

Review: Plant Growth Promoting Rhizobacteria: Blessing to Agriculture

Twisha S. Patel^{1*}, Farida P. Minocheherhomji²

¹Research Scholar, ²Associate Professor,

Department of Microbiology, B.P. Baria Science Institute, Navsari, Gujarat, India

*Corresponding Author E-mail: twishapatel.1489@gmail.com

Received: 31.03.2018 | Revised: 22.04.2018 | Accepted: 25.04.2018

ABSTRACT

Soil microbes are vital components of soil important for soil fertility and plant growth as well as yield of crop. The plant secretes various metabolites as root exudates which attract bacteria for colonization. Bacteria are involved in various biotic activities of the soil ecosystem. They stimulate plant growth through solubilizing nutrients in soils, producing numerous plant growth regulators, protecting plants from phytopathogens by controlling or inhibiting them and improving soil quality. This naturally occurring root bacteria are beneficial for plant growth viz directly and indirectly known as plant growth promoting rhizobacteria (PGPR). The direct mechanisms include facilitating resource acquisition (nitrogen, phosphorus, Potassium, zinc and essential minerals), ACC deaminase activity and modulating plant hormone levels (Auxin, cytokinin, gibberellic acid, ethylene, abscisic acid). In indirect mechanisms by decreasing the inhibitory effects of various pathogens on plant growth and development in the forms of biocontrol agents, Such as lytic enzyme production, antibiotics, HCN production, siderophore, antifungal activity, exopolysaccharide. Indeed, the bacteria which are present around/in the plant roots (rhizobacteria) are more versatile in transforming, mobilizing, solubilizing the nutrients. Therefore, the rhizobacteria are the dominant driving forces in recycling the soil nutrients and increasing soil fertility.

Key word: Rhizobacteria, Rootexudates, Phytopathogens.

INTRODUCTION

The demand of food products consisting of fruits, vegetables, dairy products, meat, poultry, and fisheries, has tremendously increased due to the global population explosion as it is a basic requirement for its ultimate survival. This demand is tried to be met by better agricultural practices aimed to maximize crop productivity employing innovative technologies. Crop productivity is increased by using agrochemicals in

agricultural activities^{20, 45}. But on the other hand, indiscriminate use of such agrochemicals consisting of fertilizers and pesticides has causing harmful effects to soil fertility and soil fauna and flora⁸¹. In the last few decades, particularly during recent times, numerous biotechnological research and expansions has been carried out in agriculture, as result of which, a new area for an increased crop productivity has arised for the overall sustenance of environment^{36,73}.

Cite this article: Patel, T.S. and Minocheherhomji, F.P., Review: Plant Growth Promoting Rhizobacteria: Blessing to Agriculture, *Int. J. Pure App. Biosci.* 6(2): 481-492 (2018). doi: <http://dx.doi.org/10.18782/2320-7051.6383>

Microorganisms are mutual partners associated with plant growth. They have a better ability for adaptation in the environment and also have the capacity to support and/ or promote the overall plant growth leading to a better crop yield. These microorganisms, known as plant growth promoting rhizobacteria (PGPR) have now been developed as/ or incorporated in biofertilizers and biopesticides to increase soil fertility and control plant disease.

The complexity of the soil ecosystem is established by numerous and diverse interactions among its physical, chemical and biological components¹⁵. Microbial communities living in soils interact with plant roots²⁵. Researchers have demonstrated that the main volume of soil in the rhizosphere zone is directly influenced by the presence of living plant roots or soil compartment influenced by the root.

Rhizosphere supports a large and active microbial population. These microorganisms were capable of beneficial, neutral and detrimental effects on the plants. Root colonizing bacteria produces beneficial effects on the growth of the host plant *via* direct or indirect mechanisms. They are termed as plant growth promoting rhizobacteria (PGPR)³¹.

The term PGPRs is coined by Kloepper and Schroth in the year 1978. It is particularly used when they are incorporated as bio inoculants to improve crop productivity as well as quality¹⁰. *Rhizobium* species were the first biofertilizers identified as PGPR³⁵. PGPR can also be described as “the live microorganisms consisting of bacteria and fungi that are utilized for improving plant growth and crop productivity, generally referred to as biofertilizers or microbial inoculants”⁷².

PGPR has also been described as “soil bacterial species occurring in plant rhizosphere which grow in, on, or around plant tissues, stimulating and promoting plant growth by various direct and indirect mechanisms”⁷⁶.

PGPR have also been described as free-living soil-borne bacteria of plants⁴². Rhizosphere is a site where the complex

interactions occur between the roots and PGPR. These interactions between microflora and plants can be classified into three categories - neutral, negative or positive⁸⁰.

The prominent characteristics of PGPR is its capability to colonize the root surface, survive, multiply and compete with other microbiota, needed to express their plant growth promoting as well as protective activities⁴⁰.

PGPR are classified based on their functional activities⁷⁰:

- a) **Biofertilizers:** Increasing the availability of nutrients to plant.
- b) **Phytohormones:** Plant growth promotion through phytohormones production.
- c) **Rhizoremediators:** By degrading organic pollutants.
- d) **Biopesticides:** Controlling diseases by the production of biocontrol agents such as antibiotics, HCN, Ammonia, antifungal metabolites, siderophore production⁴.

Different researchers have concluded that a single PGPR has multiple modes of direct and indirect mechanisms for plant growth promotion, which is known as multitrait PGPR^{41, 76}.

