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Role of Plant Growth Promoting Rhizobacteria to Suppress Phytopathogens

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Abstract

Crops destruction by pests has a serious impact on agricultural practices for a long period of time. Its losses are creating a major threat to the food production with about 27 to 42% loss in global food production. Different approaches may be used to prevent, or to control plant diseases, pest population, and its damages. Previously growers often heavily use agro chemicals (pesticides) to control plant diseases and pest damage. Use of agrochemicals has raised a number of environmental issues causing health hazards. Besides contaminating the environment pesticide residues also affect useful organisms like soil micro flora, earth worms, bees, spiders, plants, furthermore; continuous use of chemical pesticides creates a selective pressure which helps in emerging of resistance pathogen generally it causes ecology disturbance. Therefore, use of plant growth promoting rhizobacterial pesticides to control plant diseases and insect pest is important to increase production and productivity of the crops and also enhance sustainable agriculture. In this regard, rhizobacterial pesticides offer better alternative to chemical pesticides and insecticides. Rhizobacterial pesticides and insecticides are not only helps to enhance food security through fighting against phytopathogens but also ensure the food safety and quality and they are environmental friendly. In this review, we have identified role of plant growth promoting rhizobacteria to control pathogens that affect plant production, productivity and critically analyzed the importance and mode of action.

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Introduction

Crops destruction by pests has a serious impact on agricultural practices for a long period of time. Its losses are creating a major threat to the food production with about 27 to 42% loss in global food production. Pest management in agriculture is important to increase production and productivity of the crops and also enhance sustainable agriculture. These pests include insects, fungi, bacteria, weeds, viruses, nematodes and animals. It has been estimated that nearly 50, 000 species of fungi, 1,800 species of weeds, 200 species of bacteria and 15, 000 species of nematodes destroy food and fiber

crops used by millions of people worldwide (Agrios, 2005). Traditional methods used to protect crops from diseases have been largely based on the use of chemical pesticides. Applications of fungicides, fumigants, herbicides, and insecticides can have drastic effects on the environment and consumers. Chemical methods may not be economical in the long run because they pollute the atmosphere, damage the environment, leave harmful residues, and can lead to the development of resistant strains among the target organisms with repeated use. Therefore, a reduction or elimination of synthetic pesticide applications in agriculture is highly desirable. One of the most promising means to achieve this goal is

by the use of BCAs for disease control alone, or to integrate with reduced doses of chemicals in the control of plant pathogens resulting in minimal impact of the chemicals on the environment. Biocontrol of pests in agriculture is a method of controlling pests including insects, mites, weeds, and plant and soil-borne diseases (Meenu *et al.*, 2013). A number of BCAs have been registered and are available as commercial products, including strains belonging to bacterial genera such as *Agrobacterium*, *Pseudomonas*, *Streptomyces*, and *Bacillus*, and fungal genera such as *Gliocladium*, *Trichoderma*, *Ampelomyces*, *Candida*, and *Coniothyrium* (Ratna *et al.*, 2014).

Plant growth promoting rhizobacteria

PGPR bacteria are beneficial bacteria which have the ability to colonize the roots and either promotes plant growth through direct action or via biological control of plant diseases. They are associated with many plant species and are commonly present in various environment. The rhizosphere, volume of soil surrounding roots and influenced chemically, physically and biologically by the plant root, is a highly favorable habitat for the proliferation of microorganisms and exerts a potential impact on plant health and soil fertility. Root exudates rich in amino acids, monosaccharides and organic acids, serve as the primary source of nutrients, and support the dynamic growth and activities of various microorganisms within the vicinity of the roots (Boddey *et al.*, 2001). On the basis of their location in rhizosphere PGPR can be classified as extracellular PGPR found in the rhizosphere, on the rhizoplane or in the spaces between the cells of the root cortex and intracellular PGPR which exist inside the root cells, generally in specialized nodular structures (Çakmakçi *et al.*, 2007). PGPR represent a wide variety of soil bacteria which grown in association with a host plant, result in stimulation of growth of their host. PGPR have the potential to contribute in the development of sustainable agricultural systems. In general, PGPR function in three different ways (Cattelan *et al.*, 1999) synthesizing particular compounds for the plants (Chandra *et al.*, 2007) facilitating the uptake of certain nutrients from the soil and preventing the plants diseases (Chen *et al.*, 1994)., Strains like *Pseudomonas*, *Klebsiella*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia* and *Serratia* are considered as PGPR traits that enhance the plant growth. The direct mechanism involved in enhancing the plant growth is by producing plant hormones like Indole Acetic Acid (IAA) and Gibberellic Acid (GA), and provides nutrients to the host plant by

producing siderophores, Phosphate solubilization and fixes atmospheric nitrogen. The indirect mechanism involves the production of antibiotics, lytic enzymes, hydrogen cyanide and catalase which acts as a biological control of plant pathogens and microbes. Interaction of beneficial microbes and plant are the primary determinants for plant health and soil fertility. Mostly 2 - 5% of rhizospheric bacteria are PGPR. Spore forming bacteria like *Bacillus* are more efficient PGPR compared with non-spore forming bacteria like *Pseudomonas* because spores are most resistant and robust compared with vegetative cells.

