

Review

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Review

Research Progress on Rhizosphere Microbial Species of Sorghum and Their Impacts on Maximizing Final Yield

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Abstract: A large number of studies have indicated that plant community modulate the yield, improve growth and promote development of host plants, and among them rhizosphere growth-promoting bacteria play an important role in increasing crop yield. Bacteria benefit from the plant nutrients provided by the roots, but plants can benefit from their rhizobacteria as well. *Rhizobia* are considered as the most important candidate for plant growth promotion in comparison with rhizobacteria due to their endophytic nature and nitrogen fixing ability. They can also provide auxins which play a notable function in plant growth and plant-microbe interactions. *Bacillus* spp., the sporulating Gram-positive bacteria, have important roles in plant growth promotion and induction of systemic resistance. *Pseudomonas* are Gram-negative aerobic chemoheterotroph and are usually found in the environment. *Streptomyces* are important groups of soil bacteria from the actinomycetes family. Most of them are efficient rhizosphere and rhizoplane colonizers, and they can also be endophytes colonizing inner tissues of host plants. The present review aims to present the most up-to-date findings and results regarding the effects of plant growth promoting bacteria on yield of different crops, especially sorghum. Furthermore, the mechanisms of the actions of different bacteria briefly illustrated, aiming to present future needs to be addressed in sustainable crop production. Plant growth promoting rhizobacteria inoculation with different plants or treating plants with microbe-to-plant signal constituents can be an effectual technique to stimulate crop growth. They are also active in protecting crops from phytopathogens and environmental stress, plant pathogens and they have positive roles in nutrient cycling.

Keywords: *Bacillus*; *Rhizobium*; *Pseudomonas*; *Streptomyces*; growth promoting rhizobacteria

1. Introduction

Rhizobium species have been successfully utilized worldwide as a biofertilizer leading to effective establishment of nitrogen fixing symbiotic association with leguminous crops. In the *Rhizobium*-legume symbiosis, the bacterial partner differentiates into non-dividing endo-cellular symbionts. The application of *rhizobia* as biofertilizer leads to increase nutrients composition and plant water uptake and tolerance to both biotic and abiotic stresses. *Rhizobia* are gram-negative rod-shaped bacteria and they are characterized and classified by different systems. Members of the genus *Bacillus* are large, gram-positive, aerobic and sporeforming rods. They are catalase positive and *Bacillus* species occur widely in nature, being found in the soil, air and water. The Bacilli are among the most investigated rhizobacterial species, after *Pseudomonas* mostly on their bio-control activities. These bacteria are capable of increasing plant growth through production of a number of substances such as antifungal and antibiotics metabolites. Members of the *Bacillus* genus are particularly popular candidates for plant growth promoting bacteria (PGPR) because they sporulate and are easier to subject to commercial formulation. *Pseudomonas* spp. is a unique microorganism for application in bioremediation due to its flexibility and plasticity of its metabolic pathways. *Streptomyces* is the type of genus of the family *Streptomycetaceae* belonging to the order *Actinomycetales* of the class *Schizomycetes*. The bacteria belonging to this genus are mainly found in soil but are also occasionally

separated from other sources such as manures. They are widely reported to have plant diseases suppression against wide variety of plant pathogens. They are one of the most important plant growth promoting bacteria due to unique characteristics like multiplication rate, cellulases, quorum sensing controlled gene expression, antibiotics, amino acid synthesis, lipase, chitinase, phytohormones, and β -1,3-glucanase production. They have wonderful ability to control plant pathogens stem because of antibiotic production, siderophore production, competition for nutrients, volatile compound secretion and synthesis of plant growth regulators.

Sorghum (*Sorghum bicolor* (L.) Moench) is a worldwide food crop with strong drought tolerance [1–3]. It is a C4 plant with a wide range of adaptations and resistance to different negative abiotic and biotic factors [4,5]. It is also the main staple food crop in many developing countries, and is a now biofuel source in some countries with 30% grain use for ethanol production [6,7]. Plant associated microorganisms, particularly plant growth promoting rhizobacteria, are known to play an important function in promoting plant growth and also in remediating soils from organic and metal pollutants by numerous mechanisms [8–11]. Plant growth promoting bacteria has a notable role in sustainable agriculture and disease management, and it acts as potential alternatives against chemical fertilizers and provides stress tolerance in addition to rhizosphere inhabitants. There are many literature reviews dealing with the role of PGPR in mobilization, phytoremediation and phytoextraction of heavy metals from soil [12–14]. By different mechanisms such as solubilizing metal minerals, increasing root surface area for heavy metal uptake, acidifying the rhizosphere environment, and increasing the release of root exudates, these PGPR effectively increase the mobilization of heavy metals [15–17]. Inoculation of plants with strains of plant growth promoting bacteria boosts plant growth and biomass production, and promoting phytoextraction, through different mechanisms including the exudation of phytohormones, siderophores, and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase enzyme, as well as phosphate solubilization, nitrogen fixation, and antibiotic synthesis [18–20]. Plant growth promoting bacteria increase drought tolerance in plant in different ways, such as the microbial enzyme ACC synthase [21]. Microorganisms stimulate plant hormones homeostasis by generating auxin and producing 1-aminocyclopropane-1-carboxylate (ACC) deaminase to modulate the concentration of the plant stress phytohormone ethylene by decomposing its precursor ACC [22,23]. Microorganisms produce cytokinins, auxin indole-3-acetic acid (IAA), and gibberellins, which help to modify plant hormone balance [24–26]. Microorganisms decrease the plant's antioxidant system to lower the number of reactive oxygen species (ROS) [27,28]. Microorganisms contribute to improving the plant-induced systemic tolerance to drought by changing the host physiology and the metabolic procedures [29]. The production of exopolysaccharides protects against extreme conditions like desiccation, forming a protective capsule around soil aggregates and increasing permeability by improving soil aggregation and maintaining a higher water potential around the roots [30,31]. Rhizosphere engineering with PGPR for sustainable ecosystem and agriculture are nitrogen fixation; Phytohormone production such as auxins, gibberellins, cytokinins, ABS; Nutrient mobilization for P, K, Zn, Ca, Fe, etc.; abiotic stress mitigation for drought, heat and salinity; control of biotic stress for 1-aminocyclopropane-1-carboxylate (ACC)-deaminase, antibiosis, siderophores, lytic enzymes, induced systemic resistance [32]. *Pseudomonas* can synthesize enzymes which can limit the available iron by production of siderophores, kill pathogen, and modulate plant hormone levels. *Pseudomonas* also have modulated the plant growth by increasing uptake of minerals into the host plants, especially by production of cytokinin, phosphate production of IAA, modulating ethylene production in roots, and solubilizing nutrients. The principle components of rhizosphere engineering and intricate connection of these components are plant (plant breeding, cultivar selection, transgenic plants), soil (application of biochar, silicon, sewage sludge, zeolites, manure, etc.), and microbes (application of microbial inoculants) [32]. The goals are improve rhizodeposition, microbial activity, root exudates, growth and yield; improve soil structure, soil aeration, organic matter, soil buffering capacity, soil fertility, and balanced nutrients; improve nutrient availability, photosynthesis, plant growth and yield, stress, soil fertility (abiotic and biotic) tolerance, and plant immunity [32]. The goal of this review article is a survey about research

progress on rhizosphere microbial species of sorghum and their impacts on increasing yield of sorghum plants by considering sustainable agriculture.

