

ORIGINAL RESEARCH ARTICLE

Rhizospheric bacteria with potential benefits in agriculture

Antonio Velasco-Jiménez, Osvaldo Castellanos-Hernández, Gustavo Acevedo-Hernández,
Rayn Clarenc Aarland, Araceli Rodríguez-Sahagún*

Centro Universitario de la Ciénega, Universidad de Guadalajara, Ocotlán 47820, México

* Corresponding author: Araceli Rodríguez-Sahagún, aracelicrs@cuci.udg.mx

ABSTRACT

Rhizobacteria are a vast and very diverse group of bacteria that live in the vicinity of roots. They develop beneficial, neutral, and even detrimental relationships, although the latter to a lesser extent. The interactions between bacteria and plant roots have played a determining role in the adaptation and productivity of plant species over time. Several studies show that rhizobacteria have improved plant growth, production, and health, both directly through mechanisms that include the assimilation of vital nutrients such as nitrogen fixation, phosphorus and potassium solubilization, and phytostimulation through the production of various phytohormones) and indirectly (by affecting the growth of important pathogens, activating plant immunity, and improving problems caused by abiotic stress). Due to their metabolic diversity, rhizobacteria could contribute positively to the improvement of agricultural productivity and the solution of environmental problems caused by the methods used in current agriculture. Several genera, such as *Acidithiobacillus*, *Aminobacter*, *Arthrobacter*, *Azoarcus*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Clostridium*, *Enterobacter*, *Gluconoacetobacter*, *Pseudomonas*, *Serratia*, and *Sphingomonas*, have demonstrated their enormous growth-promoting capacity. This review provides a focus on the mechanisms by which rhizobacteria enhance plant growth, their contribution to sustainable agriculture, and their commercialization, a field that continues to grow steadily.

Keywords: plant growth promoting bacteria; biological nitrogen fixation; rhizosphere; phosphate solubilization

1. Introduction

Agricultural productivity has increased incredibly in the last forty years, thanks to technologies developed during the green revolution and the expansion of the use of land, water, and other natural resources^[1]. However, this modern farming process has included the indiscriminate use of pesticides and fertilizers (nitrogen and phosphorus), which has resulted in various environmental problems caused by the pollution of these natural resources^[2]. On the other hand, according to FAO^[1] agriculture will face a great challenge since, by 2050, it will have to produce almost 50% more food, fodder, and biofuel than it produced in 2012, due to a trend in population increase. In addition, the high variability of temperature, rainfall, droughts and floods, pests, and diseases resistant to different chemical compounds that have been abused in their use will be important factors that will damage crop yields. The above poses great challenges for agriculture, which has to look for systems that allow optimal food production with cost reduction and conservation of natural resources in the long term^[3].

ARTICLE INFO

Received: 2 January 2022 | Accepted: 22 February 2022 | Available online: 15 March 2022

CITATION

Velasco-Jiménez A, Castellanos-Hernández O, Acevedo-Hernández G, et al. Rhizospheric bacteria with potential benefits in agriculture. *Advances in Modern Agriculture* 2022; 3(1): 2040. doi: 10.54517/ama.v3i1.2040

COPYRIGHT

Copyright © 2022 by author(s). *Advances in Modern Agriculture* is published by Asia Pacific Academy of Science Pte. Ltd. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), permitting distribution and reproduction in any medium, provided the original work is cited.

Nature is a key point in the solution of these problems. Over time, plants and microorganisms have co-evolved and developed diverse relationships that have conferred adaptive advantages in diverse habitats on earth^[4,5]. First, plants, because of their ability to convert solar energy into chemical energy, have positioned themselves at the top of trophic chains, providing other organisms, such as rhizobacteria, with food (photosynthates and secondary metabolites), an ideal place to inhabit, and an essential element in the metabolism of cellular aerobic respiration (oxygen)^[6]. While rhizobacteria incredibly improve growth, health, and adaptability against different biotic and abiotic stress conditions in plants^[6,7].

In recent years, research on the understanding of plant-microorganism interactions has been encouraged to replace agrochemicals (fertilizers and pesticides) with highly effective products that contribute to improved plant productivity and are also environmentally friendly^[2].

2. Rhizobacteria

Rhizobacteria are bacteria that inhabit the rhizosphere, an area of soil attached to the root and extending a few millimeters from the surface of the root system. This zone is characterized by the unique and dynamic interaction of biogeochemical processes occurring between plant roots and soil microorganisms, which are highly influenced by root exudates^[8]. In addition, it harbors a large number of microorganisms that generally stimulate plant growth and reduce the incidence of diseases^[7]. This bacterial group has also been assigned the name *Plant Growth Promoting Rhizobacteria* (PGPR)^[9].

In the process of establishing relationships with rhizobacteria, plants invest up to 20% of the carbon sources obtained during photosynthesis, in exchange for the improvement of root architecture, nutrient uptake, and stimulation of the plant immune system carried out by PGPR^[6]. One of the best-known examples of such benefits is found in the case of *Rhizobium* bacteria^[6].

The impact of rhizobacteria is highly influenced by root exudates, which also play an important role in signaling and recognition processes between plants and microorganisms^[10]. The mechanisms of attraction of the bacteria to the rhizosphere of their host are mediated by a specific bacterial chemotaxis towards particular plant exudates; likewise, good adhesion and colonization on the root surface are factors that can influence the functionality of the associative symbiosis^[7,10] (**Figure 1**).

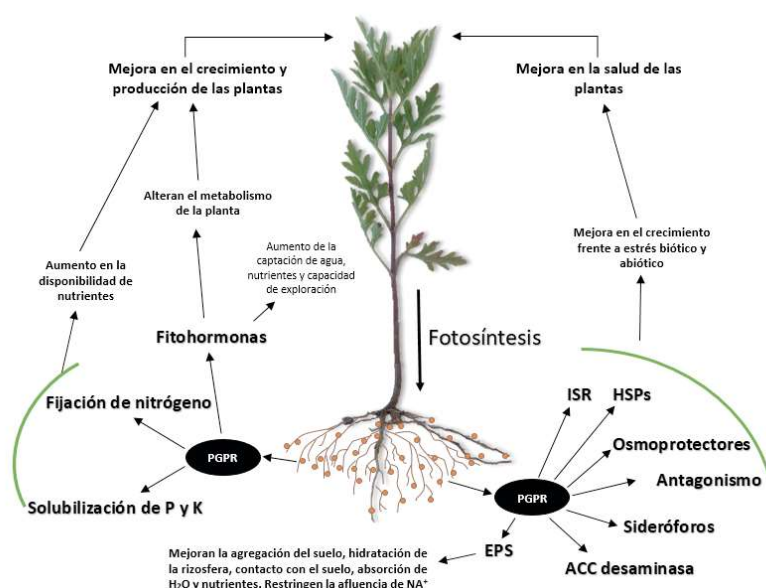


Figure 1. Mechanisms of action of PGPR.

EPS: Exopolysaccharides; ISR: Induced Systemic Resistance; HSPs: Heat shock proteins.