Bacillus is most efficient PGPR that enhances the plant growth by producing a vast variety of substances (Ajay Ku *Bacillus* and *Pseudomonas* sps are most predominant colonies in the rhizosphere, suppresses the plant pathogens by producing antifungal compounds. PGPR and their application to reduce the usage of chemical fertilizers and pesticides and achieve sustainable crop yield in agriculture and horticulture. PGPR also induces the Induced systemic resistance (ISR) in host plant and reduces the incidence of disease severity in host plants against pathogens. It is called as rhizobacteria mediated Induced Systemic Resistance (ISR).

Classification of plant growth promoting rhizobacteria

On the basis of their location in rhizosphere PGPR can be classified as extracellular PGPR found in the rhizosphere, on the rhizoplane or in the spaces between the cells of the root cortex and intracellular PGPR which exist inside the root cells, generally in specialized nodular structures (Deepmala and Bharti, 2016). PGPR represent a wide variety of soil bacteria which grown in association with a host plant, result in stimulation of growth of their host. PGPR have the potential to contribute in the development of sustainable agricultural systems. Fig 1 Major Plant growth-promoting groups used in commercial bio-inocula for plant growth promotion (Deepmala and Bharti, 2016).

General futures of PGPR involved in biological control of pathogens

Several microorganisms including bacteria, viruses, fungi, protozoa and nematodes, which inhabit the soil or plant rhizosphere, have been identified to suppress the diseases of agricultural crops caused by various pathogenic bacteria and fungi. Many rhizosphere bacteria that possess different traits for killing of pathogens are

well suited to be used as biocontrol agents. PGPR are characterized by the following features (i) they must be able to colonize the root surface (efficient colonisation of the roots, tubers, hypocotyle, etc) (ii) they must survive, multiply and compete with other microbes so that they will be able to express their plant growth promotion/protection activities, and (iii) they must promote plant growth (Avinash *et al.*, 2016). (iv) ability to utilise a variety of organic substrates usually found in root and seed exudates (v) production of a variety of secondary metabolites and (vi) their compatibility with commonly used pesticides and other biocontrol agents (Satyavir *et al.*, 2009).

Mechanism of plant growth promotion

There are array of mechanisms by which PGPR stimulate the growth of plants. They are broadly classified as direct and indirect mechanisms, as plant growth promoters and biological control agents. The main mechanisms by which PGPR directly contribute to the plant growth are phytohormone production like auxins, cytokinins and gibberellins, enhancing plant nutrition by solubilization of minerals like phosphorus and zinc, production of siderophores and enzymes, lowering of ethylene levels and induction of systemic resistance PGPR indirectly benefit the plant growth by the biocontrol of deleterious microorganisms or root pathogens that inhibit plant growth, including antibiotic production, parasitism, competition for nutrients and niches within the rhizosphere, synthesis of extracellular enzymes to hydrolyze the fungal cell wall, decreasing pollutant toxicity (kundan *et al.*, 2015)

Direct Mechanism

The direct mechanism of PGPR is the major step involved to support plant growth in a forward and direct manner. Direct mechanism includes nitrogen fixation, phytohormones production, phosphate solubilization and increasing iron availability. These mechanisms influence the plant growth activity directly but the ways by which it influences will vary from species to species as well as strain to strain. In the presence of PGPR direct enhancement of mineral uptake has been reported due to increases in specific ion fluxes at the root surface. Organic substances that stimulate plant growth are known as plant growth regulators. They stimulate plant growth by influencing the physiological and morphological processes at very low concentrations. Several microorganisms are capable of producing auxins, cytokinins, gibberellins, ethylene (ET), or abscisic acid

(ABA). Auxins are produced by several rhizobacterial genera, e.g. *Azospirillum*, *Agrobacterium*, *Pseudomonas* and *Erwinia* (kundan *et al.*, 2015).

Phytohormone production

Phytohormones are the chemical messengers that play crucial role in the natural growth and occur in low concentration. These phytohormones shape the plant, also affecting seed growth, time of flowering, sex of flowers, senescence of leaves, and fruits.

