Research and Innovation Article
Salud UIS ISSN: 2145-8464

Culturable Plant Growth-Promoting Bacteria from a High-Altitude Páramo Soil Ecosystem as Potential Sources of Biofertilizers

Bacterias cultivables promotoras del crecimiento vegetal de un ecosistema de suelo de páramo como posibles fuentes de biofertilizantes

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Received: 26/09/2025. Approved: 6/11/2025

Abstract

Introduction: High-altitude páramo ecosystems, characterized by harsh and fluctuating environmental conditions that significantly influence soil ecological and biological processes, harbor diverse and potentially beneficial microbial communities. **Objective:** This study aimed to isolate and characterize culturable plant growth-promoting bacteria from rhizosphere and bulk soils associated with *Espeletia conglomerata* in a high-altitude páramo ecosystem to screen for potential microbial biofertilizers. **Methodology:** The study site was the Santurbán Páramo Regional Natural Park, Colombia. Soil samples were collected from different altitudes for the isolation and identification of potential plant growth-promoting bacteria and evaluated by phenotypic (nitrogen fixation and phosphate solubilization) and genotypic (presence of three marker genes) approaches. The efficacy of the isolates as plant growth promoters was validated using assays conducted on tomato seedlings in controlled environments. **Results:** Twenty bacterial isolates were recovered and taxonomically classified, with the majority belonging to the genera *Pseudomonas*, *Serratia*, and *Paraburkholderia*. Functional and molecular screening revealed that 80% of the isolates could fix atmospheric nitrogen, 75% could solubilize phosphate, and 60% possessed genes associated with auxin production. Six of the isolates exhibited all the tested plant growth-promoting traits and were further evaluated in tomato seedling growth assays. Compared with the control plants, the inoculated plants presented significant increases in height, hypocotyl length, and biomass, particularly when treated with isolates of *Pseudomonas yamanorum*, *Pseudomonas fluorescens*, *Serratia proteamaculans*, and *Rhodococcus qingshengii*. **Conclusion:** These results highlight the biotechnological potential of cold-adapted bacteria from páramo ecosystems for promoting plant growth and as biofertilizer candidates. The multifunctional traits and ecological resilience of these bacteria support their application in sustainable agriculture and ecological restoration efforts in high-altitude or stressful soil environments.

Keywords: Páramo; *Espeletia*; Soil Microbiology; Plant Growth Promotion; Biofertilizer; Microbial Consortia; Plant Development; *Pseudomonas yamanorum*

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Suggested citation: Carreño JV, Fuentes-Marín S, Rangel D, Fajardo M, Archila-Durán L, Zafra G. Culturable Plant Growth-Promoting Bacteria from a High-Altitude Páramo Soil Ecosystem as Potential Sources of Biofertilizers. Salud UIS. 2026; 58: e26v58a02. doi: https://doi.org/10.18273/saluduis.58.e26v58a02

Resumen

Introducción: Los ecosistemas de páramo, caracterizados por condiciones ambientales duras y fluctuantes que influyen significativamente en los procesos ecológicos y biológicos del suelo, albergan comunidades microbianas diversas y potencialmente beneficas. **Objetivo:** Este estudio tuvo como objetivo aislar y caracterizar bacterias cultivables promotoras del crecimiento vegetal a partir de suelos de rizosféricos de *Espeletia conglomerata* y suelos no rizosféricos, en un ecosistema de páramo de gran altitud, para seleccionar posibles biofertilizantes microbianos. **Metodología:** El sitio de estudio fue el Parque Natural Regional Santurbán Páramo, Colombia. Se recolectaron muestras de suelo de diferentes altitudes para el aislamiento e identificación de posibles bacterias promotoras del crecimiento de plantas y posteriormente fueron evaluadas mediante ensayos funcionales (fijación de nitrógeno y solubilización de fosfatos) y moleculares (presencia de tres genes marcadores). La eficacia de los aislados como promotores del crecimiento vegetal se evaluó mediante ensayos de crecimiento realizados en plántulas de tomate en entornos controlados. **Resultados:** Se obtuvieron e identificaron veinte aislamientos bacterianos, la mayoría pertenecientes a los géneros *Pseudomonas*, *Serratia* y *Paraburkholderia*. El *screening* funcional y molecular reveló que el 80% de los aislados podían fijar nitrógeno atmosférico, el 75% podían solubilizar fosfato y el 60% poseían genes asociados con la producción de auxinas. Seis de los aislados exhibieron todos los rasgos de promoción del crecimiento de plantas probados y fueron evaluados posteriormente en ensayos de crecimiento de plántulas de tomate. En comparación con las plantas de control, las plantulas inoculadas presentaron aumentos significativos en su altura, longitud del hipocótilo y biomasa, particularmente cuando fueron tratadas con aislamientos de *Pseudomonas yamanorum*, *Pseudomonas fluorescens*, *Serratia proteamaculans* y *Rhodococcus qingshengii*. **Conclusiones:** Estos resultados destacan el potencial biotecnológico de las bacterias adaptadas al frío de los ecosistemas de páramo para promover el crecimiento de las plantas y como candidatos a biofertilizantes. Las características multifuncionales y la resiliencia ecológica de estas bacterias respaldan su aplicación en la agricultura sostenible y los esfuerzos de restauración ecológica en entornos de alta altitud o suelos estresantes.