Different Kinds of Plant Growth Promoting Bacteria

Among PGPB, bacteria belonging to *Serratia* genus are recognized to be capable to serve as phytostimulators, biocontrol, biofertilizer agents, and biopesticides with ability to suppress both fungal (e.g., *Rhizoctonia solani* and *Fusarium culmorum*), and bacterial plant pathogens (e.g., *Pectobacterium carotovorum* and *Erwinia amylovora*) [33–35]. It is a Gram-negative bacterium belonging to the family *Enterobacteriaceae* [36,37]. *Serratia* spp. Includes multiple plant growth promoting characteristics and stimulate, and colonize the growth of multiple (non-homologous, homologous) hosts, and they lead to root hair development controlled by their IAA-production and acyl homoserine lactones (AHLs) signaling procedures [38,39]. Hanaka et al. [39] reported that *Serratia plymuthica* (with and without inoculation) influenced most physiological factors of *Phaseolus coccineus* grown with copper and indicated some impacts on biomass, and inoculation decreased catalase and guaiacol peroxidase activities, while organic acids content was higher. It has been reported that *Serratia marcescens*, strain S27 is important for the bioremediation of environments contaminated with Cr and Cd in tropical regions [40]. Abreo et al. [41] reported that *Serratia ureilytica* which has activity as a biological control parameter and dimethyl disulfide (DMDs) produced by this bacterial strains actively involved in seedling and seed protection against *Pythium cryptotirregulare*. *Serratia* sp. S119 is a potential important biofertilizer for maize and peanut [42]. *Serratia proteamaculans* suppressed *R. solani* *in vivo* and *in vitro* and it modulated tomato defence machinery [43].

Klebsiella is one of the principle PGPB that improve plant growth by fixing nitrogen; producing 1-aminocyclopropane-1-carboxylate deaminase, gibberellic acid, indole-3-acetic acid (ACC), and siderophores, and induction of systemic resistance [44–46]. Singh et al. [47] concluded that *Klebsiella* sp. SBP-8 promoted growth of the host wheat plants and protected them from salt stressors via more than one mechanism such as K⁺/Na⁺ ration, and the effect of 1-aminocyclopropane-1-carboxylatedeamine (ACCD) activity in plants. Noman et al. [48] displayed that *Klebsiella pneumoniae* strain NST2 as nanofactories for green copper nanoparticles (CuNPs), biogenic CuNPs positively promoted antioxidative defense response of maize plant against salinity, and boosted the maize growth under salt stress.

Streptomyces is the important genus of actinobacteria, and a filamentous bacteria presenting the family *streptomycetaceae* and other actinomycetales, and it has been extensively applied for biofortification, plant growth improvement, mineral availability, nutrient assimilation, and biologic control of both plant pathogens and insect pests of agriculturally important crops [49,50]. *Streptomyces* is a bacterial genus with biotechnological activity [51]. Samgani and Gopalakrishnan [52] reported that the application of strains of *Streptomyces griseus* (MMA-32 and KAI-26) revealed a significant enhancement of Fe, K, Mn, and Zn contents in the harvested chickpea grains. Puppala et al. [53] reported that *Streptomyces* sp. having the capability to produce acidic and thermostable phytase as well as plant growth promoting characteristics showing increased plant growth could have implications in soils having acidic nature and in arid region. Djuidje et al. [54] indicated the probability of using endophytic *Streptomyces* strains, particularly isolate PERM2 in the protection of cocoyams (*Xanthosoma sagittifolium* L. Schott) against root rot disease and the improvement of root growth. Kaur and Manhas [55] showed that *Streptomyces hydrogenans* strain DH16 and extracellular metabolites produced by it can be utilized as soil amendment as biofertilizer and biofungicide with several benefits over the chemical fungicides and fertilizers. *Streptomyces eurocidicus* has antagonistic activity against a broad spectrum of phytopathogenic fungi, and it has a positive impact on soybean plants growth and development [56]. *Streptomyces microflavus* G33 application efficiently controlled tomato bacterial wilt disease, and showed strong antagonistic activity against *Ralstonia solanacearum* [57]. The most important points about plant growth promoting bacteria is shown in Table 1.

Table 1. Key points about plant growth promoting bacteria and their effects on different crops.

Plant Growth Promoting Bacteria	Plant	Bacteria Species	Key Points	Reference
<i>Serratia</i>	Chickpea (<i>Cicer arietinum</i> L.)	<i>Serratia</i> sp. 5D	* <i>Serratia</i> sp. 5D can act as effective microbial inoculants, especially in nutrient-deficient soils.	[58]
	Corn (<i>Zea mays</i> L.)	<i>Serratia</i> sp. CP-13	* <i>Serratia</i> sp. CP-13 restricted Cd uptake and concomitant lipid peroxidation in maize cultivars. * <i>Serratia</i> sp. CP-13 is a potential candidate for plant growth augmentation and Cd remediation plants.	[59]
		<i>Serratia liquefaciens</i> KM4	*Its inoculation significantly reduced oxidative stress markers. *Its inoculation promoted the maize growth and biomass production along with better leaf gas exchange, osmoregulation, antioxidant defense systems, and nutrient uptake under salt stress.	[60]
	Eggplant (<i>Solanum melongena</i> L.)	<i>Serratia rubidaea</i> SNAU02	*It is effective against <i>Fusarium oxysporum</i> f. sp. melongenae.	[61]
	Latjeera (<i>Achyranthes aspera</i> L.)	<i>Serratia</i> sp. AL2-16	*Its inoculation significantly increased shoot length, fresh shoot weight, fresh root weight, and area of leaves.	[62]
	Lentil (<i>Lens culinaris</i>)	<i>Serratia</i> sp. KUJM3	* <i>Serratia</i> sp. KUJM3 offers multiple benefits of metal(loid)s bioremediation, As(V) reduction, and plant growth promotion.	[63]
	Onion (<i>Allium cepa</i> L.)	<i>Serratia</i> sp.	* <i>Serratia</i> sp., and <i>Pseudomonas</i> sp., promoted germination of <i>A. cepa</i> seeds.	[64]
	Quinoa (<i>Chenopodium quinoa</i> Willd.)	<i>Serratia rubidaea</i> ED1	*It stimulated quinoa seeds germination and seedlings growth under salt stress conditions. *PGPR treated rhizomes showed higher amounts of secondary metabolites, primarily curcumin and additional compounds such as 4-Hydroxy-2-methylacetophenone, 2,4-curcumin and additional compounds such as 4-Hydroxy-2-methylacetophenone, 2,4-Di-tertbutyl phenol, aR-Turmerone, and (Z)-gamma-Atlantone.	[65]
	Turmeric (<i>Curcuma longa</i>)	<i>Serratia nematodiphila</i> RGK		[66]
<i>Klebsiella</i>	Cotton (<i>Gossypium herbaceum</i> L.)	<i>Klebsiella oxytoca</i> Rs-5	*Encapsulated Rs-5 is effective in relieving salt stress for cotton growth. *It can significantly promote the growth of maize seedlings.	[67]
	Corn (<i>Zea mays</i> L.)	<i>Klebsiella jilinsis</i> 2N3	*It may induce resistance of maize to the northern corn leaf blight.	[68]