Plant growth is generally supported directly and or indirectly by PGPR. Direct mechanisms include facilitating acquisition of resources like nitrogen, phosphorus, Potassium and essential minerals, ACC (1-aminocyclopropane-1-carboxylate) deaminase activity and modulating plant hormone levels like that of Auxin, cytokinin, gibberellic acid, ethylene and abscisic acid. Indirect mechanisms includes decreasing the inhibitory effects of various pathogens on plant growth and development in the form of biocontrol agents such as antibiotics, HCN, siderophore, lytic enzyme, induced systemic resistance (ISR), exopolysaccharides production and antifungal activity²⁵.

A. Direct Mechanisms:

I. Nutrient Solubilizing Traits:

1. Phosphorus solubilization: Phosphorus is one of the major and essential macronutrient for plant growth and development. Phosphorus is present in soil as organic and inorganic

phosphates. Both organic and inorganic insoluble phosphates are converted in to soluble form by PGPR, which is an important trait for the increase in plant yields⁷⁵. The mechanism of phosphate solubilization by phosphate solubilization bacteria (PSB) is associated with the release of low molecular weight organic acids through which their hydroxyl and carboxyl groups chelate the cations bound to the phosphate, ultimately converting it into soluble forms. Some phosphate solubilisation bacteria produce phosphatase that hydrolyse organic forms of phosphate compounds efficiently. These bacteria are referred to as phosphobacteria⁴³.

2. Potassium Solubilisation: Potassium (K) is an essential macronutrient in plant growth. It is mostly absorbed in abundance as cations, playing an important role in the growth, metabolism and development of plants. Imbalanced fertilizer applications have led to potassium deficiency, which is emerging as one of the major problems in crop production⁶⁸. Hence it has become necessary to find an alternative indigenous source of potassium for plant uptake and also to maintain optimum potassium level in soil for good crop production. Soil microbes have been reported to play a key role in the natural potassium cycle. Potassium solubilizing rhizobacteria present in the soil could provide potassium to plants for uptake⁸.

3. Nitrogen Fixation: Nitrogen is one of the most common nutrients required for plant growth and productivity. It forms an integral part of proteins, nucleic acids and other essential biomolecules¹³. More than 80 % of nitrogen is present in the atmosphere as inert gas which is unavailable to the plants. Nitrogen is required to be converted into ammonia, a form available to plants. In biological nitrogen fixation, nitrogen is unavailable for use by most microorganisms because of the presence of a triple bond between the two nitrogen atoms. Nitrogen to be used for growth must be “fixed” in form of ammonia NH₄ or as nitrate NO₃ ions. Nitrogen fixation fixes approximately 60% of the

available nitrogen on earth⁴⁶. It is an economically beneficial and environmental friendly alternative to chemical fertilizers, referred to as BNF (Biological nitrogen fixation). It is the process in which atmospheric nitrogen (N₂) is reduced to ammonia in the presence of nitrogenase³⁸. The process of nitrogen fixation is carried out by the nitrogenase enzyme which is coded by nif genes³⁸. Nitrogen fixing organisms are generally categorized as:

- a) Symbiotic Nitrogen Fixing Bacteria includes members of the family rhizobiaceae which forms symbiosis with leguminous plants like *Rhizobia*¹ and non-leguminous trees such as *Frankia*.
- b) Non-symbiotic or free living, associative and endophytes nitrogen fixing forms such as cyanobacteria like *Anabaena*, *Nostoc*, *Azospirillum*, *Azotobacter*, *Gluconoacetobacter diazotrophicus* and *Azocarus*¹¹.

II. Phytohormone Production:

Promotion of plant growth by one of the direct mechanisms by PGPR is by the production of plant growth regulators or phytohormones²⁵. Researchers have reported the beneficial use of auxins, cytokinins, gibberellins, ethylene and abscisic acids (ABA) in plants, which helped in boosting their growth and increasing the plant yield^{21, 54, 59, 71}.

1. Ethylene (ACC deaminase production):

Ethylene is essential for the growth and development of plants, bearing different effects on plant growth depending on its concentration in root tissues. At higher concentrations, it induces defoliation and cellular processes that lead to inhibition of stem and root growth and premature senescence. This leads to reduced crop performance which ultimately lowers crop yield⁴⁷. Under different types of environmental stress such as cold, draught, flooding, infections with pathogens, presence of heavy metals, plants synthesizes 1-aminocyclopropane-1- carboxylate (ACC), which is the precursor for ethylene^{16,29}. Some amount of ACC is secreted into the rhizosphere and is reabsorbed by the roots,

which is then converted into ethylene. Such accumulation of ethylene leads to a detrimental effect like poor root growth. It leads to a reduced ability to acquire water and nutrients which causes further stress. PGPR have an ability to degrade ACC in the rhizosphere. They can help to break this detrimental cycle and re-establish a healthy root system (Figure 1) needed to cope in the environmental stress condition⁷⁸.

The primary mechanism of rhizobacteria is to degrade ethylene by the ACC deaminase. This enzyme can prevent the harmful effects of high ethylene levels²⁶. ACC deaminase acts on ACC degrading it and converting it into α -ketobutyrate and ammonia^{26,29,52}, which is useful for plant growth. PGPR with ACC deaminase activity belonging to the *Achromobacter* and *Pseudomonas*²⁸, *Bacillus*²², 2003), *Enterobacter*⁴⁷, and *Rhizobium*¹⁹ have been isolated from different soils.

