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Characterization of a Salt-Tolerant Plant Growth-Promoting *Streptomyces levis* Strain H from the Rhizosphere Soil of *Oryza sativa*

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Abstract

Salt-tolerant plant growth-promoting (PGP) actinobacteria play an important role in enhancing plant tolerance to salinity stress and improving crop productivity. Here, 9 morphologically distinct actinobacterial isolates (A-I) were isolated from the rhizosphere soil of *Oryza sativa* cultivated in the Nalgonda district, Telangana, screened for PGP characteristics (nitrogen fixation, indole-3-acetic acid production (IAA), and phosphate solubilisation) and salt tolerance. Among them, isolate H exhibited superior PGP activity and salt tolerance, growing in media containing up to 10% NaCl. Hence, it was selected for further work. Isolate H produced cellulase, lipase, amylase and showed a positive catalase reaction. It utilised glucose, fructose, galactose, and sucrose, but not maltose. Antibiotic susceptibility analysis indicated that isolate H was partially resistant to penicillin but sensitive to tetracycline, ciprofloxacin, and vancomycin. Molecular identification based on 16S rDNA sequencing (1,356 bp) revealed that isolate H shared 99.78% sequence similarity and 99% query coverage with *Streptomyces levis* NBRC 15423^(T), suggesting that the isolate belongs to the genus *Streptomyces*. Seed germination efficiency (%) revealed that the 24 hrs culture (T₁) of isolate H had a significantly greater effect on rice seed germination than the 48 hrs culture (T₂). The germination rate of rice seeds in T₁ was 86.67%, followed by T₂ (72.00%), the control (62.33%), and distilled water (55.67%), indicating that the 24 hrs grown culture of isolate H may be used to enhance rice seed germination under salt stress. This study provides preliminary evidence of the potential of a *Streptomyces levis* strain as a PGP bacterium under saline conditions.

Keywords: Actinobacteria, Plant Growth-Promoting Characteristics, Salt-Tolerant Strain, Antibiotic Susceptibility Analysis, 16S rDNA Sequencing

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INTRODUCTION

Numerous microorganisms affected by biotic and abiotic stresses can be found in the rhizosphere or within the zone of influence surrounding plant roots. These include the predominant rhizobacteria known as plant growth-promoting rhizobacteria (PGPR), which are essential for soil health and plant growth because they inhabit the rhizosphere and root surfaces.¹ These bacterial groups are important because they participate in a number of biochemical processes in the soil, such as the fixation of atmospheric nitrogen, solubilisation of minerals, such as phosphorus and potassium, production of siderophores that sequester and mobilise iron, and synthesis of plant growth regulators.² Nitrogenase is a key enzyme involved in biological nitrogen fixation that converts atmospheric nitrogen into forms available to plants, thereby enhancing soil fertility. This is a cost-effective and environmentally friendly alternative to chemical fertilisers.³

Rice (*Oryza sativa* L.) is a staple food crop in Asia that is affected by various biotic (including rice blast)⁴ and abiotic stresses.⁵ Modern agriculture often depends on PGPR with biocontrol traits to improve agricultural production while reducing reliance on chemical fungicides.⁶

Most of the currently available information on PGPR is related to the phyla Bacteroidetes, Firmicutes, and Proteobacteria. However, very few studies have focused on the PGP characteristics of Actinobacteria.^{7,8}

Actinobacteria (actinomycetes), a phylum of Gram-positive, filamentous bacteria that resemble fungi and possess a high G+C content,⁹ have the capacity to produce lytic enzymes and secondary metabolites, including PGP substances and antibiotics, making them valuable in agriculture, industry, and medicine.¹⁰⁻¹²

Salinity stress is one of the major abiotic factors limiting rice productivity worldwide, adversely affecting seed germination, nutrient uptake, plant metabolism, and crop yield.¹³⁻¹⁵ Under saline conditions, rhizosphere microbial communities play an important role in enhancing plant tolerance and maintaining soil fertility.⁷ Salt stress mitigation mechanisms employed by PGPR include osmolyte production,¹⁶ ACC deaminase activity,¹⁷ ion homeostasis and regulation,¹⁸

and other general mechanisms associated with salinity stress tolerance.¹⁹ Among rhizospheric microorganisms, actinomycetes, particularly *Streptomyces* species, are recognised for their ability to survive under stressful environmental conditions and produce various PGP metabolites, such as indole-3-acetic acid, siderophores, ammonia, phosphate-solubilising enzymes, and ACC deaminase. These traits can improve nutrient availability, root development, and plant stress tolerance.²⁰⁻²³

