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Review Article

Root Colonization and Quorum Sensing are the Driving Forces of Plant Growth Promoting Rhizobacteria (PGPR) for Growth Promotion

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Plant growth promoting rhizobacteria (PGPR) exhibit an intricate and interdependent relationship with plants, which involves biotic and abiotic factors of the rhizosphere region other than the two partners. Success of PGPR is dependent on their survival and establishment on the root/rhizosphere. In this article, we have highlighted root colonization and cell-density dependant quorum sensing as the two important factors that play a key role in determining the outcome of the interaction.

Key Words: PGPR; Root Colonization; Quorum Sensing; Biological Control; Plant Growth

1. Introduction

Plant growth is influenced by several abiotic and biotic factors. Rhizosphere is the thin layer of soil immediately surrounding plant roots which is an extremely important and dynamic area for root activity and metabolism. Currently, it is acknowledged that the genome of the microbial component in and around the plant, especially the endophytic and rhizospheric microbes, constitute the second genome of the plant. The concept of rhizosphere introduced by Hiltner describes the narrow zone of soil surrounding the roots where microbial 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 are changed by root growth and activity. A large number of microorganisms including bacteria, fungi, protozoa and algae coexist in the rhizosphere with bacteria being the most abundant. Plants select the bacteria contributing most to their fitness by releasing organic compounds through exudates creating a very selective environment where diversity is low. Since bacteria are the most abundant microorganisms in the rhizosphere, it is highly probable that they influence the plant's physiology to a greater extent, especially considering their competitiveness in root colonization.

The different physical, chemical and biological properties of root-associated soil are responsible for changes in microbial diversity and increase in number and activity of microorganisms in the rhizosphere micro-environment [1, 2]. The microflora of the rhizosphere includes both deleterious and beneficial components that have the potential to influence plant growth and crop yield significantly. The beneficial rhizobacteria include symbiotic rhizobia, certain actinomycetes and mycorrhizal fungi and free-living bacteria that increase the availability of nutrients or plant growth substances to plants and/or suppress parasitic and non-parasitic pathogens [3]. Plant growth promoting rhizobacteria (PGPR) are a group

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of free-living bacteria that colonize the rhizosphere and contribute to increased growth and yield of crop plants [4]. Bacteria of diverse genera have been identified as PGPR of which *Bacillus* and *Pseudomonas* spp. are predominant [5]. The root colonizing bacteria are the most sought-after group of beneficial bacteria for their multifaceted qualities, which include plant growth promotion, disease control, and bioremediation. The impact of PGPR, the mechanisms of action and the interaction of PGPR with other microbes have been periodically reviewed [3, 6-14].

The beneficial effects of PGPR seen under greenhouse conditions are often not repeatable in the field. Understanding the influence of environmental factors is widely recognized as a key to improve the level and reliability of PGPR. To establish sufficient population on the host roots, compatibility with the host root exudates and other compounds released by rhizosphere microorganisms (which directly or indirectly influence the rhizosphere environment) appear to be more critical for success of the PGPR. The use of PGPR offers an attractive way to reduce the usage of chemical fertilizers, pesticides, and supplements. Application of most of the PGPR isolates result in a significant increase in plant height, root length, and dry matter production of shoot and root of plants. PGPR help in the disease control in plants. Some PGPR, especially if they are inoculated on the seed before planting, establish on the crop roots. PGPR are a major component as biocontrol agents in the integrated management systems in which reduced rates of agrochemicals and cultural practices are used. Such an integrated system could be used for transplanted vegetables to produce more vigorous transplants that would be tolerant to nematodes and other diseases for at least a few weeks after transplanting to the field. Selected strains of beneficial PGPR trigger a plant mediated induced systemic resistance (ISR) response that is effective against a broad spectrum of plant pathogens. ISR is a plant-mediated mechanism, which resembles classic pathogen-induced resistance, in which non-infected parts of previously pathogen-infected plants become more resistant to further infection. This review critically examines root colonization and quorum sensing as two important aspects of plant-PGPR interaction to find ways for further advancement in this area of plant-microbe interactions.

2. Inefficiency to Sufficiently Colonize the Host Roots Determines the Outcome of Plant-PGPR Interactions

The most important characteristic of PGPR for field application is the ability to establish on the host roots and move along with the growing roots. Sufficient populations of the PGPR on the rhizoplane ensure the desired effects on growth promotion and disease control. Root colonization by a bacterium is the result of interactions with physical, chemical, and biological characters of the environment as well as properties of the bacterium itself. A clear understanding of the colonization process is required to screen or develop strains possessing good growth promoting and biocontrol activity in field.

