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Root Colonization by Microorganisms and The Effects of PGPR 1

On Plant Growth: A Mini-Review 2

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ABSTRACT

- This brief review provides a concise overview of the impact of microorganisms that colonize 12
- roots on plant growth, with a particular focus on plant growth-promoting rhizobacteria (PGPR). 13
- At the root-soil interface, microorganisms such as bacteria and fungi interact with plants, 14
- providing various advantages, including nutrient acquisition, pathogen protection, and stress 15
- tolerance. PGPR, which are bacteria that promote plant growth through mechanisms such as 16
- nitrogen fixation, potassium solubilization, induction of plant stress resistance and siderophore 17
- production, are among the most beneficial of these microorganisms. The colonization process 18
- entails chemotaxis, adhesion, and colonization of both the rhizosphere and endosphere, which 19
- are facilitated by exopolysaccharides, biofilm formation, and signaling molecules. PGPR has 20
- been shown to boost root and shoot growth, enhance nutrient and water use efficiency, and 21
- enhance plant resistance to biotic and abiotic stressors. These effects are mediated by direct 22
- and indirect interactions between PGPR and plants, which involve modulation of plant immune 23
- responses and systemic resistance. Understanding these mechanisms is critical to the 24
- exploitation of PGPR in sustainable agriculture. PGPR can reduce reliance on chemical 25
- fertilizers and pesticides, but further research is required to unravel the complex interactions 26
- between microorganisms and plants, identify key signaling molecules in root colonization, and
- optimize the use of PGPR in various crops. This brief review underlines the importance of root 28
- colonization by microorganisms, particularly PGPR, in promoting plant growth and sustainable 29
- 30 agriculture.

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- **Keywords:** Plant Growth-Promoting Rhizobacteria (PGPR); Plant-microbe Interactions; 32
- Root Colonization; Rhizosphere; Mycorrhiza. 33

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Introduction

As plants are the major terrestrial primary producer, it should come as no surprise that many microorganisms in the soil have evolved close relationships with them as a vast number of these soil microbes are heterotrophs that depend on other organisms for their food (Willey et al., 2008). It is believed that terrestrial plants evolved from aquatic ones and this was possible through cooperation with soil microbes, many of which still remain today. These interactions could be commensalism where only the microbes benefit, mutualistic where both the plants and microbes benefit, or parasitic where the microbes induce harm to the plants (Willey et al., 2008). The balance between saprophytic and pathogenic microorganisms in soil and plant rhizospheres is a major factor affecting root diseases. In this case, the soil is referred to as disease suppressive when the nonpathogenic microbes supersede the pathogenic ones (Schroth & Weinhold, 1986).

According to Lareen *et al.* (Lareen et al., 2016), these plant-microbe relationships could impact a plant's health and development in one of such ways: change in the quantity and quality of crop yield, enhancing plant development and tolerance to biotic and abiotic stressors.

The root is an organ of the plant responsible for anchorage, uptake of nutrients and water from the surrounding soil, and release of nutrients in the form of exudates with growth regulatory properties (Ahmad et al., 2011). The root-soil interface or rhizosphere is the layer of soil surrounding the plant roots where exudates migrate and are characterized by an exceptionally high microbiological activity (Podile et al., 2014). Various groups of microorganisms including bacteria, actinomycetes, fungi, algae, and protozoans inhabit the rhizospheric soil among which bacteria are the most abundant (Mehmood et al., 2018; Podile et al., 2014). This could, according to Saharan and Nehra (Saharan & Nehra, 2011), be probably because they have the greatest influence on plant physiology, especially considering their competitiveness in root colonization.

The number of microorganisms in the rhizosphere has been said to be more than those in the rhizosphere-free soil, this could be attributed to the physical and chemical changes in the rhizosphere brought about by the root's secretion of important compounds into the rhizosphere, such compounds include fatty acids, organic acids, sugars, vitamins, amino acids, nucleotides, polyphenols, flavonoids, hormones, and nutrients, which attracts microorganisms, serve as a food source for the microorganisms within the rhizosphere and serve to keep the soil moist which is essential for the development of soil microbes (Compant et al., 2019; Mendes et al., 2013). This impact of the plant root on the growth of soil microorganisms is known as the Rhizosphere effect.

Microbial interaction in the rhizosphere is a complex one, the different groups of microbes do not interact only with the plant, but also with themselves. It has been observed that the formation of nodules by nitrogen-fixing bacteria in leguminous plants and the establishment of Arbuscular Mycorrhizae often occur simultaneously and synergistically. The presence of genes responsible for the fixation of nitrogen in an endosymbiotic bacterium, *Burkholderia* was demonstrated in Arbuscular Mycorrhizal hyphae by Minerdi *et al.* (Minerdi et al., 2001).