Streptomyces	Cucumber (<i>Cucumis sativus</i> L.)	<i>Klebsiella oxytoca</i> P620	*Its application reduces <i>p</i> -hydroxybenzoic acid (PHBA) concentration in soil, activates antioxidant and soil enzymes, and also influences metabolites in leaves by affecting plant transcriptome, mitigating PHBA stress in cucumber.	[69]
	Mung bean (<i>Vigna radiata</i> L.)	<i>Klebsiella</i> sp. Strain TIU20 (KTIU20)	*KTIU20 maybe employed as an effective plant growth candidate in agricultural soil, contaminated with heavy metals and fungal pathogen near industrial area.	[70]
	Oat (<i>Avena sativa</i> L.)	<i>Klebsiella</i> sp. IG3	*Its inoculation to oat seedlings under salt stress positively modulated the expression profile of <i>rbcL</i> and <i>WRKY1</i> genes.	[71]
	Rice (<i>Oryza sativa</i>)	<i>Klebsiella</i> sp. PD3	*PD3 improved the phenanthrene degradation in rice plants.	[72]
		<i>Klebsiella michiganensis</i> MCC3089	*PD3 showed plant growth promoting properties such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity.	[73]
		<i>Klebsiella michiganensis</i> MCC3089	*It has efficiency to alleviate cadmium-induced toxicity in rice, and enhanced growth and reduced oxidative stress in presence of the bacterium.	[74]
	Soybean (<i>Glycine max</i> L.)	<i>Klebsiella variicola</i> FH-1	*A Cadmium (Cd) resistant PGPR strain reduced Cd uptake in rice plant by Cd bioaccumulation.	[75]
	Sunflower (<i>Helianthus annuus</i> L.)	<i>Klebsiella</i> sp. Straint CPSB4 (MH266218)	*It exhibited the biological control potential by inducing resistance in soybean against <i>Sclerotinia sclerotiorum</i> infection.	[76]
	Tomato (<i>Solanum lycopersicum</i> L.)	<i>Klebsiella</i> sp. CPSB4	*CPSB4 enhanced plant biomass, plant growth, nutrient uptake, anti-oxidative enzymes, and chromium bioremediation.	[77]
	Wheat (<i>Triticum aestivum</i> L.)	<i>Klebsiella pneumonia</i> strain SN35	*It enhanced the levels of superoxide dismutase, catalase, peroxidase, total phenolic, and ascorbic acid in tomato plant under different levels of chromium stress conditions.	[78]
Streptomyces	Chickpea (<i>Cicer arietinum</i> L.)	<i>Streptomyces griseus</i> ; <i>Streptomyces africanus</i> ; <i>Streptomyces coelicolor</i>	*It is potent in the green synthesis of copper nanoparticles (CuNPs), and CuNPS could immobilize the Chromium (Cr) in the soil.	[79]
	Chili (<i>Capsicum frutescens</i> L.)	<i>Streptomyces</i> spp. KPS-E004 and KPS-A032	*They have a great potential for biological control of <i>Fusarium</i> wilt disease and PGP in chickpea.	[80]
			*Their mixture could suppress root know infestation and promote plant growth.	
			*Co-inoculation of these two strains increased yield of chili.	

Pepper (<i>Capsicum annuum</i> L.)	<i>Streptomyces pactum</i> Act12	*Its soil application enhances pepper fruit quality in the field.	[81]
	<i>Streptomyces griseocarneus</i> R132	*It controls the development of anthracnose symptoms in pepper fruits and plants.	[82]
Rice (<i>Oryza sativa</i> L.)	<i>Streptomyces hygroscopicus</i> OsiSh-2	*It could protect plants against Fe-deficient stress by a sophisticated interaction with the host, including modulation Fe chelation, solubilization, reduction and translocation, and leading to enhanced fitness of plant.	[83]
	<i>Streptomyces corchorussi</i> TKR8 and JAS2; <i>Streptomyces misionensis</i> TBS5	*They can be considered as biocontrol agents against bacterial panicle blight (PBP) <i>Burkholderia glumae</i> and bioformulations for rice crops.	[84]
Tomato (<i>Solanum lycopersicum</i> L.)	<i>Streptomyces</i> sp. Strain FJAT-31547	*It has high biocontrol efficiency against tomato <i>Fusarium</i> wilt and bacterial wilt and a growth promoting effect on tomato plants.	[85]
	<i>Streptomyces</i> strain UT4A49	*It showed the promising production of indole acetic acid (IAA), ammonia, siderophore, amylase, protease and cellulase.	[86]
Tea (<i>Camellia sinensis</i> L.)	<i>Streptomyces</i> sp. SLR03	*It is a promising biocontrol agent for tomato bacterial disease control (<i>Ralstonia solanacearum</i>).	[87]
	<i>Streptomyces griseus</i> ; <i>Streptomyces lydicus</i>	*It is a prospective option for forthcoming biological control programme of <i>Pestalotiopsis theae</i> .	
		*They can be considered as biocontrol agents and a promising alternative for effective management of red root rot disease in tea plants.	[88]

Enterobacter, any of a group of rod-shaped bacteria of the family *Enterobacteriaceae*. *Enterobacter* are gram-negative bacteria that are categorized as facultative anaerobes, which means that they are capable to thrive in both aerobic and anaerobic environments [89–91]. *Enterobacter* sp. SA187 increased the yield of the forage crop alfalfa when submitted to different saline irrigation in field trials. Luo et al. [92] showed that highly Cd-resistant alkalizing strain *Enterobacter* sp. LYX-2, as a novel microbial passivator, has considerable ability and reuse value to acquire the remediation of Cd-contaminated soil together with safe production of vegetables simultaneously. Luduena et al. [93] discovered that strain *Enterobacter* sp. J49 is an endophytic plant growth promoting bacteria, is a notable source of information to continuing the research of its potential industrial production as a biofertilizer of maize, peanut and other economically important crops. *Enterobacter cloacae* had strong insoluble P/Cd mobilization capabilities, improved diversity of rhizospheric microbial community, and could be applied as bio-inoculants for assisting phytoremediation of Cd-polluted soil in the *Solanum nigrum* L. rhizosphere [94]. Application of *Enterobacter ludwigii* CDP-14 resulted in meaningful increase in the Zn content in wheat plant under metal stress, and also promoted the various compatible solutes such as total soluble sugar, proline content, and decreased the malondialdehyde (MDA) content as compared to control [95]. *Enterobacter* sp. P23 was shown to improve rice seedling growth under salt stress, and the impact was connected with a decrease in

antioxidant enzymes and stress-induced ethylene [96]. Sabir et al. [97] concluded that combined application of biochar and *Enterobacter* sp. MN17 retrieved negative impacts of Cd in *Brassica napus*, mobilized Cd in soil, but reduced Cd uptake by plants. Ghosh et al. [98] also displayed that *Enterobacter cloacae* AS10 significantly promoted rice plant growth at the seedling stage through Cd immobilization, and it prevented the surge of stress ethylene and oxidative stress in rice seedlings, leading to plant growth improvement.

The entomopathogenic fungus *Beauveria bassiana* is extensively applied for insect pest control and can produce three distinctive infective unit kinds under different nutritional and environmental conditions: blastospores, aerial conidia, and submerged conidia [99–103]. Espinoza et al. [104] concluded that *Beauveria bassiana* could be applied to promote the yield of active chemical components in cultivated medicinal plants such as chive (*Allium schoenoprasum* L.). *Beauveria bassiana* had great potential to be applied in the integrated management of *Hypothenemus hampei* (Ferrari) in coffee crops [105]. Its strain GHA is the main component of an area-wide pest management study for coffee berry borer [106]. *Beauveria bassiana* strains were effective to kill almost all the Colorado potato beetles, and it can be suggested for the development of a new biopesticide [107]. *Beauveria bassiana* strains RGM-644, RGM-557, and RGM-721 showed fewer nymphs of whiteflies (*Trialeurodes vaporariorum*), RGM-577 and RGM-731 produced the highest plant height, and RGM-731 obtained the greatest plant biomass in tomato [108]. It can alleviate Fe chlorosis symptoms in both wheat and tomato plants during early growing stages, but the intensity of the impact related to the plant species and available Fe on substrate [109]. *Beauveria bassiana* (Balsamo) Vuillemin, can exist as an endophyte in banana (*Musa* spp.) and potentially provide management against the banana weevil *Cosmopolites sordidus* (Germar) [110]. *Beauveria bassiana* ARP14 can decrease the egg period of *Bemisia tabaci* [111]. It can promote bean plant growth, and it has important benefits as seed inoculants to suppress spider mites in bean and the technique appears to have no conflict with application of predatory mites [112]. *Beauveria bassiana* displayed promising nematocidal activity, particularly against *Meloidogyne incognita* in both cucumber and tomato [113]. It can be utilized for management of two hemipteran cotton insect pests, namely, *Phenacoccus solenopsis* Tinsley and *Dysdercus cingulatus* Fab. [114]. The yields of experimental maize samples showed a significant improvement after *Beauveria bassiana* treatment, and it produced a notable mortality rate in grasshopper [115]. *Beauveria bassiana* endophytically colonized cotton, melon, and tomato plants [116]. Ramakuwela et al. [117] demonstrated the ability to establish endophytic *B. bassiana* in pecan and the potential to use this ability in pecan pest management. The application of *B. bassiana* strain Naturalis in the presence of *Ditylenchus destructor* and *D. dipsaci* might lead to a detrimental interaction leading to higher nematode population densities and higher potato tuber damage [118]. Donga et al. [119] showed that *B. bassiana* foliar spray and soil drench improved the numbers of sugarcane sett roots. In one experiment, it has shown that the large pine weevil (*Hylobius abietis*) adults may be infected by *B. bassiana* after only a short exposure to carriers [120].