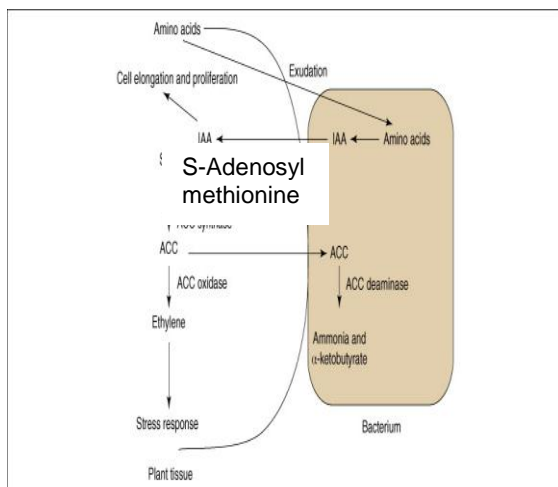


Figure – 1: ACC deaminase response in PGPR⁶³

2. Indole - 3 – acetic acid: The production of IAA by microorganisms can be achieved in the presence of the precursor tryptophan or peptone⁵⁵. Auxins help the plant for cell division, cell enlargement, root initiation, increased growth rate, phototropism, geotropism, apical dominance²¹. 80% of microorganisms isolated from the rhizosphere of various crops have the ability to produce auxins as secondary metabolites⁴⁸. Bacteria belonging to the genera *Pseudomonas*, *Xanthomonas*, and *Rhizobium*, *Alcaligenes*

faecalis, *Enterobacter cloacae*, *Acetobacter diazotrophicus* and *Bradyrhizobium japonicum* have shown to produce auxins which helps in stimulating plant growth⁵⁸.

For IAA production various metabolic pathways are involved:

- Indole-3-acetamide pathway,
- Indole-3-pyruvic acid pathway,
- Tryptophan side chain pathway,
- Tryptamine pathway,
- Indole-3-acetonitrile pathway.

3. Gibberellic acid: Plant growth regulators such as gibberellins are important economical biotechnological products. They are commonly used in agriculture, horticulture, gardening activities. Gibberellins (GAs) are a large group of diterpenoid acids among commercial phytohormones. Gibberellins act as plant growth regulators, influencing a range of developmental processes in crop such as stem elongation, germination, sex expression, dormancy, flowering, enzyme induction, and leaf and fruit senescence⁶². Gibberellic acid is naturally produced by higher plants, fungi and bacteria. Till today, a total of 126 Gibberellic acids have been identified in plants, fungi and bacteria⁶⁴.

4. Cytokinins: Cytokinins play key regulatory roles in plant growth and development. They promote seed germination, de novo bud formation, release of buds from apical dominance, stimulation of leaf expansion and reproductive development, retardation of senescence, enhanced cell division, enhanced root development, enhanced root hair formation, inhibition of root elongation, shoot initiation, or certain other physiological responses^{3, 30}. Cytokinin production in several plant-associated microbes has been well characterized^{32, 33} and these micro-organisms, which belong to diverse genera such as *Pseudomonas*, *Azospirillum*, and *Bacillus* have been isolated from a wide range of plant species.

B. Indirect Mechanisms:

1. Enzyme activity: Several bacteria produce enzymes that are able to hydrolyze chitin, proteins, cellulose and hemicelluloses; thus contributing to direct suppression of plant

pathogens. Majority of rhizobacteria have an ability to produce lytic enzyme which prevents the deleterious effects of plant pathogens on plants by production of inhibitory substances or by increasing the natural resistance of the host. This involves synthesizing the lytic enzymes including chitinases, cellulases, 1,3-glucanases, proteases, and lipases that can lyse a portion of the cell walls of many pathogenic fungi. It has also been reported that hydrolytic enzymes like chitinases, proteases, lipases that degrade virulence factors or pathogen cell-wall components act indirectly for plant growth promotion mechanisms¹⁸.

2. Antibiosis: Different antibiotics are produced to control the proliferation of plant pathogens. But excessive dependence on antibiotic producing bacteria as biocontrol agents may prove to be disadvantageous because of the host resistance developed against specific antibiotics. The mechanism of the ability of plant growth promoting bacteria to act as antagonistic agents against phytopathogens is due to the production of one or more antibiotics²³. The mechanism of antibiosis is to produce low molecular weight compounds that are deleterious and critical to major enzymes and metabolism of other microorganisms which thus retards the plant growth.

A variety of antibiotics have been identified, which includes compounds such as amphisin, 2,4-diacetylphloroglucinol (DAPG), oomycin A, phenazine, pyoluteorin, pyrrolnitrin, tensin, tropolone, and cyclic lipopeptides produced by *pseudomonads*⁴⁹ and oligomycin A, kanosamine, zwittermicin A, and xanthobaccin produced by *Bacillus*, *Streptomyces*, and *Stenotrophomonas* species to prevent the proliferation of plant pathogens, generally fungi.

