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Plant Growth Promoting Rhizobacteria: Mechanism and Current Prospective

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Abstract

Despite the phytotoxicity of olive-mill solid waste (OMSW) due to its high polyphenols content, OMSW have fertilizer characteristics, which make it a potential source for organic fertilization. Composting of OMSW treatment process was conducted in this study to eliminate the phytotoxicity and solve the environmental impact of this waste. Recycling of OMSW was carried out via composting of six batches of trials using equal proportions of OMSW, cow manure (C) and wheat straw (W). The treatment process was performed at two time intervals (two and five months), after each one, the recipient species (*Vicia faba* L.) was planted. The results showed the efficiency of composting in reducing OMSW original toxicity after two months than five months. The germination percentage and the plumule and radicle lengths of *V. faba* showed a significant improvement when the OMSW was composted with C at different proportions before using as soil amendments. Besides, the total biomass was noticeably increased at the high concentration of C-OMSW. Similarly, the total pigments concentration in *V. faba* was increased by using various composts after two months, where the highest pigment content was observed at 40% W-OMSW treatment.

The maximum uptake of potassium and sodium was recorded through the application of W-OMSW compost to soil after two months. Furthermore, the C-OMSW composts showed the highest concentration of nitrogen, calcium, iron and manganese. However, the C-W-OMSW composts recorded the highest concentration of phosphorous, magnesium and copper. Finally, this study developed a low cost treatment that will enable the growers to convert OMSW into a natural nontoxic compost rich with essential nutrients which have positive effects on plants growth.

Keywords: Plant growth promoting *Rhizobacteria*; Phytohormones; Biocontrol; Phosphate solubilization; Siderophore production

Introduction

Out of the world India has one of the richest and wide varieties of plant cultures. Ancient Indian literature incorporates a remarkably broad definition of plants and considers all plants and their products to be essential.

Today about 25% of modern pharmacopoeia are derived from plants. World Health Organization (WHO) estimated that about 80% of the developing country's population still relies on traditional medicines, mostly plant drugs, to help meet *their health care needs [1]*. Also there is an increase in the demand for plant products in both developing and developed countries because of several advantages such as no side effects, non-toxic, and affordable prices.

Plants provide raw material for industries producing pharmaceuticals, cosmetics, and fragrance flavor imparting biochemical. Therefore, there is an urgent need for conservation, sustainable utilization and management of plant genetic resources of the region so as to meet the growing requirements of food, fodder, fibre, health, water and other needs.

This led to the idea that bacteria present in the roots are beneficial for the growth of plants. Hiltner described for the first time that many microorganisms are attracted by nutrients exuded from plant roots and this effect is known as "rhizosphere effect" [2]. He observed higher numbers and activity of microorganisms in the vicinity of plant roots. From decades soil bacteria have been used for increasing the productivity.

The major role of these bacteria [3] are: (a) to supply nutrients to crops; (b) to stimulate plant growth, e.g., through the production of phytohormones; (c) to control or inhibit the activity of plantpathogens; (d) to improve soil structure; and (e) bioaccumulation or microbial leaching of inorganic compounds [4].

These microorganisms are found in association with the roots. The region of soil surrounding the roots which is highly active for the metabolism and is influenced by associated microorganisms is called rhizosphere. Hiltner introduced the concept of rhizosphere first to describe the narrow zone of soil surrounding the root where microbe populations are stimulated by root activities**.** However, the original concept has now been extended to include the soil surrounding a root in which physical, chemical and biological properties have been changed by root growth and activity**.**

Rhizosphere is the rich source of microbes and microbial activity and thus better known as store house of microbes. The rhizoshpere consists of large number of microorganisms mainly bacteria. These bacteria can be symbiotic or non-symbiotic on the basis that not only the plants get benefitted by their presence but bacteria also derive the nutrients for their survival.

Rhizomicrobiome can be referred as the corresponding microbial community associated with plant roots. Its composition differs from that of the microbial community of the surrounding soil, a direct

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consequence of bacterial competition for nutrients liberated in the vicinity of plant roots [5,6]. Since root exudate composition changes along the root system, according to stages of plant development and plant genotypes, the rhizomicrobiome composition differs accordingly [7].

