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Article

Morphological, biochemical, molecular characterization and evaluation of plant growth promoting traits of *Proteus mirabilis* PSCR17, a potential potassium solubilizing rhizobacterium

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Abstract: Potassium is an essential macronutrient for living creatures on earth and in plants, it plays a very significant role in determining the overall health of the plants. Although potassium is present in the soil, it is present in a form that is inaccessible to the plants, and hence synthetic harmful non-eco-friendly potassium fertilizers are used. To overcome this problem, the use of eco-friendly potassium-solubilizing bacteria comes into play. The goal of the present study was to assess the potassium-solubilizing bacteria that inhabit the farm rhizosphere, which demonstrate the presence of enzymes associated with plant growth promotion and antagonistic properties. A total of thirty-four isolates were isolated from the rhizosphere. All these isolates were subjected to a potassium solubilization test on Aleksandrov agar medium, out of which fourteen were found to possess potassium solubilizing ability. On the basis of the 16S rRNA gene sequencing, the most potential potassium-solubilizing bacterium was identified as *Proteus mirabilis* PSCR17. The plant growth promoting abilities and production of biocontrol enzymes of this isolate were evaluated, and the results indicated, in addition to potassium solubilization, the isolate was positive for indole acetic acid production, hydrogen cyanide production, amylase, catalase, cellulase, chitinase, and protease. The use of potassium fertilizers is harmful to the environment and ecosystem; hence, this study concludes that *P. mirabilis* PSCR17 can be used as a substitute for chemical potassium fertilizers to improve the growth and biocontrol traits of the plants in a sustainable manner after further research.

Keywords: potassium solubilization; *Proteus mirabilis* PSCR17; natural microflora; biofertilizer; sustainable crop production

1. Introduction

Potassium is an essential and vital macronutrient that plays an imperative function in ensuring plant growth and development. This element participates in the regulation of several important processes related to plant growth. Potassium is required by the plants right from the germination stage to the fruit development stage to improve plant yield and quality. The presence of potassium in high concentrations within the plant cells aids the plants in overcoming abiotic stresses such as salinity, drought, and temperature fluctuations [1]. Potassium regulates the activation of enzymes, calcium signaling route, protein synthesis, and osmoregulation, along with controlling other major physiological functions such as cell growth, sugar transport, water content of xylem and phloem, metabolism of nitrogen and carbon, stomatal control, and photosynthesis [2,3].

The major reserves of K are present in the soil in the form of silicate minerals such as vermiculite, mica, and biotite, due to which they are inaccessible to the plants,

and hence only a small fraction of soluble K is present in the soil for plant absorption, which leads to K scarcity, causing distortion of numerous functions in plants [4]. Potassium deficiency causes a disturbance in the activation of the adenosine triphosphate (ATP) synthase enzyme, reduces the carbon dioxide fixation, and causes damage to the chlorophyll, which thereby ultimately leads to the reduction of photosynthesis [1].

Numerous rhizosphere microorganisms create intricate biological communities that either directly or indirectly impact plant development. Within these are a group of bacteria called the plant growth promoting rhizobacteria (PGPR) that promote plant growth through processes such as solubilization of potassium and zinc, production of siderophore and IAA, and fixation of nitrogen [5]. The technique of fertilization of crops using PGPR is an environment-friendly, sustainable, and economical approach [6].

Potassium-solubilizing bacteria (KSB) are considered as an alternative to the chemical fertilizers that adversely affect the properties of the soil to convert the insoluble K in the soil into soluble forms that can be easily absorbed by the plants to increase the agricultural productivity [7]. These KSB solubilize the insoluble K minerals to soluble forms through mechanisms such as acidification, protonation, and the production of organic acids, including oxalic and tartaric acids. A wide range of bacteria have been studied for their K solubilizing potential, including *Acidithiobacillus* sp., *Bacillus* sp., *Paenibacillus* sp., *Burkholderia* sp., and *Pseudomonas* sp. [4].