Frankia are Gram-positive actinobacteria, filamentous nitrogen-fixing actinobacteria that are free-living microbes in the soil and in symbiotic associations with actinorhizal plants [121,122]. *Frankia* can fix nitrogen by converting atmospheric N₂ into biologically practical ammonia and provide the host plants with a source of reduced nitrogen [123–125]. Some *Frankia* strains are resistant to abiotic stresses including heavy metal, pH, salinity and temperature and have developed complicated mechanisms to adapt to these conditions [126,127]. The *Frankia* species can cause the development of nodules on the roots of an immeasurable variety of actinorhizal plants [128–130]. Marappa et al. [131] reported that *Frankia casuarinae* is an effectual biofilm inhibition agent against *Pseudomonas* sp. and *Candida* sp.

The genus *Microbacterium* belongs to the family *Microbacteriaceae* within the surborder *Micrococcineae* [132,133]. *Microbacterium* are nonspore-forming, Gram-positive, and rod-shaped bacteria [134]. *Microbacterium* species have been recently characterized as effective plant growth-promoting bacteria under abiotic and biotic stresses [135], and it is also found that members of this genus could be effectual against phytopathogenic bacteria, nematodes, and fungi [136–138]. Suarez-Estrella et al. [139] reported that *Microbacterium aerolatum*, *Microbacterium profundum*, and *Microbacterium*

foliorum showed positive results in the *in vitro* germination promotion test in lettuce seeds, increasing the radicle weight at levels close to 45%, and indicating significant palliative impacts of *Botrytis cinerea* and promoting the development of lettuce seedlings both at root and aerial levels.

Burkholderia species have various lifestyles establishing mutualism or pathogenic associations with animals and plants [140]. Bacteria of the genus *Burkholderia* are very heterogeneous, consisting of over 30 species (Gram-negative, β -Proteobacteria) that occupy extensively differing ecological niches, and the members are usually encountered in the rhizosphere of crop plants and their connection with plants ranges from pathogenic to plant-growth-promoting and symbiotic associations [141]. *Burkholderia phytofirmans* strain PsJN promoted maize plants biomass production even in heavy metal contaminated soil, and its inoculation alone had just minor impacts on alter microbiome structures [142]. Bernabeu et al. [143] discovered that seedling inoculation with *Burkholderia tropica* led to efficient root colonization of tomato plants followed by bacterial spreading to aerial tissues. *Burkholderia* sp. SSG suppressed diverse pathogens: 5 bacteria, 9 fungi and 6 oomycetes, and it provided significant control of twelve plant diseases, and it is a favorable broad-spectrum biocontrol agent for plant disease management [144]. Inoculation of *Burkholderia* sp. AQ12 promoted the rice growth, improved the cellular levels of antioxidant enzymes and boosted the expression of tillering related genes [145]. Application of *Burkholderia phytofirmans* PsJN and tree twigs biochar together improved grain quality parameters, and growth physiology of mung bean (*Vigna radiata*), immobilized Pb in soil and decreased its uptake, translocation and bioaccumulation in *V. radiata* tissues, reduced Pb induced oxidative stress by intensifying antioxidant activities while meaningfully decreasing activities of ROS [146]. *Burkholderis* sp. CC-AI74-infected maize show improved growth, and N, P contents, increased *in planta* P-utilization rate and reveal significant escalation of root phosphatase activity [147].

Bacillus is an aerobic, Gram-positive, and endospore-forming bacteria [148,149]. Manasa et al. [150] observed that *Bacillus* spp. Discovered from the marine water and the rhizosphere of the medicinal plant *Coscinium fenestratum* increased plant growth, iron content, and yield of sorghum. Sorghum plants inoculated with *Bacillus* spp. strains showed better growth in terms of root biomass and shoot length with dark greenish leaves due to high chlorophyll content, and inoculation also increased leaf relative water content and soil moisture content under water stress conditions [151]. Prathibha and Siddalingeshwara [152] reported that application of *Pseudomonas fluorescens* and *Bacillus subtilis* were effective in improving seed quality such as vigour index, seed germination and nutritional quality such as carbohydrate and protein content. *Bacillus* is one of the highly studies plant growths promoting rhizobacteria [153,154], and they are common in rhizosphere communities [155]. Most important bioactive molecules from the genus *Bacillus* are non-ribosomally synthesized peptides and polyketide compounds, lipopeptides, bacteriocins and siderophores [156]. *Bacillus mojavensis* strain PRC101 is a close relative of *Bacillus subtilis* which have been reported to reduce mycotoxin accumulation and disease incidence of *Fusarium verticillioides* in maize [157]. *Bacillus* sp. CHEP5 acts synergistically with *Bradyrhizobium* sp. SEMIA6144 increasing the symbiotic interaction with peanut even in *Sclerotium rolsii* challenged plants [158]. Kim et al. [159] reported that *Bacillus velezensis* M75 was separated from cotton waste and its application as biocontrol agent against fungal plant pathogens in agricultural fields. *Bacillus amyloliquefaciens* subsp. *plantarum* strain 32a significantly colonized and persisted in the rhizoplane of tomato plants, promoted the growth of tomato plants, and decreased the severity of crown gall disease in tomato plants [160]. Rocha et al. [161] observed that among the *Bacillus* strains, there are potential biocontrol agents against multiple races of *Fusarium* wild. *Bacillus* sp. strain PnD is a potential plant growth promoting bacterium, and the seed biopriming procedure can effectively mitigate inhibitory impacts of salinity stress in rice plants [162]. It has been reported that *Bacillus megaterium* BM18-2 could be used as a potential agent for Cd bioremediation, increasing growth and Cd absorption of hybrid *Pennisetum* in Cd contaminated soil [163]. *Bacillus amyloliquefaciens* B9601-Y2 treatment promoted maize growth parameters and yield, and revealed potential to promote maize grown and suppress corn leaf blight (*Bipolaris maydis*) [164]. *Bacillus amyloliquefaciens* PDR1 from root of karst adaptive plant increased *Arabidopsis thaliana* roots to absorb ions, promoted rhizosphere acidification capacity, and improved

Arabidopsis thaliana to resist alkaline stress [165]. *Bacillus velezensis* OEE1 effectively colonize and increase growth of *in vitro* olive plants, and its antifungal components inhibit growth of *Verticillium dahliae* [166]. Gowtham et al. [167] reported that *Bacillus subtilis* Rhizo SF 48 enhanced the plant growth parameters in tomato plants subjected to drought stress, and down-regulation of *Le25* and *SIERF84* confirm positive impact of Rhizo SF 48 in tomato plants subjected to drought stress. *Bacillus* sp. KUJM2 offered considerable potential as a PTE remediating parameter, plant growth promoter of a plant (*Lens culinaris*) and regulator of potentially toxic elements (PTEs; Cd, As, Ni, Cu) translocation curtailing human health and environmental risks [168]. *Bacillus pumilus* improves tomato growth and N uptake under N fertilization, but it does not effect tomato growth or N uptake under no N fertilization [169]. *B. Pumilus*-induced N₂ fixation is connected with bacterial *nifH* gene [169]. *Bacillus pumilus* strain JPVS11 is vital for rice growth promotion, improves photosynthetic pigments, antioxidant activity, and proline, improved microbial count, soil enzyme activity, and soil properties in salt stress [170]. *Bacillus licheniformis* induced resistance against gray mold in pepper plants, and both *Bacillus pumilus* and *Bacillus licheniformis* inhibited the growth of *Fusarium solani* and *Botrytis cinerea* [171].

Arthrobacter is a genus obligate aerobes bacteria distinguished by rod-coccus growth cycle, and it is usually are found in aerial surface of plants, soils, and wastewater sediments [172,173]. *Arthrobacter* genus belongs to the family *Micrococcaceae* within the surborder *Micrococcineae* [174,175]. Vanissa et al. [176] reported that *Arthrobacter* sp. strains can assist the growth of maize in salinity-affected and P deficient soils in a genotype-dependent fashion, and the bacterial strains was shown as able to produce the phytohormones auxin, gibberellins, abscisic acid, and cytokinins. Jiang et al. [177] indicated that *Arthrobacter* sp. DNS10 application increased nitrogen utilization by increasing the expression of genes involved in nitrogen metabolism in soybean leaves.

