Rhizospheric bacteria with potential benefits in agriculture Rhizospheric bacteria with potential benefits in agriculture

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, 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 in sustainable agriculture and their commercialization, a field that continues to grow steadily.

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

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 (FAO, 2017). 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 (Gupta et.al, 2015). On the other hand, according to FAO (2017) agriculture will face a great challenge, since by 2050 it will have to produce almost 50% more food, fodder and biofuel than what it produced in 2012, this 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, which have been abused in their use, will be important factors that will damage crop yields. The above poses great challenges for agriculture having to look for systems that allow obtaining optimal food production with cost reduction and conservation of natural resources in the long term (Pretty et al., 2018).

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 (Werner et al., 2014; Upson et al., 2018). 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) (Stringlis et al., 2018). While rhizobacteria incredibly improve growth, health and adaptability against different biotic and abiotic stress conditions of plants (Molina-Romero et al., 2015; Stringlis et al., 2018).

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 (Gupta et al., 2015).

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 (McNear, 2013), in addition, it harbors a large number of microorganisms that generally stimulate plant growth and reduce the incidence of diseases (Molina-Romero et al., 2015). This bacterial group has also been assigned the name Plant Growth Promoting Rhizobacteria (PGPR) (Kloepper and Schroth, 1978).

In the process of establishing relationships with rhizobacteria plants invest up to 20% of carbon sources obtained during photosynthesis, this in exchange for the improvement of root architecture, nutrient uptake and stimulation of the plant immune system carried out by PGPR (Stringlis et al., 2018). One of the best known examples of such benefits is found in the case of Rhizobium bacteria (Stringlis et al., 2018).

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 (Venturi and Keel, 2016). 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 a good adhesion and colonization on the root surface are factors that can influence the functionality of the associative symbiosis (Molina-Romero et al., 2015; Venturi and Keel, 2016) (Figure 1).

Direct Mechanisms in the Promotion of Plant Growth

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 (Ahemad and Kibret, 2014). A common feature of microorganisms involved in FBN is the presence of nitrogenase enzymes, which reduce atmospheric nitrogen into the assimilable ion $NH4^{+}$. 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 (Mayz-Figueroa, 2004).

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 地， fixing bacteria in which members of the family Rhizobiaceae and the genus Frankia are found (Ahemad and Kibret, 2014) and free-living, associative and endophytic non-symbiotics, such as cyanobacteria (Anabaena, Nostoc), Azospirillum, Azotobacter, Gluconoace tob ac te r diazotrophicus, Azocarus (Bhattacharyya and Jha, 2012), Paraburkholderia (Perin et al., 2006).

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 (Razaq et al., 2017). 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} (Brady and Weil, 2002), 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 (Yadav and Verma, 2012).

However, plants only take up phosphate in monobasic form: $H_2PO_4^{-1}$ and dibasic form: HPO_4^{-2} (Lugtenberg and Kamilova, 2009).

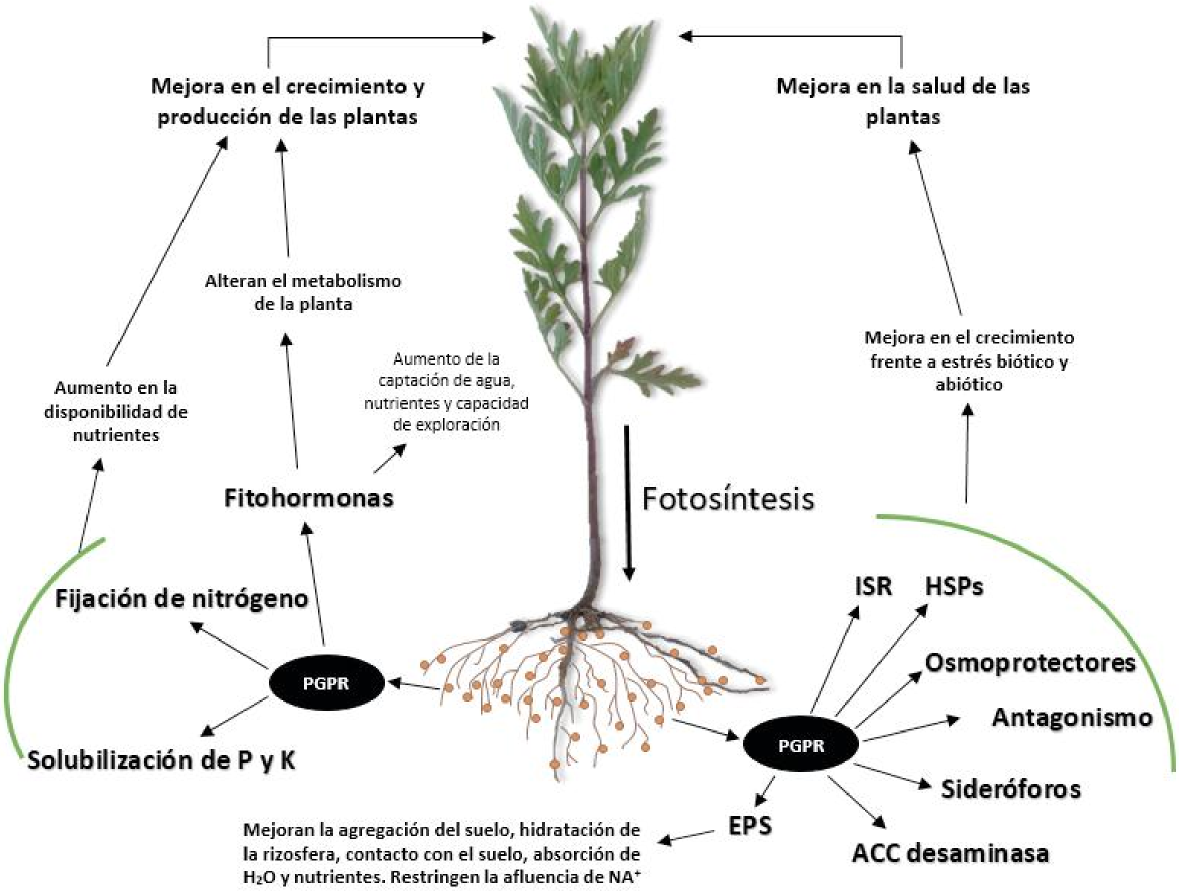

Figure 1. Mechanisms of action of PGPR. EPS: Exopolysaccharides; ISR: -Induced Systemic Resistance.- HSPs: Heat shock proteins.

