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Dual Benefits of Compost Tea Bacteria: Boosting 'San Andreas' Strawberries' Productivity and Fruit Quality

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Abstract

Bacteria represent promising tools for reducing the use of synthetic inputs in crop production. In this study, we evaluated the effects of two bacterial strains isolated from chicken compost tea—*Bacillus licheniformis* and *Pseudomonas mendocina*—on the yield and quality of strawberry. Experimental assays were conducted in two seasons (2023 and 2024) under macro-tunnel conditions, with the following treatments: control without applications (Con); commercial NPK fertilizer (FerC); application of *B. licheniformis* (BL) and *P. mendocina* (PM) solution in soil once a month. Both bacterial treatments enhanced soil properties. Fruit individual weight significantly increased in BL treatment compared to the control. Similar trends were observed for anthocyanin and ascorbic acid content (increases > 25%), as well as for antioxidant activity (increases of more than 20% and 13% for BL and PM, respectively). The differences were more significant in 2023. In addition, both strains showed positive in vitro results for phytase, siderophore, and IAA production (5.8–8.8 and 9.3–13 μg IAA/mL for BL and PM after 15 days). Although further field validation is required, these results indicate that bacteria (particularly *B. licheniformis*) show strong potential as bioinoculants to enhance the productivity and quality of strawberry.

Keywords: plant growth promoting bacteria; biological agents; biofertilizer; strawberry; 'San Andreas'

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1. Introduction

Soils are extremely complex and highly dynamic, multifunctional systems in which components interact through multiple chemical, physical, and biological processes [1]. For this, the imbalance of any of these components can affect soil health, altering its capacity to sustain biological productivity and environmental quality [2]. In recent decades, global population growth and the resulting demand for increased food production have contributed to reduced arable land availability and a decline in agricultural soil productivity, manifested by decreased organic matter content, erosion, pollution, and biodiversity loss [3]. Although many parameters influence soil degradation (tillage, monoculture, compaction, irrigation, and others), the repeated use of synthetic fertilizers to sustain crop yield and quality is

among the main contributing factors [4]. These fertilizers provide nutrients to plants immediately, but they do not improve soil health or replace its organic matter; rather, damage to the soil and contamination of surface and groundwater occur mainly, among others, to the rapid mineralization of organic matter and excessive accumulation of nutrients [5,6]. This scenario highlights the need to seek alternatives to conventional fertilization that allow for achieving the highest possible yield and quality without compromising soil health.

The Plant Growth Promoting Bacteria (PGPB) have generated great interest in the agricultural sector for the formulation of biological inoculants [7]. PGPB are microorganisms that can transform soil nutrients (through mobilization and solubilization processes) so that they are available to plants [8]. These microorganisms employ diverse mechanisms of action that promote both crop development and plant health across a wide range of agricultural systems [8–10]. In particular, the genera *Bacillus* and *Pseudomonas* are considered dominant in most compost teas [11,12]. Several studies have highlighted the mechanisms of action associated with these genera. Among the most important are the ability to generate Induced Systemic Resistance (ISR) in plants, synthesize plant growth–related hormones (indoleacetic acid, abscisic acid, and gibberellins), fix atmospheric nitrogen and solubilize phosphates, produce siderophores, and synthesize a wide range of antibiotics active against plant pathogens [8,13–15].

Regarding strawberry cultivation, Argentina produces approximately 45,000 to 50,000 tons annually on 1500–1700 ha, corresponding to an average yield of 34 tn/ha [16,17]. The province of Santa Fe is one of the country's main strawberry producers and, together with Tucumán province, defines national strawberry prices due to high production volumes and the timing of market entry (September and November) [18]. According to the Central Market of Buenos Aires (Argentina's largest fruit and vegetable trading center), the San Andreas, Camino Real, and Benicia cultivars are the most widely cultivated in Santa Fe. Between 50 and 70% of production is destined for the fresh market, while the remainder is directed to the industrial sector for the production of jams, juices, and frozen products, with the United States being the primary export destination [17,19].

While the potential applications of the genera *Bacillus* and *Pseudomonas* in different agricultural soils have been widely explored, evidence regarding the effects of *B. licheniformis* and *P. mendocina* on strawberry productivity and fruit quality remains scarce. For this reason, a preliminary study was conducted in the present work to evaluate the effects of *B. licheniformis* and *P. mendocina* (isolated from a chicken compost tea) on the strawberry cultivar 'San Andreas'.

2. Materials and Methods

2.1. Bacteria Isolation and Identification

Bacteria were isolated from chicken compost tea (TC). TC was supplied by EnBio, an agricultural bio-inputs company based in Rafaela city, Santa Fe province. Briefly, 200 µL of TC dilutions were inoculated onto Petri dishes containing Luria–Bertani (LB) medium and incubated at 37 °C for 48 h. Six randomly selected colonies with different morphologies, sizes, and colors were selected and subcultured onto fresh LB agar plates. These isolates were initially identified by MALDI-TOF MS (Matrix Assisted Laser Desorption/Ionization-Time of Flight Mass Spectrometry, Bruker Daltonics, Bremen, Germany), revealing the presence of five *Bacillus* (two *Bacillus cereus* and three *Bacillus* sp.) and one *Pseudomonas* (*P. mendocina*). Two *Bacillus* (one *Bacillus* sp., B1, and one *B. cereus*, B2) and the *Pseudomonas* (P1) isolate were subsequently selected for molecular identification.

Genomic DNA was extracted using the Quick-DNA™ Fungal/Bacterial Miniprep Kit (Tanirel Biotechnology, Montevideo, Uruguay). Molecular identification was based on the amplification and sequencing of the *16S rRNA* gene and two additional housekeeping

genes, *gyrA* and *rpoD*, which provide higher taxonomic resolution than *16S rRNA* within the genera *Bacillus* and *Pseudomonas*, respectively. PCR amplification of the *16S rRNA* gene was performed using universal bacterial primers 27F (5′-AGAGTTTGATCCTGGCTCAG-3′) and 1492 R (5′-GGTTACCTTGTTACGACTT-3′) [20]. Partial fragments of the *gyrA* gene were amplified using primers *gyrA*-42F (5′-CAGTCAGGAAATGCGTACGTCCTT-3′) and *gyrA*-1066R (5′-CAAGGTAATGCTCCAGGCAATGCT-3′) [21], and partial fragments of the *rpoD* gene were amplified using primers PsEG30F (5′-ATYGAAATCGCCAARCG-3′) and PsEG790R (5′-CGGTTGATKTCCTTGA-3′) [22].

