Current **A**pplied **S**cience and **T**echnology e-ISSN: 2586-9396

Curr. Appl. Sci. Technol. 2026, Vol. 26 (No. 2), e0266217

Research article

Isolation, Screening, and Molecular Identification of Plant Growth-Promoting Rhizobacteria from Maize Rhizosphere Soil

Bartholomew Saanu Adeleke* and Soji Fakoya

Microbiology Programme, Department of Biological Sciences, Olusegun Agagu University of Science and Technology, P.M.B. 353, Okitipupa, Ondo State, Nigeria

Received: 6 February 2025, Revised: 21 May 2025, Accepted: 23 May 2025, Published: 8 July 2025

Abstract

The biotechnological relevance of rhizosphere microbiomes with diverse mechanisms underlining their survival under harsh environments for improved plant nutrition and resilience against drought and phytopathogens cannot be over-emphasized. We aimed to isolate, screen, and molecularly identify plant growth-promoting bacteria from the maize soil sourced from different farmlands in the coastline areas of Ondo State, Nigeria. The bacteria isolated were identified molecularly using 16S rRNA gene sequencing. Twenty culturable bacterial isolates were subjected to plant growth-promoting screening, biocontrol test, and drought, heavy metals [lead ($PbSO_4$), cadmium ($CdSO_4$), zinc ($ZnSO_4$), and copper ($CuSO_4$)], and salt (NaCl) tolerance tests. The three bacteria with positive results for the tests were selected and identified as *Serratia marcescens* BSE_1*, Bacillus cereus* BSA_1*,* and *Proteus mirabilis* BSI_1. *P. mirabilis* BSI_1 exhibited biocontrol activities of 2.9 mm against the pathogenic fungus, *Sclerotium rolfsii,* and high tolerance of 41% and 46% to $ZnSO_4$ and $CdSO_4$ at 0.1% and 0.2%, respectively. The high $PbSO_4$ tolerance of 89% and $CuSO_4$ tolerance of 98% by *S. marcescens* BSE_1 and *B cereus* BSA_1 were recorded in an inoculated medium supplemented with 0.3% $PbSO_4$ and $CuSO_4$. The high salt (NaCl) tolerance of 76% at 0.1% and 0.2% were recorded for *B. cereus* BSA_1*,* and *P. mirabilis* BSI_1 compared to the control. The experimental trials involving greenhouse and field bioinoculation showed a significant effect of mixed drought-tolerant bacteria on maize growth compared to the control. Therefore, harnessing these rhizobacteria as bioinoculants to maximize coastal agricultural productivity can help ensure food security.

Keywords: beneficial soil bacteria; cereal-grain-maize; heavy metal-induced stress; coastal line microbial resources; 16S rRNA gene sequencing; sustainable agriculture

1. Introduction

Environmentally induced stresses due to drought and heavy metals pose serious threats to agricultural productivity in major countries of the world and these have resulted in the loss of crop yield and economic values, food shortage and limited raw materials supply to

*Corresponding author: E-mail: bs.adeleke@oaustech.edu.ng; microbade@yahoo.com
https://doi.org/10.55003/cast.2025.266217

Industries, and food insecurity (Barbetti et al., 2012; Gamalero & Glick, 2022; Ghanem et al., 2024). For more than 5 decades, drought stress has caused a reduction in cereal-grain production by 10%, and a loss of arable land due to drought is envisaged to result in a 50% loss of grain productivity by 2050 (Ghanem et al., 2024). Also, an insufficient supply of water to plants can result in plant stress, thereby affecting diverse plant functional processes by retarding plant growth, causing loss of membrane integrity, reducing photosynthetic rate, lowering growth hormone synthesis, etc. (Muhammad et al., 2023; Adeleke et al., 2024). To this premise, it is important to devise stringent approaches to mitigate the impact of water deficiency on plant nutrition by boosting plant resilience to drought stress. One such approach employed recently is the exploration of beneficial plant growth-promoting rhizobacteria (PGPR) in managing diverse agricultural problems for improvement of plant nutrition and defense against pathogens (Wang et al., 2021; Khan & Mehmood, 2023).

Maximizing the use of beneficial soil microorganisms plays a vital role in restoring soil nutrients, controlling plant pathogens, and enhancing plant resilience to drought, ultimately improving agricultural productivity (Oyedoh et al., 2023). Recently, a study by Agunbiade et al. (2024) validated the efficacy of PGPB in the genera *Aeromonas* upon inoculation in ameliorating drought stress in maize at varied water regimes, improving its parameters such as plant fresh weight, plant height, chlorophyll content, electrolyte leakage, stem girth, and number of leaves. The effect of rhizobacteria *Acinetobacter pittii*, *Bacillus lichiniformis*, and *Pseudacidovorax intermedius* inoculation on sorghum are known to enhance the seedlings' growth in terms of increase in root length and shoot length and improve seedling vigor index and total dry matter production under drought stress (Umapathi et al., 2022). Bacteria adopt resistance mechanisms to drought damage through the production of growth factors, such as gibberellins, indole-3-acetic acid, and siderophores (Ghanem et al., 2024). The diverse rhizobacteria genera, *Pantoea* (Noori et al., 2021), was reported to enhance plant growth and alleviate drought stress in Alfafa; similarly, the impact of *Bacillus* and *Agrobacterium* from wheat (Zafar-ul-Hye et al., 2019), *Bradyrhizobium*, *Azospirillum*, *Rhizobium* from soybean (Igiehon et al., 2019; Silva et al., 2019) was reported to enhance plant growth under drought stress, boosting crop production.

Despite the work on beneficial maize-soil-associated bacteria (Qaisrani et al., 2019; Efthimiadou et al., 2020; Peng et al., 2021), less information is available on the identifiable rhizobacteria from maize rhizosphere in the coastal line regions of Ondo State, Nigeria, which necessitated this research. This research, therefore, focused on how rhizobacteria could be harnessed to boost maize resilience to drought and metal stresses. We hypothesized that the soil collected from drought-prone farmlands may harbor multifaceted beneficial microorganisms that can actively participate in regulating soil osmotic threshold, thereby mitigating drought stress impact on crops for improved yield. In this study, we reveals the plant growth-promoting attributes of the identifiable rhizobacterial isolates, their tolerance to different concentrations of salt and heavy metals, and the bioinoculation efficacy on maize growth.

2. Materials and Methods

2.1 Soil sample collection from agricultural farmlands

A modified method described by Kifle et al. (2016) was employed for soil sample collection. Maize soil samples were randomly collected from four different points at a depth of 8-10

cm in mixed farmlands in the by-pass area of Ayeka and Supreme Court Street, Igodan in Okitipupa Local Government and Igbobini in Ilaje Local Government in Ondo State, Nigeria. The farmlands in Okitipupa have coordinates of N 6°38'45.58188" Latitude and E 4°46'31.23012" Longitude (Ayeka) and N 6°45'34.578" Latitude and E 4°77'70.879" Longitude (Igodan). The farm was in its 4th year of use with planting at intervals. Natural manure was used to condition the soil for plant growth. The plants were about 3-4 months old. Also, the farmland in Igbobini has coordinates of N 6°30'57.51648" Latitude and E 4°52′25-56372" Longitude. The farmland was subsistent in nature and had been cultivated for more than 24 years of farming, both mono and mixed cropping practices. The maize growth was enhanced by fertilizer (20:20:10) application. The plants were about 2 weeks old. The maize soil samples collected from Ayeka, Igodan, and Igbobini were designated as AYMS, IGDMS, and IGMS, respectively (i.e., AYMS – Ayeka maize soil, IGDMS – Igodan maize soil, and IGMS – Igbobini maize soil). A total of 12 maize samples (i.e., 3 from each point), along with adhering rhizosphere soil, were collected from each farmland. Then, the rhizosphere soils from healthy maize samples were placed in sterile Ziplock bags, labeled, and transported to the Microbiology Laboratory, Olusegun Agagu University of Science and Technology, Okitipupa, Ondo State for further analysis. Triplicate samples were randomly collected from four points within the agricultural farmlands.

2.2 Bacterial isolation from maize soils

Bacterial isolation was achieved by serial dilution and pour-plating techniques. First, the point soil samples from each farmland were mixed, and 1.0 g of each was aseptically dispensed into a 9.0 mL test tube containing sterile distilled water and serially diluted up to 10^6 dilutions. A 0.1 mL aliquot from the dilutions 10^{-4} and 10^{-5} folds was pipetted and gently dispensed into sterile Petri dishes in triplicate before pour-plating with already sterilized nutrient agar (ReadyMED®-RDM-NA-01, Chaitanya Group of Industries, Chaitanya Agro Biotech PVT. Ltd, India). The plates were allowed to solidify and incubated for 24 h at 37°C. The distinct bacterial colonies were counted and recorded. The observed colonies were selected based on their morphology and further purified by streaking to obtain pure cultures. The pure bacterial isolates were preserved in 25% sterile glycerol in 2.0 mL Eppendorf tubes, incubated at 37°C, and stored in a refrigerator for further microbial analysis. The morphological features of the colonies: shape, size, color, elevation, margin, optical characteristics, consistency, colony surface, and arrangement, were observed and recorded after incubation of the culture plates. Following Gram staining of the purified bacterial isolates, the following biochemical tests were conducted: catalase, motility, hydrogen sulfide production, indole, and starch hydrolysis, according to the standard procedures described by Clarke and Cowan (1952). Sugar fermentation tests were also performed using the following sugars: glucose, fructose, lactose, maltose, and sucrose.

2.3 Rhizobacteria screening for plant growth-promoting properties

2.3.1 Phosphate solubilization screening

The ability of the bacterial isolates to solubilize phosphates was tested on modified Pikovskaya agar composed of 0.2 g KCl, 10 g glucose, 0.1 g $MgSO_4.7H_2O$, 0.5 g yeast extract, 5 g $Ca_3(PO_4)_2$, 0.002 g $FeSO_4.7H_2O$, 0.5 g $(NH_4)_2SO_4$, 0.2 g NaCl, 0.002 g $MnSO_4.H_2O$, 15 g agar, and 1000 mL sterile distilled water. The medium was sterilized at 121°C for 15 min, allowed to cool, and pour-plated. The Petri dishes were spot-inoculated

at the center with the selected isolates and incubated at 35°C for 3-5 days. The development of clear zone around a colony showed positive results, while the un-inoculated plates served as control. For the quantitative screening, the bacterial isolates, *S. marcescens, B. cereus,* and *P. mirabilis* were inoculated into the sterilized Pikovskaya's broth medium supplemented with tricalcium phosphate and incubated for 72 h at 35°C. The medium was centrifuged at 6,000 rpm for 10 min and the optical density was determined using a spectrophotometer (INESA, China) at 882 nm. The solubilizing ability of the bacterial isolates was calculated using the standard curve (Arruda et al., 2013).

2.3.2 Screening for Indole-3-acetic acid (IAA)

The screening of the bacterial isolates for IAA production was achieved using Salkowski reagent technique. The freshly 24-h cultured bacterial isolates were inoculated into the nutrient broth amended with 0.1% L-tryptophan and without L-tryptophan inside test tubes and incubated on a rotary shaker at 180 rpm for 48 h before centrifugation at 8,000 rpm for 10 min. Three drops of orthophosphoric acid and 4 mL Salkowski reagent were added to the 2 mL supernatant of the culture filtrate and then incubated in the dark for 30 min. The development of pink coloration indicated a positive result for IAA production. The quantity of the IAA produced was estimated by measuring the optical density (OD) of the IAA medium inoculated with the bacterial isolates using a spectrophotometer (INESA, China) at 535 nm and the values obtained were compared to a standard curve (Arruda et al., 2013).