Pseudomonas are oxidase positive, Gram-negative, and non-spore forming bacteria that are known for inhabiting a diversity or environments [178,179]. The genus *Pseudomonas* contains different species considered to be plant growth promoting rhizobacteria, and it is one of the most and largest diverse in the bacterial kingdom [180]. Among the *Pseudomonas* species, the *P. syringae* complex including many *P. syringae* pathovars, *P. cichorri*, *P. viridiflava*, and other species, has been associated with diseases on a broad spectrum of plant hosts [181–184]. *Pseudomonas putida* strain SAESo11 inoculation keeps the redox state of tomato plants at exposure to drought stress, and resist to drought stress [185]. Moin et al. [186] reported that *Pseudomonas* EFP-121 was significantly effectual in improving fresh shoot weight and plant height of sunflower. *Pseudomonas* S4, S1 serve as PGPR and improved biomass accumulation in spinach, tomato, and lettuce; S2 and S4 root inoculation boosted chlorophyll content in tomato and lettuce leaves [187]. *Pseudomonas lurida* strain E0026 showed high metal and wide pH tolerance, and able to resist broad range of antibiotics and adapt drought stressed conditions, and copper phytoremediation by *Helianthus annuus* [188]. The inoculation with the *Pseudomonas putida* KT2440 mutant strains is an important technique to increase the growth of corn and soybean plants, so they might be applied for promoting regional crops growth at field scale utilizing natural saline soils [189]. Sahebani and Gholamrezaee [190] showed the capability of *Pseudomonas fluorescens* CHA0 to control *Meloidogyne javanica* and induction of systemic resistance of cucumber and tomato plants.

Rhizobia play a vital function to establish a symbiotic connection between leguminous plants and environmental productivity [191,192]. *Rhizobia* inhabit root nodules and they can convert the atmospheric nitrogenous molecule to ammonia and consequently make it available to the plant [193]. Rhizobial-mediated nitrogen fixation is a significant agriculture, and its inoculum has been applied frequently as biofertilizers [194,195]. It seems that rhizobia and legumes co-evolved to change important elicitors/microbe-associated molecular patterns (MAMPs) and their corresponding receptors to prevent the development of defense reactions, as the plant immunity mechanisms depend on the recognition of microbe-associated molecular patterns [196]. *Rhizobium* triggers enzyme-mediated induced resistance reactions [197]. *Rhizobium* infection of common bean increased the production of N-based nutritive compounds, while inhibited the production of C-based organic compounds associated with plant resistance, and probably increasing host plant tolerance to the

pathogen [197]. *Rhizobium* plays the main function in mutualistic interactions with plants, and *Rhizobium* sp., isolated from *Chlorella vulgaris*, enhances green algal growth [198]. *Rhizobium* decreased Cu-induced growth inhibition and promoted nitrogen content, reduced oxidative stress through boosting antioxidant ability, and regulated antioxidant, phytochelatin, gene expressions, and metallothioneins [199]. *Rhizobium alarii* strains promoted plant growth and tolerance to water stress, and they influenced on the plant growth and root-associated microbiota changed according to the strain [200]. The most important points about the effects different species of *Rhizobium* several crops are shown in Table 2.

Table 2. Key points about *Rhizobium* and their impacts on different crops.

Plant	Bacteria Species	Key Points	Reference
Chickpea (<i>Cicer arietinum</i> L.)	<i>Rhizobium leguminosarum</i> BHURC04	*It has shown better PGPR activities.	[201,202]
Common bean (<i>Phaseolus vulgaris</i>)	<i>Rhizobium tropici</i>	*It may contribute to a synergistic manner to the promotion of growth and the control of damping off in the common bean.	[203]
	<i>Rhizobium tropici</i> CIAT889	*It is a promising candidate for developing new and more efficient inoculants for common bean.	[204]
		*The inoculation increased the number and mass nodules, nitrogenase activity, leghaemoglobin content of nodule, mycorrhizal colonization, dry mass of root and shoot was reported.	
Faba bean (<i>Vicia faba</i> L.)	<i>Rhizobium leguminosarum</i> bv. <i>viciae</i>	*The inoculation increased the total plant growth, enhanced soil fertility, efficient farming, and an alternative chemical fertilizer.	[205]
Finger millet (<i>Elusine coracana</i>)	<i>Rhizobium mayense</i>	*They enhanced plant growth promotion with higher shoot length, root length, dry weight, and nodule number.	[206]
Groundnut (<i>Arachis hypogaea</i>)	<i>Rhizobium phaseoli</i> S18; <i>Rhizobium phaseoli</i> S19	*Its inoculation can increase seed germination rate, length and dry biomass of plant organs.	[207]
Mung bean (<i>Vigna radiata</i> L.)	<i>Rhizobium pusense</i>	*Inoculation with it can be used for unraveling and amelioration of crop production in barren, polluted and agricultural soils.	[208]
	<i>Rhizobium</i> sp. BD1		[209]

Pea (<i>Pisum sativum</i> L.)	<i>Rhizobium leguminosarum</i> bv. <i>viciae</i> 3841	*It can increase the growth and final yield of pea under saline conditions.	[210]
	<i>Rhizobium</i> MRP1	*Its inoculation increased growth parameters and it can be used as a bio-inoculant under fungicide-stress.	[211,212]

Mechanism of Plant Growth Promoting Bacteria

The application of plant growth-promoting bacteria (PGPB) is considered as one of the the techniques to improve phytoremediation procedure and plant growth under various abiotic stress condition [213]. The PGPB can remain under abiotic stress conditions by different mechanisms including biofilm formation, synthesis of heat shock proteins (Hsps), osmoprotective compounds, etc. Plant growth-promoting microorganisms can be applied to increase soil characteristics, improve plant growth, alleviate abiotic stresses and promote phytoremediation effectiveness is considered as an effective and environmentally friendly process [214,215]. The PGPB can improve plant growth and phytoremediation process by providing plant growth promoting (PGP) metabolites such as indole-3-acetic acid (IAA), siderophores, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, and as well as solubilizing phosphate (P) [216–219]. Certain PGPB are able to immobilizing Cr by reducing Cr⁶⁺ to Cr³⁺ can also decrease Cr toxicity in plants. Some PGPB may also lead to abiotic stress tolerance to plants by stimulating gene expression and antioxidant enzyme activity such as ascorbate peroxidase (APX), superoxide dismutase (SOD), catalase (CAT), etc. [220–222]. Plant growth-promoting microbes support plants to tolerate abiotic stress (drought, Cd, temperature, etc.) by producing indole-3-acetic acid (IAA) and siderophores, solubilizing phosphate, reducing stress ethylene content by synthesis of 1-aminocyclopropane-1-carboxylate (ACC) deaminase, and producing antioxidant enzymes like catalase (CAT), superoxide dismutase (SOD) and ascorbic peroxidase (APX) to scavenge ROS and promote nutrient uptake [223,224]. Orozco-Mosqueda et al. [225] discovered that the enzyme activity of ACC deaminase results I the production of ammonia and α-ketobutyrate, which, by reducing ACC levels, hinders excessive increases in the synthesis of ethylene under different stress environments, and it one of the most effective mechanisms to lead to plant tolerance to salt stress.

Alijani et al. [226] reported that *Serratia rubidaea* Mar61-01 succeeded in controlling *Botrytis cinerea*, the causal factor of strawberry gray mold, because of reduce mycelial growth, conidial germination and fruit decay development under in *in vivo* and *in vitro* experiments, but also that prodigiosin influenced the activity of some fruit enzymes related to the defense mechanism and resistance to gray mold infection.