Palabras clave: Páramo; *Espeletia*; Microbiología del Suelo; Promoción del Crecimiento Vegetal; Biofertilizante. Consorcios Microbianos; Desarrollo de la Planta, *Pseudomonas yamanorum*

Introduction

Páramos are unique, high-mountain tropical wetland ecosystems located primarily in the Andean mountains in Colombia, Perú, Ecuador, and Venezuela, covering approximately 35,000 km² at altitudes between 2,800 and 4,700 m.a.s.l.[1]. The significance of páramos lies in their crucial role in South America's hydrology, influencing water regulation processes and serving as important water suppliers, contributing up to 70% of the water requirements of large urban centers [2]. Páramos are home to an extraordinary amount of plant and animal diversity and are also fast-evolving biodiversity cold hot spots, with high species endemism[3]. Although the composition of plant species may vary depending on the region and altitude, plants of the genus *Espeletia* are among the most emblematic and dominant vegetal species of páramos. They play a key role in water regulation by capturing and storing atmospheric water, which is subsequently released through their roots into the soil, thereby forming subterranean water reservoirs[4]. *Espeletia* constitute the majority of the biomass present in páramos, prevent soil erosion, and regulate carbon storage[5]. The dynamic environmental conditions of the páramo, including sudden fluctuations in fog density, dew formation, solar radiation, temperature, atmospheric moisture demand, and soil water availability, play crucial roles in shaping its ecological and biological processes.

The diversity and function of microbial communities are essential for the ecological balance of páramos, not only because of their abundance but also because they participate in a wide variety of biological processes, such as the transformation and decomposition of organic matter, biogeochemical cycles, enzyme and secondary metabolite production, and plant growth promotion (PGP)[6]. Microorganisms are the main actors in soil sustainability and plant growth promotion, either by transforming substances present in the environment into bioavailable forms for plants, exerting biocontrol over phytopathogens, or through the secretion of hormones and other compounds that promote foliar and root development[7]. There are only scarce reports regarding the microbial diversity associated with *Espeletia* in páramo ecosystems, but the structure of the endophytic and epiphytic bacterial communities in the *Espeletia* phylosphere seems to vary according to the plant zone and is apparently determined by specific niche characteristics[8]. These microbial communities may influence plant traits such as nutrient uptake, stress tolerance, and pathogen resistance, and their composition could also contribute to phenotypic variation among *Espeletia* individuals.

Páramo soils can be hot spots for microbial diversity, as they constitute habitats with increased nutrient availability and distinctive environmental conditions. These microbial communities may produce enzymes with a wide range of biochemical, physiological, and molecular characteristics that enable microbial populations to adapt to and survive in harsh environments and could also have enormous biotechnological potential, especially for the promotion of plant growth[6]. Furthermore, the unique microbial communities found in páramo soils, particularly those associated with *Espeletia* spp., may offer significant advantages as potential biofertilizers. These plant growth-promoting bacteria (PGPB) and fungi, including phosphate-solubilizing, nitrogen-fixing, auxin-producing, and cellulolytic microorganisms, among others, could increase nutrient availability and promote plant growth, making them valuable for sustainable agriculture and ecological restoration efforts in harsh environments such as páramos[9]. Several studies have identified diverse microbial populations in the rhizosphere and phyllosphere of *Espeletia* species, highlighting their potential role in supporting plant health and development[8,10]. Leveraging these native PGP microbes could improve the growth and resilience of *Espeletia* spp., contributing to the conservation and restoration of páramo ecosystems. Thus, the aim of this study was to isolate and characterize indigenous soil microorganisms with plant growth-promoting activity from a high-altitude páramo ecosystem to screen for potential microbial biofertilizers.

Methodology

Study site and soil collection

The study site was the Santurbán páramo regional natural park, located in Vetas, Santander, Colombia. Samples of *Espeletia conglomerata* rhizosphere and bulk (non-*Espeletia*-rhizosphere) soils were collected from November 2022 to March 2023 at four points ranging from 3,652 to 4,032 m above sea level (m.a.s.l.) in different páramo locations (**Table 1**). *Espeletia* rhizosphere samples (n=4) were collected by gently shaking away the soil that adhered to *Espeletia* roots at a depth of 0-30 cm and then mixed. Bulk soil samples (n= 4) were also collected adjacent to *Espeletia* plants at 0-30 cm depth. The samples were refrigerated and immediately transported to the laboratory for further analysis.

Table 1. Site description of the soil sampling locations at Santurbán Páramo.

Location	Altitude (m.a.s.l.) [a]	Coordinates	Soil type [b]	Temperature range (mean)
Ciénaga – Las calles lagoon complex	3,652	N 07° 20.062' W 072° 50.685'	Rhizosphere	10 – 20 °C (15 °C)
		N 07° 20.062' W 072° 50.685'	Bulk	
	3,661	N 07° 19.934' W 072° 50.813'	Rhizosphere	
		N 07° 19.934' W 072° 50.813'	Bulk	
Cuntas lagoon complex	3,974	N 07° 17.004' W 072° 52.509'	Rhizosphere	1 – 8 °C (4 °C)
		N 07° 17.004' W 072° 52.509'	Bulk	
	4,032	N 07° 16.685´ W 072° 52.256	Rhizosphere	
		N 07° 16.685´ W 072° 52.256	Bulk	

[a]: m.a.s.l.: meters above sea level. [b]: Rhizosphere: *Espeletia conglomerata* rhizosphere; Bulk: Nonrhizospheric soil.