(a) The Biotic and Abiotic Environment of the Rhizosphere is Influenced by the Root Exudates

Roots perform more important functions than anchoring plants and providing water and nutrients to the plants. Plant roots exude potentially valuable small molecular weight compounds into the rhizosphere. Since the number of microorganisms on plant roots is usually higher than in distant soil, the plant root is thought to be a major source of nutrients for microorganisms living in the rhizosphere. Root exudation includes compounds ranging from ions, free oxygen and water, enzymes, mucilage, and a diverse array of carbon-containing primary and secondary metabolites [15, 16]. Chemical signalling between plant roots and other soil organisms is often based on root-derived chemicals eliciting dissimilar responses from different recipients. Chemical components of root exudates may deter one organism while attracting another. On the other hand, two very different organisms may be attracted with differing consequences to the plant. Increase or decrease in soil nutrient availability due to change in soil chemistry and soil biological processes by root exudates is also possible. These effects can influence the outcome of resource competition especially if the limiting resources are targeted [17]. Competition

between the strains in response to difference in chemotaxis to root exudates has been a major factor in root colonization [18]. Acidification of the rhizosphere as a result of exudation of organic acids from the root also plays a pivotal role in determining the surrounding population [19]. A pH below 5.5 can cause a decrease in major macronutrients, besides increasing concentration and activity of micronutrients such as manganese, iron and aluminium resulting in phytotoxic effects on plant roots and beneficial microbes [20]. Exudation of high concentrations of organic acid anions from roots due to deficiency of phosphorous also decreases the rhizosphere pH, thereby making phosphorus and micronutrients such as manganese, iron, and zinc more available in calcareous soils [21]. These changes in nutrient and physical status of rhizosphere affect the resident PGPR. Besides having direct effect on activity of PGPR, pH also affects the co-aggregation among different PGPR strains [22].

Duffy and Defago [23] described the effect of several minerals on antibiotic production by *P. fluorescens* CHA0. Production of diacetyl phloroglucinol (DAPG) and its precursor compound monoacetyl phloroglucinol in *P. fluorescens* CHA0 was stimulated by zinc, ammonium molybdate, and glucose, while the production of pyoluteorin (PLT) was stimulated by zinc, cobalt, and glycerol, but was repressed by glucose. High molar C/N ratios increased cell yield and phenazine production by *P. fluorescens* strain 2-79 [24]. Mineral effects on antibiotic biosynthesis may explain the association between chemical and physical properties of soil and the variable performance of biocontrol strains between field sites [25]. Zinc stimulated antibiotic production was known in a number of biocontrol strains [25-27]. It was further confirmed when a strain of *P. fluorescens* CHA0 was found to be ineffective in disease-conducive soils that contain less zinc [28]. Inorganic phosphate also represses antibiotic production by rhizobacteria, posing a major concern about potential adverse effects of phosphate fertilizers commonly used in agriculture on not only introduced biocontrol agents but also on indigenous populations of antagonists [23]. Phosphate represses biosynthesis of polyketide antibiotics like anthracycline and tetracycline, phenazines in *Pseudomonas*, [29] and zwittermycin A and kanosamine in *Bacillus* [30, 31] indicating that it may be a common phenomenon in soil bacteria.

The effect of root exudates on patterns of bacterial gene expression is relatively much less known. Root exudates of two varieties of sugar beet that select for genetically distinct pseudomonad populations in the rhizosphere showed only a partial overlap on the *P. aeruginosa* PA01 transcriptome [32]. Expression of a majority of genes was altered in response to only one of the two exudates. Genes with altered expression included those with functions related to different aspects of metabolism, chemotaxis, and type III secretion, etc. Use of mutants with targeted disruptions showed no genes with host-specific effects. Similarly, van Overbeek and van Elsas [33] found that expression of the ß-galactosidase gene in a transgenic *P. fluorescens* mutant was induced by proline but not by 125 other substrates present in root exudates of different plants. Carbon sources commonly found in plant root exudates had a differential influence on the spectrum of antibiotics produced by individual biocontrol strains irrespective of their effects on bacterial growth [23]. The effect of root exometabolites of tomato plants on the growth and antifungal activity of plant growth promoting *Pseudomonas* strains indicated that the antifungal activity of PGPR in the plant rhizosphere depends on the sugar and organic acid composition of root exudates [34]. To understand the variation in bacterial gene expression in response to various root exudates, an elaborate study involving a molecular genetics approach is much needed.

