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- Review -

# Current Perspectives on the Effects of Plant Growth-promoting Rhizobacteria

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The rhizosphere is the active zone where plant roots communicate with the soil microbiome, each responding to the other's signals. The soil microbiome within the rhizosphere that is beneficial to plant growth and productivity is known as plant growth-promoting rhizobacteria (PGPR). PGPR take part in many pivotal plant processes, including plant growth, development, immunity, and productivity, by influencing acquisition and utilization of nutrient molecules, regulation of phytohormone biosynthesis, signaling, and response, and resistance to biotic- and abiotic-stresses. PGPR also produce secondary compounds and volatile organic compounds (VOCs) that elicit plant growth. Moreover, plant roots exude attractants that cause PGPR to aggregate in the rhizosphere zone for colonization, improving soil properties and protecting plants against pathogenic factors. The interactions between PGPR and plant roots in rhizosphere are essential and interdependent. Many studies have reported that PGPR function in multiple ways under the same or diverse conditions, directly and indirectly. This review focuses on the roles and strategies of PGPR in enhancing nutrient acquisition by nutrient fixation/solubilization/mineralization, inducing plant growth regulators/phytohormones, and promoting growth and development of root and shoot by affecting cell division, elongation, and differentiation. We also summarize the current knowledge of the effects of PGPR and the soil microbiota on plants.

**Key words** : Nutrient, PGPR, phytohormone, plant growth and development, rhizosphere

## Introduction

Plant–microbe interactions occur in the rhizosphere and endosphere (Fig. 1). Endophytic bacteria are those that colonize the internal tissues of plants without having negative effects on their host [99]. Endophytes often promote plant growth and development [29]. The rhizosphere is the active microbial region surrounding the root system and is influenced by root exudates (Fig. 1) [47, 112]. The rhizosphere bacterial population is estimated to be 10 to 100 times higher than the bulk soil population [17]. Root exudates contain abundant ions, oxygen, water, and carbon-containing compounds [72, 112]. Root exudates can serve as attractants or repellents that accumulate favorable microbes or protect plants from pathogens, according to the physiological condition of the plant [5]. The various plant–microbiome interactions in the rhizosphere affect plant growth and development, influencing crop yields [18, 102]. Beneficial bacteria in the rhizosphere, termed plant growth-promoting rhizobacteria (PGPR), enhance plant health, growth, and yield [64, 107, 109].

PGPR affect plant growth and development via direct and indirect mechanisms (Fig. 1) [43, 48]. PGPR directly/indirectly affect plant developmental and metabolic processes, not only by the bacteria themselves but also by the production and secretion of various compounds, including phytohormones, anti-oxidants, proline, antifreeze proteins, volatile organic compounds (VOCs), antibiotics, and lytic enzymes. In direct mechanisms, the PGPR and their products improve the mobility and availability of nutrients for easy uptake by plants [76], regulating plant growth and development. Indirectly, PGPR products induce abiotic stress tolerance, change the properties of the soil environment by attracting a beneficial microbiome or repelling phytopathogens, and modify soil structure by solubilizing or sequestering heavy metal elements [2, 76]. Table 1 lists recent studies of PGPR. In this review, we update the information on the important effects of PGPR for enhancing plant growth directly by facilitating resource acquisition and stimulating phytohormones.

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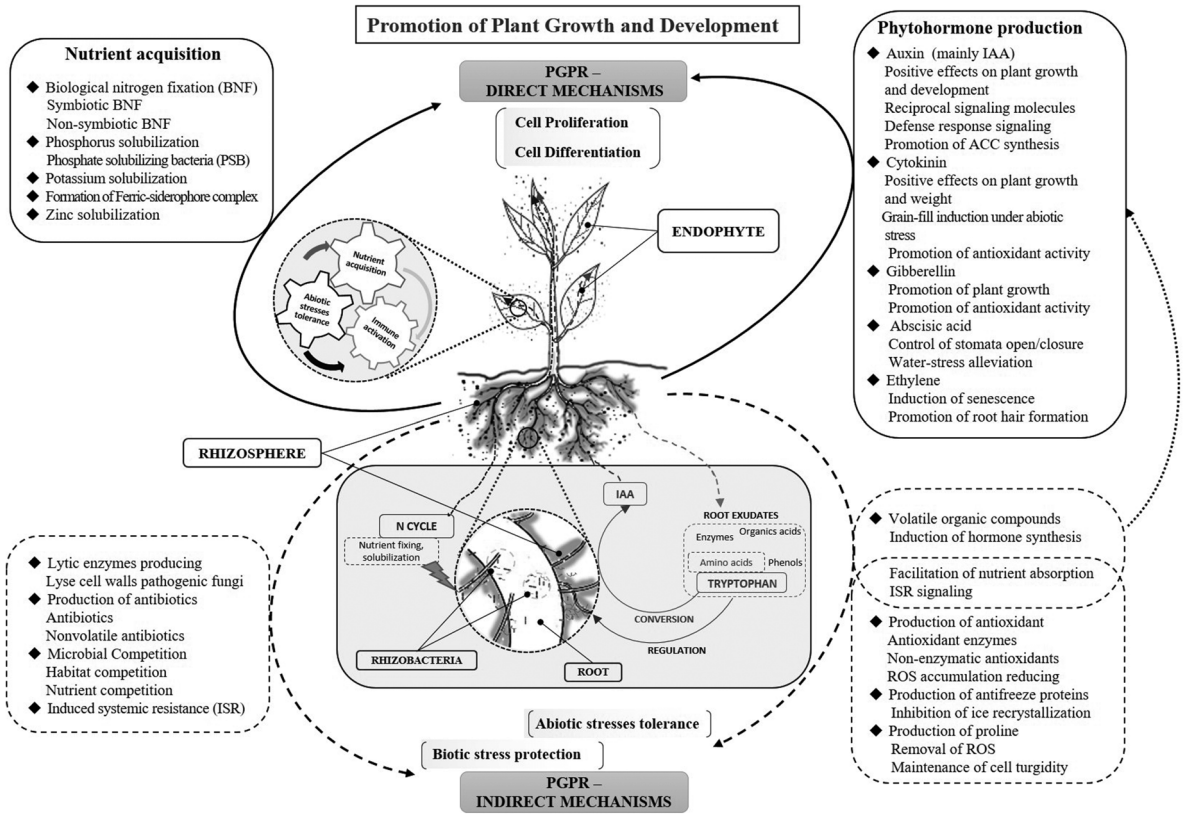


Fig. 1. Direct and indirect mechanisms of the effects of PGPR on plants. PGPR inhabit the rhizosphere or are endophytes and affect cell growth, including cell proliferation, expansion, and differentiation, thereby modifying plant growth and fitness. Direct mechanisms increase the availability of essential nutrients and the production or release of phytohormones. The indirect mechanisms improve plant tolerance of abiotic or biotic stresses. VOCs can also promote PGPR hormone production directly. The solid arrows and boxes indicate direct mechanisms; the dashed arrows and boxes indicate indirect mechanisms of PGPR on host plants; and the dotted arrow shows the effect of VOCs on hormone-producing PGPR. A middle gray box at the bottom shows an example of the direct signals between rhizobacteria and plant roots.

## PGPR and nutrient acquisition

Numerous factors affect plant growth, including external and internal cues. Nutrients are important factors that induce plant growth and productivity and increase plant biomass. PGPR improve the mobility of nutrients in the soil and rhizosphere, which facilitates plant uptake. The following paragraphs outline the mechanisms by which PGPR increase the bioavailability of soil-borne nutrients.

### *Biological nitrogen fixation*

Nitrogen (N) is an essential constituent of proteins and nucleic acids [104] and is the most important plant nutrient. More than 78% of all N is present in gaseous form. PGPR can reduce $N_2$ in the atmosphere to ammonia ($NH_3$), a usable organic form, through biological nitrogen fixation (BNF) via nitrogenase [63]. At mild temperatures, PGPR induce BNF [96]. There are two main groups of BNF bacteria: symbiotic (endophytic) (*Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Mesorhizobium*, and *Frankia*) [117], and non-symbiotic (free-living) (*Azoarcus*, *Azotobacter*, *Acetobacter*, *Azospirillum*, *Burkholderia*, *Cyanobacteria*, *Enterobacter*, *Gluconacetobacter*, and *Pseudomonas*) BNF bacteria [19]. The symbiotic BNF bacteria are responsible for more than 80% of global BNF, and the remaining 20% is supplied by non-symbiotic free-living BNF bacteria [32].

