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Phosphate- and potassium-solubilizing *Siccibacter colletis* promotes wheat growth, yield, and nutrient uptake

Pawan Kumar[1], Sandeep Kumar[1], Parkriti Jhilta[1], Vikram Poria[1], Rajpaul Yadav[2], Surender Singh[1]*

[1]Department of Microbiology, Central University of Haryana, Mahendragarh, Haryana, India.
[2]Department of Soil Science, Krishi Vigyan Kendra, CCSHAU, Hisar, Haryana, India.

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ABSTRACT

Wheat is one of the staple crops cultivated worldwide and it requires the application of chemical fertilizers for better yield. However, excessive use of these fertilizers can pollute the environment. The aim of this study was to assess the potential of plant growth-promoting rhizobacteria (PGPR) *Siccibacter colletis* isolated from foothill fields of the Aravalli Hills with different fertilizer levels on wheat growth, yield, and nutrient content. The ability of the isolate to produce IAA, ammonia, ACC deaminase, and HCN and to solubilize potassium and phosphorous makes *S. colletis* a good candidate for its use as PGPR. *S. colletis* produced 577.52 ± 0.64 nmol/mg/h and 50.36 ± 3.23 µg/mL ACC deaminase and IAA, respectively, besides solubilizing P (745.56 ± 39.07 mg/L) and K (14.6 ± 0.08 mg/L). The potential of the culture was assessed *in vivo* using pot and field experiments. Under both recommended and reduced doses of chemical fertilizers, application of *S. colletis* significantly improved plant biomass, biometric, and physiological parameters in both pot and field conditions. The findings revealed *S. colletis* as a suitable candidate for improving wheat yield with a reduced fertilizer dose, which can help to reduce cultivation cost and pollution.

1. INTRODUCTION

Wheat (*Triticum aestivum* L.) is one of the world's principal food crops. Worldwide, approximately 808 million tons of wheat is produced on 219 million hectares [1]. Approximately half of India's population depends on wheat for food and other needs; the average land under wheat cultivation was 30.38 million hectares from 2017 to 2022 [2]. However, rapid human population growth indicates that food demand will be more than quadruple by 2050 compared to its current level [3]. Heavy doses of chemical fertilizers, especially nitrogenous and phosphatic fertilizers, are applied to meet the nutrient demand of the crop. The non-judicious use of these chemical fertilizers is non-economical and increases environmental pollution. Potassium (K) and phosphorus (P) are among the most essential nutrients for growth and development. Even though most soils contain sufficient phosphorus and potassium minerals, most of which are bonded to other soil minerals, making them unavailable to plants in a free soluble state.

Under these circumstances, the use of biofertilizers can be a valuable approach to increase their availability. It has been demonstrated that the application of microbial inoculants along with chemical fertilizers is a successful strategy to increase crop yields [4,5]. Due to their beneficial interactions with plants, microbial communities such as rhizobacteria, which live in the rhizosphere and have traits that encourage plant growth, are more prevalent and are participating in this endeavor. The rhizosphere, which is a hotspot for the colonization of beneficial microorganisms, is home to the majority of plant growth-promoting rhizobacteria (PGPRs), which have been reported to enhance plant growth by direct mechanisms such as mineral solubilization, nitrogen fixation, and production of phytohormones such as auxin, gibberellin, and cytokines [4]. Furthermore, PGPR can produce ammonia, hydrogen cyanide (HCN), and bioactive metabolites such as siderophores and biosurfactants [6]. Due to their indirect effects on the synthesis of stress-alleviating enzymes, such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase [7], antibiotic production, and induced systematic resistance, PGPR can modify plant stress responses under abiotic and biotic stress conditions.

P and K solubilization are also among the most commonly reported mechanisms of action linked to increasing the quantity of accessible P and K in the soil that might be readily absorbed by plants under P- and K-limited conditions in the soil [8]. Rhizosphere contains a wide range of P- and K-solubilizing bacterial populations, such as *Azotobacter*, *Acinetobacter, Serratia, Bacillus, Enterobacter, Paenibacillus, Pantoea, Pseudomonas Methylobacterium, Ochrobactrum, Rhizobium*, and *Acetobacter*. Although their population is low, this necessitates the use of outside inoculation to get desirable effects.

*Corresponding Author:
Surender Singh,
Department of Microbiology, Central University of Haryana, Mahendergarh, Haryana, India.
E-mail: surendersingh@cuh.ac.in

Low P and K availability in the soils of many wheat-growing regions also hinders the performance of these crops. An effective way to mitigate the effects of mineral deficits could be to inoculate plants with efficient P- and K-solubilizing PGPR. Moreover, semiarid regions have limitations such as water scarcity, high temperatures, less organic content, and low fertility. The commercially available P and K solubilizers are not effective in such conditions. Therefore, indigenous P- and K-solubilizing microbes isolated from stressful regions can be more appropriate candidates for use as biofertilizers in semiarid conditions. Thus, we aimed to study the effect of newly isolated P- and K-solubilizing bacterial isolates on wheat growth with various combinations of chemical fertilizers under semiarid conditions, emphasizing PGPR as a biologically sustainable fertilizer to enhance plant's growth under P and K deficiency.

2. MATERIALS AND METHODS

2.1. Isolation of Bacteria

Soil samples were collected from the semiarid region of Aravalli Hill (28.376296°N; 76.129993°E) from the *T. aestivum* (wheat) rhizosphere at a depth of 6 cm in triplicate from each sampling site. The samples were stored at 4°C until further use. The soil samples were serially diluted and plated on Pikovskaya's [9] and Aleksandrov [10] agar medium for the isolation of P- and K-solubilizing bacteria, respectively. Isolates showing clear zones around bacterial colonies were selected and preserved for further analysis.

2.2. Qualitative Estimation of P and K Solubilization

All the isolates were screened for P and K solubilization based on clear halo zones on Pikovskaya's and Aleksandrov solid medium enriched with tri calcium phosphate (TCP) and potassium alumino-silicate (PAS), respectively. The halo zones were measured, and the solubility index (SI) was calculated by using the following formula [11]:

$$SI = \frac{H - B}{B} \times 100$$

where H is the diameter of the halo zone around the colony and B is the diameter of the bacterial colony.

2.3. Quantitative Screening

Isolates with higher solubility indices were selected for quantitative analysis using Pikovskaya's and Aleksandrov broth media with different inorganic sources of phosphate (tricalcium phosphate (TCP) and rock phosphate (RP)) and potassium (potassium alumino silicate (PAS), mica, and K-feldspar (K-Feld)), respectively [12,13].