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, phosphonatases and C-P lyases has been reported (Lugtenberg and Kamilova, 2009; Molina-Romero et al., 2015), 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 (Ahemad and Kibret, 2014; Molina-Romero et al., 2015; Oteino et al., 2015). Thus, phosphate solubilizing rhizobacteria represent an alternative in improving the application of chemical phosphate fertilizers and agricultural productivity, as they have the ability to provide available forms of phosphorus to plants (Khan et al., 2007).

Potassium solubilization. Potassium (K) is the third essential macronutrient needed in plant growth, so its limitation significantly affects crop production (Parmar and Sindhu, 2013; Gouda et al., 2018). In plants, K plays a very important role in processes such as photosynthesis, in which it regulates stomatal opening and closing and therefore CO? 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 in nitrogen absorption, thus being vital for better plant development (Ahmad and Zargar, 2017). K deficit generates plants with poorly developed roots, low growth rate and low seed production, which is reflected in lower yield (Bhagyalakshmi et al., 2017). Potassium deficiencies are not usually the same as nitrogen or phosphorus deficiencies, however, inadequate application, runoff, leaching, and soil erosion are often serious problems (Ahmad and Zargar, 2017).

Recently, rhizobacteria have been identified with the ability to solubilize minerals such as K, which can contribute to resource conservation and thus increase productivity (Parmar and Sindhu, 2013). Likewise, the positive effect of rhizobacteria on K availability in soil (Bakhshandeh et al., 2014) and K uptake in crops such as maize (Abou-el-Seoud and Abdel- Megeed, 2012), tobacco (Zhang and Kong, 2014) and wheat (Singh et al., 2010) 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 (Saiyad etal., 2015). Some genera such as Acidithiobacillus, Aminobacter, Arthrobacter, Bacillus, Burkholderia, Cladosporium, Enterobacter, Paenibacillus and Sphingomonas have been reported as potassium solubilizing rhizobacteria (Etesami et al., 2017).

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 (Damam et al., 2016; Gouda et al., 2018). Some rhizobacteria have the ability to produce phytohormones, being this one of the most studied mechanisms associated in the promotion of plant growth, such as B. amyloliquefaciens in potato crop (Calvo et al., 2010), Azospirillum and Klebsiella in corn crops (Carcaño-Montiel etal., 2006), Bacillus, Lysinibacillus, Arthrobacter and Rahnella in Eucalyptus nitens plantations (Angulo et al., 2014). Some of the groups influenced by rhizobacteria include auxins, cytokinins, gibberellins, abscisic acid, ethylene and jasmonic acid (Pereira et al., 2016; Egamberdieva et al., 2017). These molecules influence plant physiology, 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 (Fibach-Paldi et al., 2011).

Auxins. Auxins are a very important type of phytohormones in plants, they influence various developmental events such as cell division, elongation, apical dominance, adventitious root formation and phototropism (Asgher et al., 2014; Egamberdieva et al., 2017). One of the most well-known auxins produced by rhizobacteria is indole-3-acetic acid (IAA) (Ali, 2015). AIA 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 (Raheem et al., 2018). Likewise, the ability of rhizobacteria to modulate and tolerate abiotic stress using this phytohormone has been demonstrated (Egamberdieva et al., 2017).

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 (Kang et al., 2017).

Cytokinins. Cytokinins are another important group of phytohormones, their structure 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, increase of root area through adventitious root formation, leaf formation, as well as prevention of senescence (Liu et al., 2013;

Molina-Romero et al., 2015).

In the early 1970s, Phillips and Torrey (1972) 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, dihydroxizeatin, 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 (Vacheron et al., 2013; Maheshwari et al., 2015).

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 (Kang et al., 2017). Gibberellins interact with other phytohormones, leading to important responses that mediate stress tolerance (Egamberdieva et al., 2017). The ability to stimulate plant growth and development under various abiotic stress conditions has also been reported (Ahmad, 2010). In addition, gibberellins induce efficient ion uptake within the plant, which enhances growth and maintains plant metabolism under normal and stress conditions (Iqbal and Ashraf, 2013).

Gibberellins produced by PGPRs promote plant growth and increase yields (Desai, 2017). Currently, activity by several gibberellin-producing PGPR species has been reported, such as: Azotobacter spp., Bacillus pumilus, B. licheniformis, Herbaspirilum seropedicea, Leifsonia xyli, Pseudomonas spp., Rhizobium meliloti and R. phaseoli which have been used to induce germination in seeds (Molina-Romero et al., 2015).

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 (Cohen et al., 2015; Egamberdieva et al., 2017; Zhou et al., 2017). 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 (Sah et al., 2016; Shahzad et al., 2017). Furthermore, during drought, ABA has been found to function as an anti-transpirant as it induces stomatal closure to minimize water loss through transpiration (Cohen et al., 2015). Similarly, it has been reported that ABA can control root growth and water content under drought stress conditions (Egamberdieva et al., 2017). Its exogenous application can ameliorate the effects caused by stresses, such as salinity, drought and cold stress, as well as wounding (Li et al., 2014; Egamberdieva et al., 2017).

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 (Egamberdieva et al., 2017; Shahzad et al., 2017), counteracting the negative effects caused by biotic and abiotic stresses.

Exopolysaccharide and biofilm production. A wide variety of rhizobacteria possess the ability to release exopolysaccharides (EPS) and form biofilms in the root (Mohammed, 2018). Thus, rhizobacterial communities form complex structures of microbial cells adhering to the root surface, which are surrounded by an extracellular polymeric matrix (biofilms) (Upadhyay et al., 2011; Gupta et al., 2017). 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 (Kasim et al., 2016; Mohammed, 2018). 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 (Gupta et al., 2017). Some PGPRs such as Rhizobium leguminosarum, Azotobacter vinelandii, Bacillus drentensis, Enterobacter cloacae, Agrobacterium sp., Xanthomonas sp. and Rhizobium sp. release exopolysaccharides (Mahmood et al., 2016; Gouda et al., 2017). The application of EPS-producing PGPRs represent a promising measure to combat drought and salinity stress, thereby increasing global food security (Naseem et al., 2018).

