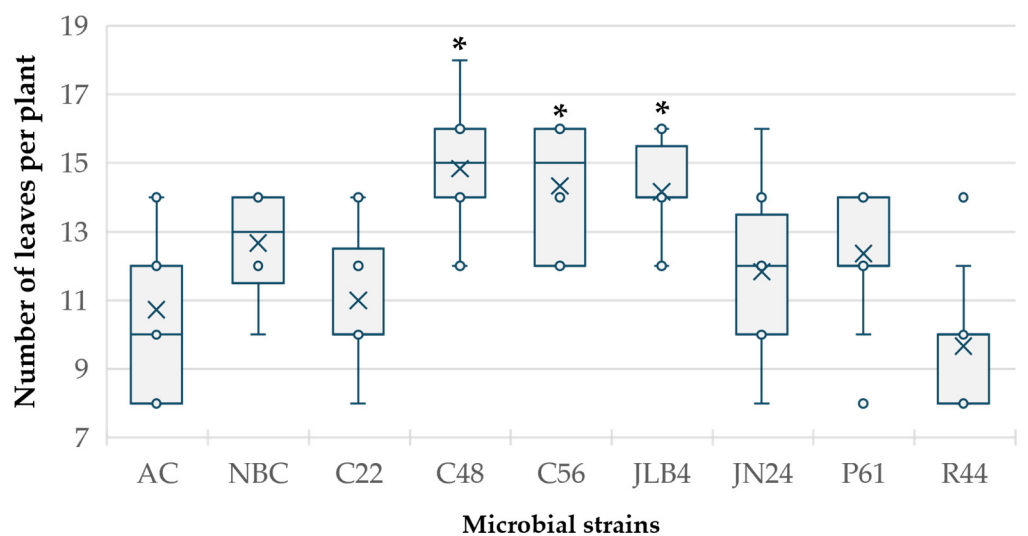


Figure 5. Effect of plant growth-promoting rhizobacteria on the number of leaves per plant in lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double 149 days after sowing. Box-and-whisker plots represent individual plant values ($n = 6\text{--}12$ per treatment), shown as circles. Boxes indicate the interquartile range (25–75%), the horizontal line within the box represents the median, the “x” indicates the mean, and whiskers indicate the minimum and maximum values. Symbols denote significant differences according to Dunnett’s test ($p \leq 0.05$): * vs. absolute control (AC). AC: Absolute control, NBC: Nutrient broth control, C22: *Bacillus pumilus*, C48: *Acinetobacter vivianii*, C56: *Achromobacter xylosoxidans*, JLB4: *Arthrobacter pokkali*, JN24: *Arthrobacter enclensis*, P61: *Pseudomonas tolaasii* and R44: *Bacillus pumilus*.