3. Hydrogen Cyanide (HCN) Production: Some rhizobacteria are capable of producing hydrogen cyanide⁶¹. HCN is a volatile, secondary metabolite produced by PGPR that suppresses the development of harmful pathogens. HCN is formed from glycine through the action of HCN synthetase enzyme. This enzyme is associated with the plasma

membrane of certain rhizobacteria¹². HCN is likely to inhibit electron transport chain and energy supply to the cell, leading to the death of cells. It also seems that PGPR inhibits proper functioning of enzymes and natural receptor reversible mechanisms of inhibition. It is a powerful inhibitor of many metal enzymes, such as copper containing cytochrome C oxidases. Many bacterial genera have shown to be capable of producing HCN, including species of *Alcaligenes*, *Aeromonas*, *Bacillus*, *Pseudomonas* and *Rhizobium*².

4. Siderophores Production: Iron (Fe) is an essential micronutrient required for the growth of almost all living microorganisms as it acts as a cofactor in enzymatic processes, oxygen metabolism, electron transfer, and DNA and RNA syntheses¹. Iron is also essential for biofilm formation because it regulates surface motility and stabilizes the polysaccharide matrix^{17, 79}. Under iron-deficient conditions, the hydrophobicity of the microbial surface decreases, leading to alteration of the bacterial surface protein composition, which then leads to limitation of biofilm formation⁶⁷. Thus, because of the low bioavailability of iron in the environment, microorganisms have developed specific uptake strategies such as production of siderophores.

Siderophores are metal-chelating agents with low molecular masses ranging between 200–2000 Da that are produced by microorganisms and plants⁶⁵. Marine organisms such as phytoplankton⁷⁴, cyanobacteria⁵ can produce siderophores especially under Fe-limiting conditions.

Siderophores are classified by the ligands used to chelate the ferric iron. These include the catecholates, hydroxamates, and carboxylates⁵³. Various studies have isolated siderophore producing bacteria belonging to the *Bradyrhizobium*³⁷, *Pseudomonas*¹⁴, *Rhizobium*, *Serratia* and *Streptomyces*⁴⁴ genera from the rhizosphere.

5. Induced Systemic Resistance (ISR): PGPR provides alternate strategy to protect plants from diseases via induced systematic resistance (ISR). The process where treatment of plant by PGPR elicits host defence as

indicated by reduction in severity or incidence of disease caused by pathogens. Induced resistance is a physiological “state of enhanced defensive capacity” elicited by plant growth promoting rhizobacteria (PGPR) such as *Pseudomonas putida*, *Serratia marcescens*, *Flavomonas oryzae*, *Bacillus pumilus*, where the innate defences of the plants, potentiated against subsequent biotic challenges, becomes a popular means of protection of the plant from pathogens through induced systemic resistance (ISR). Biopriming plants with some plant growth promoting rhizobacteria can also provide systemic resistance against a broad spectrum of plant pathogens. Induced systemic resistance involves jasmonate and ethylene signalling within the plant, wherein, these hormones stimulate the defence responses of the host plants against a variety of plant pathogens¹⁸. Many individual bacterial components induce induced systemic resistance such as lipopolysaccharides (LPS), flagella, siderophores, cyclic lipopeptides, 2, 4-diacetylphloroglucinol, homoserine lactones, and volatiles like acetoin and 2, 3-butanediol⁵⁴.

6. Exopolysaccharide production or Biofilm production

Biofilm is a complex association of bacterial cells attached to different biotic and abiotic surfaces that can retain moisture and protects plant roots from various pathogens⁹. This association on the surface involves different polymers of sugars called EPS that protects bacteria from stress⁷⁷. Exopolysaccharides production by bacteria in saline soil can be helpful against osmotic stress. Biofilms are established on various surfaces like roots and soil particles. This can improve crop productivity and physiochemical properties of soil^{6, 9}.

The important roles exhibited by EPS are:

- a) Protective
- b) Surface attachment
- c) Biofilm formation
- d) Microbial aggregation
- e) Plant–microbe interaction, and
- f) Bioremediation⁵¹

Commercialization of PGPR

Several PGPR bacterial strains are commercially available in the form of formulated products which are used as biofertilizers and biocontrol agents^{27,30,66}. Fungal biofertilizers are usually prepared either as powder formulations or granular powder and or fluid-bed granules using dextrin as binder. Bacterial biofertilizers available in the market are formulated in a variety of ways.

Gram-positive micro-organisms possess heat-resistant spores that are exploited to formulate a stable and dry powder product³⁵. Several Gram-negative bacterial strains are known to possess efficient biocontrol ability, they are difficult to formulate as they do not produce spores, their formulations have a short shelf life, and the bacteria gets easily killed when the formulations are desiccated^{34,66}.

Another problem faced by biocontrol developers is that crops are grown under a multiplicity of climatic and environmental conditions which mainly includes temperature, rainfall, soil type and crop variety. Such variations cause disparity in the potentiality of PGPR-based biofertilizers³⁴. However, over the period of time, researchers have been able to develop better biofertilizers with improved shelf life and possessing better and efficient strains. From the present scenario for the use of PGPR in sustainable agriculture, there is still a huge scope of enhancing agricultural productivity²⁴.

The success and commercialization of plant growth promoting rhizobacterial strains depend on the linkages between the scientific organizations and industries. Moreover, commercial success of PGPR strains requires an economical and viable market demand with a consistent and broad spectrum of action, with safety, stability, longer shelf life, low capital costs and easy availability of career materials. Research carried out in the different stages of the process before commercialization has led to the isolation of antagonist strains, screening, fermentation methods, mass production,

formulation viability, toxicology, industrial linkages, quality control and field efficacy⁵⁷.