### *Bio-available phosphorous for plant uptake*

Phosphorus (P) plays a key role in energy transfer, photosynthesis, macromolecule biosynthesis, and vital metabolic processes in plant growth [9, 51]. P is present in both organic and inorganic forms [61]. However, the mobility of P is affected by the soil structure and soil quality, and the amount of usable P in soil is low. PGPR can solubilize and activate

the P from soil. Phosphate-solubilizing bacteria (PSB) can convert phosphate from many unavailable forms, such as rock phosphate and mono-calcium or di-calcium phosphate, into available forms by producing enzymes and acids [25, 88]. PGPR involved in the solubilization and mineralization of P including *Arthrobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Pseudomonas*, and *Rhizobium* (Table 1). Recent studies have shown that the performance of PSB is affected by external factors, particularly stress conditions [4, 65].

### *Potassium solubilization*

Potassium (K) is important for photosynthesis, enzyme activation, and protein synthesis. K deficiency causes poor root structure, represses growth, and lowers productivity. Soluble K is present in soil in low concentrations and more than 90% of K is in inactive forms such as silicate minerals and rocks [39, 90]. *Bacillus mucilaginosus*, *Bacillus edaphicus*, *Burkholderia* sp., *Acidithiobacillus ferrooxidans*, *Pseudomonas* sp., and *Paenibacillus* sp. are PGPR that release soluble K from K-bearing soil (Table 1) [69]. The application of PGPR as K bio-fertilizer to reduce the use of chemical fertilizers and support eco-sustainable agriculture has been reported [100].

### *Iron chelate produced by siderophores*

Iron (Fe) is an essential protein co-factor involved in vital metabolic processes such as photosynthesis and respiration [30, 89]. Fe is mainly present as ferric ions ($Fe^{3+}$), which living organisms cannot absorb [8]. Fortunately, some rhizosphere bacteria increase the solubility of iron by producing siderophores, a ferric-iron-specific chelating agent [41, 114]. Representative PGPR that produce siderophores include *Pseudomonas*, *Azotobacter*, *Bacillus*, *Enterobacter*, *Serratia*, *Azospirillum*, and *Rhizobium*. The siderophore complex reduces ferric ions ($Fe^{3+}$) into ferrous ions ($Fe^{2+}$), which easily enter cells (Table 1) [95]. These siderophores also form complexes with other metals such as molybdenum, manganese, cobalt, and nickel, increasing their availability to plants and other microorganisms.

### *Zinc solubilization*

In plants, zinc (Zn) deficiency affects membrane integrity, protection against abiotic stress, and the synthesis of chlorophyll, carbohydrates, auxins, and nucleotides [56, 106]. The majority of Zn in soil is in insoluble sphalerite form (ZnS) or in various mineral ores; a minority is in soluble form, and plants can acquire divalent zinc. Communication among PGPR is involved in the solubilization and activation of Zn through soil acidification, proton and siderophore production, and oxidoreductive systems, which increase the ability of plants to absorb Zn [44]. Zn-solubilizing PGPR include *Pseudomonas aeruginosa*, *Bacillus aryabhattai, Gluconacetobacter diazotrophicus*, *Pseudomonas striata*, *Pseudomonas fluorescence*, *Burkholderia cenocepacia*, *Serratia liquefaciens*, *Serratia marcescens*, and *Bacillus thuringiensis* (Table 1). Inoculation with these Zn-solubilizing bacteria increased the Zn content of straw and grains, promoting growth and increasing yield in soybean, rice, maize, and wheat (Table 1) [1].

## PGPR produce phytohormones

Plants synthesize phytohormones to regulate their developmental and physiological processes and to recognize internal and external environmental changes as signals and ligands. There are 11 classes of phytohormones: auxins, abscisic acid (ABA), cytokinins (CKs), gibberellins (GAs), ethylene, brassinosteroids, jasmonates (JA), nitric oxides, polyamines, salicylic acids, and strigolactones [12, 20]. Many studies of genetic mutants of Arabidopsis have recognized the interactions between plants and particular phytohormones. The beneficial microbiota stimulates the biosynthesis of phytohormones, which promotes plant growth and nutrient acquisition. The interactions of plants with symbiotic or non-symbiotic bacteria influence plant growth, development, health, and yield by producing and secreting various metabolically active compounds [11, 38]. Not surprisingly, microbial regulators, which are very similar to phytohormones, affect plants. These microbial phytohormones have similar effects on the supply of exogenous phytohormones. The PGPR genera *Arthrobacter*, *Bradyrhizobium*, *Mesorhizobium*, *Bacillus*, *Rhizobium*, *Rhanella*, *Pantoea*, *Pseudomonas*, *Herbaspirillum*, *Enterobacter*, *Brevundimonas*, and *Burkholderia* can produce phytohormones (Table 1), which affects cell division and differentiation and the root structure, ultimately altering plant growth and development (Fig. 1) [11, 38].

### *Auxin*

Auxins are important hormones that contribute to the overall architecture of the plant from the cellular to the individual plant level. Auxins participate in polar signaling in the elongation of sub-apical meristem cells, organ for-

Table 1. Recent studies on the interaction of plant-PGPR and plant-growth promoting effects

| Category | | Function | PGPR | Plant | Ref. |
|---|---|---|---|---|---|
| Nutrient acquisition | Nitrogen | - Enhance root nodule and nitrogen uptake | *Bradyrhizobium* | Soybean | [7] |
| | | - Enhance total N in shoot and nodule | *Bradyrhizobium japonicum* (CIAT88, CIAT89, CIAT104 and CIAT105) | Soybean | [111] |
| | | - Enhance N content and total yield | *Burkholderia vietnamiensis* MGK3 | Rice | [46] |
| | | - Enhance N uptake and total biomass | *Herbaspirillum seropedicae* Z67 | Rice | [53] |
| | Phosphate | - Produce hydrogen cyanide<br>- Release exopolysaccharide compounds<br>- Enhance N and P content and grain yield | *Azotobacter chroococcum*<br>*Pseudomonas striata*<br>*Glomus fasciculatum* | Wheat | [119] |
| | | - Produce $NH_3$<br>- Enhance salinity tolerance<br>- Promote pharmaceutical content | *Pseudomonas florescence* CL12 | Turmeric | [66] |
| | | - Produce hydrogen cyanide<br>- Release exopolysaccharide compounds<br>- Increase N and P content and seed yield and protein | *Pseudomonas aeruginosa* PS1 | Mung bean | [3] |
| | | - Produce siderophore<br>- Enhance root and shoot elongation<br>- Enhance toxic heavy metal tolerance | *Pseudomonas* sp. NBRI 4014 | Soybean | [49] |
| | | - Active the detoxification process (induction of element P, K, S, Ca)<br>- Enhance toxic heavy metal tolerance<br>- Enhance biomass and grain yield | *Azospirillium lipoferum* 137<br>*Arthobacter mysorens* 7<br>*Agrobacterium radiobacter* 10<br>*Flavobacterium* sp. L30 | Barley | [16] |
| | | - Produce Enzymes (phosphatase and phytase)<br>- Enhance total organic P and K content | *Bacillus amyloliquefaciens*<br>*Bacillus flexus*<br>*Bacillus licheniformis*<br>*Bacillus methylotrophicus*<br>*Bacillus pumilus*<br>*Bacillus subtilis*<br>*Bacillus tequilensis*<br>*Brevibacillus formosus* | Wheat, Rice, Banana, Maize, Sorghum | [13] |
| | | - Promote potassium solubilization<br>- Enhance total organic P, K content<br>- Inhibit pathogenic microorganisms | *Paenibacillus kribensis* CX-7 | Wheat | [122] |
| | Potassium | - Promote nutrient uptake<br>- Enhance total N-P-K content in seedling, plant dry weight | *Agrobacterium tumefaciens*<br>*Burkholderia cepacia*<br>*Enterobacter asburiae*<br>*Enterobacter aerogenes*<br>*Enterobacter cloacae*<br>*Klebsiella variicola*<br>*Microbacterium foliorum*<br>*Myroides odoratimimus*<br>*Pantoea agglomerans* | Tobacco | [123] |
| | Iron | - Produce hydrogen cyanide<br>- Release exopolysaccharide compounds<br>- Enhance grain yield | *Azotobacter chroococcum*<br>*Glomus fasciculatum*<br>*Pseudomonas striata* | Wheat | [119] |
| | | - Enhance salinity tolerance<br>- Promote pharmaceutical content. | *Pseudomonas florescence* CL12 | Turmeric | [66] |
| | | - Produce hydrogen cyanide<br>- Release exopolysaccharide compounds<br>- Increase Zn, chlorophyll, leghemoglobin content, seed yield, and seed protein | *Pseudomonas aeruginosa* PS1 | Mung bean | [3] |
| | Zinc | - Promote P solubilization,<br>- Produce siderophore<br>- Enhance ACC-deaminase activity<br>- Improve grain yield | *Bacillus thuringiensis*<br>*Serratia liquefaciens*<br>*Serratia marcescens* | Wheat | [1] |