Serratia marcescens strains not only increased plant growth, but also induced systemic defense responses in the host plant, and the induction of entomopathogenic bacterium *Serratia marcescens* with the ability to produce IAA during the early establishment of rice seedlings can be beneficial [227]. Many studies have shown the potential of *Serratia marcescens* that induces plant growth by modulating phosphate solubilization and phytohormone producing [228,229]. Li et al. [230] reported that *Klebsiella* sp. strain San01 extracted from sweet potato increased the expression of the *IbLEA* gene in sweet potato under drought and salinity, and the results lead to the encouraging biotechnological approach via San01 interaction to promote stress-tolerant sweet potato (*Ipomoea batatas* L.) plants. Abbasi et al. [231] reported that *streptomyces* decrease drought stress in tomato plants and adjust the expression of transcription parameters of ERF1 and WRKY70 genes, and *streptomyces* strains inhibit stress signals, at biochemical and molecular levels to hinder the plants understanding of stress while, through boosting relative water content (RWC), compensated for the decline in the yield. The plant growth promotion by *streptomyces* is discovered which has association with the production of growth regulators including two kinds of pathways for the biosynthesis of IAA which have role in tryptophan-dependent, indole acetic acid (IAA), and tryptophan-independent have been proposed [232].

Enterobacter species sustain productivity and plant growth include nitrogen fixation, solubilization of inorganic phosphate, production of plant hormones, reduction of ethylene levels, improvement of nutrient uptake and production of antimicrobial components [233,234]. *Enterobacter cloacae* MG00145 (OS03) isolated from surface disinfected stem of *Ocimum sanctum*, which has multigrowth-promotion characteristics (IAA production, siderophore, phosphate solubilisation, and ammonia production), and promotes the growth of *Oryza sativa*, *Vigna mungo*, *Arachis hypogaea*, and *Brassica rapa* Var. Toria. Panneerselvam et al. [235] demonstrated that *Enterobacter* species were significantly increased the below and above ground response in rice plants. Inoculation of *Enterobacter cloacae* MSR1 and *Pisum sativum* significantly improved the growth parameters like dry weight of *Medicago sativa* [236].

According to the 16S rRNA gene sequence analysis SCAUK0330 was discovered as *Burkholderia cepacia*. SCAUK0330 grew at 10-40°C and pH 4.0-10.0, tolerated up to 5% NaCl, and indicated antagonism against some pathogenic fungi [237]. The expression of a single SCAUK0330 gene gave *E. coli* a pH reduce ability to solubilize phosphate, and the nucleotide and the deduced amino acid sequences of this phosphate solubilization connected with gene indicated the high degree of sequence identity with *B. cepacia* E37gabY [237]. Jiang et al. [238] concluded that *Burkholderia* sp. J62 on the basis of the 16S rDNA gene sequence analysis, show various multiple heavy metal and antibiotic resistance characteristics, as the isolate produced siderophore, indole acetic acid and 1-aminocyclopropane-1-carboxylate deaminase, and the isolate also solubilized inorganic phosphate. *Burkholderia vietnamiensis* C12 from *Ficus tikoua* Bur. showed an important biocontrol factor for rice sheath blight, and lead to the defense enzyme in rice against rice sheath blight by improving the activities of defense enzymes SOD, POD, PAL, CAT, and PPO [239]. It was identified as *Burkholderia* sp. based on 16S rDNA sequence analysis presented nitrogenase activity, phosphate solubilizing ability and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity; suppressed the growth of *Sclerotinia sclerotiorum*, *Verticillium dahliae*, and *Gibberella zeae*, and produced small quantities of indole acetic acid (IAA) [240]. *Burkholderia ambifaria* T16 showed extraordinary plant growth-promoting characteristics, such as phosphate-solubilization, siderophore production, 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, *in vitro* antagonism against *Fusarium* spp. and enhancement of grain yield when inoculated to barley grown under greenhouse conditions [241].

Bacterial species from genus *Bacillus* can produce IAA, solubilize phosphate and can fix nitrogen and develop biocontrol attributes like HCN, antibiotics, hydrolytic enzymes, and siderophore [242]. Both *Bacillus paranthracis* NT1 and *Bacillus megaterium* NCT-2 showed cadmium resistance; *Bacillus paranthracis* NT1 sequestered 96.75% of the adsorbed Cd²⁺ on the cell wall, *Bacillus megaterium* NCT-2 accumulated 43.11% of the adsorbed Cd²⁺ intracellularly, and the procedure modulated by the genes *cadA*, *khtT*, *trkA*, *zitB*, *czcD*, and *bshA*, respectively [243]. It has been reported that improved effectiveness of *Bacillus safensis* primed plants in alleviating heat stress is mainly connected with preserving functional and structural integrity of essential cellular organelles like mitochondria and chloroplast through elimination of excess reactive oxygen species (ROS) [244]. Two *Bacillus* species, *B. altitudinis* FD48 and *B. methylotrophicus* RABA6 indicated efficient groups representing abscisic acid (ABA) in rice plants, and as co-inoculant priming triggered ROS enzyme activity *viz.*, super oxide dismutase, ascorbate peroxidase, peroxidase, and catalase [245]. Tahir et al. [246] reported that consortium of *Bacillus* strains may modulate sodium (Na⁺)/potassium (K⁺) efflux and antioxidant activities of potato under salt stress; under NaCl stress, the species were positive for P-solubilization, IAA and ACC deaminase, and consortium inoculation to potato improve RWC while decreases antioxidant enzyme activity and MDA contents. Myo et al. [247] concluded that *Bacillus velezensis* NKG-2 secreted the fungal cell wall degrading enzymes and volatile organic compounds (VOCs), and it meaningfully decreased the disease severity of *Fusarium oxysporum* wilt disease on tomato plants both under *in vivo* and *in vitro* conditions. The expression of plant hormone, DNA replication and Fe-Zn transporter related proteins in wheat roots was improved in the presence of *Bacillus megaterium* strain N3 compared with uninoculated roots under Cd stress [248]. *Bacillus subtilis* exhibits both a indirect and direct biocontrol mechanism to suppress disease attributed to pathogen, and the indirect process includes the stimulation of plant growth and the induction of needed

systemic resistance, and the direct process consists of the synthesis of several secondary hormones, metabolites, cell-wall-degrading enzymes, and antioxidants that help the plant in its defense against pathogen attack [249,250]. *Bacillus* produced various types of antimicrobial peptide substances such as subtilin, bacilysin, oligomycin A, iturin, zwittermicin A, and kanosamine and, which may be accountable for the inhibition of pathogen [251–253]. It also have a basic function in plant growth promotion by production of IAA and GA3, production of cytokinin, synthesize different kinds of lipopeptides and zinc solubilization [254–256]. Sampathkumar et al. [257] also reported that *Bacillus amyloliquefaciens* (ETL2) secreted number of antibacterial secondary metabolites and endophytic *Bacillus* spp. decreased cotton bacterial blight disease in cotton plants. Chi et al. [258] illustrated that both *Bacillus megaterium* NCT2 and *Bacillus paranthracis* NT1 could modulate phytohormones secretion, decrease oxidative stress and promote *Solanum nigrum* growth when exposed to Cd, and according to the results of qPCR the two strains impacted the detoxification of Cd in *Solanum nigrum* by influencing the expression of antioxidant enzyme genes and gene PDR2, and differential expression of heavy metal transport genes HMA and IRT1 may lead to the difference Cd accumulation in *Solanum nigrum*. Dhali et al. [259] reported that horse gram (*Macrotyloma uniflorum*) inoculated with *Bacillus* sp. (AS03) has notably lesser chromosomal aberration in the roots, and the photosynthetic performance of Cr treated plants co-inoculated with AS03 was meaningfully increased compared with non-inoculated Cr treated plants on the basis of photosynthetic yield. *Azospirillum brasilense* Sp245, a diazotrophic plant growth-promoting bacterium impacts host plants through distinctive mechanisms, gene interactions and confers biotic and abiotic stress tolerance mediated by signaling molecules [260].