PCR reactions were carried out in a final volume of 25 µL containing 0.5 µL of each primer, 0.1 µL of Taq DNA polymerase (5 U/µL), 2.5 µL of 10× reaction buffer, 0.7 µL of dNTPs (10 mM), 1 µL of genomic DNA, and Milli-Q water to volume. Thermal cycling conditions for *16S rRNA* gene amplification consisted of an initial denaturation at 94 °C for 5 min, followed by 30 cycles of denaturation at 94 °C for 1 min, annealing at 55 °C for 30 s, and extension at 72 °C for 1 min 30 s, with a final extension at 72 °C for 7 min. Amplification of the *gyrA* gene was performed using an initial denaturation at 94 °C for 5 min, followed by 30 cycles of 94 °C for 30 s, 58 °C for 45 s, and 72 °C for 1 min 30 s, with a final extension at 72 °C for 10 min. For the *rpoD* gene, PCR conditions consisted of an initial denaturation at 94 °C for 5 min, followed by 35 cycles of 94 °C for 1 min, 52.3 °C for 30 s, and 72 °C for 1 min 30 s, with a final extension at 72 °C for 5 min.

PCR products were verified by electrophoresis on 0.8% agarose gels, and amplicons of the expected size were submitted to Macrogen Inc. (Seoul, Republic of Korea) for Sanger sequencing. The resulting sequences were analysed using the BLASTn algorithm (MEGA 12.1) against sequences from type strains deposited in the GenBank database (https://blast.ncbi.nlm.nih.gov/Blast.cgi, accessed on 27 October 2025). Species-level identification using the *16S rRNA* gene was considered reliable when sequence identity values were ≥98.65%, in accordance with widely accepted thresholds for bacterial species delineation [20].

For protein-coding housekeeping genes (*gyrA* and *rpoD*), no universally accepted similarity thresholds have been formally established. Therefore, species assignment was based on high sequence similarity to type strain sequences.

2.2. Experimental Design in Strawberry Cultivar 'San Andreas'

The experiments were conducted under a macro-tunnel located on the FAVE Campus in Esperanza city (Santa Fe, Argentina) (Figure 1). The use of macro-tunnels in strawberry cultivation is a technology that has been implemented in Santa Fe for several years. This relatively recent innovation offers several structural and productive advantages, e.g., as it can be assembled and disassembled during the growing season, it protects against adverse weather, and reduces fruit deformation problems [23]. Figure 2 summarizes the meteorological conditions (average temperature and total precipitation) for the period in which the crop was grown (June to December). Cultivar 'San Andreas' was used, supplied by Patagonia Agrícola S.A. from Coronda city (Santa Fe). Their vigor and health characteristics were similar at the time of implant. The seedlings were implanted in pots (3 L) using sandy loam soil, collected from a plot of land dedicated to this crop, at a depth of 0 to 15 cm. A completely randomized design was established, considering the following treatments: control without applications (Con); application of 1 g/pot of a commercial fertilizer with a composition of 18% N, 8% P, and 14.7% K at trial initiation (FerC); application of 100 mL of *B. licheniformis* suspension once a month (BL); and application of 100 mL of *P. mendocina* suspension once a month (PM). The bacterial suspensions were adjusted to the 0.5 McFarland turbidity standard, which corresponds to a concentration of 1.5×10^8 CFU/mL [24]. Four plants per treatment were used. The experiment was conducted twice (in 2023 and

2024) under the conditions described above, from June to December (complete vegetation cycle in Santa Fe). The optimal rainfall for this period in the region ranges between 450 and 550 mm. Optimal temperatures for strawberry development and reserve accumulation range between 2 and 12 °C (June to August), whereas during the flowering and fruiting period (September to December), optimal temperatures are approximately 15 to 25–30 °C [25]. During the experiments, the plants were irrigated with demineralized water according to their water requirements.

Figure 1. Illustrative photographs of strawberry trials under the macro-tunnel, FAVE Campus (Esperanza, Santa Fe).

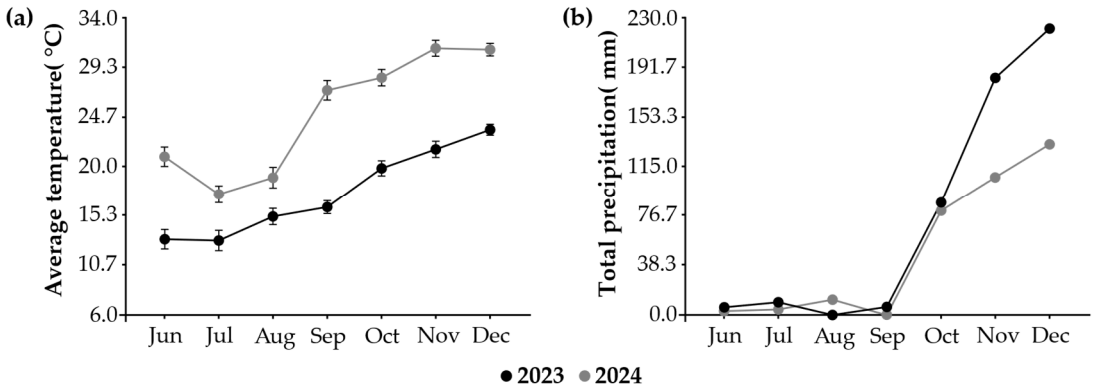

Figure 2. (**a**) Average temperature and (**b**) total precipitation during the crop cycle (June to December). The data were obtained from the meteorological station at the FAVE Campus.

2.3. Analysis of Soil

For each treatment, soil chemical properties were evaluated both initially (before planting) and at the end of the cropping cycle to assess the nutritional contributions of the proposed treatments and the residual nutrient levels in the soil. To assess the chemical properties at the end of the cycle, the four pots from the same treatment were combined to produce a homogeneous sample. Organic matter (OM) was quantified using the Walkley–Black method [26] and expressed in g/kg. For this, 0.2 g of soil was weighed, to which 1 mL of $H_2Cr_2O_7$ solution and 3 mL of H_2SO_4 were added. Finally, a titration was carried out with an indicator solution and Mohr's salt until a green endpoint was reached.

Total nitrogen (Total N) was determined using the Kjeldahl method [27] and expressed in g/kg. For this, the organic matter was digested by heating the sample with H_2SO_4 in the presence of catalysts, promoting oxidation and the conversion of organic nitrogen to ammonia. The released ammonia was subsequently distilled with NaOH, trapped in a boric acid solution, and titrated with sulfuric acid. Total phosphorus (Total P) was determined by digesting the sample in an acidic solution (HNO_3 and H_2O_2) and quantifying it using

Inductively Coupled Plasma Mass Spectrometry (ICP-MS) [28]. Results were expressed in mg/kg. Available phosphorus (Av. P) was quantified using the Bray–Kurtz method [29] and expressed in mg/kg. The sample was first extracted with a solution of NH_4F and HCl. Subsequently, a reagent mixture (H_2SO_4, ammonium molybdate, antimony potassium tartrate, and ascorbic acid) was added, and the absorbance was measured at 880 nm using a spectrophotometer. Total potassium (Total K) and sodium (Total Na) were quantified following wet digestion with HNO_3 and H_2O_2, and measurements were performed using ICP-MS [28]. Results were expressed in mg/kg.

pH was measured in a soil–water suspension (1:2.5) using a potentiometric pH meter [30]. Electrical conductivity (EC) was determined by a saturation paste and expressed in dS/m [31]. For this, a specific volume of soil was weighed, water was added until saturation, and the mixture was allowed to equilibrate for 24 h. The paste was then filtered under vacuum, and EC was measured with a conductivity meter.

