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Chapter 7

The Role of Soil Beneficial Bacteria in Wheat Production: A Review

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Abstract

Free-living plant growth-promoting rhizobacteria (PGPR) have favourable effect on plant growth, tolerance against stresses and are considered as a promising alternative to inorganic fertilizer for promoting plant growth, yield and quality. PGPR colonize at the plant root, increase germination rates, promote root growth, yield, leaf area, chlorophyll content, nitrogen content, protein content, tolerance to drought, shoot and root weight, and delayed leaf senescence. Several important bacterial characteristics, such as biological nitrogen fixation, solubilization of inorganic phosphate and mineralization of organic phosphate, nutrient uptake, 1-aminocydopropane-1-carboxylic acid (ACC) deaminase activity and production of siderophores and phytohormones, can be assessed as plant growth promotion traits. By efficient use, PGPR is expected to contribute to agronomic efficiency, chiefly by decreasing costs and environmental pollution, by eliminating harmful chemicals. This review discusses various bacteria acting as PGPR, their genetic diversity, screening strategies, working principles, applications for wheat and future aspects in terms of efficiency, mechanisms and the desirable properties. The elucidation of the diverse mechanisms will enable microorganisms developing agriculture further.

Keywords: PGPR, wheat, abiotic stress, enzymes, nitrogen fixation

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1. Introduction

Wheat (*Triticum aestivum* L.) is one of the three major cereals (together with maize and rice), major source of energy, renewable resource for food, feed and industrial raw material, protein and fibre source in human diet, staple food crop for more than one-third of the world population [1], grown both as a spring and winter crop.

Plant growth-promoting bacteria (PGPR), typically colonizing at the rhizosphere, is known to increase the yield and help alleviating the effects of biotic or abiotic stresses [2]. The practice of PGPRs is promising in reducing the use of chemical fertilisers, at the same time maintaining yields at commercially viable levels and/or maintaining grain protein content [3]. As such, PGPR contributes to the improvement of both local and global environments, reducing dependence on non-renewable resources while still being economically competitive (both price and quality aspect) [4–6].

Several beneficial free-living rhizobacteria have been termed as PGPR, including, but not limited to, *Acinetobacter, Acetobacter, Alcaligenes, Arthrobacter, Azotobacter, Azospirillum, Bacillus, Burkholderia, Beijerinckia, Enterobacter, Flavobacterium, Methylobacterium, Pseudomonas, Rhizobium, Paenibacillus* and *Pantoea* [7–10]. These bacteria enhance growth through numerous mechanisms [2, 11–15]. A short list of mechanisms cover:

- The biological nitrogen fixation (BNF) and phosphate solubilization
- Secretion of hormones, for example, auxins, indole acetic acid (IAA), cytokinins, gibberellins and ethylene
- Facilitating the uptake of essential nutrients (N, P, Fe, Zn, etc.) from the atmospheric air and soil
- Zinc and iron solubilization and organic matter mineralization
- Secretion of certain volatiles and lowering of plant ethylene level
- Induction of systemic resistance
- Production of 1-aminocyclopropane-1-carboxylate deaminase (ACC)
- Quorum sensing (QS) signal interference and inhibition of biofilm formation
- Promoting beneficial plant-microbe symbioses
- Exhibiting antifungal activity, exhibition of antagonistic activity against phytopathogenic microorganisms by producing siderophores, b-1,3-glucanase, chitinases and antibiotics
- Interference with pathogen toxin production.

A non-exhaustive list of Plant Growth Promoting Rhizobacteria (PGPR)s used to alleviate various stresses is given in **Table 1**, and the various other uses of these bacteria are listed in **Table 2**. Two important mechanisms employed by PGPR are the production of different phytohormones,

Stress type	Bacterial inoculate	Properties of the crop	Reference
Drought/water	*Azospirillum brasilense* Sp245	Wheat, growth rate of coleoptiles	[132]
Drought	*Azospirillum brasilense* INTA Az-39 wheat roots	Wheat (*T. aestivum*)	[133]
Drought	*Azospirillum lipoferum*	Wheat (*T. aestivum* L.)	[134]
Drought	*Burkholderia phytofirmans*	Wheat (*T. aestivum*) Grain yield, photosynthetic rate, water use efficiency, chlorophyll content	[135]
Drought	*Bacillus safensis, Ochrobactrum pseudogregnonense*	Wheat (*T. aestivum*)	[137]
Heavy metal-stressed	*Bacillus sp*	Wheat (*T. aestivum*) Indole-3-acetic acid Antioxidant defence system SOD shoots and roots Shoot POD and CAT	[198]
Heavy metal	*Bacillus thuringiensis, Azotobacter chroococcum, Paenibacillus ehimensis, Pseudomonas pseudoalcaligenes*	Higher heavy metal resistance Siderophore,, indole acetic acid, HCN, P solubilization	[151]
Osmotic stress	*Azospirillum*	Wheat (*T. aestivum*)	[199]
Osmotic stress	*Azospirillum brasilense* sp. 245	Wheat (*T. aestivum*)	[200]
Cold	*Pseudomonas* spp.	IAA, P solubilization, rhamnolipids, siderophores	[201]
Cold	*Bacillus megaterium* M3, *Bacillus subtilis* OSU142, *Azospirillum brasilense* Sp245, *Raoultella terrigena*	Root and shoot dry weight, leaf total chlorophyll content, stomatal conductance, leaf relative water content	[171]
Temperature	*Bacillus amyloliquefaciens* and *Azospirillum brasilense*	Wheat (*T. aestivum*)	[202]
Heat stress	*Pseudomonas putida* AKMP7	Wheat (*Triticum* spp)	[98]
Temperature	*Pseudomonas fluorescens, Pantoea agglomerans, Mycobacterium* sp	Wheat (*T. aestivum*)	[203]
Salinity	*Azospirillum*	Wheat (*T. aestivum*)	[62]
Salinity	*Pseudomonas putida, Pseudomonas extremorientalis, Pseudomonas chlororaphis* and *Pseudomonas aurantiaca.*	Wheat (*T. aestivum* cv. Turon) wheat root tip coloniser, tolerated salt	[125]
Salinity	*Pseudomonas fluorescens* 153, 169, *Pseudomonas putida* 108	Wheat (Triticum aestivum) grain yield, 1000 grain weight, grain yield	[143]
Salinity	*Pseudomonas putida* N21, *Pseudomonas aeruginosa* N39 and *Serratia proteamaculans* M35	Wheat (*Triticum aestivum* L.)	[142]
Salinity	*Azospirillum* sp	Durum wheat (*Triticum durum*)	[128]