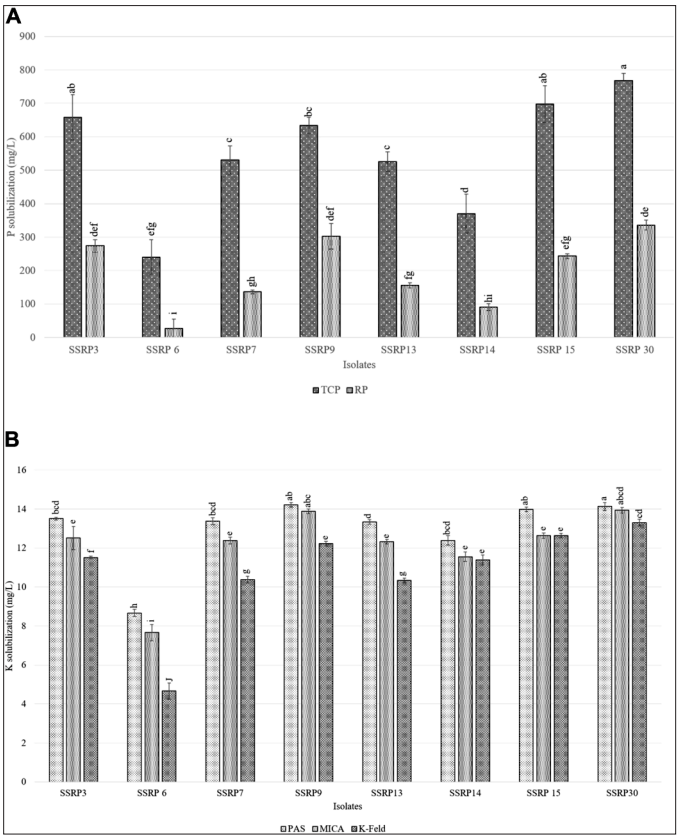

Figure 1: The graph represents quantified values of **(A)** phosphate solubilization with two phosphate sources, i.e., TCP and rock phosphate and **(B)** potassium solubilization with three sources, i.e., PAS, MICA, and K-feldspar. The error bar corresponds to SE ($n = 3$), bars with different letters indicate a statistically significant difference (Tukey test: $P < 0.05$) among different isolates.

2.4. Plant Growth-Promoting Traits (PGP Traits)

The bacterial isolates were screened for indole acetic acid (IAA) production using the Salkowski colorimetric assay [14]. Siderophore production was detected by the Chrome-Azurol S (CAS) method

Table 1: Plant growth-promoting attributes of bacterial isolates screened in vitro.

Isolates	IAA (µg/mL)	ACCD nmol/mg/h	Ammonia	HCN	Siderophores
SSRP3	40.77 ± 3.9^{bc}	497.89 ± 1.40^{b}	+++	+++	++++
SSRP6	23.11 ± 2.8^{ef}	34.60 ± 1.46^{e}	++	+++	++++
SSRP7	35.63 ± 2.2^{cd}	358.73 ± 2.88^{c}	+++	+	-
SSRP9	54.44 ± 2.5^{a}	575.80 ± 3.65^{a}	++	+	-
SSRP13	16.17 ± 1.6^{f}	209.99 ± 1.89^{d}	++	-	-
SSRP14	26.34 ± 2.6^{de}	50.11 ± 2.07^{e}	+++	-	-
SSRP15	50.35 ± 2.5^{ab}	577.52 ± 0.78^{a}	++	+	-
SSRP30	58.8 ± 2.4^{a}	347.27 ± 1.75^{c}	++	++	+

Responses are categorized as "+" low, "++" moderate, and "+++" high, and "-"' corresponds to negative result.
*Values are the mean ± SE (n = 3), columns with different letters indicate a statistically significant difference (Tukey test: p < 0.05).

Table 2: Percent homology with corresponding bacteria and accession numbers of isolates submitted.

Isolate Name	Percent Similarity	Organisms	Accession No.
SSRP3	98.87%	*Pseudomonas hunanensis*	OR352453
SSRP6	98.54%	*Pseudomonas aeruginosa*	OR352454
SSRP7	99.11%	*Lelliottia jeotgali*	OR352455
SSRP9	98.97%	*Kosakonia oryzendophytica*	OR352456
SSRP13	99.44%	*Acinetobacter baumannii*	OR352457
SSRP14	98.75%	*Acinetobacter pittii*	OR352458
SSRP15	99.41%	*Enterobacter cloacae*	PP140923
SSRP30	98.59%	*Siccibacter colletis*	OR150488

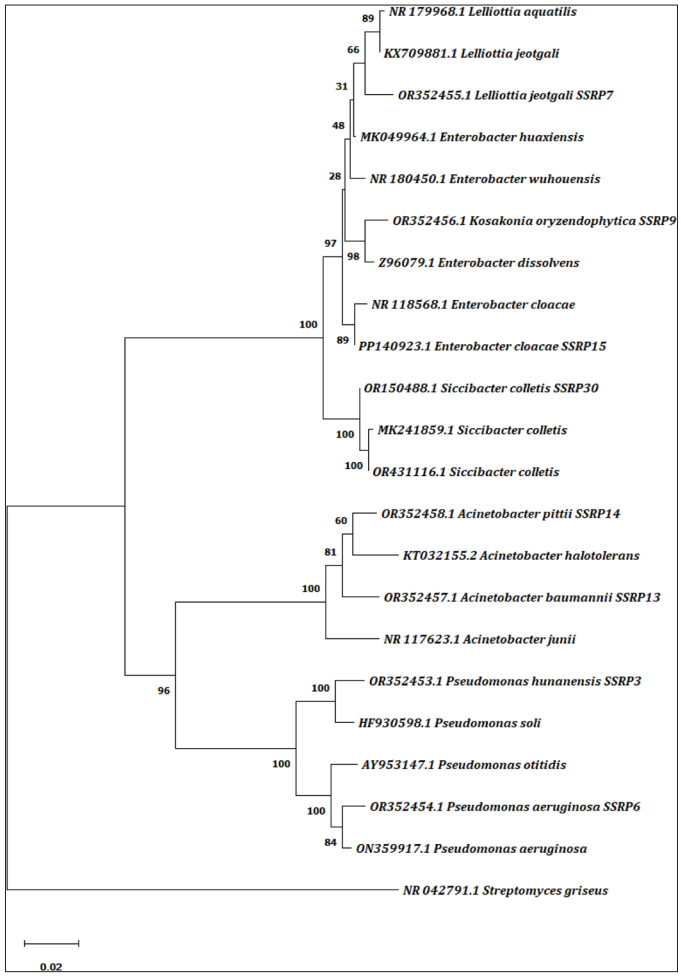

Figure 2: Phylogenetic tree showing the relationships of native bacterial isolates based on partial 16S rRNA sequences constructed via the neighbor-joining method with the MEGA-XI software. The evolutionary distance was calculated using the maximum composite likelihood method with a bootstrap of 1000 replications. The number on the scale indicates the distance level with relative units.

Table 3: Physiological growth parameters of wheat plants under pot and field conditions.