Cation Exchange Capacity (CEC) was determined by extraction with ammonium acetate [31]. Excess extractant was removed with 70% ethanol, followed by the addition of 10 mL NaCl and centrifugation to obtain the ammonium-containing supernatant. Distillation was then performed with 10 mol/L NaOH and boric acid, and the distillate was titrated with standardized H_2SO_4. Results were expressed in cmolc/kg. Finally, exchangeable cations Ca^{2+}, Mg^{2+}, Na^+, and K^+ (Ex. Ca^{2+}, Mg^{2+}, Na^+, and K^+) were quantified from the CEC extract and expressed in mg/kg. Ex. Ca^{2+} and Ex. Mg^{2+} were determined by complexometric titration with ethylenediaminetetraacetic acid (EDTA), while Ex. Na^+ and Ex. K^+ were measured directly using a flame spectrophotometer [32].

2.4. Production and Quality Parameters of Strawberry Cultivar 'San Andreas'

Once a month, the leaf area (cm^2) of each plant was registered; for this, all leaf length and width were measured and multiplied by a conversion factor (0.85) calculated using a non-destructive method [33]. At three crop stages (July, October, and December), two leaves per plant (8/treatment) were collected to determine foliar concentrations of nitrogen by the Kjeldahl method (%), phosphorus by the ascorbic acid method (ppm), and potassium by nitric acid extraction and ICP-MS (ppm). When the fruits reached harvest maturity (≈90% of the surface red), they were manually harvested. Methods for measuring fruit quality parameters are summarized in Table 1. Fruit weight, firmness, and color were recorded immediately after harvest. Juice from ten randomly selected fruits per treatment was used to quantify acidity, TSS, and TSS/acid ratio (Table 1). Anthocyanin, ascorbic acid, and phenolic compounds content, as well as the antioxidant activity, were determined following ethanol extraction from the fruit samples. For the extractions, twelve fruits were randomly selected from each treatment, ground, and 750 mg of sample was weighed into hemolysis tubes (twelve tubes per treatment). Subsequently, 2 mL of analytical ethanol (96.6%) was added to each tube and kept in the dark for 24 h. Finally, the tubes were centrifuged to separate the pellet from the extract.

Table 1. Methods for measuring fruit quality parameters.

Parameter	Technique
Weight (g)	Fruits were weighed using a digital scale. The fruits were classified into three categories: weight < 7 g (very small fruit), weight between 7 and 20 g, and weight > 20 g.
Color index (CI)	L*, a* and b* registered with digital colorimeter; CI = (a* × 1000)/(L* × b*)

Table 1. *Cont.*

Parameter	Technique
Firmness (°Shore)	Firmness was measured using a digital penetrometer at two points in the equatorial zone.
Total Soluble Solids-TSS (°Brix)	TSS of fruit juice was determined using a digital refractometer.
Acidity (eq. citric acid/mL)	Fruit juice acid-base titration with NaOH 0.1 N; Acidity = mL NaOH consumed × NaOH normality × (citric acid molecular weight/citric acid number of equivalents)
Ratio	Relationship between TSS content and acidity
Anthocyanins in mg cyanidin-3-glucoside (mg C3G/g)	Direct measurement of the extract using a spectrophotometer at 540 nm [34]
Ascorbic acid in mg ascorbic acid (mg AA/g)	Reaction: 200 µL of extract + 250 µL of sodium acetate buffer (400 mM, pH 4) + 80 µL of 2,6-dichloroindophenol + 1470 µL of distilled water. Absorbance was measured at 515 nm [35]
Phenolic compounds in mg gallic acid (mg GA/g)	Reaction: 250 µL of extract + 1250 µL of distilled water + 100 µL of Folin–Ciocalteu reagent + 200 µL of 7.5% Na_2CO_3 (water bath at 50 °C for 5 min). Absorbance was measured at 765 nm [36].
Antioxidant activity (reduction in ABTS· radical in %)	Reaction: 250 µL of extract + 250 µL of radical ABTS· ± 0.7 Abs. Absorbance was measured at 734 nm [37].

2.5. Mechanisms of Bacterial Action In Vitro

To evaluate the ability of bacteria to solubilize phosphates, a specific medium was prepared and adjusted to pH 7.2 [38]. The medium was poured into 90 × 15 mm Petri dishes, and 10 µL of each bacterium was inoculated in triplicate. The plates were incubated at 37 °C for 48 h. The formation of a clear halo around the bacteria indicates a positive result for phosphate solubilization.

For phytases production, the specific culture medium was adjusted to a pH of 5.5 [39]. The medium was poured into 90 × 15 mm Petri dishes, and 10 µL of each bacterium was inoculated in triplicate. The plates were incubated at 37 °C for 48 h. The formation of a clear halo around the bacteria indicates a positive result for phytase production.

Siderophore production was assessed with a chrome azurol sulfonate (CAS) agar plate assay and Grimm Allen medium as a base [40]. Each bacterial strain was inoculated at the center of the plate and incubated at 25 °C for 2 days. The presence of a siderophore was indicated by a color change from blue to orange surrounding the streaks of growing cultures.

Indoleacetic acid (IAA) production was quantified according to the methodology described by Karimi et al. [41]. Bacteria were inoculated in quadruplicate into Erlenmeyer flasks containing 25 mL of a liquid culture medium composed of peptone, yeast extract, NaCl, and tryptophan. Two Erlenmeyer flasks of each bacterium were incubated at 37 °C, and two were incubated at room temperature (approximately 25 °C) for 15 days. IAA concentration was measured at four time points (3, 6, 9, and 15 days). For this, an aliquot of the culture medium was centrifuged to remove the bacterial pellet. For the reaction, 1 mL of the supernatant, 50 µL of 10 mM phosphoric acid, and 2 mL of IAA reagent (composed of $FeCl_3$ and $HClO_4$) were used. The reaction was incubated at room temperature for 30 min in darkness; the appearance of an orange-pink color suggests the possible production of IAA, and its absorbance was recorded at 530 nm in a spectrophotometer [42]. The IAA level was estimated using the calibration curve (y = 52,805 x + 0.8007) and expressed in micrograms per milliliter (µg/mL).

2.6. Statistical Analysis

Experimental assays were conducted in two seasons (2023 and 2024) under identical experimental conditions. Data were subjected to a one-way analysis of variance (ANOVA), and Dunnett's test at $p < 0.05$ was used to compare means between FerC, BL, and PM treatments with respect to the control without applications (Con). All variables were analyzed separately for each experimental assay.

3. Results

3.1. Bacteria Isolation and Identification

Analysis of the *16S rRNA* gene sequence confirmed the genus-level assignments previously obtained by MALDI-TOF MS, identifying the isolates B1 and B2 as belonging to the genera *Bacillus* (*Bacillus* sp. and *B. cereus*) and P1 as *Pseudomonas* (*P. mendocina*). Additionally, sequence analysis of the housekeeping genes *gyrA* and *rpoD*, which provide improved resolution within the genera *Bacillus* and *Pseudomonas*, respectively, allowed a more refined taxonomic assessment (Table 2).