Isolation of potential plant growth-promoting bacteria

The isolation and screening of potential PGPB from páramo soils were performed on the basis of the ability of the isolates to fix nitrogen and grow in nitrogen-deficient Mannitol-Ashby media (composition per liter: mannitol, 20.0 g; K_2HPO_4, 0.2 g; $MgSO_4$, 0.2 g; NaCl, 0.2 g; K_2SO_4, 0.1 g; $CaCO_3$, 5.0 g), and solubilize the inorganic phosphate present in the National Botanical Research Institute's phosphate (NBRIP) growth media (composition per liter: glucose, 10 g; $Ca_3(PO_4)_2$, 5 g; $MgCl_2 \cdot 6H_2O$, 5 g; $MgSO_4 \cdot 7H_2O$, 0.25 g; KCl, 0.2 g; and $(NH_4)_2SO_4$, 0.1 g). Isolation was carried out by adding 1 g of each soil (rhizosphere or bulk) sample to 99 ml of

sterile physiological saline solution and vortexing for 2 min. The soil suspensions were then serially diluted, and 100 μl from dilutions 10^{-3}, 10^{-4}, 10^{-5} and 10^{-6} were spread directly into the NBRIP and mannitol-ashby plates. The plates were incubated at 15 °C for 7-14 days. Individual colonies were picked and transferred onto new plates of NBRIP and mannitol-ashby media, and then, the colonies were picked and transferred onto tryptic soy agar (TSA, Difco, USA) plates for purification. These axenic isolates were subjected to further analysis. All experiments were performed in triplicate.

Molecular identification of native bacterial isolates

Genomic DNA extraction from bacterial axenic isolates was performed via the Quick-DNA Fungal/Bacterial Miniprep Kit (Zymo Research Corporation, USA) according to the manufacturer's instructions. DNA quantity and quality were measured via agarose gel electrophoresis and by the ratio of the absorbances at 260 nm and 280 nm. Amplification of the bacterial 16S rRNA gene was performed using the primers P27F (GAGTTTGATCCTGGCTCA) and P1525R (GAAAGGAGGAGATCCAGC) according to the conditions described by Lane[11]. The PCR products were purified using the Biospin PCR purification kit (Bioer Technology, China) and sequenced in a 3730xl DNA analyzer (Applied Biosystems, USA) with oligonucleotides P27F and P1525R as sequencing primers. Partial ribosomal sequences were quality-checked and aligned using the BioEdit V7.2.5 software. The resulting sequences were used for bacterial identification via the BLAST algorithm, based on the percentage of similarity in comparison with sequences stored in the GenBank database. Ribosomal sequences were deposited in the NCBI GenBank database (https://www.ncbi.nlm.nih.gov/genbank/).

Molecular detection of microbial plant growth-promoting traits

The microbial isolates obtained from the soil were screened for the presence of three marker genes associated with plant growth-promoting traits. The detection of the nitrogenase reductase (*nifH*) gene, a marker gene used to identify nitrogen-fixing bacteria and archaea, was carried out using the primers nifHg1_for (GGTTGTGACCCGAAAGCTGA) and nifHg1_rev (GCGTACATGGCCATCATCTC)[12]. The amplification program consisted of initial denaturation at 95 °C for 5 min followed by 35 cycles of 94 °C for 30 s, 57 °C for 30 s and 72 °C for 45 s. The detection of the pyrroloquinoline quinone (*pqq*) gene, a marker gene of phosphate-solubilizing microorganisms, was carried out using the primers pqqCf1 (CATGGCATCGAGCATGCTCC) and pqqCr1 (CAGGGCTGGGTCGCCAACC)[13]. The amplification program consisted of initial denaturation at 95 °C for 5 min followed by 30 cycles of 94 °C for 30 s, 63 °C for 30 s and 72 °C for 45 s. The detection of the indole-3-pyruvate decarboxylase (*ppdC*) gene, related to 3-indole acetic acid (IAA) production by bacteria, was carried out using the primers 3FppdC (GGCGACTGCCTGTTCACC) and 3RppdC (CCAGCTGGCGTTGTTGAAC)[14]. The amplification program consisted of initial denaturation at 95 °C for 5 min followed by 30 cycles of 95 °C for 45 s, 61 °C for 30 s and 72 °C for 30 s. *nifH*, *pqq*, and *ppdC* gene amplification was detected by 1% agarose gel electrophoresis. All experiments were performed in triplicate.

Screening of plant growth-promoting effects of páramo bacterial isolates

The plant experiments were conducted in seedling trays with a cell size of 3.8 cm width, 3.8 cm length and 6 cm height, each containing 33 g of a substrate mixture consisting of 50% peat and 50% commercial compost (Anasac, Colombia). Commercial tomato (*Solanum lycopersicum* var. Milano) seeds (Anasac, Colombia) were used as the plant material in this study. The seeds were surface sterilized by rinsing with a solution of 1% sodium hypochlorite for 10 s, washed three times with sterile water, and then dried. Three sterile seeds were planted in each tray cell. To determine the ability of the bacterial isolates to promote the growth of tomato seedlings, tray cells containing the substrate mixture and seeds were inoculated with 6 x 10^8 CFU of individual bacterial isolates with all the evaluated phenotypic and molecular PGP traits, along with fast-growing isolates (forming visible colonies within 24-48 h) on Mannitol-Ashby and NBRIP plates. Two consortia composed of different mixtures of these isolates were also evaluated. The plant growth assays were carried out for 45 days at 20 °C under a relative humidity of 65–80% and a 12-hour photoperiod. After incubation, the seedlings were carefully collected from the substrate to remove the whole plant (shoots + roots), cleaned and subjected to measurements of plant characteristics. The average plant height (cm), hypocotyl height (cm), and plant fresh

weight (mg) were documented using a measuring tape for each treated tomato seedling. The controls consisted of uninoculated tomato seeds, which were planted and incubated under the same conditions as the inoculated seeds. All experiments were performed in triplicate.

Statistical analysis

The data from the plant growth experiments were analyzed via analysis of variance (ANOVA) in GraphPad Prism version 8.02 (GraphPad Software, USA), followed by Tukey's test at $p \leq 0.05$ for multiple comparisons of the means.

Results

Microbial isolation from páramo soils

A total of 20 bacterial isolates were successfully recovered from soil samples collected from the páramo ecosystem, eight from the *Espeletia* rhizosphere and 12 from bulk soil, based on their ability to grow either in nitrogen-deficient Manitol-Ashby media or NBRIP media containing insoluble tricalcium phosphate. In general, the isolates exhibited small colony sizes and typical halo zones of phosphate solubilization (**Figure 1**).