Pseudomonas spp. belong to *Pseudomonadaceae* family (10 groups on the basis of rRNA-DNA hybridization) categorized into 6-subgroups of rRNA gene homology and RFLP [261,262]. *Pseudomonas* species produce antagonistic procedure such as induced growth resistance (ISR) and components like cell wall degradation enzymes, and antibiotics to keep a mutualistic connection with the associated plant, and they can synthesize auxins having characteristics similar to phytohormones like indole-3-acetic acid (IAA), which behave as signaling molecules for modulating plant growth [261]. *Pseudomonas* spp. significantly decreased the stress ethylene emission and promoted a significant increase in plant growth in comparison with single inoculation and non-inoculated control, as catalase activity which was significantly boosted in co-inoculated red pepper plants prove its ability to effectively neutralize the hydrogen peroxide ions formed because of oxidative stress in plants under salinity stress, and significant decline in malondialdehyde (MDA) content can be associated to the increased salt tolerance in co-inoculated red pepper plants [263]. *Pseudomonas fragi* stimulated tomato immunity to control *Meloidogyne incognita* by jasmonic acid and salicylic acid dynamic defence, as it increased the expression of *PR1*, *PR2*, *PR3*, *PR5*, and *PDF1.2* [264]. Anand et al. [265] reported methyltransferase positive *Pseudomonas oleovorans* as most efficient strain for reduced grain As content due to presence of *arsM* gene, and improve plant nutrient status of rice.

PGBP inoculation tends to modify the expression of the genes associated to phytohormones such as Jasmonic acid and ABA which assists plants to tolerate salt-stressed environments [266]. There are reports that indicate that PGPB can promote expression of some principle genes associated to phosphate transport and increase PO_4^{2-} in plants under salinity stress [267]. It has been showed that the inoculation of *Arthrobacter protophormiae* in wheat plants reduced concentration of ethylene and ABA and regulated the expression of regulatory *TaDREB2* and *TaCTR1* transcription parameters in ethylene signaling pathway [268]. Inoculation of salt-tolerant PGPB with protective and suitable carrier materials will not just increase crop yield but also significantly reduce electrical conductivity (EC) and regulate Na^+ content in plants and rhizosphere [266]. *Pseudomonas simiae* up-regulated genes include Peroxidase (POX), catalase (CAT), vegetative storage protein (VSP), and nitrate reductase (NR), and down-regulated genes include high affinity K⁺ transporter (HKT1), lipoxygenase (LOX), polyphenol oxidase (PPO), and pyrroline-5-carboxylate synthase (P5CS) of soybean which are responsible for antioxidative enzymes, nitrite reduction, vegetative storage protein, and ion transporters related genes [269]. *Bacillus amyloliquefaciens* upregulated genes include *AT1G17420*, *AT1G72520*, *AT2G26010*, *AT5G44420*, *ACS2*, *ACS8* and *ACS11* which have roles in ACC synthase, and

Brassinostereoids regulator genes of *Arabidopsis thaliana* [270]. *Burkholderia phytofirmans* may modify genes of *Arabidopsis* K + Transporter 1 (AKT1), High-affinity K + Transporter 1 (HKT1), Sodium Hydrogen Exchanger 2 (NHX2), and *Arabidopsis* Salt Overly Sensitive 1 (SOS1), RD29A, and RD29B, Ascorbate Peroxidase 2 (APOX2), Glyoxalase 17, and down-regulated the expression of Lipoxxygenase 2(LOX2) which have roles in ion homeostasis-related genes, desiccation, ROS scavenging, detoxification, and jasmonic acid biosynthesis-related genes of *A. thaliana* [271]. *Bacillus firmus* induced expression of genes APX, CAT, POD, Fe-SODGmVSP, GmPHD2, GmbZIP62, GmWRKY54, GmOLPb, and CHS which have roles as antioxidant enzymes and salt tolerance related genes of soybean [272]. *Bacillus subtilis* up-regulated *PtHKT1;5* and *PtSOS1* down-regulated *PtHKT2;1* gene expression and ion transporter genes of *Puccinellia tenuiflora* [273]. *Pseudomonas* sp. enhanced expression of genes *TaP5CS*, *TaP5CR*, and *TaOAT* which are associated with proline synthesis of wheat [274]. *Bacillus oryzicola* enhanced expression of RD29A, RD22, KIN1, RD29B, RD20, RD22, and ERD1 which may lead to salt stress-responsive genes of *A. thaliana* [275]. *Enterobacter* sp. has roles in upregulation of ROS pathway genes CAT, APX, GR, and DHAR and antioxidative enzymes related genes of Okra [276]. *Pseudomonas knackmussii* modulated NHX1, HKT1, SOS2 and SOS3, PR1 as well as SAG13 which are related to salt stress, defense-related gene and senescence associated gene of *A. thaliana* [277]. *Azotobacter chroococcum* modulated the expression of NRT2.1 and LATE EMBRYOGENESIS ABUNDANT (LEA) of tomato [278]. *Arthrobacter woluwensis* up-regulated genes include GmLAX1, GmAKT2, GmST1, and GmSALT3, and down-regulated genes include GmNHX1 and GmCLC1 [279,280].

Plant Growth-Promoting Bacteria and Sorghum

The physiological responses and growth of sorghum plants, nitrogen metabolites, and nitrogen fixation efficiency increased after inoculation. PGBP decreased free ammonia, increased soluble protein and nitrate in sorghum plants [281]. El-Meihy et al. [282] reported that utilization of heavy metal-tolerant plant growth promoting bacterial strains (HMT-PGPB) namely *Alcaligenes faecalis* MG966440.1, *Alcaligenes faecalis* MG257493.1 and *Bacillus cereus* MG257494.1 to lessen the heavy metal's toxic impacts on sorghum plant, in addition to their along with increase in plant growth. Beneficial bacteria are notably enhanced in the rhizosphere of sorghum, and they have positive interaction with sorghum nitrogen uptake under low nitrogen environment [283,284]. Sahib et al. [285] indicated that *Pseudomonas* sp., *Pseudomonas poae*, *Microbacterium* sp., *Serratia marcescens*, *Pantoea agglomerans* and *Bacillus pumilus* may improve total productivity, and soil-plant interactions under inadequate resources. El-Meihy et al. [282] concluded that the usage of these HTM-PGPB strains as biofertilizer of sorghum support plant to avoid the toxic impacts of heavy metals and enhance growth parameters. Bruno et al. [286] found that the chromium reducing-thermotolerant inoculation with plant growth promoting bacteria (CRT-PGPB) strains selected from Cr contaminated plots and distinguished as *Myroides odoratimimus* TCR22, *Providencia rettgeri* TCR21 and *Bacillus cereus* TCR17 through molecular characterization, indicated the possibility of reduction of Cr⁶⁺ to Cr³⁺, produce siderophores, solubilize phosphate and indole-3-acetic acid. Inoculation of sorghum with CRT-PGPB boosted antioxidant status such as catalase, superoxide dismutase and ascorbate peroxidase, plant growth, and declined malondialdehyde contents and decreased proline in plants under Cr stress; moreover, escalation of atmospheric temperature (IAT), and Cr+IAT stress proved that PGPB was appropriate to decrease stress induced oxidative damage [286]. Under IAT stress, inoculation of CRT-PGPB reduced the accumulation of Cr in plants in comparison with uninoculated control propose that CRT-PGPB may have the capability to increase phytostabilization procedure in Cr contaminated soils [286]. Dhawi et al. [287] indicated that among treatment group, PGPB group induced to maximum number of upregulated proteins, and PGPB in combination with arbuscular mycorrhizal (AM) fungi or alone decreased the adverse influences of radical scavenging system (ROS), and boosted levels of particular proteins as a result changing the metabolism towards carbohydrates synthesis in sorghum biomass and absorption of nutrients. Plant growth promoting actinobacterial strains selected from metal-polluted soils and identified as *Nocardiopsis* sp. strain RA07 and *Streptomyces* sp. strain RA04 showed diversified plant growth promoting parameters like production of indole-3-acetic acid, siderophores, 1-aminocyclopropane-1-carboxylate deaminase, and phosphate solubilization under