Stress type	Bacterial inoculate	Properties of the crop	Reference
Salinity	*Pseudomonas putida, Enterobacter cloacae, Serratia ficaria*, and *Pseudomonas fluorescens*	Wheat	[204]
	Bacillus, Burkholderia, Enterobacter, Microbacterium, Paenibacillus	Wheat (*T. aestivum*)	[46]
Salinity	*Bacillus pumilus, Pseudomonas mendocina, Arthrobacter* sp., *Halomonas* sp., and *Nitrinicola lacisaponensis*	P solubilization, indole acetic acid (IAA), siderophore, ammonia,proline accumulation, salt tolerance, choline oxidase activity	[140]
	Streptomyces sp	Wheat (*T. aestivum*)	[85]
Salinity	*B. subtilis, Arthrobacter* sp.	Wheat (*T. aestivum*)	[97]
	Azospirillum sp.	Wheat (*T. aestivum*)	[95]
Salinity	*Pseudomonas putida, Enterobacter cloacae, Serratia ficaria* and *P. fluorescens*	Wheat (*T. aestivum*) Germination rate percentage and index and improved nutrient status	[205]
Salinity	*Hallobacillus* sp. SL3 and *Bacillus halodenitrificans* PU62	Root length, root elongation, dry weight	[1]
Salinity	*Enterobacter asburiae, Moraxella pluranimalium, Pseudomonas stutzeri*	Number of tillers, grain weight, growth and yield	[138]

Table 1. PGPB-mediated IST against abiotic stress.

PGPR	Source	Plant growth regulation	Results of addition of bacteria to plants	References
Azospirillum sp.	Wheat rhizospheric	N2 fixation	Grain yield, dry matter, N content	[32]
Azospirillum brasilense	Mutant	Indole-3-acetic acid (IAA)	Number and length of lateral roots, distribution of root hairs.	[206]
Cyanobacteria	Rhizospheric	N2 fixation	Root dry weight, N content root and hoot	[207]
Azorhizobium caulinodans	Wheat	N2 fixation	Dry weight, nitrogen content	[192]
Azotobacter chroococcum	Wheat Rhizospheric	P solubilization, N2 fixation, IAA	Seed emergence radicle and plumule length	[114]
Azotobacter sp. *Azotobacter chroococcum*	Wheat Rhizospheric	N2 fixation	Growth	[73]
Paenibacillus polymyxa	Wheat	Cytokinin, N2 fixation	Plant growth	[208]
Azospirillum brasilense Sp7	Digitaria decumbens	Lectins, N_2 fixation	Activities of a-glucosidase, b-glucosidase and b-galactosidase in wheat-seedling	[209]
Azospirillum brasilense 75, 80 and Sp245	Non-sterilised and surface-sterilised wheat roots	N2 fixation	Root-hair deformation colonization	[99]

PGPR	Source	Plant growth regulation	Results of addition of bacteria to plants	References
Azospirillium brasilense	Wheat rhizospheric	N2 fixation	Plant growth, N accumulation and content, biomass, grain yield and protein concentration	[164]
Klebsiella pneumoniae 342	Maize	N2 fixation	Dry weight of roots and shoots, total N per plant colonized the interior of wheat roots	[26]
Pseudomonas denitrificans Pseudomonas rathonis		Auxin	Plant growth	[210]
Bacillus simplex BS BNM-10, *Bacillus firmus* BF BNM-4	Wheat roots,		Biomass number of ears nitrogen accumulation, N content	[172]
Azotobacter chroococcum Pantoea agglomerans	Geographically and climatically diverse locations	Gibberellic acid (GA), IAA	Increase in number root hairs, thickening of roots, root and shoot biomass	[11]
Pseudomonas spp	Rhizosphere of wheat	P solubilization, siderophore Indole acetic acid ACC deaminase, diacetyl-phloroglucinol	Protein content, yield and grain quality	[162]
Bacillus RC01, *Bacillus* RC03	Rhizosphere of wheat	P solubilization, N_2 fixation	Root and shoot weight, total biomass	[111]
Azotobacter chroococcum	Various sources	N_2 fixation	Grain and straw yield, N content in grain and straw	[211]
Rhizobium leguminismarum Thal-8/ SK8), *Pseudomonas* sp. 54RB	Rice	N_2 fixation P solubilization	Root and shoot weight, plant height, spike length, grain yield, seed P content, leaf protein and sugar content	[185]
Pseudomonas putida, P. extremorientalis, P. chlororaphis, P. aurantiaca	Rhizosphere of wheat grown in saline soil	Hydrogen cyanide (HCN), IAA, ACC deaminase, protease, cellulases competitive colonisers, tolerated salt	Shoot and root length, shoot, root and dry matter of wheat	[125]
Acinetobacter calcoaceticus	Rhizospheres of wheat.	P solubilization, siderophore IAA	Wheat growth, increase in the rate of germination, in the root length and dry weight	[106]
Azospirillum brasilense		N_2 fixation	uptake of several macro and micronutrients	[5]
Acinetobacter calcoaceticus, A. baumannii, A. lwoffii		N_2 fixation, siderophores, P solubilization	Root growth Root length	[45]
Bacillus simplex KBS1F-3, *Bacillus megaterium* NAS7-L, *Bacillus cereus* KFP9-F, *Paenibacillus alvei* NAS6G-6	Grass	IAA, siderophores P solubilization	Shoot and root Weight colonisation	[212]