A numbers of microorganisms that promote the growth of plants are found in the rhizosphere. Plants thus secrete several chemicals into the rhizoshpere and these chemicals allow the microorganisms to colonize the root. Microorganisms of the rhizosphere can be classified based on their effects on plants and the way they interact with roots. Some may be pathogenic whereas other may be beneficial.

Plant microbe interactions are symbiotic in which costs and benefits are shared by both of them [8]. Rhizoshpere mainly consists of bacteria termed rhizobacteria which by direct or indirect means exert a positive effect on plants [9]. These free living soil bacteria that colonize the root and benefit the plants by stimulating its growth are termed as PGPR (plant growth promoting rhizobacteria).

PGPR – plant growth promoting rhizobacteria

From the last few decades, PGPR have gained considerable interest in research because of stimulation of plant growth, increasing crop yields, being less harmful to the environment and also reducing the cost of chemical fertilizers. PGPR can also be termed as plant health promoting rhizobacteria (PHPR) or nodule promoting rhizobacteria (NPR). Based on their relationship with the plants, PGPR can be divided into two groups: symbiotic bacteria and free-living rhizobacteria [10].

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 (Figure 1).

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 [11]. 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 [12]. 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* [13].

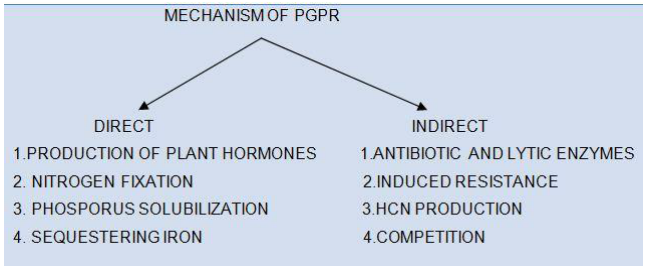

Figure 2: Mechanisms of PGPR used for plant growth promotion.

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 [14]. While this strategy is sometimes successful, rhizosphere microorganisms may also produce or modulate phytohormones under *in vitro* conditions. So that many PGPB can alter phytohormone levels and thereby affects the plant's hormonal balance and its response to stress [15].

Indole acetic acid: Indole-3-acetic acid (indole acetic acid, IAA) is one of the most common as well as the most studied auxins, and much of the scientific literature considers auxin and IAA to be interchangeable terms [16]. 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 [17]. The variation of IAA production among the PGPR was reported by Prakash and Karthikeyan, 2013 in which ten bacterial strains isolated from *Acoruscalamus*rhizospheric soil of Melaiyar and Nagapattinam districts in Tamil Nadu and were identified as *Azospirillum* spp., *Bacillus* spp., *Pseudomonas* spp., and *Azotobacter*spp [18]. These were tested for IAA production. The IAA production varied among them with Pseudomonas (94%), Azospirillumspp (80%), Azotobacter spp. (65%) and Bacillus spp. (40%). Similarly, Production of IAA by *Bacillus is* a general characteristic of rhizobacterial isolates [19].

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 [20]. Tryphtophan 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 (Figure 2). Thus tryptophan plays vital role in IAA production by negative feedback regulation.

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 (Figure 3). 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 (C_2H_4), influences many aspects of plant growth and development [21]. 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 [22]. 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. [23]

Cytokinins and gibberellins: 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.

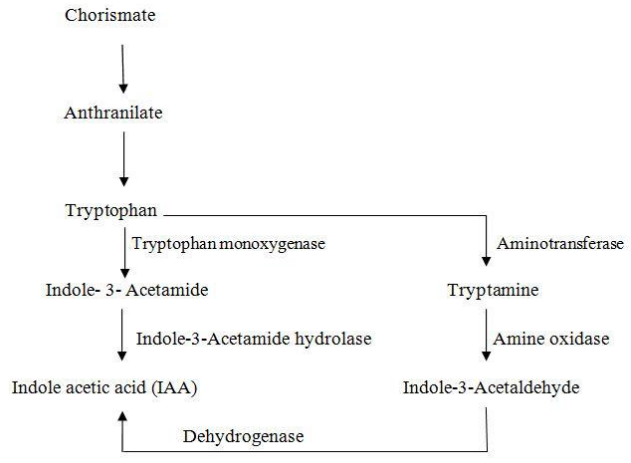

Figure 2: IAA synthesis by tryptophan dependent pathway.