The species classified under the genus *Proteus* were initially explored, analyzed, and described in the year 1885 [8]. Generally, while the genus *Proteus* is often overlooked in discussions of their PGPR and bioremediation potential, *P. mirabilis* has been widely studied for the bioremediation properties, which include toxic pollutant degradation and heavy metal immobilization [9–12]. These species have also been known to demonstrate the capability to mitigate various harmful herbicides and pesticides that could lead to significant pollution in both terrestrial and aquatic ecosystems [13–16]. *P. mirabilis*, along with other species of *Proteus*, has been identified to exhibit plant growth-promoting traits such as solubilization of potassium, phosphate, and zinc, along with protecting the plants from phytopathogens [4,17–23].

Therefore, the present study was aimed at isolating the highest KSB from the rhizosphere of farm plants and assessing the production of enzymes linked to plant growth promotion and antagonistic characteristics, which can be used as a feasible option for enhancing plant growth in the future after further studies to sustainably grow crops.

2. Materials and methods

2.1. Sample collection and isolation of potassium solubilizing bacteria (KSB)

The soil was collected from the roots of plants from a farm in Chennai, Tamil Nadu. The serial dilution plate method was used to isolate bacteria using Nutrient agar medium. The plates were inoculated and incubated at 28 ℃ for 24 h. After the incubation period, the isolates were transferred onto fresh nutrient agar plates to obtain

pure colonies and maintained [24]. The isolates were spot inoculated on Aleksandrov agar medium (per liter—Glucose—5 g; Potassium Aluminosilicate—3 g; $CaCO_3$—2 g; $MgSO_4$—0.005 g; $CaPO_4$—2 g; $FeCl_3$—0.1 g; Agar—15 g; pH—7.0) for screening for potassium solubilization and observed after 5 d of incubation at 32 °C [25]. The bacterial isolates with potassium-solubilizing ability form a clear zone around their colony, while negative isolates do not form this zone [25]. The potassium solubilization index was calculated using the formula: Diameter of zone of clearance ÷ Diameter of growth [26].

2.2. Molecular identification and Phylogenetic tree construction of PSCR17

The highest potassium solubilization was observed in the isolate PSCR17 and hence it was taken up for identification and further morphological and biochemical tests, along with testing for the production of the enzymes linked to plant growth promotion and antagonistic characteristics.

The genomic DNA was isolated using the NucleoSpin® Tissue Kit (Macherey-Nagel) following the manufacturer's protocols. A microcentrifuge tube was used to hold the culture. After adding 180 µL of T1 buffer and 25 µL of proteinase K, the tube was incubated in a water bath at 56 ℃. Following lysis, 5 µL of 100 mg/mL of RNase A was added, and the mixture was incubated for 5 min at room temperature. B3 buffer (200 µL) was added, and the mixture was incubated for 10 min at 70 ℃. 210 µL of 100% ethanol was added, and the mixture was vortexed. After pipetting the mixture into a NucleoSpin® Tissue column placed in a 2 mL collecting tube, it was centrifuged for 1 min at 1000 g. After being moved to a fresh 2 mL tube, the NucleoSpin® Tissue column was cleaned with 500 µL of BW buffer. Washing was repeated using 600 µL of B5 buffer. Following washing, 50 µL of BE buffer was used to elute the DNA from the NucleoSpin® Tissue column, which was placed in a sterile 1.5 mL tube [27]. The 16S rRNA gene of the isolate was amplified by using a PCR thermal cycler (GeneAmp PCR System 9700, Applied Biosystems). For the PCR analysis, 0.25 µL of each of the universal Forward Primer 16S-RS-F-(5'CAGGCCTAACACATGCAAGTC3') and Reverse Primer 16S-RS-R-(5'GGGCGGWGTGTACAAGGC3') was used, along with 1 µL of DNA, 5 µL of 2X Phire Master Mix and 4 µL of distilled water [28]. The amplification conditions were as follows: 95 ℃ for 5 min, followed by 35 cycles at 95 ℃ for 30 s, 60 ℃ for 40 s, and 72 ℃ for 60 s. A final extension step was performed for 7 min at 72 ℃. The reaction was then held at 4 ℃ [27]. To identify the nucleotide sequences, a BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, USA) was used. The obtained 16S rRNA sequence of PSCR17 was deposited in the GenBank under the Accession no. OR782201 [29]. Using the BLAST tool of the GenBank NCBI database, the 16S rRNA gene sequence was compared, aligned, and identified. The phylogenetic tree was constructed using the neighbor-joining algorithm in the MEGA 11 software (https://www.megasoftware.net/) [30]. SPSS software (version 20) was used to perform the statistical analysis. The results were considered to be significant at $P < 0.05$.

