



Communication of Plant Growth Promoting Rhizobacteria in Agricultural Sustainability: An overview

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ABSTRACT

Microorganisms in the soil are commonly associated with every plant tissue. Plants control the physical and chemical composition of the soil which can affect colonization capacity of plant growth promoting rhizobacteria (PGPR). The degree of plant influence over the microbial community is highest nearer the root surface. This zone is now generally referred to as a rhizosphere. Rhizosphere soil is normally a moist environment but contains high amount of reduced carbon which supports the growth of these microbes. Plants protect endophytic bacteria from the environment that can colonize and establish plantations. In return, microbes in the soil promote plant growth through nitrogen fixation, phytohormone production, nutrient acquisition (solubilization of minerals, absorption of iron by production of siderophores), the production of antimicrobial substances to lessen or prevent the deleterious effects of phytopathogens on plants, phytoremediation, protection of plants by induced systemic resistance, production of natural products, and by conferring tolerance to various environmental stresses. These mechanisms can increase crop tolerance for the abiotic stresses such as drought, heat and salinity that become more frequent as changes in the climate continue to develop. This review is an update about the potential activities of microorganisms in the rhizosphere of various plant species. It also provides an overview of the endophytic bacteria associated with various plants and benefits that host plants derive from them.

Keywords: Rhizobacteria, endophytes, phytohormones, biocontrol agents, tolerance.

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INTRODUCTION

PGPR and their host relationships can be classified into two levels of complexity: i) rhizospheric and ii) endophytic. Rhizosphere is the layer of soil under the influence of root exudate, is much richer in bacteria than the surrounding bulk soil. Studies based on culture-independent molecular analysis have found over 4,000 microbial species per gram of soil [1]. In rhizospheric relationships, PGPR can colonize the rhizosphere, root surface, or even superficial intercellular spaces. By definition, plants can alter the physical and chemical composition of the soil, affecting the ability of PGPR to colonize the rhizosphere. In many rhizospheric relationships, PGPR remains attached to the plant surface.

The term endophyte was first coined by De Bary in 1866 [2]. Endophytes are bacterial or fungal microorganisms that spend all or part of their life cycle within healthy tissue inside host plant and show no external signs of host infection or adverse effects on their host [3]. In an endophytic relationship, PGPR is actually located in the apoplastic space within the host plant. There is some evidence that endophytes occupy intracellular spaces, but these reports are rare. Depending on the host plant and the endophyte, PGPR can be found in all plant parts: seeds, roots, stems, leaves, fruits, etc. [4, 5]. There is evidence that endophytes reside in apoplastic intercellular spaces within the parenchyma tissue [6]. Several endophyte species are usually associated with a single plant, and at least one of these exhibits host specificity. There are about 300,000 species of plants in the world, each one hosts several to hundreds of endophytes generating enormous biodiversity [7]. The endophytic niche provides protection from the environment for bacteria that can colonize and establish *in planta*. These bacteria generally colonize the intercellular spaces and are isolated from all plant compartments, including seeds [8]. Endophytic bacteria have been

isolated from both monocotyledonous and dicotyledonous plants, ranging from woody tree species such as oak and pear to herbaceous crops such as sugar beet and maize [9].

PGPR is now commercialized as a novel inoculum to promote plant growth through direct and indirect mechanisms. The direct growth-promoting mechanisms are [10] nitrogen fixation, [11] increased nutrient availability in the rhizosphere (mineral solubilization, iron uptake through siderophores production), and [12] production of phytohormones such as auxins, cytokinins and gibberellins [13]. Indirect mechanisms of plant growth promotion include the production of antimicrobials substances to reduce or prevent the detrimental effects of plant pathogens on plants or to enhance host natural resistance [14]. Indirect mechanisms of plant growth promotion are (1) biocontrol agents (2) competition for sites on roots and displacement of plant pathogens (3) induced systemic resistance (4) production of natural products (5) tolerance under stress conditions [15]. Along with the production of novel chemicals, many endophytes have displayed a natural ability of xenobiotic degradation. This natural ability of xenobiotics degradation has been studied for improving phytoremediation [16].