PGPR	Source	Plant growth regulation	Results of addition of bacteria to plants	References
Pseudomonas sp.	Wheat	P solubilization, ACC deaminase, siderophores, IAA	Increased soil enzyme activities, total productivity, and nutrient uptake, nutrient assimilation	[102]
Pseudomonas jessenii R62; *Pseudomonas synxantha* R81 and arbuscular *mycorrhizal* fungi (AMF)	Wheat roots	P solubilization, IAA, siderophores, ACC deaminase, diacetyl-phloroglucinol	Grain yield Protein and mineral nutrient concentration (P, K, Cu, Fe, Zn, Mn) alkaline and acid phosphatase, urease, dehydrogenase.	[163]
Pseudomonas putida AKMP7	sorghum	Phytohormones(IAA, GA), HCN, ammonia, Siderophore, P-solubilization	Increased root, shoot length, dry biomass, chlorophyll content	[98]
Bacillus sp. (AW1), *Providencia* sp. (AW5), *Brevundimonas diminuta* (AW7)	Rhizosphere of wheat	P-solubilization, N_2 fixation, ACC deaminase siderophore, ammonia, HCN	Seedling length, germination, plant height, panicle weight, root weight	[40]
Pseudomonas fluorescens 153 and 169, *P. putida* 4 and 108		ACC deaminase, IAA-like products, P solubilization	Height, tillers, number of grains/spike, garain and straw yield, N, P and K uptake	[54]
Pseudomonas lurida	Radish	P solubilization IAA, HCN, siderophores	Growth and nutrient uptake parameters	[64]
Providencia sp. PW5	Wheat rhizosphere	Ammonia siderophore, HCN, IAA, P solubilization Zn solubilization	N uptake in wheat grain. protein content grain Fe, Zn, Mn, and Cu content	[161]
Pseudomonas fluorescens MKB37	Barley	Siderophore ACC deaminase. Protease phytate	Grain number, weight and yield	[23]
Azospirillum sp., Azotobacter sp. *Bacillus megaterium*	Wheat	N_2 fixation, P solubilization	Plant height, number spikes, grain yield, protein content	[213]
Azospirillum brasilense	Wheat	N_2 fixation	Agronomic performance and yield of wheat	[35]
P. fluorescens and *Serratia* sp.	Rubus and wheat	P solubilization	Shoot length, root and shoot dry weight, P uptake	[214]
Hallobacillus sp. SL3, *Bacillus halodenitrificans* PU62	Naturally saline habitats	ACC deaminase, IAA, HCN, siderophores, P solubilization,	Seed germination, root length, root elongation, dry weight root biomass	[1]
A. chroococcum (W5), *Mesorhizobium ciceri* (F 75), *P.striata* (P27), *S.marcescens* (L11) *A.torulosa*		N_2 fixation P solubilization,	Nutrient status of soil and plants, plant biomass, N and P uptake	[177]

PGPR	Source	Plant growth regulation	Results of addition of bacteria to plants	References
Bacillus OSU-142, *Bacillus* M3, *A. brasilense* sp. 245, *B. megaterium* RC07, *P. polymyxa* RC05, *B. licheniformis* RC08, *R. terrigena, B. cepacia* FS Tur		N_2 fixation P solubilization	Grain and straw N content, root and shoot weight. grain and total biomass yield, protein content, grain weight per spike	[3]
Bacillus spp.	Rhizospheres of wheat and tomato	IAA, lipase, protease, siderophore, P solubilization salt tolerant	Germination, root length, root weight, panicle weight	[52]
B. subtilis IB-22 *B. subtilis* IB-21		Zeatin type cytokinins	Shoot concentrations of zeatin, total chlorophyll and nitrogen contents of wheat leaves	[90]
Streptomyces spp.	Wheat roots	P solubilization, phytase, chitinase, IAA, siderophore	Growth, biomass, Fe, Mn and P content antifungal activity	[43]
P. brassicacearum subsp. *brassicacearum* RZ310 *Pseudomonas* sp. PO283, *Pseudomonas* sp. PO366	Rhizosphere of wheat	IAA, ACC deaminase	Both coleoptiles and root elongation, root length, wheat seedling growth, growth and biomass of Wheat coleoptiles	[215]
S.liquefaciens, S. marcescens, B. thuringiensis	Wheat rhizosphere	Zn solubilizing	Enhance grain yield and Zn content of wheat	[160]
Bacillus sp., *Pseudomonas*, sp., *Arthrobacter* sp.	Wheat rhizosphere	P solubilization	Plant biomass P, K, Mg, Zn and Mn contents at harvest	[216]

Table 2. Examples of plant growth-promoting substances released by some commonly employed PGPR.

including auxins, cytokinins and gibberellins, and the synthesis of several enzymes, such as phosphatase and catalase, modulating plant growth and development as well as strengthening their immune system [16, 17]. In a review, Palacios et al. compiled many molecules facilitating interactions of PGPB with plants [18]. The list includes plant hormones, hydrolytic enzymes, antibiotics, flavonoids, other signal molecules, toxic molecules, siderophores, exopolysaccharide, volatiles, polyamines, lectins and vitamins. The PGPR efficiency, in turn, depends upon a number of factors like soil mineral content, type of crop and its genotype, specific PGPR strain and its combination with the plant, competition with indigenous strains, environmental conditions and the growth parameters evaluated, as illustrated in greenhouse and field trials [3] and other studies [19–22].

Despite the promising features from agronomic efficiency and crop yield perspective, the key bottleneck for the commercial use of PGPRs is their varying performance under field conditions: the results obtained in a field are not always similar to those of laboratory [23], which calls for immediate further research on the agricultural use of these PGPRs.

2. Mechanisms of plant growth promotion

2.1. Biological nitrogen fixation

PGPR improve plant growth by multiple mechanisms. A well-established mechanism is the biological nitrogen fixation (BNF), as described in extensive literature available on diazotrophic association in wheat and subsequent addition of nitrogen to the ecosystem [24], contributing to the total N_2 requirement of wheat [25–27]. Nitrogen fixation is considered to be a direct plant growth-promoting trait and the nitrogen-fixing rhizobacteria provide an alternative source to inorganic nitrogen fertilizers.