In addition, the functional advantages of actinobacteria over other PGPR groups include their ability to produce diverse secondary metabolites,²⁴ extracellular enzymes, stress-resistant spores, and disease-suppressive compounds, as well as their enhanced adaptability to harsh environmental conditions.^{13,20} Despite several reports on PGPR under salinity stress, studies focusing on salt-tolerant actinomycetes associated with the rice rhizosphere remain limited.^{22,24,25} Therefore, the isolation and characterisation of salt-tolerant, PGP actinomycetes from the rice rhizosphere are important for identifying potential candidates for sustainable enhancement of rice growth under saline conditions.

Rice cultivation is widely practised in the Nalgonda district of Telangana, and certain agricultural soils are frequently exposed to salinity stress owing to irrigation practices, groundwater quality, and climatic conditions. Hence, the present study emphasises the isolation and identification of salt-tolerant PGP actinobacteria from the rhizosphere of *Oryza sativa* in the Nalgonda district, evaluation of their PGP traits, and assessment of their potential to promote rice seed germination.

MATERIALS AND METHODS

Soil sample collection

Rhizosphere soil samples of *Oryza sativa* were collected during the crop-growing season from a depth of 10-12.5 cm below the soil surface in Nalgonda district, Telangana, India, at the following GPS coordinates: 17.116634° N, 79.235241° E; 17.115542° N, 79.234527° E; and 17.117239° N, 79.233776° E, using a random sampling method. Three soil samples were collected at each location. Each experiment was performed in triplicate to ensure the reproducibility of the results. After

collection, samples were properly sealed in sterile polythene bags and transported to the laboratory.

Isolation of actinomycetes

One gram of soil sample was serially diluted up to 10^{-6} , and 0.1 mL of different dilutions was plated on starch casein agar (g/L): soluble starch, 10; K_2HPO_4 , 2; KNO_3 , 2; casein, 0.3; $MgSO_4 \cdot 7H_2O$, 0.05; $CaCO_3$, 0.02; $FeSO_4 \cdot 7H_2O$, 0.01; and agar, 15 (pH 7.0 ± 0.2). Starch casein agar contained 80 μ g/mL of cycloheximide and 75 μ g/mL of nalidixic acid (HiMedia, Mumbai, India) to limit fungal and bacterial growth, respectively. A sterilised glass spreader was used to evenly distribute the diluted soil samples on starch casein agar plates. These inoculated plates were incubated at $28 \pm 2^\circ C$ for 21 days.

Different actinomycete isolates were selected based on specific colony characteristics, including colony colour, texture, size, margin, elevation, aerial mycelium formation, and pigmentation. Colonies were sub-cultured, purified, and stored as slants at $4^\circ C$ for further analysis.

PGP tests

The purified actinobacterial isolates were subjected to various PGP tests, including atmospheric nitrogen fixation, IAA production, and phosphate solubilisation. Among all the isolates, a high-potential PGP isolate was selected for further studies.

The nitrogenase activity of the purified actinobacterial isolates was determined by stabbing the isolates separately into Burk's agar, a nitrogen-free medium (HiMedia, India),^{26,27} followed by incubation for 3-5 days at $28-30^\circ C$ and assessment of growth. The appearance of growth by the isolates indicated a positive result.

IAA production by purified actinobacterial isolates was determined by inoculating them separately into Jensen's broth (g/L): sucrose, 20; K_2HPO_4 , 1; $MgSO_4 \cdot 7H_2O$, 0.5; NaCl, 0.5; $FeSO_4$, 0.1; $NaMoO_4$, 0.005; and $CaCO_3$, 2, supplemented with 2 mg/mL L-tryptophan.²⁸ The test (with the isolate) and control (without the isolate) tubes were kept at $37^\circ C$ for 48 hrs with rotation at 125 rpm.²⁹ According to Gordon and Weber, approximately 2 mL of test and control solutions were centrifuged for 1 min at $18,800 \times g$ after the incubation period.