Indirect Mechanisms in the Promotion of Plant Growth

Stress drivers. Stress is defined as any factor that negatively influences plant development (Foyer et al., 2016). 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 (Gouda et al., 2018). 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.

ACC deaminase. Ethylene is an essential metabolite for growth and senescence of leaves, flowers and fruits. This hormone 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 (Barnawal et al., 2017). 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 (Stearns et al., 2012; Vacheron et al., 2013; Sarkar et al., 2018). 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 (Shen et al., 2012; Molina- Romero et al., 2015). 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 (Cedeño-García et al., 2018).

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 (Molina-Romero et al., 2015; Patil et al., 2016).

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, Arthrobacter nitroguajacolicus, have been able to enhance plant growth under water stress conditions through accumulation of free amino acids such as proline and soluble sugars (Vurukonda et al., 2016).

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 (Vurukonda et al., 2016).

Heat shock proteins. High temperatures (>40 °C) is a major problem affecting the production of many crops worldwide (Ali et al., 2011). 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, 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 (Palacio-Rodríguez et al., 2016).

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 were irreversibly damaged. The activity of such chaperones is essential for cell survival during heat shock and for subsequent recovery (Grover et al., 2011).

Induced systemic resistance (ISR). Some rhizobacteria increase the defensive capacity in plants for prolonged periods, a mechanism known as ISR (induced systemic resistance) (Lucas et al., 2013). This response keeps the whole plant on alert and is induced in distant or unaffected parts (Chaturvedi and Paul Khurana, 2017). 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 (Sunar et al., 2015). During interaction with the plant, rhizobacteria release cellular structures such as: lipopolysaccharides (LPS), flagella, salicylic acid, siderophores, cyclic lipopeptides, among others, which induce ISR (Poupin et al., 2013; Molina-Romero et al., 2015). Induction of ISR by rhizobacteria is a useful tool to reduce diseases caused by pathogens.

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 (Bloemberg and Lugtenberg, 2001). 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 (Molina-Romero et al., 2015). 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
Pseudomonas gessardii BLP141, P. fluorescens A506 and P. fluorescens LMG 2189	Sunflower (Helianthus annuus)	Greenhouse	Improved plant growth, physiology, yield and antioxidant activities, as well as proline accumulation.	Saleem et al. (2018)
Bacillus sp. JS	Tobacco (Nicotiana tabacum 'Xanthi') and Lettuce (Lactuca sativa 'Crispa')	In vitro	Fresh weight and shoot length increased.	Kim et al. (2018)
Klebsiella sp. Br1, Klebsiella pneumoniae Fr1, Bacillus pumilus S1r1, B. subtilis and Acinetobacter sp. S3r2	Corn (Zea mays L.)	Greenhouse	It increased top and root dry biomass and total nitrogen content.	Kuan et al. (2016)

P luteola IMPCA244, O. anthropi IMP311, Aeromonas salmonicida N264, Burkholderia cepacia N172, P fluorescens N50 and S. maltophilia	Sugar cane (Saccharum officinarum)	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. (2015)
Pseudomonas putida, Azospirilium, Azotobacter	Artichoke (Cynara scolymus)	In vitro	Shoot length, shoot weight and germination time increased.	Jahanian et al. (2012)
Pseudomonas sp.	Soybeans and wheat	Field	Increased soil enzymatic activities, total productivity and nutrient uptake.	Sharma et al (2011)
Bradyrhizobium sp., Pseudomonas sp., Ochrobactrum cytisi	Lupinus luteus	Field	Both biomass and nitrogen content increased.	Dary et al. (2010)
Pseudomnas putida strain R-168, P. fluorescens strain R-93, P. fluorescens DSM 50090, P. putida DSM291, Azospirillum lipqferum DSM 1691, A. brasilense DSM 1690	Corn (Zea mays L.)	Field	Plant height, seed weight, number of seeds, and leaf area increased.	Gholami et al. (2009)
Azospirillum amazonense	Rice (Oryza sativa 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. (2008)
Pseudomonas sp.	Rice (Oryza sativa), maize (Zea mays)	In vitro	They showed ability to control root fungal pathogens.	Lawongsa et al. (2008)
Azospirillum brasilense Sp245	Bean (Phaseolus vulgaris)	Greenhouse	Increased root growth.	Remans et al. (2008)
Bacillus subtilis, Pseudomonas aeruginosa	Solanum lycopersicum, Abelmoschus esculentus, Amaranthus sp.	Greenhouse	Dry biomass increased by 31% for Solanum lycopersicum, 36% for Abelmoschus esculentus and 83% for Amaranthus sp.	Adesemoye et al. (2008).
Pseudomonas jessenii PS06, Mesorhizobium ciceri C-2/2	Cicer arietinum	Greenhouse	The co-inoculation treatment increased seed yield (52% more than the control) and nodule fresh weight.	Valverde et al. (2006)
Azotobacter chroococcum	Brassica juncea	Greenhouse	It protected the plant from metal	Wu et al.

HKN-5, Bacillus megaterium		toxicity and stimulated plant growth.	(2006)

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 (Beneduzi et al., 2012). Antibiotic production is one of the most studied biocontrol strategies of rhizobacteria and include a wide variety of antibiotics (amphisin, 2,4-diacetylphloroglucinol (DAPG), oomycin-A, phenazine, pyroluteorin, pyrrolnitrin, tensin, oligomycin A, kanosamine, zwittermicin A, and xanthobaccin) (Odoh, 2017) (Odoh, 2017).

Some genera of antibiotic-producing rhizobacteria correspond to Burkholderia (Tenorio- Salgado et al., 2013), Streptomyces (Rajesh and Prakash, 2011), Bacillus, Pseudomonas and Stenotrophomonas (Odoh, 2017).