2.3. Morphological and biochemical characterization of PSCR17

Morphological characterization of the KSB including color, size, form, elevation, margin, texture, and gram staining was carried out using Bergey's Manual of Systematic Bacteriology [31]. Standard protocols were followed for the biochemical characterization of the isolate. The biochemical characterization of the isolate was carried out as follows: oxidase test was carried using oxidase discs which when changes color to purple indicates a positive oxidase test and no color change indicates a negative test [32]. The production of oxygen bubbles upon the addition of hydrogen peroxide on the smeared isolate reveals a positive catalase test while no bubble formation reveals a negative test [33]. For citrate test, the isolate was streaked on Simmons Citrate agar medium and no color change of the medium indicates a negative result while change of color of the medium to blue indicates a positive result [34]. The gelatinase test was carried out using nutrient gelatin agar medium and post the inoculation and incubation of the isolate, the observation of a halo zone around the colony upon flooding with ammonium sulphate indicates a positive test, while no zone indicates a negative test [35]. The isolate was inoculated on Christensen's urea agar medium, and the change of the color of the medium to pink indicates a positive urease test, while no color change indicates a negative result [36]. The Triple Sugar Iron (TSI) test was carried out by inoculating the isolate on Triple-Sugar Iron Agar (TSI) medium, and after incubation, the change of color of the medium to yellow or black indicates the fermentation of carbohydrates and the production of hydrogen sulfide gas, while no change of color of the medium indicates no fermentation of carbohydrates [37]. The Methyl Red (MR) and Voges-Proskauer (VP) tests were carried out by inoculating the isolate on Glucose phosphate broth and a positive MR test is indicated by the red color formation of the medium upon the addition of methyl red solution, a positive VP test is indicated by the change of the medium to red after the addition of Barrit reagent A and Barrit reagent B, and no color change in both the test mediums indicates a negative MR and VP test [38].

2.4. Production of enzymes and other mechanisms by PSCR17 that aid in plant growth promotion and defense

The ability of the isolate to solubilize phosphate and zinc was tested by spot inoculating the isolate on Pikovskaya's agar medium and Tris-minimal salt medium amended with Zinc oxide. Positive tests are indicated by the production of halo zones on both the medium, and negative results are indicated by no zone formation [39,40]. The production of ammonia was tested using peptone water broth and the change of the color of the broth upon the addition of Nessler's reagent to slight yellow or orange indicates a positive result, while a negative result is indicated by no color change [41]. Indole-3-acetic acid (IAA) production by the bacteria was determined using Salkowski's reagent, and the change of the color of the broth to a reddish pink color indicates a positive IAA test while no color change indicates a negative test [42]. Analysis was done on several biocontrol enzymes produced by PSCR17. Spot inoculation of the isolate was done to test the activity of chitinase and amylase enzymes on Colloidal Chitin agar medium and Starch agar medium, and positive tests are indicated by the formation of halo zones while negative results are indicated by no

zone formation [24,35]. The production of extracellular protease and cellulase was tested on Skim Milk agar medium and Carboxymethylcellulose agar medium, and positive tests are characterized by the presence of halo zones, whereas negative results are indicated by the absence of such zones [43]. The hydrogen cyanide (HCN) test was carried out in King's B agar medium amended with glycine, and no color change of the picric acid-dipped filter paper indicates a negative result, while the change of color to moderate brown indicates a positive result [41].