Table 1. Continued

| Category | | Function | PGPR | Plant | Ref. |
|---|---|---|---|---|---|
| Phytohormone production | Auxin | - Promote root morphogenesis | *Aeromonas punctate* PNS-1 | *Arabidopsis thaliana* | [52] |
| | | - Dehydrogenase activity<br>- Enhance Fluorescein diacetate hydrolysis<br>- Enhance Plant growth and yield | *Alcaligenes* sp. WRB10<br>*Anabaena oscillarioides* WRC3<br>*Anabaena torulosa* WRC4<br>*Providencia* sp. WRB4<br>*Triticum aestivum variety* PBW343 | Wheat | [74] |
| | | - Enhance salinity tolerance<br>- Promote pharmaceutical content | *Pseudomonas florescence* CL12 | Turmeric | [66] |
| | CK | - Increase shoot and root weight | *Bacillus sp.*739<br>*Bacillus subtilis* IB-15<br>*Bacillus subtilis* IB-22 | Lecture | [10] |
| | | - Promote antioxidant biosynthesis<br>- Delay leaf senescence<br>- Enhance tolerance to severe drought stress | *Sinorhizbium meliloti* | Alfalfa | [115] |
| | GA | - Up regulate $GA_4$ and SA production<br>- Enhance chlorophyll content under osmotic and salinity stress | *Acinetobacter calcoacetius* SE370<br>*Burkholderia cepacia* SE4<br>*Promicromonospora* sp. SE188 | Cucumber | [59] |
| | | - Regulate 3β hydroxylated GAs production<br>- Enhance endogenous GA synthesis | *Bacillus pumilus*<br>*Bacillus licheniformis* | Alder | [50] |
| | | - Enhance endogenous salicylic acid | *Bacillus amyloliquefaciens* RWL-1 | Rice | [101] |
| | | - Up regulate GAs and ABA production<br>- Enhance salinity tolerance | *Azospirillum lipoferum* USA 59b | Maize | [27] |
| | Abscisic acid | - Down regulate the ABA production<br>- Enhance chlorophyll content under osmotic and salinity stress | *Acinetobacter calcoacetius* SE370<br>*Burkholderia cepacia* SE4<br>*Promicromonospora* sp. SE188 | Cucumber | [59] |
| | | - Enhance proline level and photosynthesis under drought condition | *Azospirillum brasilense* Sp245 | *Arabidopsis thaliana* | [28] |
| | | - Decrease endogenous ABA and JA<br>- Enhance endogenous salicylic acid | *Bacillus amyloliquefaciens* RWL-1 | Rice | [101] |
| | Ethylene | - Produce ACC deaminase<br>- Promote root morphogenesis | *Aeromonas punctate* PNS-1 | *Arabidopsis thaliana* | [52] |
| | | - Metabolize ACC by ACC deaminase<br>- Decrease ACC level in rosette leaves | *Variovorax paradoxus* 5C-2 | *Arabidopsis thaliana* | [68] |
| Promotion of cell growth | Root | - Produce *acetoin* and volatiles compounds | *Bacillus megaterium* UMCV1 | Bean, *Arabidopsis thaliana* | [71] |
| | | - Regulate expression of auxin and ethylene signaling related genes | *Burkholderia phytofirmans* PsJN | *Arabidopsis thaliana* | [94] |
| | | - Local ethylene emission activation | *Phyllobacterium brassicaearum* STM196 | *Arabidopsis thaliana* | [40] |
| | | - Enhance auxin regulated gene expression | *Pseudomonas fluorescens* WCS417 | *Arabidopsis thaliana* | [120] |
| | | - Produce substrate lumichrome<br>- Increase number of nodules | *Mesorhizobium loti* | Lotus | [45] |
| | Shoot (Leaves & Stem) | - Up regulate 3β hydroxylated GAs | *Bacillus licheniformis*<br>*Bacillus pumilus* | Alder | [50] |
| | | - Release lipo-chitooligosaccharide<br>- Release lumichrome | *Bradyhizobium japonicum* | Maize, Soybean | [62] |
| | | - Release lumichrome | *Sinorhizobium melioti* | Maize, Sorghum | [77] |
| | | - Up regulate GAs and ABA | *Azospirillum lipoferum* USA 59b | Maize | [27] |
| | | - Produce lumichrome | *Sinorhizobium melioti* | Soybean, Cowpea | [77] |
| | Yield | - Promote solubilization<br>- Produce siderophore<br>- Enhance ACC-deaminase activity | *Bacillus thuringiensis*<br>*Serratia liquefaciens*<br>*Serratia marcescens* | Wheat | [1] |
| | | - Release lumichrome | *Glomus intraradices/Glomus mossea* | Tomato | [45] |
| | | - Release rhizobacterial VOCs<br>- Regulate auxin homeostasis | *Bacillus sbutilis* GB03 | *Arabidopsis thaliana* | [121] |

mation, shoot elongation, and root development via phototropism and gravitropism. Auxin signaling and plant biosynthesis are tightly regulated [33, 37]. The most essential auxin is indole-3-acetic acid (IAA), which has major effects in intact plants and is the most potent native auxin [67, 105, 110]. IAA is biosynthesized by both PGPR and pathogenic bacteria [37, 54, 91]. IAA-producing bacteria have the potential to interfere with plant auxin homeostasis. Whether bacterial IAA promotes or inhibits plant growth depends on the plant endogenous IAA level and amount of bacterial IAA produced [75, 91]. Some reports describe the negative effects of bacterial IAA, such as reduced root motility, debilitation of the plant defense system by loosening the plant cell wall and altering the hypersensitive response, and promoting pathogen colonization [83, 91]. However, most research has found that auxin-producing bacteria positively affect important steps in plant growth and development. Rhizobacteria producing IAA promote plant growth when bacterial IAA is within an ideal concentration range. IAA-producing bacteria, such as *Agrobacterium*, *Bradyrhizobium*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, and *Rhizobium*, promote root elongation and lateral root formation in canola, *Medicago*, and wheat in host specific- and dose-dependent manners as PGPR (Table 1) [91, 104]. PGPR producing IAA also promote root hair formation, resulting in root system development, improved water and nutrient acquisition, and root anchoring in the soil as well as increased plant biomass. Some research shows that auxin-producing PGPR can directly stabilize the auxin level of host plants by supplying auxin in root nodules [41]. Most auxin-producing rhizobial knock-out mutants are still involved in plant growth and development, suggesting the existence of other mechanisms that act in combination with IAA biosynthesis, such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase, phosphate solubilization, or dinitrogen fixation, on biomass [35]. ACC deaminase production by PGPR represses the inhibition of root growth by converting ACC into ammonia and alpha-ketobutyrate [35]. Bacterial IAA induces the activation of key enzymes in the tricarboxylic acid cycle, which enhances nitrogen fixation in plant nodules and increases plant biomass [124]. IAA is also a reciprocal signaling molecule that sustains symbiotic relationships that have co-evolved between plants and bacteria. Despite the characterization of IAA synthesis pathways from isolated IAA-producing bacteria, the details of the interactions between plants and PGPR are still unclear. Nevertheless, the co-cultivation of plants and IAA-producing bacteria should improve biofertilization, phytostimulation, and biocontrol to reduce the use of chemical fertilizers and herbicides.

### *Cytokinin*

Cytokinin (CK) is also an important hormone that is involved in developmental processes throughout plant life, including meristematic cell division and differentiation, organ formation, root hair induction, and leaf expansion and senescence delay in plants [24, 33]. CK is also involved in chloroplast and xylem differentiation, apical dominance, blooming and fruiting, nutrient signals, and plant–pathogenic bacteria interactions [98]. CK produced by *Bacillus subtilis* accumulates in plants, resulting in increased plant growth and weight (Table 1) [10]. Several CK-producing bacteria have been shown to improve the drought tolerance of alfalfa and enhance rhizobacterial colonization in the rhizosphere [115]. The increased CK concentration under abiotic stress is linked to a stay-green phenotype and improved grain filling and antioxidant production (Table 1) [22, 80, 108].