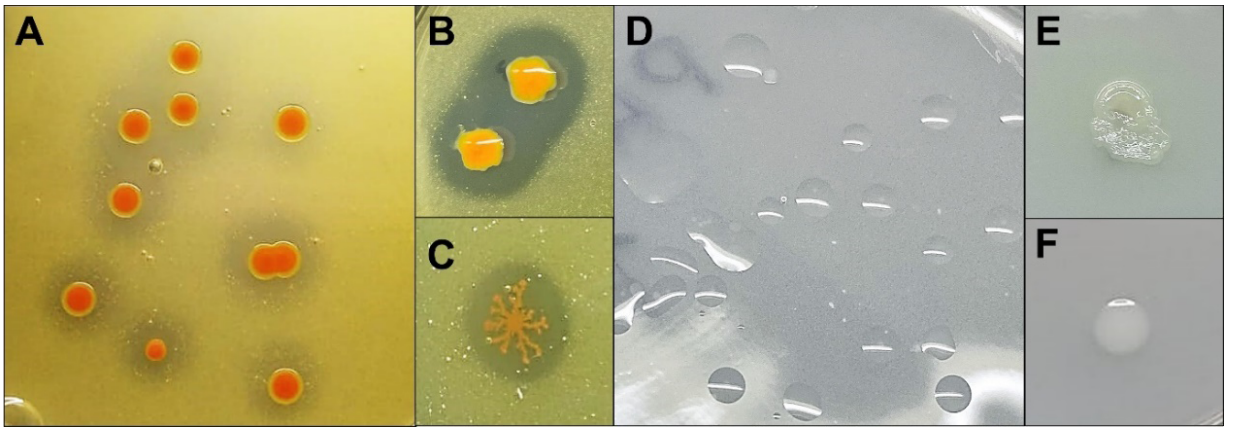

Figure 1. Morphological characteristics of bacterial isolates from páramo soils.
Colony morphology and halo zones of isolates SN03 (A), SP03 (B), and SP05 (C) growing in solid NBRIP media containing insoluble tricalcium phosphate; colony morphology of isolates SN04 (D), SN01 (E), and SP07 (F) growing in nitrogen-deficient Mannitol-Ashby media.

Taxonomic classification based on 16S rRNA gene sequencing grouped the isolates into four major bacterial classes (Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, and Actinomycetia). Among these classes, Gammaproteobacteria was the most represented class, comprising 70% of the total isolates. This dominance was especially evident among the isolates derived from bulk soil (9 of 12 isolates). At the genus level, *Pseudomonas*, *Serratia*, and *Paraburkholderia* were predominant, accounting for 40%, 20%, and 15% of the total isolates, respectively. Other isolated genera included *Caballeronia, Rhizobium*, *Rahnella*, and *Rhodococcus*. Thirteen isolates were identified at the species level, whereas the remaining seven were identified only at the genus level because of slightly lower identity percentages and broader taxonomic resolution. The identity percentages ranged from 98.49% to 100%, with most isolates exhibiting values above 99.50% with those reported in GenBank (**Table 2**). The isolates assigned to the same species (e.g., *Pseudomonas fluorescens* SN01 and SN09; *Pseudomonas yamanorum* SN02, SN04, and SP07; *Rahnella aquatilis* SN05 and SP10) were not 100% similar, exhibiting slight variations in their 16S rRNA gene sequences. With respect to the altitude of isolation, most isolates (17 out of 20) were obtained from elevations close to 3,974 m.a.s.l., with a few collected from higher elevations (4,032 m.a.s.l.). or lower elevations (3,661 and 3,652 m.a.s.l.) reflecting the altitudinal gradient typical of páramo ecosystems.

Table 2. Identification of native bacterial isolates based on 16S rRNA gene sequences.

Isolate ID	Major taxonomic group (Class)	Taxon group (species)	Identity (%) [a]	Isolation altitude (m.a.s.l)	Soil type[b]	GenBank accession[c]
SN01	Gammaproteobacteria	*Pseudomonas fluorescens*	100	4,032	Bulk	PV784136.1
SN02	Gammaproteobacteria	*Pseudomonas yamanorum*	100	3,974	Rhizo	PV784137.1
SN03	Gammaproteobacteria	*Serratia liquefaciens*	99.38	3,974	Bulk	PV784138.1
SN04	Gammaproteobacteria	*Pseudomonas yamanorum*	99.93	3,974	Rhizo	PV784139.1
SN05	Gammaproteobacteria	*Rahnella aquatilis*	100	3,974	Bulk	PV784140.1
SN06	Gammaproteobacteria	*Pseudomonas* sp. (*P. fluorescens* group)	100	3,974	Bulk	PV784141.1
SN07	Gammaproteobacteria	*Serratia* sp.	98.51	3,974	Bulk	PV784142.1
SN09	Gammaproteobacteria	*Pseudomonas fluorescens*	99.92	3,974	Bulk	PV784143.1
SN10	Alphaproteobacteria	*Rhizobium lusitanum*	99.90	3,661	Bulk	PV784144.1
SN11	Betaproteobacteria	*Paraburkholderia* sp.	99.86	3,661	Bulk	PV784145.1
SN12	Betaproteobacteria	*Paraburkholderia sediminicola*	99.93	3,661	Bulk	PV784146.1
SP01	Gammaproteobacteria	*Pseudomonas* sp.	99.86	3,974	Rhizo	PV784147.1
SP02	Gammaproteobacteria	*Pseudomonas* sp.	100	3,974	Rhizo	PV784148.1
SP03	Gammaproteobacteria	*Serratia* sp.	100	3,974	Bulk	PV784149.1
SP04	Gammaproteobacteria	*Serratia proteamaculans*	99.82	3,974	Bulk	PV784150.1
SP05	Actinomycetia	*Rhodococcus qingshengii*	100	3,974	Rhizo	PV784151.1
SP07	Gammaproteobacteria	*Pseudomonas yamanorum*	100	3,974	Rhizo	PV784152.1
SP08	Betaproteobacteria	*Caballeronia mineralivorans*	100	3,661	Rhizo	PV784153.1
SP09	Betaproteobacteria	*Paraburkholderia* sp.	98.49	3,661	Rhizo	PV784154.1
SP10	Gammaproteobacteria	*Rahnella aquatilis*	99.50	3,652	Rhizo	PV784155.1