3. Results

3.1. Isolation and screening for potassium solubilizing bacteria (KSB)

Thirty-four rhizobacterial isolates were obtained from the farm rhizosphere. A total of fourteen isolates were found to be potassium solubilizers, which showed a clear halo zone around the colonies on Aleksandrov agar medium, indicating the ability to solubilize potassium from an insoluble potassium source. Out of the fourteen isolates, isolate PSCR17 was found to have the highest potassium solubilization index of 5. The range of the potassium solubilization index of the fourteen isolates varied from 1.5 to 5 (**Figure 1**).

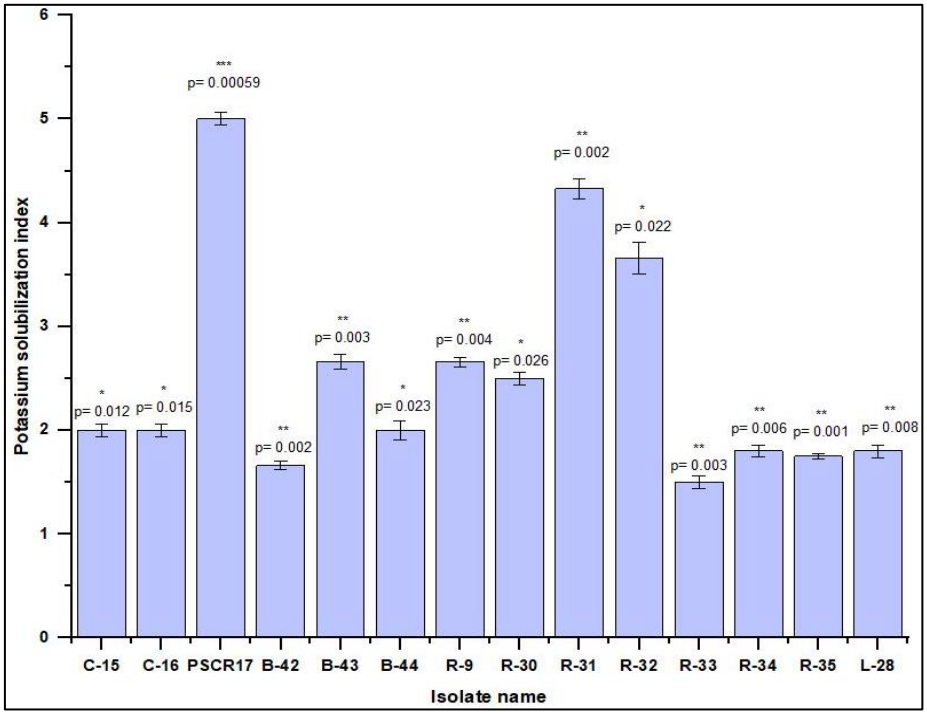

Figure 1. Potassium solubilization Index of the fourteen isolates. The highest potassium solubilization was found in the isolate PSCR17 showing an index of 5. Each bar represents the mean ± standard error. One asterisk (*) indicates *p* value smaller than 0.05 ($p < 0.05$). Two asterisk (**) indicates *p* value smaller than 0.01 ($p < 0.01$). Three asterisks (***) indicate *p* value smaller than 0.001 ($p < 0.001$).

3.2. Molecular identification and Phylogenetic tree construction of PSCR17

The BLAST analysis of PSCR17 showed 99.32% similarity to *Proteus mirabilis*. According to the phylogenetic tree created using the results of the BLAST analysis,

the isolate was found to be from a previously identified and thoroughly studied species. Therefore, the isolate PSCR17 (Accession no. OR782201) was identified as *Proteus mirabilis* [29] (**Figure 2**).