### *Gibberellin*

Gibberellins (GA), which are synthesized from diterpenoid acids via the terpenoid pathway, stimulate stem elongation [36, 118] and promote chlorophyll biogenesis and the photosynthetic rate of plants [60, 116]. GA production has been detected in both fungi and bacteria [23]. The fungus *Gibberella fujikuroi* GA pathway is distinct from the host plant pathway [21]. GA have been also detected in *Achromobacter xylosoxidans*, *Acinetobacter calcoaceticus*, *Azotobacter* spp., *Azospirillum* spp., *Bacillus* spp., *Gluconobacter diazotrophicus*, *Herbaspirillum seropedicae*, and *Bradyrhizobium* and *Rhizobium* strains (Table 1) [34]. Some nitrogen-fixing bacteria, including a soybean symbiont (*Bradyrhizobium japonicum*) and a broad-host-nodulating species (*Sinorhizobium fredii*), contain a putative GA biosynthetic operon/gene cluster necessary to produce $GA_9$ [85], suggesting that a GA biosynthetic pathway evolved independently in bacteria (Table 1). Under abiotic stress, especially osmotic stress in plants, the presence of GA can promote antioxidant enzyme production by reducing the level of reactive oxygen species, thereby improving the plant host fitness [73].

### *Abscisic acid*

Abscisic acid (ABA) is biosynthesized in plants by an indirect pathway in which ABA is converted from the car-

otenoid lycopene enzymatically [82]. ABA plays roles in abiotic stress protection (salinity, drought, and metal toxicity), bud dormancy, fruit ripening, stomata opening and closing, suppression of seed germination, and inhibition of root elongation [33, 103]. Based on many in vitro studies, it was proposed that PGPR produce ABA [26], including *Azospirillum brasilense* and *Bradyrhizobium japonicum*. *Azospirillum brasilense* grown on defined media produced ABA. In vitro, the ABA concentration doubled in plant tissues when Arabidopsis seedlings were treated with *Azospirillum brasilense* suspension, indicating that PGPR promote plant ABA levels (Table 1) [26]. A similar result was reported when aseptic maize seedlings were inoculated with *Azospirillum lipoferum* USA59b, which may help to alleviate water stress in plants [27].

### *Ethylene*

Ethylene or ripening hormone plays an important role in physiological processes, including stimulation of fruit ripening, cell expansion, seed germination, and senescence [33]. Ethylene represses primary root elongation and lateral root formation [84, 92]. Recent research focused on the effect of rhizobacteria on plant ethylene levels via ACC deaminase [42, 78, 81], which is found in 34 bacterial genera, and *Azospirillum brasilense* Sp245 was one of the best-known PGPR [15]. This enzyme is a key factor in PGPR activity to stimulate root elongation via a reduction in endogenous ethylene.

## PGPR affect plant growth and development

Through direct (such as the production of phytohormones and facilitation of soil nutrient acquisition) and indirect (such as competition with pathogens and improvement of soil properties) mechanisms, PGPR affect host plant growth and development, from the molecular level to crop yield. Because PGPR inhabit the rhizosphere, many studies have focused on the effects of PGPR on root systems. Of the various hormones produced by PGPR, auxins influence root architecture [113] and development [55] by altering cell division and differentiation. Auxin-producing PGPR evoked transcriptional changes in root elongation induction and cell wall-related genes and increased root biomass and stomata size, while reducing stomata density [70].

PGPR affect both cell division at the root meristem and the sites of lateral root formation in cell division and differentiation. Inoculating Arabidopsis seedlings with PGPR, such as *Bacillus megaterium* UMCV1 or *Pseudomonas simiae* WCS417, altered maintenance of the root stem cell niche and the transition from cell proliferation to cell differentiation (Table 1) [71, 120]. *Pseudomonas simiae* increases cell division in the root meristematic zone [120], whereas *Bacillus megaterium* decreases cell division [71]. However, inoculation with these bacteria caused a decrease in primary root length, due to decreased cell elongation in the elongation zone by 40% and 50%, respectively [71, 120]. PGPR also affect the formation of root hairs, which emerge closer to the root tip. The changes in root development caused by PGPR result from modification of the plant hormone response. *Pseudomonas simiae* WCS417 induced increased meristematic cell division and lateral root numbers, suggesting increased auxin-responsive gene expression. By contrast, *Bacillus megaterium* UMCV1 induced decreased meristematic cell division (Table 1) [71, 120]. The cellular and genetic effects of PGPR on the root system accompany changes in the endogenous phytohormone response. Inoculating plants with IAA-producing rhizobacteria strains induced growth in root length and leaves under saline conditions [6]. *Bacillus subtilis* GB03, which produces IAA, initiated growth by modifying auxin homeostasis and cell-wall-loosening enzymes [97, 121].

Bacteria, including PGPR, produce and secret quorum-sensing molecules, which are involved in cell-to-cell communication to monitor cell density and the composition of the microbial community in the extracellular environment by adjusting their gene expression and physiological processes [113]. Quorum sensing negatively regulates IAA production in bacteria. A few strains of *Azospirillum lipoferum* produce quorum-sensing N-acyl-homoserine lactone (AHL) molecules that reduce IAA production via AHL inactivation [113]. AHL alters root development in Arabidopsis by inhibiting primary root growth, altering lateral root formation, and causing the proliferation of root hairs, thereby increasing the absorptive surface [86, 87]. Depending on the concentration and length of AHLs, AHL-producing rhizobacteria induce distinct changes in root systems. For example, high AHL concentrations promote lateral root development and inhibit primary root growth, perhaps by altering cytokinin signaling rather than the auxin response [86]. Conversely, at low concentrations, short-chain AHLs promote primary root elongation by inducing increased numbers of meristematic cells and increasing cell size in the elongation zone [124]. Similarly, VOCs produced by PGPR affected the growth of

*Arabidopsis thaliana* [121] and *Lactuca sativa* [79] by up-regulating the expression of auxin synthesis genes, modifying the cell well by promoting the expression of expansion genes (*EXP1*, *EXP6*, and *EXPA5*), and regulating auxin homeostasis (Table 1). PGPR are also reported to affect other plant parts, such as leaves and stems. Tomato plants inoculated with the PGPR *Promicromonospora* sp. SE188 had longer shoots and greater biomass, exhibiting GA-production and phosphate-solubilization activities [57]. GA-deficient mutant soybean plants had increased total weight, plant height, and chlorophyll content when inoculated with GA-producing *Pseudomonas putida* H-2-3 [58]. The PGPR *Burkholderia phytofirmans* PsJN enhanced primary root growth, root hair development and growth, and aerial growth, including increasing the size of leaf epidermal cells [93]. The secondary metabolites and VOCs produced by PGPR can improve plant growth and development. PGPR-produced VOCs accelerate increased shoot length and biomass [14], shorten leaf emergence, or increase leaf size via lumichrome and riboflavin [31]. Many studies have reported that PGPR exudates, VOCs, secondary metabolites, and phytohormones influence root permeation and the transport of nutrients to the shoot, and promote cell division and expansion, ultimately resulting in increased plant growth. Although further studies of the physiological, molecular, and genetic interactions between plants and PGPR are required, the appropriate coordination of crop species and PGPR should provide renewable methods to enhance crop yield.

## Conclusion

Plants have evolved reciprocally beneficial interactions in the rhizosphere with various rhizobacteria and have used them to recognize and adapt to changes in the external environment. This review summarized the effects of PGPR in promoting various characteristics of plant growth via direct mechanisms. PGPR help to increase the availability of essential nutrients by mobilizing, solubilizing, or producing siderophore compounds, thereby promoting plant growth. Phytohormones produced or released by PGPR play dual roles: modifying the physiological processes of the host and protecting plant processes under biotic or abiotic stresses. Rhizobacteria-produced exudates, including secondary metabolites, VOCs, and quorum-sensing molecules, can modify the physical, chemical, and biological properties of the rhizosphere environment. These modifications directly or indirectly stimulate cell division and expansion, facilitate nutrient acquisition, and activate defenses against abiotic and biotic stresses. However, the details of the mechanisms of the effects of PGPR on plants at the cellular, genetic, and molecular levels remain poorly understood. It is important to investigate these effects of PGPR under controlled conditions to reveal the precise mechanisms by which PGPR promote plant growth and increase crop yields. Ultimately, PGPR are a promising approach to replace chemical fertilizers, synthesized hormones, and chemical pesticides in agriculture.