3. Direct mechanisms in the promotion of plant growth

3.1. Biological nitrogen fixation (BNF)

Nitrogen (N) is one of the vital nutrients for plant growth and productivity. This element is present in amino acids inherent in proteins, amides, chlorophyll, hormones, nucleotides, vitamins, alkaloids, and nucleic acids^[11]. A common feature of microorganisms involved in FBN is the presence of nitrogenase enzymes, which reduce atmospheric nitrogen into the assimilable ion NH_4^+ . Enzymatic activity is generally susceptible to the concentration of oxygen in the medium; therefore, microorganisms have adopted adaptive mechanisms such as respiratory protection, conformational protection, and cellular compartmentalization^[12].

On land, N_2 constitutes approximately 78% of the gases in the atmosphere; however, this form is not assimilable by plants. Nitrogen-fixing organisms are generally classified into symbiotic, fixing bacteria in which members of the family Rhizobiaceae and the genus *Frankia* are found^[11] and free-living, associative, and endophytic non-symbiotics, such as cyanobacteria (*Anabaena*, *Nostoc*), *Azospirillum*, *Azotobacter*, *Gluconoacetobacter diazotrophicus*, *Azocarus*^[13], *Paraburkholderia*^[14].

3.2. Phosphate solubilization

Phosphorus (P) is the second-most important nutrient involved in plant growth and productivity. This element is essential in cell division, signal transduction, macromolecular biosynthesis, photosynthesis, and plant respiration, with energy acquisition, storage, and use being one of its main functions^[15]. Unlike nitrogen, phosphorus is not available in the atmosphere, so its main source is more limited as it comes mainly from primary and secondary minerals present in the soil. Another problem is that this element is usually found in lower concentrations than other elements, ranging from 0.001 to 1 mg L⁻¹^[16], further decreasing its availability to plants. Phosphorus in soil is usually found in three categories: (I) as an inorganic compound forming complexes with aluminum (Al), iron (Fe), manganese (Mn), and calcium (Ca); (II) organic compounds, such as humus, inositol, phytic acid, phytin, sugar phosphates, nucleotides, phosphoproteins, phosphonates, and phospholipids; and (III) as organic and inorganic compounds associated with living cell matter^[17]. However, plants only take up phosphate in monobasic form (H_2PO_4^-) and dibasic form (HPO_4^{2-})^[18].

Some rhizobacteria have the ability to solubilize phosphates from inorganic or organic compounds using different pathways. For example, the activity of enzymes such as non-specific phosphatases, phytases, phosphonatas, and C-P lyases has been reported^[7,18], which solubilize phosphorus from organic compounds in the soil. Likewise, one of the most studied mechanisms is the obtaining of this element compound by rhizobacteria through the release of organic acids such as gluconic or 2-ketogluconic acid, capable of chelating the bioavailable phosphorus in the soil using its hydroxyl and carboxyl radicals. The production of these acids can be variable and depends on root exudates^[7,11,19]. Thus, phosphate-solubilizing rhizobacteria represent an alternative to improving the application of chemical phosphate fertilizers and agricultural productivity, as they have the ability to provide available forms of phosphorus to plants^[20].

3.3. Potassium solubilization

Potassium (K) is the third essential macronutrient needed in plant growth, so its limitation significantly affects crop production^[21,22]. In plants, K plays a very important role in processes such as photosynthesis, in which it regulates stomatal opening and closing and therefore CO_2 absorption, and has also been found to be involved in enzyme activation, protein synthesis, maintenance of cell turgor, reduction of respiration, transport of sugars, and nitrogen absorption, thus being vital for better plant development^[23]. K deficiency generates plants with poorly developed roots, a low growth rate, and low seed production, which is reflected in lower

yield^[24]. Potassium deficiencies are not usually the same as nitrogen or phosphorus deficiencies; however, inadequate application, runoff, leaching, and soil erosion are often serious problems^[23].

Recently, rhizobacteria have been identified with the ability to solubilize minerals such as K, which can contribute to resource conservation and thus increase productivity^[21]. Likewise, the positive effects of rhizobacteria on K availability in soil^[25] and K uptake in crops such as maize^[26], tobacco^[27] and wheat^[28] have been previously reported. The main mechanisms related to mineral potassium solubilization include the production of organic acids such as oxalic acid, tartaric acid, gluconic acid, 2-ketogluconic acid, citric acid, malic acid, succinic acid, lactic acid, propionic acid, glycolic acid, malonic acid, fumaric acid, and proton production^[29]. Some genera, such as *Acidithiobacillus*, *Aminobacter*, *Arthrobacter*, *Bacillus*, *Burkholderia*, *Cladosporium*, *Enterobacter*, *Paenibacillus*, and *Sphingomonas*, have been reported as potassium-solubilizing rhizobacteria^[30].

3.4. Production of phytohormones

Phytohormones are organic molecules that, in small concentrations (<1 mM), regulate the expression of genes involved in plant growth and development. These can be synthesized in different locations of the plant, and their action varies according to environmental changes that modify the gene expression of the organism, so they have a prominent impact on plant development and productivity^[22,31]. Some rhizobacteria have the ability to produce phytohormones, being one of the most studied mechanisms associated with the promotion of plant growth, such as *B. amyloliquefaciens* in potato crop^[32], *Azospirillum* and *Klebsiella* in corn crops^[33], *Bacillus*, *Lysinibacillus*, *Arthrobacter*, and *Rahnella* in *Eucalyptus nitens* plantations^[34]. Some of the groups influenced by rhizobacteria include auxins, cytokinins, gibberellins, abscisic acid, ethylene, and jasmonic acid^[35,36]. These molecules influence plant physiology by increasing root volume, host plant root respiration rate, and proton flux in the root membrane, causing an increase in the uptake of soluble nutrients and minerals^[37].

3.5. Auxins

Auxins are a very important type of phytohormone in plants; they influence various developmental events such as cell division, elongation, apical dominance, adventitious root formation, and phototropism^[36,38]. One of the most well-known auxins produced by rhizobacteria is indole-3-acetic acid (IAA)^[39]. IAA released by rhizobacteria mainly affects the root system, increasing its size, weight, branching number, and surface area in contact with the soil. All these changes lead to an increase in their ability to explore the soil for nutrient exchange, thus improving plant nutrition and growth capacity. In addition, this auxin has been found to act as an important molecule in plant-microorganism signaling and interaction^[40]. Likewise, the ability of rhizobacteria to modulate and tolerate abiotic stress using this phytohormone has been demonstrated^[36].

Rhizobacteria use L-tryptophan that is secreted into the rhizosphere to synthesize IAA, mainly through the indole-3-pyruvic acid (IPyA) pathway. Some genera, such as *Azospirillum*, *Rhizobium*, and *Bradyrhizobium*, synthesize the hormone through this pathway^[41].

3.6. Cytokinins

Cytokinins are another important group of phytohormones; their structure is generally derived from adenine, where the N6 position of adenine is substituted with an isoprenoid, such as in zeatin, or an aromatic side chain, such as in kinetin. These types of hormones promote processes such as cell division and differentiation, an increase in root area through adventitious root formation, leaf formation, and the prevention of senescence^[7,42].