Azospirillum is a kind of nitrogen-fixing bacterium that lives in close association with plants in the rhizosphere. Its beneficial effects on wheat yields in both greenhouse and field conditions have been reported [28, 29]. Balandreau found that *Azosprillum lipoferum* inoculation increased yield around 1.8 t/ha and wheat grain by up to 30% [30, 31]; Okon and Labandera-Gonzalez by inoculation with *Azospirillum brasilense* [31]. In an earlier study, Boddey et al. were unable to observe fixed N in wheat from similar organisms [32]. Further, Ruppel and Merbach investigated the dinitrogen-fixing ability strain of *Pantoea agglomerans* and *Azospirillum* spp. and in hydroponic experiments with wheat found that bacterial strain inoculation affected plant growth, by nitrogen uptake and the amount of biologically fixed dinitrogen. In this sense, when *Azospirillum* brasilense is inoculated using seed inoculation, it increases the productivity of wheat [33–35]. *P. agglomerans*, as a diazotroph, is able to fix molecular N_2 with wheat [36]. Ruppel et al. reported *P. agglomerans* to be superior strain for winter wheat, reporting a grain yield increase for different wheat cultivars ([37], also in Ref. [38]). Moreover, a nitrogen-fixing *P. agglomerans* Lma2 was isolated from wheat rhizosphere, it was found to have the ability to produce IAA, siderophores and solubilize P, and growth performance of plant was significantly better in the presence of salt [39].

Acinetobacter strains also possessed BNF properties, siderophore and ammonia production as well as mineral solubilization. Rana et al. reported a positive correlation of BNF potential of *Providencia* spp. AW4 and *Brevundimonas diminuta* AW7 strains with panicle weight and plant height in wheat, indicating the enhancing plant growth role of BNF [40].

2.2. Phosphate solubilization and mineralization

Soil stores several structures and forms of phosphate, both organic and inorganic. Phosphorus plays a key role in photosynthesis, respiration, root development, signal transduction, energy transfer, macromolecular biosynthesis and the resistance ability of plants to diseases and adverse conditions. However, majority of soil phosphorus is insoluble that is not available to plants. The secondary significant contributing factor to promoted growth is the availability of phosphorous in the rhizospheric region, as a result of phosphate solubilization by the PGPR [41].

PGPRs serve as phosphate (and zinc) solubilizer (PSB). This is due to the decreased pH of the medium, indicating the possible involvement of organic acids such as gluconic acid. Plant growth promotion can be achieved through solubilization of inorganic phosphates by these

organic acids. de Werra et al. showed that this happens with not only gluconate but also malate [42, 43]. These results were consistent with earlier report on the P and Zn solubilizing properties of *Acinetobacter* sp. [44]. Nearly all the *Acinetobacter* species isolated from rhizosphere soil of the three wheat varieties in the present study were efficient phosphate and zinc solubilizers and produced iron chelating siderophores [45]. Phosphate solubilizing bacteria (PSB) belong largely to the genera pseudomonads, bacilli and rhizobia [46].

Phosphorus-solubilizing *Bacillus* strains have been reported to increase the plant biomass and yield of wheat as well as uptake of nutrients [47]. Similar results have been reported by Afzal et al. when a combination of nitrogen-fixing Rhizobium leguminosarum with P-solubilizing *Pseudomonas* sp. strain 54RB have been used [48]. Similarly, several *Pseudomonas* spp. strains have been tested in the field for their efficacy to increase growth and yield of wheat [49]. Four P solubilizer (*Arthrobacter* WP-2, *Bacillus* MP5, *Rhodococcus* M28 and *Serratia* 5D) and one phytohormone producer (*Azospirillum* WS1) strains tested as single-strain inocula resulted in improved growth of wheat plants [50]. Some *Bacillus* species can improve phosphate solubilization of the soil [51, 52]. On the other hand, Baig et al. reported a positive correlation between P-concentration in soil, P-solubilization activity of the Bacillus strains and P uptake by wheat plants [53]. Along the same line, improvement of growth and yield of wheat was observed and reported upon inoculation with P-solubilizing microorganisms. Both PGPR (*Bacillus* and *Pseudomonas* spp.) are similar in effectively solubilizing phosphate. A short list of phosphate-solubilizing bacteria (PSB) includes *P. fluorescens* 153, *P. fluorescens* 169, *P. putida* 4 and *P. putida* 108 together with their capability in natural soil ecosystem to synthesize ACC deaminase and IAA-like products [54].

Combined application of PSB with conventional fertilizer (50% PSB, 25 kg/ha P_2O_5) improves plant growth. Similarly, a combination of PGPRs are more effective when compared with isolated applications as reported by Hassan et al. for wheat crops and by Baig et al. for wheat yield and P uptake [53, 55].

2.2.1. Mineralization

Mineralization of most organic phosphorous compounds is carried out by means of phosphatase enzymes. The conversion of insoluble inorganic P to a form accessible by plants is achieved by PSB via organic acids, chelation and exchange reactions [56]. However, organic P forms, particularly phytates, are predominant in most soils (10–50% of total P) and must be mineralized by phytases (myo-inositol hexakisphosphate phosphohydrolases) to be available P for plants [57, 58]. Previous research has shown that *Bacillus* sp., *Providencia* sp., *Brevundimonas* and *Alcaligenes* were recorded positive for P solubilization [40, 59].

Singh et al. reported that phytase-producing bacteria from Himalayan soils showed ability to solubilize inorganic phosphate, producing phytase, siderophores, ammonia and IAA and increased availability of P, IAA and ammonia leading to increased plant growth [57]. The role of PGPR in production of phosphataes, β-gluconase, dehydroginase, antibiotic, solubilization of phosphates and other nutrients, stabilization of soil aggregates, improved soil structure and organic matter contents has been recognized.

2.3. Production of plant hormones and other beneficial plant metabolite

There are five groups of plant hormones of well-known PGRs, namely auxins, gibberellins, cytokinins, ethylene and abscisic acid [60]. Direct plant growth promotion includes symbiotic and non-symbiotic PGPR, which functions through production of these plant hormones [11, 61–63]. Much attention has been given on the role of phytohormone auxin. Production of indole-3-ethanol or indole-3-acetic acid (IAA), the compounds belonging to auxins, which is known to stimulate in cell elongation, division and differentiation responses in plants, has been reported for several bacterial genera [12, 17, 64]. PGPR promote root growth by increasing root surface area, which, in turn, promotes nutrient uptake, thereby indirectly stimulating plant growth positively [52, 65]. Khalid et al. reported a correlation between *in vitro* auxin production and increase in early growth parameters of inoculated wheat seeds [66].