Then, 1 mL aliquots of both test and control supernatants were separately mixed with 2 mL of Salkowski's reagent (150 mL of concentrated H_2SO_4 , 250 mL of distilled water, and 7.5 mL of 0.5 M $FeCl_3 \cdot 6H_2O$) and incubated for 20 min at $28-30^\circ C$. IAA production was confirmed by a change in the broth colour to pink-red compared with the control.³⁰

To determine phosphate solubilisation activity of purified actinobacterial isolates, they were grown on Pikovskaya's agar.³¹ Pikovskaya's agar contained (g/L): dextrose, 10; yeast extract, 0.5; $(NH_4)_2SO_4$, 0.5; $Ca_3(PO_4)_2$, 0.5; KCl, 0.2; $MgSO_4$, 0.1; $FeSO_4$, 0.0001; $MnSO_4$, 0.0001; and agar, 15. After inoculation, Petri plates were incubated at $28-30^\circ C$ for 7 days. A clear halo zone surrounding the isolates indicated a positive phosphate solubilisation test (conversion of insoluble phosphate into its soluble form).

Effect of % NaCl on growth of actinobacterial isolates

Purified actinobacterial isolates were subjected to NaCl (0%-12%, at 1% intervals) to determine their tolerance levels and the amount of NaCl required for optimal growth. The growth of the isolates was evaluated at 24 hrs and 48 hrs based on measurements of optical density (at 600 nm) using a colorimeter.

Enzyme activities

Based on the PGP traits and salinity tolerance described above, a high-potential PGP isolate (showing high salinity tolerance) was selected from among the purified actinobacterial isolates. Subsequently, it was tested for the production of different hydrolytic enzymes, including cellulase, lipase, and amylase, on carboxymethyl cellulose (CMC), Tween 80 lipase, and starch agar plates.

The cellulase activity of the selected PGP isolate was investigated by inoculating the organism on CMC agar, where 1% CMC was used as the soluble cellulose derivative and substrate. CMC hydrolysis was detected by flooding the agar plate with 1% Congo red dye solution. After 15 min, the dye solution was poured off, and the plate was further flooded with 0.1% NaCl for 15 min and observed for the formation of a clear zone. The undegraded cellulose portions were stained red,

whereas clear zones appeared around the colonies where the CMC was degraded.³²

The amylase activity of the selected PGP isolate was determined using the clear-zone method on starch agar plates. The plate was flooded with iodine solution for 1 min after incubation for 72 hrs. Formation of a clear zone surrounding the culture indicated a positive starch hydrolysis test, whereas the absence of a zone indicated a negative test.³³

The selected PGP isolate was tested for lipase production on 0.1% Tween 80 lipase agar plates.^{34,35} The formation of a clear zone around the isolate indicated a positive lipase test, whereas the absence of a zone indicated a negative test.

Effect of temperature and pH on growth of the PGP isolate

The selected high-potential PGP isolate was subjected to different temperatures (room temperature (28-30 °C), 28 °C, 37 °C, and 45 °C) to optimise its growth and evaluate pigment production. Different pH conditions (pH 6-9, at intervals of 1 pH unit) were used to identify the optimal pH for growth. Isolate growth was evaluated at 24 hrs and 48 hrs based on measurements of the optical density at 600 nm using a colorimeter.

Biochemical characterisation of the PGP isolate

Different carbohydrate utilisation tests (glucose, fructose, galactose, maltose, and sucrose) were performed for the selected PGP isolate to determine its ability to utilise specific carbohydrates according to the carbohydrate fermentation protocol.³⁶ Phenol red carbohydrate broth was inoculated with the selected PGP isolate, and a colour change from orange-red to yellow after 24 hrs of incubation indicated a positive test (acid production). This test was performed along with a control (without the isolate) for comparison.