(b) Flagella and Pili Influence the Root Colonization Ability of PGPR

The root exudates and soil nutrient status decide the fate of establishment of microbes in the rhizosphere. Properties of the bacterial partner, including the morphological and biochemical characteristics, are equally important in determining their survival on plant roots. Bacteria are likely to locate plant roots through cues exuded from the root such as carbohydrates and amino acids stimulating

chemotaxis on root surfaces [35]. Bacterial motility is considered as an important factor in root colonization. Motility can potentially enhance rhizoplane competence both in terms of movement from bulk soil to roots as well as along the roots [36], while motility of *P. fluorescens* does not affect the root colonization when applied as seed or soil inoculums [37]. The importance of motility for pathogens and beneficial microbes for competitive advantage in rhizosphere has been established [38-40]. Involvement of motility in virulence of several plant pathogenic bacteria such as *Agrobacterium tumefaciens, Ralstonia solanacearum, Pseudomonas syringae* pv. *tabaci,* and *Erwinia carotovora* subsp. *atroseptica* was shown [41-44]. It was also established that active bacterial motility towards the root hair zone is important for the initiation of root colonization by *Azospirillum brasilense* at these sites [45]. Thus, efficient motility of beneficial and pathogenic bacteria facilitates competition and/or colonization in rhizosphere/ rhizoplane. Flagella-mediated motility has been thought to be advantageous to the bacteria to search for favourable environment or to escape from detrimental conditions and also for successful competition with other organisms [46]. Based on short-term *in vitro* studies with *A. brasilense*, a two-step attachment mechanism was proposed [47]. The first step, termed the adsorption step, consists of a rapid and weak binding of the bacteria to the plant root surface mediated by the polar flagellum of the bacteria. The second step, termed the anchoring step, occurs in high C/N ratio containing medium and is mediated by a bacterial polysaccharide. By means of this polysaccharide, the bacteria firmly attach to the plant root and additional free bacteria are entrapped to form large clusters on the root surface. *Azospirillum* polar flagellum or a component located on the polar flagellum was reported to function as a wheat root adhesin in short-term incubation studies [48]. Non-flagellated mutants showed a severely reduced adsorption capacity to wheat roots, possibly due to loss of the bacterial root adhesin located at the polar flagellum, mediating attachment to the receptor sites at the root hair zones. Bacterial flagellins play a crucial role in recognizing host and non-host plants for beneficial bacteria.

Plants sense the presence of a broad range of rhizobacteria using a transmembrane receptor-like kinase that responds to fragments of the eubacterial flagellin peptides [49]. Another important determinant of bacterial motility is type IV pili, which are involved in the adhesion of animal and human pathogenic bacteria to eukaryotic cells [50-52]. Type IV pili play a role in plant colonization by endophytic bacteria such as *Azoarcus* spp. [50, 53]. Pilin precursors are the building blocks of pili on the surface of bacteria. Budzik *et al*. [54] described the chemical bonds that assemble BcpA pilin subunits on the surface of *Bacillus cereus*. Sortase D cleaves BcpA precursor between the threonine and the glycine residues of its LPXTG sorting signal and catalyzes formation of an amide bond between threonine of the sorting signal and lysine in the YPKN motif of another BcpA subunit. Three CNA B domains of BcpA generate intramolecular amide bonds, and one of these contributes to pilus formation. Thus, the amide bonds establish the crucial link to assemble pili on the surface of bacilli and other Gram-positive bacteria.