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## References

1. Abaid-Ullah, M., Hassan, M. N., Jamil, M., Brader, G., Shah, M. K., Sessitsch, A. and Hafeez, F. Y. 2015. Plant growth promoting rhizobacteria: an alternate way to improve yield and quality of wheat (*Triticum aestivum*). *Int. J. Agric. Biol.* **17**, 51-60.
2. Ahemad, M. 2012. Implications of bacterial resistance against heavy metals in bioremediation: a review. *J. Inst. Integr. Omics Appl. Biotechnol.* **3**, 39-46.
3. Ahemad, M. and Khan, M. S. 2010d. Phosphate-solubilizing and plant growth promoting *Pseudomonas aeruginosa* PS1 improves greengram performance in quizalafop-p-ethyl and clodinafop amended soil. *Arch. Environ. Contam. Toxicol*. **58**, 361-372.
4. Ahemad, M. and Khan, M. S. 2012a. Effect of fungicides on plant growth promoting activities of phosphate solubilizing *Pseudomonas putida* isolated from mustard (*Brassica compestris*) rhizosphere. *Chemosphere* **86**, 945-950.
5. Ahemad, M. and Kibret, M. 2014. Mechanisms and applications of plant growth promoting rhizobacteria: Current perspective. *J. King Saud Univ. Sci.* **26**, 1-20.
6. Albacete, A., Ghanem, M. E., Martínez-Andújar, C., Acosta, M., Sánchez-Bravo, J., Martínez, V., Lutts, S., Dodd, I. C. and Pérez-Alfocea, F. 2008. Hormonal changes in relation to biomass partitioning and shoot growth impairment in salinized tomato (*Solanum lycopersicum L.*) plants. *J. Exp. Bot.* **59**, 4119-4131.
7. Alves, B. J. R., Boddey, R. M. and Urquiaga, S. 2004. The success of Biological Nitrogen Fixation (BNF) in soybean in Brazil. *Plant Soil*. **252**, 1-9.
8. Ammari, T. and Mengel, K. 2006. Total soluble Fe in soil solutions of chemically different soils. *Geoderma* **136**, 876-885.
9. Anand, K., Kumari, B. and Mallick, M. A. 2016. Phosphate

solubilizing microbes: An effective and alternative approach as biofertilizers. *Int. J. Pharm. Pharm. Sci.* **8**, 37-40.
10. Arkhipova, T., Veselov, S., Melentiev, A., Martynenko, E. and Kudoyarova, G. 2005. Ability of bacterium *Bacillus subtilis* to produce cytokinins and to influence the growth and endogenous hormone content of lettuce plants. *Plant Soil.* **272**, 201-209.
11. Arora, N. K., Tewari, S. and Singh, R. 2013. Multifaceted plant-associated microbes and their mechanisms diminish the concept of direct and indirect PGPRs, pp. 411-449. In: Arora, N. K. (ed) *Plant microbe symbiosis: fundamentals and advances*. Springer, New Delhi, India.
12. Arshad, M. and Frankenberger, W. T. 1998. Plant growth-regulating substances in the rhizosphere: Microbial production and functions. *Adv. Agron*. **62**, 46-151.
13. Bahadur, I., Maurya, B. R., Meena, V. S., Saha, M., Kumar, A. and Aeron, A. 2017. Mineral release dynamics of tricalcium phosphate and waste muscovite by mineral-solubilizing rhizobacteria (MSR) isolated from Indo-Gangetic Plain (IGP) of India. *Geomicrobiol. J.* **34**, 454-466.
14. Bailly, A. and Weisskopf, L. 2012. The modulating effect of bacterial volatiles on plant growth: current knowledge and future challenges. *Plant Signal. Behav*. **7**, 79-85.
15. Belimov, A. A., Dodd, I. C., Hontzeas, N., Theobald, J. C., Safronova, V. I. and Davies, W. J. 2009. Rhizosphere bacteria containing ACC deaminase increase yield of plants grown in drying soil via both local and systemic hormone signaling. *New Phytol*. **181**, 413-423.
16. Belimov, A. A., Kunakova, A. M., Safronova, V. I., Stepanok, V. V., Iudkin, L. Iu., Alekseev, Iu. V. and Kozhemiakov, A. P. 2004. Employment of rhizobacteria for the inoculation of barley plants cultivated in soil contaminated with lead and cadmium. *Microbiologia* **73**, 99-106.
17. Berendsen, R. L., Pieterse, C. M. and Bakker, P. A. 2012. The rhizosphere microbiome and plant health. *Trends Plant Sci*. **17**, 478-486.
18. Berg, G. and Smalla, K. 2009. Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiol. Ecol*. **68**, 1-13.
19. Bhattacharyya, P. N. and Jha, D. K. 2012. Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. *World J. Microbiol. Biotechnol.* **28**, 1327-1350.
20. Bishopp, A., Mahonen, A. P. and Helariutta, Y. 2006. Signs of change: Hormone receptors that regulate plant development. *Development* **133**, 1857-1869.
21. Bömke, C. and Tudzynski, B. 2009. Diversity, regulation and evolution of the gibberellin biosynthetic pathway in fungi compared to plants and bacteria. *Phytochemistry* **70**, 1876-1893.
22. Borrell, A. K., Hammer, G. L. and Henzell, R. G. 2000. Does maintaining green leaf area in sorghum improve yield under drought? II. Dry matter production and yield. *Crop Sci*. **40**, 1037-1048.
23. Bottini, R., Cassán, F. and Piccoli, P. 2004. Gibberellin production by bacteria and its involvement in plant growth promotion and yield increase. *Appl. Microbiol. Biotechnol*. **65**, 497-503.
24. Cassán, F., Vanderleyden, J. and Spaepen, S. 2014. Physiological and agronomical aspects of phytohormone production by model plant-growth-promoting rhizobacteria (PGPR) belonging to the genus *Azospirillum*. *J. Plant Growth Regul*. **33**, 440-459.
25. Chen, Y. P., Rekha, P. D., Arun, A. B., Shen, F. T., Lai, W. A. and Young, C. C. 2006. Phosphate solubilizing bacteria from subtropical soil and their tricalcium phosphate solubilizing abilities. *Appl. Soil Ecol.* **34**, 33-41.
26. Cohen, A. C., Bottini, R. and Piccoli, P. N. 2008. *Azospirillum brasilense* Sp245 produces ABA in chemically-defined culture medium and increases ABA content in Arabidopsis plants. *Plant Growth Regul*. **54**, 97-103.
27. Cohen, A. C., Travaglia, C. N., Bottini, R. and Piccoli, P. N. 2009. Participation of abscisic acid and gibberellins produced by endophytic *Azospirillum* in the alleviation of drought effects in maize. *Botany* **87**, 455-462.
28. Cohen, A. C., Bottini, R., Pontin, M., Berli, F. J., Moreno, D., Boccanlandro, H., Travaglia, C. N. and Piccoli, P. N. 2015. *Azospirillum brasilense* ameliorates the response of *Arabidopsis thaliana* to drought mainly via enhancement of ABA levels. *Physiol. Plant.* **153,** 79-90.
29. Conrath, U., Beckers, G. J. M., Flors, V., García-Agustín, P., Jakab, G. and Mauch, F. 2006. Priming: getting ready for battle. *Mol. Plant Microbe. Interact.* **19**, 1062-1071.
30. Crowley, D. E. 2006 Microbial Siderophores in the Plant Rhizosphere, pp 169-198. In: Barton L.L. and Abadia J. (eds), *Iron Nutrition in Plants and Rhizospheric Microorganisms*. Springer Publisher: Dordrecht, The Netherland.
31. Dakora, F., Matiru, V. and Kanu, A. 2015. Rhizosphere ecology of lumichrome and riboflavin, two bacterial signal molecules eliciting developmental changes in plants. *Front. Plant Sci*. **6**, 700.
32. Das, A. J., Kumar, M. and Kumar, R. 2013. Plant growth promoting rhizobacteria (PGPR): An alternative of chemical fertilizer for sustainable, environment friendly agriculture. *Res. J. Agric. For. Sci.* **1**, 21-23.
33. Davies, P. J. 2010. Introduction, pp. 1-35. In: Davies, P. J. (ed.), *Plant hormones: Biosynthesis, signal transduction, action! revised 3rd edition*. Springer Publisher: Dordrecht, The Netherland.
34. Deka, H., Deka, S. and Baruah, C. 2015. Plant growth promoting rhizobacteria for value addition: mechanism of action, pp 305-321. In: Egamberdieva, D., Shrivastava, S., Varma, A. (Eds.), *Plant-Growth-Promoting Rhizobacteria (PGPR) and Medicinal Plants*. Springer International Publishing, Cham, New York, U. S. A.
35. Dobbelaere, S., Vanderleyden, J. and Okon, Y. 2003. Plant growth promoting effects of diazotrophs in the rhizosphere. *Crit. Rev. Plant Sci.* **22**, 107-149.
36. Dodd, I. C., Zinovkina, N. Y., Safronova, V. I. and Belimov, A. A. 2010. Rhizobacterial mediation of plant hormone status. *Ann. Appl. Biol*. **157**, 361-379.
37. Duca, D., Lorv, J., Patten, C. L., Rose, D. and Glick, B. R.