CHARACTERISTICS AND APPLICATIONS OF PGPR

Biological nitrogen fixation

Biological nitrogen fixation (BNF) is a biological process in which nitrogen is converted to ammonia by nitrogen fixing microorganisms with the help of nitrogenase enzyme. BNF is estimated to contribute 180×10^6 metric tonnes/year globally, of which 80% comes from symbiotic associations and the rest from free-living or associative systems [17]. These include symbiotic nitrogen fixing (N_2 -fixing) forms, viz. *Rhizobium*, the obligate symbionts in leguminous plants and *Frankia* in non-leguminous trees, and non-symbiotic N_2 -fixing forms like cyanobacteria, *Azospirillum*, *Azotobacter*, *Acetobacter diazotrophicus*, *Azoarcus* etc [18]. *Frankia* forms root nodules on more than 280 species of woody plants from 8 different families. However, its symbiotic relationship is not well understood [19]. The most studied and longest exploited PGPR are the rhizobia for their ability of N_2 fixation in legume hosts. Sahgal and Johri (2003) outlined the status of rhizobial taxonomy and enlisted 36 species distributed among seven genera such as *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Methylobacterium*, *Rhizobium* and *Sinorhizobium*. Non-symbiotic N_2 fixation has a great agronomic significance [20]. One main limitation is the requirement of carbon and energy source for the energy intensive nitrogen fixation process. However, this limitation can be compensated by moving closer to or inside the plants viz., in diazotrophs present in rhizosphere, rhizoplane or those growing endophytically. Some important non-symbiotic nitrogen-fixing bacteria include *Azoarcus* sp., *Gluconacetobacter diazotrophicus*, *Herbaspirillum* sp., *Azotobacter* sp., *Achromobacter*, *Acetobacter*, *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Azomonas*, *Bacillus*, *Beijerinckia*, *Clostridium*, *Corynebacterium*, *Derxia*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, *Rhodospirillum*, *Rhodopseudomonas* and *Xanthobacter* [21, 22].

2. Solubilization of minerals

Next to nitrogen, phosphorus is essential element for plant productivity. Plants have the ability to absorb phosphorus in two soluble forms, the monobasic ($H_2PO_4^-$) and the dibasic (HPO_4^{2-}) ions [23]. Soil pH is more than 7.5 and at this pH, very low amount (3-10 mg/kg) of phosphorus is in available form. A survey of Indian soils revealed that 98% of this need phosphorus fertilization either in the form of chemical or biological fertilizer [24]. The solubilization of phosphate in the rhizosphere is the most common mode of action implicated in PGPR that increase nutrient availability to host plants [64]. The most efficient phosphate solubilizing microorganism (PSM) belong to genera *Azotobacter*, *Enterobacter*, *Bacillus*, *Rhizobium* and *Pseudomonas* amongst bacteria, and *Aspergillus*, *Cladosporium* and *Penicillium* amongst fungi. Within rhizobia, two species nodulating chickpea, *Mesorhizobium ciceri* and *Mesorhizobium mediterraneum*, are well-known as good phosphate solubilizers [25].

Many rhizobacteria and rhizofungi are able to solubilize phosphate by secreting organic acids [26]. PSM have been identified, but their effectiveness in the soil-plant system is still unclear. The application of PSM and PGPR together can reduce phosphate application by 50% without any significant reduction of grain yield in corn, *Zea mays* [27]. The PSB inoculation with mineral phosphorus raises the efficiency of phosphate fertilizer and decreases the required phosphate rate to plants.

3. Production of siderophores for uptake of iron

Siderophores are low molecular weight iron binding molecules produced by several microorganisms under low iron conditions [28]. Microbial siderophores may stimulate plant growth directly by increasing the availability of iron in the soil surrounding the roots [29]. Marschner and Römheld (1994) revealed that plants may also use siderophores synthesized by microorganisms that colonizing the rhizosphere. Thus, this would be a source of soluble iron for the host plants. Plants such as sorghum, oats, peanut, cotton, cucumber and sunflower demonstrated the ability to use radiolabelled microbial siderophores as a sole source of iron [30]. Growth of cucumber in the presence of microbial siderophores resulted in

enhanced plant biomass and chlorophyll content [31]. However, there is a controversy as regards to the significance of bacterial Fe³⁺ siderophore uptake to the iron nutrition of plants. In fact, the vast majority of research on microbial siderophores in the rhizosphere is associated with their biocontrol activities due to their competitive effects with plant pathogens.

