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Plant Growth Promoting Rhizobacteria A review

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ABSTRACT

Abstract : *Plant Growth Promoting Rhizobacteria (PGPR) are the rhizospheric bacteria that can affect positively plant growth by several mechanisms like phosphate solubilization, siderophore production, biological nitrogen fixation, production of 1-Aminocyclopropane-1-carboxylate deaminase (ACC), quorum sensing (QS) signal interference and inhibition of biofilm formation, phytohormone production, exhibiting antimicrobial activity, induction of systemic resistance (ISR), promoting beneficial plant-microbe symbioses, and many others mechanismms. It is the biological way to replace the use of chemical fertilizers, pesticides in agriculture practices. The PGPR strains present a high taxonomic and metabolic diversity. This review synthesizes the different aspects of PGPR studies, from their applications to the stress tolerance, via the different modes of action.*

I. Introduction

The rhizosphere is a narrow area adjacent to the plant roots and influenced by strong microbial activity in the soil, in and around the roots [1,2] affecting plant growth [3,4]. "Strictly speaking, the rhizosphere is the region of the soil under the root influence............It is the fabulous place where organisms communicate with each other by exchanging signal molecules (especially quorum sensing) and/or growth molecules (simple metabolites, hormones,...), or even toxic molecules and others" this is how Gobat and his collaborators [5] described the rhizosphere.

In this same perspective, a considerable number of studies have focused on the beneficial effects of bacterial species that colonize the rhizosphere of many plant species. They have proven their beneficial effects on plant growth, yield and productivity as well as their role in reducing their susceptibility to diseases caused by plant pathogens, fungi, viruses and nematodes and even against abiotic stresses [6]. These activities result from the synthesis of metabolites such as antibiotics, siderophors, growth promoters, hydrocyanic acid, lipopolysaccharides [7,8]. These bacteria have been called "Plant Growth Promoting Rhizobacteria" (PGPR) [9,10]. In this regard, the number of bacterial species identified as PGPRs has recently increased due to numerous studies of a wider range of plant species, advances in bacterial taxonomy, and advances in understanding the different mechanisms of action of these rhizobacteria. Consequently, PGPRs include a wide variety of bacterial taxa, including species of the genera *Pseudomonas, Azospirillum, Azotobacter, Klebsiella, Enterobacter, Alcaligenes, Arthobacter, Burkholderia, Pantoea, Bacillus, Serratia* and *Rhizobium* have shown an ability to improve plant growth [4,11,12].

This review is a modest contribution to highlight the importance of PGPRs for the health, growth and proper development of the plant. Indeed, this work synthesizes the main data on these original bacteria through their functioning, diversity and application.

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II. Rhizobacteria Promoting Plant Growth

In recent decades, a very large number of rhizobacteria have shown an ability to improve plant growth [11,13]. The latter are often mentioned as rhizobacteria promoting plant growth (Plant Growth Promoting Rhizobacteria: PGPR) [14,15] and are associated with the root surfaces of many plants [16]. Kloepper and Schroth [17] first used this expression specifically for *Pseudomonas fluorescens* strains. The PGPR include symbionts, those that form a symbiotic relationship, which involves the formation of specialized structures or nodules on the roots of host plants and free saprophytes, those that live freely in the soil; the latter are often found near, on or even inside the roots of plants [14]. On the other hand, non-symbiotic rhizobacteria with the ability to colonize intensively roots belong to different genera and species of which the most studied are *Agrobacterium radiobacter, Azospirillum spp, Bacillus spp, Pseudomonas spp.* fluorescent lamps [18].