2014. Indole-3-acetic acid in plant–microbe interactions. *Antonie van Leeuwenhoek* **106**, 85-125.
38. Egamberdieva, D. and Lugtenberg, B. 2014. Use of Plant Growth-Promoting Rhizobacteria to Alleviate Salinity Stress in Plants, pp 73-96. In: Miransari, M. (ed) *Use of Microbes for the Alleviation of Soil Stresses, Volume 1*. Springer Publisher: New York, U. S. A.
39. Etesami, H., Emami, S. and Alikhani, H. A. 2017. Potassium solubilizing bacteria (KSB): Mechanisms, promotion of plant growth, and future prospects - A review. *J. Soil Sci. Plant Nutr*. **17**, 897-911.
40. Galland, M., Gamet, L., Varoquaux, F., Touraine, B., Touraine, B. and Desbrosses, G. 2012. The ethylene pathway contributes to root hair elongation induced by the beneficial bacteria *Phyllobacterium brassicacearum* STM196. *Plant Sci.* **190**, 74-81.
41. Ghosh, S. and Basu, P. S. 2006. Production and metabolism of indole acetic acid in roots and root nodules of *Phaseolus mungo*. *Microbiol. Res*. **161**, 362-366.
42. Glick, B. R., Penrose, D. M. and Li, J. P. 1998. A model for the lowering of plant ethylene concentrations by plant growth-promoting bacteria. *J. Theor. Biol.* **190**, 63-68.
43. Glick, B. R. 2012. Plant Growth-Promoting Bacteria: Mechanisms and Applications. *Scientifica (Cairo)* **2012,** 963401.
44. Gontia-Mishra, I., Sapre, S., Sharma, A. and Tiwari, S. 2016. Alleviation of mercury toxicity in wheat by the interaction of mercury-tolerant plant growth-promoting rhizobacteria. *J. Plant Growth Regul*. **35**, 1000-1012.
45. Gouws, L. M., Botes, E., Wiese, A. J., Trenkamp, S., Torres-Jerez, I., Tang, Y., Hills, P. N., Usadel, B., Lloyd, J. R., Fernie, A. R., Kossmann, J. and van der Merwe, M. J. 2012. The plant growth-promoting substance, lumichrome, mimics starch, and ethylene-associated symbiotic responses in lotus and tomato roots. *Front. Plant Sci*. **3**, 120.
46. Govindarajan, M., Balandreau, J., Kwon, S. W., Weon, H. Y. and Lakshminarasimhan, C. 2008. Effects of the inoculation of *Burkholderia vietnamensis* and related endophytic diazotrophic bacteria on grain yield of rice. *Microb. Ecol*. **55,** 21-37.
47. Gray, E. J. and Smith, D. L. 2005. Intracellular and extracellular PGPR: commonalities and distinctions in the plant bacterium signaling processes. *Soil Biol. Biochem*. **37**, 395-412.
48. Gupta, G., Parihar, S. S., Ahirwar, N. K., Snehi, S. K. and Singh, V. 2015. Plant growth promoting rhizobacteria (PGPR): current and future prospects for development of sustainable agriculture. *Microb. Biochem. Technol*. **7**, 96-102.
49. Gupta, A., Meyer, J. M. and Goel, R. 2002. Development of heavy metal-resistant mutants of phosphate solubilizing *Pseudomonas* sp. NBRI 4014 and their characterization. *Curr. Microbiol*. **45**, 323-327.
50. Gutierrez-Manero, F. J., Ramos-Solano, B., Probanza, A., Mehouachi, J., Tadeo, F. R. and Talon, M. 2001. The plant-growth-promoting rhizobacteria *Bacillus pumilus* and *Bacillus licheniformis* produce high amounts of physiologically active gibberellins. *Physiol. Plant*. **111**, 206-211.
51. Ham, B. K., Chen, J., Yan, Y. and Lucas, W. J. 2018. Insights into plant phosphate sensing and signaling. *Curr. Opin. Biotechnol*. **49**, 1-9.
52. Iqbal, A. and Hasnain, S. 2013. *Aeromonas punctata* PNS-1: a promising candidate to change the root morphogenesis of *Arabidopsis thaliana* in MS and sand system. *Acta Physiol. Plant*. **35**, 657-665.
53. James, E. K., Gyaneshwar, P., Mathan, N., Barraquio, W. L., Reddy, P. M., Iannetta, P. P. M., Olivares, F. L. and Ladha, J. K. 2002. Infection and colonization of rice seedlings by the plant growth promoting bacterium *Herbaspirillum seropedicae* Z67. *Mol. Plant Microbe. Interact*. **15**, 894-906.
54. Jameson, P. 2000. Cytokinins and auxins in plant-pathogens interactions—an overview. *Plant Growth Regul*. **32**, 369-380.
55. Jha, C. K. and Saraf, M. 2015. Plant growth promoting rhizobacteria (PGPR): a review. *E3 J. Agric. Res. Dev*. **5**, 108-119.
56. Kamran, S., Shahid, I., Baig, D. N., Rizwan, M., Malik, K. A. and Mehnaz, S. 2017. Contribution of zinc solubilizing bacteria in growth promotion and zinc content of wheat. *Front. Microbiol*. **8**, 2593.
57. Kang, S. M., Khan, A. L., Hamayun, M., Hussain, J., Joo, G. J., You, Y. H., Kim, J. G. and Lee, I. J. 2012. Gibberellin-producing *Promicromonospora* sp. SE188 improves *Solanum lycopersicum* plant growth and influences endogenous plant hormones. *J. Microbiol*. **50**, 902-909.
58. Kang, S. M., Radhakrishnan, R., Khan, A. L., Kim, M. J., Park, J. M., Kim, B. R., Shin, D. H. and Lee, I. J. 2014. Gibberellin secreting rhizobacterium, *Pseudomonas putida* H-2-3 modulates the hormonal and stress physiology of soybean to improve the plant growth under saline and drought conditions. *Plant Physiol. Biochem*. **84**, 115-124.
59. Kang, S. M., Khan, A. L., Waqas, M., You, Y. H., Kim, J. H., Kim, J. G., Hamayun, M. and Lee, I. J. 2014. Plant growth-promoting rhizobacteria reduce adverse effects of salinity and osmotic stress by regulating phytohormones and antioxidants in *Cucumis sativus*. *J. Plant Interact*. **9**, 673-682.
60. Khan, A. L., Waqas, M., Hussain, J., Al-Harrasi, A., Hamayun, M. and Lee, I. J. 2015. Phytohormones enabled endophytic fungal symbiosis improve aluminum phyto extraction in tolerant *Solanum lycopersicum*: an example of *Penicillium janthinellum* LK5 and comparison with exogenous $GA_3$. *J. Hazard Mater*. **295**, 70-78.
61. Khan, M. S., Zaidi, A., Wani, P. A. and Oves, M. 2009. Role of plant growth promoting rhizobacteria in the remediation of metal contaminated soils. *Environ. Chem. Lett*. **7**, 1-19.
62. Khan, W., Prithiviraj, B. and Smith, D. L. 2008. Nod factor [Nod Bj V (C18:1, MeFuc)] and lumichrome enhance photosynthesis and growth of corn and soybean. *J. Plant Physiol*. **165**, 1342-1351.
63. Kim, J. and Rees, D. C. 1994. Nitrogenase and biological nitrogen fixation. *Biochemistry* **33**, 389-397.
64. Kloepper, J. W., Schroth, M. N. and Miller, T. D. 1980. Effects of rhizosphere colonization by plant growth promoting rhizobacteria on potato plant development and yield. *Phytopathology* **70**, 1078-1082.