To perform the catalase test, a small amount of the selected PGP organism was placed onto a microscope slide without any agar after 24 hrs of growth in nutrient broth. Using a dropper or Pasteur pipette, one drop of 3% H₂O₂ was placed on the organism on the microscope slide. The formation of bubbles against a dark background, which enhances visibility, indicated a positive result.³⁷

Antimicrobial susceptibility test of the PGP isolate

The antimicrobial susceptibility test of the selected PGP isolate was performed according to CLSI guidelines³⁸ to determine the sensitivity of the organism to penicillin (10 µg), tetracycline (30 µg), ciprofloxacin (5 µg), and vancomycin (30 µg). This test was performed by placing the respective antibiotic discs on the culture and measuring zones of inhibition using the Kirby–Bauer disc diffusion method.³⁹

Molecular characterisation of the PGP isolate

The selected PGP isolate was characterised at the molecular level by isolating its DNA through incubation of a bacterial colony in 50 µL of molecular biology-grade distilled water at 96 °C for 10 min in a thermal cycler. Polymerase chain reaction (PCR) was then performed using the extracted DNA under the following conditions: initial denaturation at 94 °C for 5 min, followed by 30 cycles of denaturation at 94 °C for 30 sec, annealing at 54 °C for 30 sec, and extension at 72 °C for 2 min, followed by a final extension at 72 °C for 5 min to amplify the 16S rDNA gene of the isolate using universal bacterial forward and reverse primers (27F and 1525R).⁴⁰ The PCR product was then subjected to 16S rDNA sequencing, which was outsourced to the National Collection of Industrial Microorganisms, Pune. The 16S rDNA sequence of the isolate was uploaded to the EzBioCloud database and compared with the 16S rDNA sequences available in this database to identify the isolate based on sequence similarity values. Phylogenetic analysis of the isolate was performed using the ClustalW alignment program in MEGA 11.⁴¹

A phylogenetic tree was constructed using the neighbour-joining method with the Kimura 2-parameter model, and bootstrap analysis was performed with 1,000 replications to assess branch support values.

Effect of strain H culture on the growth of rice seeds under salt stress

Seed germination experiments were conducted to study the effects of isolate H on rice seed growth under salt stress. Initially, rice seeds were surface-sterilised in 70% ethanol, followed by treatment with sodium hypochlorite solution, and rinsed thoroughly with sterile distilled water

before treatment. The bacterial inoculum was prepared at an approximate density of 10^8 colony-forming units/mL. Sterilised rice seeds were immersed in distilled water, a nutrient medium consisting of 5% NaCl without isolate H (control), a nutrient medium containing 5% NaCl with isolate H grown for 24 hrs (T_1), and a nutrient medium containing 5% NaCl with isolate H grown for 48 h (T_2) for 2 hrs each. The rice seeds were then placed separately in four petri dishes containing moist tissue paper and sprinkled daily with sterile distilled water. Seed germination analysis was performed under controlled incubation conditions at 28 ± 2 °C. The percentage germination of rice

seeds was observed in triplicate after 7 days. All experiments were conducted in triplicate.

The percentage germination of rice seeds was calculated using the following formula:

$$\% \text{ Seed germination} = \left[\frac{\text{Number of seeds germinated}}{\text{Total number of seeds used for germination}} \right] \times 100$$

Rice seed germination data were statistically analysed using one-way analysis of variance to compare the distilled water, control, T_1 , and T_2 treatments. Statistical analysis was performed using SPSS version 25.0, and differences were considered statistically significant at $P < 0.05$. Post-hoc analysis was conducted using Tukey's honest significant difference test to determine significant differences among treatment means.

RESULTS AND DISCUSSION

Isolation of actinomycetes

Morphologically, nine different actinomycete colonies (serially labelled A-I) were isolated and purified on starch casein agar from rhizosphere soil samples of *Oryza sativa*. All nine isolates were subjected to PGP tests to determine their PGP potential.