Consequently, these rhizobacteria can directly stimulate plant growth by increasing the removal of soil nutrients such as atmospheric nitrogen fixation, minerals solubilization of phosphorus and iron, production of siderophors and enzymes, inducing and producing plant growth regulators and activating induced resistance mechanisms in plants. Therefore, they indirectly stimulate plant growth through their antagonistic effect on harmful microflora by transforming toxic metabolites and through the production of antibiotics or hydrogen cyanide, competition for nutrients, production of extracellular enzymes [11,19,20,21,22,23]. Cerains species are well known such as: *Pseudomonas, Bacillus, Azospirillum, Rhizobium* and *Serratia*. Indeed, Amir et al [24] concluded that the application of bacterial inoculations significantly improves the absorption of the plant's main mineral nutrients (NPK). In addition, the inoculation process with *Azospirillum* and *Bacillus spp.* showed a clear accumulation of these minerals in the plant tissues. Furthermore, Bashan and Holguin [25] suggested that bacteria with both PGP and protective effects could be reclassified into a single category: Biocontrol of Plant Growth Promoting Rhizobacteria (PGPR Biocontrol). Moreover, several studies have highlighted the phytobeneficial effect of rhizobacteria in plants under abiotic stress. Some bacterial species have a real potential to improve plant growth under stressful conditions, by reducing ethylene production through deaminase ACC activity [26] in *Solanum tuberosum* through induction of changes in ROS antioxidant enzyme expression and improved photosynthesis [27]. Under water deficit conditions, Pseudomonas fluorescens improves *Ajmalicin* growth and production in *Catharanthus roseus* [28].

On the other hand, the diversity and composition of bacterial taxa in the rhizosphere can be affected by several factors, including plant type, soil type, soil management practices and microbial interactions [29,30]. Hence, Gram positive PGPR include coryneform bacteria, *Bacillus cereus, B.circulans, B.subtilis, B. spp,* while Gram negative PGPR include fluorescent and non-fluorescent Pseudomonas and various members of the Enterobacteriaceae family [31].They belong mainly to the following four phyla: Proteobacteries, Firmicutes, Actinobacteries and Bacteroidetes [32].

III. Applications of PGPR

III.1. Biological nitrogen fixation

The biological fixation of molecular nitrogen (N_2) by rhizobacteria appears among one of the most important mechanisms of plant association with its microbiota. Moreover, N_2-binding bacteria are called "diazotrophs" and are classified as both symbiotic (*Rhizobia* and *Frankia* species) or as free endophyte (associative) and/or root endophyte microorganisms [33] such as *Azotobacter, Acetobacter, and Azospirillum* …etc. Therefore, *Azospirillum* was originally selected for its ability to fix atmospheric nitrogen (N_2), and since the mid-1970s, it has consistently been a very promising PGPR [34].

III.2. PGPR in HCN production

The production of volatile inhibitory substances can increase the survival rate of bacteria in soil, eliminating potential competitors for nutrients [35]. Bacteria of *Pseudomonas* genus emit some volatile compounds, such as hydrogen cyanide (HCN). They have antibiotic effects, and play a role in protecting the host plant [7]. HCN is a broad-spectrum antimicrobial compound involved in the biological control of root diseases [36]. This element accompanied by CO_2 is formed from glycine [37].

III.3. Plant growth producers

PGPR are considered as plant growth regulators or phytohormone producers. In fact, the Indol-Acetic-Acid (IAA) is the largest class of the auxins family [38]. The role of bacterial IAA in stimulating plant growth and in phytopathogenesis has already been reported [39]. Loper and Schroth [40] were able to demonstrate that bacterial IAA secreted in the rhizosphere could influence the root elongation of sugar beet. In addition, IAA and its active analogues in most plants synthesized from tryptophan as the major precursor of which root exudates are the major sources in soil [39]. Moreover, certains PGPR are capable of stimulating plant growth by directly lowering plant ethylene levels through the action of

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1-aminocyclopropane-1-carboxylic acid (ACC) deaminase [41], which is involved in plant growth enhancement [42]. This enzyme can cleave the precursor of ethylene ACC and thus reduce the level of ethylene in the plant.