Table 2. Molecular identification parameters of bacteria isolated from compost tea.

Gen	Sp. Identified by MALDI-TOF	BLAST Analysis		
		% Identity (Id.)	E-Value	Sequence with the Highest ID in Genbank (Access)
GyrA	B1-*Bacillus* sp. B2-*B. cereus*	100 99.79	0.0 0.0	*B. licheniformis* culture SZMC:27712 DNA gyrase subunit alpha(*gyrA*) gene, partial cds (OP620082)
rpoD	P1-*P. mendocina*	96.00	0.0	*P. mendocina* ATCC 25411partial *rpoD* gene for DNA-directed RNA polymerase subunit D (AJ633567.1)

Based on *gyrA* sequence analysis, *Bacillus* isolates B1 and B2 were assigned to *B. licheniformis*. For the *Pseudomonas* isolate (P1), *rpoD* sequence analysis revealed the highest sequence similarity to *P. mendocina*, with a percentage of identity of 96.00% (Table 2). This value suggests a close phylogenetic relationship rather than an unequivocal species-level assignment. Accordingly, this isolate was considered a *Pseudomonas* sp. closely related to *P. mendocina*. According to these results, the *Bacillus* sp. (*B. licheniformis*) and *P. mendocina* strains were selected for the strawberry plant trials.

3.2. Analysis of Soil

Initial and final chemical soil parameters are summarized in Table 3. OM increased slightly towards the end of the cycle in both trials with respect to initial soil analysis; however, the final soil analysis revealed comparable OM values across all treatments (10–11.2 g/kg in 2023 and 13.7–14.6 g/kg in 2024). A similar trend was observed for Total N, except in 2024, when the BL and PM treatments showed values lower than those of the control (Table 3). Regarding phosphorus, while the Total P content of the bacterial treatments did not exceed that of the control, available P (Av. P) was higher in BL and FerC, particularly in 2024. Total K decreased towards the end of the cycle in both trials, with similar values for all treatments (Table 3). As for Total Na, a higher content was observed in the treatments with FerC and the bacteria (mainly BL). The pH was not affected by the application of bacteria (pH between 6 and 7), nor was the EC (EC between 0.4–0.5 and 0.2–0.3 dS/m for 2023 and 2024, respectively) (Table 3). Regarding the exchangeable complex, a slightly higher CEC was recorded for the BL and PM treatments, and a higher content of the cations K^+, Na^+, and Mg^{2+}; however, in 2024, the values for these variables

were similar in all treatments, except for the Ca^{2+} and Mg^{2+} content, which was higher in the PM treatment (Table 3).

Table 3. Initial and final chemical soil characteristics for each treatment.

Parameter	Initial Soil	2023				2024			
		Con	FerC	BL	PM	Con	FerC	BL	PM
OM (g/kg)	6.4	10.5	11.2	10.0	10.8	14.6	14.2	13.7	13.9
Total N (g/kg)	0.3	0.7	1.3	1.0	0.8	0.6	0.5	0.3	0.4
Av. P (mg/kg)	53.7	47.4	53.9	51.1	51.4	36.9	124.9	80.7	38.3
Total P (mg/kg)	157.5	242.5	204.5	179.9	220.5	448.3	402.9	439.2	461.9
Total K (mg/kg)	1149.0	938.0	854.0	974.0	961.0	927.9	867.9	907.9	992.9
Total Na (mg/kg)	1062.0	909.0	1132.1	1268.0	1171.0	793.8	918.5	1032.8	809.4
pH	6.1	7.3	6.1	6.9	6.8	7.0	7.0	6.5	7.0
CE (dS/m)	0.7	0.4	0.4	0.5	0.5	0.3	0.2	0.3	0.3
CEC (cmolc/kg)	6.1	4.4	4.9	5.0	5.1	4.2	3.8	4.2	4.6
Ex. Ca^{2+} (mg/kg)	400.8	258.0	433.4	270.0	279.0	400.8	440.9	416.8	440.9
Ex. K^{+} (mg/kg)	391.0	97.7	89.9	113.4	101.7	154.0	127.0	107.0	121.0
Ex. Na^{+} (mg/kg)	46.0	46.0	32.2	69.0	92.0	64.0	60.0	58.0	65.0
Ex. Mg^{2+} (mg/kg)	133.8	122.0	117.2	158.0	147.0	158.1	121.6	133.8	170.2

3.3. Vegetative Parameters of Strawberry Cultivar 'San Andreas'

In 2023, bacterial treatments exhibited higher leaf area values across all evaluated months; however, these differences were not statistically significant compared with the control (Con); significant differences were only detected in June 2023 between the FerC and Con treatments (Figure 3a). In 2024, leaf development was similar among all treatments (Figure 3b). The analysis of total leaf nutrients revealed, in general terms, a similar pattern across all treatments (Figure 4). Nitrogen concentration declined toward the end of the cycle, ranging between 1.5 and 3.5%. For phosphorus, FerC, BL, and PM treatments presented the highest values in both 2023 and 2024, particularly in the measurements taken in October. Finally, potassium content in leaves was comparable between treated and control (Con) groups in 2023 (Figure 4a), whereas in 2024 (Figure 4b), higher levels of this nutrient were detected in the FerC, BL, and PM treatments, especially in the samples collected in October and December.

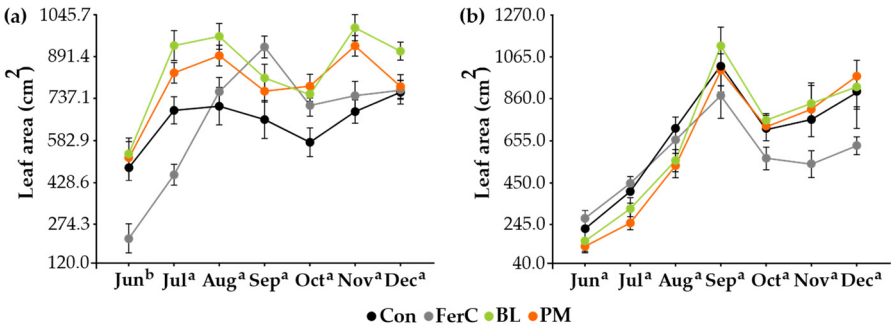

Figure 3. Leaf area measured monthly throughout the crop cycle in (**a**) 2023 and (**b**) 2024. Different letters within each month indicate statistically significant differences among treatments (FerC, BL, and PM) compared with the control (Con) (Dunnett's test, $p < 0.05$); the lines above the dots indicate the standard error.