Plant Growth Promontory Bioformulation:

Bioformulations meant for plant growth promotion continue to inspire research and development in other fields also. Bioformulations are defined as biologically active products containing one or more beneficial microbial strains in an easy to use and economical carrier material. Increase in soil fertility, plant growth promotion, and suppression of phytopathogens are the targets of the bioformulation industry that leads to the sustainable of ecofriendly environment. Bioformulations of PGPR should be consist of a superior carrier material possessing high water holding as well as high water retention capacities, no exothermic heat generation during wetting, nearly sterile, both chemically and physically uniform, nontoxic in nature, non-polluting and easily biodegradable, having nearly neutral pH and or easily adjustable pH, and also supporting bacterial growth and their survival. Most bioformulations are also used to maintain cell viability under adverse environmental conditions⁶⁹.

The synthetic chemicals used in agriculture to increase yields, kill pathogens, pests, and weeds, have a big harmful impact on the ecosystem. So, bioformulations offer an environmentally sustainable approach to increase crop production and health, contributing substantially in making the twenty-first century the age of biotechnology.

Further Aspects and Strategies in Research and Development of PGPR:

Need of today's world is higher yield and enhanced production of food crops with an eco-friendly approach.

- New concepts of rhizo-engineering
- Research in rhizosphere biology consisting of molecular & biotechnological approaches
- Integrated management of soil microbial population
- Bioinoculants for high value crops like vegetable, fruits & flowers
- Application of multi strain bacterial consortium over single inoculation

- Addition of ice-nucleating PGPR
- Comprehensive research on potassium solubilisation
- Biosafety data required for the registration of PGPR
- Non-phytotoxic PGPR
- PGPR tolerant to adverse environment condition
- Cost effective PGPR product.

REFERENCES

1. Aguado-Santacruz, G.A.A., Moreno-Gómez, B.A., Jiménez-Francisco, B.B., García-Moya, E.B., Preciado-Ortiz, R.E., Impact of the microbial siderophores and phytosiderophores on the iron assimilation by plants: a synthesis. *Rev Fitotec Mex.*, **35**: 9–21 (2012).
2. Ahmad, F., Ahmad, I., & Khan, M. S., Screening of free-living rhizospheric bacteria for their multiple plant growth promoting activities. *Microbiological research*, **163(2)**: 173-181 (2008).
3. Amara, U., Khalid, R., & Hayat, R., Soil bacteria and phytohormones for sustainable crop production. In D. K. Maheshwari (Ed.), *Bacterial metabolites in sustainable agroecosystem (pp. 87–103)*. Springer International. doi: 10.1007/978-3-319-24654-3 (2015).
4. Antoun, H., Kloepper, J.W., Plant growth promoting rhizobacteria (PGPR) in Encyclopedia of Genetics. Academic Press, New York. Edited by Brenner S, Miller JH, 1477–1480 (2001).
5. Armstrong J.E., Van Baalen C., Iron transport in microalgae: the isolation and biological activity of a hydroxamate siderophore from the blue-green alga *Agmenellum quadruplieatum*. *J Gen Microbiol*, **111**: 253–262 (1979).
6. Ashraf, M., Hasnain, S., Hussain, F., Proc. Int. Conf. Environmentally Sustainable Development, Exo-polysaccharides (exopolysaccharide) producing biofilm bacteria in improving physico-chemical characteristics of the salt affected soils (2005).