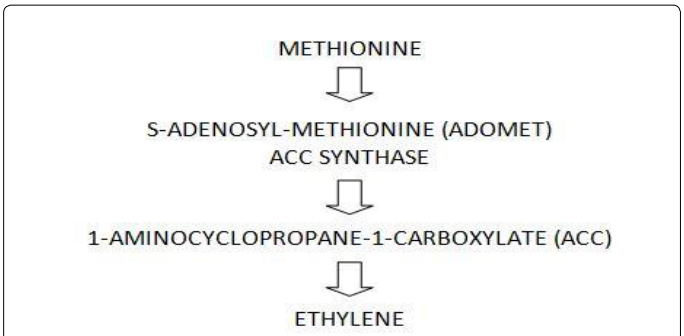

Figure 3: Formation of ethylene from methionine.

The cytokinin balance is influenced by the levels of other growth regulators, e.g. auxins [24] 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 [25]. 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 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 soil bacteria in general, and PGPB in particular, can produce either cytokinins or gibberellins or both [26].

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 [27]. The nitrogenase complex is a complex enzyme which carries out the process of N_2 fixation [28]. Structure of nitrogenase was elucidated [29] as a two-component metalloenzyme consisting of (i) dinitrogenasereductase which is an iron protein and (ii) dinitrogenase consists of a metal cofactor. Dinitrogenasereductase provides electrons with high reducing power while dinitrogenase utilizes these electrons to reduce N_2 to NH_3.

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.

Nitrogen fixers: A variety of bacterial species belonging to genera *Azospirillum*, *Alcaligenes*, *Arthrobacter*, *Acinetobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Pseudomonas*, *Rhizobium* and *Serratiacolonize* with the plant rhizosphere are able to exert many beneficial effects on plant growth [30].

Biological nitrogen fixation contributes about 180×10^6 metric tons/year of nitrogen globally, out of which symbiotic association produces 80% and the rest comes from free-living or associative systems [31].

The nitrogen fixers include symbiotic nitrogen fixers like *Rhizobium*. Inoculation of *Rhizobium* sp. causes a greater increase in growth and yield of the plant. Also the number of nodules per root system is significantly larger in plants inoculated with *Rhizobium* sp. than the plants without *Rhizobium* sp. under field condition [32]. Rhizobia also mobilize inorganic and organic phosphorus.

Both phosphate-solubilizing strains and the N_2-fixing bacterial strains have been found to have great ability of being formulated and used as biofertilizers [33].

It also includes non-symbiotic nitrogen fixers which have great economic significance. *Azoarcus*sp, *Gluconacetobacterdiazotrophicus*, *Herbaspirillium*sp, and *Azotobacter*sp are some of the important non-symbiotic nitrogen-fixing bacteria [34].

Azotobacter is a free living aerobic nitrogen fixer and has been reported to increase seed germination and growth of seedlings. Out of all most abundant species in the rhizoshpere is *Bacillus*. These strains release a number of metabolites [35] that strongly affect the environment by increasing nutrient availability to the plants.

*Bacillus subtilis*can maintain a stable contact with higher plants and can stimulate their growth whereas inoculation of *Bacillus licheniformis*on tomato and pepper shows considerable colonization that can be used as a biofertilizers without altering normal management in greenhouses [36].

Pseudomonas also acts an efficient PGPR and most important strain is fluorescent *Pseudomonas* species and increases yield if used in combination with biofertilizers. *Pseudomonas putida* is also considered beneficial in growth promotion. Different nitrogen fixing bacteria along with their relationship with their host plants are summarized in Table 1.