III.4. Production of siderophore

Iron is an essetial mineral growth element for plants. Therefore, Fe^{3+} must first be reduced to Fe^{2+} before being absorbed by the plant. Once Fe^{3+} chelated at the root surface, the phytosiderophore-Fe complex is directly assimilated [43]. The plants capture these bacterial complexes and the latter can play a significant role in nutrition and growth [41]. In addition, this mechanism is involved in PGPR biocontrol activities and is linked to competitive effects with phytopathogens and other harmful microorganisms in the rhizosphere [44].

III.5. Phosphates Solubilizing Bacteria (PSB)

Phosphorus is an indispensable and irreplaceable element for the vital needs of plants. The microbial processes mediated largely the organic phosphorus mineralization in soil (Figure 1), so microorganisms play an important role in maintaining phosphorus availability [41]. In agricultural soils, the inorganic phosphates solubilization related closely to soil microorganisms' activity. Therefore, phosphate solubilizing microorganisms (PSM) are characterized by their ability to solubilize precipitated forms of phosphorus when grown invitro and include a wide range of symbiotic and non-symbiotic organisms [41]. Several growth promoting rhizobacteria such as Rhizobia, *Pseudomonas* and *Bacillu*s have been described as phosphate solubilizing bacteria (PSB) [45]. The beneficial effects of inoculating cultures with these phosphate solubilizing microorganisms have been described by several authors [46,47,48]. In addition, phosphatases are necessary for hydrolysis (mineralization) of organic phosphorus and, in bulk soil; microbial mineralization of organic phosphorus contributes significantly to its availability for plants [49].

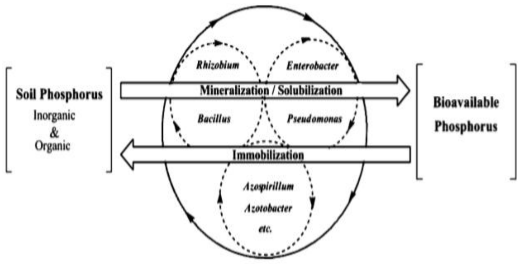

Figure 1. *Schematic diagram of mineralization, solubilization and immobilization of phosphorus by rhizobacteria [50]*

III.6. Biocontrol Agents

Certain rhizobacteria are capable of controlling plant diseases caused by soil pathogens [51]. The different mechanisms of biocontrol (Figure 2) include the secretion of extracellular metabolites such as hydrogen cyanide, siderophors, antibiotics, hydrolytic enzymes and/or competition for nutrients [23,51,52,53]. The first biocontrol mechanism exercised by PGPR involves the production of anibiotics, such as phenazine 1-carboxylic acid, 2,4-Diacetyl phloroglucinol, oomycin, pyoluteorin, pyrrolnitrin, kanosamine, zwittermycin A and pantocin [23].

In the same perspective, soil microorganisms compete for nutrients and energy sources [15]. The main competitive mechanisms of PGPRs are their ability to absorb and destroy nutrients in roots [54,55], to colonize the largest area on the root [56], to destroy pathogenic fungi by the action of lytic enzymes (e.g. chitinase) that degrade the fungal cell wall [11,13]. Moreover, the rhizobacteria ability to inhibit the germination of fungal spores in soil characterized competition for nutrients, including carbon [59] while competition for iron occurs in siderophore production [57]. Indeed, this competition appears as a very important mode of action for bacteria and fungi in biological control [58,59].

III.7. Antifungal activity

PGPR antifungal activity against phytopathogenic fungi have been reviewed (Table 1). Several bacterial species can produces a range of enzymes (chitinase, glucanase, lipase and protease) such as *Myxobacteria*, capable of inhibiting invitro growth of *Maghnaporthe poae* [60]. In addition, the lytic ability of *Serratia marcescens* and *Lysobacter* played a role in the control of phytopathogenic fungi: *Sclerotium rolfsii*, *Bipolaris* and *Pythium sp*, phytopathogenic fungi [61,62]. Moreover, *Pseudomonas* have strong antifungal activity against *Pyricularia oryzae* and *Rhizoctonia solani* mainly through the production of antifungal metabolites. For example, *Pseudomonas stutzeri* produces extracellular chitinase and laminarinase that lyses the mycelium of *Fusarium solani* [63].