7. Bandelier, S., Renaud, R., and Durand, A., Production of gibberellic acid by fed-batch solid state fermentation in an aseptic pilot-scale reactor. *Process Biochemistry*, **32(2)**: 141-145 (1997).
8. Basak, B. B. and Biswas, D. R., Co-inoculation of potassium solubilizing and nitrogen fixing bacteria on solubilization of waste mica and their effect on growth promotion and nutrient acquisition by a forage crop. *Biology and fertility of soils*, **46(6)**: 641-648 (2010).
9. Batool R., Hasnain, S., Growth stimulatory effects of *Enterobacter* and *Serratia* located from biofilms on plant growth and soil aggregation. *Biotechnol.*, **4(4)**: 347–353 (2005).
10. Bhardwaj, D., Ansari, M. W., Sahoo, R. K., and Tuteja, N., Biofertilizers function as key player in sustainable agriculture by improving soil fertility, plant tolerance and crop productivity. *Microb Cell Fact*, **13**, 66 (2014).
11. Bhattacharyya, P. N. and Jha, D. K., Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. *World Journal of Microbiology and Biotechnology*, **28(4)**: 1327-350 (2012).
12. Blumer, C. and Haas, D., Mechanism, regulation, and ecological role of bacterial cyanide biosynthesis. *Archives of Microbiology*, **173(3)**: 170-177 (2002).
13. Bockman, O.C., Fertilizers and biological nitrogen fixation as sources of plant nutrients: Perspectives for future agriculture. *Plant Soil*, **194**: 11-14 (1997).
14. Boopathi, E., & Rao, K. S, A siderophore from *Pseudomonas putida* type A1: structural and biological characterization. *Biochimica et Biophysica Acta (BBA)-Protein structure and molecular enzymology*, **1435(1)**: 30-40 (1999).
15. Buscot, F., What are Soils. In: Micro-Organisms in Soils: Roles in Genesis and Functions, Buscot, F. and A. Varma (Eds.) *Springer-Verlag, Heidelberg, Germany*, pp: 3-18 (2005).
16. Chen X., Liu, M., Hu, F., Mao, X. and Li, H., Contributions of soil micro-fauna (protozoa and nematodes) to rhizosphere ecological functions, *Acta. Ecol. Sin.*, **27(8)**: 3132-3143 (2007).
17. Chhibber, S., Nag, D., Bansal, S., Inhibiting biofilm formation by *Klebsiella pneumoniae* B5055 using an iron antagonizing molecule and a bacteriophage, *BMC Microbiol. Jul* **26**; **13**: 174 (2013).
18. Compant, S., Reiter, B., Sessitsch, A., Nowak, J., Clément, C., Endophytic colonization of *Vitisvinifera* L. by plant growth-promoting bacterium *Burkholderia sp. strain 45*. *PsJN. Appl Environ Microbiol* **71**: 1685-1693 (2005).
19. Duan, J., Müller, K. M., Charles, T. C., Vesely, S., & Glick, B. R, 1-aminocyclopropane-1-carboxylate (ACC) deaminase genes in rhizobia from southern Saskatchewan. *Microbial ecology*, **57(3)**: 423-436 (2009).
20. Fox, J.E., Gullledge, J., Engelhaupt, E., Burow, M.E. and McLachlan, J.A., Pesticides reduce symbiotic efficiency of nitrogen-fixing rhizobia and host plants. *PNAS*, **104**: 10282-10287 (2007).
21. Frankenberger, Jr. W.T. and Arshad, M., *Phytohormones in Soil: Microbial Production and Function*. Marcel Dekker Inc., *New York, USA*, ISBN: 0824794427: 503 (1995).
22. Ghosh, S., Penterman, J. N., Little, R. D., Chavez, R. and Glick, B. R., Three newly isolated plant growth-promoting bacilli facilitate the seedling growth of canola, *Brassica campestris*. *Plant Physiology and Biochemistry*, **41(3)**: 277-281 (2003).
23. Glick, B.R., Cheng, Z., Czarny, J., Duan, J., Promotion of plant growth by ACC deaminase producing soil bacteria, *Eur J of Plant Pathol* **119**: 329-339 (2007).
24. Glick, B. R., Bacteria with ACC deaminase can promote plant growth and help to feed the world. *Microbiological Research*, **169**, 30–39. doi:10.1016/j.micres.2013.09.009 (2014).

25. Glick, B.R., The enhancement of plant growth by free living bacteria. *Canadian Journal of Microbiology*, **41 (2)**: 109–114 (1995).
26. Glick, B.R., Penrose, D.M. and Li, J. A model for the lowering of plant ethylene concentrations by plant growth promoting bacteria. *J. Theor. Biol.*, **190**: 63-68 (1998).
27. Gohel, V., Singh, A., Vimal, M., Ashwini, P., & Chhatpar, H. S., Bioprospecting and antifungal potential of chitinolytic microorganisms. *African Journal of Biotechnology*, **5**, 54–72 (2006).
28. Govindasamy, V., Senthilkumar, M., Gaikwad, K., & Annapurna, K., Isolation and characterization of ACC deaminase gene from two plant growth-promoting rhizobacteria. *Current microbiology*, **57(4)**: 312-317 (2008).
29. Grichko, V.P. and Glick, B.R., Amelioration of flooding stress by ACC deaminase-containing plant growth-promoting bacteria. *Plant Physiol. Biochem.*, **39**: 11-17 (2001).
30. Jha, C. K., & Saraf, M., Plant growth promoting rhizobacteria (PGPR): A review. *E3 Journal of Agricultural Research and Development*, **5**, 108–119 (2015).
31. Juanda, J. I. H., Screening of soil bacteria for Plant Growth Promoting Activities in Vitro. *J. Agri. Sci.* **4**:27-31 (2005).
32. Kado C.I., Phytohormone mediated tumorigenesis by plant pathogenic bacteria. In DPS Verma, TH Hohn, eds, *Genes Involved in Microbe* (1984).
33. Kaiss-Chapman, R.W., Morris, R.O., Trans-zeatin in culture filtrates of *Agrobacterium tumefaciens*. *Biochem Biophys Res Commun* **76**: 453-459 (1977).
34. Kamilova, F., Okon, Y., de Weert, S., & Hora, K., Commercialization of microbes: Manufacturing, inoculation, best practice for objective field testing, and registration. In B. Lugtenberg (Ed.), *Principles of plant-microbe interactions*(pp. 319–327). *Springer International*. doi: 10.1007/978-3-319-08575-3_33(2015).
35. Kannaiyan, S. (Ed.). , *Biotechnology of biofertilizers. Alpha Science Int'l Ltd* (2002).
36. Khan, M.S., Zaidi, A., Ahemad, M., Oves, M. and Wani, P.A., Plant growth promotion by phosphate solubilizing fungi– current perspective. *Arch. Agron. Soil Sci.*, **56**: 73-98 (2010).
37. Khandelwal, S. R., Manwar, A. V., Chaudhari, B. L., & Chincholkar, S. B., Siderophoregenic bradyrhizobia boost yield of soybean. *Applied biochemistry and biotechnology*, **102(1-6)**, 155-168 (2002).
38. Kim, J. and Rees , D.C., Nitrogenase and biological nitrogen fixation , *Biochemistry*, **33**: 389–397(1994).
39. Kloepper, J. W. and Schroth, M. N., Plant growth-promoting rhizobacteria on radishes, Proc. 4th Int. Conf. on Plant Pathogenic Bacteria, Station de Pathologie Vegetale et Phytobacteriologie, *INRA, Angers, France*, **2**: 879-882 (1978).
40. Kloepper, J.W., Plant Growth-Promoting Rhizobacteria (Other Systems). In: *Azospirillum/Plant Associations* Okon, Y. (Eds.). CRC Press, Boca Raton, FL., USA. 111-118 (1994).
41. Kloepper, J.W., A review of mechanisms for plant growth promotion by PGPR In: Reddy, M.S., Anandaraj, M., Eapen, S.J., Sarma, Y.R., Kloepper, J.W. (Eds.), *Abstracts and Short Papers. 6th International PGPR Workshop*.d, Indian Institute of Spices Research, Calicut, India, 81–92 (2003).
42. Kloepper, J.W., Leong, J., Teintze, M., Schroth, M.N., Enhanced plant growth by siderophores produced by plant growthpromoting rhizobacteria. *Nature*, **286**: 885–886 (1980).
43. Kloepper, J.W., Zablotowics, R.M., Tipping, E.M. and Lifshitz, R., Plant Growth Promotion Mediated by Bacterial Rhizosphere Colonizers. In: *The Rhizosphere and Plant Growth*, Keister, D.L. and P.B. Cregan (Eds.). *Kluwer Academic Publishers, USA*, 315-326 (1991).