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 (Rajkumar et al., 2010). For microorganisms, the availability of this element is critical in the success or failure of 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 (Stearns et al., 2012). PGPRs with the ability to produce siderophores gain competitive advantages in root colonization, competition for the ecological niche and inhibition of the growth of f'itopathogenic fungi due to the low concentration of Fe^{3+} available in soils (Sunar et al., 2015).

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 (Farag et al., 2013). Recently, about 846 different VOCs produced by 350 bacterial species have been reported, among which the most representative are acetoin and 2,3-butanediol (Tahir et al., 2017). 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 (Gouda et al., 2018).

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 a 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.

REFERENCES

Adesemoye, A. O., M. Obini, and E. O. Ugoji. 2008. Comparison of plant growth-promotion with Pseudomonas aeruginosa and Bacillus subtilis in three vegetables. Braz. J. Microbiol. 39: 423¬426. doi: https://doi.org/10.1590/S1517-83822008000300003.

Abou-el-Seoud, I. I. and A. Abdel-Megeed. 2012. Impact of rock materials and biofertilizations on P and K availability for maize (Zea mayz L.) under calcareous soil conditions. Saudi J. Biol. Sci. 19: 55-63. doi:

https://doi.org/10.1016/j.sjbs.2011.09.001.

Ahemad, M. and M. Kibret. 2014. Mechanisms and applications of plant growth Promoting rhizobacteria: Current perspective. J. King Saud Univ. Sci. 26: 1-20. doi: https://doi.org/10.1016Zj. jksus.2013.05.001.

Ahmad, P. 2010. Growth and antioxidant responses in mustard (Brassica juncea L.) plants subjected to combined effect of gibberellic acid and salinity. Arch. Agron. Soil Sci. 56: 575¬588. doi: https://doi.org/10.1080/03650340903164231.

Ahmad, M. S. and M. Y. Zargar. 2017. Characterization of potassium solubilizing bacteria (KSB) in rhizospheric soils of apple (Malus domestica Borkh.) in temperate Kashmir. J. Appl. Life Sci. Int. 15: 1-7. doi: https://doi.org/10.9734/ JALSI/2017/36848.

Ali, S. Z., V Sandhya, M. Grover, V R. Linga, and V Bandi. 2011. Effect of inoculation with a thermotolerant plant growth promoting Pseudomonas putida strain AKMP7 on growth of wheat (Triticum spp.) under heat stress. J. Plant Interact. 6: 239-246. doi: https://doi.org/10.1080/17429145.2010.545147.

Ali, B. 2015. Bacterial auxin signaling: Comparative study of growth induction in Arabidopsis thaliana and Triticum aestivum. Turk J. Bot. 39:1-9. doi. https://doi.org/10.3906/bot- 1401-31.

Angulo, V C., E. A. Sanfuentes, F. Rodríguez, and K. E. Sossa. 2014. Characterization of growth-promoting rhizobacteria in Eucalyptus nitens seedlings. Rev. Argent. Microbiol. 46: 338¬347. doi: https://doi.org/10.1016/S0325-7541(14)70093-8.

Asgher, M., M. I. R. Khan, N. A. Anjum, and N. A. Khan. 2014. Minimising toxicity of cadmium in plants-role of plant growth regulators. Protoplasma 252: 399-413. doi: https://doi. org/10.1007/s00709-014-0710-4.

Bakhshandeh, E., H. Rahimian, H. Pirdashti, and G. A. Nematzadeh. 2014. Phosphate solubilization potential and modeling of stress tolerance of rhizobacteria from rice paddy soil in northern Iran. World J. Microbiol. Biotechnol. 30: 2437-2447. doi: https:// doi.org/10.1007/s11274-014-1669-1.

Barnawal, D., S. S. Pandey, N. Bharti, A. Pandey, T. Ray, S. Singh, C. S. Chanotiya, and A. Kalra. 2017. ACC deaminase-containing plant growth-promoting rhizobacteria protect Papaver somnifcrum from downy mildew. J. Appl. Microbiol. 122: 1286-1298. doi: https://doi.org/10.1111/jam.13417.

Beneduzi, A., A. Ambrosini, and L. M. P. Passaglia. 2012. Plant growth promoting rhizobacteria (PGPR): Their potential as antagonists and biocontrol agents. Genet. Mol. Biol. 35: 1044-1051. doi: https://doi.org/10.1590/s1415-47572012000600020.

Bhagyalakshmi, B., P. Ponmurugan, and A. Balamurugan. 2017. Potassium solubilization, plant growth promoting substances by potassium solubilizing bacteria (KSB) from southern Indian Tea plantation soil. Biocatal. Agric. Biotechnol. 12: 116-124. doi: https://doi.org/10.1016/j.bcab.2017.09.011.

Bhattacharyya, P. N. and D. K. Jha. 2012. Plant growth-promoting rhizobacteria (PGPR): Emergence in agriculture. World J. Microbiol. Biotechnol. 28: 1327-1350. doi: https://doi. org/10.1007/s11274-011-0979-9.

Bloemberg, G. V. and B. J. Lugtenberg. 2001. Molecular basis of plant growth promotion and biocontrol by rhizobacteria. Curr. Opin. Plant Biol. 4: 343-350. doi: https://doi.org/10.1016/ S1369-5266(00)00183-7.

Brady, N. C. and R. R. Weil. 2002. The nature and properties of soils. Prentice Hall. New Delhi, India.

Calvo, P., E. Ormeño-Orillo, E. Martinez-Romero, and D. Zuñiga. 2010. Characterization of Bacillus isolates of potato rhizosphere from andean soils of Peru and their potential PGPR characteristics. Braz. J. Microbiol. 41: 899-906. doi: http://dx.doi.org/10.1590/S1517-83822010000400008.

Carcaño-Montiel, M. G., R. Ferrera-Cerrato, J. Pérez-Moreno, J. D. Molina-Galán, and Y. Bashan. 2006. Nitrogenase activity, production of phytohormones, siderophores and antibiosis in strains of Azospirillum and Klebsiella isolated from maize and teosintle. Terra Latinoamericana 24: 493-502.

Cedeño-García, G. A., M. Gerding, G. Moraga, L. Inostroza, S. Fischer, M. Sepúlveda-Caamaño, and P. Oyarzúa. 2018. Plant growth promoting rhizobacteria with ACC deaminase activity isolated from Mediterranean dryland areas in Chile: Effects on early nodulation in alfalfa. Chil. J. Agric. Res. 78: 360-369. doi: http://dx.doi.org/10.4067/S0718-58392018000300360.