Phosphate solubilization

Phosphorus is another essential nutrient and plants need adequate amount of phosphorus for optimum growth. However, phosphorus is present mostly in insoluble forms and hence not able to support plants. Thus both in PGPB and plant growth-promoting fungi such as *mychorriza,* solubilization and mineralization of phosphorus by phosphate-solubilizing bacteria are an important trait [51]. The action of low molecular weight organic acids synthesized by various soil bacteria cause solubilization of inorganic phosphorus [52]. Conversely, the synthesis of a variety of different phosphorus, catalyzing the hydrolysis of phosphoric esters, causes mineralization of organic phosphorus (Figures 4 and 5). Importantly, both phosphate solubilization and mineralization can coexist in the same bacterial strain [53].

The microorganism mediated solubilization of insoluble phosphates is associated with the organic acids detachment which are often combined with other metabolites, as found in vitro, that the potential for phosphate solubilization by microorganisms is directly related to production of siderophores, lytic enzymes, and phytohormones [54].

Since most soils are poor in phosphorus and also phosphate fertilizer not affordable by farmers due to its high cost, this has led to the advantage of using soil microorganisms as inoculum for phosphate mobilization.

Phosphate solubilizing bacteria are beneficial bacteria capable of hydrolyzing insoluble inorganic phosphorus into soluble organic phosphorus which is absorbed as a nutrient by the plants (Figure 4). The most efficient phosphate solubilizing bacteria belong to genera *Bacillus, Rhizobium* and *Pseudomonas.*

Phosphate solublizing bacteria (PSB): The form of phosphorus that the plants needed the most for growth and development is present in the inorganic form and is made available to the plants by converting it into soluble form by PSB (phosphate solubilizing bacteria) and inoculating plants with PSB increases growth and yield directly. Among bacteria the most efficient PSM belong to genera *Bacillus, Rhizobium* and *Pseudomonas*. Within *Rhizobia*, two species nodulating chickpea, *Mesorhizobiumciceri*and *Mesorhizobiummediterraneum*, are known as good phosphate solubilizers [55].

Bacteria generally use two mechanisms to solubilize phosphate, i.e.: 1) by releasing organic acids and affecting the mobility of phosphorus by means of ionic interactions; and 2) by means of phosphatases that help to unbind the phosphate groups from organic matter. These mechanisms are mostly beneficial in basic soils. For the PGPR to be effective it must be introduced into the soils and sometimes it can be effective or sometimes completely inefficient due to the soil composition or variation in soils.

This knowledge of their mechanisms and ecology in the rhizosphere will play a vital role in their use in sustainable agriculture [56]**.** In addition to lowering the rhizospheric pH, PSB dissolves the soil phosphate through production of low molecular weight organic acids such as gluconic and ketogluconic acids [57]. The rhizospheric pH is lowered through biotic production of proton/bicarbonate release (anion/cation balance) and gaseous (O_2/CO_2) exchanges. Phosphorus

PGPR	Relationship	Host plant	References
Azospirillum sp.	Non-symbiotic	Rice, wheat, maize, sugarcane	[37–40]
Azotobacter sp.	Non-symbiotic (aerobic)	Paspalumnotatum grass, maize, wheat	[41–43]
Azoarcus sp.	Non-symbiotic (aerobic/microaerophillic	Kallar grass, sorghum	[44,45]
Acetobacter sp.	Non-symbiotic (obligatory aerobic)	Sugarcane	[46,47]
Rhizobium leguminosarum	Symbiotic (endosymbiotic)	Wheat, maize, barley	[48]
Bradyrhizobium betae	Symbiotic	Sugar beets	[49]
Bradyrhizobium japonicum	Symbiotic	Cowpeas, mungbeans, soybeans	[49]
Burkholderia sp.	Symbiotic (endo)	Rice	[50]

Table 1: Nitrogen fixing bacteria and their relationship with the host plants.

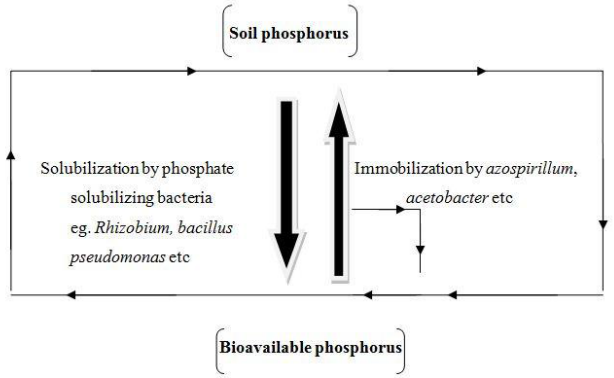

Figure 4: Solubilization of soil phosphorus by rhizobacteria.