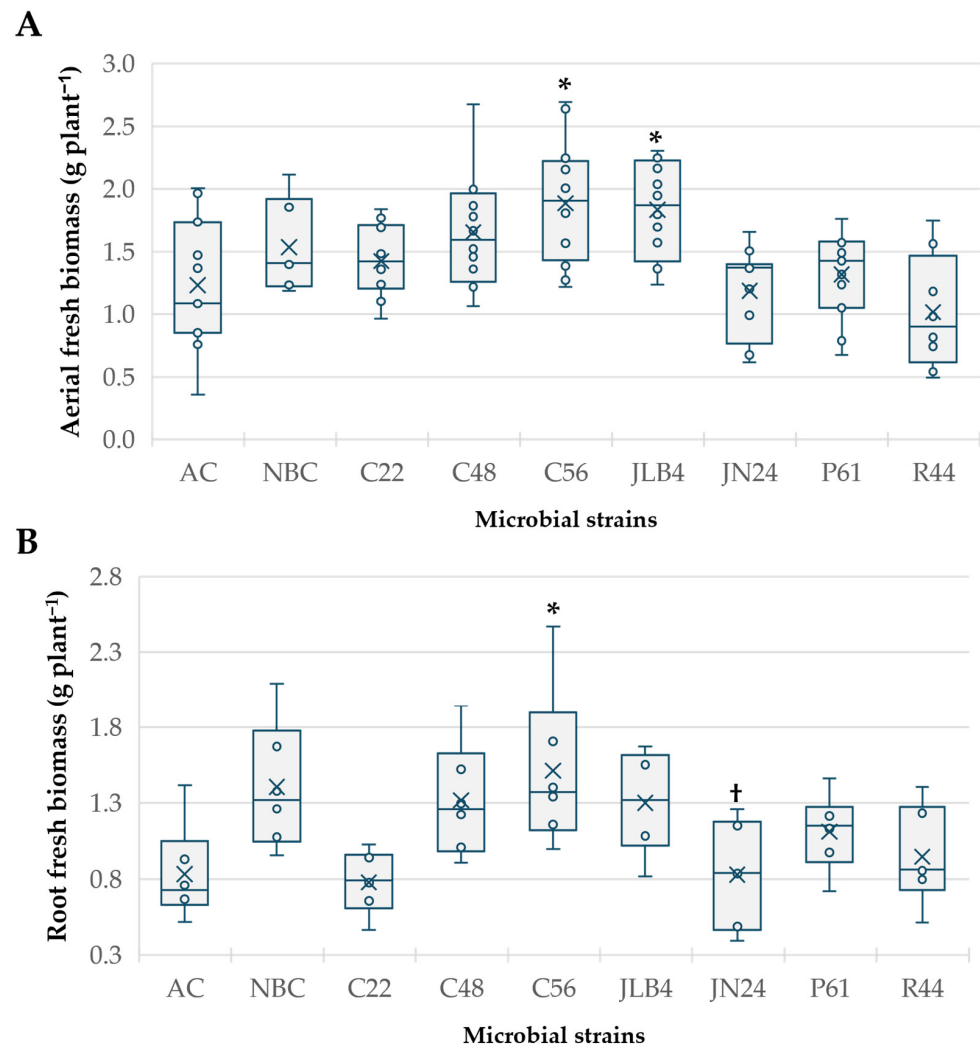


Figure 6. Effect of plant growth-promoting rhizobacteria on fresh biomass of lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double plants 149 days after sowing. **(A)** Aerial fresh biomass and **(B)** root fresh biomass. Box-and-whisker plots represent individual plant values, displayed as circles. For aerial biomass, $n = 6$ – 12 per treatment; for root biomass, $n = 6$ per treatment. Boxes indicate the interquartile range (25–75%), the horizontal line within the box represents the median, the “x” indicates the mean, and whiskers indicate the minimum and maximum values. Symbols denote significant differences according to Dunnett’s test ($p \leq 0.05$): * vs absolute control (AC) and † vs nutrient broth control (NBC). AC: Absolute control, NBC: Nutrient broth control, C22: *Bacillus pumilus*, C48: *Acinetobacter vivianii*, C56: *Achromobacter xylosoxidans*, JLB4: *Arthrobacter pokkali*, JN24: *Arthrobacter enclensis*, P61: *Pseudomonas tolaasii* and R44: *Bacillus pumilus*.

Shoot dry biomass increased significantly with inoculation of strains C56 and JLB4, which exceeded the absolute control by 74.5 and 61.3%, respectively (Figure 7A). Regarding root dry biomass, strains C56, JLB4 and C48 showed significant increases compared to the absolute control, with increments of 106.3 and 83.9 and 79.7%, respectively (Figure 7B).

3.2. Nutrient Contents

Inoculation with strains C22, C48, C56, JLB4 and P61 significantly increased shoot N content compared to the absolute control (Figure 8A). The increases were 45.5, 70.1, 88.2 and 71.4, and 20.1%, respectively. Compared to the nutrient broth control, only C48, C56 and JLB4 showed higher values, with increases of 29.9, 43.8 and 30.9%, respectively. In contrast, strains JN24 and R44 exhibited significantly lower N content compared to the nutrient broth control.

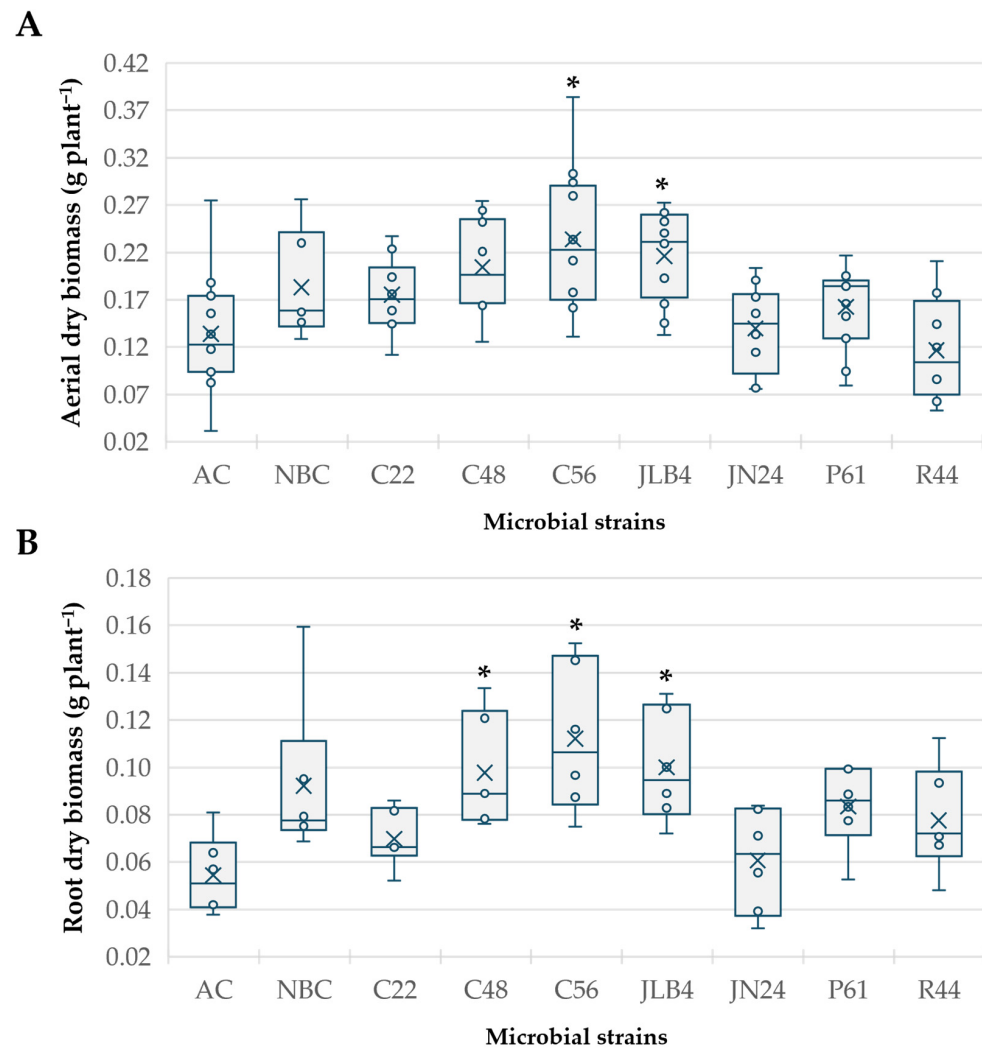


Figure 7. Effect of plant growth-promoting rhizobacteria on dry biomass of lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double plants 149 days after sowing. **(A)** Aerial dry biomass and **(B)** root dry biomass. Box-and-whisker plots represent individual plant values, displayed as circles. For aerial biomass, $n = 6$ –12 per treatment; for root biomass, $n = 6$ per treatment. Boxes indicate the interquartile range (25–75%), the horizontal line within the box represents the median, the “x” indicates the mean, and whiskers indicate the minimum and maximum values. Symbols denote significant differences according to Dunnett’s test ($p \leq 0.05$): * vs absolute control (AC). AC: Absolute control, NBC: Nutrient broth control, C22: *Bacillus pumilus*, C48: *Acinetobacter vivianii*, C56: *Achromobacter xylosoxidans*, JLB4: *Arthrobacter pokkali*, JN24: *Arthrobacter enclensis*, P61: *Pseudomonas tolaasii* and R44: *Bacillus pumilus*.