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Table 1. *Antifungal activity of PGPR strains*

Bacterial strains	Target fungi	Plant affected	Author
Fluorescents Pseudomonads	*Rhizoctonia solani*	Bean	Ahmadzadeh and Tehrani [64]
Fluorescents Pseudomonads	*Thielaviopsis basicola*	Tobacco	Stutz et al [65]
Azospirillum, Azotobacter	*Rhizoctonia solani*	Wheat	Fatima et al [66]
Peudomonas fluorescens	*Gaeumannomyces graminis*	Wheat	Tomashow and Weller [67]
Burkholderia cepacia	*Fusarium oxysporum and F. culmorum*	Potato	Recep et al [68]

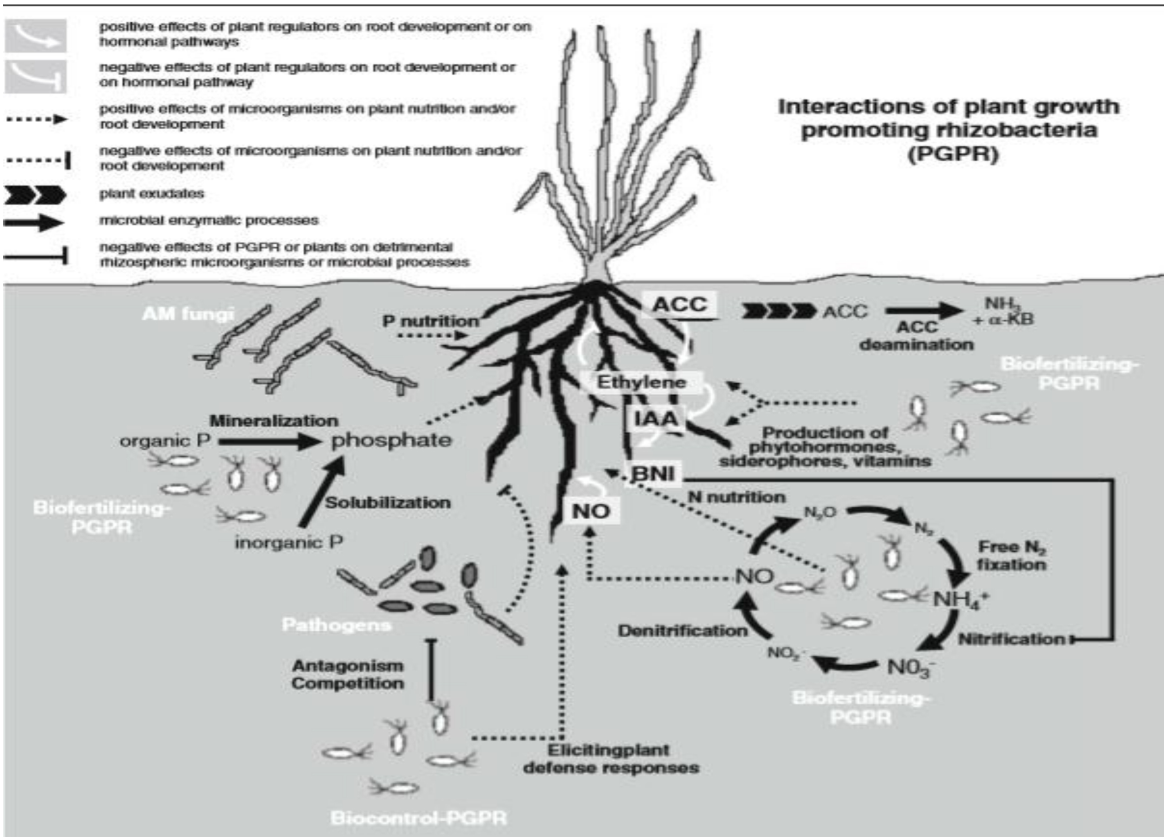

Figure 2. *Mechanisms for promoting plant growth (positive and negative effects) associated with soil and rhizosphere microorganisms. Biofertilizer-PGPR and arbuscular mycorrhizal (AM) fungi stimulate plant nutrition by directly increasing the supply of nutrients to plants (e.g. by nitrogen fixation, solubilization and/or mineralization of P, vitamin and siderophora production) or by increasing plant access to nutrients by increasing root volume. Root growth promotion is related to the ability of the PGPR to produce phytohormones (e.g., IAA, ethylene, NO) or by direct influences on plant hormone levels (e.g., deamination of the ACC precursor to plant ethylene). Biocontrol-PGPR improves plant health by inhibiting plant pathogen growth or eliciting plant defence responses [41].*

IV. PGPR action under stressed conditions

Changes in the environmental state of the rhizosphere can affect survival and activities PGPR. To this end, physiological approaches are an essential step to study PGPR activities and species identification.

IV.1. Tolerance to pHs

Soil pH plays a major role in the survival and prosperity of rhizobacteria, and therefore in the growth of their host plant. However, acidity is generally more harmful than alkalinity [69]. The rhizosphere acidification by exudation of organic acids from the root also plays a central role in determining the surrounding population [70]. A pH below 5.5 may result in a decrease in major macronutrients and an increase in the concentration and activity of micronutrients such as manganese, iron and aluminum, resulting in phytotoxic effects on plant roots and beneficial microorganisms [71]. Therefore, tolerance to pHs could be a distinguishing parameter between species such as the genus *Burkholderia* whose *B. brasilensis* grows at a pH

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between 4 and 6, and *B. tropica* grows at a pH above 5 [72].