Production of phytohormones

One of the direct mechanisms by which PGPR promote plant growth is by production of plant growth regulators or phytohormones [32]. Diverse bacterial species have the ability to produce the auxin phytohormone IAA. Bacteria belonging to the genera such as *Azospirillum*, *Pseudomonas*, *Xanthomonas*, *Rhizobium*, *Alcaligenes faecalis*, *Enterobacter cloacae*, *Acetobacter diazotrophicus* and *Bradyrhizobium japonicum* have been shown to produce auxins which enhance the plant growth [33]. Although there is not a strong evidence of Gibberellins (GA) production being a common method of growth promotion by PGPR, it does suggest that it may have a role and indicates that more research in this area is warranted.

PGPR as biocontrol agents

Indirect mechanism of plant growth occurs when PGPR lessen or prevent the detrimental effects of plant pathogens on plants by production of inhibitory substances or by increasing the natural resistance of the host. The mechanisms used by biocontrol-PGPR to phytopathogens can be chemical, environmental, or metabolic [34]. A major group of rhizobacteria with potential for biological control is the *Pseudomonads* [35]. Among various biocontrol agents, fluorescent *Pseudomonads*, equipped with multiple mechanisms for biocontrol of phytopathogens are being employed commonly as they produce a wide variety of antibiotics, chitinolytic enzymes, siderophores, HCN and catalase [36]. *Pseudomonas fluorescens* MSP-393, a PGPR is an efficient biocontrol agent in rice grown in saline soils of coastal ecosystems [37]. Cole-tolerant fluorescent *Pseudomonas* isolated from Garhwal Himalayas act as potential plant growth promoting and biocontrol agents in pea [38]. *P. fluorescens* produces 2, 4-diacetyl phloroglucinol which inhibits growth of phytopathogenic fungi [39]. One of the isolates of a fluorescent *Pseudomonas* spp. EM85 is found to be strongly antagonistic to *Rhizoctonia solani*, a causal agent of damping-off of cotton [40]. The *P. oryzihabitans* and *X. nematophila* strains produce secondary metabolites and suppress *Pythium* and *Rhizoctonia* species which also cause damping-off of cotton [41]. *Bacillus subtilis* is also used as a biocontrol agent. In addition, due to its broad host range, its ability to form endospores and produce different biologically active compounds with broad spectrum of activity, *B. subtilis* as well as other *Bacilli* are potentially useful as biocontrol agents [42].

Bacillus megaterium from tea rhizosphere is able to solubilize phosphate, produce IAA, siderophore and antifungal metabolite and thus it helps in the plant growth promotion and reduction of disease intensity [43]. Two strains viz., *B. thuringiensis* and *B. sphaericus* have the ability to solubilize inorganic phosphates and help in the control of the lepidopteron pests [44]. Arbuscular Mycorrhizal (AM) fungi are ubiquitous in nature and constitute an integral component of terrestrial ecosystems, forming symbiotic associations with plant root systems of over 80% of all terrestrial plant species. One of the particular importance of AM fungi is the bioprotection conferred to plants against many soil-borne pathogens such as species of *Aphanomyces*, *Cylindrocladium*, *Fusarium*, *Macrophomina*, *Phytophthora*, *Pythium*, *Rhizoctonia*, *Sclerotinium*, *Verticillium* and *Thielaviopsis* and various nematodes by AM fungal colonization of the plant root [45].

Siderophore production is an important characteristic for the inhibition of plant pathogens and promotion of plant growth. PGPR produce extracellular siderophores which efficiently complex environmental iron, making it less available to certain native microflora [29]. Some biocontrol-PGPR produce a wide range of low molecular weight metabolites with antifungal potential. The best known is hydrogen cyanide (HCN). HCN produced by bacteria can inhibit the black root rot pathogens of tobacco. In soil, a biocontrol pseudomonad was capable of using seed exudates of sugar beet to produce substances inhibitory to the pathogen *Pythium ultimum* [34]. Certain PGPR can also produce enzymes that can lyse fungal cell walls, but not plant cell walls and thereby prevent fungal phytopathogens. For example, *Pseudomonas stutzeri* produces extracellular chitinase and laminarinase which lyses the mycelia of *Fusarium solani* [46].