They also affect gene expression and transcription levels, cellular division and growth. In targeted cells phytohormones also regulate cellular processes, pattern formation, vegetative and reproductive development and stress responses. Thus, all the major activities like formation of leaf, flowers and development and ripening of fruit are regulated and determined by hormones. In order to decrease the negative effects of the environmental stressors caused due to growth limiting environmental conditions, plants mostly attempt to adjust the levels of their endogenous phytohormones.

PGPR can promote plant development with the production of different phytohormones like IAA, gibberellic acid and cytokinins (Satyavir *et al.*, 2009). There are five classes of well-known Plant growth promoting hormones, namely auxins, gibberellins, cytokinins, ethylene and abscisic acid. Much attention has been given on the role of phytohormone auxin. With the production of different phytohormones like indole-3-acetic acid (IAA), gibberellic acid and cytokinins, PGPR can increase root surface and length and thus help in the growth and development of plants (Premachandra *et al.*, 2016).

Indole acetic acid

Indole-3-acetic acid (indole acetic acid, IAA) is one of the most common phytohormones and much of the scientific literature considers auxin and IAA to be interchangeable terms (Spaepen *et al.*, 2007). Its main function is cell division, cell elongation, differentiation, and extension. But it has been known that plant responses to IAA vary from plant to plant in terms of sensitivity. Generally, IAA released by rhizobacteria interferes with many plant developmental processes because the endogenous pool of plant IAA may be altered by the acquisition of IAA that has been secreted by soil bacteria (Glick, 2012). The production of IAA

among the PGPR are vary (Prakash and Karthikeyan, 2013).

IAA is synthesized by several independent biosynthetic pathways and mostly produced in bud and young leaves of plant. In young stems IAA causes a rapid increase in cell wall extensibility. IAA seems to promote growth of auxiliary bud and bud formation. There are several ways by which IAA supports the plant. IAA helps in the apical dominance, and also stimulates lateral and adventitious root development and growth. Besides development, IAA plays crucial role in leaf and flower abscission. Thus IAA can be considered as major auxin involved because it plays overall role in growth stimulation by being involved in DNA synthesis.

Tryptophan is an important molecule that alters the level of IAA synthesis which is also identified as the main precursor for IAA and thus plays a vital role in modulating the level of IAA biosynthesis. Tryptophan stimulates the IAA production and thus regulates the IAA biosynthesis by inhibiting anthranilate that is a major precursor for tryptophan because it seems to reduce IAA synthesis. Thus tryptophan plays vital role in IAA production by negative feedback regulation (kundn *et al.*, 2015).

Ethylene

Ethylene hormone in plants is the simplest molecule with a wide range of biological activities. It is produced by plant endogenously and induces different physiological changes in plants at molecular level. The production of ethylene varies within the plant species and types of tissues. This gaseous hormone is formed by breakdown of methionine that is present in all the cells. The production of ethylene is entirely dependent on its rate of production versus its rate of escaping into the atmosphere. It is produced more in dividing cells mostly in darkness. It effects plant growth by root initiation, fruit ripening, seed germination, and inhibiting root elongation. The major effect seen is fruit ripening and thus called aging hormone in plants. Ethylene, because of its simple structure (C₂H₄), influences many aspects of plant growth and development (kundn *et al.*, 2015). During severe conditions like extreme temperature, flooding, toxic metals and radiations exposure, ethylene is synthesized. Under these stressed conditions the endogenous production of ethylene is induced more to have the adverse effect on root growth and eventually on whole plant. 1-aminocyclopropane- 1-carboxylate (ACC) deaminase is a vital enzyme present in plant growth

promoting rhizobacteria (PGPR), which regulates ethylene production by metabolizing ACC (an immediate precursor of ethylene biosynthesis in higher plants) into alpha-ketobutyrate and ammonia. Inoculation with PGPR combined with ACC deaminase activity could be quite helpful in promoting plant growth and development under stress conditions by reducing stress-induced ethylene production. By lowering the abundance of the ethylene precursor ACC, the PGPR ACC activity is thought to decrease root ethylene production, which in turn can alleviate the repressing effect of ethylene on root growth (kundn *et al.*, 2015). Ethylene that is synthesized as a response to various stresses is called “stress ethylene”. This increases plant survival in such extreme conditions. Thus for the optimum growth under stressful condition introduction of ACC deaminase genes could be done to maintain ethylene level in plants. Currently, bacterial strains exhibiting ACC deaminase activity have been identified in a wide range of genera such as *Acinetobacter*, *Achromobacter*, *Agrobacterium*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Ralstonia*, *Serratia* and *Rhizobium* etc. (kundn *et al.*, 2015).