	Pot trial						*Field trial*						
Treatment	Chl a mg/g tissue	Chl b mg/g tissue	Total chl mg/g tissue	Proline µmol/g tissue	Sugar content mg/g tissue	RWC	MTS	Chl a mg/g tissue	Chl b mg/g tissue	Total chl mg/g tissue	Proline µmol/g tissue	Sugar content mg/g tissue	RWC	MTS
T1	1.53 ± 0.36^{c}	0.60 ± 0.05	2.23 ± 0.41^{c}	3.94 ± 0.06	6.41 ± 0.37^{d}	79.13 ± 4.69	13.04 ± 1.89	1.59 ± 0.26^{d}	0.60 ± 0.04	2.19 ± 0.30^{d}	3.87 ± 0.07^{c}	7.35 ± 0.36^{c}	79.55 ± 3.53	12.70 ± 1.86^{c}
T2	2.62 ± 0.17^{ab}	0.63 ± 0.04	3.51 ± 0.24^{ab}	4.33 ± 0.24	8.49 ± 0.55^{bc}	84.78 ± 2.16	15.38 ± 0.92	2.20 ± 0.22^{c}	0.68 ± 0.11	3.14 ± 0.09^{b}	4.31 ± 0.17^{b}	8.38 ± 0.73^{b}	81.97 ± 0.87	14.19 ± 1.89^{abc}
T3	2.61 ± 0.25^{ab}	0.63 ± 0.40	3.30 ± 0.36^{ab}	4.64 ± 0.34	9.04 ± 0.80^{ab}	82.11 ± 6.67	14.21 ± 3.29	2.70 ± 0.23^{b}	0.58 ± 0.29	3.28 ± 0.28^{b}	4.82 ± 0.04^{a}	9.35 ± 0.76^{a}	82.74 ± 4.98	16.50 ± 2.49^{a}
T4	3.18 ± 0.28^{a}	0.67 ± 0.38	3.89 ± 0.26^{a}	4.75 ± 0.55	9.46 ± 0.28^{a}	82.41 ± 7.23	16.01 ± 2.35	3.19 ± 0.25^{a}	0.83 ± 0.10	3.87 ± 0.20^{a}	4.96 ± 0.17^{a}	9.67 ± 0.12^{a}	82.79 ± 5.62	15.13 ± 0.96^{ab}
T5	1.97 ± 0.09^{bc}	0.63 ± 0.12	2.71 ± 0.16^{bc}	3.94 ± 0.35	7.80 ± 0.30^{c}	79.78 ± 0.37	13.44 ± 1.11	2.03 ± 0.07^{c}	0.66 ± 0.05	2.69 ± 0.12^{c}	4.30 ± 0.21^{b}	8.31 ± 0.41^{b}	79.74 ± 0.27	13.18 ± 1.31^{bc}
T6	3.04 ± 0.24^{a}	0.65 ± 0.13	3.86 ± 0.16^{a}	4.80 ± 0.29	8.88 ± 0.67^{ab}	82.10 ± 4.21	13.81 ± 3.16	3.15 ± 0.25^{a}	0.73 ± 0.13	3.88 ± 0.12^{a}	4.83 ± 0.23^{a}	9.05 ± 0.32^{a}	81.83 ± 3.24	14.32 ± 1.99^{abc}
T7	1.61 ± 0.43^{c}	0.62 ± 0.03	2.04 ± 0.46^{c}	4.17 ± 0.52	6.63 ± 0.35^{d}	79.13 ± 4.69	13.14 ± 1.69	-	-	-	-	-	-	-
T8	2.60 ± 0.19^{ab}	0.64 ± 0.15	3.58 ± 0.15^{a}	4.44 ± 0.38	8.79 ± 0.56^{ab}	85.48 ± 1.28	15.50 ± 0.81	-	-	-	-	-	-	-

*Values are the means ± SDs (n = 3); columns with different letters indicate a statistically significant difference (Tukey test: $p < 0.05$). However, no letters indicate that there is no significant difference.

Table 4: Biometric growth parameters of wheat plants under pot conditions (a) and field conditions (b).

(a)

	Pot Trial						
Treatment	**Shoot Length cm**	**Root Length cm**	**Wet mass g/Plant**	**Dry mass g/Plant**	**P % in Straw**	**N % in straw**	**K % in straw**
T1	63.96 ± 0.54^{d}	26.67 ± 1.27^{d}	11.34 ± 0.60^{c}	4.51 ± 0.03^{c}	0.12 ± 0.00^{bc}	0.51 ± 0.01^{c}	0.83 ± 0.03^{d}
T2	69.23 ± 1.10a^{bc}	31.75 ± 1.27^{bc}	12.44 ± 0.85a^{bc}	5.46 ± 0.19^{ab}	0.14 ± 0.01^{cd}	0.64 ± 0.02^{b}	0.98 ± 0.10b^{c}
T3	70.15 ± 1.76^{ab}	32.17 ± 1.94^{b}	12.41 ± 0.33^{abc}	5.89 ± 0.37^{a}	0.14 ± 0.00^{cd}	0.56 ± 0.04^{c}	0.93 ± 0.03^{c}
T4	71.30 ± 1.82^{a}	35.56 ± 1.27^{a}	13.16 ± 0.29^{a}	6.06 ± 0.26^{a}	0.16 ± 0.01^{a}	0.73 ± 0.01^{a}	1.17 ± 0.03^{a}
T5	66.46 ± 3.67^{bcd}	29.63 ± 1.94^{c}	11.80 ± 0.30^{bc}	5.07 ± 0.05^{bc}	0.14 ± 0.00^{bc}	0.66 ± 0.04^{b}	1.03 ± 0.05^{b}
T6	70.07 ± 2.64^{ab}	32.60 ± 1.94^{b}	12.70 ± 0.23^{ab}	5.73 ± 0.25^{a}	0.14 ± 0.00^{b}	0.67 ± 0.04^{b}	1.04 ± 0.07^{b}
T7	64.41 ± 1.23^{d}	30.90 ± 0.73^{bc}	11.62 ± 0.22^{bc}	4.66 ± 0.04^{c}	0.13 ± 0.01^{d}	0.56 ± 0.04c	0.91 ± 0.02^{cd}
T8	65.62 ± 3.20^{cd}	32.17 ± 0.73^{b}	12.66 ± 0.29^{ab}	5.60 ± 0.31^{ab}	0.14 ± 0.01^{bcd}	0.67 ± 0.04^{b}	1.00 ± 0.08^{bc}

*Values are the means ± SDs (n = 3); columns with different letters indicate a statistically significant difference (Tukey test: $P < 0.05$). However, no letters indicate that there is no significant difference.