2.3.3 Hydrogen cyanide (HCN) production

This test was performed by placing a sterilized Whatman filter paper soaked in 2% sodium carbonate and 0.05% picric acid solution inside test tubes containing sterile nutrient broth amended with glycine (4.4 g/L). The mouth of each test tube was plugged with sterile cotton wool and incubated at 30°C for 4 days. The color change of the filter paper from yellow to red-brown indicated a positive result for hydrogen cyanide production. The test tubes without bacterial inoculation served as a control (Agbodjato et al., 2015).

2.3.4 Ammonia production

The ammonia test was performed by inoculating bacterial isolates into 10 mL sterilized peptone water and then incubating at 30°C for 48 h on a rotary shaker. After incubation, 0.5 mL of Nessler’s reagent was added to each test tube and allowed to stand for 5 min. The observed slight yellow to brown indicated a positive reaction. Un-inoculated tubes served as control (Agbodjato et al., 2015).

2.3.5 Exopolysaccharide production

An exopolysaccharide test was performed by supplementing nutrient broth with 10% sucrose. The pH of the medium was adjusted to pH 7 and sterilized at 121°C for 15 min. A sterile Whatman paper (3 mm diameter) was gently placed on the Petri dishes. A 24-h-old bacterial culture was inoculated directly on the Whatman paper and then incubated at 30°C for 24 h. The formation of mucoid appearance on the filter paper indicated a positive test. Un-inoculated plates served as control (Igiehon et al., 2019).

2.3.6 Nitrogen fixation

The nitrogen fixation test was performed using Jensen's medium composed of 20 g sucrose, 0.5 g NaCl, 0.5 g $MgSO_4.7H_2O$, 1.0 g K_2HPO_4, 0.005 g Na_2MoO_4, 2.0 g $CaCO_3$, 0.1 g $FeSO_4.7H_2O$ and 15 g agar in 1,000 mL sterile distilled water. The broth medium was adjusted to pH 7.2, sterilized at 121°C for 15 min, allowed to cool, and poured plated aseptically. The Petri dishes were inoculated and incubated at 30°C for 5 days. The observed growth of bacterial isolates on the incubated Petri dishes indicated a positive result for the nitrogen-fixing ability of the rhizobacteria. Un-inoculated plates served as control (Igiehon et al., 2019).

2.4 Rhizobacterial screening for extracellular enzymes

The bacterial isolates were qualitatively screened for the following enzymes, which include mannanase, cellulase, amylase, and lipase.

2.4.1 Mannanase

A medium containing 0.5 g magnesium sulfate ($MgSO_4$), 1 g dipotassium hydrogen phosphate (K_2HPO_4), 1 g ammonium chloride (NH_4Cl), 0.001 iron sulphate ($FeSO_4$), 0.1 g calcium chloride ($CaCl_2$), 0.5 g sodium chloride (NaCl), 3 g locust bean gum, 13 g agar, and 1000 mL sterile distilled water was prepared. The pH of the medium was adjusted to 7.2 before sterilization. The sterilized medium was aseptically dispensed into the sterile Petri dishes and allowed to solidify. The Petri dishes were spot-inoculated at the center with the 24-h-old bacterial cultures and incubated at 28°C for 48 h. The plates were flooded with iodine solution for 15 min, decanted, and further flooded with sodium chloride (1 M) for 15 min. The clear zones around the colony indicated mannanase production. The plates without bacterial inoculation served as a control (Adeleke et al., 2022).

2.4.2 Cellulase

Carboxymethyl cellulose (CMC) was used as a substrate for cellulase screening. The CMC-amended nutrient agar was sterilized, pour-plated, and allowed to cool. The Petri dishes were inoculated with fresh bacterial cultures and incubated at 28°C for 48 h. Then flooded with 1% (w/v) Congo red for 5 min and later washed with NaCl (1 M) for 10 min. The zone of clearance around the colony indicated a positive for cellulase production. An un-inoculated plate served as a control (Adeleke et al., 2022).

2.4.3 Amylase

The amylase production medium was composed of 0.5 g magnesium sulphate ($MgSO_4$), 5 g peptone, 0.01 g iron sulphate ($FeSO_4$), 5 g yeast extract, 0.01 g sodium chloride (NaCl), 10 g soluble starch, 15 g agar, and 1000 mL sterile distilled water. The starch medium was sterilized and pour-plated. The Petri dishes were spot-inoculated and incubated at 37°C for 24 h. The incubated plates were flooded with Lugol's iodine solution (0.2% iodine, 0.4% potassium iodide, and 100 mL distilled water) and allowed to stand for 10 min. The clear zones around the colony indicated positive results for amylase production while the un-inoculated plate served as control (Adeleke et al., 2022).

2.4.4 Lipase

A lipase medium composed of peptone (0.4%), KH_2PO_4 (0.15%), $(NH_4)_2SO_4$ (0.1%), NaCl (0.05%), $MgSO_4 \cdot 7H_2O$ (0.05%), peanut oil emulsion (12%), and agar (2%) was used for the lipase-producing potential of the identifiable rhizobacteria. The pH of the medium was adjusted to 7.8 and sterilized in an autoclave at 121°C for 20 min. The medium was allowed to cool, pour-plated, inoculated, and incubated at 37°C for 2 days. The zone of clearance around the colony indicated lipase production, while un-inoculated plates served as control (Ma et al., 2010)

2.5 Rhizobacteria response to salinity and heavy metals

This was achieved by amending nutrient broth inside test tubes with salt (NaCl) at different concentrations (1, 3, and 5%). The medium was sterilized, allowed to cool, inoculated with freshly grown bacterial culture, and incubated at 30°C on a rotary shaker at 150 rpm for 72 h. Similarly, for heavy metals, $PbSO_4$, $CdSO_4$, $ZnSO_4$, and $CuSO_4$, tolerance was performed by amending nutrient broth with 100 mg/L of each heavy metal. The medium was sterilized at 121°C for 15 min, inoculated with fresh bacterial culture, and incubated at 30°C on a rotary shaker at 150 rpm for 72 h. The salt (NaCl) and heavy metal tolerance were measured at 520 nm using a spectrophotometer (Fasusi et al., 2021).

2.6 Antagonistic potential of screened rhizobacterial isolates

A dual culture technique was employed in evaluating the antagonistic activities of the bacterial isolates on the *S. rolfsii.* The pathogenic fungus, *S. rolfsii*, was obtained from the research laboratory of the Department of Crop, Soil and Pest Management of the Olusegun Agagu University of Science and Technology, Okitipupa, Nigeria. The fungus was made viable by growing on sterilized potato dextrose agar plates and incubated at 28°C for 5 days. Then, approximately 5 mm fungal disc-like mycelia were aseptically picked with cork borer and placed on the center of the PDA plates containing bacterial cultures at opposite corner equidistance of 2.5 cm. A plate with pathogenic fungus without bacteria served as a control. The inoculated plates were incubated at 30°C for 72 h and observed daily for the zone of inhibition. The zone of inhibition indicated antagonistic activity against the fungal pathogens, and the diameter of inhibition was measured and recorded (cm). The percentage of fungal mycelial inhibition rate was calculated as:

$$\% \text{ inhibition} = \frac{(A - B)}{A} \times 100$$

where: A = fungal mycelium growth (mm) on the control plates, B = fungal pathogen mycelium (mm) in the inoculated plates (Farhaoui et al., 2022).

2.7 Identification of isolated maize rhizosphere bacteria by molecular techniques

The plant growth-promoting bacteria were identified by 16S rRNA gene sequencing. The bacterial genomic DNA was extracted using Quick-DNA™ Fungal/Bacterial Miniprep Kit (Zymo Research, Catalogue No. D6005) according to the manufacturer's guide. The quality and quantity of the extracted DNA were measured using a Nanodrop A260/280 ratio

(Thermo Scientific™ NanoDrop™ One Micro-volume UV-Vis Spectrophotometer) and recorded. The extracted DNA was subjected to polymerase chain reaction (PCR) using the forward primer, 27F – (5'AGAGTTTGATCMTGGCTCAG 3'), and reverse primer, 1492R – (5'CGGTTACCTTGTTACGACTT 3') purchased from Inqaba Biotechnological Industrial (Pty) Limited, Ibadan, Nigeria. The target region of the PCR product was amplified using OneTaq® Quick-Load® 2X Master Mix (NEB, Catalogue No. M0486). A total 25 µL reaction mixture composing 1 µL in template DNA, 0.5 µL (10nM) for 10µM forward primer was used for the PCR, 0.5 µL (10 nM) for 10 µM reversed primer, 12.5 µL of One Taq Quick Load 2X Master Mix with standard buffer, and 10.5 µL of nuclease free water. The samples were then subjected to thermal cycling conditions using the Eppendorf Mastercycler nexus gradient 230 at initial denaturation at 94^{o}C for 5 min, followed by 35 cycles denaturation at 94^{o}C for 30 s, annealing at 50^{o}C for 30 s, extension at 68^{o}C for 1 min, and final extension at 68^{o}C for 10 min, and holding at 4^{o}C till infinity (Altschul et al., 1997). Then, 2 µL of each PCR products were run on 1% agarose gel, stained with Safe View Red (5 µL), and photographed using a gel documentation system (E-BOX, Vilber Lourmat, Italy). Furthermore, the PCR product was purified and sequenced. The PCR product was purified using an enzymatic method with the ExoSAP master mix, prepared in a 0.6 mL microcentrifuge tube. The ExoSAP master mix was composed of 50 µL of Exonuclease I (20 U/µL, Catalogue No. NEB M0293L) and 200 µL of shrimp alkaline phosphatase (1 U/µL, Catalogue No. NEB M0371). The reaction mixture was prepared by combining 10 µL of the amplified PCR product with 2.5 µL of the ExoSAP master mix. The resulting mixture was incubated at 37°C for 15 min, followed by 80°C for 15 min to inactivate the enzymes. The PCR products were sequenced using a Nimagen, Brilliant Dye™ Terminator Cycle Sequencing Kit V3.1, BRD3-100/1000 and purified (Zymo Research, ZR-96 DNA Sequencing Clean-up Kit™, Catalogue No. D4050) following the manufacturer's instructions. The sequencing reaction was done using internal sequencing primers: 785F: (5'GGATTAGATACCCTGGTA 3') forward, and 907R: (5'CCGTCAATTCMTTTRAGTTT 3') reverse. The labeled products were then cleaned with a ZR-96 DNA Sequencing Clean-up Kit (Catalogue no. D4053). The cleaned DNA products of each sample were injected and analyzed on the Applied Biosystems ABI 3500XL Genetic Analyser (Applied Biosystems, ThermoFisher Scientific) with a 50 cm array, using POP7 and sequence data was collected. The sequenced PCR products were analyzed using BioEdit Sequence Alignment Editor version 7.2.5. ClustalW alignment on the BioEdit program was used to align multiple sequences. The consensus sequencing results were obtained by a Basic Local Alignment Search Tool (BLAST) search on the National Center for Biotechnology Information (NCBI) to match the nucleotide sequences to the GenBank database (https://blast.ncbi.nlm.nih.gov/Blast.cgi). The evolutionary analyses were performed using the Neighbor-Joining method with the Maximum Composite Likelihood model and 1,000 bootstrap replications at uniform rates, using Molecular Evolutionary Genetics Analysis version 11 (MEGA 11) (Kumar et al., 2018).