Cytokinins

Cytokinins are phytohormones that promote cell division in plant roots and shoots. Their main function is cell growth and differentiation. As they also affect apical dominance so they are used by the farmers to increase the overall yield. Cytokinins help the plant by delaying the senescence or aging of tissues and thus effect the leaf growth.

The cytokinin balance is influenced by the levels of other growth regulators, e.g. auxins (Kaminek *et al.*, 1997) as well as by environmental cues. The apical dominance induced by auxins is countered by cytokinins; they in conjunction with ethylene promote abscission of leaves, flower parts, and fruits (Sipes *et al.*, 1983). Cytokinins can be produced in soil and pure culture by PGPR and this is an emerging alternate to enhance plant growth to improve yield and quality of crops, playing crucial role in sustainable development.

Gibberellins

Gibberellins are chemicals produced naturally by plants and are involved in several aspects of germination. They stimulate the enzyme (alpha amylase) and help in hydrolysis of starch present in many seeds into glucose to be used in cellular respiration. Gibberellins are plant

hormones that influence and control plant developmental processes like stem elongation, germination, dormancy, flowering, sex expression and leaf and fruit senescence. Lastly gibberellins act as a chemical messenger and help by breaking dormancy. Several studies revealed that many soilbacteria in general, and PGPB in particular, can produce either cytokinins or gibberellins or both (kundu *et al.*, 2015).

Abscissic acid

Abscissic acid (ABA) plays a primary role in water-stressed environment, such as found in arid and semiarid climates where it helps in combating the stress through stomatal closure of leaves. Therefore, its uptake by and transport in plant and its presence in the rhizosphere could be extremely important for plant growth under water stress condition. In addition, abscissic acid (ABA) has also been detected by radioimmunoassay or TLC in supernatants of *Azospirillum* and *Rhizobium* sp. cultures (Yunus *et al.*, 2016).

Nitrogen fixation

Nitrogen fixation is the conversion of atmospheric nitrogen into utilizable nitrogen that changes to ammonia. This is essential for all life forms because nitrogen is the basic building block of plants and all life forms. Biological nitrogen fixation occurs generally at mild temperatures by nitrogen fixing microorganisms, which are widely distributed in nature. The nitrogenase complex is a complex enzyme which carries out the process of N₂ fixation [28]. Structure of nitrogenase was elucidated as a two-component metalloenzyme consisting of (i) dinitrogenase reductase which is an iron protein and (ii) dinitrogenase consists of a metal cofactor. Dinitrogenase reductase provides electrons with high reducing power while dinitrogenase utilizes these electrons to reduce N₂ to NH₃ (kundu *et al.*, 2015).

This process consumes enormous amount of energy in the form of ATP. The nitrogen fixation process requires nitrogenase gene (*nif*) which is sensitive to oxygen; therefore to prevent oxygen from inhibiting nitrogen fixation while at the same time providing sufficient oxygen for the bacteroides within the nodule to respire, it is possible to introduce bacterial hemoglobin, which binds free oxygen. The *nif* genes include structural genes that activate Fe protein, molybdenum, and other regulatory genes that are directly involved in the function and synthesis of enzyme and seem to be present in both symbiotic and free living systems. Since nitrogen

fixation is a very energy consuming process, requiring at least 16 moles of ATP for each mole of reduced nitrogen, it would be beneficial if bacterial carbon resources are directed toward oxidative phosphorylation, which results in the synthesis of ATP, rather than glycogen synthesis, resulting in the storage of energy in the form of glycogen. A variety of nitrogen fixer bacterial species belonging to genera *Azospirillum*, *Alcaligenes*, *Arthrobacter*, *Acinetobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Pseudomonas*, *Rhizobium* and *Serratia* colonize with the plant rhizosphere are able to exert many beneficial effects on plant growth.

Phosphate solubilization

Phosphorus (P), the second important plant growth-limiting nutrient after nitrogen, is abundantly available in soils in both organic and inorganic forms. Despite of large reservoir of P, the amount of available forms to plants is generally low. This low availability of phosphorous to plants is due to the fact that the majority of P present in the soil is found in insoluble forms, while the plants are able to absorb it only in two soluble forms, the monobasic (H₂PO₄) and the dibasic (HPO₄)⁻² ions. To overcome the P deficiency in soils, there are frequent applications of phosphatic fertilizers in agricultural fields. Plants absorb fewer amounts of applied phosphatic fertilizers and the rest is rapidly converted into insoluble complexes in the soil (Kundan *et al.*, 2015). But regular application of phosphate fertilizers is not only costly but is also environmentally undesirable.