For P content, strains C22, C48, C56 and JLB4 significantly increased values relative to the absolute control (Figure 8B), with increments of 19.6, 38.6, 48.6 and 38.4%, respectively. However, relative to the nutrient broth control, only C56 showed a significant increase, whereas JN24, R44 and P61 exhibited significantly lower P content.

For K content, several strains differed significantly from the absolute control (Figure 8C). The highest value was recorded with strain JLB4, which increased K content by 62.9 and 22.1% relative to the absolute and nutrient broth controls, respectively. Strain C56 also exhibited a marked increase relative to the absolute control, although to a lesser extent as compared to JLB4.

In Ca content (Figure 8D), strain C56 showed the strongest response, increasing Ca by 61.1 and 15.5% compared to the absolute and nutrient broth controls, respectively. Other strains,

including C22, C48 and JLB4, also showed significant differences relative to the absolute control, although the magnitude of the response was lower than that observed for C56.

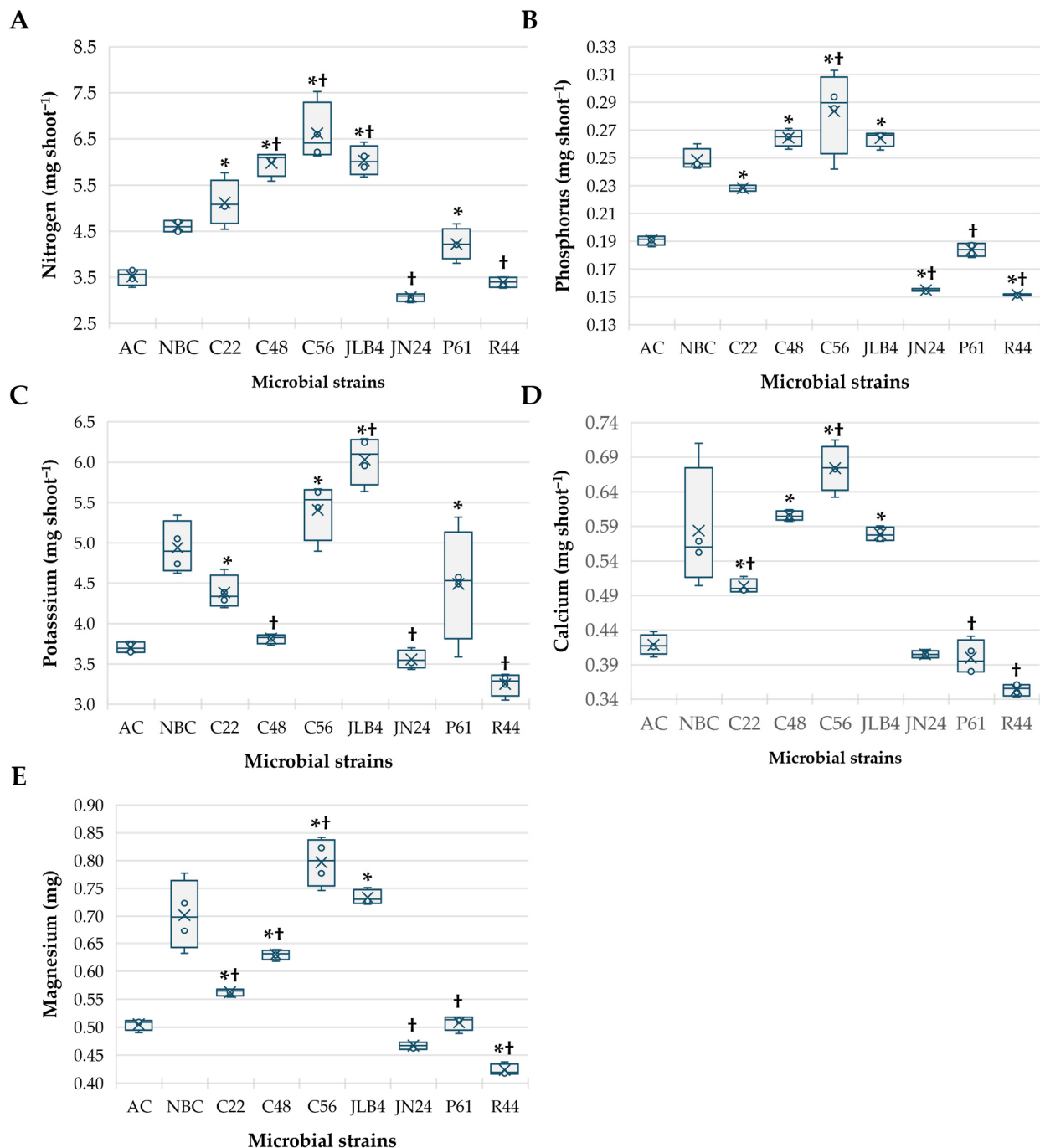


Figure 8. Effect of plant growth-promoting rhizobacteria on the macronutrient content in the aerial part of lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double plants 149 days after sowing. (A) Nitrogen (N), (B) Phosphorus (P), (C) Potassium (K), (D) Calcium (Ca) and (E) Magnesium (Mg). Box-and-whisker plots represent composite shoot samples ($n = 4$ composite samples per treatment), displayed as circles. Boxes indicate the interquartile range (25–75%), the horizontal line within the box represents the median, the “x” indicates the mean, and whiskers indicate the minimum and maximum values. Symbols denote significant differences according to Dunnett’s test ($p \leq 0.05$): * vs. absolute control (AC) and † vs. nutrient broth control (NBC). AC: Absolute control, NBC: Nutrient broth control, C22: *Bacillus pumilus*, C48: *Acinetobacter vivianii*, C56: *Achromobacter xylosoxidans*, JLB4: *Arthrobacter pokkali*, JN24: *Arthrobacter enclensis*, P61: *Pseudomonas tolaasii* and R44: *Bacillus pumilus*.