2.8 Greenhouse experiment

The beneficial response of *S. marcescens, B. cereus,* and *P. mirabilis* on the maize seed growth was tested following the methods modified from Kifle et al. (2016). The soil was collected at a depth of 0-15 cm from University Agricultural Farmlands and prepared by removing the debris and unwanted plant materials using a stainless-steel sieve 2 mm pore-size. Then, placed in sterile plastic bags approximately 5 kg and sterilized at 121°C for 15 min. Next, 10 bacterialized maize seeds were planted in containers containing sterile soil

randomly arranged at 5 cm apart. The germinated maize seedlings were thinned to one seedling after 7 days of planting and inoculated with potent bacterial cultures. The light conditions of the experiment were a 12-h photoperiod, 10 h of dark, and a temperature of 37°C was used. The growth parameters were measured and recorded after 28 days of planting.

2.9 Field experiment

The field experiment was conducted from June to July 2024 at the University Research Farm to determine the bioinoculation effects of rhizobacterial strains on maize growth. The experiment was performed using a randomized complete block design in triplicate for each bacterial treatment. The field experiment was arranged with plants spaced 20 cm apart within rows, and rows spaced 50 cm apart (Kifle et al., 2021).

2.10 Statistical analysis

The data obtained were subjected to the analysis of variance (ANOVA) on the Statistical Package for Social Science (SPSS) program, version 22.0, and presented as the average mean. The significant level was obtained at $p<0.05$. The experimental data were presented in triplicate.

3. Results and Discussion

3.1 Morphological and biochemical characterization of the rhizobacteria from maize soil

The results of the morphological observation and biochemical tests of bacteria isolated from maize soil are presented in Table 1. All the bacterial isolates were morphologically circular in shape, big in size, creamy in color, opaque, and shiny on the surface. Similarly, the colonial view under the light microscope revealed their chain-like arrangement. The biochemical tests showed a positive reaction of the rhizobacterial isolates to catalase, motility, hydrogen sulfide, and starch hydrolysis.

The bacteria fermented the sugars with a few producing both acid and gas. The phylogeny information similarity indexes of the identified rhizobacterial isolates based on 16S rRNA sequencing results are presented in Figure 1 and Table 2, respectively. The rhizome-compartment designating soil-root environment is characterized as a reserved hotspot for high microbial biomass build-up and fosters plant-soil microbe interactions due to profuse root exudation and release of complex organic compounds (Wu et al., 2023). Harnessing the beneficial rhizosphere microbes for improved plant nutrition can be a leverage in the management of diverse problems facing agricultural productivity (Akanmu et al., 2021). The exploration of copious microbial strains with distinct growth traits and colonization dynamics remains fundamental in their selection for real-time production and commercialization (Agunbiade et al., 2024).

The selection of microorganisms in diverse environments can be somewhat challenging due to their ability to compete with autochthonous microorganisms (Adeleke et al., 2024). In this research, we isolated and characterized rhizobacteria from maize soil with a further selection of three potent PGPR to validate their bioinoculation efficacy on maize growth by inoculation, *in vitro* using plate assay, under screen-house, and field

Table 1. Morphological observation and biochemical tests of rhizobacteria from maize soil

Morphology	**IGDMS**	**AYMS**	**IGMS**
Shape	Circular	Circular	Circular
Size	Big	Big	Big
Color	Creamy	Creamy	Creamy
Elevation	Flat	Raised	Raised
Margin	Lobate	Entire	Entire
Optical characteristics	Opaque	Opaque	Opaque
Consistency	Mucoid	Mucoid	Mucoid
Colony surface	Shiny	Shiny	Shiny
Colonial arrangement	Chains	Chains	Chains
Biochemical tests			
Gram reaction	-	+	-
Morphology	Rods	Rods	Rods
Catalase	+	+	+++
Motility	**+**	**+**	**+**
Hydrogen sulphide	**++**	**++**	**+++**
Indole	**+**	**-**	**++**
Starch hydrolysis	**+**	**++**	**+**
Glucose	Ag	AG	AG
Fructose	Ag	AG	AG
Lactose	Ag	Ag	Ag
Maltose	AG	AG	AG
Sucrose	Ag	AG	AG

Key: - - negative, + - positive, IGDMS – Igodan maize soil, AYMS – Ayeka maize soil, IGMS – Igbobini maize soil, AG – gas and acid production, Ag – acid production without gas

experiments. The bacteria isolated were circular in shape, large in size, creamy, opaque, and mucoid in terms of consistency. The bacteria had a shiny surface and arranged in chains of which two were Gram-negative and one Gram-positive. The bacteria isolates exhibited positive reactions to catalase, motility, hydrogen sulfide, and starch hydrolysis. The biochemical results aligned with the findings of Babu et al. (2024), who reported the response of rhizobacteria from rice to some biochemical tests under experimental conditions. The biochemical characteristics including catalase, starch hydrolysis, motility, and hydrogen sulfide of sulfur-oxidizing bacteria from the rhizosphere of mustard were reported with varied degrees of responses to each test (Chaudhary et al., 2022). Compared to other bacteria, extensive work on the characterization of *Bacillus* and *Pseudomonas* species from plant rhizosphere has confirmed them as the most predominant rhizobacteria and their ecological functions cannot be overemphasized (Ríos-Ruiz et al., 2024; Solórzano-Acosta & Quispe, 2024; Świątczak et al., 2024).

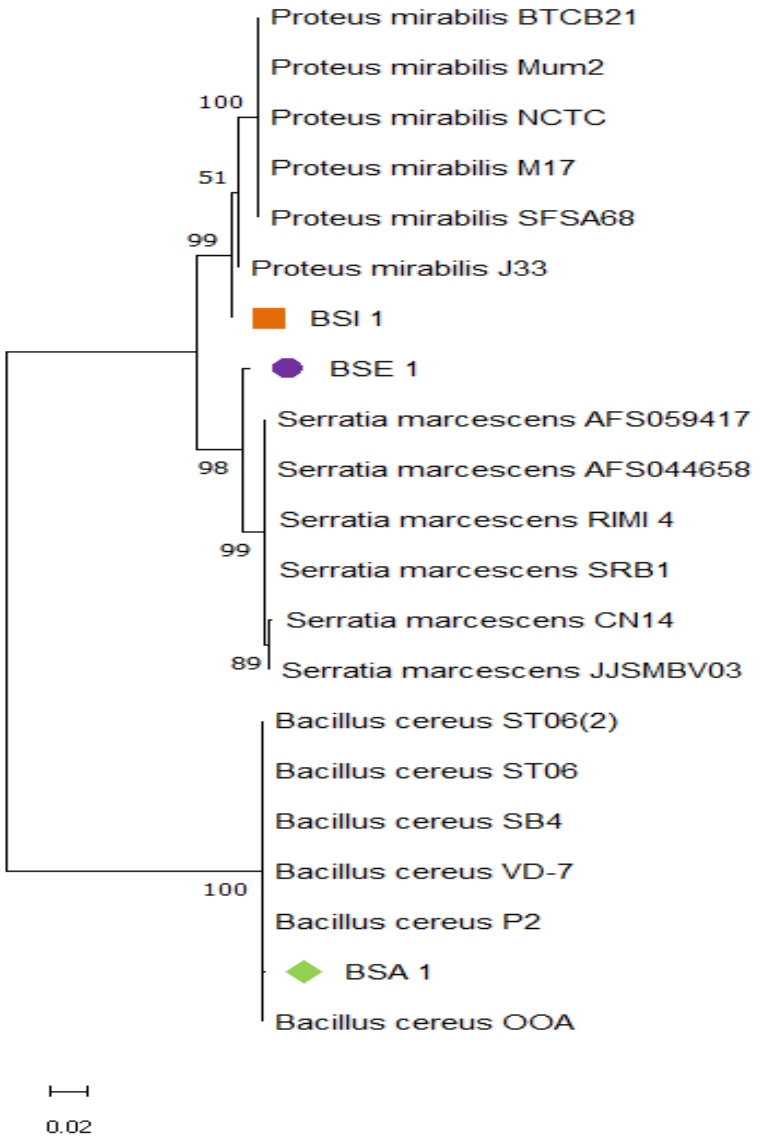

Figure 1. The phylogeny plot of the identifiable rhizobacteria from maize soil

Table 2. Similarity indexes of isolated rhizobacteria based on 16S rRNA sequencing results

Strains	Best Closest Match	Accession No. NCBI (GenBank)	Similarity (%)
BSA_1	*Bacillus cereus*	OR702892.1	(99.80%)
BSE_1	*Serratia marcescens*	OP986805.1	(98.26%)
BSI_1	*Proteus mirabilis*	PQ325712.1	(100.00%)

3.2 The qualitative and quantitative screening of rhizobacteria for plant growth traits

The results of the plant growth-promoting screening of the rhizobacteria are presented in Table 3. The screened bacterial isolates showed positive responses to phosphate solubilization, nitrogen fixation, ammonia production, IAA production, exopolysaccharide production, and cellulase production. Only *S. marcescens* BSE exhibited hydrogen cyanide activity, while only *P. mirabilis* BSI_1 showed antifungal activities against *Sclerotium rolfsii* (Figure 2). The quantitative screening of plant growth traits exhibited by the isolated rhizobacteria is presented in Figure 3.

Screening of isolated bacteria for multiple PGP traits, such as nitrogen fixation, ammonia production, IAA, exopolysaccharide, and enzyme production was evident in this study. Also, the monitoring of maize seeds treated with the bacterial isolates *in vitro* and the biocontrol potential of *P. mirabilis* against the growth of the pathogenic fungus, *S. rolfsii* was achieved. Moreover, the tolerance of bacterial isolates to heavy metals, salinity, and pH were unraveled. The multiple PGP traits of rhizobacteria from maize soil and their phytopathogen control ability showed that maize soil harbored beneficial bacteria with distinct plant growth-stimulating traits (Agunbiade et al., 2024). The isolation and screening of PGP *B. cereus*, *S. marcescens,* and *P. mirabilis* from the maize rhizosphere showed multi-dimensional promises with prospects and opportunities, which therefore required deeper investigation into the rhizosphere biology.

Phosphorus is an essential element needed for plant nutrition and some beneficial soil microbiomes play significant roles in making bound phosphorus accessible to plants for easy absorption and uptake from the soil (Gomez-Ramirez & Uribe-Velez, 2021).

Table 3. Identifiable screened plant growth-promoting rhizobacteria

Isolates	Qualitative Screening Tests										
	PS	**NF**	**NH_3**	**IAA**	**HCN**	**EPS**	**Man**	**Amy**	**Cel**	**Lip**	**Biocontrol**
S. marcescens BSE	+	+	+	+	+	+	+	+	+	+	-
B. cereus BSA	+	+	++	+	-	++	+	+	+	-	-
P. mirabilis BSI	+	+	+	++	-	++	-	-	+	-	+

Legend: + = positive, ++ – highly positive, - = negative, PS – phosphate solubilization, NF – nitrogen fixation, NH_3 – ammonia, IAA – indole-acetic acid, HCN – hydrogen cyanide, EPS – exopolysaccharide, Man – mannanase, Amy – amylase, Cel – cellulase, Lip – lipase

The incorporation of phosphate-solubilizing rhizobacteria in agriculture as bio-adjuvants holds sustainable alternatives to conventional phosphorus-containing fertilizers, which are eco-friendly and enables the reduction of dangers linked to chemical fertilizer usage (Korir et al., 2017). The phosphate-solubilizing potential of isolated bacteria from this study suggested that they can be explored as bioinoculants in boosting the phosphorus pool in the soil and the reclamation of phosphorus-deficient soil. Therefore, the phosphate solubilizing potential of *B. megaterium* was reported to underscore its effectiveness at strengthening root architecture, boosting nutrient absorption, increasing soil phosphorus pool, and conferring plant resistance to abiotic stress (Lee et al., 2024). Kulkova et al. (2024) documented the application of *Serratia* species in promoting plant growth by alleviating salinity and drought stresses and improving essential nutrient supply for improved plant nutrition and crop productivity.