Materials and Methods

To assess the current state of the research on importance of Microorganisms and The Effects of PGPR, a review of the existing journal literature, books, report, blogs, and newspaper were carried out. Keywords (Plant growth-promoting rhizobacteria (PGPR); Plant-microbe interactions; Root Colonizatio; Rhizosphere; Mycorrhiza) search in the google, google scholar, web of science database (www.thomsonreuters.com/web-of-science), and a full – text search of the Science Direct (www.sciencedirect.com) database were carried out. The reviews or literature reviews will be examined to identify further studies for inclusion, and the results of meta-analyses will not be included in the analysis.

Conflict of Interests and Data Sharing

The authors declare that there are no conflicts of interests. No new data was analyzed or created; hence, data sharing is not applicable to this article.

Results and Discussion

1. Plant-Microbe Interactions

It is well documented that just as the growth of plants is positively influenced by biotic and abiotic factors, they can as well be hindered by these plant stressors. Stressors such as phytopathogens, and draught hinders plant growth (Saharan & Nehra, 2011).

There is a high demand of plant-microbe interactions all around the world, this is due to the fact that they are seen as potential alternatives to the use of chemical fertilizers and pesticides, and the ability of the microbes to relieve plants of the various biotic and abiotic stresses are plaguing the agricultural industry (Romano et al., 2020; Turan et al., 2021). Turan *et al.* (Turan et al., 2021) describe agriculture as a vital part of every country's economic well-being, hence improving the yield and quality of crops has gained more focus as it is considered a global agricultural problem (Zhang et al., 2023).

Plant-microbe interactions are complex and multifaceted relationships between plants and microorganisms that live in and around them. These microorganisms are mainly bacteria and fungi and the invasion could be beneficial or detrimental to the plants (Dolatabadian, 2020). Fungal mycorrhizae, rhizobial bacteria, and endophytes are groups of microorganisms that establish a beneficial relationship with plant roots (Narula et al., 2012; Slonczewski et al., 2015).

a. Fungal Mycorrhizae

Mycorrhizae is a mutualistic interaction established between plant roots and soil fungi. It is observed in the rhizosphere of most – about 80% – terrestrial plants (Narula et al., 2012). Unlike most fungi, mycorrhizal fungi obtain photosynthetically derived carbohydrates from their host plant (hence most mycorrhizal fungi are not saprophytic), on the other hand, the plant host benefits from this interaction through a number of ways, including enhanced nutrient uptake as fungi provide access to immobile nutrients, such as phosphorous being the most valuable service provided by mycorrhizae to the plant (Slonczewski et al., 2015; Willey et al., 2008).

Mycorrhizae can either remain extracellular forming interconnected sheaths of hyphae around the root as in the case of ectomycorrhizae, or penetrate the root cells as in the case of endomycorrhizae.

b. Nitrogen-Fixation Symbiosis

This is another essential plant-microbe interaction (Narula et al., 2012). Gramnegative nitrogen-fixing bacteria and legumes are the parties involved in this interaction. The most extensively studied groups of nitrogen fixers are *Rhizobium* and *Frankia* (Mehmood et al., 2018; Saharan & Nehra, 2011). Bacteria such as the nitrogen fixers are attracted to the root by exudates released by plants, this is accompanied by the formation of nodules for nitrogen fixation upon entry of the bacteria into the root cells (Mehmood et al., 2018). It has been documented that 80% of nitrogen available for plant assimilation is derived from biological nitrogen fixation by these bacteria and the remaining 20% is attributed to non-symbiotic processes (Mehmood et al., 2018). Nitrogen fixers are not only beneficial to their symbiont but also to other plants not involved in the relationship as some nitrogen can be leaked and taken up by them (Slonczewski et al., 2015).

c. Growth Promoters (PGPR)

A group of soil bacteria, capable of enhancing plant growth and increasing the yield and quality of crops were recognized several years back and are successfully used today in field experiments (Saharan & Nehra, 2011). PGPR are widely distributed among the

following bacterial taxa; *Actinobacteria, Bacteroidetes, Cyanobacteria, Firmicutes*, and *Proteobacteria* (Martínez-Viveros et al., 2010).

This group of bacteria and the mechanisms through which they promote plant growth is discussed in detail in a subsequent section of this review.

2. Root Colonization by Microbes

Root colonization by microorganisms can be initiated through a number of ways, the first of which includes, recognition of specific chemical molecules released by the plants through the roots. The next step involves the adherence of microorganisms to the surface of the root or penetration into the roots for endophytes. The last step involves the colonization of plant roots by increasing microbial density and cell-cell communication. Research has shown that plants and microbes have developed the potential to communicate among themselves. These microorganisms identify/sense signaling molecules produced by plants. Microbes respond to these signals by releasing compounds that are in turn recognized by plants thus initiating a plant-microbe conversation. Once the relationship is initiated, the plants and microbes continue to monitor the physiology of their partner and adjust accordingly (Lareen et al., 2016; Lyu & Smith, 2022).