Chaturvedi, S. and S. M. Paul Khurana. 2018. Induced systemic resistance. J. Microbiol. Biotechnol. 3: 1-2. doi: https://doi. org/10.23880/oajmb-16000126.

Cohen, A. C., R. Bottini, and P. Piccoli. 2015. Role of abscisic acid producing PGPR in sustainable agriculture. pp. 259-282. In: D. K. Maheshwari (ed.). Bacterial metabolites in sustainable agroecosystem. Sustainable development and biodiversity. V)l. 12. Springer. doi: https://doi.org/10.1007/978-3-319- 24654-3_9.

Damam, M., K. Kaloori, B. Gaddam, and R. Kausar. 2016. Plant growth promoting substances (phytohormones) produced by rhizobacterial strains isolated from the rhizosphere of medicinal plants. Int. J. Pharm. Sci. Rev. Res. 37: 130-136.

Dary, M., M. A. Chamber-Pérez, A. J. Palomares, and E. Pajuelo. 2010. "In situ" phytostabilisation of heavy metal polluted soils using Lupinus luteus inoculated with metal resistant plant-growth Promoting rhizobacteria. J. Hazard. Mater. 177: 323-330. doi: https://doi.org/10.1016/j.jhazmat.2009.12.035.

Desai, S. A. 2017. Isolation and characterization of gibberellic acid (GA3) producing rhizobacteria from sugarcane roots. Biosci. discov. 8: 488-494.

Egamberdieva, D., S. J. Wirth, A. A. Alqarawi, E. F. Abd-Allah, and A. Hashem. 2017. Phytohormones and beneficial microbes: Essential components for plants to balance stress and fitness. Front. Microbiol. 8: 1-14. doi: https://doi.org/10.3389/ fmicb.2017.02104.

Etesami, H., S. Emami, and H. A. Alikhani. 2017. Potassium solubilizing bacteria (KSB): Mechanisms, promotion of plant growth, and future prospects - A review. J. Soil Sci. Plant Nutr. 17: 897-911. doi: http://dx.doi.org/10.4067/S0718-95162017000400005.

FAO (Food and Agriculture Organization of the United Nations. 2017. The future of food and agriculture: trends and challenges. http://www.fao.org/3/a-i6881s.pdf (Accessed: March 03, 2019).

Farag, M. A., H. Zhang, and C. M. Ryu. 2013. Dynamic chemical communication between plants and bacteria through airborne signals: Induced resistance by bacterial volatiles. J. Chem. Ecol. 39: 1007-1018. doi: https://doi.org/10.1007/s10886-013- 0317-9.

Fibach-Paldi, S., S. Burdman, and Y. Okon. 2011. Okon. 2011. Key physiological properties contributing to rhizosphere adaptation and plant growth promotion abilities of Azospirillum brasilense. FEMS Microbiol. Lett. 326: 99-108. doi: https://doi.org/10.1111/ j.1574-6968.2011.02407.x.

Foyer, C. H., B. Rasool, J. W. Davey, and R. D. Hancock. 2016. Cross-tolerance to biotic and abiotic stresses in plants: A focus on resistance to aphid infestation. J. Exp. Bot. 67: 2025-2037. doi: https://doi.org/10.1093/jxb/erw079.

Gholami, A., S. Shahsavani, and S. Nezarat. 2009. The effect of plant growth promoting rhizobacteria (PGPR) on germination, seedling growth and yield of maize. Int. J. Biol. Sci. 3: 35-40.

Gouda, S., R. G. Kerry, G. Das, S. Paramithiotis, H. S. Shin, and J. K. Patra. 2018. Revitalization of plant growth promoting rhizobacteria for sustainable development in agriculture. Microbiol. Res. 206: 131-140. doi: https://doi.Org/10.1016/j. micres.2017.08.016.

Gupta, G., S. Singh Parihar, N. Kumar Ahirwar, S. Kumar Snehi, and V Singh. 2015. Plant growth promoting rhizobacteria (PGPR): Current and future prospects for development of sustainable agriculture. Microbiol. Biochem. Technol. 7: 096¬102. doi: https://doi.org/10.4172/1948-5948.1000188.

Gupta, G., S. K. Snehi, and V. Singh. 2017. Role of PGPR in biofilm formations and its importance in plant health. pp. 27-42. In: I. Ahmad and F. Mabood Husain (eds.). Biofilms in Plant and Soil Health. doi: https://doi.org/10.1002/9781119246329.ch2. Online ISBN: 978111919246329.

Grover, M., S. Z. Ali, V Sandhya, A. Rasul, and B. Venkateswarlu. 201 1. Role of microorganisms in adaptation of agriculture crops to abiotic stresses. World J. Microbiol. Biotechnol. 27: 1231-1240. doi: https://doi.org/10.1007/s11274-010-0572-7.

Iqbal, M. and M. Ashraf. 2013. Gibberellic acid mediated induction of salt tolerance in wheat plants: growth, ionic partitioning, photosynthesis, yield and hormonal homeostasis. Environ. Exp. Bot. 86: 76-85. doi: https://doi.org/10.1016/j. envexpbot.2010.06.002.

Jahanian, A., M. R. Chaichi, K. Rezaei, K. Rezayazdi, and K. Khavazi. 2012. The effect of plant growth promoting rhizobacteria (pgpr) on germination and primary growth of artichoke (Cynara scolymus). Int. J. Agric. Crop Sci. 4: 923¬929.

Kasim, W. A., R. M. Gaafar, R. M. Abou-Ali, M. N. Omar, and H. M. Hewait. 2016. Effect of biofilm forming plant growth Promoting rhizobacteria on salinity tolerance in barley. Ann. Agric. Sci. 61: 217-227. doi: https://doi.org/10.1016/j. aoas.2016.07.003.