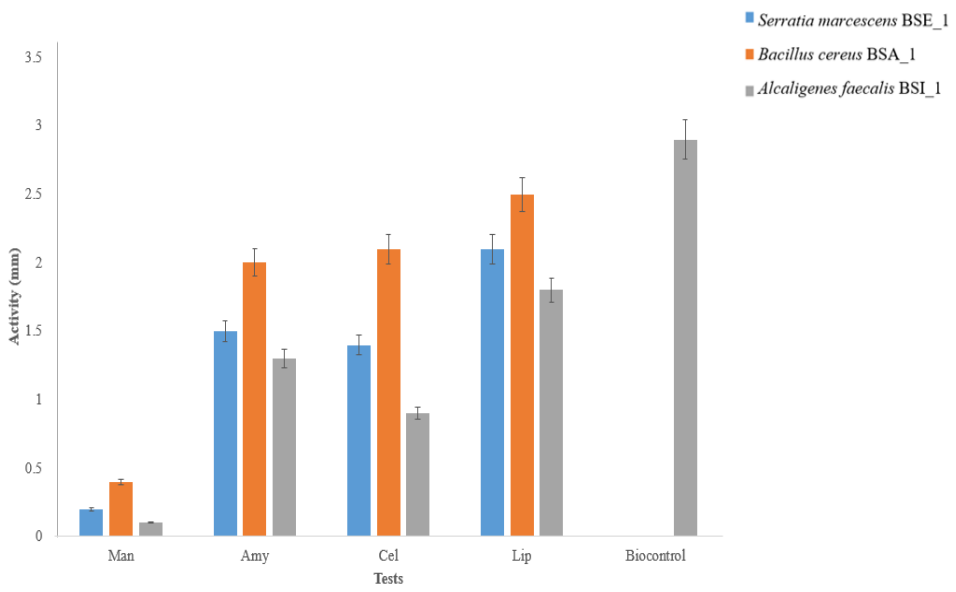

Figure 2. Enzyme screening and biocontrol activity of plant growth-promoting rhizobacteria. **Legend:** Man – mannanase, Amy – amylase, Cel – cellulase, Lip – lipase

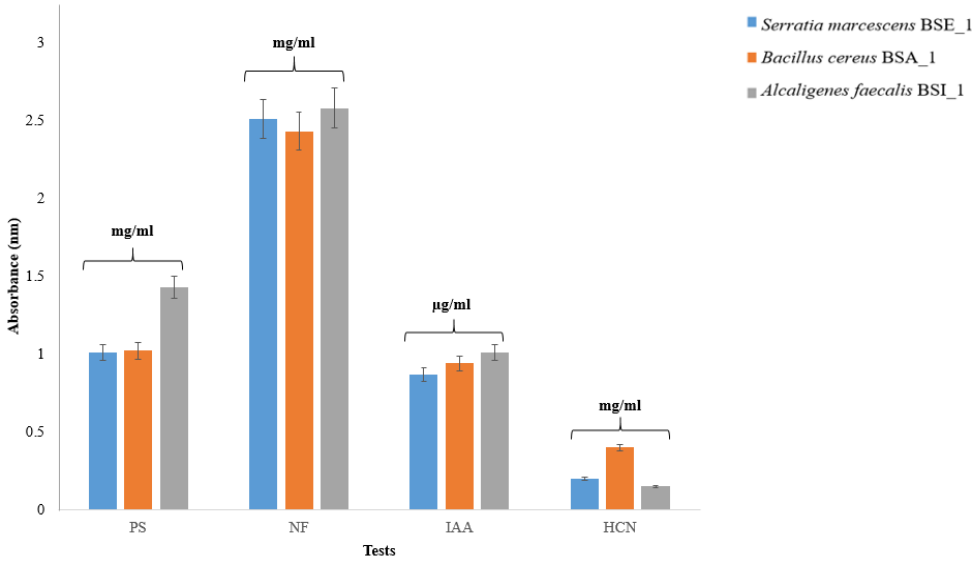

Figure 3. Quantitative screening of rhizobacteria for plant growth-promoting traits. **Legend**: PS – phosphate solubilization, NF – nitrogen fixation, IAA – indole-acetic acid, HCN – hydrogen cyanide

The isolation and screening of PGPR such as *Bacillus, Burkholderia, Pantoea,* and *Rhizobium* from plant rhizosphere as phosphate solubilizers and biocontrol agents with the target in sustaining soil and plant health were reported (Igiehon et al., 2019; Chen et al., 2024; Sharma et al., 2024). Other findings also validated the exploration of the multifunctional PGPR as phosphate solubilizers in ameliorating ecological problems associated with the use of phosphate-containing chemical fertilizers (Cui et al., 2019; Lebrazi et al., 2020; Muleta et al., 2021). Biological nitrogen fixation by microorganisms, mostly the PGPR and arbuscular mycorrhiza fungi, plays a critical role in improving soil nitrogen availability and consequently, plant nutrition (Tirry et al., 2024). Nitrogen is an essential macronutrient that promotes plant growth, and its bioavailability in the soil is a key factor in boosting the productivity of crops such as maize and other legumes (Ayilara et al., 2022). Nitrogen deficiency in the soil negatively affects plant growth and crop yield (Meena et al., 2017); however, this has necessitated researchers to devise biorational techniques using nitrogen-fixing microorganisms as soil conditioners. The response of rhizobacteria to fix nitrogen relies largely on their ability to produce nitrogenase, an enzyme mediating nitrogen fixation (Abd-Alla et al., 2019). Some notable rhizobacteria genera associated with maize have been reported to fix nitrogen in maize and other crops, thus contributing to sustainable agricultural practices (Kuan et al., 2016; Zhiyong et al., 2024). However, information on *Bacillus, Serratia,* and *Proteus* from maize soil collected from Okitipupa and Igbobini, Ondo State Nigeria was not previously reported. The use of *B. cereus* as bioinoculants demonstrated an increase of the nitrogen pool in the soil and an enhancement of plant growth (Babalola et al., 2021). Ding et al. (2005) reported a nitrogen-fixing bacterium, *B. cereus*, isolated from the maize rhizosphere with the ability to produce nitrogenase. Notably, *Peribacillus, Pseudomonas,* and *Rhizobium* were reported to contribute to overall plant development based on their ability to fix nitrogen in the soil and production of phytohormones, which enhance root development and nutrient uptake (Dhole et al., 2023; Świątczak et al., 2024). The synergistic interactions of *S. marcescens* with plants can mediate certain mechanisms, such as their ability to potentially fix nitrogen, solubilize phosphate, and produce siderophores, stimulating plant responses to environmental stresses (Kulkova et al., 2024). The possession of nitrogenase genes in *Azospirillum brasilense* and *B. megaterium* CY5 and *B. mycoides* CA1 from wheat and sugarcane rhizosphere were reported to underline the nitrogen-fixing activities with major influence on plant growth, tolerance to stress, and yield improvement (Santos et al., 2017; Singh et al., 2020).

In recent years, the production of ammonia by microorganisms has garnered significant attention due to its role in plant growth promotion and soil health (Ke et al., 2019). *Bacillus cereus*, a well-known Gram-positive, rod and soil inhabitants has been extensively studied for its ability to produce ammonia, causing an improvement in nitrogen in the soil and plant resilience to stresses (Parvin et al., 2023). Similarly, ammonia production by PGPR suggested them as suitable candidates with functional roles in boosting plant growth and resilience to biotic and abiotic stresses (Adeleke et al., 2024). Mehmood et al. (2023) reported the ammonia-producing ability of *P. lurida* from maize with multifaceted impact in suppressing plant pathogens and enhancing crop yield.

Indole-3-acetic acid plays an important role in plant growth promotion, such as root development, and root elongation which are critical in the uptake of nutrients for plant use (Kumari et al., 2018). The IAA production potential of selected rhizobacteria from this study signaled their ability to increase root biomass and formation. The utilization of substrate, L-tryptophan in the IAA medium revealed the bacteria's potency in IAA production, which corroborates the findings of Adeleke et al. (2022) on the IAA production by *B. cereus* isolated from sunflower.

The ability of rhizobacteria to produce hydrogen cyanide can contribute to their effective biocontrol mechanism against pathogens affecting maize crops (Sehrawat et al., 2022). Patel et al. (2024) reported the HCN production potential of *in vitro Serratia marcescens* and *Pseudomonas fluorescens*, with a direct effect on plant protection and sustainable growth. Overall plant resilience to biotic stress was linked to the ability of the isolated rhizobacteria to synthesize HCN, suggesting their future exploration as bioinoculants and biopesticides.

Drought amelioration in plants due to exopolysaccharide production by microorganisms has gained much attention recently with the projection of incorporating beneficial rhizobacteria in integrated crop management to boost agricultural productivity through plant growth enhancement, plant resistance to drought, nutrient accessibility, stability of soil aggregate, and biocontrol of pathogens (Prasad et al., 2022). *Bacillus* and other rhizobacteria have been reported to produce exopolysaccharides with significant positive effects on maize and soybean growth (Igiehon et al., 2019; Naseem et al., 2024).

Plant disease control remains a strategic measure in ensuring food security and agricultural productivity. The use of some microorganisms as biocontrol agents, such as *Bacillus thuringiensis* as biopesticide, has been widely explored and reported on the control of plant pests (Adeniji et al., 2021). The biocontrol efficacy of soil bacteria against plant fungal pathogens may be due to their antibiosis, genetic constituents, and production of lytic enzymes by interfering with the fungal cell wall integrity, spore germination, and mycelia growth, protein synthesis, and potassium ions linkage (Soni et al., 2021). Also, the ability of rhizobacteria to produce secondary metabolites underlines their biocontrol activities against plant pathogens. However, out of the three rhizobacteria identified in this study, only *P. mirabilis* showed antifungal activity against *S. rolfsii*, and this conformed with the findings of Rasool et al. (2021), who reported the antifungal activities of *Brevibacterium frigoritolerans* AIS-3 and *Bacillus aryabhattai* AIS-10 against *S. rolfsii.* The ability of some notable PGP rhizobacteria in controlling plant pathogens was reported by Belabess et al. (2024) while testing the efficacy of the volatile compounds from microorganisms from tomatoes in the control of tomato diseases caused by *Cladosporium fulvum*. Shin et al. (2024) reported the use of rhizobacterium, *Pseudomonas* sp. SH-26 isolated from peat soil, in the control of plant pathogenic fungi. A study by Ghazy and El-Nahrawy (2021) documented the control of *Cephalosporium maydis*, responsible for late wilt disease in maize, using *Bacillus subtilis* MF497446 and *Pseudomonas koreensis* MG209738. Nevertheless, information on the biocontrol efficacy of *P. mirabilis* in the control of a potent pathogenic fungus, *S. rolfsii,* was less documented in the literature, highlighting the need for further research on this bacterium.