Inoculation with *A. brasilense* Cd and the application of pure IAA to the roots both increased root length, number of lateral roots and number of root hairs in wheat as observed by earlier workers [67, 68]. IAA-producing *Azospirillum* sp. also promoted alterations in the growth and development of wheat (*Triticum aestivum* L.) plants [69–72]. Bacteria of the *Azotobacter* genus synthesize auxins, cytokinins and GA-like substances, and these growth materials are the primary substances controlling the enhanced growth [73]. These hormonal substances, which originate from the rhizosphere or root surface, affect the growth of the closely associated higher plants. The highest concentration of IAA is produced by bacterial strain *P. fluorescens* and *Kocuria* varians [74]. Specifically for wheat, the positive effect of PGPR via IAA has been reported [75–78].

When applied in optimum concentrations, bacterial indole-3-acetic acid (IAA), synthesized by gram-positive and -negative, photosynthetic, methylotrophic and cyanobacteria, is reported to stimulate root hair formation, at the same time increasing the length and the number of primary and lateral roots [66, 72, 79]. IAA synthesis by these bacteria is reported to be affected by tryptophan, vitamins, salt and oxygen levels, as well as pH, temperature, carbon and nitrogen source. For example, IAA from *Azospirillum brasilense* Sp245 stimulates early plant development and increases significantly the plants and roots yield (in dry weight) and the N-uptake efficiency of wheat [71, 80]. The ability to synthesize ABA, particularly under stressful conditions, for example, salinity, and to affect the ABA level in plants was detected in PGPB from the genera *Azospirillum, Bacillus, Pseudomonas, Brevibacterium* and *Lysinibacillus* [15, 81, 82]. Both plants and bacteria can be synthesized via several pathways, including the indole-3-pyruvic acid (IPA), indole-3-acetamide (IAM) and indole-3-acetonitrile (IAN) pathways, which are often regulated by tryptophan, carbon and nitrogen availability, a reduction in growth rate and abiotic factors such as temperature, pH and oxygen [79].

As a PGPR application to wheat seedlings, Sachdev et al. reported that IAA producing *Klebsiella* strains significantly increased the root length and shoot height, when compared with the control, in pot experiments [83, 84]. Similarly, Khalid et al. reported up to 28% higher grain yields in wheat grown in field as a result of seed inoculation in peats with high auxin-producing rhizobacteria [66]. The capability of auxin synthesis detected in many bacterial strains from the genera *Azospirillium, Pseudomonas, Bacillus*, etc., is thought to underlie the activation of plant root growth by these microorganisms [81]. Sadeghi et al. demonstrated

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that a *Streptomyces* isolate increased plant growth in wheat and produced indole acetic acid and auxin in presence of salt [85]. Phytohormone-producing *Bacillus* sp. and *B. subtilis* have potential at field level to improve wheat productivity and may be helpful in formulation of an effective biofertilizer for wheat [52, 79, 86–89]. A complete understanding of the IAA system can further mediate the efficient use of these PGPRs for biofertilizer.

Cytokinins can be produced by representative strains of *Bacillus, Rhizobium, Arthrobacter, Azotobacter, Azospirillium* and *Pseudomonas*. The plants inoculated with cytokinin-producing bacteria *B. subtilis* showed the increased chlorophyll content and cytokinin accumulation, which led to the increase in weight of shoots and roots [90, 91]. On the other hand, treatment of plant with a substance obtained from cytokinin-producing microorganisms, typically colonizing in wheat roots [92, 93], increased chlorophyll content in leaf; in this case, the level of chlorophyll was comparable to that observed in the plants treated with a synthetic cytokinin benzyladenine. Cytokinins can promote stomatal opening, stimulate shoot growth and decrease root growth.

2.3.1. Accumulation of osmolytes

Proline is a known osmoprotectant, promoting the protection of the plant from drought, salt and other stresses [94]. Alternative to proline accumulation, another defence strategy is to increase total soluble sugar level in plants under salinity stress. PGPRs have been demonstrated to enhance wheat stress tolerance via osmolyte accumulation as reported in Refs. [95–97]. Ali et al. used *P. putida* AKMP7 resulting in significant increase in proline levels in heat-stressed wheat plants [98].

Yegorenkova et al. suggested that lectin-carbohydrate interactions are involved in the initial stages of bacterial-plant root attachment [99]. Additionally, PGPR producing extracellular polymeric substance are reported to enhance greatly the soil volume macropores and the rhizosphere aggregation of soil, which results in increased water and fertiliser availability to plants [46].

2.4. Siderophore and exopolysaccharide production by PGPR

With its unique physico-chemical properties, iron (Fe) has a key role in plant growth, taking part in several metabolic pathways including TCA cycle, nitrogen fixation, respiration and ETC, oxidative phosphorylation and photosynthesis, biosynthetic regulation (chlorophyll, toxin, vitamins, antibiotic, cytochrome and pigment) and as cofactor for numerous enzymes [100]. Following this, iron deficiency (typically caused by low iron bioavailability) is frequently seen at elevated pH, alkali soils in dry regions, as well as in case of excessive fertilizer and pesticides application.

Siderophores are small iron carriers, chemically high-affinity iron chelating compounds secreted by PGPRs and are among the strongest soluble Fe^{3+} binding agents known. Comprehensive information on the role of siderophores in increasing iron oxide solubility and promoting dissolution in soils requires the consideration of the rates of various processes such as siderophore exudation, the uptake, and the degradation rates [101]. In BNF, siderophores are expected to play significant role, since in its very essence, nitrogenase requires Fe [102], also supported by a high correlation between N and Fe uptake.

Siderophore productions promote the crop growth, or protect the plant against pathogens. Produced by microorganisms, these are found in soil solutions and influence Fe nutrition of plants [103]. The role of siderophores has been reported as signalling molecules and as such, their use points to avenues for novel agricultural applications [54].