Cd stress (CdS), high-temperature stress (HTS), and drought stress (DS) conditions [288]. Silambarasan et al. [288] also reported that the actinobacterial inoculants decreased malondialdehyde concentration and increased antioxidant enzymes in plants cultivated under different abiotic stress environments, revealing that actinobacterial inoculants alleviated oxidative damage. Both strains RA07 and RA04 increased the translocation of Cd from root to shoot, and accumulation of Cd in plant tissues, which proves they could be effectual bio-inoculants to escalate phytoremediation of Cd polluted soil even in high-temperature stress and drought stress conditions [288]. Dhwai et al. [289] reported that plant growth promoting bacteria enhanced metabolic activities which resulted in increase in element uptake and sorghum root biomass whether accompanied with mycorrhiza or used solely, as treated plants two biochemical pathways, fatty acid biosynthesis and galactose metabolism were regulated in all treatment groups. Three heavy metals tolerant-plant growth promoting bacteria (HMT-PGBP) (*Alcaligenes faecalis* MG966440.1, *Alcaligenes faecalis* MG257493.1 and *Bacillus cereus* MG257494.1) increased the microbial activities such as improving dehydrogenase activity (DHA), decrease of heavy metal bioaccumulation in plants and roots, and stimulate heavy metals bioaccumulation parameter in rhizosphere and sorghum plants, as well as improved the microbial activities and decreased the accumulation of heavy metals in soil sorghum plants [290].

Li et al. [291] showed that the endophytic bacterial strain K3-2 may be applied for improving sorghum biomass production and Cu phytostabilization in the Cu mining wasteland soils. Shinde and Borkar [292] showed that *Serratia marcescens* strain L2FmA4 and *Serratia marcescens* strain L1SC8 promoted 1-aminocyclopropane-1-carboxylic acid deaminase and indole-3-acetic acid (IAA) production, increased germination, functional leaves, promoted height and final yield of sorghum in semi-arid and arid regions. *Streptomyces pactum* (Act 12) promoted potential toxic trace elements (PTEs) absorption in root and shoot of sorghum and it increased soil and plant enzymatic activities in polluted soil [293]. Sorghum root, shoot dry weight and chlorophyll significantly improved after Act 12, also β -glucosidase, alkaline phosphatase and urease activities were significantly increased by Act12, however lipid peroxidation (MDA) and antioxidant enzymatic activities were decreased after the consumption of Act12 [293]. The AgNPs were synthesized by extracellular extract of *Streptomyces griseoplanus* SAI-25, and it has shown antifungal activity against charcoal rot pathogen *Macrophomina phaseolina* of sorghum [294]. Gopalakrishnan et al. [295] reported that five strains of *Streptomyces* (CAI-121, CAI-24, KAI-32, CAI-127, and KAI-90) significantly increased all PGP parameters such as plant height, stem weight, leaf area, leaf weight, root surface area, root length, root volume, and root dry weight over the control. Alekhya et al. [296] concluded that two streptomyces strains, CAI-8 and BCA-546 have the potential to control charcoal rot disease in sorghum. Gopalakrishnan et al. [297] indicated that *Streptomyces albus* strain CAI-21 and its active metabolite organophosphate have the ability to control charcoal rot in sorghum. *Enterobacter* sp. K3-2 was identified from the roots of sorghum which exhibited Cu resistance and produced 1-aminocyclopropane-1-carboxylate (ACC) deaminase, indole-3-acetic acid (IAA), arginine decarboxylase and siderophores [297]. Chiarini et al. [298] reported that *Enterobacter* sp. strain BB23T4d was capable of colonize the root system of sorghum, but it could not stimulate plant growth such as *Pseudomonas fluorescens* strain A23T3c and *Burkholderia cepacia* strain PHP7. Singh and Jha [299] concluded that under salinity stress, *Enterobacter* sp. SBP-6 can be applied for promoting the sorghum plants growth. *Beauveria bassiana* strain GHA could possibly control *Melanaphis sacchari* infestations in sorghum if utilized under suitable environmental conditions [300]. *Beauveria bassiana* can become an endophyte in sorghum and lead to protecting from stem borer, and it has been suggested that stem tunneling by shoot borer was significantly greater compared to *Beauveria bassiana* treated sorghum plants [301]. The endophytic colonization of sorghum by *Beauveria bassiana* indicates that this isolate is well adjusted to a wide range of conditions consisting of endophytic in plants and pathogenic to insects, and it can recognize as an endophyte in sorghum without negatively impacting plant growth [302]. Ramos et al. [303], and Liu et al. [304] reported that *Beauveria bassiana* resulted in appropriate endophytic colonization in crop tissues and regulated stem height, fresh root, fresh stem weight, and root length, and it has been suggested due to its high application potential in eco-agricultural fields including biofertilizers and biopesticides. Raya-Diaz et al. [305] showed that *Beauveria bassiana* boosted the Fe nutrition of

the sorghum plants, but their impacts associated to the inoculation method. Schlemper et al. [306] reported that *Burkholderia tropica* strain IAC/BECa 135 is an appropriate PGPB strain for application as inocula for sustainable sorghum cultivation because it can notably improved the plant biomass of sorghum plants. A significant increase in the yield level of sorghum because of combined inoculation of phosphate solubilizing bacteria and *Azospirillum brasilense* over single inoculation showing a positive interaction between the 2 groups of bacteria [307]. The interactions between *Azospirillum brasilense* and *endomycorrhizae* may increase shoot-to-root ratios, plant dry weight, and the nitrogen content of infected plants [308]. *Pseudomonas* sp. P17 strain as a potential PGPR for plant growth and nutrient uptake in sorghum, as inoculation lead to better growth, higher nutrient uptake and seedlings treated, as well as appropriate root volume, maximum dry mass, shoot length, chlorophyll, leaf area, phosphorus, nitrogen, carbohydrates and other nutrients [309–312]. Saad and Abo-Koura [313] reported that inoculation of sorghum plants with *Bacillus cereus* could improved vegetative growth, RWC% but reduced antioxidant enzymes under drought stress. Wu et al. [314] found that *Bacillus amyloliquefaciens* can be applied to manipulate the microbial communities of the sorghum rhizosphere soil.

Conclusions

Plant growth promoting bacteria are described as bacteria that can increase plant growth and protect plants from abiotic stresses and diseases through different types of mechanisms. They can increase nutrient uptake by changing the level of plant hormone that increases root surface area by improving its shape, so promoting in absorbing more nutrients. *Rhizobium* are known to form colonies on the root surface stimulating biological nitrogen fixations and providing nitrogen to the leguminous crops and they are known as an important procedure for improving both soil fertility and yield. *Bacillus* strain are aerobic, Gram-positive, endospore-forming, rod-shaped bacteria. The *Bacilli* rhizobacteria are known for many unique properties and functions in plant rhizospheres such as biofertilization, bioprotection and phytostimulation. *Bacilli* rhizobacteria can present both environmentally-friendly and an efficient technology. *Pseudomonas* are Gram-negative aerobic chemoheterotrophs are commonly found in the environment. They show diverse enzymatic systems and are capable of conducting different biochemical transformation. *Streptomyces* are marine- and soil-dwelling microbes that need to survive dramatic fluctuations in nutrient levels and environmental conditions. The importance of *Streptomyces* strains in plant growth promotion is clearly expressed in their antipathogenic activities. Most of the activities of the *Streptomyces* genus come from its unique capability to produce secondary metabolites. Under different environmental conditions, and on the basis of the abundance and function of microbial strains in sorghum producing regions, appropriate application of rhizosphere growth-promoting bacteria can effectively improve the yield of sorghum. The plant growth promoting bacteria can be active under abiotic stress conditions by various mechanisms such as synthesis of heat shock protein, biofilm formation, osmoprotective compounds, etc. They can be used to increase soil characteristics, increase plant growth, reduce abiotic stresses, and improve phytoremediation effectiveness in an environmentally friendly process. The plant growth-promoting bacteria can change the rhizosphere bacteria community composition, boosting the activity of soil bacteria and upregulating gene expression. A lot of researches have shown the significant roles of plant growth promoting bacteria in nutrient absorption, plant root development and disease resistance improvement, however, more researches are needed to survey the influence of different plant growth promoting bacteria on sorghum yield and yield components.

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