The communication however depends on the specific group of microorganisms in question. In legumes, the symbiotic association starts with mutual recognition of signal molecules, Rhizobia produce a lipo-chitooligosaccharide signal in response to a plant-derived flavonoid (Nod factor). Perception of Nod factor by legume plant result in the activation of subsequent symbiotic reactions that lead to rhizobial infection and nodule organogenesis (Dolatabadian, 2020; Lareen et al., 2016).

In an arbuscular mycorrhizal association, recognition initiates when plants release strigolactone that stimulates spore germination and promotes hyphae growth, on the other hand, fungi produce mycorrhizal factors, such as lipo-chitooligosaccharides and chitooligosaccharides, to activate the signaling pathway of the symbiosis in the root (Dolatabadian, 2020; Lyu & Smith, 2022).

Interaction between plants and pathogenic microbes initiates when Pattern Recognition Receptors (PRRs) on the cell membrane of plant cells bind microbe/pathogen-associated molecular patterns (MAMPs/PAMPs) and control plant immune responses. The binding triggers PAMP-Triggered Immunity (PTI)/basal resistance, which is a defense response in plants called the first line of defense. This mechanism is effective in restricting infection in most plant species (Chen et al., 2022; Dolatabadian, 2020; Nishad et al., 2020).

3. Plant Growth Promoting Rhizobacteria (PGPR)

The terminology "plant growth promoting rhizobacteria" was used to describe the enhanced growth of plant and crop yield by specific bacteria that colonizes the root of plants. PGPR describe root-colonizing bacteria that cause this effect, to differentiate them from other rhizospheric microorganisms that did not enhance plant growth (Schroth & Weinhold, 1986). The term plant growth-promoting rhizobacteria was coined by Kloepper and Schroth (Kloepper & Schroth, 1978) to illustrate the group of beneficial microbes that promote plant growth by effective colonization of the roots of plants (Mehmood et al., 2018). Some plant growth-promoting rhizobacteria and their mechanism of action are listed in Table 1.

Table 1: Mechanism of PGPRs (Singh & Sachdev, 2018)

PGPR	Mechanism	Plant/Crop Affected
Azoarcus sp.	Nitrogen fixation	Rice
Azotobacter vinelandii	Cytokinin production	Cucumber (tomato)
Azorhizobium	Nitrogen fixation	Wheat
	Cytokinin and gibberellin	Potato, cucumber, pepper
	production	
	Siderophore production	
Bacillus licheniformis		
	Induction of plant stress	Maize, pepper
	resistance	
	Potassium solubilization	Cucumber, pepper
Burkholderia vietnamiensis	Nitrogen fixation	Rice
Chryseobacterium	Siderophore production	Tomato
Frankia	Nitrogen fixation	Alnus
Mycobacterium	Induction of plant stress	Maize
	resistance	
Rhizobium	Induction of plant stress	Peanut
	resistance	
	Hydrogen cyanide production	Legumes
	Nitrogen fixation	Legumes, rice
Pseudomonas	ACC deaminase synthesis	Mung beans, wheat
Streptomyces	Indole acetic acid synthesis	Indian lilac

Plant growth-promoting Rhizobacteria (PGPR) can influence plant growth directly and indirectly in several ways but majorly grouped into four which include: nutrient transfer, growth enhancement through phytoregulators, biocontrol, and induction of stress tolerance (Dolatabadian, 2020; Tsukanova et al., 2017; Turan et al., 2021). The direct effect includes: producing phytoregulators (such as cytokinins, auxin, and gibberellins), lowering ethylene concentrations in plants, solubilizing inorganic and mineralizing organic phosphates, symbiotic nitrogen fixation, organic matter (amino acids and enzymes) synthesis, and activating disease-resistance pathways. Indirect benefits of PGPR to plants include biocontrol by antagonizing and outcompeting pathogens and pests, and induction of plant-stress tolerance to harsh environmental conditions and pathogens of plants (Dolatabadian, 2020; Tsukanova et al., 2017; Turan et al., 2021).

a. Nutrient availability

The impact of PGPR on plant growth is observed in its ability to enhance nutrient availability for plant uptake. It does this by either converting some otherwise inaccessible minerals in the soil to plant-accessible forms or by sequestering them thereby preventing them from leaching out (Vejan et al., 2016).

Although nitrogen gas constitutes 80% of the atmospheric nitrogen, it is the most limiting nutrient for plants. The provision of fixed nitrogen enables the growth of plants in soils that would otherwise be nitrogen-limiting. This can be achieved through nitrogen fixation which is a uniquely prokaryotic process. *Azobacter* is an example of a bacterium that can fix nitrogen (Vejan et al., 2016; Willey et al., 2008).