[a] Percent identity of matches with aligned sequences in the NCBI database. [b] Rhizo: Rhizosphere; Bulk: Non-rhizospheric soil. [c] Reported accession number in the NCBI GenBank database.

Detection of plant growth-promoting traits in native bacterial isolates

All bacterial isolates presented either nitrogen fixation or phosphate solubilization traits, as confirmed by phenotypic and molecular assays (**Table 3**). Among the 20 isolates evaluated, 16 (80%) exhibited visible growth in Mannitol-Ashby medium, indicating their ability to fix nitrogen. All seven isolates obtained from bulk soil were able to fix nitrogen, and the four isolates that did not fix nitrogen (*Pseudomonas* sp. SN01, *Caballeronia mineralivorans* SP08, *Paraburkholderia* sp. SP09, and *Rahnella aquatilis* SP10) were all isolated from rhizosphere samples. The amplification of the *nifH* gene, which was conducted to complement the phenotypic screenings, was absent in the same four isolates that failed to grow in the Mannitol-Ashby medium, indicating strong agreement between the molecular and phenotypic assessments.

Table 3. Detection of plant growth-promoting traits in native bacterial isolates from páramo soils.

Isolate	Taxon group (species)	Isolation source (soil type)	Plate screening		PCR screening		
			N_2 fixation	PO_4 solubilization	*nifH* gene	*pqq* gene	*ppdC* gene
SN01	*Pseudomonas fluorescens*	Bulk	+	–	+	–	–
SN02	*Pseudomonas yamanorum*	Rhizosphere	+	+	+	+	+
SN03	*Serratia liquefaciens*	Bulk	+	+	+	+	+
SN04	*Pseudomonas yamanorum*	Bulk	+	+	+	+	+
SN05	*Rahnella aquatilis*	Bulk	+	+	+	–	–
SN06	*Pseudomonas* sp. (*P. fluorescens* group)	Bulk	+	–	+	–	+
SN07	*Serratia* sp.	Bulk	+	+	+	+	+
SN09	*Pseudomonas fluorescens*	Bulk	+	+	+	+	+
SN10	*Rhizobium lusitanum*	Bulk	+	–	+	–	+
SN11	*Paraburkholderia* sp.	Bulk	+	–	+	–	+
SN12	*Paraburkholderia sediminicola*	Bulk	+	–	+	–	+
SP01	*Pseudomonas* sp.	Rhizosphere	–	+	–	+	+
SP02	*Pseudomonas* sp.	Rhizosphere	+	+	+	–	+
SP03	*Serratia* sp.	Bulk	+	+	+	+	+
SP04	*Serratia proteamaculans*	Bulk	+	+	+	+	+
SP05	*Rhodococcus qingshengii*	Rhizosphere	+	+	+	+	+
SP07	*Pseudomonas yamanorum*	Rhizosphere	+	+	+	+	+
SP08	*Caballeronia mineralivorans*	Rhizosphere	–	+	–	+	+
SP09	*Paraburkholderia* sp.	Rhizosphere	–	+	–	+	+
SP10	*Rahnella aquatilis*	Rhizosphere	–	+	–	–	+

+: Indicates growth (in plate screening) or amplification detected (in PCR screening); –: Indicates no growth (in plate screening) or no amplification detected (in PCR screening).

Phosphate solubilization ability, based on growth on NBRIP medium, was detected in 15 (75%) isolates. All the rhizosphere-derived isolates were positive in this assay, and remarkably, the four isolates that did not fix nitrogen in Mannitol-Ashby medium (SP01, SP08, SP09, and SP10) were capable of solubilizing phosphate on the NBRIP medium. Except for isolate SN05 (*Rahnella aquatilis*), the *pqq* gene, associated with phosphate solubilization through gluconic acid synthesis, was successfully amplified in all the isolates showing phosphate solubilization in the NBRIP medium, again confirming the consistency between the results of the PCR detection and plate growth assays. Although not all of them exhibited both traits, a total of 11 isolates, including 4 rhizosphere-derived and 7 bulk soil-derived isolates, demonstrated the ability to simultaneously fix nitrogen and solubilize phosphate in culture media.

The presence of the *ppdC* gene, which is involved in indole-3-acetic acid (IAA) biosynthesis, was detected in 12 isolates (60%), regardless of whether they were from bulk soil or the rhizosphere. While some isolates positive for *ppdC* also demonstrated phosphate solubilization and nitrogen-fixation abilities (e.g., SN03, SN07), others, such as SP01 and SP08, were positive only for a subset of PGP traits. The rhizosphere isolate SP10 (*Rahnella aquatilis*) presented a unique profile, lacking nitrogen fixation and the *nifH* gene and negative for *pqq*; however, it presented positive phosphate solubilization in the plate assay and harbored the *ppdC* gene. The isolates SN02

(*Pseudomonas yamanorum*), SN03 (*Serratia liquefaciens*), SN09 (*Pseudomonas fluorescens*), SP07 (*Pseudomonas yamanorum*), and SP04 (*Serratia proteamaculans*), which are derived from bulk soil, exhibited the complete set of PGP traits in both plate-based and molecular assays, including nitrogen fixation, phosphate solubilization, and the presence of the *nifH*, *pqq*, and *ppdC* genes, along with fast growth rates on culture medium plates; conversely, among rhizosphere isolates, only *Rhodococcus qingshengii* SP05 exhibited fast colony growth and all tested PGP traits. These six individual isolates isolates (*Pseudomonas yamanorum* SN02, *Serratia liquefaciens* SN03, *Serratia proteamaculans* SP04, *Pseudomonas fluorescens* SN09, *Rhodococcus qingshengii* SP05, and *Pseudomonas yamanorum* SP07) were further evaluated in plant growth assays.