3.3 Heavy metal and salt tolerance

Tables 4a–c show the percentage of heavy metal tolerance exhibited by rhizobacteria isolated from maize soil. The bacterial isolates demonstrated high tolerance levels of 32% and 41% at a 0.1% $ZnSO_4$ concentration after 72 h of incubation (Table 4c). At a 0.2% $CdSO_4$ concentration, high tolerance values of 34% and 35%, 45% and 44%, and 45% and 46% were recorded for all bacterial isolates at 48 and 72 h of incubation, respectively (Tables 4a and 4c).

Table 4a. Percentage of heavy metal tolerance of the rhizobacteria at 24 h incubation

Bacterial Isolates	Heavy Metal Conc. (g/mL)	$ZnSO_4$	$CdSO_4$	$PbSO_4$	$CuSO_4$
S. marcescens BSE_1 (OD: 21%)	0.1	32.00±0.00^b	26.03±0.02^a	31.63±1.09^b	58.00±0.01^c
	0.2	26.02±0.03^a	28.00±0.00^b	86.01±0.02^d	76.01±0.04^c
	0.3	24.02±0.04^a	28.00±0.01^b	83.97±0.07^c	25.96±0.07^a
B. cereus BSA_1 (OD: 21%)	0.1	23.00±0.00^a	27.02±0.03^b	26.02±0.03^b	68.01±0.02^c
	0.2	23.00±0.00^b	20.00±0.00^a	82.01±0.02^d	74.02±0.03^c
	0.3	14.00±0.00^a	20.00±0.00^b	85.00±0.00^c	79.00±0.01^d
P. mirabilis BSI_1 (OD: 21%)	0.1	17.00±0.00^b	13.00±0.00^a	37.01±0.02^c	79.01±0.02^d
	0.2	24.00±0.00^a	28.00±0.00^b	81.01±0.02^d	70.00±0.01^c
	0.3	12.00±0.00^a	24.00±0.00^b	85.00±0.00^d	79.01±0.02^c

Table 4b. Percentage of heavy metal tolerance of the rhizobacteria at 48 h incubation

Bacterial Isolates	Heavy Metal Conc. (g/mL)	$ZnSO_4$	$CdSO_4$	$PbSO_4$	$CuSO_4$
S. marcescens BSE_1 (OD: 21%)	0.1	27.34±0.57^a	28.96±0.07^b	29.00±0.00^b	73.00±0.00^c
	0.2	27.01±0.02^a	34.00±0.01^b	87.00±0.01^c	87.00±0.00^c
	0.3	22.01±0.03^a	26.00±0.00^b	90.01±0.02^d	86.01±0.02^c
B. cereus BSA_1 (OD: 21%)	0.1	27.00±0.00^b	21.02±0.03^a	56.02±0.04^c	91.02±0.04^d
	0.2	28.00±0.00^a	45.00±0.01^b	89.01±0.01^c	96.01±0.02^d
	0.3	23.00±0.00^a	34.01±0.02^b	93.00±0.00^c	97.01±0.01^d
P. mirabilis BSI_1 (OD: 21%)	0.1	38.00±0.00^a	39.00±0.01^a	90.00±0.00^b	94.01±0.01^c
	0.2	31.33±0.56^a	45.01±0.02^b	91.00±0.00^c	93.01±0.01^d
	0.3	24.00±0.00^a	39.02±0.03^b	93.01±0.01^c	96.01±0.02^d

Table 4c. Percentage of heavy metal tolerance of the rhizobacteria at 72 h incubation

Bacterial Isolates	Heavy Metal Conc. (g/mL)	$ZnSO_4$	$CdSO_4$	$PbSO_4$	$CuSO_4$
S. marcescens BSE_1 (OD: 22%)	0.1	32.96±0.06^b	28.00±0.00^a	38.00±0.00^c	88.01±0.02^d
	0.2	26.00±0.00^a	35.01±0.02^b	88.00±0.00^c	93.00±0.00^d
	0.3	24.02±0.03^a	31.01±0.02^b	89.00±0.00^c	90.01±0.02^c
B. cereus BSA_1 (OD: 22%)	0.1	32.01±0.02^b	28.02±0.03^a	61.00±0.00^c	89.01±0.01^d
	0.2	25.02±0.03^a	44.00±0.00^b	83.01±0.02^c	99.01±0.02^d
	0.3	22.00±0.00^a	32.00±0.00^b	84.01±0.01^c	98.00±0.00^d
P. mirabilis BSI_1 (OD: 22%)	0.1	41.00±0.00^a	40.00±0.00^a	76.01±0.02^b	95.01±0.01^c
	0.2	30.00±0.00^a	46.00±0.00^b	83.01±0.02^c	98.01±0.01^d
	0.3	22.00±0.00^a	37.01±0.02^b	86.01±0.01^c	96.00±0.00^d

Values are presented as mean±standard deviation of triplicate readings. The different superscript letters (small alphabets) across the same row represent a significant difference: OD – optical density of the inoculated broth culture (control).

At 0.2% and 0.3% $PbSO_4$ concentrations, the bacterial isolates showed higher percentages of $PbSO_4$ tolerance. *Serratia marcescens* BSE_1, *Bacillus cereus* BSA_1, and *Proteus mirabilis* BSI_1 exhibited high $CuSO_4$ tolerance levels of 93%, 99%, and 98%, respectively, at a 0.2% $CuSO_4$ concentration after 72 h of incubation (Table 4c). The heavy metal tolerance varied upon inoculating the heavy metal broth with each bacterial isolate. Also, the percentage salt (NaCl) tolerance of the rhizobacteria from maize soil is shown in Figures 3a-3c. The salt (NaCl) tolerance level increased with incubation time. A high salt (NaCl) tolerance level of 76% was recorded for *B. cereus* BSA and *P. mirabilis* BSI at 0.1 and 0.2 salt (NaCl) concentrations at 72 h of incubation. Salinity and heavy metal stress pose serious ecological threats to plant survival, thus necessitating their amelioration (Adeleke et al., 2021). The bacteria response to salt and heavy metals, $PbSO_4$, $CdSO_4$, $ZnSO_4$, and $CuSO_4$ varied under experimental conditions based on their tolerance levels, as they negatively influenced the overall plant performance. The tolerance of PGPR under salt (NaCl) and heavy metals was evaluated under optimized conditions by measuring the process parameters to ascertain their tolerance levels (Agunbiade et al., 2024). The presence of heavy metal in the environment poses a great challenge to agricultural productivity, a situation that needs bioremediation (Chaudhary et al., 2021). The observed variation in heavy metal tolerance of rhizobacteria tested in this study might be due to their remarkable ability in the detoxification of environmental pollutants. A study by Anusha & Natarajan (2020) reported 97.17% ($PbSO_4$), 77.44% ($ZnSO_4$), and 91.98% ($CuSO_4$) tolerance of *B. cereus* in the growth medium. The growth of rhizobacterial strains in a medium supplemented with heavy metals, such as $PbSO_4$, $Cr_2(SO_4)_3$, and $CdSO_4$ has established the potency of maize-associated *Aeromonas* spp. tolerance to heavy metals, possibly due to the presence of heavy metal tolerant genes in their genome (Agunbiade et al., 2024)

3.4 Maize seed inoculation: Greenhouse, and field experiments

The results of greenhouse and field experimental values are presented in Figures 4a and 4b. A root length of 17.70 cm was recorded for the maize inoculated with the bacteria consortia while the number of adventitious roots of 118.40 and plant fresh weight of 167.00 g were recorded for the maize inoculated with three bacteria compared with other treatments and the control. Microbial bioinoculation is important in measuring the effect of beneficial microorganisms on certain ecological functions (Jangra et al., 2024). The isolated rhizobacteria contributed to maize growth significantly compared to un-inoculated. The variations in the growth parameters measured were likely due to the multiple mechanisms exhibited by the bacterial consortia with better performance on maize growth as bioinoculants. The maize inoculation with multiple bacterial strains showed significant growth effects compared to single and duo treatments and the control, relative to the seed germination and reduction of pathogenic phytopathogens. The use of putative rhizobacteria as plant growth promoters has been reported to enhance maize growth (Ghorchiani et al., 2018). The combined effect of beneficial rhizobacteria, *B. megaterium, B. pumilus,* and *Enterobacter asburiae* was also reported to enhance groundnut growth under experimental conditions (Beshah et al., 2024). Also, the functionality of soil microbes in enhancing plant growth can be linked to their genetic constituents comprising genes mediating plant growth promotion and secondary metabolite synthesis in sustaining plant health.

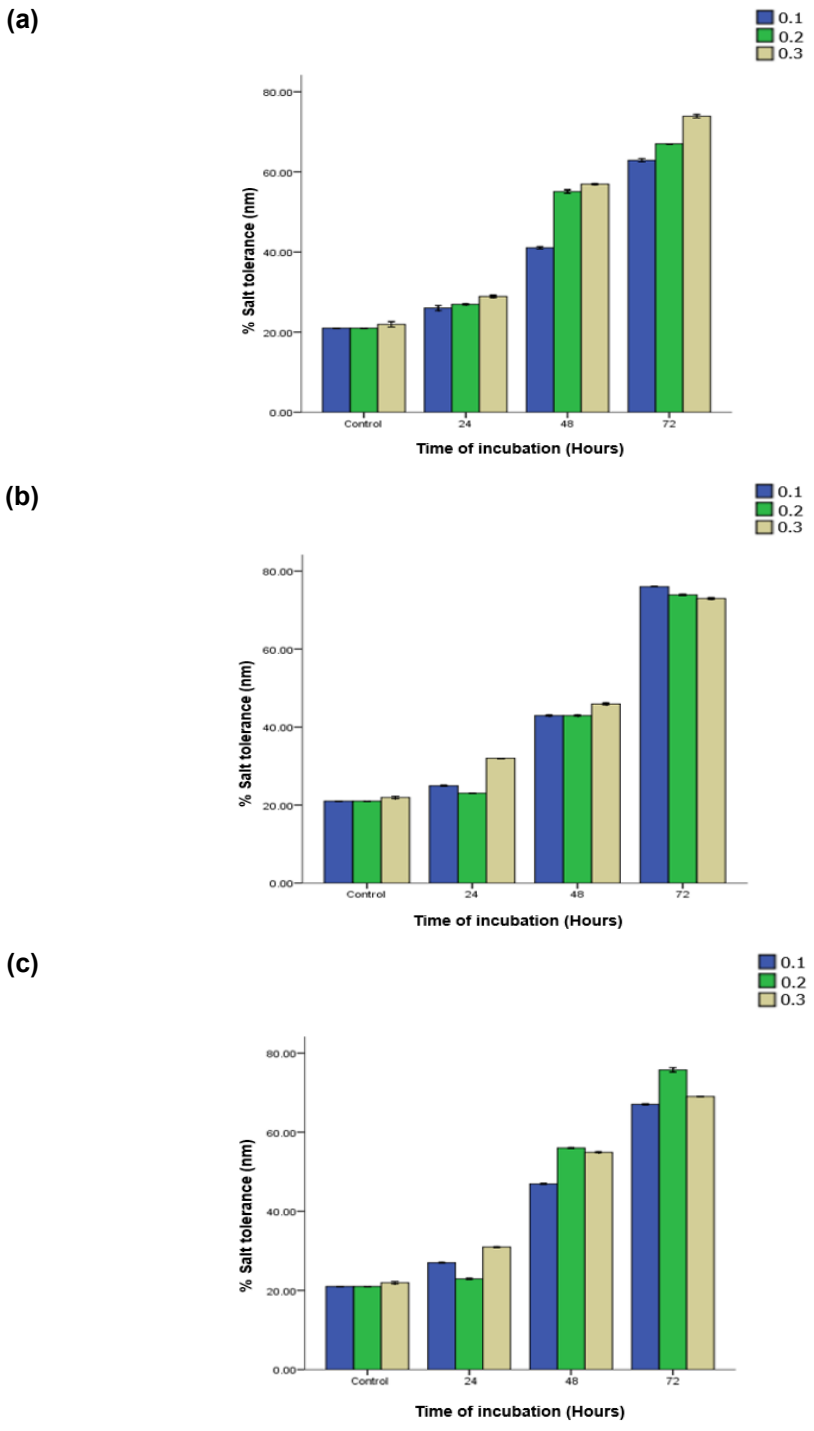

Figure 3. Percentage salt (NaCl) tolerance of the rhizobacteria
(a) *S. marcescens* BSE_1; **(b)** *B. cereus* BSA_1; **(c)** *P. mirabilis* BSI_1