This has led to search for an ecologically safe and economically reasonable option for improving crop production in low P soils. In this context, microorganisms such as PGPR possessing phosphate solubilizing activity, often termed as phosphate solubilizing microorganisms (PSM), may provide the available forms of P to the plants and hence a viable substitute to chemical phosphatic fertilizers. Typically, the solubilization of inorganic phosphorus occurs as a consequence of the action of low molecular weight organic acids which are synthesized by various soil bacteria. The mineralization of organic phosphorus occurs through the synthesis of a variety of different enzymes such as phosphatases, catalyzing the hydrolysis of phosphoric esters. Importantly, phosphate solubilization and mineralization can coexist in the same bacterial strain (Tao *et al.*, 2008).

Table.1 Some of the PGPR available in market with their brand name (Figueiredo *et al.*, 2010).

S. No.	PGPR used	Brand name
1	Agrobacterium radiobacter K 1026	N0gs11®
2	Bacillus Pumilus QST 2808	Sonata®TM
3	B.pumilus GB34	Yield Shield®
4	B.subtilis GB03	Kodiak®
5	Pantoeaagglomerans C9-1	Blight Ban®
6	P.agglomerans E325	Bloom time®
7	Pseudomonas aureofaciens Tx-1	Spot-Les®T
8	P.syringae ESC-10 and ESC-11	Bio-save®
9	P.fluorescens A506	Blight Ban®
10	P.chlororaphis MA 342	Cedomon®
11	Streptomyces griseoviridis K61	Mycostop®
12	S.lydicus WYEC 108	Actinovate®

Fig.1 Major Plant growth-promoting groups used in commercial bio-inocula for plant growth promotion (Deepmala and Bharti, 2016).