For Mg (Figure 8E), strains C22, C48, C56 and JLB4 significantly increased Mg content relative to the absolute control. Among them, C56 showed the highest increment (57.8 and 13.6% compared to the absolute and nutrient broth controls, respectively). In contrast, strains JN24 and P61 exhibited significantly lower Mg content compared to the nutrient broth control, whereas strain R44 showed significantly lower values relative to both controls.

Plants inoculated with strains C22, C48, C56 and JLB4 showed significantly higher Fe content compared to the absolute control (Figure 9A). Among them, JLB4 exhibited the greatest increase (78.3% relative to the absolute control), although it did not differ significantly from the nutrient broth control. In contrast, strains JN24, P61 and R44 showed significantly lower Fe values relative to the nutrient broth control.

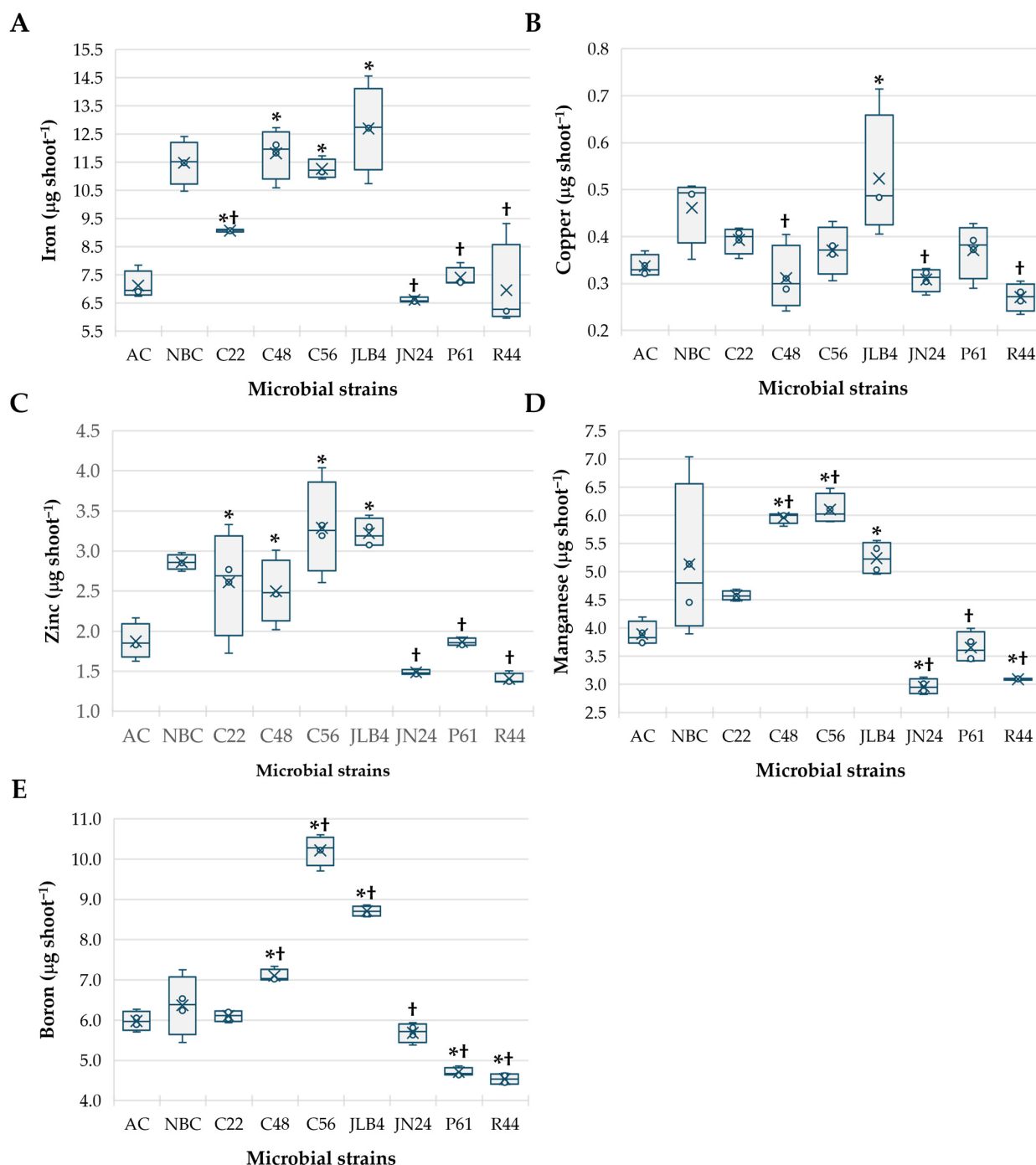


Figure 9. Effect of plant growth-promoting rhizobacteria on the micronutrient content in the aerial part of lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double plants 149 days after

sowing. (A) Iron (Fe), (B) Copper (Cu), (C) Zinc (Zn), (D) Manganese (Mn) and (E) Boron (B). Box-and-whisker plots represent composite shoot samples ($n = 4$ composite samples per treatment), displayed as circles. Boxes indicate the interquartile range (25–75%), the horizontal line within the box represents the median, the “×” indicates the mean, and whiskers indicate the minimum and maximum values. Symbols denote significant differences according to Dunnett’s test ($p \leq 0.05$): * vs. absolute control (AC) and † vs. nutrient broth control (NBC). AC: Absolute control, NBC: Nutrient broth control, C22: *Bacillus pumilus*, C48: *Acinetobacter vivianii*, C56: *Achromobacter xylosoxidans*, JLB4: *Arthrobacter pokkali*, JN24: *Arthrobacter enclensis*, P61: *Pseudomonas tolaasii* and R44: *Bacillus pumilus*.