In the early 1970s, Phillips and Torrey^[43] reported a cytokinin-like substance in culture filtrates of *Rhizobium leguminosarum* and *Bradyrhizobium japonicum*, which was later identified as zeatin. At present, more than 30 different plant growth-promoting cytokinin compounds produced by plant-associated microorganisms have been found, such as zeatin, isopentenyladenine, and dihydrozeatin, among others. Likewise, a large number of species producing this phytohormone have been reported, such as *Arthrobacter giacomelloi*, *Azospirillum brasilense*, *Bradyrhizobium japonicum*, *Bacillus licheniformis*, *Paenibacillus polymyxa*, *Pseudomonas fluorescens*, and *Rhizobium leguminosarum*, among others^[44,45].

3.7. Gibberellins

Gibberellins are a group of phytohormones consisting of about 136 molecules with different structures that regulate plant growth in various metabolic processes, including seed germination, stem elongation, flowering, fruit formation, and plant height^[41]. Gibberellins interact with other phytohormones, leading to important responses that mediate stress tolerance^[36]. The ability to stimulate plant growth and development under various abiotic stress conditions has also been reported^[46]. In addition, gibberellins induce efficient ion uptake within the plant, which enhances growth and maintains plant metabolism under normal and stress conditions^[47].

Gibberellins produced by PGPRs promote plant growth and increase yields^[48]. Currently, activity by several gibberellin-producing PGPR species has been reported, such as: *Azotobacter* spp., *Bacillus pumilus*, *B. licheniformis*, *Herbaspirillum seropedicea*, *Leifsonia xyli*, *Pseudomonas* spp., *Rhizobium meliloti* and *R. phaseoli* which have been used to induce germination in seeds^[7].

3.8. Abscisic acid

Abscisic acid (ABA) is a phytohormone with a sesquiterpenoid structure that plays a very important role in plant physiology, mainly in adaptive responses to biotic and abiotic stresses^[36,49,50]. ABA is involved in processes such as seed dormancy and organ abscission. Likewise, it has been reported that, under abiotic stress conditions, ABA up-regulates the expression of stress-responsive genes, leading to improved performance in tolerance responses^[51,52]. Furthermore, during drought, ABA has been found to function as an anti-transpirant as it induces stomatal closure to minimize water loss through transpiration^[49]. Similarly, it has been reported that ABA can control root growth and water content under drought stress conditions^[36]. Its exogenous application can ameliorate the effects caused by stresses, such as salinity, drought and cold stress, as well as wounding^[36,53].

The study related to ABA-producing rhizobacteria and their metabolism has been a bit more limited compared to that of other phytohormones, however, there are some species such as: *Azospirillum brasilense*, *Arthrobacter koereensis*, *Bacillus amyloliquefaciens*, *B. licheniformis* that have demonstrated the ability to produce this phytohormone^[36,52], counteracting the negative effects caused by biotic and abiotic stresses.

3.9. Exopolysaccharide and biofilm production

A wide variety of rhizobacteria possess the ability to release exopolysaccharides (EPS) and form biofilms in the root^[54]. Thus, rhizobacterial communities form complex structures of microbial cells adhering to the root surface, which are surrounded by an extracellular polymeric matrix (biofilms)^[55,56]. Rhizobacteria within the biofilm significantly protect plants from external stress, because they maintain greater adherence to surfaces, improving the soil aggregation state of the rhizosphere, which increases the availability of water and nutrients, likewise, the microbial density increases, which improves plant growth^[54,57]. In addition, rhizobacterial exopolysaccharides function as signal molecules that activate the defense response during the process of pathogen infection. Some EPS bind cations, including Na⁺, suggesting a role in mitigating salinity

stress by reducing the Na⁺ content available for plant consumption^[56]. Some PGPRs such as *Rhizobium leguminosarum*, *Azotobacter vinelandii*, *Bacillus drentensis*, *Enterobacter cloacae*, *Agrobacterium* sp., *Xanthomonas* sp. and *Rhizobium* sp. release exopolysaccharides^[22,58]. The application of EPS-producing PGPRs represent a promising measure to combat drought and salinity stress, thereby increasing global food security^[59].

4. Indirect mechanisms in the promotion of plant growth

4.1. Stress drivers

Stress is defined as any factor that negatively influences plant development^[60]. Plants are sessile organisms and are frequently subjected to various types of stresses such as: high temperatures, cold, drought, salinity, alkalinity, UV radiation, and pathogen infection. These factors are often unpredictable and come to significantly impair agricultural productivity^[22]. In the face of the present climate change, the aforementioned problems represent a challenge in the improvement of agricultural sustainability and production. In the following, mention is made of the participation of PGPRs and their role in stress management.

4.2. ACC deaminase

Ethylene is an essential metabolite for the growth and senescence of leaves, flowers, and fruits. This hormone, which is produced endogenously and at optimal levels, is important for inducing physiological changes in plants as it functions as a signal molecule that activates transcription of various genes that influence progression, reproductive success, and organ longevity, thus regulating plant lifespan^[61]. However, under stress conditions such as those generated by salinity, drought, heavy metals, and pathogenicity, endogenous ethylene levels are deliberately increased, causing defoliation, inhibition of cell elongation, senescence, and other cellular processes that negatively affect plant development^[44,62,63]. Therefore, alternatives have been sought to help counteract and decrease stress in plants caused by unpredictable environmental changes.

The direct precursor in the synthesis of ethylene in plants is ACC (1-aminocyclopropane-1-carboxylate acid). Rhizobacteria, with the ability to produce the enzyme ACC deaminase, facilitate and help plant growth and development under stress conditions as they decrease ethylene levels by metabolizing the precursor into a source of carbon (alpha-ketobutyrate) and nitrogen (ammonia), which they use as food^[7,64]. In addition, it has been found that in some legumes, this can increase the number of nodules, producing changes in root architecture and promoting the development of lateral roots^[65].

Currently, bacterial strains exhibiting ACC deaminase have been identified in a wide range of genera, such as *Achromobacter*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Rhizobium*, *Rhodococcus*, *Enterobacter*, *Klebsiella*, *Methylobacterium*, *Mesorhizobium*, *Pseudomonas*, and *Sinorhizobium*^[7,66].

4.3. Osmoprotectants

Under drought stress conditions, many rhizobacteria produce molecules that function as osmoprotectants (glutamate, trehalose, proline, glycine betaine (GB), proline betaine, ectoine etc.), maintaining fluid balance in cells and stimulating plant growth under unfavorable conditions. Some rhizobacterial species, such as *Bacillus polymyxa*, *Pseudomonas jessenii*, *Pseudomonas synxantha*, *Azospirillum lipoferum*, and *Arthrobacter nitroguajacolicus*, have been able to enhance plant growth under water stress conditions through the accumulation of free amino acids such as proline and soluble sugars^[67].

Some strains, such as *Bacillus subtilis*, *Klebsiella variicola*, *Pseudomonas fluorescens*, and *Raoultella planticola*, have shown the ability to enhance the biosynthesis and accumulation of cholines, a precursor in

GB metabolism, resulting in increased accumulation of this compound, thus improving relative leaf water content and dry weight^[67].

4.4. Heat shock proteins

High temperatures (>40 °C) are a major problem affecting the production of many crops worldwide^[68]. It promotes protein denaturation and aggregation, causing serious problems in plants. Some rhizobacteria, such as *Bacillus subtilis*, have the ability to induce thermotolerance in plants by synthesizing high-molecular-weight proteins (8–90 kDa), known as heat shock proteins (HSPs: *Heat Shock Proteins*). The main function of HSPs is the protection of other proteins that are affected by high temperatures^[69].