Members of *Streptomyces* and related actinomycetes play important ecological roles in organic matter decomposition, nutrient recycling, production of bioactive metabolites, and enhancement of plant growth under



Figure 1. Growth of isolate H on Burk's agar

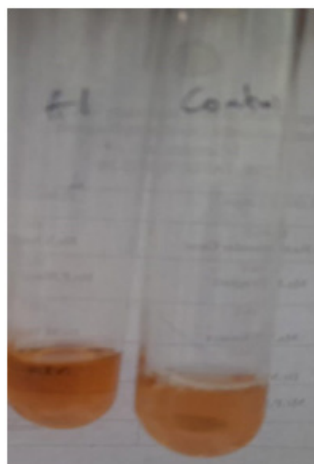


Figure 2. IAA production by isolate H



Figure 3. Phosphate solubilisation on Pikovskaya's agar by isolate H

stress conditions. Their adaptation to saline environments may improve plant tolerance to salt stress through mechanisms, such as phytohormone and siderophore production, phosphate solubilisation, and osmotic stress regulation. A similar ecological significance and functional diversity of actinomycetes have been previously reported.^{20,42-44} Three isolates, HB6J2, HB8P1, and HB4N3, were reported to have significant salt tolerance and were isolated from 18 soil samples collected from saline soils in Haryana State.⁴⁵

PGP tests

Among the 9 isolates (A-I) tested, isolate H grew effectively on Burk's agar, indicating its nitrogen-fixing capacity (Figure 1). The conclusion regarding nitrogen fixation was based on growth in a nitrogen-free medium and associated PGP traits. However, additional direct assays, such

as the acetylene reduction assay and nif-gene detection, would further confirm the nitrogen-fixing ability. Compared with the other isolates purified in this study, isolate H also showed IAA production when the broth changed to a reddish colour after addition of salkowski reagent (Figure 2). Many PGP actinomycete isolates produce IAA, which is responsible for enhancing the number of adventitious roots, thereby helping plants absorb more water and nutrients and secrete increased amounts of root exudates that are beneficial to bacteria.⁴⁶

A clear halo zone formed around isolate H on Pikovskaya's agar, indicating positive phosphate solubilisation after 7 days of incubation (Figure 3) compared with that observed for the other eight isolates purified in this investigation. In a study of 98 rhizospheric actinomycetes isolated from different wheat and tomato fields in Punjab, Pakistan, only 6 *Streptomyces* isolates were positive for phosphate solubilisation.⁴⁷

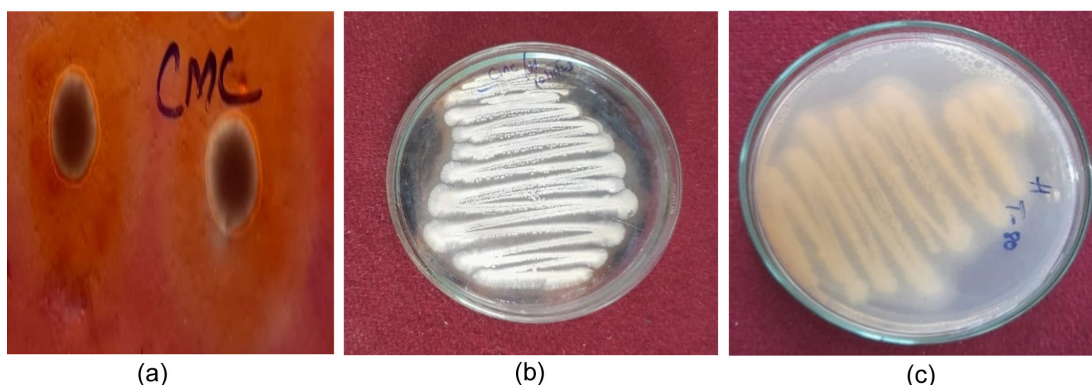


Figure 4. Different enzyme activities of isolate H: (a) cellulase activity on carboxymethyl cellulose (CMC) agar; (b) amylase activity on starch agar; and (c) lipase activity on Tween 80 lipase agar



Figure 5. Effect of temperature on growth and pigment production by isolate H

Effect of % NaCl on growth of actinobacterial isolates

Eight actinobacterial isolates exhibited lower salt tolerance (below 2% NaCl) than that of isolate H, which grew in a medium containing up to 10% NaCl. However, the optimum growth of isolate H was recorded at 2% NaCl. PGPR can reduce the harmful effects of increased salt concentrations on plants and enhance their development in two ways: first, by regulating plant response systems during salt exposure and, second, by producing anti-stress molecules.⁴⁸

Because isolate H exhibited promising PGP activities and comparatively better salinity tolerance than the other isolates purified in this study, it was chosen for further studies.