Plant growth-promoting effects of páramo native bacterial isolates

The application of the six bacterial isolates with full PGP traits had different effects on the evaluated tomato seedling development parameters (**Figure 2**). Compared with the control, the inoculation of individual isolates SN02 (*Pseudomonas yamanorum*), SN09 (*Pseudomonas fluorescens*), and SP07 (*Pseudomonas yamanorum*) resulted in substantial increases in overall seedling length (**Figure 2A**) ($p < 0.05$), with average values ranging from 10 to 12 cm. Compared with the control, inoculation with the SN09 isolate resulted in the highest values (~11.5 cm), representing an approximately 2.0-fold increase. The consortia consisting of SN02 (*Pseudomonas yamanorum*) + SN03 (*Serratia liquefaciens*) + SP04 (*Serratia proteomaculans*) (SN02+SN03+SP04) and that consisting of SN09 (*Pseudomonas fluorescens*) + SP07 (*Pseudomonas yamanorum*) + SP05 (*Rhodococcus qingshengii*) (SN09+SP07+SP05) also performed significantly better than the control; however, there were no appreciable differences compared with the most successful individual treatments. Similarly, significant increases in hypocotyl length (**Figure 2B**) were obtained when individual isolates SN02, SN09, and SP07 were inoculated, especially in the consortium (SN09+SP07+SP05), which presented values comparable to those of the most effective individual treatments (~8.5 cm), indicating an approximately 1.8-fold increase compared with those of the control.

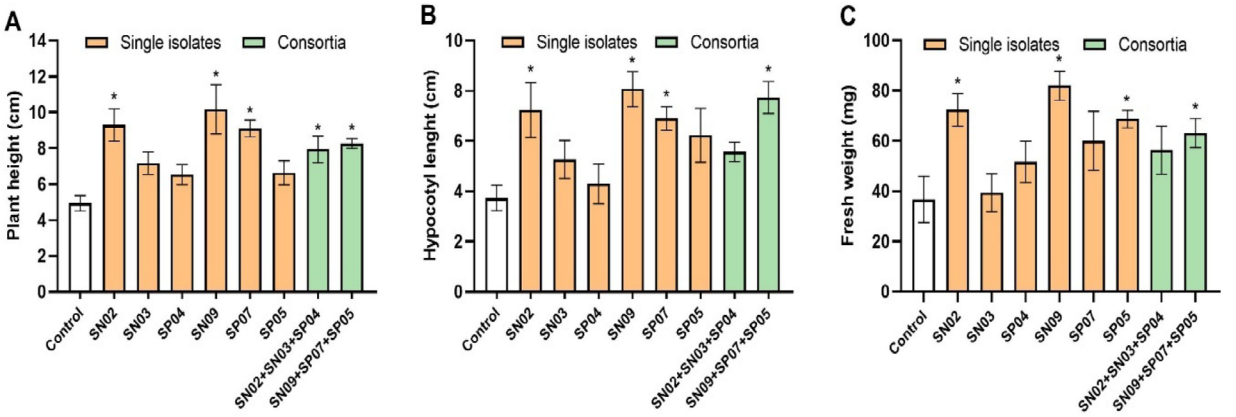

Figure 2. Influence of different plant growth-promoting (PGP) bacterial isolates on the growth of tomato seedlings after 45 days. The effects of inoculation on (A) plant height, (B) hypocotyl length, and (C) plant fresh weight are shown. *Indicates a significant difference ($p \leq 0.05$) compared with the control. SN02: *Pseudomonas yamanorum*; SN03: *Serratia liquefaciens*; SP04: *Serratia proteamaculans*; SN09: *Pseudomonas fluorescens*; SP05: *Rhodococcus qingshengii*; SP07: *Pseudomonas yamanorum*.

Significant increases in seedling fresh weight (**Figure 2C**) were also detected when isolates SN02, SN09, SP07, SP05, and both consortia were inoculated. The treatment with isolate SN09 (*Pseudomonas yamanorum*) presented the highest value at approximately 85 mg, which was double that of the control, closely followed by SN02 at approximately 80 mg, indicating an increase of almost 1.9-fold. For at least two of the examined variables, the analyzed microbial treatments produced values that were greater than those of the control. The treatments with the SN02 and SN09 isolates were particularly noteworthy since they continuously presented the greatest relative increases (up to twofold) and statistically significant differences ($p < 0.05$) across all three variables, indicating greater potential as plant growth promoters under controlled conditions.