HSPs are constituted by chaperones (such as GroEL, DnaK, DnaJ, GroES, ClpB, ClpA, ClpX, small heat shock proteins (sHSPs), and proteases). Chaperones are involved in the proper folding of proteins that are denatured, whereas proteases are responsible for the degradation of proteins that are irreversibly damaged. The activity of such chaperones is essential for cell survival during heat shock and for subsequent recovery^[70].

4.5. Induced systemic resistance (ISR)

Some rhizobacteria increase the defensive capacity of plants for prolonged periods, a mechanism known as ISR (induced systemic resistance)^[71]. This response keeps the whole plant on alert and is induced in distant or unaffected parts^[72]. The ISR response is dependent on jasmonic acid and ethylene signaling in the plant. Accumulation of these molecules coordinates at the systemic level the activation and enhancement of defense capabilities such as cell wall strengthening, production of antimicrobial phytoalexins, peroxidase, chitinase, β -1,3-glucanase, phenylalanine ammonium lyase, pathogenesis-related proteins and biosurfactant production^[73]. During interaction with the plant, rhizobacteria release cellular structures such as: lipopolysaccharides (LPS), flagella, salicylic acid, siderophores, cyclic lipopeptides, among others, which induce ISR^[7,74]. Induction of ISR by rhizobacteria is a useful tool to reduce diseases caused by pathogens.

5. Biocontrol mechanisms (antagonism)

Some PGPRs naturally eliminate phytopathogens (bacteria, fungi, weeds and insects) by producing various secondary metabolites that are excreted locally or near the plant surface^[75]. The molecules released by these microorganisms are biodegradable and are needed in small quantities, unlike some agrochemicals that are resistant to degradation and are applied in large quantities to agricultural crops^[7]. Some of the main inhibitory compounds produced by some rhizobacteria are presented below (**Table 1**).

Table 1. Biotechnological potential of rhizobacteria in agriculture.

Rhizobacteria	Plant	Conditions	Results	Reference
<i>Pseudomonas gessardii</i> BLP141, <i>P. fluorescens</i> A506 and <i>P. fluorescens</i> LMG 2189	Sunflower (<i>Helianthus annuus</i>)	Greenhouse	Improved plant growth, physiology, yield and antioxidant activities, as well as proline accumulation.	Saleem et al. ^[76]
<i>Bacillus</i> sp. JS	Tobacco (<i>Nicotiana tabacum</i> 'Xanthi') and Lettuce (<i>Lactuca sativa</i> 'Crispa')	<i>In vitro</i>	Fresh weight and shoot length increased.	Kim et al. ^[77]
<i>Klebsiella</i> sp. Br1, <i>Klebsiella pneumoniae</i> Fr1, <i>Bacillus pumilus</i> S1r1, <i>B. subtilis</i> and <i>Acinetobacter</i> sp. S3r2	Corn (<i>Zea mays</i> L.)	Greenhouse	It increased top and root dry biomass and total nitrogen content.	Kuan et al. ^[78]

Table 1. (Continued).

Rhizobacteria	Plant	Conditions	Results	Reference
<i>P. luteola</i> IMPCA244, <i>O. anthropi</i> IMP311, <i>Aeromonas salmonicida</i> N264, <i>Burkholderia cepacia</i> N172, <i>P. fluorescens</i> N50 and <i>S. maltophilia</i>	Sugar cane (<i>Saccharum officinarum</i>)	Greenhouse	Plant height (27.75%), stem diameter (30.75%), number of tillers (38.5%), leaf area (49%), and aerial and root dry matter weight increased.	Morgado González et al. ^[79]
<i>Pseudomonas putida</i> , <i>Azospirillum</i> , <i>Azotobacter</i>	Artichoke (<i>Cynara scolymus</i>)	<i>In vitro</i>	Shoot length, shoot weight and germination time increased.	Jahanian et al. ^[80]
<i>Pseudomonas</i> sp.	Soybeans and wheat	Field	Increased soil enzymatic activities, total productivity and nutrient uptake.	Sharma et al. ^[81]
<i>Bradyrhizobium</i> sp., <i>Pseudomonas</i> sp., <i>Ochrobactrum cytisi</i>	<i>Lupinus luteus</i>	Field	Both biomass and nitrogen content increased.	Dary et al. ^[82]
<i>Pseudomonas putida</i> strain R-168, <i>P. fluorescens</i> strain R-93, <i>P. fluorescens</i> DSM 50090, <i>P. putida</i> DSM291, <i>Azospirillum lipqferum</i> DSM 1691, <i>A. brasilense</i> DSM 1690	Corn (<i>Zea mays</i> L.)	Field	Plant height, seed weight, number of seeds, and leaf area increased.	Gholami et al. ^[83]
<i>Azospirillum amazonense</i>	Rice (<i>Oryza sativa</i> L.)	Greenhouse	It increased grain dry matter accumulation (7%–11.6%), panicle number (3%–18.6%) and nitrogen accumulation at grain maturity (3.518%–5%).	Rodrigues et al. ^[84]
<i>Pseudomonas</i> sp.	Rice (<i>Oryza sativa</i>), maize (<i>Zea mays</i>)	<i>In vitro</i>	They showed ability to control root fungal pathogens.	Lawongsa et al. ^[85]
<i>Azospirillum brasilense</i> Sp245	Bean (<i>Phaseolus vulgaris</i>)	Greenhouse	Increased root growth.	Remans et al. ^[86]
<i>Bacillus subtilis</i> , <i>Pseudomonas aeruginosa</i>	<i>Solanum lycopersicum</i> , <i>Abelmoschus esculentus</i> , <i>Amaranthus</i> sp.	Greenhouse	Dry biomass increased by 31% for <i>Solanum lycopersicum</i> , 36% for <i>Abelmoschus esculentus</i> and 83% for <i>Amaranthus</i> sp.	Adesemoye et al. ^[87]
<i>Pseudomonas jessenii</i> PS06, <i>Mesorhizobium ciceri</i> C-2/2	<i>Cicer arietinum</i>	Greenhouse	The co-inoculation treatment increased seed yield (52% more than the control) and nodule fresh weight.	Valverde et al. ^[88]
<i>Azotobacter chroococcum</i> HKN-5, <i>Bacillus megaterium</i>	<i>Brassica juncea</i>	Greenhouse	It protected the plant from metal toxicity and stimulated plant growth.	Wu et al. ^[89]

5.1. Antibiotics

Many rhizobacteria secrete molecules that eliminate or decrease the growth of some phytopathogens by inhibiting cell wall synthesis, structural destabilization of the cell membrane, or inhibition of translation in phytopathogens, among others^[90]. Antibiotic production is one of the most studied biocontrol strategies of rhizobacteria and includes a wide variety of antibiotics (amphisin, 2,4-diacetylphloroglucinol (DAPG), oomycin-A, phenazine, pyrroluteorin, pyrrolnitrin, tensin, oligomycin-A, kanosamine, zwittermicin-A, and xanthobaccin)^[91].