44. Kuffner, M., Puschenreiter, M., Wieshammer, G., Gorfer, M., & Sessitsch, A., Rhizosphere bacteria affect growth and metal uptake of heavy metal accumulating willows. *Plant and Soil*, 304(1-2), 35-44 (2008).
45. Kumar, J.I.N., Bora, A. and Amb, M.K., Chronic toxicity of the triazole fungicide tebuconazole on a heterocystous, nitrogen-fixing rice paddy field cyanobacterium, *Westiellopsis prolifica* Janet.J. *Microbial. Biotechnol*, **20**: 1134-1139 (2010).
46. Ladha, J. K., De Bruijn, F. J. and Malik, K. A., Introduction: assessing opportunities for nitrogen fixation in rice—a frontier project. In *Opportunities for Biological Nitrogen Fixation in Rice and Other Non-Legumes*. Springer Netherlands. 1-10 (1997).
47. Li, J., Ovakim, D.H., Charles, T.C. and Glick, B.R., An ACC deaminase minus mutant of *Enterobacter cloacae* UW4 no longer promotes root elongation. *Curr. Microbiol*, **41**: 101-105 (2000).
48. Loper, J.E. and Schroth, M.N., Influence of bacterial sources of indole-3-acetic acid on root elongation of sugar beet. *Phytopathology*, **76**: 386-389 (1986).
49. Lugtenberg B, Kamilova F, Plant-growth-promoting rhizobacteria. *Annu Rev Microbiol* **63**: 541-556 (2009).
50. Ahemad, M., Khan, M.S., Effect of pesticides on plant growth promoting traits of *Mesorhizobium* strain MRC4.J. *Saudi Soc. Agric. Sci.*, **11**: 63 – 71 (2012).
51. Manca de Nadra, M.C., Strasser, A.M., de Saad, A.A., de Ruiz Holgado, P., Oliver, G., Extracellular polysaccharide production by *Lactobacillus bulgaricus* CRL 420. *Milchwissenschaft*, **40**: 40 (1985).
52. Mayak, S., Tivosh, T. and Glick, B.R., Effect of wild type and mutant plant growth-promoting rhizobacteria on the rooting of mung bean cuttings. *J. Plant Growth Regul*, **18**: 49-53 (1999).
53. Miethke, M. and Marahiel, M. A., Siderophore-based iron acquisition and pathogen control. *Microbiol. Mol. Biol. Rev.* **71**: 413–451 (2007).
54. Mohamed, H. I. and Gomaa, E. Z., Effect of plant growth promoting *Bacillus subtilis* and *Pseudomonas fluorescens* on growth and pigment composition of radish plants (*Raphanus sativus*) under NaCl stress. *Photosynthetica*, **50(2)**: 263-272 (2012).
55. Nassar, A. H., El-Tarabily, K. A. and Sivasithamparam, K., Promotion of plant growth by an auxin-producing isolate of the yeast *Williopsis saturnus* endophytic in maize (*Zea mays* L.) roots. *Biology and Fertility of Soils*, **42(2)**: 97-108 (2005).
56. Naznin, H.A., Kimura, M., Miyazawa, M., Hyakumachi, M., Analysis of volatile organic compounds emitted by plant growth promoting fungus *phoma* sp. GS8-3 for growth promotion effects on tobacco. *Microbe Environ*, **28**: 42-49 (2005).
57. Parada, M., Vinardell, J., Ollero, F., Hidalgo, A., Gutiérrez, R., *Sinorhizobium fredii* HH103 mutants affected in capsular polysaccharide (KPS) are impaired for nodulation with soybean and *Cajanus cajan*. *Mol Plant Microbe Interact* **19**: 43-52 (2006).
58. Patten, C.L. and Glick, B.R., Bacterial biosynthesis of indole-3-acetic acid. *Can. J. Microbiol.*, **42**: 207-220 (1996).
59. Puga-Freitas, R. and Blouin, M., A review of the effects of soil organisms on plant hormone signalling pathways. *Environmental and Experimental Botany* (2014).
60. Raaijmakers JM, de Bruijn I, Nybroe O and Ongena M., Natural functions of lipopeptides from *Bacillus* and *Pseudomonas*: More than surfactants and antibiotics. *FEMS Microbiol Rev*, **34**: 1037-1062 (2010).
61. Rezzonico, F., Zala, M., Keel, C., Duffy, B., Moënné-Loccoz, Y. and Défago, G., Is the ability of biocontrol fluorescent *pseudomonads* to produce the antifungal metabolite 2, 4-diacetylphloroglucinol really synonymous with higher plant