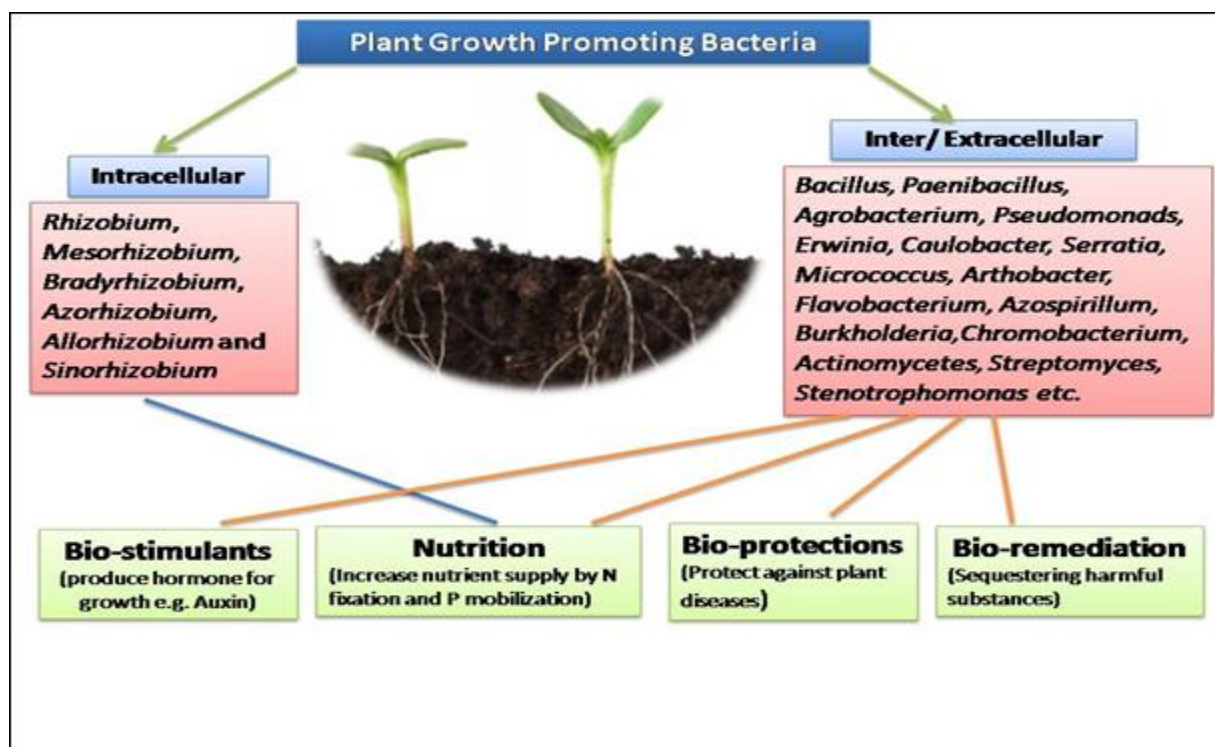


Fig.2

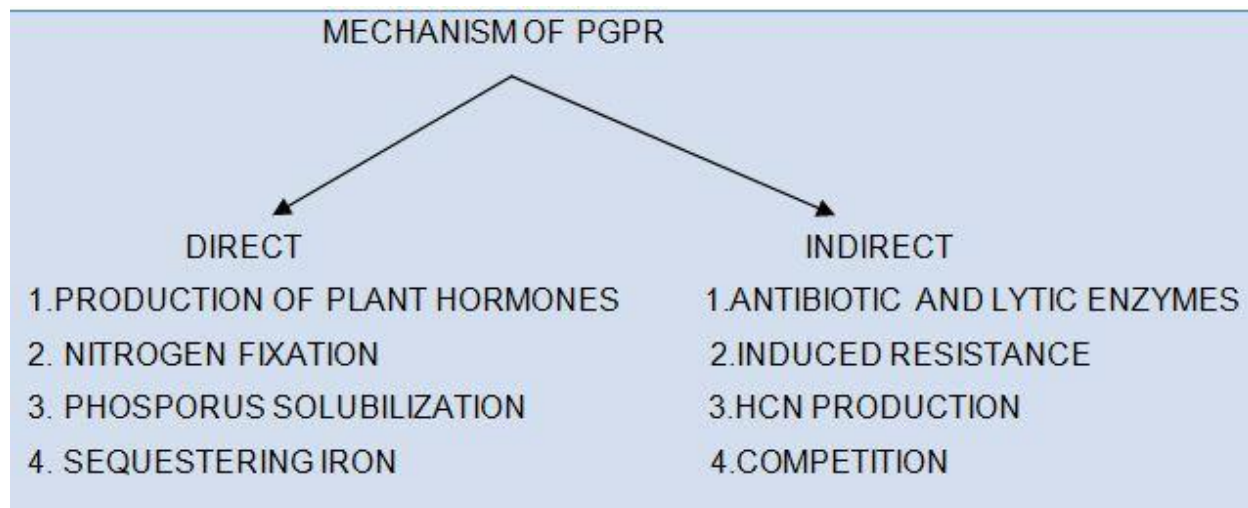
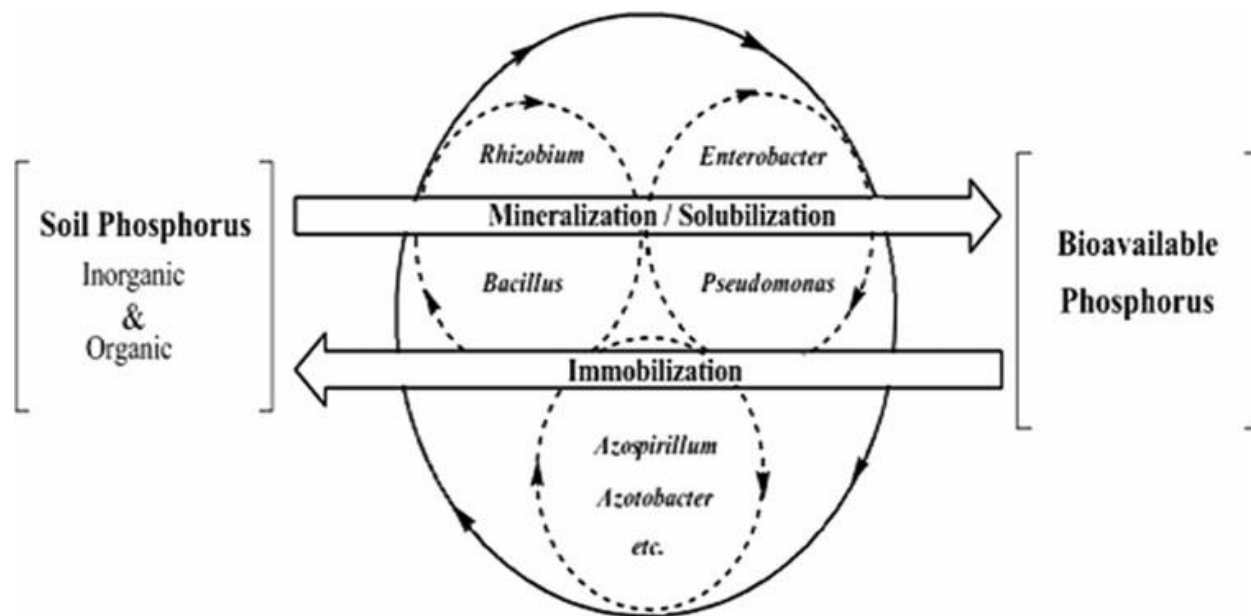