IV.2. Temperature tolerance

Several studies have examined the tolerance of PGPRs to a temperature range [73,74]. Invitro seeds and soil treatment with *Pseudomonas fluorescens, P. fluorescens, Bacillus megaterium* and *Paenibacillus macerans* reported to suppress fusarium wilt in chickpeas (*Cicer arietinum*) by *Fusarium oxysporum* f. *sp. ciceris* occurred at optimal temperatures for bacterial growth and production of inhibitory metabolites [75]. Moreover, co-inoculation of rhizobacteria promoting plant growth (PGPR) with *Bradyrhizobium* increased legume nodulation and nitrogen fixation at optimal soil temperatures [76].

IV.3. Tolerance to salinity

Like acidity, saline soils are an unfavourable environment for the growth of most plants and their endophytic bacteria. Unlike their host plants, symbiotic and associative endophytes can tolerate and survive under important soil salinity [77]. The bacteria adaptation to high salt concentrations is due to their ability to synthesize and accumulate compatible intracellular solutions. These solutions have an osmoregulating and protecting potential against the saline stress effects. Therefore, the main solutes found in bacteria are: K^+ ion, glycine, betaine, proline, glutamate, various carbohydrates and N-acetylglutaminyl-glutamine amide [78,79].

IV.4. Intrinsic resistance to antibiotics

Intrinsic antibiotic resistance is a very important marker for identifying a newly introduced bacterial strain in a given soil [80]. Antibiotic tolerance depends on the bacteria strain, type and concentration of antibiotic in the medium [81]. On the other hand, various strains belonging to *Burkholderia*, including *B.vietnamiensis* isolated from the rice rhizosphere, and species belonging to *Rhizobium sp*. have shown resistance to different types of antibiotics [82, 83].

IV.5. Intrinsic resistance to heavy metals

Some metals are essential for biological functions, such as growth, reproduction and survival, while others have no known biological function [84]. Therefore, the toxicity of heavy metals depends on their concentration in the soil, their nature, the presence of other metals and the affected organism type. Moreover, Excess manganese reported to alter the exopolysaccharides composition in *Sinorhizobium meliloti* [85]. The selection of resistant strains to heavy metals would be of paramount importance for field inoculation.