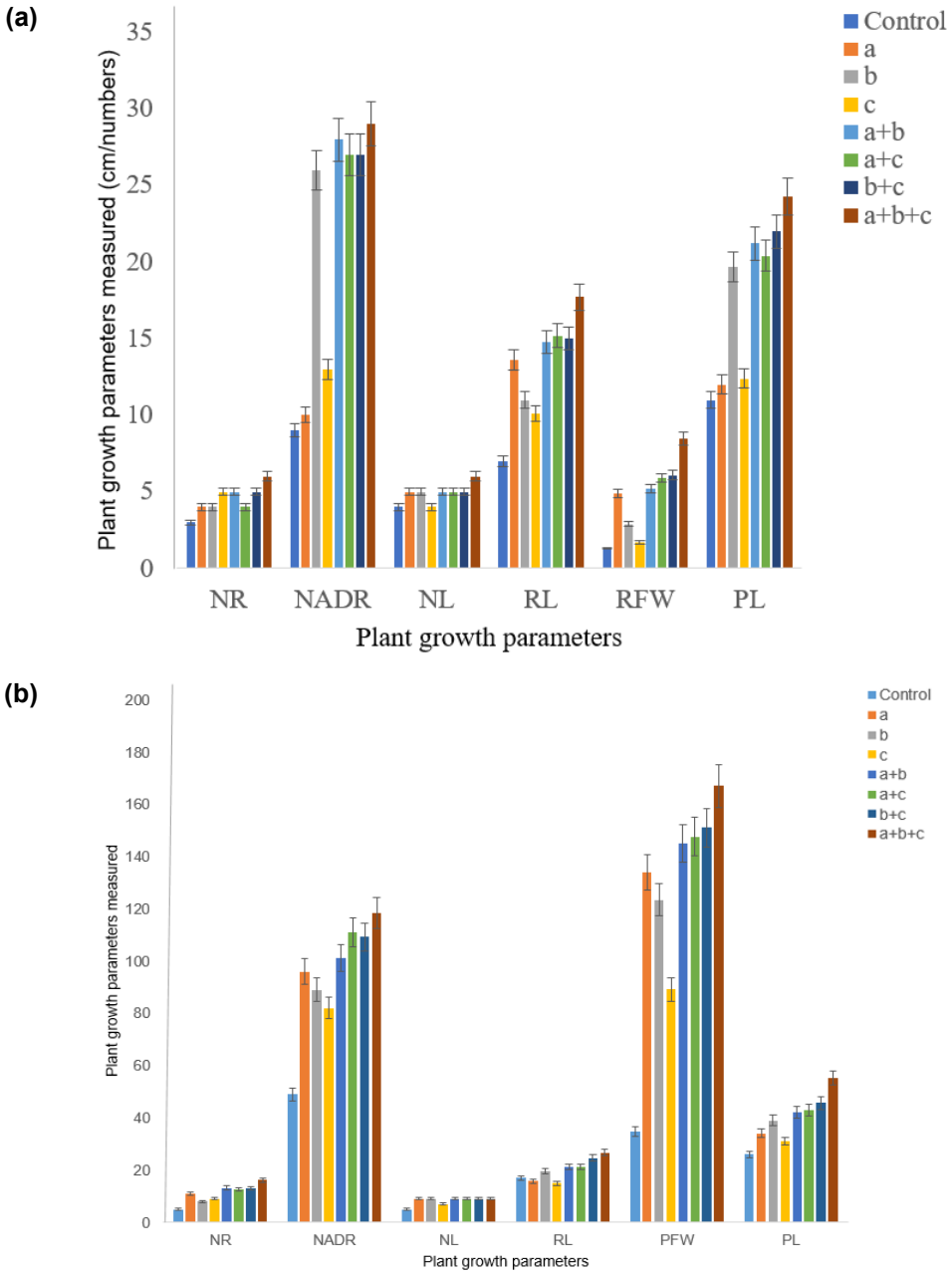

Figure 4. (a) Greenhouse experiment; **(b)** Field experiment. **Key:** NR – number of the roots, NADR – number of adventitious roots, NL – number of leaves, PL – plant length, PFW – plant fresh weight, RL – root length, **a** - *S. marcescens* BSE_1, **b** - *B. cereus* BSA_1, **c** - *A. P. mirabilis* BSI_1, **a+b** - *S. marcescens* BSE_1 + *B. cereus* BSA_1, **a+c** - *S. marcescens* BSE_1 + *P. mirabilis* BSI_1, **b+c** - *B. cereus* BSA_1 + *P. mirabilis* BSI_1, **a+b+c** - *S. marcescens* BSE_1 + *B. cereus* BSA_1 + *P. mirabilis* BSI_1

4. Conclusions

This study demonstrates that the isolated PGPR from the maize rhizosphere in Okitipupa and Igbobini holds great promise for improving maize growth under various experimental conditions. The selected bacterial strains exhibited plant growth-promoting properties, and their inoculation significantly improved maize growth parameters compared to the non-inoculated control. The observed tolerance of each bacterium to heavy metals and salinity highlighted their potential to survive in environments with toxic metals and high salinity, suggesting their use as effective agents in the bioremediation of environmental pollutants. The antifungal activities of *P. mirabilis* underscore its potential for inclusion in integrated pest management as an alternative to chemical fungicides for controlling maize pathogens. This suggests the dual functionality of this bacterium, both as a biofertilizer to enhance plant growth and as a biocontrol agent to manage pathogens. In conclusion, the indigenous PGPR isolated in this study showed great potential as bioinoculants for developing eco-friendly agriculture and promoting sustainable maize production in diverse environments.

5. Acknowledgements

The authors gratefully acknowledge their affiliated institution and the support of the Tertiary Education Trust Fund (TETFund) through the Institution-Based Research (IBR) Intervention, Research Project (RP) for 2022/2024 (merged), under reference number: OAUSTECH/TETFund/IBR/VOL.4/020.

6. Authors' Contributions

Bartholomew Saanu Adeleke: Designed and performed research; contributed new reagents/analytical tools; analyzed data; coordinated research; and wrote the paper. Soji Fakoya: designed and coordinated research; and wrote the paper.

7. Conflicts of Interest

The authors declare no conflicts of interest.

ORCID

Bartholomew Saanu Adeleke https://orcid.org/0000-0001-7707-8816

Soji Fakoya https://orcid.org/0000-0001-7675-3226

References

Abd-Alla, M. H., Nafady, N. A., Bashandy, S. R., & Hassan, A. A. (2019). Mitigation of effect of salt stress on the nodulation, nitrogen fixation and growth of chickpea (*Cicer arietinum* L.) by triple microbial inoculation. *Rhizosphere,* 10, Article 100148. https://doi.org/10.1016/j.rhisph.2019.100148

Adeleke, B. S., Ayangbenro, A. S., & Babalola, O. O. (2022). *In vitro* screening of sunflower associated endophytic bacteria with plant growth-promoting traits. *Frontiers in Sustainable Food Systems,* 6, Article 903114. https://doi.org/10.3389/fsufs.2022.903114

Adeleke, B. S., Babalola, O. O., & Glick, B. R. (2021). Plant growth-promoting root-colonizing bacterial endophytes. *Rhizosphere,* 20, Article 100433. https://doi.org/10.1016/j.rhisph.2021.100433

Adeleke, B. S., Chaudhary, P., Ayilara, M. S., Ojo, F. M., Erinoso, S. M., Upadhayay, V. K., Adeyemo, A. I., & Akinola, S. A. (2024). Rhizosphere microbiomes mediating abiotic stress mitigation for improved plant nutrition. *Ecologies,* 5(3), 375-401. https://doi.org/10.3390/ecologies5030024

Adeniji, A. A., Ayangbenro, A. S., & Babalola, O. O. (2021). Genomic exploration of *Bacillus thuringiensis* MORWBS1. 1-candidate biocontrol agent, predicts genes for biosynthesis of zwittermicin, 4, 5-DOPA dioxygenase extradiol, and quercetin 2, 3-dioxygenase. *Molecular Plant-Microbe Interactions*, 34, 602-605. https://doi.org/10.1094/MPMI-10-20-0272-SC

Agbodjato, N. A., Noumavo, P. A., Baba-Moussa, F., Salami, H. A., Sina, H., Sèzan, A., Bankolé, H., Adjanohoun, A., & Baba-Moussa, L. (2015). Characterization of potential plant growth promoting rhizobacteria isolated from Maize (*Zea mays* L.) in central and Northern Benin (West Africa). *Applied and Environmental Soil Science*, 2015, Article 901656. https://doi.org/10.1155/2015/901656

Agunbiade, V. F., Fadiji, A. E., Agbodjato, N. A., & Babalola, O. O. (2024). Isolation and characterization of plant-growth-promoting, drought-tolerant rhizobacteria for improved maize productivity. *Plants,* 13(10), Article 1298. https://doi.org/10.3390/plants13101298

Akanmu, A. O., Babalola, O. O., Venturi, V., Ayilara, M. S., Adeleke, B. S., Amoo, A. E., Sobowale, A. A., Fadji, A. E., & Glick, B. R. (2021). Plant disease management: Leveraging on the plant-microbe-soil interface in the biorational use of organic amendments. *Frontiers in Plant Science,* 12, Article 1590. https://doi.org/10.3389/fpls.2021.700507

Altschul, S. F., Madden, T. L., Schäffer, A. A., Zhang, J., Zhang, Z., Miller, W., & Lipman, D. J. (1997). Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. *Nucleic Acids Research,* 25(17), 3389-3402. https://doi.org/10.1093/nar/25.17.3389

Anusha, P., & Natarajan, D. (2020). Bioremediation potency of multi metal tolerant native bacteria *Bacillus cereus* isolated from bauxite mines, kolli hills, Tamilnadu-a lab to land approach. *Biocatalysis and Agricultural Biotechnology,* 25, Article 101581. https://doi.org/10.1016/j.bcab.2020.101581

Arruda, L., Beneduzi, A., Martins, A., Lisboa, B., Lopes, C., Bertolo, F., Passaglia, L. M. P., & Vargas, L. K. (2013). Screening of rhizobacteria isolated from maize (*Zea mays* L.) in Rio Grande do Sul State (South Brazil) and analysis of their potential to improve plant growth. *Applied Soil Ecology*, 63, 15-22. https://doi.org/10.1016/j.apsoil.2012.09.001