(b)

	Field trial												
Treatment	**Plant Height cm**	**Ear Height cm**	**Spikelet/ Plant**	**Ear Weight g/Ear**	**Grain_ yld q/ha**	**Gtraw_ yld q/ ha**	**Biological_ yld q/ha**	**Harvest Index**	**P% Straw**	**N% Straw**	**K% straw**	**P% grain**	**N% grain**	**K% grain**
T1	90.40 ± 4.04^{b}	10.42 ± 1.04	43.80 ± 12.79	1.99 ± 0.37	41.89 ± 1.22^{c}	56.80 ± 1.70^{c}	98.89 ± 2.86^{c}	0.41 ± 0.02^{ab}	0.12 ± 0.00^{d}	0.51 ± 0.00^{e}	0.83 ± 0.02^{c}	0.29 ± 0.01^{c}	1.02 ± 0.04^{d}	0.47 ± 0.01^{d}
T2	94.60 ± 3.58^{a}	10.76 ± 0.45	49.80 ± 5.72	2.42 ± 0.51	45.15 ± 2.11^{b}	65.11 ± 2.6^{b}	110.81 ± 4.68^{b}	0.41 ± 0.00^{ab}	0.14 ± 0.00^{bc}	0.62 ± 0.02^{c}	0.91 ± 0.00^{b}	0.33 ± 0.01^{b}	1.10 ± 0.04^{c}	0.51 ± 0.01^{c}
T3	101.00 ± 4.06^{a}	11.32 ± 0.61	52.80 ± 5.93	2.65 ± 0.29	54.49 ± 0.73^{a}	75.79 ± 0.66^{a}	130.08 ± 0.71^{a}	0.42 ± 0.00^{a}	0.14 ± 0.00^{c}	0.56 ± 0.03^{d}	0.91 ± 0.02^{b}	0.34 ± 0.00^{b}	1.12 ± 0.02^{bc}	0.52 ± 0.01^{bc}
T4	95.40 ± 4.34^{a}	11.64 ± 0.41	53.20 ± 5.81	2.60 ± 0.66	55.36 ± 0.86^{a}	77.19 ± 1.12^{a}	132.33 ± 1.34^{a}	0.42 ± 0.01^{a}	0.16 ± 0.00^{a}	0.73 ± 0.01^{a}	0.96 ± 0.01^{a}	0.37 ± 0.01^{a}	1.20 ± 0.01^{a}	0.54 ± 0.00^{a}
T5	96.80 ± 4.92^{a}	10.56 ± 0.89	48.40 ± 5.55	2.10 ± 0.37	43.49 ± 1.63^{bc}	66.29 ± 3.61^{b}	110.21 ± 4.88^{b}	0.40 ± 0.01^{b}	0.14 ± 0.00^{b}	0.66 ± 0.03^{b}	0.95 ± 0.02^{a}	0.33 ± 0.01^{b}	1.12 ± 0.02^{bc}	0.51 ± 0.00^{c}
T6	100.20 ± 4.5^{a}	10.60 ± 0.76	49.00 ± 8.15	2.47 ± 0.75	54.85 ± 0.76^{a}	75.73 ± 0.30^{a}	130.40 ± 1.06^{a}	0.42 ± 0.00^{a}	0.14 ± 0.00^{b}	0.61 ± 0.01^{c}	0.94 ± 0.01^{aa}	0.36 ± 0.00^{a}	1.15 ± 0.03^{ab}	0.53 ± 0.00^{ab}

*Values are the means ± SDs (n = 3); columns with different letters indicate a statistically significant difference (Tukey test: $p < 0.05$). However, no letters indicate that there is no significant difference.

[15]. The purified cultures were assessed for their nitrogen-fixing capacity using nitrogen-free media [16] and ammonia production [17]. The 1-aminocyclopropane-l-carboxylate deaminase (ACCD) enzymatic activity was evaluated using both agar plate and in-broth culture techniques on Dworkin and Foster (DF) media supplemented with 1-aminocyclopropane-1-carboxylic acid as the only nitrogen source. The production of ACC deaminase was determined by estimating the amount of α-ketobutyrate produced by hydrolysis of ACC [18].

2.5. Molecular Characterization

Total genomic DNA of eight bacterial isolates was extracted using the sDNA isolation kit (Zymo Research, USA) following the manufacturer's instructions. Gene amplification using 16S rRNA was performed using the universal bacterial-specific primer sets 27F (5′ AGAGTTTGATCCTGGCTCAG 3′) and 1492R (5′ CGGTTACCTTGTTACGACTT 3′). The PCR products were purified using a GeNei™ gel purification kit and subsequently sent to Barcode Bioscience, Bangalore (India), for sequencing. Sequence alignment

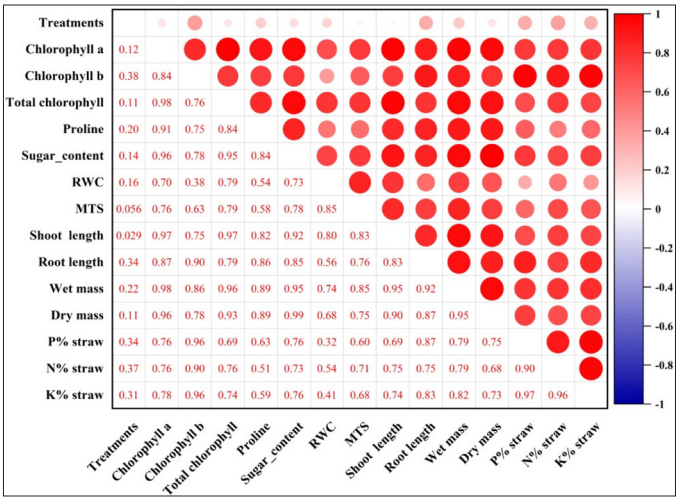

Figure 3: Correlation coefficient matrix illustrating the impact of *Siccibacter colletis* on wheat straw nutritional content, physiological characteristics, and biometric measurements in pots with different fertilizer levels. In the matrix, the correlation coefficient (r) values are indicated by the dark red circles and are significantly positive at $p < 0.01$.

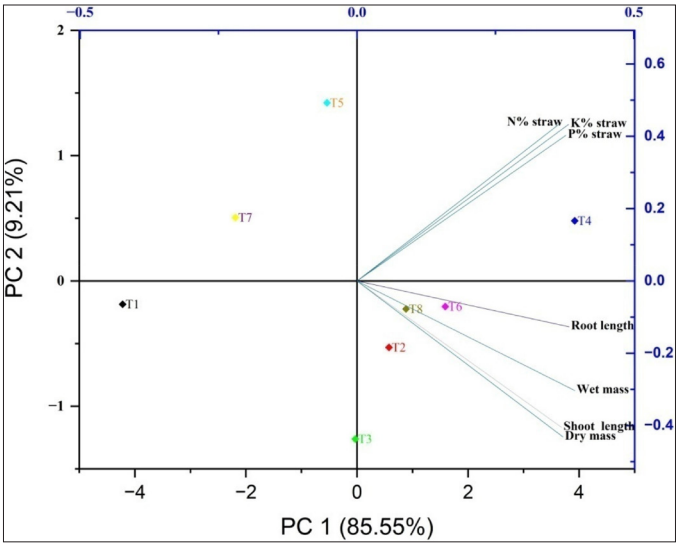

Figure 5: The 2D biplot depicts the variables of wheat crop characteristics that are grouped according to their PC scores (PC1 and PC2) that are obtained from biometric data, nutrient content in straw, and treatment levels under pot conditions.