Enzyme activities

Clear-zone formation around the culture was observed for isolate H on CMC, starch, and

Tween 80 lipase agars, indicating positive cellulase, amylase, and lipase activities, respectively (Figure 4).

Cellulase production by *Streptomyces* spp. helps degrade complex cellulose materials present in the rhizosphere, thereby releasing nutrients for plant uptake and supporting microbial colonisation around plant roots.⁴³ Production of extracellular enzymes by actinomycetes also improves rhizosphere colonisation efficiency by enabling microorganisms to utilise diverse organic substrates released from plant roots and soil debris.⁴³

Amylase activity contributes to the breakdown of starch and other polysaccharides into simpler sugars, which enhances nutrient cycling, microbial survival in the rhizosphere, and plant growth.⁴² Protease production may assist in the degradation of proteinaceous organic matter and suppress certain phytopathogens through



Figure 6. Different carbohydrate utilisation tests were performed with isolate H



Figure 7. Catalase test of isolate H

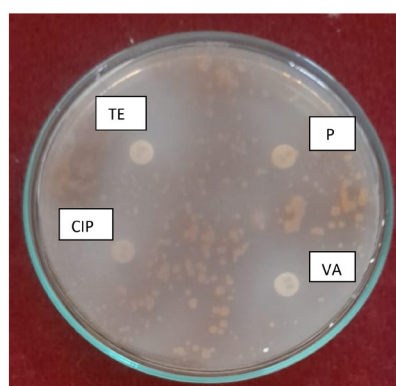
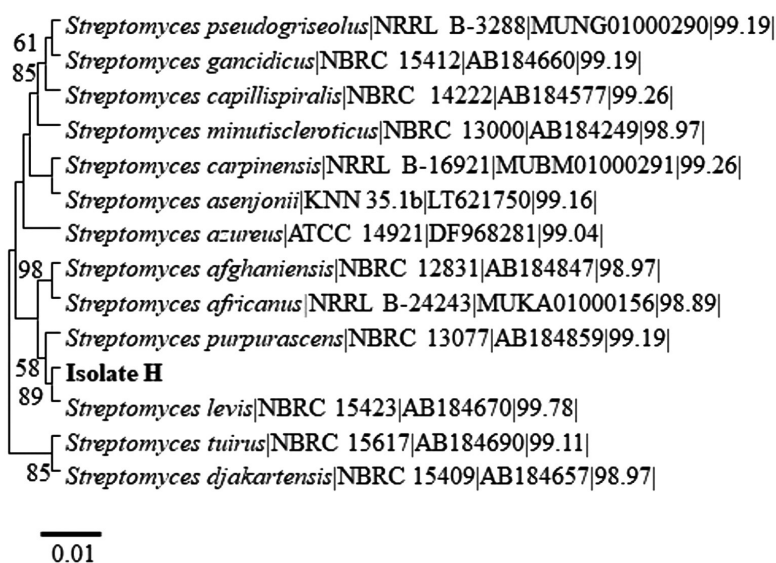


Figure 8. Antibiotic susceptibility test of isolate H
Note: P = penicillin (10 µg); TE = tetracycline (30 µg); CIP = ciprofloxacin (5 µg); and VA = vancomycin (30 µg)

Table. Effect of isolate H on rice seed germination percentage

No.	Rice seed treatment	Seed germination (%) in replicates			Mean $\pm$ Standard deviation (SD) seed germination (%)	Group
1	T ₁ (24-hour-grown strain H in nutrient medium with 5% NaCl)	88	87	85	86.67 $\pm$ 1.53	a
2	T ₂ (48-hour-grown strain H in nutrient medium with 5% NaCl)	74	72	70	72.00 $\pm$ 2.00	b
3	Control (nutrient medium containing 5% NaCl without isolate H)	64	62	61	62.33 $\pm$ 1.53	c
4	Distilled water	58	54	55	55.67 $\pm$ 2.08	d

**Figure 9.** Phylogenetic tree of isolate H constructed using the neighbour-joining method. Bar = 0.01 nucleotide substitutions per site

the hydrolysis of pathogenic proteins, thereby indirectly promoting plant health.²⁰

Effect of temperature and pH on growth of isolate H

Isolate H showed good growth at room temperature but was not able to produce pigment under these conditions. It produced a darker brown pigment at 28 °C and 37 °C. However, pigment production was lower at 45 °C (Figure 5). The growth of isolate H was observed up to pH 8, but the optimum pH was 7.