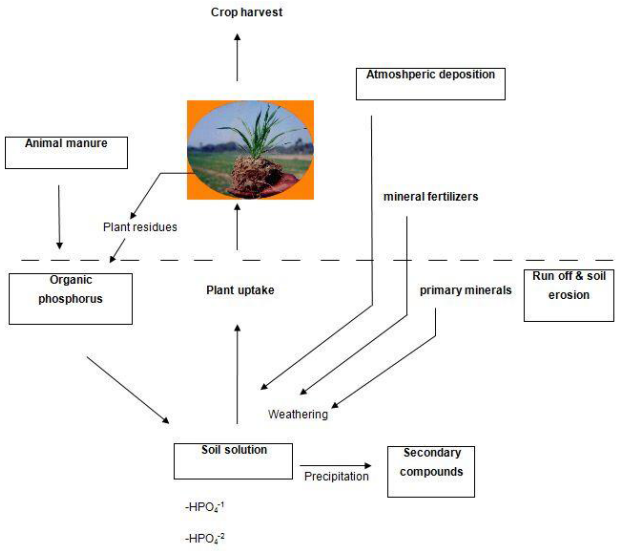

Figure 5: Phosphorus mobilization in soils.

solubilization ability of PSB has direct correlation with pH of the medium. Phosphate solubilizing bacteria and their host plants are summarized in Table 2.

Sequestering iron

Iron is one of the most abundant elements on the earth but still is not readily available to the plants because it is present as ferric ions which have very low solubility and are the predominant form of iron in nature. Plants require large amount of iron.

The microorganisms surviving under aerobic conditions also need iron for the essential purposes including heme formation and ATP synthesis. Some bacteria have developed iron uptake systems. These systems involve production of siderophores. Siderophores are microbial Fe-chelating low molecular weight compounds. Siderophores are released by microbes to scavenge iron from these mineral phases by the formation of soluble Fe^{3+} complexes that are taken up by active transport mechanisms but mechanism of siderophores is active only under low availability of iron.

Siderophores are usually stable complexes and can be of different types such as hydroxamates, phenolcatecholates and carboxylates. Siderophore mediated iron scavenging in gram negative transport is better studied PGPR than gram positive PGPR [65]. Till date there are about 500 known siderophores of which chemical structures of 270 of these compounds have been determined [66].

In case of stresses such as heavy metal pollution, siderophores help the plants to bear these stresses. Besides scavenging iron from the surrounding and making mineral availability to microbes, siderophores also have precious role in virulence mechanism in plants as well as animals as many pathogenic microbes are critical to sufficient iron supply.

The knowledge of mechanistic pathways of siderophores has helped in designing small molecule inhibitors that block siderophore biosynthesis and therefore bacterial growth and virulence in iron limiting environments.

Indirect mechanism

Antibiotic production and lytic enzymes

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. But excess dependence on antibiotic producing bacteria as biocontrol agent may be a disadvantage because of the resistance developed against specific antibiotics. The production of one or more antibiotics is the mechanism most commonly associated with the ability of plant growth promoting bacteria to act as antagonistic agents against phytopathogens [67].

The mechanism of antibiosis is to produce low molecular weight compounds that are deleterious and critical to major enzymes and metabolism of other microorganisms and thus retards the growth.

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 [68].

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 [69]. Therefore the indirect mechanism seems to be beneficial both in

PGPR	HOST PLANT	REFERNCES
Azotobacter chroococcum	Wheat	[58]
Bacillus circulans, Cladosporium herbarum	Mungbeans	[59]
Bradyrhizobium japonicum	Soybeans	[60]
Enterobacter agglomerans	Tomato	[61]
Pseudomonas chlororaphis, Pseudomonas putida	Soybeans	[62]
Rhizobium leguminosarum	Beans (*Phaseolus vulgaris*)	[63]
Bacillus megaterium	Tea	[64]

Table 2: Examples of phosphate solubilizing bacteria with their host plants.