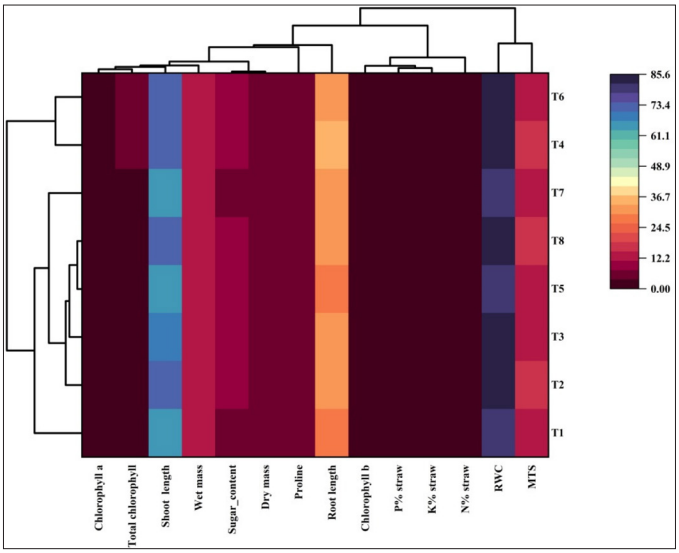

Figure 4: Heatmap demonstrating that *Siccibacter colletis* interacts with various growth parameters and the nutritional content of wheat straw at different fertilizer levels in pots. *The color codes (lowest to highest: violet to yellow and blue) directly correlate to the values of the correlation coefficient (r).

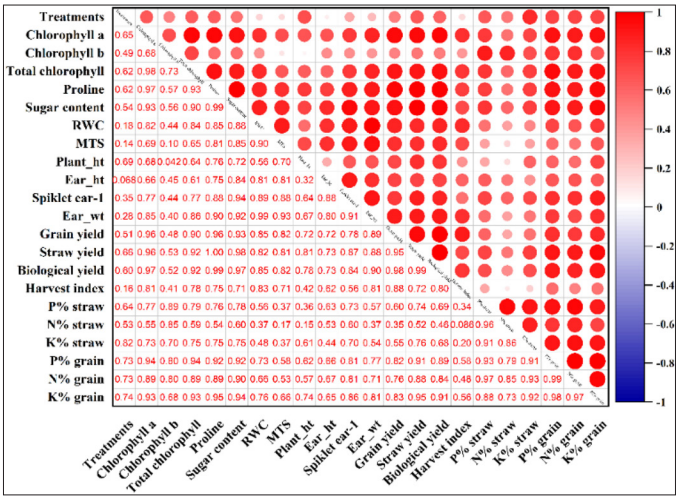

Figure 6: Correlation coefficient matrix illustrating the impact of *Siccibacter colletis* wheat straw and grain nutritional content, physiological characteristics, and biometric measurements in the field under different fertilizer levels. In the matrix, the correlation coefficient (r) values are indicated by the dark red circles and are significantly positive at $p < 0.01$.

and gap filling were performed using SeaView, and the taxonomic relationships were confirmed via NCBI database. A cladogram was constructed by the neighbor-joining method with bootstrap method using MEGA 11.

2.6. Effect of *Siccibacter colletis* Inoculation on the Growth and Yield of Wheat

Siccibacter colletis SSRP30 was selected as the best isolate on the basis of P, K, and other PGP traits in vitro and evaluated their effect on wheat variety HD 2967 in pot and field.

2.6.1. Layout of treatment and physicochemical properties of soil

Treatments

T1 absolute control

T2 bacterial inoculum

T3 recommended dose of NPK (150 kg N, 60 kg P, and 60 kg K/ha)

T4 recommended dose of NPK + bacterial inoculum

T5 50% recommended dose of NPK

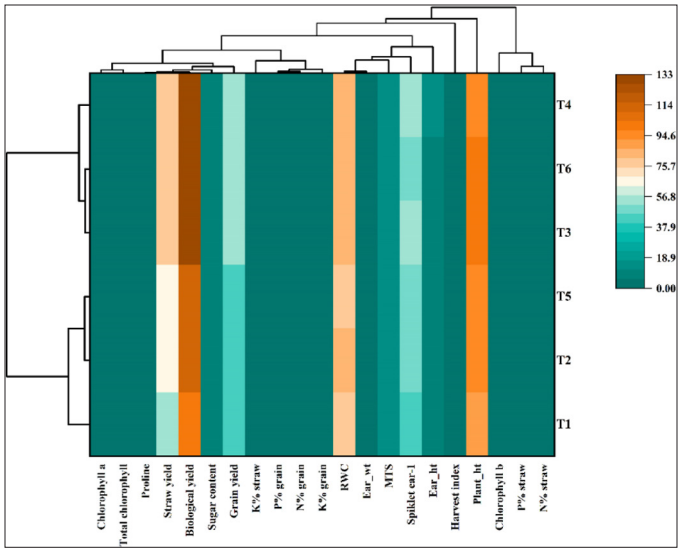

Figure 7: Heatmap demonstrating the relationships between the physiological, biometric, and mineral contents of wheat straw and *Siccibacter colletis* plants grown in the field under various treatment conditions. **The color codes (lowest to highest: violet to yellow and blue) directly correlate to the values of the correlation coefficient (r).

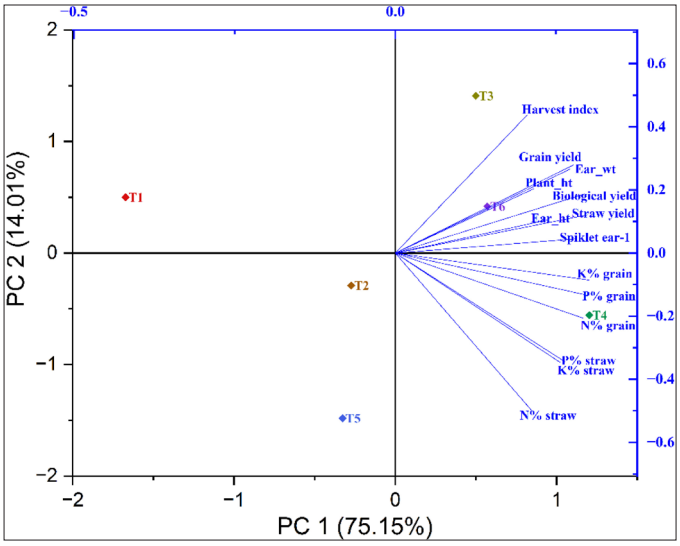

Figure 8: The 2D biplot depicts the variables of wheat crop characteristics that are grouped on PC scores (PC1 and PC2) that are obtained from mineral content in grain and straw and biometric parameters along with treatment levels in the field.