Some genera of antibiotic-producing rhizobacteria correspond to *Burkholderia*^[92], *Streptomyces*^[93], *Bacillus*, *Pseudomonas*, and *Stenotrophomonas*^[91].

5.2. Siderophore production

Iron (Fe) is an essential element for virtually all living things in important cellular functions such as DNA synthesis, respiration, and free radical detoxification^[94]. For microorganisms, the availability of this element

is critical to the success or failure of their colonization of a given environment. To solve this problem, many organisms, such as rhizobacteria, secrete low-molecular-weight molecules (0.5 to 1.0 kDa) called siderophores which specifically act as chelating agents to sequester iron in the presence of other metals and reduce it to Fe^{2+} , a much more soluble and usable form for their nutrition^[62]. PGPRs with the ability to produce siderophores gain competitive advantages in root colonization, competition for the ecological niche, and inhibition of the growth of phytopathogenic fungi due to the low concentration of Fe^{3+} available in soils^[73].

5.3. Volatile organic compounds (VOCs)

VOCs are diverse molecules of low molecular weight (300 g mol^{-1}), among which are aldehydes, alcohols, ketones, hydrocarbons, indoles, fatty acid derivatives, terpenes, and jasmonates^[95]. Recently, about 846 different VOCs produced by 350 bacterial species have been reported, among which the most representative are acetoin and 2,3-butanediol^[96]. A large number of rhizobacterial genera, such as *Pseudomonas*, *Bacillus*, *Arthrobacter*, *Stenotrophomonas*, and *Serratia*, have demonstrated the ability to produce volatile organic compounds that positively affect plant growth^[22].

6. Conclusions

Rhizobacteria represent a biotechnological alternative in agriculture, mainly due to the large number of molecular mechanisms that allow improving yield and plant health. Inoculants based on rhizobacteria are a biotechnological alternative in sustainable agriculture that can increase yields and reduce production costs in agricultural practice. Likewise, rhizobacteria can help reduce the use of chemical fertilizers, pesticides, and artificial regulators that have negative effects on natural ecosystems and contribute to more environmentally friendly agriculture. More research is needed to understand the mechanisms of phytostimulation in different environmental conditions and different crops, as well as to find strains that can be controlled in different scenarios.

Acknowledgments

To CONACYT for funding under grant No. 819029 in the Graduate Program in Science, University of Guadalajara.

Conflict of interest

The authors declare no conflict of interest.

References

1. Food and Agriculture Organization of the United Nations. The future of food and agriculture: Trends and challenges. Available online: <http://www.fao.org/3/a-i6881s.pdf> (accessed on 3 March 2019).
2. Shailendra Singh GG. Plant growth promoting rhizobacteria (PGPR): Current and future prospects for development of sustainable agriculture. *Journal of Microbial & Biochemical Technology* 2015; 7(2). doi: 10.4172/1948-5948.1000188
3. Pretty J, Benton TG, Bharucha ZP, et al. Global assessment of agricultural system redesign for sustainable intensification. *Nature Sustainability* 2018; 1(8): 441–446. doi: 10.1038/s41893-018-0114-0
4. Werner GDA, Cornwell WK, Sprent JI, et al. A single evolutionary innovation drives the deep evolution of symbiotic N_2 -fixation in angiosperms. *Nature Communications* 2014; 5(1). doi: 10.1038/ncomms5087
5. Upson JL, Zess EK, Bialas A, et al. The coming of age of EvoMPMI: Evolutionary molecular plant-microbe interactions across multiple timescales. *Current Opinion in Plant Biology* 2018; 44: 108–116. doi: 10.1016/j.pbi.2018.03.003
6. Stringlis IA, Proietti S, Hickman R, et al. Root transcriptional dynamics induced by beneficial rhizobacteria and microbial immune elicitors reveal signatures of adaptation to mutualists. *The Plant Journal* 2017; 93(1): 166–180. doi: 10.1111/tbj.13741
7. Molina-Romero D, Bustillos-Cristales MR, Rodríguez-Andrade O, et al. Mechanisms of phytostimulation by

- rhizobacteria, isolates in America and biotechnological potential (Spanish). *Biologicas* 2015; 17(2): 24–34.
8. McNear DH. The rhizosphere - roots, soil and everything in between. Available online: https://www.researchgate.net/publication/303919396_The_rhizosphere-roots_soil_and_everything_in_between (accessed on 19 December 2019).
 9. Kloepper JW, Schroth MN. Plant growth-promoting rhizobacteria on radishes. In: Proceedings of the 4th International Conference on Plant Pathogenic Bacteria; 27 August–2 September 1978; Angers, France. pp. 879–882.
 10. Venturi V, Keel C. Signaling in the rhizosphere. *Trends Plant Science* 2016; 21: 187–198. doi: 10.1016/j.tplants.2016.01.005
 11. Ahemad M, Kibret M. Mechanisms and applications of plant growth promoting rhizobacteria: Current perspective. *Journal of King Saud University – Science* 2014; 26(1): 1–20. doi: 10.1016Zj. jksus.2013.05.001
 12. Mayz J. Biological nitrogen fixation. *Revista Científica UDO Agrícola* 2004; 4: 1–20.
 13. Bhattacharyya PN, Jha DK. Plant growth-promoting rhizobacteria (PGPR): Emergence in agriculture. *World Journal of Microbiology and Biotechnology* 2011; 28(4): 1327–1350. doi: 10.1007/s11274-011-0979-9
 14. Perin L, Martínez-Aguilar L, Castro-González R, et al. Diazotrophic *Burkholderia* species associated with field-grown maize and sugarcane. *Applied and Environmental Microbiology* 2006; 72: 3103–3110. doi: 10.1128/aem.72.5.3103-3110.2006
 15. Razaq M, Zhang P, Shen H long, et al. Influence of nitrogen and phosphorous on the growth and root morphology of Acer mono. *PLoS ONE* 2017; 12(2): e0171321. doi: 10.1371/journal.pone.0171321
 16. Weil RR, Brady NC. *The Nature and Properties of Soils*. Prentice Hall; 2002.
 17. Yadav BK, Verm A. Phosphate solubilization and mobilization in soil through microorganisms under arid ecosystems. In: Ali M (editor). *The Functioning of Ecosystems*. IntechOpen; 2012. doi: 10.5772/35917
 18. Lugtenberg B, Kamilova F. Plant-growth-promoting rhizobacteria. *Annual Review of Microbiology* 2009; 63(1): 541–556. doi: 10.1146/annurev.micro.62.081307.162918
 19. Oteino N, Lally RD, Kiwanuka S, et al. Plant growth promotion induced by phosphate solubilizing endophytic *Pseudomonas* isolates. *Frontiers in Microbiology* 2015; 6: 1–9. doi: 10.3389/fmicb.2015.00745
 20. Khan MS, Zaidi A, Wani PA. Role of phosphate-solubilizing microorganisms in sustainable agriculture—A review. *Agronomy for Sustainable Development* 2007; 27: 29–43. doi: 10.1051/agro:2006011
 21. Parmar P, Sindhu SS. Potassium solubilization by rhizosphere bacteria: Influence of nutritional and environmental conditions. *Journal of Microbiology Research* 2013; 3: 25–31. doi: 10.5923/j.microbiology.20130301.04
 22. Gouda S, Kerry RG, Das G, et al. Revitalization of plant growth promoting rhizobacteria for sustainable development in agriculture. *Microbiological Research* 2018; 206: 131–140. doi: 10.1016/j.micres.2017.08.016
 23. Ahmad MS, Zargar MY. Characterization of potassium solubilizing bacteria (KSB) in rhizospheric soils of apple (*Malus domestica* Borkh.) in temperate Kashmir. *Journal of Applied Life Sciences International* 2017; 15: 1–7. doi: 10.9734/JALSI/2017/36848
 24. Bagyalakshmi B, Ponmurugan P, Balamurugan A. Potassium solubilization, plant growth promoting substances by potassium solubilizing bacteria (KSB) from southern Indian tea plantation soil. *Biocatalysis and Agricultural Biotechnology* 2017; 12: 116–124. doi: 10.1016/j.bcab.2017.09.011
 25. Bakhshandeh E, Rahimian H, Pirdashti H, et al. Phosphate solubilization potential and modeling of stress tolerance of rhizobacteria from rice paddy soil in northern Iran. *World Journal of Microbiology and Biotechnology* 2014; 30(9): 2437–2447. doi: 10.1007/s11274-014-1669-1
 26. Abou-el-Seoud II, Abdel-Megeed A. Impact of rock materials and biofertilizations on P and K availability for maize (*Zea Maize*) under calcareous soil conditions. *Saudi Journal of Biological Sciences* 2012; 19(1): 55–63. doi: 10.1016/j.sjbs.2011.09.001
 27. Zhang C, Kong F. Isolation and identification of potassium-solubilizing bacteria from tobacco rhizospheric soil and their effect on tobacco plants. *Applied Soil Ecology* 2014; 82: 18–25. doi: 10.1016/j.apsoil.2014.05.002
 28. Singh G, Biswas DR, Marwaha TS. Mobilization of potassium from waste mica by plant growth promoting rhizobacteria and its assimilation by maize (*Zea mays*) and wheat (*Triticum aestivum* L.): A hydroponics study under phytotron growth chamber. *Journal of Plant Nutrition* 2010; 33(8): 1236–1251. doi: 10.1080/01904161003765760
 29. Saiyad SA, Jhala YK, Vyas RV. Comparative efficiency of five potash and phosphate solubilizing bacteria and their key enzymes useful for enhancing and improvement of soil fertility. *International Journal of Scientific and Research Publications* 2015; 5(2): 1–6.
 30. Etesami H, Emami S, Alikhani HA. Potassium solubilizing bacteria (KSB): Mechanisms, promotion of plant growth, and future prospects—A review. *Journal of Soil Science and Plant Nutrition* 2017; 17(4): 897–911. doi: 10.4067/S0718-95162017000400005
 31. Damam M, Kaloori K, Gaddam B, Kausar R. Plant growth promoting substances (phytohormones) produced by rhizobacterial strains isolated from the rhizosphere of medicinal plants. *International Journal of Pharmaceutical Sciences Review and Research* 2016; 37(1): 130–136.