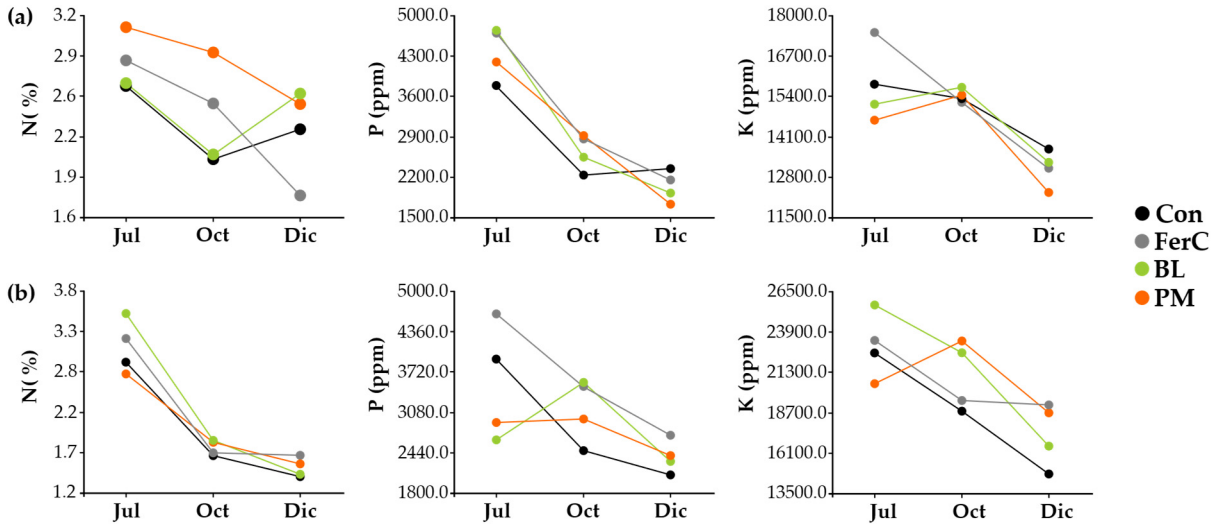

Figure 4. Leaf nutrient concentrations at three crop stages (Jul, Oct, and Dec) in (**a**) 2023 and (**b**) 2024. Nutrients: nitrogen (N) in %, phosphorus (P) in ppm, and potassium (K) in ppm.

3.4. Productive Parameters of Strawberry Cultivar 'San Andreas'

BL produced the largest fruits in terms of individual fruit weight (16.4 ± 7.12 g and 14.0 ± 5.06 g in 2023 and 2024, respectively), and this difference was statistically significant compared to the control (Con) (Figure 5). In accordance with Figure 5, Table 4 indicates that BL and PM treatments resulted in the lowest percentage of small fruits (<7 g) and the highest percentage of fruits exceeding 20 g, in both 2023 and 2024. Colorimetric analysis indicated that the BL and FerC treatments resulted in the highest color index in 2023, showing statistically significant differences compared to Con; in 2024, the color index was similar across all treatments (51.5–54.8 g/kg), and no significant statistical differences were observed (Table 5). Additionally, BL produced slightly firmer fruits in both 2023 and 2024; however, this difference was not statistically significant compared to Con (Table 5). The bacterial and FerC treatments showed higher fruit acidity, but no significant differences were observed compared to the control (Table 5). In 2023, the TSS content of FerC, BL, and PM was slightly lower, while in 2024 it was similar for all treatments (4.3–4.9 °Brix); however, as with acidity, no statistically significant differences were observed (Table 5). Ratio values were similar across all treatments in both trials (0.5–0.7 in 2023 and 0.3–0.4 in 2024), with no statistically significant differences relative to Con (Table 5).

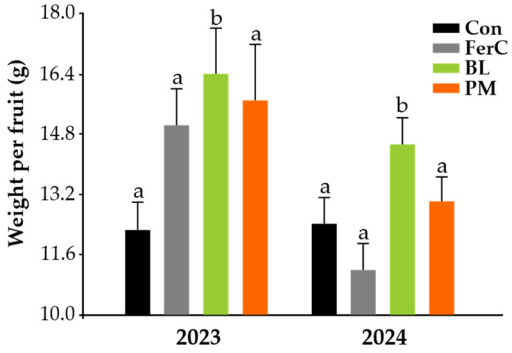

Figure 5. Fruit weight per treatment. Different letters among treatments indicate statistically significant differences compared to the control (Con) (Dunnett's test, $p < 0.05$); the lines above the bars indicate the standard error.

Table 4. Percentage of fruits by individual weight (%). Categories: fruits weighing less than 7 g (<7 g); fruits weighing between 7 and 20 g (7–20 g); and fruits weighing more than 20 g (>20 g). Values calculated from fruits collected per treatment throughout the growing cycle.

Trial	Treatment	Fruit Categorization Based on Individual Weight (%)		
		<7 g	7–15 g	>20 g
2023	Con	17.5	74.6	7.90
	FerC	18.6	61.4	21.4
	BL	10.0	62.5	30.0
	PM	16.7	61.1	25.0
2024	Con	27.5	65.2	6.2
	FerC	28.8	67.2	8.1
	BL	4.60	88.4	9.3
	PM	4.5	88.6	9.1

Table 5. Color index, firmness, acidity, and total soluble solids (TSS) of fruits (mean ± standard error). Different letters among treatments indicate statistically significant differences compared to the control (Con) (Dunnett's test, $p < 0.05$).

Trial	Treatment	Color Index	Firmness (°Shore)	Acidity (eq. Citric Acid/mL)	TSS (°Brix)	Ratio
2023	Con	53.9 ± 3.1 [a]	44.0 ± 2.0 [a]	9.9 ± 1.1 [a]	6.8 ± 0.7 [a]	0.7 ± 0.1 [a]
	FerC	65.8 ± 1.6 [b]	45.5 ± 1.9 [a]	11.8 ± 0.9 [a]	6.2 ± 0.3 [a]	0.5 ± 0.04 [a]
	BL	65.7 ± 3.5 [b]	46.1 ± 2.3 [a]	10.5 ± 0.7 [a]	5.6 ± 0.4 [a]	0.5 ± 0.06 [a]
	PM	57.0 ± 2.8 [a]	42.0 ± 2.5 [a]	13.7 ± 2.9 [a]	6.2 ± 0.2 [a]	0.5 ± 0.1 [a]
2024	Con	51.5 ± 1.7 [a]	43.2 ± 1.3 [a]	10.2 ± 0.7 [a]	4.3 ± 0.2 [a]	0.4 ± 0.01 [a]
	FerC	53.0 ± 2.1 [a]	42.8 ± 1.7 [a]	14.2 ± 1.1 [a]	4.9 ± 0.3 [a]	0.3 ± 0.03 [a]
	BL	54.8 ± 3.0 [a]	44.5 ± 2.1 [a]	14.1 ± 1.9 [a]	4.7 ± 1.9 [a]	0.4 ± 0.04 [a]
	PM	53.9 ± 2.9 [a]	41.0 ± 2.4 [a]	14.6 ± 1.8 [a]	4.3 ± 0.4 [a]	0.3 ± 0.03 [a]

With respect to anthocyanin content, all treatments showed significantly higher values compared to the control in both seasons (Figure 6). Additionally, BL and PM exhibited significantly higher ascorbic acid contents, whereas FerC showed a statistically significant increase only in 2024. FerC and BL presented the higher phenolic compounds contents; these increases were statistically significant in both trials for FerC and only in 2023 for BL (Figure 6). Finally, antioxidant activity was higher in BL and PM, although statistically significant differences were only observed between BL and the control from both seasons (Figure 6).