Discussion

In contrast to the extensive microbiological research conducted in tundra and subantarctic environments, the potential of microbes from Andean páramo ecosystems as PGPB remains relatively underexplored. High-altitude páramo ecosystems pose unique challenges for microbial adaptation and metabolism due to harsh environmental conditions, including extremely low temperatures, reduced oxygen availability, strong UV radiation, and drastic temperature fluctuations. The use of PGPB as biofertilizers has garnered increasing interest in recent years as a sustainable approach to increase plant productivity, particularly in stress-prone environments such as cold and high-altitude regions[15]. In this context, the isolation and characterization of PGPB adapted to páramo conditions is critically important for the development of sustainable agricultural practices and ecological restoration strategies in cold mountain ecosystems. In this study, native bacteria isolated from páramo soils, including genera such as *Pseudomonas*, *Serratia*, *Rhizobium*, *Paraburkholderia*, *Rahnella*, *Rhodococcus*, and *Caballeronia,* were found to exhibit a broad range of beneficial traits for plant growth and stress resistance. Among them, a majority exhibited the ability to fix nitrogen and/or solubilize phosphate under *in vitro* conditions, with 11 isolates showing both capabilities.

The ability to fix atmospheric nitrogen and the presence of the *nifH* gene were detected in 16 of the 20 bacterial isolates, predominantly among members of the *Pseudomonas*, *Serratia*, *and Paraburkholderia* genera. Isolates of *Pseudomonas yamanorum* and *Serratia liquefaciens* displayed consistent phenotypic nitrogen fixation activity and *nifH* gene presence, which is consistent with prior findings that *Pseudomonas*[16] and *Serratia*[17] are effective diazotrophs in a variety of soils, including cold or high-altitude environments, highlighting their robust nitrogen-fixing potential in cold environments such as páramo. Phosphate solubilization, another critical PGP trait, was confirmed in 13 of the 20 isolates. The presence of the *pqq* gene, which encodes a cofactor (pyrroloquinoline quinone) involved in phosphate solubilization via glucose dehydrogenase, was also confirmed in 11 isolates. These included both rhizosphere and bulk soil isolates, indicating that phosphate-solubilizing mechanisms are widespread across microhabitats in the páramo soil ecosystem. Similarly, the *ppdC* gene, which is involved in the biosynthesis of indole-3-acetic acid (IAA), a major plant auxin, was detected in 14 isolates, with strong representation among *Pseudomonas* and *Paraburkholderia* isolates. The presence of *ppdC* suggests that these isolates can potentially stimulate root elongation and branching, thus increasing nutrient uptake efficiency in host plants, a key trait for successful plant establishment in nutrient-poor soils[18].

Notably, six isolates presented all the phenotypic and molecular traits evaluated in this study, including nitrogen fixation, phosphate solubilization, and IAA-related gene presence, along with fast growth rates. Three of these isolates corresponded to species of the *Pseudomonas fluorescens* complex (*P. fluorescens* and *P. yamanorum*), which are well known for their PGP capabilities, including phosphate solubilization, siderophore production, and the synthesis of phytohormones such as indole-3-acetic acid (IAA). Additionally, their antifungal properties are reported to contribute to the biocontrol of soilborne pathogens[19]. Cold-tolerant strains of *P. fluorescens* have also been demonstrated to be effective at promoting growth in alpine and temperate crops[20], supporting their potential as candidates for biofertilizer development in high-altitude ecosystems. Remarkably, in this study, *Pseudomonas yamanorum*, a psychrotolerant species previously isolated from subantarctic cold environments[21], was the most prevalent of the identified PGPB isolates, suggesting an adaptive advantage in high-altitude conditions and a promising candidate for bioinoculant development in harsh agroecosystems. Two other promising isolates belong to species of the genus *Serratia* (*Serratia liquefaciens* and *Serratia proteamaculans*), which are versatile bacteria known for their nitrogen-fixing ability, production of indole-3-acetic acid (IAA), antagonistic activity against phytopathogens, and role in promoting plant growth, particularly under cold or stress-associated conditions. The adaptability of PGPB to various environmental conditions, including low temperatures, enhances their potential as PGPB in mountainous regions[22]. For example, *Serratia liquefaciens* isolates have been isolated from soils in cold regions and shown to promote wheat growth under stress conditions[23]. *Rhodococcus qingshengii,* on the other hand, although less commonly associated with PGPB, has been shown to promote root elongation[24] and degrade environmental pollutants[25]. Its cold-adaptive physiology and metabolic versatility may benefit high mountain environments, where multifunctional bioinoculants are highly desirable. The convergence of multiple beneficial traits among the microbial taxa isolated from páramo soils underscores their potential as components of biofertilizer consortia intended for agriculture in cold-climate settings.

The efficacy of the isolates as plant growth promoters was validated through assays conducted on *Solanum lycopersicum* seedlings in controlled environments, where most of the microbial treatments resulted in substantial increases in critical physiological parameters: total seedling length, hypocotyl length, and fresh weight. The effects of isolates SN09 (*Pseudomonas fluorescens*, bulk soil), SN02, and SP07 (*Pseudomonas yamanorum*, rhizosphere) were particularly remarkable, consistently demonstrating substantial effects across all three variables, with certain increases surpassing twofold relative to the uninoculated control. The observed increase in total seedling length could be attributed to the synergistic effects of various mechanisms, including biological nitrogen fixation, phosphate solubilization, and indole-3-acetic acid (IAA) production, which are processes that promote cell elongation and the accessibility of vital nutrients[20]. This effect was reinforced by *in vitro* functional assays, as these isolates exhibited the capacity to fix nitrogen, solubilize phosphate, and concurrently harbor the three principal molecular markers linked to PGP traits (*nifH*, *pqq*, and *ppdC*), thereby confirming their multifunctionality and enhancing their potential as biofertilizers. Such comprehensive functionality traits likely result in additive or synergistic effects, improving nitrogen and phosphorus acquisition while modulating root architecture and shoot development through IAA production[20,22]. The performance of these isolates also highlights the ecological plasticity of PGPs across soil microhabitats. The length of the hypocotyl, which is markedly responsive to hormonal signals and phosphorus availability, notably increased in the SN09, SN02, SP07, and consortium (SN09+SP07+SP05) treatments. This finding indicates a potential synergistic interaction between bacterial IAA synthesis and phosphate mobilization, promoting cellular growth in juvenile tissues[26]. Consequently, fresh weight significantly increased across nearly all the treatments, indicating that the modification of primary metabolism and water equilibrium was instigated by the microorganisms. In contrast, individual isolates SN03 and SP04 exhibited relatively modest effects, demonstrating that the mere presence of functional genes does not ensure superior performance as plant growth promoters. This may result from limitations in their rhizosphere colonization ability or reduced expression of PGP-related genes under plant-dependent conditions. These findings are consistent with previous observations that certain soil-derived strains exhibit minimal functional or ecological specialization, which can hinder their effectiveness as plant growth promoters despite harboring relevant genetic traits[27].