For Cu, only strain JLB4 significantly increased Cu content relative to the absolute control, with an increment of 65.2%. Conversely, strains C48, JN24 and R44 showed significantly lower Cu values compared to the nutrient broth control (Figure 9B).

Regarding Zn, strains C22, C48, C56 and JLB4 significantly increased Zn content relative to the absolute control, with C56 and JLB4 showing the strongest responses, with increases of 75.6 and 72.1%, respectively. In contrast, strains JN24, P61 and R44 exhibited significantly lower Zn values compared to the nutrient broth control (Figure 9C).

Mn content increased by 53.1 and 56.8% in plants inoculated with strains C48 and C56, respectively, compared to the absolute control (Figure 9D). Strain JLB4 also showed a significant increase (34.6%) relative to the absolute control, although to a lesser extent. In contrast, strains JN24 and R44 exhibited significantly lower Mn contents compared to both controls.

B content was higher than in the controls in plants inoculated with strains C56 and JLB4 (Figure 9E). In C56, the increases were 70.9 and 60.5% compared to the absolute and nutrient broth controls, respectively. In strain JLB4, the increases were 45.6 and 36.8%, respectively. Strain C48 also showed a significant increase in B content relative to both the absolute and nutrient broth controls (18.7 and 11.5%, respectively). In contrast, inoculation with strains JN24 and P61 significantly reduced B content compared to the nutrient broth control, while strain R44 showed significantly lower B contents compared to both controls.

3.3. Principal Component Analysis

Principal component analysis of growth variables showed that the first two components explained 81.1% of the total variance (PC1 = 67.4%, PC2 = 13.7%) (Figure 10). PC1 was associated with overall vegetative vigor, integrating plant height, leaf area, number of leaves, and shoot and root biomass. Treatments located on the positive side of PC1 corresponded to plants with greater growth performance. In particular, strains C56, C48 and JLB4 were positioned on the positive side of the axis, indicating a stronger promotion of vegetative development. In contrast, the absolute control and strains C22, JN24 and R44 were located on the negative side of PC1, reflecting lower plant growth. The separation of R44 in this region supports its negative effect on *lisianthus* development observed in the univariate analyses. PC2 explains a smaller proportion of the variance and mainly reflects differences in growth patterns among treatments.

Principal component analysis based on shoot nutrient contents showed that the first two components explained 89.6% of the total variance (PC1 = 78.7%, PC2 = 10.9%) (Figure 11). PC1 was positively associated with higher nutrient contents and separated treatments with greater nutrient accumulation from those with lower values. Strains C56, C48 and JLB4 were located on the positive side of PC1, indicating a stronger overall contribution to plant nutrient accumulation. In contrast, the absolute control, JN24 and R44 were positioned on the negative side of PC1, reflecting lower nutrient contents in the shoot. PC2 mainly differentiated treatments according to variation in nutrient content among strains,

separating JLB4 and P61 from strains such as C48 and C56, suggesting differences in the relative accumulation of macro- and micronutrients among treatments.

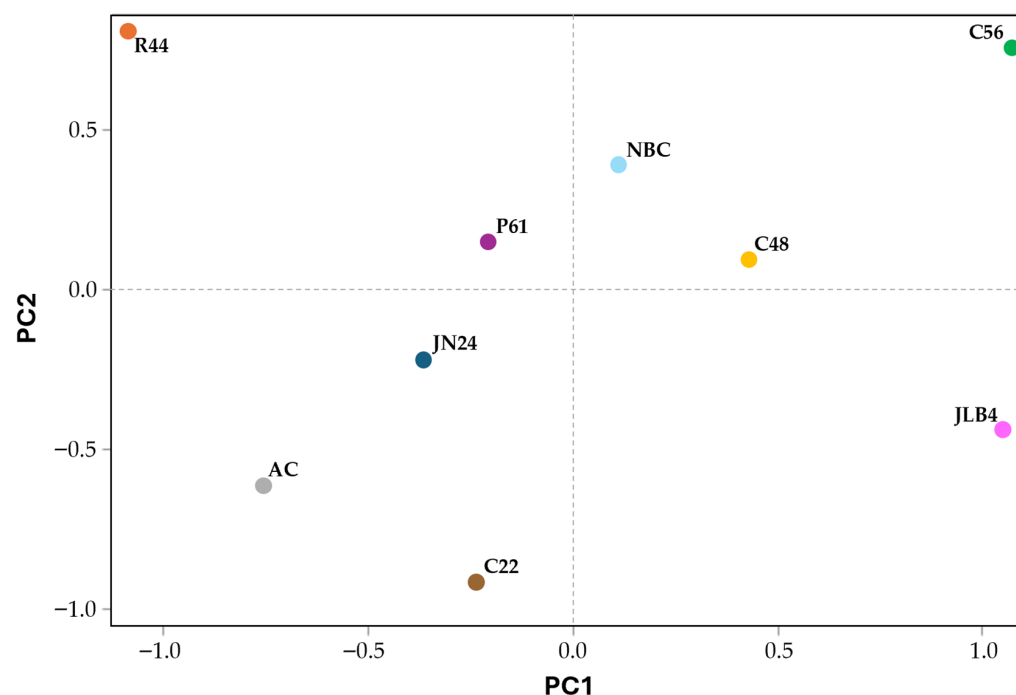


Figure 10. Principal component analysis (PCA) of the growth parameters in lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double plants inoculated with different plant growth-promoting rhizobacterial strains. Points represent mean PCA scores for each treatment. PC1 and PC2 explained 67.4% and 13.7% of the total variance, respectively.