Competition and displacement of pathogens

Competition for nutrients and suitable niches among pathogens and biocontrol-PGPR is another mechanism of biocontrol of some plant diseases. For example, high inoculum levels of a saprophytic *Pseudomonas syringae* protected pears against *Botrytis cinerea* (gray mold) and *Penicillium expansum* (blue mold). *Azospirillum brasilense* was able to displace the causal agent of bacterial speck disease of tomato, *P. syringae* pv. *Tomato*, on tomato leaves and consequently decreased disease development. Similarly, when a non-pathogenic strain of *P. syringae* pv. *Tomato* was co-inoculated on to leaves with a pathogenic strain; disease incidence was significantly reduced. An ice-nucleation-deficient mutant of *P.*

syringae displaced pathogenic *P. syringae* and protected tomato and soybean against early frost induced by the pathogen [34].

Induced systemic resistance

Plants can be protected against pathogens for long periods and across a broad spectrum of disease-causing microbes by making them more resistant against infection. Exposure to pathogen, non-pathogens, PGPR and microbial metabolites stimulate a plant's natural self-defence mechanisms before a pathogenic infection can be established, effectively 'immunizing' the plant against fungal, viral and bacterial infections. Protection occurs via accumulation of compounds like salicylic acid which plays a central protective role in acquired systemic resistance or by enhancement of the oxidative enzymes of the plant. The feasibility of protecting plants by induced systemic resistance (ISR) has been demonstrated for several plant diseases. The plant growth promoting *Pseudomonas* strains which induced resistance systemically in watermelon to gummy stem rot are investigated on their ISR-related characteristics by Lee et al. (2001). The concept that PGPR can protect plants against the pathogens by inducing defence mechanisms by iron binding siderophore, HCN and other associates. PGPR induced systemic protection against tomato late blight [47]. Under *in vitro* conditions *P. fluorescens* (ENPF1) and *P. chlororaphis* isolate (BCA) promote plant growth and induce systemic resistance against stem blight pathogen *Corynespora cassiicola* in *Phyllanthus amarus* [48]. Several PGPR strains release a blend of volatile organic compounds that promote growth in Arabidopsis seedlings and induce resistance against *Erwinia carotovora* subsp. *carotovora* [49]. Plant growth promotion induced by the antagonistic fungus, *Pythium oligandrum*, is the result of a complex interaction which includes an indirect effect through control of pathogens in the rhizosphere and/or a direct one mediated by plant-induced resistance [50].

Phytoremediation

The use of living organisms for the remediation of soils contaminated with heavy metals, radionuclide or polycyclic aromatic hydrocarbon is known as 'bioremediation' [12]. The soil microbes, PGPR, mycorrhizal-helping fungi and AM fungi in the rhizosphere of the plants growing on trace metal contaminated soils play a crucial role in phytoremediation [51]. AM are involved in phytoremediation activities, particularly in phytostabilization [52]. Among the possible mechanisms by which AM fungi improve the resistance of plants to heavy metals (HMs) is the ability of the AM fungi to sequester HMs through the production of chelates or by absorption. AM plants typically translocate less HM to their shoots than the corresponding non-AM controls. The role of AM fungi in phytoextraction is thought to be less significant. The metal resistant PGPR can also serve as an effective metal sequestering and growth promoting bioinoculant for plants in metal stressed soil [53]. A plant growth promoting bacterium, *Kluyvera ascorbata* SUCD165 contains high levels of HMs, is resistant to the toxic effects of Ni²⁺, Pb²⁺, Zn²⁺ and CrO₄. This bacterium decreases nickel toxicity in the seedlings [54]. Wu et al. (2006) carried a greenhouse study with *Brassica juncea* to critically evaluate effects of bacterial inoculation on the uptake of HMs from Pb-Zn mine tailings by plants. The presence of beneficial bacteria stimulated plant growth and protected the plant from metal toxicity and altered metal bioavailability in the soil. The hydroxamate siderophores contained in culture filtrates of *Streptomyces acidiscabies* E13 promotes cowpea growth under nickel contamination by binding iron and nickel, thus playing a dual role of sourcing iron for plant use and protecting against nickel toxicity [55]. Engineered endophytic *Burkholderia cepacia* G4 strains improved phytoremediation and promoted plant tolerance to toluene [56]. Siciliano et al. (2001) revealed that plants cultivated in soil contaminated with xenobiotics naturally recruited endophytes with the necessary contaminant degrading genes. Indeed, in field sites contaminated with nitro-aromatics, genes encoding for nitro-aromatic compound degradation were more prevalent in endophytic strains than within rhizospheric or soil microbial communities [57]. Van Aken et al. (2004) also showed that a phytosymbiotic strain of *Methylobacterium*, which was isolated from hybrid Poplar trees (*Populus deltoidea* x *nigra*), was capable of biodegrading numerous nitro-aromatic compounds such as, 2, 4, 6-trinitro-toluene [58]. Lodewyckx et al. (2001) demonstrated that endophytes of yellow lupin, genetically constructed for nickel resistance, were able to enhance the nickel accumulation and tolerance of inoculated plants [59]. Germaine et al. (2006) inoculated pea plants with a *Pseudomonas* endophyte capable of degrading the organochlorine herbicide, 2, 4-dichlorophenoxyacetic acid (2, 4-D). When inoculated plants were exposed to 2, 4-D, they showed no accumulation of the herbicide into their tissues and experienced little or no signs of phytotoxicity. Thus, phytoremediation playing a crucial role in the clean-up of contaminated land and water, it is envisaged that endophytes will play a major role in enhancing both the range of contaminants that can be remediated and the rate of their degradation [60].