65. Kumar, A., Kumar, A. and Pratush, A. 2014. Molecular diversity and functional variability of environmental isolates of *Bacillus* species. *Springerplus* **3**, 312.
66. Kumar, A., Singh, V., Singh, M., Singh, P. P., Singh, S. K., Singh, P. K. and Pandey, K. D. 2016b. Isolation of plant growth promoting rhizobacteria and their impact on growth and curcumin content in *Curcuma longa L. Biocatal. Agric. Biotechnol*. **8**, 1-7.
67. Li, M., Guo, R., Yu, F., Chen, X., Zhao, H., Li, H. and Wu, J. 2018. Indole-3-acetic Acid biosynthesis pathways in the plant-beneficial bacterium *Arthrobacter pascens* ZZ21. *Int. J. Mol. Sci*. **19**, 443.
68. Chen, L., Dodd, I. C., Theobald, J. C., Belimov, A. A. and Davies, W. J. 2013. The rhizobacterium *Variovorax paradoxus* 5C-2, containing ACC deaminase, promotes growth and development of *Arabidopsis thaliana* via an ethylene-dependent pathway. *J. Exp. Bot*. **64**, 1565-1573.
69. Liu, D., Lian, B. and Dong, H. 2012. Isolation of *Paenibacillus* sp. and assessment of its potential for enhancing mineral weathering. *Geomicrobiol. J*. **29**, 413-421.
70. Llorente, B. E., Alasia, M. A. and Larraburu, E. E. 2016. Biofertilization with *Azospirillum brasilense* improves in vitro culture of *Handroanthus ochraceus*, a forestry, ornamental and medicinal plant. *N. Biotechnol*. **33**, 32-40.
71. López-Bucio, J., Campos-Cuevas, J. C., Hernández-Calderón, E., Velásquez-Becerra, C., Farías-Rodríguez, R., Macías-Rodríguez, L. I. and Valencia-Cantero, E. 2007. *Bacillus megaterium* rhizobacteria promote growth and alter root-system architecture through an auxin- and ethylene-independent signaling mechanism in *Arabidopsis thaliana*. *Mol. Plant Microbe Interact*. **20**, 207-217.
72. Lynch, J. and Whipps, J. 1990. Substrate flow in the rhizosphere. *Plant Soil* **129**, 1-10.
73. Manjili, F. A., Sedghi, M. and Pessarakli, M. 2012. Effects of phytohormones on proline content and antioxidant enzymes of various wheat cultivars under salinity stress. *J. Plant Nutr*. **35**, 1098-1111.
74. Manjunath, M., Prasanna, R., Sharma, P., Nain, L. and Singh, R. 2011. Developing PGPR consortia using novel genera *Providencia* and *Alcaligenes* along with cyanobacteria for wheat. *Arch. Agron. Soil Sci*. **57**, 873-887.
75. Manulis, S., Haviv-Chesner, A., Brandl, M. T., Lindow, S. E. and Barash, I. 1998. Differential involvement of indole-3-acetic acid biosynthetic pathways in pathogenicity and epiphytic fitness of *Erwinia herbicola* pv. *gypsophilae*. *Mol. Plant Microbe Interact.* **11**, 634-642.
76. Martínez-Viveros, O., Jorquera, M. A., Crowley, D. E., Gajardo, G. M. L. M. and Mora, M. L. 2010. Mechanisms and practical considerations involved in plant growth promotion by rhizobacteria. *J. Soil Sci. Plant Nutr*. **10**, 293-319.
77. Matiru, V. N. and Dakora, F. D. 2005a. The rhizosphere signal molecule lumichrome alters seedling development in both legumes and cereals. *New Phytol*. **166**, 439-444.
78. Mayak, S., Tirosh, T. and Glick, B. R. 2004. Plant growth-promoting bacteria that confer resistance to water stress in tomatoes and peppers. *Plant Sci*. **166**, 525-530.
79. Minerdi, D., Bossi, S., Maffei, M. E., Gullino, M. L. and Garibaldi, A. 2011. *Fusarium oxysporum* and its bacterial consortium promote lettuce growth and expansion A5 gene expression through microbial volatile organic compound (MVOC) emission. *FEMS Microbiol. Ecol*. **76**, 342-351.
80. Mohapatra, P. K., Panigrahi, R. and Turner, N. C. 2011. Chapter five - Physiology of spikelet development on the rice panicle: is manipulation of apical dominance crucial for grain yield improvement? *Adv. Agron*. **110**, 333-360.
81. Morgan, P. W. and Drew, M. C. 1997. Ethylene and plant responses to stress. *Physiol. Plant*. **100**, 620-630.
82. Nambara, E. and Marion-Poll, A. 2005. Abscisic acid biosynthesis and catabolism. *Annu. Rev. Plant Biol*. **56**, 165-185.
83. Navarro, L., Dunoyer, P., Jay, F., Arnold, B., Dharmasiri, N., Estelle, M., Voinnet, O. and Jones, J. D. G. 2006. A plant miRNA contributes to antibacterial resistance by repressing auxin signaling. *Science* **312**, 436-443.
84. Negi, S., Sukumar, P., Liu, X., Cohen, J. D. and Muday, C. K. 2010. Genetic dissection of the role of ethylene in regulating auxin-dependent lateral and adventitious root formation in tomato. *Plant J*. **61**, 3-15.
85. Nett, R. S., Montanares, M., Marcassa, A., Lu, X., Nagel, R., Charles, T. C., Hedden, P., Rojas, M. C. and Peters, R. J. 2017. Elucidation of gibberellin biosynthesis in bacteria reveals convergent evolution. *Nat. Chem. Biol*. **13**, 69-74.
86. Ortíz-Castro, R., Martínez-Trujillo, M. and López-Bucio, J. 2008. N-Acyl-L-homoserine lactones: a class of bacterial quorum-sensing signals alter post-embryonic root development in *Arabidopsis thaliana*. *Plant Cell Environ*. **31**, 1497-1509.
87. Ortiz-Castro, R., Díaz-Pérez, C., Martínez-Trujillo, M., del Río, R. E., Campos-García, J. and López-Bucio, J. 2011. Transkingdom signaling based on bacterial cyclodipeptides with auxin activity in plants. *Proc. Natl. Acad. Sci. USA*. **108**, 7253-7258.
88. Oteino, N., Lally, R. D., Kiwanuka, S., Lloyd, A., Ryan, D., Germaine, K. J. and Dowling, D. N. 2015. Plant growth promotion induced by phosphate solubilizing endophytic *Pseudomonas* isolates. *Front. Microbiol*. **6**, 745.
89. Pahari, A. and Mishra, B. B. 2017. Antibiosis of siderophore producing bacterial isolates against phytopathogens and their effect on growth of okra. *Int. J. Curr. Microbiol. App. Sci*. **6**, 1925-1929.
90. Parmar, P. and Sindhu, S. S. 2013. Potassium solubilization by rhizosphere bacteria: influence of nutritional and environmental conditions. *J. Microbiol. Res*. **3**, 25-31.
91. Patten, C. J., Blakney, A. J. C. and Coulson, T. J. D. 2013. Activity, distribution and function of indole-3-acetic acid biosynthetic pathways in bacteria. *Crit. Rev. Microbiol*. **39**, 395-415.
92. Pierik, R., Tholde D., Poorter H., Visser E. J. W. and Voesenek, L. A. C. J. 2006. The Janus face of ethylene: growth inhibition and stimulation. *Trends Plant Sci*. **11**, 176-183.
93. Poupin, M. J., Timmermann, T., Vega, A., Zuñiga, A. and González, B. 2013. Effects of the plant growth-promoting Bacterium *Burkholderia phytofirmans* PsJN throughout the life cycle of *Arabidopsis thaliana*. *PLoS One* **8**, e69435.