The wheat seed inoculation was tested for their effect on wheat in terms of healthier germination and productivity. The organisms used were siderophoregenic pyoverdin-producing *Pseudomonas putida* and *Pseudomonas aeruginosa* strains from two diverse habitats. Inoculation with siderophoregenic PGPR increased percentage germination, shoot height, shoot and root length, weight of spikelets, chlorophyll content, grain yield and iron content [100, 104, 105]. Inoculated wheat plants showed increase in total iron uptake and physiologically available iron contents. *Acinetobacter calcoaceticus* obtained from wheat rhizosphere produces catechol type of siderophores during exponential phase, which is influenced by iron content of medium [106]. Ca, Cd and Mg ions and succinic acid stimulated the synthesis of the siderophore examined, whereas Zn and Pb ions partially decreased its level.

Some PGPR strains may also protect plants from salt and drought stress by producing exopolysaccharides (EPS), binding, in turn, Na+ or by biofilm formation [107]. Resultingly, reduced Na+ results in lower Na+ uptake and high K+/Na+ ratio, promoting survival in salt-stressed conditions [107, 108]. Another example is the wheat seedling inoculation by EPS producing strain of *Pantoea agglomerans* (NAS206) isolated from the wheat rhizosphere, growing in a Moroccan vertisol. It had a positive effect on aggregation and stabilization of root-adhering soil, by increased mean aggregate diameter and macroporosity [109].

2.5. PGPR and plant nutrient uptake

Seed inoculation with the bacterium has been found to improve the growth and nutrient uptake of wheat seedlings via promotion of the plant growth and increased root surface area or the general root architecture [110]. With enlarged root hairs, nutrient uptake is promoted [21, 71, 77, 111].

The PGPR effects also increase N and P uptake in field trials [112], presumably, by stimulating greater plant root growth. Both *A. chroococcum* and *P. agglomerans* were found to increase plant growth, plant dry matter, as well as N and P uptake [25, 113]. *Azospirillum*-inoculated plants under drought conditions had increased Mg, K and Ca contents compared to non-inoculated plants [62, 114–117]. The increase in nutrient accumulation/uptake due to biofertilizers/PGPR was previously reported in wheat [118–120]. Sharma et al. reported that the majority of 13 tested *Pseudomonas* spp. strains increased the macro (N, P, K and S) and micronutrients uptake (Cu, Fe, Zn and Mn) in wheat [102, 121].

Inoculation of efficient plant-growth-promoting actinobacterial *Streptomyces* species significantly improved the Fe, Mn and P content of wheat plants when compared with an uninoculated control [43, 105]. Yasin et al. investigated the effects of selenate fertilization and bacterial inoculation on Se uptake and plant growth [122]. They found that *Bacillus pichinotyi* enhanced wheat growth, dry weight, shoot length and spike length, Se and Fe concentration in wheat kernels and stems. Selenium (Se) is an essential trace element for humans [123], and

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they reported that inoculation with rhizospheric microorganisms significantly enhanced wheat Se content.

2.6. Alleviation of abiotic stress in wheat by PGPR

Abiotic stress is the major cause of decreasing crop productivity worldwide. The application of the combination of PGPR and mycorrhizal fungi alleviates the stress conditions, as reported by Nadeem et al., via the regulation of hormones, nutrition uptake and growth [124]. Similar outcomes have been reported by Cakmakci et al. for wheat and spinach plants [77]. Enzymatic activities in the leaves of these plants such as glucose-6-phosphate dehydrogenase, 6-phosphogluconate dehydrogenase, glutathione reductase and glutathione S-transferase have been observed.

Additionally, numerous studies suggested that both IAA and ACC deaminase-producing bacteria protect plants most effectively, against a wide range of different stresses [125]. Notable reports among those are *Azospirillum* strains helping to cope with salt stress [126–128] and *Bacillus* and *Azospirillum* leading to improve heat tolerance in wheat [129].

2.6.1. Drought

Drought stress, exhibited as limited water supply, usually causes a severe loss in plant yield, where the combination of severity and duration are critical factors for plant survival [130]. The application of PGPR can counteract damaging effects of moisture stress, and therefore boost crop yields. Creus et al. reported that growing *Azospirillum brasilense* Sp245-primed wheat under drought stress conditions resulted in large increase in water content and potential, and apoplastic water function in both shoots and roots compared to the non-primed plants [62].

Moreover, Pereyra et al. reported that *Azospirillum* inoculation provided a better water status in wheat seedlings under osmotic stress due to morphological modifications of the coleoptile xylem architecture [131]. *Azospirillum*-inoculated wheat seedlings subjected to osmotic stress developed significant higher coleoptiles, with higher fresh weight and better water status than non-inoculated seedlings [132]. In this regard, ABA-producing bacteria *Azospirillum* promoted resistance of *Arabidopsis*, maize and wheat plants to soil drought [81]. *Azospirillum brasilense* INTA Az-39-inoculated wheat plants under typical dry land farming conditions exhibited better growth and increased vegetative growth, shoot and root dry matter accumulation, grain number and grain yield [133]. According to Arzanesh et al. results, inoculation of wheat with *Azospirillum* spp. can alleviate drought stress on plant growth and yield through adjusting plant water characters [134].

Inoculation of wheat with *Burkholderia phytofirmans* PsJN significantly diluted the adverse effects of drought on relative water contents and CO_2 assimilation rate, thus improving the photosynthetic rate, water use efficiency and chlorophyll content over the uninoculated control [135]. In a similar study conducted on wheat under water stress environment showed that mycorrhizal inoculation enhanced the activities of antioxidant enzymes such as peroxidase and catalase compared to those in uninoculated control plants [136]. Several other studies report similar outcomes [137].

2.6.2. Salinity

Salinity decreases the yield of many crops because salt inhibits plant photosynthesis, protein synthesis and lipid metabolism. Nutrient contents decrease in the roots and shoots with increasing NaCl concentration in the growth medium. PGPR counteract osmotic stress and help plant growth. Investigations on interaction of PGPR with other microbes and their effect on the physiological response of crop plants under different soil salinity regimes are still in incipient stage.