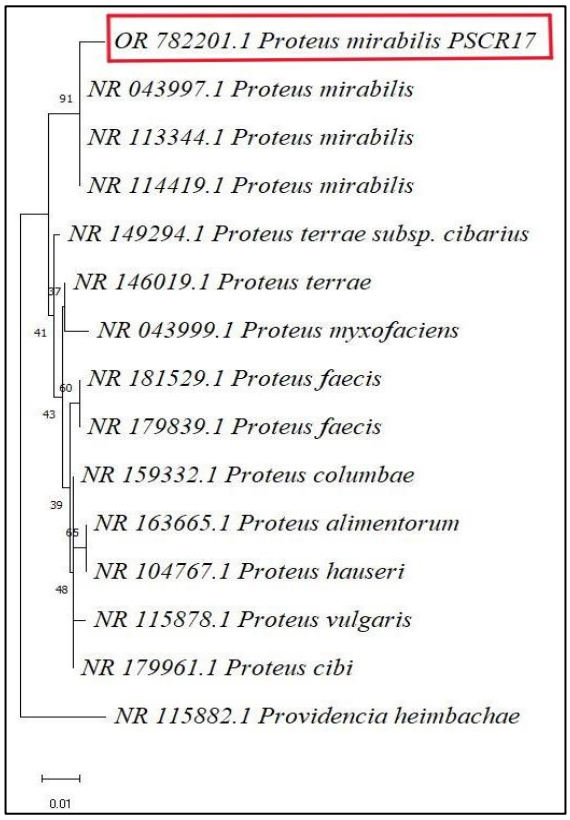

Figure 2. Phylogenetic tree was constructed using the Neighbor joining method (using MEGA 11) with the bootstrap analyzes of 1000 cycles, based on the 16S rRNA gene sequences which shows the relationship between *Proteus mirabilis* PSCR17 and other members of the *Proteus* sp. *Providencia heimbachae* was used as an outgroup. The scale bar represents 0.01 substitution per nucleotide position.

3.3. Morphological, biochemical, plant growth promoting and defense characterization of PSCR17

The isolate *P. mirabilis* PSCR17 was found to be moderate in size, whitish-yellow in color, and smooth in texture, with a raised elevation, irregular form, and lobate margin, and was found to be gram negative. *P. mirabilis* PSCR17 was found to grow in the pH range of 1 to 9, at temperatures of 10 to 50 °C, with NaCl tolerance up to 15%, and with incubation periods from 2 to 50 h. With respect to the biochemical tests, the isolate was found to be positive for oxidase, catalase, citrate, gelatinase, urease, and TSI tests. The isolate *P. mirabilis* PSCR17 was found to contain plant growth-promoting characteristics through the production of enzymes. The results explained that the isolate showed IAA production by the development of a reddish-pink-colored complex, and positive ammonia production was indicated by the development of the color of the medium to a slight yellow or brownish color. The production of multifarious biocontrol enzymes was also observed. A clear halo zone was formed around the colonies when tested for chitin, amylase, cellulase, and

protease. The isolate was also observed to be an effective HCN producer due to the change in color of the filter paper from yellow to moderate brown. A detailed characterization of *P. mirabilis* PSCR17 is listed in **Table 1** and illustrated in **Figure 3**.

Table 1. Morphological and biochemical characterization, along with the production of enzymes for plant growth promotion and plant defense by *P. mirabilis* PSCR17.