94. Poupin, M. J., Greve, M., Carmona, V. and Pinedo, I. 2016. A complex molecular interplay of auxin and ethylene signaling pathways is involved in Arabidopsis growth promotion by *Burkholderia phytofirmans* PsJN. *Front. Plant Sci*. **7**, 492.
95. Rajkumar, M., Ae, N., Prasad, M. N. V. and Freitas, H. 2010. Potential of siderophore-producing bacteria for improving heavy metal phytoextraction. *Trends Biotechnol*. **28**, 142-149.
96. Raymond, J., Siefert, J. L., Staples, C. R. and Blankenship, R. E. 2004. The natural history of nitrogen fixation. *Mol. Biol. Evol*. **21**, 541- 554.
97. Ryu, C. M., Farag, M. A., Hu, C. H., Reddy, M. S., Wei, H. X., Paré, P. W. and Kloepper, J. W. 2003. Bacterial volatiles promote growth in Arabidopsis. *Proc. Natl. Acad. Sci. USA*. **100**, 4927-4932.
98. Sakakibara, H. 2006. Cytokinins: activity, biosynthesis, and translocation. *Annu. Rev. Plant Biol*. **57**, 431-449.
99. Schulz, B. and Boyle, C. 2006. What are Endophytes?, pp. 1-13. In: Schulz B. J. E., Boyle C. J. C. and Sieber T. N. (eds), *Microbial Root Endophytes. Soil Biology, vol 9*. Springer, Berlin, Heidelberg.
100. Setiawati, T. C. and Mutmainnah, L. 2016. Solubilization of Potassium containing mineral by microorganisms from sugarcane rhizosphere. *Agri. Sci. Procedia* **9**, 108-117.
101. Shahzad, R., Waqas, M., Khan, A. L., Asaf, S., Khan, M. A., Kang, S. M., Yun, B. W. and Lee, I. J. 2016. Seed-borne endophytic *Bacillus amyloliquefaciens* RWL-1 produces gibberellins and regulates endogenous phytohormones of *Oryza sativa*. *Plant Physiol. Biochem*. **106**, 236-243.
102. Shaikh, S., Wani, S. and Sayyed, R. 2018. Impact of Interactions between Rhizosphere and Rhizobacteria: A Review. *J. Bacteriol. Mycol*. **5**, 1058.
103. Sharp, R. E. and Le Noble, M. E. 2002. ABA, ethylene and the control of shoot and root growth under water stress. *J. Exp. Bot*. **53**, 33-37.
104. Shilev, S. 2013. Soil rhizobacteria regulating the uptake of nutrients and undesirable elements by plants, pp 147-150. In: Arora, N. K. (ed), *Plant microbe symbiosis: fundamentals and advances*. Springer, New Delhi, India.
105. Simon, L., Bousquet, J., Lévesque, R. C. and Lalonde, M. 1993. Origin and diversification of endomycorrhizal fungi and coincidence with vascular land plants. *Nature* **363**, 67-69.
106. Singh, B., Natesan, S. K. A., Singh, B. K. and Usha, K. 2005. Improving zinc efficiency of cereals under zinc deficiency. *Curr. Sci*. **88**, 36-44.
107. Singh, M., Kumar, A., Singh, R. and Pandey, K. D. 2017a. Endophytic bacteria: a new source of bioactive compounds. *3 Biotech*. **7**, 315.
108. Singh, S. and Prasad, S. M. 2014. Growth, photosynthesis and oxidative responses of *Solanum melongena* L. seedlings to cadmium stress: mechanism of toxicity amelioration by kinetin. *Sci. Hortic*. **176**, 1-10.
109. Singh, V. K., Singh, A. K. and Kumar, A. 2017b. Disease management of tomato through PGPB: current trends and future perspective. *3 Biotech*. **7**, 255.
110. Spaepen, S., Vanderleyden, J. and Remans, R. 2007. Indole-3-acetic acid in microbial and microorganism plant signaling. *FEMS Microbiol. Rev*. **31**, 425-448.
111. Torres, A. R., Kaschuk, G., Saridakis, G. P. and Hungria, M. 2012. Genetic variability in *Bradyrhizobium japonicum* strains nodulating soybean *Glycine max* (L.) Merrill. *World J. Microbiol. Biotechnol*. **28**, 1831-1835.
112. Uren, N. C. 2000. Types, amounts, and possible functions of compounds released into the rhizosphere by soil-grown plants, pp. 1-21. In: Pinton, R., Varanini, Z. and Nannipieri, P. (eds.), *The Rhizosphere: Biochemistry and Organic Substances at the Soil-Plant Interface, second edition*. CRC Press: Boca Raton, FL, U. S. A.
113. Vacheron, J., Desbrosses, G., Bouffaud, M. L., Touraine, B., Moenne-Loccoz, Y., Muller, D., Legendre, L., Wisniewski-Dyé, F. and Prigent-Combaret, C. 2013. Plant growth-promoting rhizobacteria and root system functioning. *Front. Plant Sci*. **4**, 356.
114. Whipps, J. M. 2001. Microbial interactions and biocontrol in the rhizosphere. *J. Exp. Bot*. **52**, 487-511.
115. Xu, J., Li, X. L. and Luo, L. 2012. Effects of engineered *Sinorhizobium meliloti* on cytokinin synthesis and tolerance of alfalfa to extreme drought stress. *Appl. Environ. Microbiol*. **78,** 8056-8061.
116. You, Y. H., Yoon, H., Kang, S. M., Shin, J. H., Choo, Y. S, Lee, I. J., Lee, J. M. and Kim, J. G. 2012. Fungal diversity and plant growth promotion of endophytic fungi from six halophytes in Suncheon Bay. *J. Microbiol. Biotechnol*. **22**, 1549-1556.
117. Zahran, H. H. 2001. Rhizobia from wild legumes: diversity, taxonomy, ecology, nitrogen fixation and *biotechnology*. *J. Biotechnol*. **91**, 143-153.
118. Zaidi, A., Ahmad, E., Khan, M. S., Saif, S. and Rizvi, A. 2015. Role of plant growth promoting rhizobacteria in sustainable production of vegetables: current perspective. *Sci. Hortic*. **193**, 231-239.
119. Zaidi, A. and Khan, M. S. 2005. Interactive effect of rhizospheric microorganisms on growth, yield and nutrient uptake of wheat. *J. Plant Nutr*. **28**, 2079-2092.
120. Zamioudis, C., Mastranesti, P., Dhonukshe, P., Blilou, I. and Pieterse, C. M. J. 2013. Unraveling root developmental programs initiated by beneficial *Pseudomonas* spp. bacteria. *Plant Physiol*. **162**, 304-318.
121. Zhang, H., Kim, M. S., Krishnamachari, V., Payton, P., Sun, Y., Grimson, M., Farag, M. A., Ryu, C. M., Allen, R., Melo, I. S. and Paré, P. W. 2007. Rhizobacterial volatile emissions regulate auxin homeostasis and cell expansion in Arabidopsis. *Planta* **226,** 839-851.
122. Zhang, A., Zhao, G., Gao, T., Wang, W., Li, J., Zhang, S. and Zhu, B. 2013. Solubilization of insoluble potassium and phosphate by *Paenibacillus kribensis* CX-7: a soil microorganism with biological control potential. *Afri. J. Microbiol. Res*. **7**, 41-47.
123. Zhang, C. and Kong, F. 2014. Isolation and identification of potassium-solubilizing bacteria from tobacco rhizo-

spheric soil and their effect on tobacco plants. *Appl. Soil. Ecol*. **82**, 18-25.
124. Zhao, Q., Zhang, C., Jia, Z., Huang, Y., Li, H. and Song, S. 2015. Involvement of calmodulin in regulation of primary root elongation by N-3-oxo-hexanoyl homoserine lactone in *Arabidopsis thaliana*. *Front. Plant Sci*. **5**, 1-11.

## 초록 : 식물생장촉진 근권미생물의 영향에 대한 연구 현황 및 전망

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근권은 식물 뿌리와 토양 미생물이 서로의 신호를 주고 받으며 끊임없이 상호반응하는 역동적인 장소이다. 근권 주위에서 식물의 생장과 생산성에 유익한 토양 미생물을 식물생장촉진근권미생물(Plant Growth Promoting Rhizobacteria, PGPR)이라 칭하며, 이 PGPR은 식물 전 생장기간동안 생물학적 및 비생물학적 스트레스에 대한 저항성, 식물 호르몬 조절, 영양분의 흡수와 이용 등에 영향을 끼침으로써 식물의 생장과 발달, 면역, 생산력 등중요한 생명 과정에 관여한다. 그리고, PGPR은 식물 생장을 유도하는 2차 대사산물이나 휘발성 유기 화합물을 생산하고, 식물의 뿌리 역시 식물 유해한 인자 혹은 병원성 인자에 대항하여 자신을 보호하거나 토양 성질 개선을 위해, PGPR을 유인하고 정착시키기 위한 물질을 생산, 분비한다. 그러므로, 식물과 PGPR 사이의 상호작용은 필수적이면서도 상호의존적이다. 현재까지, PGPR에 대한 많은 연구는 직간접적 개념에 대하여 공통적 또는 다양한 조건들에서 여러 방식으로 PGPR의 기능을 밝히는 방향으로 전개되어 왔다. 본 총설에서는 세포분열과 팽창, 분화에 의한 식물의 생장과 발달의 촉진, 식물생장조절인자와 호르몬의 유도, 영양물질의 고정, 용해, 무기화를 촉진하기 위한 PGPR의 역할과 전략을 소개하였다. 또한 PGPR와 토양 미생물군의 효과에 대한 현재까지의 연구 정보를 요약하였다.