T6 50% recommended dose of NPK + bacterial inoculum

T7 recommended dose of N + potassium aluminosilicate + TCP

T8 recommended dose of N + potassium aluminosilicate + TCP + bacterial inoculum

A total of eight (T1–T8) and six (T1–T6) treatment combinations were laid out in pots and fields, respectively, in a completely randomized design with three replications. Sandy loam soil was collected from the experimental field of Central University of Haryana, Mahendergarh (India) for the pot experiment, and the field experiment was conducted in the farmer's field. The soil was sieved through a 10-mm mesh sieve and subsequently dried to determine the physicochemical properties, including pH, EC, organic carbon [19], available N [20], phosphorous [21], and potassium [22] [Supplementary Table 1].

2.6.2. Pot experiment

Pot experiments were conducted during the Rabi season (2021–22) to study the individual and combined effects of the strains. A total of 15 bacteria-treated seeds were sown in 10-inch diameter pots and thinned to 10 after full emergence of the first leaf. The uninoculated plants treated with nutrient broth without any bacterial strain were taken as controls. Physiological parameters, namely, chlorophylls a and b, total chlorophyll [23], total sugar [24], proline, [25], relative water content (RWC), and membrane thermal stability (MTS) [26], were analyzed at the flag leaf stage in the laboratory by using standard protocols. Biometric parameters such as plant height, root length, and wet and dry weights of roots and shoots were analyzed in vitro. Available nitrogen [27], phosphorous [28], and potassium [29] in wheat straw were measured at the Department of Soil Science laboratory of Chaudhary Charan Singh Haryana Agricultural University, Hisar (Haryana).

2.6.3. Field evaluation of S. colletis

A field experiment was conducted during rabbi 2022–23 at the farmers' field in Manheru (28.7143"N; 76.2345"E), Haryana, India, in 15 × 3 m plots. The plants in each plot were basely dressed according to the treatment with an N:P:K ratio of 150:60:60 kg/ha. Seeds were treated with overnight grown bacterial suspension (10^7 CFU/mL) in a ratio of 1:5, i.e., 1 L of bacterial suspension for 50 kg of seeds, along with a sticker solution (10% gum arabic) for 30 min prior to sowing. Bacterial-treated seeds (150 kg/ha) were sown in each plot. The plants were raised by following standard agronomical practices. All the physiological parameters were analyzed at the flag leaf stage. At maturity, field crops were harvested, biometric parameters were measured, and the plants were threshed after drying. The grain weight, straw weight, biological yield, and harvest index were recorded for field experiments.

2.7. Statistical Analysis

The experiment was designed using a completely randomized design (CRD) with three replications. All the data collected in the study were analyzed by one-way and two-way analysis of variance (ANOVA) using the OriginPro 2023b software, version 10.0. Significant differences among treatments were compared using the Tukey test at $p < 0.05$.

3. RESULTS

3.1. Isolation, Screening, and Quantitative Determination of P- and K-Solubilizing Bacteria

In the present study a total of 87 isolates were initially isolated, which were then screened thrice on Pikovskaya's and Aleksandrov's agar medium to confirm their efficacy and stability. Notably, 20 of the 87 isolates were categorized as PSB and KSB based on their P and K solubilization efficacy, while only 8 isolates based on their P- and K-solubilizing index and pH reduction were tested further for

different attributes. There were significant differences ($p < 0.05$) in P solubilization between all strains and the control in the presence of TCP, which varied from 240.48 ± 28.62 to 786.362 ± 21.86 mg/L, and in the presence of RP, soluble P concentrations also varied significantly ($p < 0.05$) ranging from 26.98 ± 7.65 to 335.996 ± 14.65 mg/L. Similarly, significant differences ($p < 0.05$) were also recorded between all strains and control in terms of soluble K concentration in the presence of PAS (8.6 to 14.2 mg/L), mica (7.6 to 13.9 mg/L), and K-feldspar (4.3 to 13.3 mg/L) [Figure 1]. Maximum P solubilization in the presence of TCP and RP (768.362 ± 21.86 mg/L and 335.996 ±14.65 mg/L, respectively) was shown by strain SSRP30. However, maximum K was solubilized by strain SSRP9 (14.2 ± 0.069 mg/L) followed by SSRP30 (14.1 ± 0.20 mg/L) in the presence of PAS, whereas in the presence of mica and K-feldspar, maximum solubilization was shown by strain SSRP30 (13.9 ± 0.15 mg/L and 13.3 ± 0.17 mg/L, respectively).

3.2. PGP Traits

The PGP traits of the isolates are presented in Table 1. Based on the screening of PGP traits, SSRP30, SSRP9, and SSRP15 showed the highest, i.e., 58.8 ± 01.23, 54.4 ± 3.96, and 50.3 ± 1.36 µg/mL IAA production, respectively, as compared to other test strains [Table 1]. Similarly, highest ACC deaminase was observed in isolate SSRP15 (577.52 ± 0.78 nmol/mg/h) followed by SSRP9 (575.8 ± 3.65 nmol/mg/h) and SSRP3 (497.8 ± 1.40 nmol/mg/h). Furthermore, siderophore production was recorded as the highest for SSRP3 followed by SSRP6 as compared to other isolates; however, all the strains were positive for ammonia and HCN production except SSRP13.

3.3. Molecular Characterization

Notably, 16S rRNA PCR amplicon of ~1500 bp was sequenced and a Basic Local Alignment of concatenated 16S rRNA gene sequence revealed homology with the corresponding organism, and it is presented in Table 2. To assess the taxonomic position of the identified strains, sequences of 14 corresponding bacterial-type strains retrieved from the NCBI were compared. The dendrogram [Figure 2] was generated with MEGA X using the neighbor-joining algorithm with a 50% bootstrap majority-rule consensus tree (1000 replications). *Streptomyces griseus* was used as an outgroup. With >90% similarity and 0.020 nucleotide substitutions per site, four major groups were clustered.

3.4. Effect of *S. colletis* Inoculation in Pot Trials

After 5 days of sowing (DAS) in pots, the bacterized wheat seeds displayed a 100% germination rate compared to those in the T1 treatment and the treatment involving non-bacterized seeds, i.e., 98%. The rhizobacterium *S. colletis* combined with RDF and 50% RDF significantly boosted plant growth. Among the physiological parameters, proline content, RWC, and MTS were found to be nonsignificant between the treatments ($P > 0.05$). However, there were significant differences in total chlorophyll and sugar contents between the treatments ($P < 0.05$), with T4 and T6 having the highest levels [Table 3]. The lowest contents of sugar and chlorophyll were observed in the plants from treatment T7, followed by those from treatment T1.