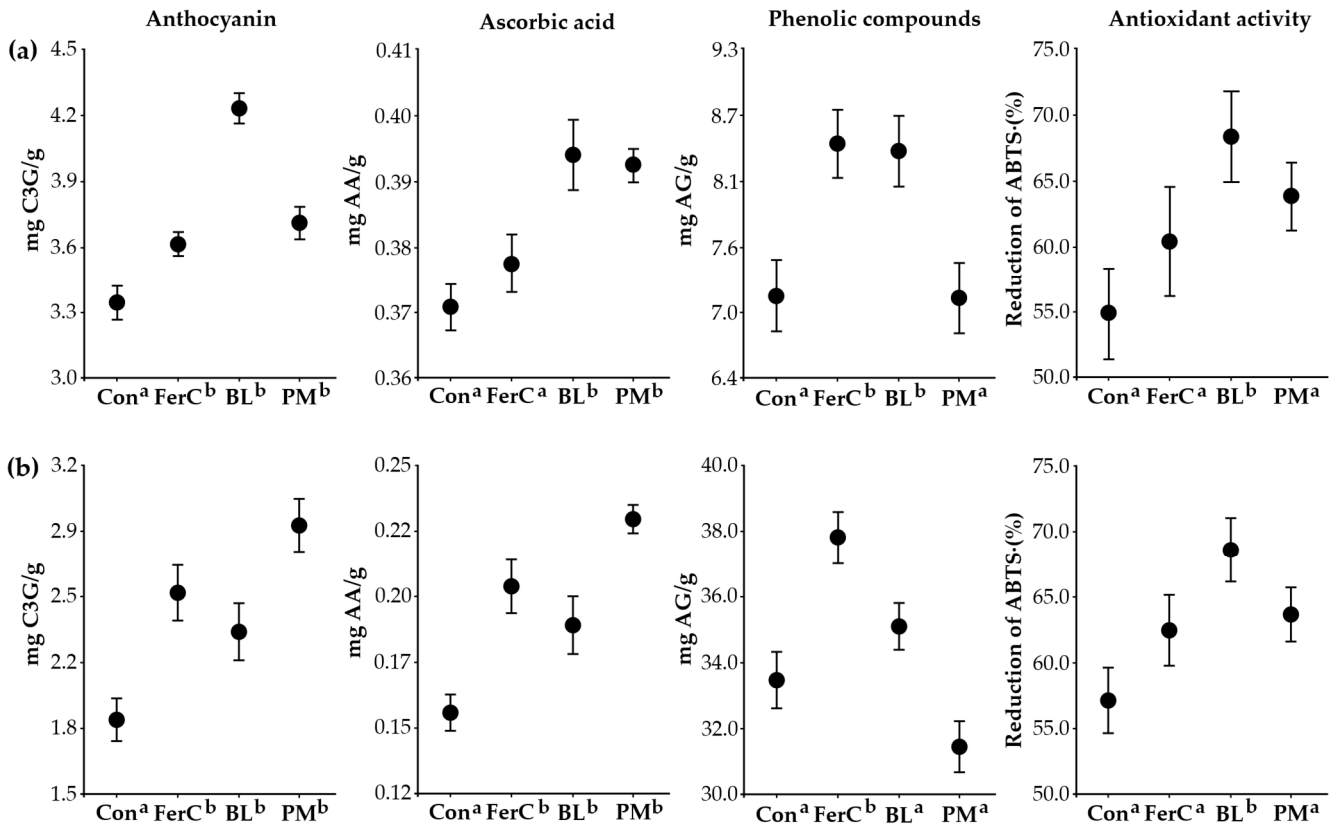

Figure 6. Biochemical properties of the harvested fruits in (**a**) 2023 and (**b**) 2024. Ref.: anthocyanin content (mg cyanidin-3-glucoside/g); ascorbic acid content (mg ascorbic acid/g); phenolic compounds content (mg gallic acid/g); and antioxidant activity (reduction of ABTS radical in %). Different letters among treatments indicate statistically significant differences compared to the control (Con) (Dunnett's test, $p < 0.05$); the lines above the dots indicate the standard error.

3.5. Mechanisms of Bacterial Action In Vitro

The positive (+) and negative (−) results of bacterial mechanisms of action are summarized in Table 6. The in vitro phosphate solubilization assay was negative, as no clear halo formed around the inoculated bacteria. However, both bacteria showed a positive response in the phytase production assay, with the formation of a clear halo around the colonies (Figure 7a). Regarding the siderophore production assay, a clear orange coloration was observed in the culture medium of PM, indicating a positive result (Table 6, Figure 7b). The BL culture also exhibited orange pigmentation in the culture medium, although with lower intensity than that observed for PM. Additionally, both BL and PM showed positive IAA production at 37 °C (Figure 8a) and at room temperature (Figure 8b) (Table 6). In particular, PM showed higher IAA production compared to BL at both temperatures, reaching 10.36 and 9.3 µg IAA/mL at 25 °C and 37 °C, respectively. BL produced IAA exponentially at 25 °C, but its production decreased at 37 °C after 15 days of culture (Figure 8).

Table 6. Positive (+) and negative (−) results of the mechanism of bacterial action in vitro.

Mechanism	*B. licheniformis* (BL)	*P. mendocina* (PM)
Phosphate solubilization	−	−
Phytase production	+	+
Siderophore production	+ (low)	+
IAA production	+	+

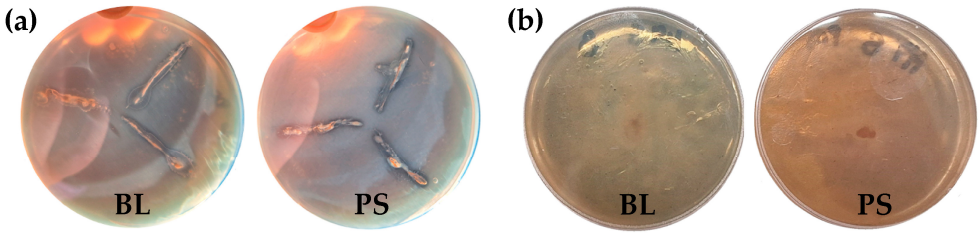

Figure 7. In vitro (**a**) phytase production and (**b**) siderophore production for *B. licheniformis* (BL) and *P. mendocina* (PM).