3. Cell Density Dependent Gene Expression Contributes to the Success of PGPR

Bacteria have complex communication mechanisms to control the expression of certain functions in a cell density-dependent manner, termed as quorum sensing (QS) [55-59]. Enormous competitive advantage is conferred on bacteria by the QS, improving their chances to survive as they can explore niches that are more complex. In bacterial communication, QS is based on the production and release of signal molecules, termed autoinducers, into the medium. On detection of the signal molecule at a given concentration, transcription of certain genes regulated by this mechanism is induced or repressed in the bacteria. There are many microbial processes regulated by QS which include DNA transferase by conjugation, siderophore production, biolumine-scence, biofilm formation, and the ability of some bacteria to move, also called ‘swarming’ [60, 61]. QS-mediated gene expression is dependent not only on signal molecules but also on bacterial population density [62]. The need for a threshold level of the

initial PGPR inocula to promote plant growth strongly supports the idea that QS by bacteria plays an important role in plant–PGPR interactions [3]. Although N-acyl homoserine lactones (AHLs) are the most common autoinducer signals [63], half a dozen other molecules like diketopiperazines in several Gram-negative bacteria [64] and γ-butyrolactone in *Streptomyces* [65], have also been implicated in density-dependent signalling. Bacteria can respond to QS-like molecules produced by other rhizobacteria [66] and by plants [67], and even destroy the QS molecules produced by other bacterial species [68]. In addition to producing regulatory peptides, *Bacillus* produces enzymes to degrade the AHL moieties produced by Gram-negative bacteria. Genes encoding for AHL degrading enzymes, *aiiA*, have been found in *B. thuringiensis* and various subspecies [69]. The presence of such proteins allows *Bacillus* strains to cleave the lactone bond of AHLs *via* hydrolysis, suggesting a mechanism for autoinducer degrading activity, allowing these bacteria to compete with other Gram-negatives.

Bacterial activity in the rhizosphere, therefore, can be altered directly by plants or other microorganisms *via* QS molecules. The rhizosphere contains a higher proportion of AHL producing bacteria as compared to bulk soil, suggesting that they play a role in colonization [70]. This suggests that plants could be using root-exuded compounds in the rhizosphere to take advantage of this bacterial communication system and influence colonizing communities [7, 39, 71]. Exudates from pea seedlings contain compounds that mimic factors of QS suggests that plants might even be able to select for microbial partners [67]. Plant host species have evolved responses to AHLs. *Medicago trunculata* on exposure to a wide concentration range of AHLs responded with an initial decrease in various protein concentrations followed by increase of the same proteins later [72]. Some of these proteins included members of defence/stress response, cytoskeleton structure/function, isoflavone production, and metabolic enzyme families. This presents an interesting area of research as to how bacteria communicate among themselves and how plants have evolved mechanisms to respond to these signal compounds.

Besides motility and QS, bacterial major outer membrane protein (MOMP) also plays an important role in early host recognition. The MOMP of *Azospirillum brasilense* showed stronger adhesion factor to extracts of cereals than extracts of legumes and tomatoes, and may act as an adhesion involved in root adsorption and cell aggregation of the bacterium [73]. Bacterial lipopolysaccharides (LPS), in particular the O-antigen chain, can also contribute to root colonization [74, 75]. However, it is strain dependent since the O-antigenic side chain of *P. fluorescens* WCS374 does not contribute to potato root adhesion [76], whereas the O-antigen chain of *P. fluorescens* PCL1205 is involved in tomato root colonization [75].

4. Concluding Remarks

As our understanding of the complex environment of the rhizosphere, the mechanisms of action of PGPR, and the practical aspects of inoculant formulation and delivery increases, we can expect to see new PGPR products becoming available. The success of these products will depend on our ability to manage the rhizosphere to enhance survival and competitiveness of these beneficial microorganisms. Rhizosphere management will require consideration of soil and crop cultural practices as well as inoculant formulation and delivery.

The results obtained with PGPR application, *in vitro*, cannot always be reproduced in the field. The variability in the performance of PGPR may be due to various environmental factors that affect growth of PGPR and/or to their effects on the plants. The environmental factors include climate, weather conditions, soil characteristics or the composition or activity of the indigenous microbial flora of the soil. To achieve the maximum benefit out of interaction between PGPR and plants, it is important to discover how the rhizobacteria exert their effects on plants and the critical factors that drive the interaction.

Genetic enhancement of PGPR strains to enhance colonization and effectiveness may involve addition of one or more traits associated with plant growth promotion. Genetic manipulation of host

crops for root-associated traits to enhance establishment and proliferation of PGPR by secreting specific chemical compounds is a topic of investigation. More details of the importance of root colonization and the role of root exudates are available, while the components of the cell-density-dependent QS in PGPR are being identified. Overall, PGPR offer a sustainable approach to increase crop production and health. The application of molecular tools will enhance our ability to understand and manage the rhizosphere and will allow us to develop new products with improved effectiveness.

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