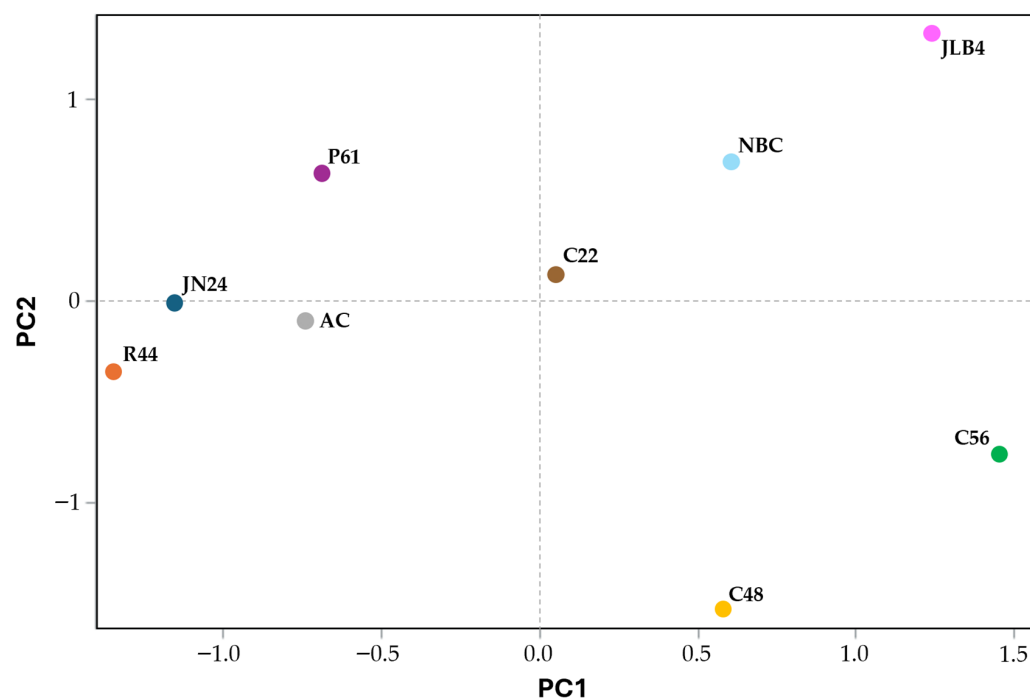


Figure 11. Principal component analysis (PCA) of the shoot nutrient contents in lisianthus [*Eustoma grandiflorum* (Raf.) Shinnery] cv. Mariachi Blue Double plants inoculated with different plant growth-promoting rhizobacterial strains. Points represent mean PCA scores for each treatment. PC1 and PC2 explained 78.7% and 10.9% of the total variance, respectively.

4. Discussion

The time required to obtain lisianthus seedlings suitable for transplanting, from seed sowing, can vary from 8 to 20 weeks, depending on the season [52]. After transplanting, this species goes through three phenological phases: a vegetative phase for plant establishment, which spans from transplanting to the onset of stem elongation (25–30 days after transplanting); a stem elongation phase (25–90 dat); and a flowering phase (90–120 dat) [21]. During the vegetative phase, the plant increases in size and mass, determined by the growth of shoots and roots [53,54]. Plant growth can be measured using biometric parameters such as dry biomass weight, stem height, and leaf area.

The duration of the vegetative phase, which occurs before floral induction, is a critical step for optimizing production [54]. In this study, inoculation of lisianthus with the strains *Acinetobacter vivianii* C48, *Achromobacter xylosoxidans* C56, and *Arthrobacter pokkalii* JLB4 improved all growth parameters, indicating that these rhizobacteria can accelerate the growth rate and thus shorten the vegetative period. Such effects may contribute to earlier attainment of transplant or production stages in lisianthus cultivation.

In cut flowers, one of the main criteria for defining plant quality is stem length and diameter. Stem strength must be sufficient to support the weight of the leaves and flowers [22]. Under our experimental conditions, inoculation with the strains *Acinetobacter vivianii* C48, *Achromobacter xylosoxidans* C56, and *Arthrobacter pokkalii* JLB4 increased plant height (Figures 1 and 2), whereas only the *Achromobacter xylosoxidans* C56 strain significantly increased stem diameter compared to absolute controls and those with nutrient broth (Figure 3). Positive effects on plant height after inoculation with strains C48 and C56 have already been reported in sugarcane (*Saccharum* spp.) seedlings [47]; in lettuce (*Lactuca sativa* L.) when inoculated with strain C56; and in chili pepper (*Capsicum annuum* L.) when a bacterial consortium composed of strains C56, JLB4 and AV5 (*Bacillus pumilus*) was used [55].

Leaf area, age, and number of leaves are key factors of vegetative growth that directly influence the photosynthesis process. Among them, leaf area in particular affects photosynthesis and transpiration in crops [56]. After inoculation with PGPR, alone or in combination with other microorganisms, leaf area and leaf number are significantly improved in several economically important crops such as poblano pepper [57,58]; bell pepper [44]; tomato [48]; and blackberry (*Rubus* spp.) [59]. In ornamental plants, particularly, inoculation with *Enterobacter* sp. CPO 2.5 combined with 50% reduced fertilization significantly increased the leaf area of both leaves and bracts of poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) var. Prestige Red [60]. In China Aster (*Callistephus chinensis* L.), the use of a growth medium composed of soil, coco peat and perlite, combined with the inoculation of *Pseudomonas putida*, increased leaf area by more than 100% in relation to control plants grown in soil and without the addition of growth-promoting bacteria [61]. The findings of this research also show that the use of PGPR at early stages significantly improves leaf area and leaf number in lisianthus plants (Figures 4 and 5), which in turn can positively impact the photosynthesis process. In particular, strain C56 stands out, with an increase of more than 49% in leaf area and 34% in leaf number compared to control plants (Figures 4 and 5).