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 [70].

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 weed control agents [71].

Also the secondary metabolite produced, that acts as an effective agent for the biocontrol of weeds, 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.

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. Some PGPR with their biocontrol properties are listed in Table 3.

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.

PGPR acts as a biofertilizers

Vessey (2003) defines biofertilizer as a substance which contains living microorganisms which, when applied to seed, plant surfaces, or soil colonizes the rhizosphere or the interior of the plant and promotes growth by increasing the supply or availability of primary nutrients to the host plant. Biofertilizers have a natural mechanism to supply nutrients to plants by solubilizing phosphorus, nitrogen fixation and by synthesis of plant growth promoting substances. There are microbes present in biofertilizers that increase the soil natural nutrient cycle and help in building soil organic matter and maintain the soil fertility. One of the preferred microorganism (bacteria) that has gained worldwide acceptance as beneficial bacteria is PGPR. Some bacteria are able to promote growth by acting as biofertlizers as well as biocontrol agents. The main advantage of using biofertilizer is being cheaper and safer than chemical pesticides.

Co-inoculation of plant with PGPR

In order to have beneficial effect on plants, it is essential to introduce PGPR into the soil. PGPR strains when inoculated with soil seem to have a positive effect on stimulation of growth. The means by which PGPR stimulates the growth is by acting as biofertilizer for growth promotion and biocontrol agent for controlling disease management.

Climatic variations also influence the effectiveness of PGPR but sometimes unfavorable growth conditions in the field are to be expected as normal functioning of agriculture. (*Azospirillium*, *Bacillus*, *Burkholderia*, *Klebsiella*, *Pseudomonas* have direct effect as PGP trait through phytohormones production, nitrogen fixation and phosphorus uptake. The first step of these bacteria in growth promotion is by colonizing the root. PGPR have a vital role in the host nodulation response [92].

Besides the direct effect, PGPR affect the plant by controlling pathogens which are mostly involved in competition and production of metabolites that affect the pathogen directly by siderophores production, lytic enzymes and antibiotics production and by induced

PGPR	Host plant	Pathogen	References
Actinobacteria	*Triticum aestivum*	*Aspergillus niger, Penicillium chrysogenum, Microsporum gypseum*	[72]
Bacillus, Brevibacillus, Lysinibacillus, Paenibacillus, Terribacillus and Jeotgalibacillus.	*Phyllanthus amarus*	*Corynespora cassiicola*	[73]
Bacillus amyloliquefacians	Bell pepper Tomato	*Myzus persicae sluzer* *Tomato mottle virus*	[74] [75]
Bacillus pumilus	Tobacco	*Blue mold*	[76]
Bacillus sp.	Cucumber Wheat	*Cotton aphids* *Gaeumannomyces graminis var. tritici, Rhizoctonia root rot*	[77] [78]
Bacillus subtilis and B. cereus	Wheat	*R. solani AG 8*	[79]
Bacillus subtilis G803	Pepper	*Myzus persicae*	[80]
Bacillus subtilis CE1	Maize	*Fusarium verticilloides*	[81]
Bacillus licheniformis	Pepper	*Myzus persicae*	[82]
Pseudomonas sp.	White clover Medicago Groundnut	*Acyrthosiphon kondoi* *Rhizoctonia bataticola*	[83] [84]
Pseudomonas chlororaphis	Sorghum	*Macrophomina phaseolina*	[85]
Pseudomonas fluorescens	Tobacco	*Tobacco necrosisvirus*	[86]
Pseudomonas fluorescens MKB 100 and MKB 249,	Wheat and barley	*Fusarium culmorum*	[87]
Pseudomonas aeruginosa	Mung bean	*Root rot*	[88]
Enterobacter sp.	Chickpea	*Fusarium avenaceum*	[89]
Azospirillum brasilense	*Prunus cerasifera* L.	*Rhizosphere fungi*	[90]
Paenibacillus polymyxa	Sesame	*Fungal E681 disease*	[91]

Table 3: PGPR with biocontrol properties against different pathogens in host plant.

systemic resistance. Induced systemic resistance (ISR) or systemic acquired resistance (SAR) is defined as the activation of chemical and physical defenses of the plant host by an inducer which could be a chemical or a microorganism, leading to the control of several pathogens [93].