Kang, S. M., M. Waqas, M. Hamayun, S. Asaf, A. L. Khan, A. Y. Kim, Y. G. Park, and I. J. Lee. 2017. Gibberellins and indole- 3-acetic acid producing rhizospheric bacterium Leifsonia xyli SE134 mitigates the adverse effects of copper-mediated stress on tomato. J. Plant Interact. 12: 373-380. doi: https://doi.org/1 0.1080/17429145.2017.1370142.

Khan, M. S., A. Zaidi, and P. A. Wani. 2007. Role of phosphate- solubilizing microorganisms in sustainable agriculture - A review. Agron. Sustain. Dev. 27: 29-43. doi: https://doi. org/10.1051/agro:2006011.

Kim, J. S., J. E. Lee, H. Nie, Y. J. Lee, S. T. Kim, and S. H. Kim. 2018. Physiological and proteomic analysis of plant growth enhancement by the rhizobacterium Bacillus sp. JS. Genes Genom. 40: 129-136. doi: https://doi.org/10.1007/s13258-017-0615-7.

Kloepper, J. W. and M. N. Schroth. 1978. Plant growth-promoting rhizobacteria on radishes. pp. 879-882. In: Proc. 4th Int. Conf. Plant Path. Bact. Vol. 12. Angers, France.

Kuan, K. B., R. Othman, K. Abdul Rahim, and Z. H. Shamsuddin. 2016. Plant growth-promoting rhizobacteria inoculation to enhance vegetative growth, nitrogen fixation and nitrogen remobilization of maize under greenhouse conditions. PLoS ONE 11: 1-19. doi: https://doi.org/10.1371/journal. pone.0152478.

Lawongsa, P., N. Boonkerd, S. Wongkaew, F. O'Gara, and N. Teaumroong. 2008. Molecular and phenotypic characterization of potential plant growth-promoting Pseudomonas from rice and maize rhizospheres. World J. Microbiol. Biotechnol. 24: 1877-1884. doi: https://doi.org/10.1007/s11274-008-9685-7.

Li, X., J. Cai, F. Liu, T. Dai, W. Cao, and D. Jiang. 2014. Exogenous abscisic acid application during grain filling in winter wheat improves cold tolerance of offspring's seedlings. J. Agron. Crop Sci. 200: 467-478. doi: https://doi.org/10.1111/jac.12064.

Liu, F., S. Xing, H. Ma, Z. Du, and B. Ma. 2013. Cytokinin¬producing, plant growth-promoting rhizobacteria that confer resistance to drought stress in Platycladus orientalis container seedlings. Appl. Microbiol. Biotechnol. 97: 9155-9164. doi: https://doi.org/10.1007/s00253-013-5193-2.

Lucas, J. A., A. García-Villaraco, B. Ramos, J. Garcia-Cristobal, E. Algar, and J. Gutierrez-Mañero. 2013. Structural and functional study in the rhizosphere of Oryza sativa L. plants growing under biotic and abiotic stress. J. Appl. Microbiol. 115: 218-235. doi: https://doi.org/10.1111/jam.12225.

Lugtenberg, B. and F. Kamilova. 2009. Plant-growth-promoting rhizobacteria. Annu. Rev. Microbiol. 63: 541-556. doi: https:// doi.org/10.1146/annurev.micro.62.081307.162918 .

Maheshwari, D. K., S. Dheeman, and M. Agarwal. 2015. Phytohormone-producing PGPR for sustainable agriculture. pp. 159-182. In: D. K. Maheshwari (ed.). Bacterial metabolites in sustainable agroecosystem. Sustainable development and biodiversity.Vol. 12. Springer. doi: https://doi.org/10.1007/978-3-319-24654-3-3_7.

Mahmood, S., I. Daur, S. G. Al-Solaimani, S. Ahmad, M. H. Madkour, M. Yasir, H. Hirt, S. Ali, and Z. Ali. 2016. Plant growth promoting rhizobac and silicon synergistically enhance salinity tolerance of mung bean. Front Plant Sci. 7: 1-14. doi: https://doi.org/10.3389/fpls.2016.00876.

Mayz-Figueroa, J. 2004. Biological nitrogen fixation. Scientific Rev. UDO Agríc. 4: 1-20.

McNear Jr, D. H. 2013. The rhizosphere - roots, soil and everything in between. Nat. Educat. Knowledge 4:1.

Mohammed, A. E. 2018. Effectiveness of exopolysaccharides and biofilm forming plant growth promoting rhizobacteria on salinity tolerance of faba bean (Vicia faba L.). Afr. J. Microbiol. Res. 12: 399-404. doi: https://doi.org/10.5897/ AJMR2018.8822.

Molina-Romero, D., M. Bustillos-Cristales, O. Rodríguez-Andrade, Y. E. Morales-Garcia, Y. Santiago-Saenz, M. Castañeda-Lucio, and J. Muñoz-Rojas. 2015. Mechanisms of phytostimulation by rhizobacteria, isolates in America and biotechnological potential. Biologicas 17: 24-34.

Morgado González, A., D. Espinosa Victoria, and F. C. Gómez Merino. 2015. Efficiency of plant growth promoting rhizobacteria (pgpr) in sugarcane. Terra Latinoamericana 33: 321-330.

Naseem, H., M. Ahsan, M. A. Shahid, and N. Khan. 2018. Exopolysaccharides producing rhizobacteria and their role in plant growth and drought tolerance. J. Basic Microbiol. 58: 1009-1022. doi: https://doi.org/10.1002/jobm.201800309.

Odoh, C. K. 2017. Plant Growth Promoting Rhizobacteria (PGPR): A Bioprotectant bioinoculant for Sustainable Agrobiology. A Review. Int. j. Adv. Res. Biol. Sci. 4: 123-142. doi: http:// dx.doi.org/10.22192/ijarbs.2017.04.05.014.

Oteino, N., R. D. Lally, S. Kiwanuka, A. Lloyd, D. Ryan, K. J. Germaine, and D. N. Dowling. 2015. Plant growth promotion induced by phosphate solubilizing endophytic Pseudomonas isolates. Front. Microbiol 6: 1-9. doi: https://doi.org/10.3389/ fmicb.2015.00745.

Palacio-Rodríguez, R., B. P. Ramos, J. L. Coria-Arellano, B. Nava Reyes, and J. Sáenz-Mata. 2016. Mechanisms of PGPRs to mitigate plant abiotic stress. Arid-Science 1: 4-11.