S. No.	Characteristics	*Proteus mirabilis* PSCR17
1	Size	Moderate
2	Color	Whitish-Yellow
3	Texture	Smooth
4	Elevation	Raised
5	Form	Irregular
6	Margin	Lobate
7	Gram staining	Negative
8	Growth condition	Facultatively Anaerobic
9	Growth pH	1–9
10	Growth temperature	10–50 ℃
11	Salt tolerance up to	1%–15%
12	Incubation Period	2–50 h
	Biochemical characteristics	
13	Oxidase	Positive
14	Catalase	Positive
15	Simmon Citrate test	Positive
16	Gelatin hydrolysis	Positive
17	Urea hydrolysis	Positive
18	TSI (H_2S production)	Yes, Black
19	TSI (Gas gap space)	Yes
20	TSI (Color)	No color change
21	Methyl Red (MR)	Negative
22	Voges-Proskauer (VP)	Negative
	Enzymes for Plant growth and defense characteristics	
23	Potassium	Positive
24	Phosphate	Negative
25	Zinc	Negative
26	Ammonia	Positive
27	IAA	Positive
28	Chitin	Positive
29	Amylase	Positive
30	Cellulase	Positive
31	Protease	Positive
32	HCN	Positive

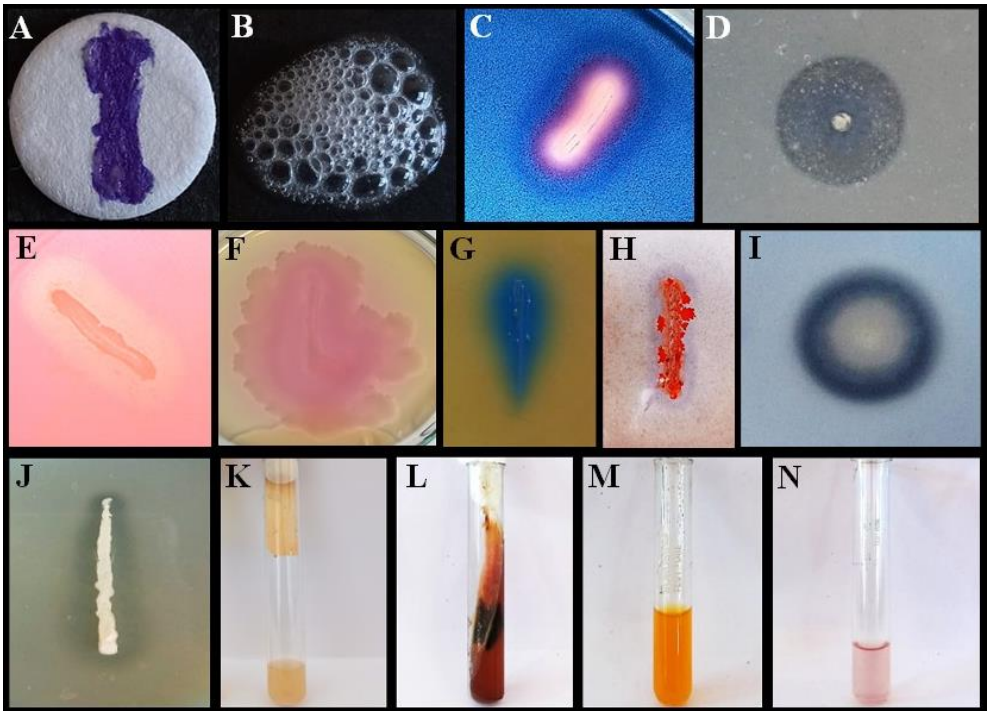

Figure 3. Characterization of *Proteus mirabilis* PSCR17. **(A)** The development of a purple color on the oxidase disc, indicated a positive oxidase test; **(B)** A positive catalase test was observed by the production of oxygen bubbles upon the addition of hydrogen peroxide; **(C)** A positive amylase test was indicated by the production of a clear halo zone around the colony of the isolate on starch agar medium upon the addition of Gram's iodine solution; **(D)** The zone of clearance around the colony observed on Aleksandrov agar medium indicated the potential of the isolate to solubilize potassium; **(E)** The formation of a clear halo zone on Carboxymethylcellulose agar medium upon the addition of Congo red and NaCl which indicated a positive cellulase test; **(F)** The change of color of the Christensen's urea agar medium from yellow to pink revealed a positive urease test; **(G)** The production of a blue color on the Simmons Citrate agar medium demonstrated a positive citrate test; **(H)** The halo zone formed around the colony on colloidal chitin agar indicated the production of the enzyme chitinase; **(I)** The isolate showing halo zone on skim milk agar medium indicated the production of the enzyme protease; **(J)** The halo zone formation on nutrient gelatin agar medium after flooding with ammonium sulphate indicated a positive gelatinase test; **(K)** The development of an orangish-brown color of the picric acid dipped filter paper suspended over the King's B agar medium supplemented with glycine indicated HCN production; **(L)** The raising of the butt of the TSI medium along with the formation of a black precipitate indicated the production of hydrogen sulfide gas by the isolate; **(M)** The change of color of the peptone water broth to slight yellow or orange upon addition of Nessler's reagent revealed a positive ammonia test; **(N)** The development of a pink color in the nutrient broth medium upon the addition of Salkowski's reagent indicated a positive IAA test.

4. Discussion