Plant protection under stress conditions

PGPR can have positive effects on vigor and productivity of plants, especially under stress conditions. Seed inoculations with PGPR in asparagus (*Asparagus officinalis* L) results in a positive response and enhances plant growth under drought [61]. The phosphate solubilizing microorganisms can interact

positively in promoting plant growth as well as phosphate uptake of maize plants, leading to plant tolerance improving under water deficit stress conditions [62]. On the basis of mutational studies of *Azospirillum*, Kadouri et al. [63] proved the role of PHB synthesis and accumulation in enduring various stresses, viz., UV irradiation, heat, osmotic pressure, osmotic shock and desiccation. *Azospirillum* inoculated wheat (*T. aestivum*) seedlings subjected to osmotic stress developed significant higher coleoptiles with higher fresh weight and better water status than uninoculated seedlings [64]. A multi-process phytoremediation system utilizes plant/PGPR interactions to mitigate stress ethylene effects, thereby greatly increasing plant biomass, particularly in the rhizosphere and it also causes the decontamination of persistent petroleum and organic contaminants in soil [65].

Production of natural products

The endophytes are now recognized as important sources of a variety of structurally novel and biologically active secondary metabolites, including terpenoids, steroids, alkaloids and isocoumarins derivatives. For example, Taxol, an effective antitumor drug produced by bark of the yew tree, *Taxus brevifolia*, could also be produced by endophytic fungi *Taxomyces andreanae* [66]. Fungal endophyte, *Trametes hirsute* isolated from *Podophyllum* spp. produces lignans (podophyllotoxin) with anticancer activity. Derivatives of podophyllotoxin, etoposide and teniposide are currently used in cancer chemotherapy [67]. The fungus isolated from inner bark of *Nothapodytes foetida* (Wight) Sleumer., produces the anticancer phytochemical camptothecin [68]. *Pseudomonas viridiflava* isolated from grass and *Streptomyces griseus* from *Kandelia candel* produced antimicrobial compounds namely ecomycins (B and C) and p-aminoacetophenoic acid, respectively [69]. Munumbicin D and coronamycin are the antimalarial phytochemicals which were produced by *Streptomyces* NRRL 30562 and *Streptomyces* spp. isolated from *Kennedia nigriscans* and *Monstera* spp., respectively [70]. Bioplastics are biomaterials that are receiving increasing commercial interest. Lemoigne (1926) first described a bioplastic, poly-3-hydroxybutyrate (PHB) produced by *Bacillus megaterium*. Genomic analysis indicates that many species of bacteria have potential to produce bioplastics [71].

CONCLUSIONS

Thus, it has been concluded that PGPR have received worldwide importance and acceptance for agricultural benefits. These microorganisms have potential applications in sustainable agriculture and the trend for the future. Therefore, several researchers have been engaged in understanding of PGPR adaptation to the rhizosphere, mechanisms of root colonization, effects of plant physiology and growth, biofertilization, induced systemic resistance, biocontrol of plant pathogens, and production of determinants. Biodiversity of PGPR and mechanisms of action for the different groups such as diazotrophs, bacilli, *Pseudomonads*, *Trichoderma*, AM fungi, rhizobia, PSM and fungi, lignin degrading, chitin degrading, cellulose degrading bacteria and fungi are shown. Thus, PGPR in agricultural field need to be explore due to their several beneficial characteristics. More study need to be carried out on genetically modified (GM) microorganisms for advance applications in agriculture field.

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