Parmar, P. and S. S. Sindhu. 2013. Potassium solubilisation by Rhizosphere Bacteria: influence of nutritional and environmental conditions. J. Microbiol. Res. 3: 25-31. doi: https://doi.org/10.5923/j.microbiology.20130301.04.

Patil, C., R. Suryawanshi, S. Koli, and S. Patil. 2016. Improved method for effective screening of ACC (1-aminocyclopropane- 1-carboxylate) deaminase producing microorganisms.J. Microbiol. Methods 131: 102-104. doi: https://doi. org/10.1016/j.mimet.2016.10.009.

Pereira, S. I. A., C. Monteiro, A. L. Vega, and P. M. L. Castro. 2016. Endophytic culturable bacteria colonizing Lavandula dentate L.plants: isolation, characterization and evaluation of their plant growth-promoting activities. Ecol. Eng. 87: 91-97. doi: https://doi.org/10.1016/j.ecoleng.2015.11.033.

Perin, L., L. Martínez-Aguilar, R. Castro-González, P. Estrada-de los Santos, T. Cabellos-Avelar, H. V. Guedes, V. M. Reis, and J. Caballero-Mellado. 2006. Diazotrophic Burkholderia species associated with field-grown maize and sugarcane. Appl. Environ. Microbiol. 72: 3103-3110. https://doi.org/10.1128/

aem.72.5.3103-3110.2006.

Phillips, D. A. and J. G. Torrey. 1972. Studies on cytokinin production by Rhizobium. Plant Physiol. 49: 11-15. doi: https:// doi.org/10.1104/pp.49.1.11.

Poupin, M. J., T. Timmermann, A. Vega, A. Zuñiga, and B. González. 2013. Effects of the plant growth-promoting bacterium Burkholderia phytofirmans PsJN throughout the life cycle of Arabidopsis thaliana. PLoS ONE 8: 1-15. doi: https://doi.org/10.1371/journal.pone.0069435.

Pretty, J., T. G. Benton, Z. P. Bharucha, L. V. Dicks, C. V. Flora, H. C. J. Godfray, D. Goulson, S. Hartley, N. Lampkin, C. Morris, G. Pierzynski, P. V V Prasad, J. Reganold, P. Smith, P. Thorne, and S. Wratten. 2018. Global assessment of agricultural system redesign for sustainable intensification. Nat. Sustain. 1: 441¬446. doi: https://doi.org/10.1038/s41893-018-0114-0.

Raheem, A., A. Shaposhnikov, A. Belimov, I. C. Dodd, and B. Ali. 2018. Auxin production by rhizobacteria was associated with improved yield of wheat (Triticum aestivum L.) under drought stress. Arch. Agron. Soil Sci. 64: 574-587. https://doi.org/10.1 080/03650340.2017.1362105.

Rajesh-Kannan, R. and S. G. Prakash-Vincent. 2011. Molecular characterization of antagonistic Streptomyces isolates from a Mangrove Swamp. Asian J. Microbiol. Biotechnol. 3: 237¬245. doi: https://doi.org/10.3923/ajbkr.2011.237.245.

Rajkumar, M., N. Ae, M. N. V. Prasad, and H. Freitas. 2010. Potential of siderophore-producing bacteria for improving heavy metal phytoextraction. Trends Biotechnol. 28: 142-149. doi: https://doi.org/10.1016/j.tibtech.2009.12.002.

Razaq, M., P. Zhang, H. Shen, and Salahuddin. 2017. Influence of nitrogen and phosphorous on the growth and root morphology of Acer mono. PLoS ONE 12: 1-13. doi: https://doi. org/10.1371/journal.pone.0171321.

Remans, R., S. Beebe, M. Blair, G. Manrique, E. Tovar, I. Rao, A. Croonenborghs, R. Torres-Gutierrez, M. El-Howeity, J. Michiels, and J. Vanderleyden. 2008. Physiological and genetic analysis of root responsiveness to auxin-producing plant growth-promoting bacteria in common bean (Phaseolus vulgaris L.). Plant Soil 302: 149-161. doi: https://doi. org/10.1007/s11104-007-9462-7.

Rodrigues, E. P., L. S. Rodrigues, A. L. M. de Oliveira, V L. D. Baldani, K. R. dos S. Teixeira, S. Urquiaga, and V M. Reis. 2008. Azospirillum amazonense inoculation: effects on growth, yield and N2 fixation of rice (Oryza sativa L.). Plant Soil 302: 249-261. doi: https://doi.org/10.1007/s11104-007-9476-1.

Saleem, M., H. N. Asghar, Z. A. Zahir, and M. Shahid. 2018. Impact of lead tolerant plant growth promoting rhizobacteria on growth, physiology, antioxidant activities, yield and lead content in sunflower in lead contaminated soil. Chemosphere 195: 606¬614. doi: https://doi.org/10.1016/j.chemosphere.2017.12.117.

Sah, S. K., K. R. Reddy, and J. Li. 2016. Abscisic acid and abiotic stress tolerance in crop Plants. Front. Plant Sci. 7: 1- 26. doi: https://doi.org/10.3389/fpls.2016.00571.

Saiyad, S. A., Y. K. Jhala, and R. V Vyas. 2015. Comparative efficiency of five potash and phosphate solubilizing bacteria and their key enzymes useful for enhancing and improvement of soil fertility. Int. J. Sci. Res. Publ. 5: 1-6.

Sarkar, A., P. K. Ghosh, K. Pramanik, S. Mitra, T. Soren, S. Pandey, M. H. Mondal, and T. K. Maiti. 2018. A halotolerant Enterobacter sp. displaying ACC deaminase activity promotes rice seedling growth under salt stress. Res. Microbiol. 169: 20¬32. doi: https://doi.org/10.1016/j.resmic.2017.08.005.

Shahzad, R., A. L. Khan, S. Bilal, M. Waqas, S. M. Kang, and I. J. Lee. 2017. Inoculation of abscisic acid-producing endophytic bacteria enhances salinity stress tolerance in Oryza sativa. Environ. Exp. Bot. 136: 68-77. doi: https://doi.org/10.1016/j. envexpbot.2017.01.010.