The biometric parameters of the wheat crops exhibited similar patterns. Treatments T3, T4, and T6 resulted in highly comparable plant biomasses in terms of wet and dry weights ($P < 0.05$). The NPK concentration in the straw varied across treatments and was significantly higher in T4, followed by T6 and T3 [Table 4], in contrast to the biometric measurements. However, when T7 and T8 were compared with the other treatments for growth characteristics, it was found that T8 tended to be nonsignificant to T4 and T6, respectively, and significantly higher than other treatments.

Positive effects were observed with observable variations in plant height among the treatment groups. Compared with those in other treatments, the shoot heights in T1 and T7 were the lowest. On the other hand, plants from treatment T4 were the tallest, while the other plants were closely related but differed significantly. Parallel trends were observed in the length of the roots of the plants among the treatments. Similarly, bacterial inoculation significantly affected the macronutrient content, i.e., NPK, in the present study. Substantial differences were recorded across the various treatment groups; in particular, treatments T4, T5, T6, and T8 exhibited the significantly highest levels of these nutrients within wheat straw, with T4 having the highest and T1 having the lowest NPK levels.

The treatments studied under controlled pot conditions demonstrated a significantly positive Pearson correlation coefficient (r), as depicted in Figure 3, when assessed in relation to the physiological and biometric parameters examined in this study. However, with the exception of the relative water content and membrane thermal stability, which demonstrated a slight inclination toward neutrality, the observed associations were consistently positive. This was also apparent in the clustered heatmap [Figure 4], which was based on similarities in correlation coefficients and displayed against growth parameters (horizontally) and treatment (vertically). Closely comparable treatments, such as T6 and T4, were grouped together. Similarly, growth characteristics with greater correlations were clustered together. As a consequence of *S. colletis* strains with RDFs or 50% RDFs, the locations of various growth metrics and macronutrient (NPK) concentrations in straw were represented by the four zones of the PCA biplot [Figure 5] according to the principal component analysis. Two main components (PC1, 85.55%; PC2, 9.21%) comprised the PCA, which explained 94.76% of the variance under potting conditions [Figure 5]. T4 had a significant effect on the N, P, and K contents of the wheat straw, as indicated by the upper right biplot. On the other hand, T8, T6, and T2 had an impact on the biometric parameters if the crop was represented by the lower right corner of the biplot, where PC1 had positive loading and PC2 had negative loading.

3.5. Effect of *S. colletis* Inoculation in Field Trials

Like in the pot experiments, we studied the effects of bacterial inoculation in conjunction with RDF or a reduced dose of 50% RDF under field conditions. The results revealed a significant increase in several biometric growth indices, including dry biomass output, plant height, and yield-related attributes. Furthermore, the investigation indicated a considerable increase in the macronutrient content in grain and straw. When comparing the treatment groups to T1, i.e., the absolute control, a significant difference in physiological parameters, was detected. Among all the treatments, T6, which had 50% RDF and bacterial inoculum, and T4, which had RDF and bacterial inoculum, exhibited the significantly highest levels of total chlorophyll. In terms of proline and sugar concentrations, there were no significant differences found between treatments T3, T4, and T6; however, they were significantly higher compared to other treatments. There were no statistically significant differences in the relative water content measured in any treatment group ($P > 0.05$). In contrast to the results of pot studies, the membrane thermal stability data revealed significant variation across the treatment groups. The plants from T3 had the highest MTS, whereas the MTS values from T2, T4, and T6 were statistically identical. Except for the number of spikelets per plant, ear

height, and weight, all the biometric parameters significantly differed among the treatment groups.

Furthermore, T4 exhibited the best yield qualities, such as straw, grain, and biological yields, followed by T6 and T3 [Table 4]. However, the harvest indices were significantly different among the groups but more or less similar throughout the treatment groups. The NPK content in the wheat straw and grain was significantly highest in T4. However, no significant difference was found in P content of the wheat straw in T6, T5, and T2. Similarly, the K contents in the wheat straw were found to be significantly higher in treatments T4, T6, followed by T5, and similar trends were generally recorded for the K content in the grains. Similarly, compared with that in the absolute control, the N content in the straw was significantly different across the treatments but was similar in the grains [Table 4].

Consistent with the findings from the controlled pot experiments and similar to those of the pot studies, Pearson's correlation coefficient between the treatments and various physiological and biometric parameters revealed an overall significant positive correlation [Figure 6]. However, parallel to the results observed under pot conditions, the RWC and MTS tended to reach neutrality, as did the ear height and harvest index. Similarly, the harvest index showed a lower positive correlation with the nitrogen content (r = 0.086) in the wheat straw.

A heatmap generated for physiological and biometric parameters (horizontally) against various treatments (vertically) depicted different groupings based on their similarities. In line with the results observed in the controlled pot experiments, treatments containing RDF, either alone or in combination with *S. colletis*, demonstrated significant positive interactions with respect to yield-related attributes under field conditions [Figure 7], which was reflected by the proximity of T6–T4 to both the inoculum control and the absolute control (i.e., T1 and T2) within the heatmap.

PCA revealed two principal components contributing 75.15% (PC1) and 14.01% (PC2) of the variance, collectively accounting for 89.16% of the total variance. It is evident from the biplot that treatment T6, with 50% RDF together with rhizobacterial inoculation, and treatment T3, involving RDF alone, predominantly influenced wheat yield attributes, as shown in the upper right quartile, having a large positive loading for both principal components [Figure 8]. The nutritional content of both the grain and straw was predominantly affected by treatment T4, as demonstrated by a positive loading on PC1 and a negative loading on PC2, placing it in the lower right quartile of the biplot, in contrast to the results from the pot trials.