Biochemical characterisation

Different carbohydrate utilisation tests performed with isolate H showed a positive reaction (broth colour changed to yellow) for all carbohydrates tested (glucose, fructose, galactose, and sucrose), except maltose (Figure 6). This test was compared with the control (without isolate H). Isolate H tested positive for catalase activity (Figure 7).

Antimicrobial susceptibility test

Isolate H was partially resistant to penicillin (10 µg), whereas it was sensitive to tetracycline (30

µg), ciprofloxacin (5 µg), and vancomycin (30 µg; Figure 8). Actinobacteria enhance plant growth not only through the production of extracellular enzymes, siderophores, and phytohormones but also through the production of antagonistic metabolites in soil ecosystems.²⁰

Molecular identification

The 16S rDNA sequence (1,356 bp) of isolate H obtained after outsourcing was uploaded to the EzBioCloud database and compared with the 16S rDNA sequences of other strains present in the database. It showed 99.78% similarity to *Streptomyces levis* NBRC 15423^(T) with 99% query coverage (Figure 9). *Streptomyces* is the largest genus of actinobacteria, members of which are commonly found in soil and contribute to the decomposition of organic matter, thereby promoting crop production. They are involved in the production of extracellular hydrolytic enzymes and antifungal compounds; therefore, they play a role in biocontrol, particularly against phytopathogens such as those causing rice blast disease.^{49,50} Some reports have also highlighted their role in improving crop tolerance to salt stress.⁵¹

Effect of isolate H on rice seed germination under salt stress

Rice seed germination results indicated (Table) that the 24 hrs grown isolate H culture (T₁) in nutrient medium in the presence of 5% NaCl showed a higher rice seed germination percentage (86.67%) than that of the 48 hrs grown isolate H culture (T₂), which showed a germination percentage of 72.00%. The control condition (nutrient medium without isolate H containing 5% NaCl) showed a lower seed germination percentage (62.33%) than that of T₂, and treatment with distilled water resulted in the lowest seed germination rate (55.67%). One-way analysis of variance revealed significant differences in rice seed germination among the treatments (P < 0.05). Tukey's honest significant difference post-hoc test showed that the T₁ treatment resulted in significantly higher seed germination than that of the T₂, control, and distilled water treatments. The difference between T₁ and T₂ in seed germination may be associated with variations in the bacterial

growth phase, cell viability, or nutrient availability. This report indicated that the more metabolically active 24 hrs grown culture may have produced higher levels of PGP substances than those of the 48 hrs grown culture. *Streptomyces* spp. are known to improve plant growth under saline conditions through multiple mechanisms, including phytohormone production, nutrient mobilisation, siderophore production, extracellular enzyme secretion, and improved rhizosphere colonisation. These activities may help plants tolerate osmotic and ionic stresses caused by salinity.²⁰ Similar observations were reported by Gopalakrishnan et al.²² and Sreevidya et al.,⁴⁴ who demonstrated the role of *Streptomyces* spp. in improving seed germination, enhancing root development and plant growth, and increasing salinity stress tolerance, which may be attributed to their PGP activities, including phytohormone production and stress tolerance mechanisms.

CONCLUSION

This report provides information on the purification of a salt-tolerant *Streptomyces levis* strain (isolate H) from Nalgonda district, Telangana, India. The isolate exhibits promising PGP traits that enhance rice seed germination under saline conditions. This report highlights that the 24 hrs grown culture of isolate H (T₁) had a significant impact on the germination of rice seeds compared with the 48 hrs grown culture (T₂), the control treatment, and distilled water. Further research on this isolate is required to enhance rice crop production.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTION

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

FUNDING

None.

DATA AVAILABILITY

All datasets generated or analyzed during this study are included in the manuscript.

ETHICS STATEMENT

Not applicable.

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