32. Calvo P, Ormeño-Orrillo E, Martínez-Romero E, et al. Characterization of *Bacillus* isolates of potato rhizosphere from andean soils of Peru and their potential PGPR characteristics. *Brazilian Journal of Microbiology* 2010; 41(4): 899–906. doi: 10.1590/s1517-83822010000400008
33. Carcaño-Montiel MG, Ferrera-Cerrato R, Pérez-Moreno J, et al. Nitrogenase activity, production of phytohormones, siderophores and antibiosis in strains of *Azospirillum* and *Klebsiella* isolated from maize and teosintle. *Terra Latinoamericana* 2006; 24(4): 493–502.
34. Angulo VC, Sanfuentes EA, Rodríguez F, Sossa KE. Characterization of growth-promoting rhizobacteria in *Eucalyptus nitens* seedlings (Spanish). *Revista Argentina de Microbiología* 2014; 46: 338–347. doi: 10.1016/S0325-7541(14)70093-8
35. Pereira SIA, Monteiro C, Vega AL, et al. Endophytic culturable bacteria colonizing *Lavandula dentata* L. plants: Isolation, characterization and evaluation of their plant growth-promoting activities. *Ecological Engineering* 2016; 87: 91–97. doi: 10.1016/j.ecoleng.2015.11.033
36. Egamberdieva D, Wirth SJ, Alqarawi AA, et al. Phytohormones and beneficial microbes: Essential components for plants to balance stress and fitness. *Frontiers in Microbiology* 2017; 8: 2104. doi: 10.3389/fmicb.2017.02104
37. Fibach-Paldi S, Burdman S, Okon Y. Key physiological properties contributing to rhizosphere adaptation and plant growth promotion abilities of *Azospirillum brasilense*. *FEMS Microbiology Letters* 2012; 326(2): 99–108. doi: 10.1111/j.1574-6968.2011.02407.x. c
38. Asgher Mohd, Khan MIR, Anjum NA, et al. Minimising toxicity of cadmium in plants—Role of plant growth regulators. *Protoplasma* 2014; 252(2): 399–413. doi: 10.1007/s00709-014-0710-4
39. Ali B. Bacterial auxin signaling: Comparative study of growth induction in *Arabidopsis thaliana* and *Triticum aestivum*. *Turkish Journal of Botany* 2015; 39(1): 1–9. doi: 10.3906/bot-1401-31
40. Raheem A, Shaposhnikov A, Belimov A, et al. Auxin production by rhizobacteria was associated with improved yield of wheat (*Triticum aestivum* L.) under drought stress. *Archives of Agronomy and Soil Science* 2018; 64(4): 574–587. doi: 10.1080/03650340.2017.1362105
41. Kang SM, Waqas M, Hamayun M, et al. Gibberellins and indole-3-acetic acid producing rhizospheric bacterium *Leifsonia xyli* SE134 mitigates the adverse effects of copper-mediated stress on tomato. *Journal of Plant Interactions* 2017; 12(1): 373–380. doi: 10.1080/17429145.2017.1370142
42. Liu F, Xing S, Ma H, et al. Cytokinin-producing, plant growth-promoting rhizobacteria that confer resistance to drought stress in *Platycladus orientalis* container seedlings. *Applied Microbiology and Biotechnology* 2013; 97(20): 9155–9164. doi: 10.1007/s00253-013-5193-2
43. Phillips DA, Torrey JG. Studies on cytokinin production by rhizobium. *Plant Physiology* 1972; 49(1): 11–15. doi: 10.1104/pp.49.1.11
44. Vacheron J, Desbrosses G, Bouffaud ML, et al. Plant growth-promoting rhizobacteria and root system functioning. *Frontiers in Plant Science* 2013; 4. doi: 10.3389/fpls.2013.00356
45. Maheshwari DK, Dheeman S, Agarwal M. Phytohormone-producing PGPR for sustainable agriculture. In: Maheshwari DK (editor). *Bacterial Metabolites in Sustainable Agroecosystem*. Springer; 2015. Volume 12. pp. 159–182. doi: 10.1007/978-3-319-24654-3_7
46. Ahmad P. Growth and antioxidant responses in mustard (*Brassica juncea* L.) plants subjected to combined effect of gibberellic acid and salinity. *Archives of Agronomy and Soil Science* 2010; 56(5): 575–588. doi: 10.1080/03650340903164231
47. Iqbal M, Ashraf M. Gibberellic acid mediated induction of salt tolerance in wheat plants: Growth, ionic partitioning, photosynthesis, yield and hormonal homeostasis. *Environmental and Experimental Botany* 2013; 86: 76–85. doi: 10.1016/j.envexpbot.2010.06.002
48. Desai SA. Isolation and characterization of gibberellic acid (GA3) producing rhizobacteria from sugarcane roots. *Bioscience Discovery* 2017; 8(3): 488–494.
49. Cohen AC, Bottini R, Piccoli P. Role of abscisic acid producing PGPR in sustainable agriculture. In: Maheshwari DK (editor). *Bacterial Metabolites in Sustainable Agroecosystem*. Springer; 2015. Volume 12. pp. 259–282. doi: 10.1007/978-3-319-24654-3_9
50. Zhou C, Li F, Xie Y, et al. Involvement of abscisic acid in microbe-induced saline-alkaline resistance in plants. *Plant Signaling & Behavior* 2017; 12(10): e1367465. doi: 10.1080/15592324.2017.1367465
51. Sah SK, Reddy KR, Li J. Abscisic acid and abiotic stress tolerance in crop plants. *Frontiers in Plant Science* 2016; 7. doi: 10.3389/fpls.2016.00571
52. Shahzad R, Khan AL, Bilal S, et al. Inoculation of abscisic acid-producing endophytic bacteria enhances salinity stress tolerance in *Oryza sativa*. *Environmental and Experimental Botany* 2017; 136: 68–77. doi: 10.1016/j.envexpbot.2017.01.010
53. Li X, Cai J, Liu F, et al. Exogenous abscisic acid application during grain filling in winter wheat improves cold tolerance of offspring's seedlings. *Journal of Agronomy and Crop Science* 2014; 200(6): 467–478. doi: 10.1111/jac.12064
54. Mohammed AE. Effectiveness of exopolysaccharides and biofilm forming plant growth promoting rhizobacteria