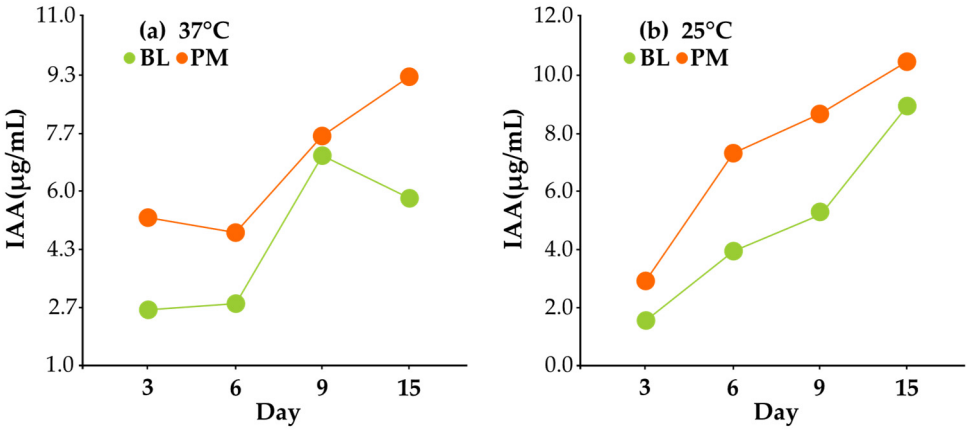

Figure 8. Indoleacetic acid (IAA) production by *B. licheniformis* (BL) and *P. mendocina* (PM) at (**a**) 37 °C and (**b**) room temperature (25 °C).

4. Discussion

Enhancing food production in terms of both quantity and quality remains one of the primary challenges in the agricultural sector. Although synthetic agrochemicals have been extensively employed to meet this demand, accumulating evidence indicates that their prolonged use contributes to soil degradation, the emergence of novel phytopathogens, and contamination of groundwater resources. Consequently, scientific efforts have increasingly focused on the development of alternative, bio-based inputs that align with the demands of both sustainable agriculture and environmental stewardship. Among these, the application of plant growth-promoting bacteria (PGPB) has garnered considerable attention due to their multifaceted benefits for soil health, plant development, and ecological balance. Particularly, soil microorganisms play a crucial role in the decomposition of organic matter, facilitating the release and biochemical transformation of nutrients into plant-available forms [43,44]. In this study, two bacteria (*B. licheniformis* and *P. mendocina*) were isolated from a chicken-waste compost tea and applied to strawberry soils. According to molecular analysis, strain *P. mendocina* is more appropriately described as a *Pseudomonas* sp. closely related to *P. mendocina*. Hence, this similarity alone is insufficient for a definitive species assignment; however, the MALDI-TOF method confirmed this strain as *P. mendocina*. Nevertheless, further taxonomic resolution would require the analysis of additional housekeeping genes (e.g., *gyrB*, *recA*, *atpD*) or a multilocus sequence analysis (MLSA) approach.

Both bacteria improved the soil's chemical parameters, increased fruit weights, and some quality parameters such as color, anthocyanin, ascorbic acid, phenolic compound contents, and antioxidant activity. In statistical terms, bacterial performance was more pronounced in the 2023 trial. Nevertheless, the trends observed in 2024 were comparable across most measured parameters. Climatic conditions influence crop development, which may account for these differences. According to meteorological data from the FAVE Campus

weather station (Esperanza, Santa Fe), average temperatures during June–December 2023 were lower than those recorded in 2024 (13.1–23.4 °C and 20.8–30.9 °C for 2023 and 2024, respectively), while cumulative precipitations was higher, particularly between October and December (507.8 mm and 333.2 mm for 2023 and 2024, respectively). In this regard, the hypothesis that meteorological parameters may have influenced bacterial performance in the soil is considered. Consequently, new trials are required to evaluate the effects of precipitation and temperature on microbial activity. On the other hand, and from a statistical standpoint, *B. licheniformis* showed a better performance than *P. mendocina* for most of the analyzed parameters. Numerous studies have documented the effects of various *Bacillus* species, such as *B. velezensis*, *B. subtilis*, *B. safensis*, and *B. megaterium* (e.g., [45–55]) as well as *Pseudomonas* species, including *P. fluorescens*, *P. putida*, and *P. monteilii* (e.g., [46,49,52,56,57]) on strawberry production parameters. However, aside from the study conducted by Seema et al. [58], no research to date has evaluated the impact of soil application of *B. licheniformis* and *P. mendocina* on strawberry yield and quality traits. Therefore, the present study represents one of the first reports addressing this gap.

4.1. Impact of Bacteria on Soil Chemical Properties

The abundance and diversity of microorganisms generated during composting processes contribute to the release of substances that activate various mechanisms of action, such as the solubilization and/or mineralization of non-labile nutrient-containing molecules. These processes increase the concentration of nutrients available in the soil and, consequently, enhance their absorption by plants [46].

In 2023, BL and PM treatments exhibited the highest values of exchangeable Na^+ and Mg^{2+}, whereas BL achieved the best performance in available P levels, particularly in 2024. Moreover, soil pH and electrical conductivity (EC) remained stable after bacterial application, showing values comparable to the initial analysis. This outcome can be attributed to the broad spectrum of mechanisms through which bacteria act in soils [13,14], facilitating nutrient availability to plants without disrupting the soil's functional dynamics. Arunrat et al. [59] reported a positive correlation between the microbial community (especially *Bacillus*) and several soil properties, including pH, EC, available phosphorus, and CEC. Similarly, optimizing CEC and exchangeable cation content following bacterial application has been associated with greater nutrient availability and uptake by plants [60]. Furthermore, the diverse interactions between bacteria and soil minerals (such as dissolution, transformation, reduction, siderophore production, and chelation) directly influence nutrient availability and enhance plant absorption [61].

Regarding nitrogen, no changes were detected in the soil N content under treatments with either the commercial fertilizer or the bacterial inoculant. However, plants treated with bacteria (particularly *P. mendocina*) exhibited higher foliar N levels, suggesting an effective transformation of nitrogen compounds into forms available for plant uptake. Evidence indicates that both *B. licheniformis* [62–64] and *P. mendocina* [65–69] are nitrogen-fixing bacteria capable of converting nitrogen fertilizers into bioavailable forms for plants.

One of the main mechanisms by which bacteria act is their ability to solubilize phosphates. Phosphorus is an essential nutrient for plants, as it plays a critical role in DNA synthesis, cell membrane formation, respiration, and photosynthesis. However, P often limits crop productivity due to its chemical binding to colloidal soil surfaces and fixation with elements such as aluminum, iron, and calcium, depending on soil pH [70]. Consequently, both chemical and biological processes are required to enhance its availability. Although total soil P content was lower in plots treated with bacteria compared to other treatments, the available P in the soil and the total foliar P content were higher in plants treated with *B. licheniformis* and *P. mendocina*. Numerous studies have demonstrated that many bacteria

solubilize phosphates through the production of organic acids and phosphatase enzymes (including phytases), thereby increasing the availability of this essential nutrient [71–75]. Despite this evidence, the in vitro phosphate solubilization assay yielded negative results for both bacterial strains tested. Timofeeva et al. [76], however, highlight conflicting reports regarding the influence of temperature on phosphate solubilization, with some studies identifying an optimal range of 20–25 °C, while others report activity up to 45 °C. This variability may explain the negative results obtained under the conditions applied in this work and suggests the need to repeat the assays at different temperature ranges, given that both *B. licheniformis* [62,63,77–79] and *P. mendocina* [65–67,80,81] are widely recognized as phosphate solubilizers. Nevertheless, positive results were obtained for phytase enzyme production in both strains. Phytases, a subclass of phosphatases, hydrolyze phytic acid (phytate) and release P, Zn^{2+}, Cu^{2+}, Ca^{2+}, Fe^{3+}, and Al^{3+} in inorganic forms, thereby improving mineral uptake by plants [82]. Several studies have confirmed the ability of bacteria, particularly those belonging to the genera *Bacillus* and *Pseudomonas*, to secrete phytases in diverse environments [82–84].