Rhizobacteria that are residing within the rhizosphere of plants growing in saline habitats may have already been adapted to salt stress that may be a valuable resource to develop crop inoculants. Raheem and Ali isolated rhizobacteria that were producing beneficial plant growth-promoting metabolites such as IAA and ACC-deaminase activity [138]. The isolation of indigenous microorganisms from the stress-affected soils and screening on the basis of their stress tolerance and PGP traits may be useful in the rapid selection of efficient strains that could be used as bio-inoculants for stressed crops [139, 140]. For several durum cultivars, PGPR efficacy in mitigating salt stress in tetraploid wheat is salt level and bacterial strain-specific [128, 141, 142]. There are some instances of ameliorating salt-stricken cereal crops by PGPR's. Salinity stress in the wheat was alleviated by inoculations with four strains of PGPR, *Pseudomonas fluorescens* 153, 169, *Pseudomonas putida* 108 and 4 [143]. Upadhyay et al. considered the impact of PGPR inoculation on the growth and antioxidant of wheat under saline conditions [46]. In a follow-up study, Upadhyay et al. investigated the effects of two salt-tolerant PGPR (*B. subtilis* and *Arthobacter* sp.) on wheat plants under different salinity regimes and the results obtained demonstrated alleviation of the salinity stress effects on plants treated with bacteria [97]. Similar outcome has been reported by Nia et al. for *Azospirillum* strains on wheat plants [144]. Several PGPR of the genus *Pseudomonas* contain ACC-deaminase enzyme, and when inoculated into plant roots may sustain plant growth under salinity [125, 142].

2.6.3. Mitigation of cold stress in wheat by PGPR

The over-wintering ability of PGPR is fundamental when considering uses in colder climates. De Freitas and Germida reported that *Pseudomonas* species are able to over-winter in sufficient quantities on the roots of winter wheat [145]. It has also been argued that antifreeze protein activity of many bacterial species may contribute to their survival in colder climates [146–148].

The effect of inoculation with 12 psychrotolerant *Pseudomona* strains on cold alleviation and growth of wheat seedling at cold temperature was investigated in Ref. [105]. Psychrotolerant PGPR inoculation improved metabolite levels, such as chlorophyll, anthocyanin, free proline, total phenolics, starch content, physiologically available iron, proteins and amino acids that are sign of alleviation of cold stress in wheat plants.

Higher chlorophyll content in leaves of cold acclimated winter wheat over control plants was also reported [105]. Proline is a dominant amino acid that accumulates in many organisms upon exposure to environmental stress and plays multiple roles in plant adaptation to stress. Also increased proline content in wheat plant at low temperature with the bacterial inoculation is an indication to chilling tolerance [105].

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Turan et al. conducted greenhouse experiments in wheat and barley under cold stress conditions to determine the growth, freezing injury, antioxidant enzyme activity effect of four different rhizobacteria and boron [149]. The authors showed that boron+PGPR treatments have positive effect on root and shoot growth, H_2O_2, and SOD, POD and CAT antioxidant enzyme activities of wheat and barley plants under cold and control conditions. This suggests that the PGPB application can ameliorate the deleterious effects of cold stress by increasing chlorophyll content, photosynthetic activity and relative water content, altering mineral uptake, and decreasing membrane damage, increasing cold tolerance in wheat and barley.

2.6.4. Metal stress tolerance in wheat

Plant growth-promoting bacteria are able to also grow in heavy metal-contaminated environment and protect plants against heavy metals toxicity in contaminated soils [150, 151]. Hasnain and Sabri reported that upon *Pseudomonas* sp. inoculation of wheat in Pakistan, growth was stimulated, less toxic ions were taken up and increased auxin content was observed [152].

Under Cr stress conditions, Shahzadi et al. reported root length, shoot length, root dry weight and shoot dry weight, respectively, as compared to uninoculated control plants upon inoculation of wheat seeds with *Pseudomonas fluorescens* Q14 and *Bacillus thuringiensis* KAP5 [153]. In this context, ACC-deaminase producing PGPR could play vital role in improving the plant growth under metal-stress condition and they may enhance bioremediation process in Cr-contaminated environment. Similarly, Jamali et al. studied the relationship of bacterial Cr mobilization in soil with total Cr accumulation in wheat [154]. Hassan et al. reported that inoculation with PGPR decreased the deleterious effects of cadmium pollution by chelating and influencing its bioavailability and increased the wheat growth [155]. Singh et al. found that PGPR having ACC-deaminase activity were resistant against Cd, Cr, Pb and Cu toxicity, and increased the wheat and pigeon pea growth [156]. Consequently, uses of rhizospheric microorganisms are generally considered as safe, cost effective and reliable technique for elimination of heavy metals from environmental compartments [150, 157, 158]. Govindasamy et al. observed that growth-promoting ability of rhizoacteria containing ACC deaminase in wheat seedlings through modulation of stress ethylene synthesis enhanced root elongation significantly and minimized ethylene synthesis in wheat seedlings under induced cadmium stress condition [159].

2.7. Improve yield and quality of wheat

Beneficial rhizobacteria associated with cereals has increased recently and several studies clearly demonstrated the positive and beneficial effects of PGPR on growth and yield of wheat at different environment under variable ecological conditions (Turan et al., 2010).

Zn solubilizing rhizobacteria significantly influenced the growth, yield and Zn concentration of wheat grain over uninoculated control and Zn fertilizer [160, 161]. Similarly, increased nutrient concentrations in wheat due to inoculation were reported in Refs. [5, 118, 162–165]. It is pointed out by Mäder et al. that microbial inoculants have been shown to be a valid option for sustainable high quality wheat production in low-input areas, promising to improve the nutritional status and health of the rural population [163]. In a survey of 20 years of experiments, Okon

and Labandera-Gonzalez reported that 60–70% of the experiments showed yield increases due to inoculation, with statistically significant increases in yield from 5 to 30% [31].