- on salinity tolerance of faba bean (*Vicia faba* L.). *African Journal of Microbiology Research* 2018; 12(17): 399–404. doi: <https://doi.org/10.5897/AJMR2018.8822>
55. Upadhyay SK, Singh JS, Singh DP. Exopolysaccharide-producing plant growth-promoting rhizobacteria under salinity condition. *Pedosphere* 2011; 21(2): 214–222. doi: 10.1016/s1002-0160(11)60120-3
 56. Gupta G, Snehi SK, Singh V. Role of PGPR in biofilm formations and its importance in plant health. In: Gupta G, Snehi SK, Singh V (editors). *Biofilms in Plant and Soil Health*. John Wiley & Sons; 2017. pp. 27–42. doi: 10.1002/9781119246329.ch2
 57. Kasim WA, Gaafar RM, Abou-Ali RM, et al. Effect of biofilm forming plant growth promoting rhizobacteria on salinity tolerance in barley. *Annals of Agricultural Sciences* 2016; 61: 217–227. doi: 10.1016/j.aoas.2016.07.003
 58. Mahmood S, Daur I, Al-Solaimani SG, et al. Plant growth promoting rhizobacteria and silicon synergistically enhance salinity tolerance of mung bean. *Frontiers in Plant Science* 2016; 7. doi: 10.3389/fpls.2016.00876
 59. Naseem H, Ahsan M, Shahid MA, et al. Exopolysaccharides producing rhizobacteria and their role in plant growth and drought tolerance. *Journal of Basic Microbiology* 2018; 58(12): 1009–1022. doi: 10.1002/jobm.201800309
 60. Foyer CH, Rasool B, Davey JW, et al. Cross-tolerance to biotic and abiotic stresses in plants: A focus on resistance to aphid infestation. *Journal of Experimental Botany* 2016; 67(7): 2025–2037. doi: 10.1093/jxb/erw079
 61. Barnawal D, Pandey SS, Bharti N, et al. ACC deaminase-containing plant growth-promoting rhizobacteria protect papaver somniferum from downy mildew. *Journal of Applied Microbiology* 2017; 122(5): 1286–1298. doi: 10.1111/jam.13417
 62. Stearns JC, Woody OZ, McConkey BJ, et al. Effects of bacterial ACC deaminase on brassica napus gene expression. *Molecular Plant-Microbe Interactions*® 2012; 25(5): 668–676. doi: 10.1094/mpmi-08-11-0213
 63. Sarkar A, Ghosh PK, Pramanik K, et al. A halotolerant *Enterobacter* sp. displaying ACC deaminase activity promotes rice seedling growth under salt stress. *Research in Microbiology* 2018; 169(1): 20–32. doi: 10.1016/j.resmic.2017.08.005
 64. Shen M, Jun Kang Y, Li Wang H, et al. Effect of plant growth-promoting rhizobacteria (PGPRs) on plant growth, yield, and quality of tomato (*Lycopersicon esculentum* Mill.) under simulated seawater irrigation. *The Journal of General and Applied Microbiology* 2012; 58(4): 253–262. doi: 10.2323/jgam.58.253
 65. Cedeño-García GA, Gerding M, Moraga G, et al. Plant growth promoting rhizobacteria with ACC deaminase activity isolated from Mediterranean dryland areas in Chile: Effects on early nodulation in alfalfa. *Chilean Journal of Agricultural Research* 2018; 78(3): 360–369. doi: 10.4067/s0718-58392018000300360
 66. Patil C, Suryawanshi R, Koli S, et al. Improved method for effective screening of ACC (1-aminocyclopropane-1-carboxylate) deaminase producing microorganisms. *Journal of Microbiological Methods* 2016; 131: 102–104. doi: 10.1016/j.mimet.2016.10.009
 67. Vurukonda SSKP, Vardharajula S, Shrivastava M, et al. Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. *Microbiological Research* 2016; 184: 13–24. doi: 10.1016/j.micres.2015.12.003
 68. Ali SZ, Sandhya V, Grover M, et al. Effect of inoculation with a thermotolerant plant growth promoting *Pseudomonas putida* strain AKMP7 on growth of wheat (*Triticum* spp.) under heat stress. *Journal of Plant Interactions* 2011; 6(4): 239–246. doi: 10.1080/17429145.2010.545147
 69. Palacio-Rodríguez R, Ramos BP, Coria-Arellano JL, et al. Mechanisms of PGPRs to mitigate plant abiotic stress. *Arid-Science* 2016; 1: 4–11.
 70. Grover M, Ali SKZ, Sandhya V, et al. Role of microorganisms in adaptation of agriculture crops to abiotic stresses. *World Journal of Microbiology and Biotechnology* 2010; 27(5): 1231–1240. doi: 10.1007/s11274-010-0572-7
 71. Lucas JA, García-Villaraco A, Ramos B, et al. Structural and functional study in the rhizosphere of *Oryza sativa* L. plants growing under biotic and abiotic stress. *Journal of Applied Microbiology* 2013; 115(1): 218–235. doi: 10.1111/jam.12225
 72. Chaturvedi S. Induced systemic resistance. *Open Access Journal of Microbiology & Biotechnology* 2018; 3(1). doi: 10.23880/oajmb-16000126
 73. Sunar K, Dey P, Chakraborty U, Chakraborty B. Biocontrol efficacy and plant growth promoting activity of *Bacillus altitudinis* isolated from Darjeeling hills. *Journal of Basic Microbiology* 2013; 55(1): 91–104. doi: 10.1002/jobm.201300227
 74. Poupin MJ, Timmermann T, Vega A, et al. Effects of the plant growth-promoting bacterium *Burkholderia phytofirmans* PsJN throughout the life cycle of *Arabidopsis thaliana*. *PLoS ONE* 2013; 8(7): e69435. doi: 10.1371/journal.pone.0069435
 75. Bloemberg GV, Lugtenberg BJ. Molecular basis of plant growth promotion and biocontrol by rhizobacteria. *Current Opinion in Plant Biology* 2001; 4(4): 343–350. doi: 10.1016/S1369-5266(00)00183-7
 76. Saleem M, Asghar HN, Zahir ZA, et al. Impact of lead tolerant plant growth promoting rhizobacteria on growth, physiology, antioxidant activities, yield and lead content in sunflower in lead contaminated soil. *Chemosphere* 2018; 195: 606–614. doi: 10.1016/j.chemosphere.2017.12.117
 77. Kim JS, Lee JE, Nie H, et al. Physiological and proteomic analysis of plant growth enhancement by the