The use of chemical and synthetic fertilizers to meet the growing food needs of the world population can adversely affect the natural components and the microflora of the soil. The innately available microbes present in the soil can act as PGPR, which helps in the betterment of the plant's health [42]. Within these groups are KSB, which solubilizes the K and other minerals in the soil and makes them available to the plants, helping with the nutrient cycling and enhancing the microbial community [4,6]. Potassium has a major impact on how well plants absorb and use other nutrients, as

there is a relationship between K and other nutrient ions, and various crops require varying amounts of K [2].

Soil samples frequently contain enteric bacteria. As a result, it has been established that enteric bacteria are frequently found in agricultural plants due to their presence in the soil [44]. The current experimental study showed that the PSCR17 isolated from a farm rhizosphere was capable of solubilizing potassium and was identified as *P. mirabilis*. In 1885, the species of Proteus was first described by a German microbiologist Gustav Hause due to their swarming ability on solid surfaces. This ability could be the possible origin of the name *P. mirabilis* which translates to marvellous, splendid and amazing in Latin [8].

The present study indicated that *P. mirabilis* PSCR17 has the capability to solubilize potassium and was also found to be positive for the production of IAA, protease, amylase, HCN, cellulase, chitin, ammonia, urease, gelatinase, etc., which aid in the direct and indirect growth and development of plants. The results of the current research were found to be in accordance with the results obtained by Verma et al. [22], where both studies report the presence of similar biochemical characteristics and PGP attributes of *P. mirabilis* PSCR17 and PD25.

In this research work, *P. mirabilis* PSCR17 formed a clear transparent zone around the colony when tested on Aleksandrov agar medium exhibiting the trait of K solubilization. The use of KSB is a promising and an environmentally friendly method to convert insoluble potassium in the soil into soluble forms that can be absorbed by the plants and the same property was detected in the case of isolate PSCR17. The potassium solubilization index of *P. mirabilis* PSCR17 was 5 and was found to be the highest when compared to the other isolates obtained in this study. Previous studies have demonstrated that KSB can function as PGPR and improve plant development. *P. mirabilis* BUFF14, T166 and PD25 with PGP activities including highest solubilization of potassium (4 cm), phosphate and zinc, nitrogen fixation and salt tolerance showed the maximum absorption of N, P, K, along with the highest enhancement of biological yield, harvest index and grain yield of *Foeniculum vulgare*, *Cicer arietinum*, *Vigna radiata* and mitigated deleterious effects of salinity in wheat [4,22,45].