Inoculation of lisianthus seedlings with strains C56 and JLB4 increased shoot fresh and dry biomass by more than 49% compared to the absolute control. On the other hand, only strain C56 significantly increased root fresh and dry biomass weight. The increases in shoot biomass could be attributed to the ability of PGPR to enhance photosynthetic activity by increasing photosynthetic pigments and electron transport efficiency, resulting in a higher photosynthetic rate [43,44,46] and, consequently, higher biomass production. Regarding root biomass, the results may be related to the ability of strain C56 to produce a significant amount of IAA. IAA can promote root growth and development, increase root surface area,

and accelerate root metabolism [62,63]. The positive results in biomass are comparable to those reported in cannabis plants inoculated with *Bacillus* sp., *Mucilaginibacter* sp. and *Pseudomonas* sp. during the vegetative stage, which increased the total dry weight of the aerial part, with PGPR inoculation providing a solid basis for the reproductive development of the plant [45]. On the other hand, *Pseudomonas chlororaphis* colonization of tomato plants under saline conditions increased shoot fresh and dry biomass weight by 60.3 and 91.1%, respectively, and root fresh and dry biomass weight by 70.1 and 92.5%, respectively, compared to uncolonized plants [43]. Likewise, the *Pseudomonas mandelii* strain increased the fresh and dry biomass of maize roots by more than 100% compared to control plants [42].

Root traits were evaluated on a destructive subsample ($n = 6$ per treatment), which is within the range commonly used in controlled plant growth experiments. Although the number of replicates was lower than that used for shoot measurements, significant treatment effects were consistently detected, supporting the robustness of the observed responses.

For rhizobacteria to exert growth-promoting mechanisms in plants, they must first be able to survive and colonize the rhizosphere. Furthermore, there must be compatibility between microorganisms and the plant's intrinsic factors, specifically root exudates [35,64]. In this study, three rhizobacterial strains (C48, C56 and JLB4) displayed the best growth-promoting effects. A likely explanation is that the lisianthus plant exudates positively modulated the colonization of these bacteria. Indeed, organic acid exudation from roots has been reported in lisianthus [65,66], while PGPR utilize root exudates (i.e., sugars, amino acids, and organic acids), as C sources and signaling molecules to colonize the rhizosphere [67]. With successful colonization, each strain exerted changes or mechanisms in the plant both directly and indirectly, enhancing nutrient uptake and phytohormone synthesis, which contributed to optimal seedling growth and development.

In this study, all bacterial strains were grown under standardized culture conditions using the same nutrient broth formulation to ensure experimental comparability. However, species-specific optimization of culture media was not performed. Therefore, it cannot be excluded that certain strains may have exhibited differential growth dynamics or metabolite production under alternative culture conditions, which could have influenced their performance after inoculation.

Strains C48 and C56 have the ability to produce indoles and solubilize phosphate [47]. With a production of $33.3 \mu\text{g IAA mL}^{-1}$, strain C56, belonging to the species *Achromobacter xylosoxidans*, demonstrated outstanding capability to synthesize and exude indoles, while strain JLB4, which solubilizes phosphates and produces IAA, belongs to the species *Arthrobacter pokkalii* [48]. In a previous study, *A. pokkalii* has been shown to form biofilms [68], an attribute that may facilitate colonization and establishment in the rhizosphere. Since plants undergo a variety of PGPR-induced changes, growth promotion is likely the result of the interaction of multiple factors acting in concert rather than in isolation [69,70]. This phenomenon, known as the additive hypothesis, involves a cumulative effect of changes in the expression of several genes that regulate the plant's multifactorial metabolic system, affecting both its development and nutrition [69,71].

Strain R44 significantly reduced plant height and leaf number in lisianthus (Figures 1 and 5). Similar results were reported in blackberry plants inoculated with this strain, with evident reduced growth [59]. In bell pepper, however, positive effects of R44 have been reported, by increasing leaf number, leaf area and root volume [44]. These contrasting responses indicate that the growth-promoting effect of PGPR is strongly host-dependent and influenced by multiple factors, including effective colonization, root exudate composition, plant developmental stage and environmental conditions [35,43,45,72].

In the literature, some PGPR have been reported to inhibit plant growth through mechanisms such as hormonal imbalance, phytotoxic metabolite production, and antagonistic interactions with the host plant or native microbiota [73]. In particular, PGPR-induced growth inhibition has been associated with altered plant hormonal balance, including increased ethylene accumulation in the host plant under certain physiological conditions [74]. In *lisianthus*, the negative response observed after inoculation with strain R44 may similarly be related to hormone-mediated effects, potentially involving enhanced ethylene signaling in the plant rather than direct bacterial ethylene production. It remains to evaluate the hormonal profiles of these plants in response to the different inoculated strains.

Another relevant result of this research was that the application of nutrient broth also had a beneficial effect on growth parameters compared to the AC and strains JN24 and R44 (Figures 1 and 4–7). However, some of these results were not statistically superior to strains C56, C48 and JLB4. Nutrient broth is a liquid medium used for the development of microorganisms with few nutritional requirements; it contains meat extract and sodium chloride, and can be supplemented with yeast extract, peptones, glucose, and other components [75]. Thanks to its composition, this medium stimulates plant growth and development by providing essential elements and compounds that are readily available.

Although nutrient broth was used as an inoculum vehicle under controlled conditions, the development of stabilized formulations suitable for commercial greenhouse or field application warrants further investigation.