Sharma, S. K., B. N. Johri, A. Ramesh, O. P. Joshi, and S. V. S. Prasad. 2011. Selection of plant growth-promoting Pseudomonas spp. that enhanced productivity of soybean-wheat cropping system in central India. J. Microbiol. Biotechnol. 21: 1127-1142. doi: https://doi.org/10.4014/jmb.1012.12018.

Shen, M., Y. Jun-Kang, H. Li-Wang, X. Sheng-Zhang, and Q. Xin- Zhao. 2012. Effect of plant growth-promoting rhizobacteria (PGPRs) on plant growth, yield, and quality of tomato (Lycopersicon esculentum Mill.) under simulated seawater irrigation. J. Gen. Appl. Microbiol. 58: 253-262. doi: https:// doi.org/10.2323/jgam.58.253.

Singh, G., D. R. Biswas, and T. S. Marwah. 2010. Mobilization of potassium from waste mica by plant growth promoting rhizobacteria and its assimilation by maize (Zea mays) and wheat (Triticum aestivum L.). J. Plant Nutr. 33: 1236-1251. doi: https://doi.org/10.1080/01904161003765760.

Stearns, J. C., O. Z. Woody, B. J. McConkey, and B. R. Glick. 2012. Effects of bacterial ACC deaminase on Brassica napus gene expression. Mol. Plant Microbe Interact. 25: 668-676. doi: https://doi.org/10.1094/mpmi-08-11-0213.

Stringlis, I. A., S. Proietti, R. Hickman, M. C. Van Verk, C. Zamioudis, and C. M. J. Pieterse. 2018. Root transcriptional dynamics induced by beneficial rhizobacteria and microbial immune elicitors reveal signatures of adaptation to mutualists. Plant J. 93: 166-180. doi: https://doi.org/10.1111/tpj.13741.

Sunar, K., P. Dey, U. Chakraborty, and B. Chakraborty. 2015. Biocontrol efficacy and plant growth promoting activity of Bacillus altitudinis isolated from Darjeeling hills. J. Basic Microbiol. 55: 91-104. doi: https://doi.org/10.1002/ jobm.201300227.

Tahir, H. A. S., Q. Gu, H. Wu, W. Raza, A. Hanif, L. Wu, M. V. Colman, and X. Gao. 2017. Plant growth promotion by volatile organic compounds produced by Bacillus subtilis SYST2. Front. Microbiol. 8: 1-11. doi: https://doi.org/10.3389/ fmicb.2017.00171.

Tenorio-Salgado, S., R. Tinoco, R. Vzquez-Duhalt, J. Caballero- Mellado, and E. Pérez-Rueda. 2013. Identification of volatile compounds produced by the bacterium Burkholderia tropica that inhibit the growth of fungal pathogens. Bioengineered 4: 236-243. doi: https://doi.org/10.4161/bioe.23808.

Upadhyay, S. K., J. S. Singh, and D. P. Singh. 2011. Exopoly saccharide producing plant growth-promoting rhizobacteria under salinity condition. Pedosphere 21: 214¬222. doi: https://doi.org/10.1016/s1002-0160(11)60120-3.

Upson, J. L., E. K. Zess, A. Bialas, Ch. Wu, and S. Kamoun. 2018. The coming of age of EvoMPMI: evolutionary molecular plant-microbe interactions across multiple timescales. Curr. Opin. Plant Biol. 44: 108-116. doi: https://doi.org/10.1016/j. pbi.2018.03.003.

Vacheron, J., G. Desbrosses, M. L. Bouffaud, B. Touraine, Y. Moenne-Loccoz, D. Muller, L. Legendre, F. Wisniewski- Dye, and C. Prigent-Combaret. 2013. Plant growth-promoting rhizobacteria and root system functioning. Front. Plant Sci. 4: 1-19. doi: https://dx.doi.org/10.3389/fpls.2013.00356.

Valverde, A., A. Burgos, T. Fiscella, R. Rivas, E. lázquez, C. Rodríguez-Barrueco, E. Cervantes, M. Chamber, and J. M. Igual. 2006. 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 287: 43-50. doi: https://doi.org/10.1007/ s11104-006-9057-8.

Venturi, V and C. Keel. 2016. Signaling in the rhizosphere. Trends Plant Sci. 21: 187-198. doi: https://doi.org/10.1016/j. tplants.2016.01.005.

Vurukonda, S. S. S. K. P., S. Vardharajula, M. Shrivastava, and A. SkZ. 2016. Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. Microbiol. Res. 184: 13-24. doi: https://doi.org/10.1016/j.micres.2015.12.003.

Werner, G. D. A., W. K. Cornwell, J. I. Sprent, J. Kattge, and E. T. Kiers. 2014. A single evolutionary innovation drives the deep evolution of symbiotic N2-fixation in angiosperms. Nat. Commun. 5: 4087. doi: https://doi.org/10.1038/ncomms5087.

Wu, C. H., T. K. Wood, A. Mulchandani, and W. Chen. 2006. Engineering plant-microbe symbiosis for rhizoremediation of heavy metals. Appl. Environ. Microbiol. 72: 1129-1134. doi: https://doi.org/10.1128/aem.72.2.1129-1134.2006.

Yadav, B. K. and A. Verma. 2012. Phosphate solubilization and mobilization in soil through soil microorganisms under arid ecosystems. pp. 93-108. In: M. Ali (ed.). The functioning of ecosystems. Intech Open. London, UK. doi: https://doi. org/10.5772/35917. ISBN: 978-953-51-0573-2.

Zhang, C. and F. Kong. 2014. Isolation and identification of potassium solubilizing bacteria from tobacco rhizospheric soil and their effect on tobacco plants. Appl. Soil Ecol. 82: 18-25. doi: https://doi.org/10.1016/j.apsoil.2014.05.002.

Zhou, C., F. Li, Y. Xie, L. Zhu, X. Xiao, Z. Ma, and J. Wang. 2017.Involvement of abscisic acid in microbe-induced saline- alkaline resistance in plants. Plant Signal. Behav. 12: 1-4. doi: https://doi.org/10.1080/15592324.2017.1367465.