V. Mechanisms shown by PGPR

PGPRs are classified into tow categories (Figure 3) according to their mode of action. The first ones are the so-called phytoprotective bacteria that can protect the plant against pathogenic microorganisms via antibiotic synthesis and resistance induction (Biocontrol). The second group are the phytobeneficial bacteria that improve plant growth through phytohormone synthesis (phytostimulation) and mineral nutrition improvement (biofertilistaion). However, growth promotion and biological disease control should be considered as two sides of the same coin [15].

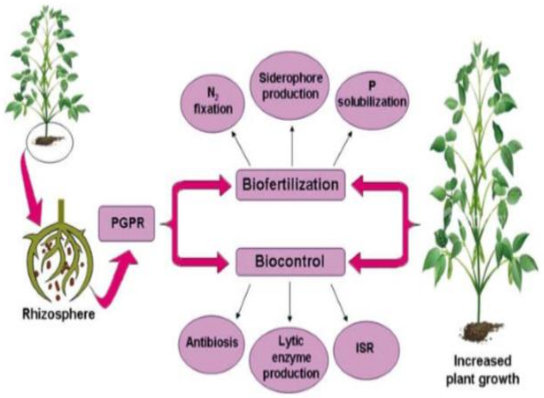

Figure 3. *Promotion of plant growth by Rhizobacteria [86].*

V.1. Phytostimulation

Phytohormones can be produced by PGPR that can stimulate plant development by affecting elongation, cell division and differentiation. In addition, they play a very important role in the plant's response to biotic and abiotic stresses [51]. Some bacteria can produce auxin such as *Azospirillum, Pseudomonas, Xanhomonas, Rhizobium*, including *Alcaligens feacalis, Enterobacter cloacae, Acetobacter diazotrophicus* and *Bradyrhizobium japonicum* [39]. In addition to auxin, *Azospirillum* can synthesize cytokinin [87] and gibberillin [88].

V.2. Biofertilisation

PGPRs used as biofertilizers are a promising alternative to chemical fertilizers application and environmental-friendly and lower costly. PGPRs facilitate removal and improve plant nutrient availability through siderophore production, nitrogen fixation, phopshates solubilization, in order to proved essential mineral nutients in the soil to plant growth.

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V.3. Improvement of plant resistance

Plant resistance to pathogens is mainly due to two signalling pathways. The first is Acquired Systemic Resistance (SAR) whose signal molecule is salicylic acid. Therefore, the plant infected responds to pathogen (virus, bacteria or fungus) by increasing salicylic acid production at the infection site as well as in the entire plant. In some plant/pathogenic models, salicylic acid, exogenously supplied by *fluorescent Pseudomonas*, has provided protection against pathogens [89]. The second plant defence pathway involves jasmonate as a signal molecule and is the Systemic Resistance Induction (SRI). This mechanism can be activated by certain non-pathogenic rhizospheric bacteria mainly by the presence of determinants embedded in their wall and synthesize diffusible molecules that are perceived by the plant and induce a resistance mechanism [90].

VI.Conclusion

The PGPR diversity in the rhizosphere along with their colonization ability of wide range of cultivated plants and mechanism of action should facilitate their application as a reliable component in the management of sustainble agricultural system. Therefore, due to their physiological approach, PGPR could be introduced on marginal, arid and/or saline soils.

Abbreviations

ACC: 1-aminocyclopropane-1-carboxylic acid, HCN: hydrogen cyanide, IAA: Indole-Acetic-Acid, ISR: Systemic Resistance Induction, NPK: nitrogen phosphorus potassium PGPR: Plant Growth Promoting Rhizobacteria, PSB: Phosphate solubilizing bacteria**,** PSM: Phosphate solubilizing microorganisms, ROS: Reactive oxygen species, SAR: Acquired Systemic Resistance.

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