4. DISCUSSION

PGPR, by virtue of its ability to provide or mobilize different nutrients and secrete other metabolites, sustains plant growth with the minimum amount of chemical fertilizers and alleviates many stresses such as salinity, high temperature, and pests. P and K being the major nutrients required by the plants are to be supplied externally in the form of chemical fertilizers frequently. However, the unfavorable soil pH renders P unavailable for plants due to the formation of insoluble complexes with aluminum or iron minerals. Similarly, K is also not present in available form in the soil for the plants. Furthermore, various abiotic stresses such as high temperature, drought, and salinity also reduce plant growth, especially in semiarid regions such as Mahendergarh, India. P- and K-solubilizing microorganisms have emerged as potential candidates for sustainable supply of these minerals to plants. Besides providing P and K, many microorganisms have the potential to alleviate or reduce the effects of various abiotic stresses in such areas. However, these microorganisms are adapted to certain soil conditions and fail to provide desirable effects under unfavorable soil conditions. So the researchers are working on different approaches to ensure the effectiveness of P- and K-solubilizing bacteria in sustaining crop yields in diverse agricultural environments. This involves several methodologies and approaches, such as analyzing the area-specific soil characteristics (soil texture, pH, and nutrient content), applying high-throughput methods for isolating and identifying area-specific indigenous microbes, molecular techniques for strain development, compatible testing with agrochemical and other beneficial microbes, and conducting several seasonal field trials to prepare area-specific bioinoculant formulations for sustaining crop yields in such areas. A large number of bacteria belonging to Enterobacteriacea, including *Enterobacter cloacae, Enterobacter* sp. CM94, *Klebsiella michiganensis* TS8, and *Lelliottia jeotgali* MR [30-32], are reported to be efficient PGPR and have been applied in the field for improving crop yields. The most efficient bacterial isolate in the present study was identified as *S. colletis* SSRP30 (acc. no. OR150488), based on the 16S rRNA gene sequence they are primarily present in the rhizosphere soil and as mutualistic endophytes [33,34]. Jackson et al. [33] published the first description of *S. colletis* as a unique species isolated from tea leaves and poppy seeds. Both *Siccibacter* and *Siccibacter*-derived genera have been reported for their various plant growth-promoting characteristics [35]. According to Chamkhi, et al. [34], *S. colletis* from alfalfa rhizosphere has an extensive capacity to colonize plant roots and shield plants from biotic and abiotic stresses. Similarly, Salazar-RamÍRez et al. [36] isolated *S. colletis* from the candelilla (*Euphorbia antisyphilitica*) rhizosphere. This is the first study in which *S. colletis* was reported from the wheat rhizosphere soil of Aravalli foothills. The foothill soils are rich in minerals, and hence the probability of finding mineral-weathering microorganisms is always high. The results of the in vitro experiment unequivocally demonstrated that the *S. colletis* SSRP30 strain, which was chosen for this study, possesses many PGP features, including IAA, ACC deaminase, siderophore production, HCN production, and biofilm formation, all of which directly or indirectly aid in plant growth and development.

The competitive saprophytic ability of the microorganisms varies and determines their fate when applied in the field. Isolates that showed promising results in the in vitro experiments failed to perform under field conditions because of several environmental and edaphic factors, which vary from soil to soil. Hence, it is imperative to evaluate the competitive saprophytic ability of isolates by means of pot and field experiments and analyze their effect on yield. The culture was able to provide significant yield benefits compared to the control, which indicated the superior competitive saprophytic ability of the isolate. Since under unfavorable soil pH conditions, the P and K form complexes with different minerals, making them unavailable for plants, the applied isolates were instrumental in the sustainable release of these macronutrients, which resulted in better biometric parameters and crop yield.

The effects of bacterial inoculation were investigated in both the field and pot. Wheat, being the staple crop in Northwest India, is being grown in stressed soil affected by salinity and water stress. The macro- and micronutrient availability in rhizospheric soil can be significantly increased by applying microbial inoculants [37,38]. In the soil ecosystem, microorganisms employ several mechanisms, including

acidolysis, production of organic acids, which lower the pH of the surroundings to mineralize/solubilize mineral nutrients, and transform them into forms that may be used by plants [39,40]. Our findings are in line with this fact, *S. colletis* SSRP30 lowered the pH in Pikovskaya's and Aleksandrov's broth to release the bound mineral in the broth, thus improving the NPK uptake in wheat crops. Similar reports were also presented for various strains of *Siccibacter* sp. having the capacity to solubilize P and K. Furthermore, growth hormones such as IAA and ACC deaminase are crucial plant hormones that increase plant biomass and play a pivotal role in exerting tolerance toward various environmental conditions. Extracellular polysaccharides produced by bacterial inoculants can assist in nutrition intake by holding nutrients and energy substrates, which also provide resistance to water and temperature stress, complemented by ACC deaminase [34,35,41-45]. *S. colletis* SSRP30 enhanced the total biomass of wheat crops in both pot and field studies, reflected through improved nutrient uptake and phytohormone production and increased chlorophyll and sugar content in plants [46-48].

With respect to wheat plants supplemented with RDF, 50% RDF, and without chemical fertilizer under net house conditions, *S. colletis* SSRP30 significantly enhanced height, wet and dry mass, yield and other yield-associated traits, grain yield, straw yield, biological yield, and the harvest index in the wheat crop. Compared with those in plants supplied with RDF, 50% lower doses of RDF, and without chemical fertilizer, the values in RDFs inoculated with bacterial inoculum plants were significantly greater, followed by those in RDFs without inoculum, 50% lower doses of RDF, and no chemical fertilizer with inoculum. This may be due to the fact that plants do not use all the nutrients applied through chemical fertilizers. A significant amount gets bound to other components of soil, reducing its availability and requiring extra energy to extract and use the same [49]. When bioinoculants such as *S. colletis* SSRP30 are applied to the field, they aid the plants in nutrient acquisition through the mechanisms discussed above. The lowest values were recorded for the absolute control without the inoculant. Plant growth and development in pot and field experiments are significantly enhanced by the application of PGPR [46,50-53].

Among the different treatments, the highest NPK content was recorded in the grain and straw of the plants inoculated with the bacterial inoculum and RDF compared to that in the other treatments. These findings are consistent with earlier research showing that PGPR inoculation of plants increased the amount of NPKs (macronutrients) in wheat straw and grain [54-56].

Based on the findings presented in this study as well as the findings of earlier research, *S. colletis* can be a potential candidate for *in vivo* application as a bioinoculant with or without combinations of insoluble P and K. Thus, *S. colletis* SSRP30 can improve plant growth and increase yield by mobilizing unavailable P and K existing in the soil and increasing plant uptake in fields.

5. CONCLUSION

Based on the findings presented in this study as well as the findings of earlier research, *S. colletis* can be a potential candidate for in vivo application as a bioinoculant with or without combinations of insoluble P and K. The results revealed that the application of *S. colletis* SSRP30 significantly enhanced yield (up to 18.31%) compared to the control (50% P and K) and reduced the doses of chemical fertilizer by up to 50%. Thus, *S. colletis* SSRP30 can be an appropriate candidate for improving plant growth and yield by mobilizing unavailable P and K existing in the soil under such unfavorable conditions.

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7. AUTHORS' CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agree to be accountable for all aspects of the work. All the authors are eligible to be an author as per the international committee of medical journal editors (ICMJE) requirements/guidelines.

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The authors report no financial or any other conflicts of interest in this work.

10. ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

11. DATA AVAILABILITY

All the data is available with the authors and shall be provided upon request.

12. USE OF ARTIFICIAL INTELLIGENCE (AI)-ASSISTED TECHNOLOGY

The authors confirm that there was no use of artificial intelligence (AI)-assisted technology for assisting in the writing or editing of the manuscript and no images were manipulated using AI.

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