- rhizobacterium *Bacillus* sp. JS. *Genes & Genomics* 2018; 40: 129–136. doi: 10.1007/s13258-017-0615-7
78. Kuan KB, Othman R, Abdul Rahim K, Shamsuddin ZH. Plant growth-promoting rhizobacteria inoculation to enhance vegetative growth, nitrogen fixation and nitrogen remobilization of maize under greenhouse conditions. *PLoS ONE* 2016; 11: 1–19. doi: 10.1371/journal.pone.0152478
 79. Morgado González A, Espinosa Victoria D, Gómez Merino FC. Efficiency of plant growth promoting rhizobacteria (PGPR) in sugarcane. *Terra Latinoamericana* 2015; 33(4): 321–330.
 80. Jahanian A, Chaichi MR, Rezaei K, et al. The effect of plant growth promoting rhizobacteria (PGPR) on germination and primary growth of artichoke (*Cynara scolymus*). *International Journal of Agriculture and Crop Sciences* 2012; 4: 923–929.
 81. Sharma SK. Selection of plant growth-promoting *Pseudomonas* spp. That enhanced productivity of soybean-wheat cropping system in central India. *Journal of Microbiology and Biotechnology* 2011; 21(11): 1127–1142. doi: 10.4014/jmb.1012.12018
 82. Dary M, Chamber-Pérez MA, Palomares AJ, et al. “In situ” phytostabilisation of heavy metal polluted soils using *Lupinus luteus* inoculated with metal resistant plant-growth promoting rhizobacteria. *Journal of Hazardous Materials* 2010; 177(1–3): 323–330. doi: 10.1016/j.jhazmat.2009.12.035
 83. Gholami A, Shahsavani S, Nezarat S. The effect of plant growth promoting rhizobacteria (PGPR) on germination, seedling growth and yield of maize. *International Journal of Agricultural and Biosystems Engineering* 2009; 3(1): 35–40.
 84. Rodrigues EP, Rodrigues LS, de Oliveira ALM, et al. *Azospirillum amazonense* inoculation: Effects on growth, yield and N₂ fixation of rice (*Oryza sativa* L.). *Plant and Soil* 2007; 302(1–2): 249–261. doi: 10.1007/s11104-007-9476-1
 85. Lawongsa P, Boonkerd N, Wongkaew S, et al. Molecular and phenotypic characterization of potential plant growth-promoting *Pseudomonas* from rice and maize rhizospheres. *World Journal of Microbiology and Biotechnology* 2008; 24(9): 1877–1884. doi: 10.1007/s11274-008-9685-7
 86. Remans R, Beebe S, Blair M, et al. Physiological and genetic analysis of root responsiveness to auxin-producing plant growth-promoting bacteria in common bean (*Phaseolus vulgaris* L.). *Plant and Soil* 2007; 302(1–2): 149–161. doi: 10.1007/s11104-007-9462-7
 87. Adesemoye AO, Obini M, Ugoji EO. Comparison of plant growth-promotion with *Pseudomonas aeruginosa* and *Bacillus subtilis* in three vegetables. *Brazilian Journal of Microbiology* 2008; 39(3): 423–426. doi: 10.1590/s1517-83822008000300003
 88. Valverde A, Burgos A, Fiscella T, et al. Differential effects of coinoculations with *Pseudomonas jessenii* PS06 (a phosphate-solubilizing bacterium) and *Mesorhizobium ciceri* C-2/2 strains on the growth and seed yield of chickpea under greenhouse and field conditions. *Plant Soil* 2006; 287: 43–50. doi: <https://doi.org/10.1007/s11104-006-9057-8>
 89. Wu CH, Wood TK, Mulchandani A, et al. Engineering plant-microbe symbiosis for rhizoremediation of heavy metals. *Applied and Environmental Microbiology* 2006; 72(2): 1129–1134. doi: 10.1128/aem.72.2.1129-1134.2006
 90. Beneduzi A, Ambrosini A, Passaglia LMP. Plant growth promoting rhizobacteria (PGPR): Their potential as antagonists and biocontrol agents. *Genetics and Molecular Biology* 2012; 35: 1044–1051. doi: 10.1590/s1415-47572012000600020
 91. Chuks Kenneth O. Plant growth promoting rhizobacteria (PGPR): A bioprotectant bioinoculant for sustainable agrobiolgy. A review. *International Journal of Advanced Research in Biological Sciences (IJARBS)* 2017; 4(5): 123–142. doi: 10.22192/ijarbs.2017.04.05.014
 92. Tenorio-Salgado S, Tinoco R, Vazquez-Duhalt R, et al. Identification of volatile compounds produced by the bacterium *Burkholderia tropica* that inhibit the growth of fungal pathogens. *Bioengineered* 2013; 4(4): 236–243. doi: 10.4161/bioe.23808
 93. Rajesh Kan R, Prakash Vi SG. Molecular characterization of antagonistic streptomycetes isolated from a mangrove swamp. *Asian Journal of Biotechnology* 2011; 3(3): 237–245. doi: 10.3923/ajbkr.2011.237.245
 94. Rajkumar M, Ae N, Prasad MNV, et al. Potential of siderophore-producing bacteria for improving heavy metal phytoextraction. *Trends in Biotechnology* 2010; 28(3): 142–149. doi: 10.1016/j.tibtech.2009.12.002
 95. Farag MA, Zhang H, Ryu CM. Dynamic chemical communication between plants and bacteria through airborne signals: Induced resistance by bacterial volatiles. *Journal of Chemical Ecology* 2013; 39: 1007–1018. doi: 10.1007/s10886-013-0317-9
 96. Tahir HAS, Gu Q, Wu H, et al. Plant growth promotion by volatile organic compounds produced by *Bacillus subtilis* SYST2. *Frontiers in Microbiology* 2017; 8: 1–11. doi: 10.3389/fmicb.2017.00171