Experimental studies showed that isolates capable of producing IAA increased the growth of crops. *P. mirabilis* TL14-1 that produced IAA improved rice plant growth properties through enhancement of germination, soil nutrients, root colonization and yield [23]. Wheat, chilli and tomato seeds were bacterized with IAA producing *P. mirabilis* R2 and BETS2 which resulted in the highest plant biomass, germination stress tolerance index, leaf water contents, leaf area, root and shoot length and the isolates showed antagonistic activity against phytopathogens *Fusarium oxysporum*, *Sclerotium rolfsii* and *Colletotrichum capsici* and were found to be resistant to antibiotics [6,44]. *P. mirabilis* PSCR17 also played a noteworthy role in the production of IAA which is a positive aspect for plant growth as IAA being a phytohormone plays an integral role in plant development. IAA stimulates the root development which increases the water and nutrient uptake. The enlargement of the root area also aids in hosting multiple microbial communities. *P. mirabilis* PSCR17 also produced hydrolytic enzymes HCN, amylase, cellulase, chitin and protease which are a part of the innate defense mechanism present within the bacterium that helps to fight against plant diseases by releasing its antagonistic activities. The production of

hydrolytic enzymes by the bacteria aids the plant in defending itself against phytopathogenic attacks.

Previous studies have reported that *P. mirabilis* ZK1 and IPSr83 showed resistance to heavy metals such as arsenic, cadmium, chromium, cobalt, copper, mercury, nickel and lead. These isolates also exhibited PGP traits and increased the plant growth of maize and *Saccharum ravennae* by increasing the plant tolerance to the heavy metals, reducing oxidative stress and increasing the production of antioxidant enzymes. Hence it was reported that *P. mirabilis* can be used in heavy metal phytoremediation [18,20]. *P. mirabilis* isolated from a lake in northeast Georgia was found to be the fastest degrader of a commonly used herbicide propanil [13]. Many other species of *Proteus* have been reported to neutralize and degrade toxic plant-used pesticides, insecticides and herbicides [8,15,46–48]. Hence, the KSB *P. mirabilis* PSCR17 can also be used to degrade and neutralize heavy metals, insecticides, pesticides and herbicides with addition to being used as a PGPR in the future after further studies are carried out. The PGPR which are capable of solubilizing minerals and producing enzymes, help in the alleviation of stress levels.

Several experiments as mentioned above have demonstrated that enteric bacteria such as *P. mirabilis* are capable of plant growth promotion by production of plant growth hormones, have antagonistic activity against phytopathogens and heavy metal degrading ability. The results of the present study are in consonance and are similar to the results obtained by other researchers using *P. mirabilis* where *P. mirabilis* isolates have shown PGP traits highlighting their importance to be used as a PGPR.

5. Conclusion

The study concludes that the utilization of PGPR is a sustainable and eco-friendly way to accomplish eco-accommodative sustainable agriculture. The work presented here exhibits that the isolate *P. mirabilis* PSCR17 was the most efficient K solubilizer along with producing IAA and hydrolytic defense enzymes such as chitinase, cellulase, protease, amylase, and HCN with antagonistic properties. This beneficial PGPR isolated in the current study could be used as an alternative technology to chemical fertilizers to promote plant growth, health, yield, and stress tolerance and to enhance the soil quality. The utilization of indigenous bacteria present within the rhizosphere of the plants aids in increased nutrient uptake, promotes root development, and assists plants to endure harsh environments. Thus, the utilization of the KSB *P. mirabilis* PSCR17 is regarded as an appealing and bold strategy, and it may offer a viable substitute for providing crops with nutrients, especially K, in an environmentally responsible and sustainable way. However, further validation, research, and evaluation are required under different conditions prior to advising its use as a bioinoculant and manufacturing commercial inoculums.

Author contributions: Formal analysis, SMJ and SL; experiment, SMJ and SL; writing—original draft preparation, SMJ; writing—review and editing, SP; supervision, SP. All authors have read and agreed to the published version of the manuscript.

Conflict of interest: The authors declare no conflict of interest.

Abbreviations

K	Potassium
PGPR	Plant Growth Promoting Rhizobacteria
KSB	Potassium Solubilizing Bacteria
IAA	Indole Acetic Acid
HCN	Hydrogen Cyanide
TSI	Triple Sugar Iron

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