Siderophore production is another widely studied bacterial mechanism that influences Fe^{3+} availability in plants. Siderophores are low-molecular-weight organic compounds that chelate Fe^{3+}, thereby facilitating iron uptake by plants and contributing to spatial competition against pathogens [77,85]. *P. mendocina* exhibited positive results in the in vitro siderophore production assay, consistent with previous reports [86–88]. In contrast, siderophore production by *B. licheniformis* was negligible, which contradicts findings reported by other authors [78,85,89,90]. However, Bordé-Pavlicz et al. [85] noted strain-dependent variability in siderophore production within *B. licheniformis*, with some strains showing positive results and others negative. This variability may explain the absence of siderophore detection in the present study.

4.2. Impact of Bacteria on Productive Parameters

Bacterial treatments affected fruit weight, with the most pronounced effects observed in plants treated with *B. licheniformis*. As previously noted, although no studies have specifically evaluated the application of *B. licheniformis* -except Seema et al. [58], who reported comparable outcomes- and *P. mendocina* in strawberry cultivation, both bacteria have shown promising results in other crop systems. Thus, soil application of *B. licheniformis* has been shown to enhance root system volume, germination rate, plant height, foliar development, and overall yield in various crops, including tomato crops [91–93], pepper [93], maize [89,94], peanut [95,96], potato [85], and quinoa [78]. Additionally, *B. licheniformis* has demonstrated efficacy under abiotic stress conditions, such as soil salinity [78,92]. The use of *P. mendocina* as a plant growth-promoting in soil crops is scarce; only a few studies in lettuce [81,97], basil [98], tomato, and wheat [99] have been reported. Most studies on this bacterium have focused on its bioremediation capacity in soils contaminated with diverse pollutants [86,100–104]. Therefore, this study represents one of the first reports on the application of *P. mendocina* in crops.

Conversely, soil microbial biomass has been shown to contribute to the synthesis of phytohormones that act as plant growth regulators, independent of nutrient availability, thereby enhancing plant development and productivity [44]. Among the predominant genera, *Bacillus* and *Pseudomonas* are recognized for their capacity to produce key plant growth-promoting hormones, including auxins, IAA, gibberellins, and abscisic acid [105]. In this study, both bacterial strains showed a progressive production of IAA over the 15 days, with a continuous increase in concentration, which may partially explain the greater fruit weight and improved quality observed under bacterial treatments. Several studies have reported the production of IAA by these bacteria, although the recorded

concentrations varied. For *B. licheniformis*, IAA levels ranging from 2.5 to 35 µg/mL have been documented [62,85,91,95,106], which are consistent with the findings of the present study. Higher IAA concentrations, reaching up to 200 µg/mL, have also been reported, depending on the specific strain used [78,107]. No studies have been found that quantify IAA production by *P. mendocina*; therefore, this study constitutes the first report.

Regarding the organoleptic properties of the fruit, plants treated with *B. licheniformis* showed significant improvements in anthocyanin content, ascorbic acid, and antioxidant activity in both 2023 and 2024, whereas the increase in phenolic compounds was significant only in 2023 for BL. For the *P. mendocina* treatment, only anthocyanin and ascorbic acid contents exhibited statistically significant increases. Fruit firmness, acidity, and total soluble solids content were similar across all treatments in both experimental years, with the exception of the color index, which was significantly higher in BL and FerC. In terms of fruit firmness, several studies have found no significant differences following bacterial treatment [49,56]. Similarly, the TSS content observed in this study was lower than values reported in previous investigations involving *Bacillus* [47,48,52,54,58,108] and *Pseudomonas* [47,52]. In contrast, the ascorbic acid content recorded here was comparable to that reported in earlier studies [52,58,108]. However, the concentrations of anthocyanins, total phenolic compounds, and antioxidant capacity measured in the present study exceeded those documented by the aforementioned authors for both bacterial genera.

Furthermore, several authors agree that fruit ripening involves various biochemical and physiological processes that lead to color changes, driven in part by the accumulation of anthocyanins and sugars, as well as alterations in acidity [109,110]. Although no significant differences were observed in TSS or acidity between the *B. licheniformis* and control treatments, the fruits harvested from plants treated with exhibited a high anthocyanin content, reflected in the highest color index recorded for this treatment. Fruits harvested from *P. mendocina*-treated plants also showed elevated anthocyanin levels (albeit lower than *B. licheniformis*), but their color index did not differ significantly from the control. Notably, *B. licheniformis* stood out for its elevated levels of ascorbic acid, phenolic compounds, and antioxidant activity. Scientific evidence supports a positive correlation among these three variables in various fruits [111]. Moreover, fruits rich in anthocyanins have been shown to possess greater antioxidant capacity [112,113], consistent with the enhanced color index and anthocyanin content observed in *B. licheniformis*. A similar trend was observed for *P. mendocina*, except for its phenolic compound content, which was comparatively low with respect to other treatments. Although phenolic compounds are known for their strong electron-donating capacity and contribution to antioxidant activity, their specific composition and distribution within different fruit tissues can significantly influence antioxidant potential, either positively or negatively [114].

5. Conclusions

Based on the results obtained, the bacteria isolated from chicken compost tea (primarily *B. licheniformis*) may be considered promising candidates for enhancing the productivity, yield, and quality of strawberries. These microorganisms not only improved several soil physicochemical properties (available P, total Na, exchangeable Na^+, and exchangeable Mg^{2+}) but also significantly increased yield and most assessed quality parameters, including color index, anthocyanin concentration, ascorbic acid content, total phenolic compounds, and antioxidant activity. Moreover, both *B. licheniformis* and *P. mendocina* demonstrated beneficial mechanisms of action, particularly in nutrient mobilization within the soil (e.g., phytase and siderophore production) and in promoting plant growth (e.g., IAA synthesis). The trends observed across all analyzed parameters were similar in 2023 and 2024; however, bacterial activity was greater in 2023 than in 2024. Although multiple

factors influence crop development, we believe that the low rainfall recorded in 2024 may have directly affected the activity of the bacteria applied to the strawberry plants. These findings highlight the need for further studies to evaluate the impact of climatic conditions on bacterial activity in crop soils. Moreover, further complementary studies, such as raised bed trials and fruit nutrient profiling, are warranted to validate these effects and investigate additional application strategies under diverse agronomic conditions. These findings may contribute to the development of more efficient and sustainable biological inputs for agricultural systems.

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