Ayilara, M. S., Adeleke, B. S., & Babalola, O. O. (2022). Bioprospecting and challenges of plant microbiome research for sustainable agriculture, a review on soybean endophytic bacteria. *Microbial Ecology,* 85, 1113-1135. https://doi.org/10.1007/s00248-022-02136-z

Babalola, O. O., Adeleke, B. S., & Ayangbenro, A. S. (2021). Whole genome sequencing of sunflower root-associated *Bacillus cereus*. *Evolutionary Bioinformatics,* 17, 1-6. https://doi.org/10.1177/11769343211038948

Babu, S. V., Gopal, A. V., Trimurtulu, N., Babu, G. K., & Bhattiprolu, S. (2024). Efficacy of silica solubilizing bacteria as plant growth promoting rhizobacteria and their biochemical characteristics. *International Journal of Environment and Climate Change,* 14(6), 199-210. https://doi.org/10.9734/ijecc/2024/v14i64221

Barbetti, M. J., Banga, S. S., & Salisbury, P. A. (2012). Challenges for crop production and management from pathogen biodiversity and diseases under current and future climate scenarios – Case study with oilseed Brassicas. *Field Crops Research,* 127, 225-240. https://doi.org/10.1016/j.fcr.2011.11.021

Belabess, Z., Gajjout, B., Legrifi, I., Barka, E. A., & Lahlali, R. (2024). Exploring the antifungal activity of Moroccan bacterial and fungal isolates and a Strobilurin fungicide in the control of *Cladosporium fulvum*, the causal agent of tomato leaf mold disease. *Plants,* 13(16), Article 2213. https://doi.org/10.3390/plants13162213

Beshah, A., Muleta, D., Legese, G., & Assefa, F. (2024). Exploring stress-tolerant plant growth-promoting rhizobacteria from groundnut rhizosphere soil in semi-arid regions of Ethiopia. *Plant Signaling and Behavior,* 19(1), Article 2365574. https://doi.org/10.1080/15592324.2024.2365574

Chaudhary, P., Parveen, H., Gangola, S., Kumar, G., Bhatt, P., & Chaudhary, A. (2021).Plant growth-promoting rhizobacteria and their application in sustainable crop production. In P. Bhatt, S. Gangola, D. Udayanga, & G. Kumar (Eds.). *Microbial technology for sustainable environment* (pp. 217-234). Springer. https://doi.org/10.1007/978-981-16-3840-4_13

Chaudhary, S., Dhanker, R., Singh, K., Brar, B., & Goyal, S. (2022). Characterization of sulfur-oxidizing bacteria isolated from mustard (*Brassica juncea* L.) rhizosphere having the capability of improving sulfur and nitrogen uptake. *Journal of Applied Microbiology,* 133(5), 2814-2825. https://doi.org/10.1111/jam.15742

Chen, X., Zhao, Y., Huang, S., Peñuelas, J., Sardans, J., Wang, L., & Zheng, B. (2024). Genome-based identification of phosphate-solubilizing capacities of soil bacterial isolates. *AMB Express,* 14(1), Article 85. https://doi.org/10.1186/s13568-024-01745-w

Clarke, P. H., & Cowan, S. (1952). Biochemical methods for bacteriology. *Microbiology,* 6, 187-197. https://doi.org/10.1099/00221287-6-1-2-187

Cui, W., He, P., Munir, S., He, P., Li, X., Li, Y., Wu, J., Wu, Y., Yang, L., He, P., & He, Y. (2019). Efficacy of plant growth promoting bacteria *Bacillus amyloliquefaciens* B9601-Y2 for biocontrol of southern corn leaf blight. *Biological Control,* 139, Article 104080. https://doi.org/10.1016/j.biocontrol.2019.104080

Dhole, A. M., Shelat, H. N., Patel, H. K., & Jhala, Y. K. (2023). Evaluation of the co-inoculation Effect of *Rhizobium* and plant growth promoting non-rhizobial endophytes on *Vigna radiata*. *Current Microbiology,* 80(5), Article 167. https://doi.org/10.1007/s00284-023-03266-4

Ding, Y., Wang, J., Liu, Y., & Chen, S. (2005). Isolation and identification of nitrogen-fixing bacilli from plant rhizospheres in Beijing region. *Journal of Applied Microbiology,* 99(5), 1271-1281. https://doi.org/10.1111/j.1365-2672.2005.02738.x

Efthimiadou, A., Katsenios, N., Chanioti, S., Giannoglou, M., Djordjevic, N., & Katsaros, G. (2020). Effect of foliar and soil application of plant growth promoting bacteria on growth, physiology, yield and seed quality of maize under Mediterranean conditions. *Scientific Reports,* 10(1), Article 21060. https://doi.org/10.1038/s41598-020-78034-6

Farhaoui, A., Adadi, A., Tahiri, A., El Alami, N., Khayi, S., Mentag, R., Ezrari, S., Radouane, N., Mokrini, F., Belabess, Z., & Lahlali, R. (2022). Biocontrol potential of plant growth-promoting rhizobacteria (PGPR) against *Sclerotiorum rolfsii* diseases on sugar beet (*Beta vulgaris* L.). *Physiological and Molecular Plant Pathology*, 119, Article 101829. https://doi.org/10.1016/j.pmpp.2022.101829

Fasusi, O. A., Amoo, A. E., & Babalola, O. O. (2021). Characterization of plant growth-promoting rhizobacterial isolates associated with food plants in South Africa. *Antonie Van Leeuwenhoek*, 114(10), 1683-1708. https://doi.org/10.1007/s10482-021-01633-4

Gamalero, E., & Glick, B. R. (2022). Recent advances in bacterial amelioration of plant drought and salt stress. *Biology,* 11(3), Article 437. https://doi.org/10.3390/biology11030437

Ghanem, M., Kamal, O., & Said, A. F. (2024). Plant growth-promoting rhizobacteria: selective screening and characterization of drought-tolerant bacteria from drought-prone soils. *Novel Research in Microbiology Journal,* 8(3), 2469-2490. https://doi.org/10.21608/nrmj.2024.293974.1607

Ghazy, N., & El-Nahrawy, S. (2021). Siderophore production by *Bacillus subtilis* MF497446 and *Pseudomonas koreensis* MG209738 and their efficacy in controlling *Cephalosporium maydis* in maize plant. *Archives of Microbiology,* 203(3), 1195-1209. https://doi.org/10.1007/s00203-020-02113-5

Ghorchiani, M., Etesami, H., & Alikhani, H. A. (2018). Improvement of growth and yield of maize under water stress by co-inoculating an arbuscular mycorrhizal fungus and a plant growth promoting rhizobacterium together with phosphate fertilizers. *Agriculture, Ecosystems and Environment,* 258, 59-70. https://doi.org/10.1016/j.agee.2018.02.016

Gomez-Ramirez, L. F., & Uribe-Velez, D. (2021). Phosphorus solubilizing and mineralizing *Bacillus* spp contribute to rice growth promotion using soil amended with rice straw. *Current Microbiology,* 78, 932-943. https://doi.org/10.1007/s00284-021-02354-7

Igiehon, N. O., Babalola, O. O., & Aremu, B. R. (2019). Genomic insights into plant growth promoting rhizobia capable of enhancing soybean germination under drought stress. *BMC Microbiology,* 19(1), Article 159. https://doi.org/10.1186/s12866-019-1536-1

Jangra, A., Kumar, K., Maikhuri, S., Bhandari, M. S., Pandey, S., Singh, H., & Barthwal, S. (2024). Unveiling stress-adapted endophytic bacteria: characterizing plant growth-promoting traits and assessing cross-inoculation effects on *Populus deltoides* under abiotic stress. *Plant Physiology and Biochemistry*, 210, Article 108610. https://doi.org/10.1016/j.plaphy.2024.108610

Ke, X., Feng, S., Wang, J., Lu, W., Zhang, W., Chen, M., & Lin, M. (2019). Effect of inoculation with nitrogen-fixing bacterium *Pseudomonas stutzeri* A1501 on maize plant growth and the microbiome indigenous to the rhizosphere. *Systematic and Applied Microbiology,* 42(2), 248-260. https://doi.org/10.1016/j.syapm.2018.10.010

Khan, N., & Mehmood, A. (2023). Revisiting climate change impacts on plant growth and its mitigation with plant growth promoting rhizobacteria. *South African Journal of Botany,* 160, 586-601. https://doi.org/10.1016/j.sajb.2023.07.051

Kifle, M. H., & Laing, M. D. (2016). Isolation and screening of bacteria for their diazotrophic potential and their influence on growth promotion of maize seedlings in greenhouses. *Frontiers in Plant Science*, 6, Article 1225. https://doi.org/10.3389/fpls.2015.01225

Korir, H., Mungai, N. W., Thuita, M., Hamba, Y., & Masso, C. (2017). Co-inoculation effect of rhizobia and plant growth promoting rhizobacteria on common bean growth in a low phosphorus soil. *Frontiers in Plant Science,* 8, Article 141. https://doi.org/10.3389/fpls.2017.00141

Kuan, K. B., Othman, R., Rahim, K. A., & Shamsuddin, Z. H. (2016). Plant growth-promoting rhizobacteria inoculation to enhance vegetative growth, nitrogen fixation and nitrogen remobilisation of maize under greenhouse conditions. *PloS ONE,* 11(3), Article e0152478. https://doi.org/10.1371/journal.pone.0152478

Kulkova, I., Wróbel, B., & Dobrzyński, J. (2024). *Serratia* spp. as plant growth-promoting bacteria alleviating salinity, drought, and nutrient imbalance stresses. *Frontiers in Microbiology,* 15, Article 1342331. https://doi.org/10.3389/fmicb.2024.1342331

Kumar, S., Stecher, G., Li, M., Knyaz, C., & Tamura, K. (2018). MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution,* 35(6), Article 1547. https://doi.org/10.1093/molbev/msy096

Kumari, S., Prabha, C., Singh, A., Kumari, S., & Kiran, S. (2018). Optimization of indole-3-acetic acid production by diazotrophic *B. subtilis* DR2 (KP455653), isolated from rhizosphere of *Eragrostis cynosuroides*. *International Journal of Pharma, Medical and Biological Sciences,* 7(2), 20-27. https://doi.org/10.18178/ijpmbs.7.2.20-27

Lebrazi, S., Niehaus, K., Bednarz, H., Fadil, M., Chraibi, M., & Fikri-Benbrahim, K. (2020). Screening and optimization of indole-3-acetic acid production and phosphate solubilization by rhizobacterial strains isolated from *Acacia cyanophylla* root nodules

and their effects on its plant growth. *Journal of Genetic Engineering and Biotechnology,* 18(1), Article 71. https://doi.org/10.1186/s43141-020-00090-2

Lee, S., Kim, J.-A., Song, J., Choe, S., Jang, G., & Kim, Y. (2024). Plant growth-promoting rhizobacterium *Bacillus megaterium* modulates the expression of antioxidant-related and drought-responsive genes to protect rice (*Oryza sativa* L.) from drought. *Frontiers in Microbiology,* 15, Article 1430546. https://doi.org/10.3389/fmicb.2024.1430546

Ma, Q., Sun, X., Gong, S., & Zhang, J. (2010). Screening and identification of a highly lipolytic bacterial strain from barbecue sites in Hainan and characterization of its lipase. *Annals of Microbiology,* 60, 429-437. https://doi.org/10.1007/s13213-010-0060-1