Fig.3 Solubilization of soil phosphorus by rhizobacteria (Khan *et al.*, 2009)



Though, PSB are commonly found in most soils; their establishment and performances are severely affected by environmental factors especially under stress conditions. Bacterial strains belonging to genera *Pseudomonas*, *Bacillus*, *Rhizobium*, *Burkholderia*, *Achromobacter*, *Agrobacterium*, *Micrococcus*, *Aerobacter*, *Flavobacterium* and *Erwinia* have the ability to solubilize insoluble inorganic phosphate compounds such as tricalcium phosphate, dicalcium phosphate, hydroxyl apatite and rock phosphate. Strains from genera *Pseudomonas*, *Bacillus* and *Rhizobium* are among the most powerful phosphate solubilizers (Satyavir *et al.*, 2009). The production of organic acids especially

gluconic acid seems to be the most frequent agent of mineral phosphate solubilization by bacteria such as *Pseudomonas* sp., *Erwinia herbicola*, *Pseudomonas cepacia* and *Burkholderia cepacia*. Another organic acid identified in strains with phosphate-solubilizing ability is 2- ketogluconic acid, which is present in *Rhizobium leguminosarum* (caroline *et al.*, 2013) and *Bacillus firmus*. Strains of *Bacillus* sp. were found to produce mixtures of lactic, isovaleric, isobutyric, and acetic acids (Satyavir *et al.*, 2009). Other organic acids, such as glycolic acid, oxalic acid, malonic acid, succinic acid, citric acid and propionic acid, have also been identified among phosphate solubilizers (Deepmalak *et al.*, 2016)

Indirect mechanism

Indirect mechanism involves the ability of PGPR to reduce the deleterious effects of plant pathogens on the growth. 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. Also different antibiotics are produced in response to proliferation of plant pathogens.

Production of antibiotics

Many PGPR have the ability to produce peptide antibiotics. These are oligopeptides that inhibit synthesis of pathogens cell walls, influence membrane structures of cells, and inhibit the formation of initiation complex on small subunit of ribosomes (Kundan *et al.*, 2015).

A variety of antibiotics have been identified, including compounds such as amphisin, 2,4 diacetylphloroglucinol, hydrogen cyanide, oomycin A, phenazine, pyoluteorin, pyrrolnitrin, tensin, tropolone, and cyclic lipopeptides produced by pseudomonads and oligomycin A, kanosamine, zwittermicin A, and xanthobaccin produced by *Bacillus*, *Streptomyces*, and *Stenotrophomonas* spp (Avinash *et al.*, 2016).

More than 12 antibiotics are synthesized by *B. subtilis* strains: bacillomycin, mycobacillin, fungistatin, iturin, phengicin, plipastatin, surfactin, bacilizin, etc. The majority of *Bacillus* sp. Antibiotics is active with both Gram positive and Gram negative bacteria (for example, polymyxin, circulin, and colistin) and pathogenic fungi *Alternaria solani*, *Aspergillus flavus*, *Botryosphaeria ribis*, *Colletotrichum gloeosporioides*, *Fusarium oxysporum*, *Helminthosporium maydis*, *Phomopsis gossypii*. Some studies reported an active influence of bacterial antibiotics in the regulation of defense system of the plant. It was revealed that *B. subtilis* surfacine is able to stimulate induced systemic resistance by activation of components like lipoxygenases, lipid peroxidases and the formation of reactive oxygen species (Satyavir *et al.*, 2009).

Secretion of lytic enzymes

Some bacteria, especially *Bacillus* and *Pseudomonas* sp. suppress growth and development of fungi both by secreting lytic enzymes such as chitinases and glucanases. Use of the bacteria producing chitinases to biological protection of crops from pathogens, especially

those that contain chitin and glucans within their cell wall structure, is the most prominent approach in the agriculture (Kundan *et al.*, 2015).