Pseudomonas strains significantly increased grain yield of wheat [23, 49, 143, 166]. Similarly, Shaharoona et al. reported that N use efficiency increased in response to inoculation with *Pseudomonas fluorescens* at all fertilizer levels in wheat [167]. PGPR isolates significantly increased shoot and root length, shoot and root dry weight, grain weight per spike, shoot and root N content and also enhanced the N contents of inoculated wheat seedlings [168]. Barneix et al. reported that inoculation of wheat with *Bacillus simplex* and *Bacillus firmis* resulted in consistent increase in dry matter and wheat grain quality. A number of other *Bacillus* spp. isolated from wheat rhizosphere have also been investigated for their growth-promoting property in wheat having similar effects on dry weight [10, 40, 169], the latter focusing on isolating and characterizing PGPRs. Trials with rhizosphere-associated plant growth-promoting N_2-fixing and P-solubilising *Bacillus* and other species indicated yield increases in many crops such as wheat [43, 51, 170, 171]. In wheat, several rhizobacteria have been reported as improving grain yield, grain protein concentration or both [3, 135, 140, 164, 172].

3. Co-inoculation of multiple PGPRs

Inoculation with mixed different strains could be an alternative to inoculation with individual strains, likely reflecting the different mechanisms used by each strain in the consortium [173]. Combined inoculation with N_2-fixing and phosphate solubilizing bacteria were more effective than a single microorganism for providing a more balanced nutrition for plants [19, 174]. There are numerous examples in wheat whereby synergistic effects of multiple PGPRs are observed [97, 175, 176]. Among those, notable is the combined inoculation of mixtures and biofilmed bio-inoculants (*Anabaena torulosa* + *Pseudomonas striata* and/or *Anabaena torulosa* + *Azotobacter chroococcum*) were superior over single inoculation and chemical fertilizer control in term of plant growth and nutrient uptake [177]. The benefits can be on nutrient uptake, but also in root physiology as exemplified by Manjunath et al. as co-inoculation of wheat with two proteobacterial (*Providencia* sp. and *Alcaligenes* sp.) and two cyanobacterial (*Anabaena oscillarioides* and *Anabaena torulosa*) inoculants, similarly in Ref. [178, 179].

Seed bacterization with both strains, *P. fluorescens* BAM-4 and *B. cepacia* BAM-12 single or combined significantly enhanced growth and yield, but increase in bacterial population, spike length, P content of shoots and grain yield was more in co-inoculation treatment than single. The best among the bioinoculation treatments was *B. cepacia* BAM-12 + TCP and *B. cepacia* BAM-12 + *P. fluorescens* BAM-4 + TCP for P content with free and immobilized cells [180].

Several authors conducted experiments on wheat either under pot and field conditions to examine the effect of co-inoculations of PGPR on the growth and yield of wheat. Kumar et al. found that *B. megaterium, A. chlorophenolicus* and *Enterobacter* significantly increased plant height, grain yield and straw yield [181]; Baris et al. concluded that *Bacillus megaterium* M3 and Mixed (*Bacillus subtilis* 05U142, *B. megaterium* M3, *Azospirillum brasilense* Sp245) inoculation provided greater plant nutrient element concentrations than mineral fertilizer application

[182]. Similar outcomes also compared with chemically fertilized soils are reported in Refs. [53, 183–185].

Nowadays, there is a greater awareness to use biological components such as PGPR and mycorrhizal fungi as a component of integrated nutrient management strategies to obtain higher input use efficiency, to maintain the desired productivity through optimization of the benefits from all possible sources, to cope with increasing fertilizer costs and their long-term adverse effects on agricultural ecosystems such as increased nutritional imbalances, declining productivity, adverse conditions prevailing in this ecosystem, and or a combination of these factors, as reported in Refs. [113, 177]. Note that some PGPR inoculants may adversely affect mutualistic associations between plants and indigenous soil microorganisms and suggest a possible reason as to why spring wheat growth was not consistently enhanced by these *pseudomonad* PGPR [186]. Co-inoculation of *Azotobacter* and *Mycorrhiza* increased grain yield and yield components of wheat [187].

Wheat rhizobacterial community structure is highly dynamic and influenced by different factors such as wheat cultivar line ages, plant's age, growth stage, distance from the soil to the root, root exudation pattern, multiple soil properties and agronomic practises [162, 188, 189]. Roesti et al. employed a consortia formed by a PGPR *Pseudomonas* spp. and an indigenous AMF to study their effect on the bacterial community structure and wheat growth [162].

All in all, greater attention should be paid to new combinations of different types and properties organisms such as N_2-fixing and P-solubilizing bacteria for improvement of biofertilizers efficiency [19].

4. PGPR reduce chemical fertilization

Due to high cost of chemical fertilizers and negative environmental effects, the use of PGPR as biofertilizer is advantageous for development of sustainable agriculture, increasing agronomic efficiency, once the use of chemical fertilizers can be reduced or eliminated if the inoculants are efficient [6]. The use of bio-fertilizers with a good management can decrease the leaching loss of nitrate and phosphate from the agricultural land and improve the ground water quality [190]. Also, the use of PGPR with low-fertilizer rate is also an environment friendly step and would be a viable supplementary strategy for further increasing crop yields [71, 78, 191].

Trials conducted under greenhouse conditions showed that most of PGPR in the absence of any fertilizer application achieved increases in root and shoot weight [3], corresponding to nitrogen treatment at the rate of 40 and 80 kg N ha^{-1} in wheat. Furthermore, co-inoculation of N_2-fixing and P-solubilizing bacteria always gave equal or higher grain yield than conventional application of nitrogen.

Rosas et al. studied the promotion effect of *Pseudomonas aurantiaca* SR1 on maize and wheat in field treatments that included phosphorus and nitrogen fertilization [166]. Both crops, when inoculated with the SR1 strain, presented significant promoting effect in growth parameters and higher yields with lower fertilization doses than conventionally applied. Additionally,

PGPR are also important with respect to an efficient use of resources such as P and N, as illustrated by a 95% increased P use efficiency of wheat grains [163].

It could be concluded that application of PGPR with low-fertilizer rates could be a viable supplementary strategy for maximum benefits and should be employed with appropriate doses of fertilizers to get maximum benefit in terms of fertilizer savings and better growth in any yield of crops. Experiments as field trials with dry land areas, the co-inoculations of PGPR strains for wheat, maize and barley with chemical fertilizers gave improved response [3, 183, 192–197].

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