Both microbial consortia, composed of combinations of the individual PGP isolates (SN02+SN03+SP04 and SN09+SP07+SP05), significantly enhanced tomato seedling development, especially in terms of hypocotyl length and fresh weight, although they did not perform better than the most effective individual isolates did. This may arise from partial complimentary interactions; however, competition or antagonism among strains may also occur, potentially hindering colonization effectiveness or the synthesis of essential metabolites. Recent studies underscore that the development of microbial consortia must consider not only individual functionalities but also the metabolic, ecological, and geographical compatibility of the constituent strains[28]. Interestingly, isolates obtained from both the *Espeletia* rhizosphere and the bulk soil and their combinations presented full PGP profiles and accounted for most of the best-performing inoculants in the plant growth assays, significantly enhancing tomato seedling growth. Taken together, these results reinforce the notion that the *Espeletia* rhizosphere acts as a selective niche that enriches functionally beneficial microbes[8] but also suggest that the harsher, less root-influenced bulk environment may select for robust or metabolically versatile microbes under páramo conditions that are able to efficiently promote plant growth.

In this study, *P. yamanorum* emerged as a dominant, highly effective PGP species, both genetically and functionally, with statistically significant improvements in height, hypocotyl length, and biomass, providing direct evidence of plant growth promotion. Like *Pseudomonas yamanorum,* the ecological relevance of other functionally diverse, plant-growth-promoting bacterial species in the páramo environment is underscored by the extreme environmental fluctuations that characterize these ecosystems, including variable temperature, fog density, UV radiation, atmospheric moisture, and soil water availability[29]. The survival and functionality of these microorganisms under such stressors highlights their potential utility, not only in agricultural applications whether as PGPB or even as biocontrol agents[30], but also in ecological restoration efforts in fragile high-altitude ecosystems. Their use as biofertilizers could support the establishment and growth of native or agriculturally relevant plants under conditions where conventional agrochemicals are ineffective or environmentally detrimental[31]. From a biotechnological perspective, the identification of cold-tolerant and multifunctional PGPB offers a strategic advantage for sustainable agriculture in mountainous or degraded soils. The global trend toward reducing synthetic fertilizer use and enhancing sustainable practices emphasizes the need for microbial inoculants

tailored to specific environments[16]. Given their origin, these páramo-derived bacteria likely possess enzymes and metabolic pathways adapted to low-temperature stressful conditions, features that may translate to more consistent performance under field conditions.

Conclusions

In conclusion, this study provides strong evidence that páramo soils host culturable, cold-adapted bacteria with considerable potential for promoting plant growth. The identified isolates present a diverse array of plant growth-promoting features, such as nitrogen fixation, phosphate solubilization, and auxin production potential, that could be effectively utilized in the development of biofertilizers suitable for cold, stress-associated ecosystems such as the Andean páramos. The integration of phenotypic screening, molecular marker detection, and plant-based bioassays demonstrated the functional diversity and application prospects of these isolates. Isolates such as *Pseudomonas yamanorum* SN02 and *Pseudomonas fluorescens* SN09 have emerged as promising biofertilizer candidates for use in cold or environmentally stressful agricultural scenarios. Their multifunctionality, genetic potential, and environmental resilience make them promising candidates for further biotechnological exploration and application in sustainable agriculture and conservation efforts tailored to páramo and other high-altitude environments. These findings underscore the broader ecological value of the páramo microbiome, not only as a support system for endemic plant species such as *Espeletia* but also as a source of microbial biodiversity with applications in biotechnology and environmental restoration. As anthropogenic pressures and climate change increasingly threaten these fragile high mountain ecosystems, harnessing native microbial resources has become a strategic approach for reinforcing ecosystem resilience, improving plant productivity, and fostering sustainable land management. Future studies should aim to assess the in-field performance of selected isolates, explore their synergistic potential in microbial consortia, and investigate their genomic adaptations to cold, acidic, and oligotrophic conditions.

Authors' contributions

JVC and SFM: Methodology, formal analysis and investigation. DRI and LAD: Methodology. MFL: Writing-original draft preparation. GZ: Conceptualization, formal analysis and investigation, writing-original draft preparation, writing-review and editing, funding acquisition, supervision. All authors read and approved the final manuscript.

Ethical considerations

This study protocol was reviewed and approved by the Ethics Committee in Scientific Research of the Universidad Industrial de Santander (CEINCI-UIS).

Acknowledgments

Sampling expeditions were performed with the supervision, approval, and collaboration of the local environmental authority (CDMB, Santander, Colombia) and under collection permission No. IDB0398 from the Colombian National Environmental Licensing Authority (ANLA). The authors would like to thank Finca El Romeral in Vetas, Santander, for the logistical support accessing some of the sampling areas.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Funding

This work was funded by Universidad Industrial de Santander project number 3726 "Diversidad microbiana asociada a la rizósfera y suelo total del frailejón (*Espeletia* sp.) en el páramo de Santurbán".

AI Technological Support

The Rubriq and Quillbot academic editing and translation tools were used to assist with grammar and style correction.

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