Some PGPR may also support the growth by acting as an agent against stresses that are induced by biotic as well as abiotic factors. These stresses act as a barrier and result in low yield of plant. The yield losses from abiotic stresses are about 50–80%. Abiotic stresses include salinity, low and high temperature, drought and pollutants.

The most important is the salinity that reduces the capacity of photosynthesis. Therefore, introducing the PGPR beneficial strain into the soil or even treating the root, leaf or plant part with PGPR will have a positive effect on growth stimulation.

Challenges in selection and characterization of PGPR strains

The process of applying *Rhizobacteria* in soil and plant parts to eradicate bacterial and fungal pathogens was pioneered in Soviet Union in 1958 [94] even though the selection of efficacious PGPR strains during that time was highly complicated. Selecting the appropriate strain is essential so that the most beneficial bacteria are screened for the experiment to be successful. For this purpose effective strategies need to be considered. The strategy can be selecting the specific PGPR strain from thousands of root colonizing bacteria and testing their efficacy for plant growth promotion. The plant parts can be then treated with the selected strain for monitoring the effects. Recently, mass screening technique has been used for the selections of efficacious PGPR strains [95]. Here physiological, nutritional and biochemical characteristics as in Bergey's Manual of Determinative Bacteriology are used for primary screening of new isolates [96].

The host plant specificity or adaptation to a particular soil, climatic conditions or pathogen should be considered in selecting the isolation conditions, and screening assays [97].

Other approaches can be selected on the basis of traits like antibiotic production, siderophores production and root colonization. Selection of superior strains can be facilitated by the development of high throughput assay systems and effective bioassays [98].

Future prospects and challenges

PGPR is now considered as safe means of agriculture due to increasing yield as it holds promising solution in being safe for the environment. The most important is to protect plants from chemicals that are used to kill pests and also cause harmful impact on the ecosystem. PGPR can also affect yield by controlling plants diseases and pests as diseases are responsible for one third of plant losses. PGPR seems to have beneficial effect on laboratory as well as greenhouse experiment. An emerging field to improve and explore the PGPR strain is by genetic engineering which enables to over-express the traits so that strains with required characters are obtained. Besides all the advancements there are environmental barriers and adverse conditions that influence the activity of PGPR. The problems of varying efficacy can be attained by strain mixing, improved inoculation techniques, or gene transfer of active genetic source of antagonists to the host plant**.** Diverse conditions can also affect PGPR as biocontrol because biocontrol agents need similar ecological niche for growth and survival. Hence under diverse environmental conditions the efficacy of biocontrol agents could be improved through the usage of compatible mixed inoculum of biocontrol agents which could have a consistent performance [99]. Besides being beneficial there are several challenges faced by PGPR. The natural variation is an issue because it is difficult to predict how bacteria will act in laboratory and when placed in field. These variations can be sudden and affect the whole experiment. Another challenge is that under field conditions PGPR need to be propagated to regain their viability and biological activity. This propagation can be according to the plant type and could be seasonal. The challenge could be in terms of working place that should be highly sterile and appropriate tools should be used because isolating and characterizing PGPR in vitro seem not be easy.

Conclusion

The use of bacterial fertilizers has made significant improvement in terms of growth, health and yield of plants. The mechanism by which PGPR stimulates can be direct or indirect. PGPR also support growth by reducing the phytopathogens which reduce the yield and growth. The outcome of PGPR inoculation is greatly influenced by plant age and by the chemical, physical and biological properties of the soil. There are several challenges for using PGPR such as natural variation but by the virtue of advance techniques and applying biotechnology can overcome the challenges faced by PGPR. Hence future prospects can be replacement of chemical fertilizers and supporting the ecosystem in terms of safety. Further understanding of the complete mechanism of PGPR could help in obtaining more specific strain that will be able to work under more adverse and varying conditions.

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