The production of lytic enzymes by rhizospheric bacteria involved in the control mechanisms against plant root pathogens including *Fusarium oxysporum* and *Rhizoctonia solani* (Nico *et al.*, 2010). Hydrolytic enzymes act as agents for prevention of plant diseases by causing lysis of deleterious microbes in the close vicinity of the plant as they secrete increased level of cell wall lytic enzymes (chitinases, glucanases and proteases) (Satyavir *et al.*, 2009). Some PGPR strains have been found to produce enzymes that can lyse fungal cell walls. Cell walls of most of the phytopathogenic fungi (except Oomycetes) are made up of chitin, which is a homopolymer of N-acetyl 21 glucosamine residues linked in P-1, 4 linkages. Chitinases which hydrolyse this polymer are produced by various organisms and have been implicated in the control of fungal diseases. Inactivation of genes involved in their biosynthesis has been used to provide evidence for their contribution in biocontrol in planta (Kundan, *et al.*, 2015). Other lytic enzymes from Proteobacteria target virulence factors, such as the phytotoxin fusaric acid produced by *F. oxysporum*, thereby enabling protection of tomato plants from wilt disease. The soil borne fluorescent *Pseudomonas* has received particular attention because of their capacity to produce a wide range of enzymes and metabolites. Antagonistic or biocontrol activity of fluorescent *Pseudomonas* may also be due to the production of different types of cell wall degrading enzymes like chitinase, protease/elastase and β -1,3glucanase. These enzymes are supposed to degrade the cell wall of various bacterial and fungal plant pathogens. Interestingly, some allelochemicals produced by PGPR are finding new uses as experimental pharmaceuticals, and this group of bacteria may offer a resource for compounds to deal with the alarming ascent of multidrug-resistant human pathogenic bacteria (Premachandra *et al.*, 2016).

Induced systemic response (ISR)

There is another mechanism called induced systemic resistance (ISR). This is the mechanism of increased resistance at particular sites of plants at which induction had occurred. The defense mechanism of ISR is activated only when there is an attack of pathogenic agent. ISR is not specific against particular pathogen but helps the plant to control diseases. ISR involves jasmonate and ethylene signaling within the plant and these hormones stimulate the host plant's defense responses to a range of

pathogens (Verhagen *et al.*, 2004). Another mechanism is the siderophore production which prevents plants from some pathogens to acquire adequate amount of iron and suppresses their ability to grow. It is reported that this mechanism is effective because of the siderophores produced by biocontrol PGPB that show a much greater affinity for iron as compared to fungal pathogens (Schipper *et al.*, 1987). Therefore the indirect mechanism seems to be beneficial both in terms of understanding the mechanism of biocontrol bacteria and use of bacterial strains instead of harmful chemical pesticides.

HCN production

The deleterious *Rhizobacteria* act as biocontrol agents of weeds that can colonize plant root surfaces and are able to suppress plant growth (Satyavir *et al.*, 2009). Cyanide being toxic is produced by most microorganisms including bacteria, algae, fungi and plants as a means of survival by competing with the counterparts. Generally there is no negative effect on the host plants by inoculation with cyanide-producing bacterial strains and host-specific *Rhizobacteria* can act as biological control agents.

Also the secondary metabolite produced, that acts as an effective agent for the biocontrol of pests, is HCN which is mostly synthesized by *Pseudomonas* and *Bacillus* species. HCN is likely to inhibit electron transport chain and energy supply to cell, leading to death of cells. It also seems that PGPR inhibit proper functioning of enzymes and natural receptors reversible mechanism of inhibition and also known to inhibit the action of cytochrome oxidase (Bhargavi *et al.*, 2016).

Competition

PGPR sometimes compete with the deleterious microbes for the nutrient which is present in trace amount and that can limit the disease causing agent. This can be explained when there are abundant non-pathogenic microbes in soil which would rapidly colonize the surfaces of plants and also utilize nutrient available and therefore inhibit the growth of pathogenic microbes.

These mechanisms are considered critical because they are difficult to study in the system but competition for the nutrient between PGPR and pathogens is considered the most important interaction that indirectly supports the growth stimulation of the plants by inhibiting the growth of pathogens (Stephane *et al.*, 2005).

Biological pesticides have been used in agriculture for many years. It is established that biological pesticides are ecofriendly, target-specific, easily biodegradable and safer alternatives. In this review, we have critically analyzed several advantages of bacterial pesticides over synthetic chemicals, including biosafety (safe for non-target organisms including human), eco-friendly (tendency to biodegrade), economic (low cost to develop) and good compatibility with IPM programs. Still, bacterial pesticides are not without critics. Drawbacks that might suggest further areas of research include limited product shelf life, unpredictable efficacy and short effective life in the field. Use of genetically modified organisms (GMO) is still controversial. When one makes crops resistant to an insect pest, this can potentially result in over-use of that pesticide. Incorporation of natural pest toxicants into the plant material might cause health-related problems. There is also concern about distributing genetic material to places where it does not occur naturally. Therefore, there is an ample scope of research for bacterial insecticide industry to face these challenges. The registrant community and the EPA, U.S. Department of agriculture, and U.S. Food and drug administration have developed high standards to ensure safety to man, animals, and the environment.

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