- protection. *New Phytologist*, **173(4)**: 861-872 (2007).
62. Rodrigues, C., Vandenberghe, L. P. D. S., de Oliveira, J. and Soccol, C. R., New perspectives of gibberellic acid production: a review. *Critical reviews in biotechnology*, **32(3)**: 263-273 (2012).
63. Saleem, M., Arshad, M., Hussain, S. and Bhatti, A. S., Perspective of plant growth promoting rhizobacteria (PGPR) containing ACC deaminase in stress agriculture. *Journal of industrial microbiology & biotechnology*, **34(10)**: 635-648 (2007).
64. Sasaki, A., Itoh, H., Gomi, K., Ueguchi-Tanaka, M., Ishiyama, K., Kobayashi, M. and Matsuoka, M., Accumulation of phosphorylated repressor for gibberellin signaling in an F-box mutant. *Science*, **299(5614)**: 1896-1898 (2003).
65. Schwyn, B., Neilands, J.B. Anal Biochem, Universal chemical assay for the detection and determination of siderophores, **160(1)**: 47-56 (1987).
66. Sethi, S. K., Sahu, J. K., & Adhikary, S. P., Microbial biofertilizers and their pilot-scale production. *Microbial Biotechnology: Progress and Trends*, 297 (2014).
67. Simões, L.C., Simões, M., Vieira, M.J., Biofilm interactions between distinct bacterial genera isolated from drinking water. *Appl Environ Microbiol*, **73(19)**: 6192-200 (2007).
68. Sindhu, S.S., Parmar, P. and Phour, M., Nutrient cycling: potassium solubilization by microorganisms and improvement of crop growth. In: Geomicrobiology and biogeochemistry: Soil biology. Parmar, N. and Singh, A., Eds. *Springer-Wien/New York, Germany* (2012).
69. Singh, S., Gupta, G., Khare, E., Behal, K.K., Arora, N.K., Effect of enrichment material on the shelf life and field efficiency of bioformulation of *Rhizobium* sp. and P-solubilizing *Pseudomonas fluorescens*. *Science Research Reporter*, **4**: 44-50 (2014).
70. Somers, E., Vanderleyden, J. and Srinivasan, M., Rhizosphere bacterial signalling: a love parade beneath our feet. *Crit. Rev. Microbiol*, **30**: 205–240 (2004).
71. Spaepen S., Vanderleyden J. and Remans R. Indole-3-acetic acid in microbial and microorganism-plant signalling. *FEMS Microbiology Review*, **31**: 425–448 (2006).
72. Subba Rao, N. S. and Dommergues, Y. R., Microbial interactions in agriculture and forestry (1998).
73. Tank, N. and M. Saraf., Salinity-resistant plant growth promoting rhizobacteria ameliorates sodium chloride stress on tomato plants. *J. Plant Interactions*, **5**: 51-58 (2010).
74. Trick CG, Andersen RJ, Gillam A, Harrison, P.J., Procentrin: An Extracellular Siderophore Produced by the Marine Dinoflagellate *Prorocentrum minimum*. *Science*. **219(4582)**: 306-8 (1983).
75. Valverde, A., Burgos, A., Fiscella, T., Rivas, R., Velazquez, E., Rodriguez-Barrueco, C., Cervantes, E., Chamber, M. and Igual, J.M., 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 (2006).
76. Vessey, K., Plant growth promoting rhizobacteria as biofertilizers. *Plant Soil* 255: 571-586. **16 (3)**: 295 – 298 (2003).
77. Vyrides, I., Stuckey, D.C., Adaptation of anaerobic biomass to saline conditions: Role of compatible solutes and extracellular polysaccharides. *Enzyme Microb. Technol*, **44**: 46–51 (2009).
78. Wang, C., Knill, E., Glick, B.R. and Defago, G., Effect of transferring 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase genes into *Pseudomonas fluorescens* strain CHAO and its gacA derivative CHA96 on their growth-promoting and disease-

- suppressive capacities. *Can. J. Microbiol.*, **46**: 898-907 (2006).
79. Weinberg, E.D., Suppression of bacterial biofilm formation by iron limitation. *Med Hypotheses*, **63(5)**: 863-5 (2004).
80. Whipps, J. M., Microbial interactions and biocontrol in the rhizosphere. *Journal of experimental Botany*, **52(suppl 1)**: 487-511 (2001).
81. Yu, Y., Chu, X., Pang, G., Xiang, Y. and Fang, H., Effects of repeated applications of fungicide carbendazim on its persistence and microbial community in soil, *J. Environ. Sci.*, **21**: 179-185 (2009).