Meena, V. S., Meena, S. K., Verma, J. P., Kumar, A., Aeron, A., Mishra, P. K., Bisht, J. K., Pattanayak, A., Naveed, M., & Dotaniya, M. L. (2017). Plant beneficial rhizospheric microorganism (PBRM) strategies to improve nutrients use efficiency: A review. *Ecological Engineering,* 107, 8-32. https://doi.org/10.1016/j.ecoleng.2017.06.058

Mehmood, N., Saeed, M., Zafarullah, S., Hyder, S., Rizvi, Z. F., Gondal, A. S., Jamil, N., Igbal, R., Ali, B., Ercisli, S., & Kupe, M. (2023). Multifaceted impacts of plant-beneficial *Pseudomonas* spp. in managing various plant diseases and crop yield improvement. *ACS Omega,* 8(25), 22296-22315. https://doi.org/10.1021/acsomega.3c00870

Muhammad, M., Waheed, A., Wahab, A., Majeed, M., Nazim, M., Liu, Y.-H., & Li, W.-J. (2023). Soil salinity and drought tolerance: An evaluation of plant growth, productivity, microbial diversity, and amelioration strategies. *Plant Stress*, 11, Article 100319. https://doi.org/10.1016/j.stress.2023.100319

Muleta, A., Tesfaye, K., Selassie, T. H. H., Cook, D. R., & Assefa, F. (2021). Phosphate solubilization and multiple plant growth promoting properties of *Mesorhizobium* species nodulating chickpea from acidic soils of Ethiopia. *Archives of Microbiology,* 203*,* 2129-2137. https://doi.org/10.1007/s00203-021-02189-7

Naseem, M., Chaudhry, A. N., Jilani, G., Alam, T., Naz, F., Ullah, R., Zahoor, M., Zaman, S., & Sohail. (2024). Exopolysaccharide-producing bacterial cultures of *Bacillus cereus* and *Pseudomonas aeruginosa* in soil augment water retention and maize growth. *Heliyon,* 10(4), Article e26104. https://doi.org/10.1016/j.heliyon.2024.e26104

Noori, F., Etesami, H., Noori, S., Forouzan, E., Jouzani, G. S., & Malboobi, M. A. (2021). Whole genome sequence of *Pantoea agglomerans* ANP8, a salinity and drought stress–resistant bacterium isolated from alfalfa (*Medicago sativa* L.) root nodules. *Biotechnology Reports,* 29, Article e00600. https://doi.org/10.1016/j.btre.2021.e00600

Oyedoh, O. P., Yang, W., Dhanasekaran, D., Santoyo, G., Glick, B. R., & Babalola, O. O. (2023). Rare rhizo-Actinomycetes: A new source of agroactive metabolites. *Biotechnology Advances*, 67, Article 108205. https://doi.org/10.1016/j.biotechadv.2023.108205

Parvin, N., Mukherjee, B., Roy, S., & Dutta, S. (2023). Characterization of plant growth promoting rhizobacterial strain *Bacillus cereus* with special reference to exopolysaccharide production. *Journal of Plant Nutrition,* 46(11), 2608-2620. https://doi.org/10.1080/01904167.2022.2160740

Patel, S. K., Singh, S., Benjamin, J., Singh, V., Bisht, D., & Lal, R. (2024). Plant growth-promoting activities of *Serratia marcescens* and *Pseudomonas fluorescens* on *Capsicum annuum* L. plants. *Ecological Frontiers,* 44(4), 654-663. https://doi.org/10.1016/j.ecofro.2024.01.002

Peng, J., Ma, J., Wei, X., Zhang, C., Jia, N., Wang, X., Wang, E. T., Hu, D., & Wang, Z. (2021). Accumulation of beneficial bacteria in the rhizosphere of maize (*Zea mays* L.) grown in a saline soil in responding to a consortium of plant growth promoting rhizobacteria. *Annals of Microbiology,* 71, Article 40. https://doi.org/10.1186/s13213-021-01650-8

Prasad, J., Dey, R., & Raghuwanshi, R. (2022). Exopolysaccharide-producing rhizospheric bacteria enhance yield via promoting wheat (*Triticum aestivum* L.) growth at early stages. *Microbiology,* 91(6), 757-769. https://doi.org/10.1134/S0026261721102622

Qaisrani, M. M., Zaheer, A., Mirza, M. S., Naqqash, T., Qaisrani, T. B., Hanif, M. K., Rasool, G., Malik, K. A., Ullah, S., Jamal, M. S., Mirza, Z., Karim, S., & Rasool, M. (2019). A comparative study of bacterial diversity based on culturable and culture-independent techniques in the rhizosphere of maize (Zea mays L.). *Saudi Journal of Biological Sciences,* 26(7), 1344-1351. https://doi.org/10.1016/j.sjbs.2019.03.010

Rasool, A., Mir, M. I., Zulfajri, M., Hanafiah, M. M., Unnisa, S. A., & Mahboob, M. (2021). Plant growth promoting and antifungal asset of indigenous rhizobacteria secluded from saffron (*Crocus sativus* L.) rhizosphere. *Microbial Pathogenesis,* 150, Article 104734. https://doi.org/10.1016/j.micpath.2021.104734

Ríos-Ruiz, W. F., Tarrillo-Chujutalli, R. E., Rojas-García, J. C., Tuanama-Reátegui, C., Pompa-Vásquez, D. F., & Zumaeta-Arévalo, C. A. (2024). The biotechnological potential of plant growth-promoting rhizobacteria isolated from maize (*Zea mays* L.) cultivations in the San Martin Region, Peru. *Plants,* 13(15), Article 2075. https://doi.org/10.3390/plants13152075

Santos, K. F. D. N., Moure, V. R., Hauer, V., Santos, A. R. S., Donatti, L., Galvão, C. W., Pedrosa, F. O., Souza, E. M., Wassem, R., & Steffens, M. B. R. (2017). Wheat colonization by an *Azospirillum brasilense* ammonium-excreting strain reveals upregulation of nitrogenase and superior plant growth promotion. *Plant and Soil,* 415, 245-255. https://doi.org/10.1007/s11104-016-3140-6

Sehrawat, A., Sindhu, S. S., & Glick, B. R. (2022). Hydrogen cyanide production by soil bacteria: Biological control of pests and promotion of plant growth in sustainable agriculture. *Pedosphere,* 32(1), 15-38. https://doi.org/10.1016/S1002-0160(21)60058-9

Sharma, P., Pandey, R., & Chauhan, N. S. (2024). Unveiling wheat growth promotion potential of phosphate solubilizing *Pantoea agglomerans* PS1 and PS2 through genomic, physiological, and metagenomic characterizations. *Frontiers in Microbiology*, 15, Article 1467082. https://doi.org/10.3389/fmicb.2024.1467082

Shin, H.-Y., Kim, D.-S., Lee, C.-H., Lee, D.-S., & Han, S.-I. (2024). Isolation and characterization of plant growth promoting bacteria *Pseudomonas* sp. SH-26 from peat soil. *Journal of the Korean Applied Science and Technology,* 41(2), 199-207. https://doi.org/10.12925/jkocs.2024.41.2.199

Silva, E. R., Zoz, J., Oliveira, C. E. S., Zuffo, A. M., Steiner, F., Zoz, T., & Vendruscolo, E. P. (2019). Can co-inoculation of *Bradyrhizobium* and *Azospirillum* alleviate adverse effects of drought stress on soybean (*Glycine max* L. Merrill.)? *Archives of Microbiology,* 201(3), 325-335. https://doi.org/10.1007/s00203-018-01617-5

Singh, R. K., Singh, P., Li, H.-B., Song, Q.-Q., Guo, D.-J., Solanki, M. K., Verma, K. K., Malviya, M. K., Song, X.-P., Lakshmanan, P., Yang, L.-T., & Li, Y.-R. (2020). Diversity of nitrogen-fixing rhizobacteria associated with sugarcane: a comprehensive study of plant-microbe interactions for growth enhancement in *Saccharum* spp. *BMC Plant Biology,* 20(1), Article 220. https://doi.org/10.1186/s12870-020-02400-9

Solórzano-Acosta, R. A., & Quispe, K. R. (2024). Assessing the role of field isolated *Pseudomonas* and *Bacillus* as growth-promoting rizobacteria on avocado (*Persea americana*) seedlings. *Journal of Sustainable Agriculture and Environment,* 3(3), Article e12114. https://doi.org/10.1002/sae2.12114

Soni, R., Rawal, K., & Keharia, H. (2021). Genomics assisted functional characterization of *Paenibacillus polymyxa* HK4 as a biocontrol and plant growth promoting bacterium. *Microbiological Research,* 248, Article 126734. https://doi.org/10.1016/j.micres.2021.126734

Świątczak, J., Kalwasińska, A., & Brzezinska, M. S. (2024). Plant growth–promoting rhizobacteria: *Peribacillus frigoritolerans* 2RO30 and *Pseudomonas sivasensis* 2RO45 for their effect on canola growth under controlled as well as natural conditions. *Frontiers in Plant Science,* 14, Article 1233237. https://doi.org/10.3389/fpls.2023.1233237

Tirry, N., Ferioun, M., Kouchou, A., Laghmari, G., Asri, M., Zouitane, I., Bahafid, W., El Omari, B., & El Ghachtouli, N. (2024). Plant growth-promoting rhizobacteria's (PGPR) effects on *Medicago sativa* growth, arbuscular mycorrhizal colonisation, and soil enzyme activities. *International Journal of Environmental Studies,* 81(3), 1190-1208. https://doi.org/10.1080/00207233.2023.2216606

Umapathi, M., Chandrasekhar, C. N., Senthil, A., Kalaiselvi, T., Santhi, R., & Ravikesavan, R. (2022). Isolation, characterization and plant growth-promoting effects of sorghum [*Sorghum bicolor* (L.) moench] root-associated rhizobacteria and their potential role in drought mitigation. *Archives of Microbiology,* 204(6), Article 354. https://doi.org/10.1007/s00203-022-02939-1

Wang, H., Liu, R., You, M. P., Barbetti, M. J., & Chen, Y. (2021). Pathogen biocontrol using plant growth-promoting bacteria (PGPR): Role of bacterial diversity. *Microorganisms*, 9(9), Article 1988. https://doi.org/10.3390/microorganisms9091988

Wu, S., Wu, K., Shi, L., Sun, X., Tan, Q., & Hu, C. (2023). Recruitment of specific microbes through exudates affects cadmium activation and accumulation in *Brassica napus*. *Journal of Hazardous Materials,* 442, Article 130066. https://doi.org/10.1016/j.jhazmat.2022.130066

Zafar-ul-Hye, M., Danish, S., Abbas, M., Ahmad, M., & Munir, T. M. (2019). ACC deaminase producing PGPR *Bacillus amyloliquefaciens* and *Agrobacterium fabrum* along with biochar improve wheat productivity under drought stress. *Agronomy,* 9(7), Article 343. https://doi.org/10.3390/agronomy9070343

Zhiyong, S., Yaxuan, G., Yuanyuan, W., Xiang, Y., Xu, G., Zhenhong, L., Jingping, N., Jianping, L., & Zhenyu, L. (2024). Nitrogen-fixing bacteria promote growth and bioactive components accumulation of *Astragalus mongholicus* by regulating plant metabolism and rhizosphere microbiota. *BMC Microbiology,* 24(1), Article 261. https://doi.org/10.1186/s12866-024-03409-y