In addition to viable bacterial cells, the applied suspensions likely contained bacterial metabolites produced during culture, including IAA and other bioactive molecules previously reported for these strains [44,47,48,55]. Such metabolites may contribute to plant physiological responses independently or synergistically with bacterial colonization. Therefore, the observed growth responses may reflect the combined effect of living bacterial cells, secreted metabolites, and residual medium components. Further studies separating cell-free supernatants from bacterial biomass would help clarify the relative contribution of these factors.

The best-performing strains differentially influenced nutrient acquisition in *lisianthus* plants (Figures 8 and 9). In particular, C48, C56 and JLB4 enhanced N and P accumulation in shoot tissues, whereas K content was primarily increased by C56 and JLB4. Strain C56 showed the highest Ca and Mg accumulation in aerial tissues. In contrast, Fe, Cu and Zn contents were mainly elevated in plants inoculated with JLB4, while Mn content increased with C48 and C56. Additionally, C56 was associated with the highest B content in shoots.

The multivariate relationships among treatments were further supported by the principal component analysis. The PCA of growth variables separated the best-performing strains (C56, C48 and JLB4) from the controls and the less effective strains along the positive side of PC1, indicating that these bacteria were consistently associated with improved vegetative vigor (Figure 10). Similarly, the PCA based on shoot nutrient contents positioned this stronger contribution to plant nutritional status (Figure 11). Together, these multivariate patterns reinforce the univariate results and highlight the consistent ability of strains C56, C48 and JLB4 to enhance both growth and nutrient accumulation in *lisianthus*.

Variation in micronutrient accumulation among PGPR treatments has been reported in the literature and may depend on the specific plant–microbe interaction and the functional traits of each strain, including differential capacities to influence nutrient mobilization, uptake regulation, and allocation within plant tissues [29–31]. In the present study, strains C48 and C56 were associated with lower Cu accumulation in shoot tissues compared to JLB4, suggesting strain-specific differences in plant Cu uptake or internal redistribution. Such variation may reflect differences in rhizosphere interactions or modulation of nutrient transport processes rather than a uniform effect across strains. Regarding B, the

higher accumulation observed particularly in plants inoculated with strain C56 is consistent with the essential role of B in cell wall formation, membrane integrity and active vegetative growth [76]. Therefore, the differential B levels detected among treatments may be associated with the distinct growth responses promoted by each strain in lisianthus.

The differences observed in macro- and micronutrient accumulation among treatments may be related to strain-specific effects on plant nutrient metabolism and regulation of uptake processes [77]. PGPR are known to influence nutrient dynamics through multiple mechanisms, including modulation of root physiology and transport activity. However, the present study did not evaluate changes in substrate nutrient availability or metal speciation; therefore, the mechanisms underlying the observed differences in Cu accumulation require further investigation.

The positive effects of PGPR on nutrient acquisition have been widely documented in diverse crops, such as blackberry [59], strawberry (*Fragaria × ananassa* Duch.) [41], tomato [48], rice (*Oryza sativa* L.) [78] and maize [42]. Increases in nutrient acquisition mediated by PGPR are closely related to increases in root surface area and changes in root morphology [63,79]. These changes are largely due to the production of IAA [80,81]. These rhizobacteria can either provide IAA directly to the plant or regulate endogenous levels of this hormone by modulating the expression of auxin-responsive genes [62]. Therefore, the more pronounced development of the roots favors a larger exploration surface, which, in turn, optimizes the plant's nutrient uptake capacity [79]. In addition, another well-documented mechanism by which some rhizobacteria enhance nutrient uptake is the upregulation of the expression of some genes or proteins related to nutrient transport and uptake. Among the reported transporters are AMT2 for NH_4^+ , IRT1 and FRO for Fe, and PHT1 for Pi in plant roots [34,79,81]. Furthermore, the increased nutrient accumulation in plant tissues promoted by PGPR is not only due to increased nutrient availability in the soil, but also to the functionality of plasma membrane proteins involved in root nutrition [78,80]. The transmembrane electrochemical gradient is the main driving force regulating ion transport across the plasma membrane [81]. This gradient is maintained by the activity of plasma membrane H^+ -ATPase, a key enzyme for solute movement [82]. Therefore, the activity of this enzyme is essential in the process of nutrient acquisition by plants [83]. Indeed, inoculation with *Herbaspirillum seropedicae* stimulates H^+ -ATPase activity in maize roots, promoting greater efficiency in nutrient uptake [84].

Overall, PGPR enhance plant physiology and metabolism through complex biochemical and molecular mechanisms of both direct and indirect action, including phytohormone production and signaling, nutrient solubilization and mobilization, siderophore production, secretion of secondary metabolites, and induced systemic responses [85,86]. These processes are regulated by key genes involved in photosynthetic efficiency, root system development, nutrient transport, and abiotic stress tolerance [40,87]. In the present study, the improved vegetative growth and nutrient acquisition observed particularly with strains C48, C56 and JLB4 are consistent with this integrated and multifactorial mode of action, where several physiological pathways may operate simultaneously rather than independently.

Our results demonstrate the potential of selected PGPR strains to improve vegetative growth and nutrient acquisition in lisianthus. Future research should evaluate the performance of these strains under commercial greenhouse conditions, their compatibility in combined microbial formulations, and their effects on flowering, stem quality and postharvest performance. Additionally, studies addressing long-term plant–microbe interactions and responses under intensive cultivation systems would contribute to the development of effective PGPR-based biostimulants for ornamental crop production.

5. Conclusions

Inoculation with the strains *Acinetobacter vivianii* C48, *Achromobacter xylosoxidans* C56, and *Arthrobacter pokkalii* JLB4 improved lisianthus plant growth parameters and nutrient uptake. These results indicate that these rhizobacteria have the ability to accelerate the growth rate, shorten the vegetative period, and promote improved vegetative performance and support subsequent productive stages. Therefore, these strains have great potential as inoculants for intensive lisianthus production.

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