Some PGPR solubilizes phosphate that is otherwise inaccessible to plants resulting in increased availability of accessible phosphate ions in the soil, which can be easily taken up by the plants. *Kocuria turfanensis* strain 2M4 isolated from rhizospheric soil was discovered to be a phosphate solubilizer (Vejan et al., 2016).

Lavakush et al. (Lavakush et al., 2014) conducted research using *Pseudomonas fluorescens*, *Pseudomonas putida*, and *Pseudomonas fluorescens* PGPR strains to study their effect on nutrient uptake by rice.

b. Growth hormones/regulators

Plant hormones also called phytohormones are organic molecules that act as chemical signals influencing the plant's capability to respond to its environment (Vejan et al., 2016). Plant Growth Regulators on the other hand are Phytohormones that are synthesized exogenously that is, not by the plants by natural and synthetic means. These substances,

required in low concentrations are synthesized in various parts of the plants and are transported along a concentration gradient (higher concentration towards lower concentration within the plant) (Mehmood et al., 2018; Vejan et al., 2016). Plants' physiological processes such as growth, differentiation and development, stomatal movement, flowering, and fruit ripening are influenced by phytohormones. Phytohormones are classified into five and these are ethylene, abscisic acid, auxins, cytokinins, and gibberellins (Mehmood et al., 2018). It is noteworthy that two or more plant hormones act together to produce an effect that could either stimulate or inhibit plant growth depending on the concentration of the hormones (Vejan et al., 2016). A prominent way through which PGPRs enhance plant growth is observed in their ability to produce or alter the concentration of phytohormones (Mehmood et al., 2018; Vejan et al., 2016).

IAA (indole-3-acetic acid) is considered the most important native Auxin. It functions as a signal molecule regulating various plant developmental stages such as organogenesis, cellular responses such as cell expansion, cell division, and differentiation, and gene regulation. Many bacterial species have been reported to possess the ability to produce the auxin phytohormone IAA (Saharan & Nehra, 2011). Tsukanova *et al.* (Tsukanova *et al.*, 2017) reported that plants inoculated with *Aeromonas punctata* PNS-1, *Serratia marcescens* 90–166 and *Azospirillum brasilense* Sp245, PGPR that produces auxin showed an increased level of endogenous auxin.

Gibberellin, another phytohormone is involved in seed germination, development of fruit and flower, and stem and leaf growth. A study by Khan *et al.* (Khan et al., 2014) showed the effect of gibberellin-producing *Sphingomonas sp.* LK11 strain in growth characteristics of tomato.

Cytokinins are another class of plant hormones that are a prerequisite for the progression of the cell cycle in plant cells, an essential aspect of every living cell. It has been confirmed that PGPR can influence plant cytokinin concentration. *Platycladus orientalis* plants inoculated with a cytokinin-producing PGPR strain of *Bacillus subtilis* (AE016877) have an increased level of cytokinin in the shoots (Tsukanova et al., 2017).

Ethylene at high concentrations, are known to be detrimental to plants, it generally causes diminished crop performance by inducing defoliation, inhibiting stem and root growth, and causing premature senescence. 1 -aminocyclopropane-1 -carboxylate (ACC), a precursor for ethylene is synthesized as a response to various environmental stressors, and secreted to the rhizosphere where it is taken up again by the roots, and converted into ethylene. This leads to the accumulation of ethylene with a downward spiral effect, thus, PGPR that can degrade ACC in the rhizosphere aids the plant in re-establishing a healthy

root system that can cope with environmental stress (Martínez-Viveros et al., 2010; Tsukanova et al., 2017).

c. Anti-stressors

Biotic stressors of plants include pathogenic fungi, bacteria, nematodes, and viruses whereas abiotic stressors include drought, air pollution, low or high temperature, moisture, and salinity (Mehmood et al., 2018). Abiotic stresses can account for about 50% to 82% loss in crop yield though this value can vary depending on the type of crop (Saharan & Nehra, 2011). Inoculation of such plants with PGPR can increase their tolerance to stress and hence prevent yield loss (Mehmood et al., 2018).

The plant hormone ethylene endogenously maintains plant homeostasis under stressed conditions such as drought and inhibits root and shoot development. However, PGPR ACC deaminase's breakdown of the ethylene precursor ACC reduces plant stress and restores regular plant development (Yang et al., 2009). Under conditions of water scarcity, seed treatment with PGPR had great results in a variety of agricultural plants, including chickpeas, maize, and asparagus (Mehmood et al., 2018).

For plants in metal-stressed soil, the metal-resistant PGPR can act as an efficient bio-inoculant that sequesters metal thereby promoting plant growth. *Pseudomonas putida* is a great choice for field application in polluted soil since it is resilient to a variety of heavy metals at greater levels (Saharan & Nehra, 2011).

d. Biocontrol

Another function of PGPR is to control plant diseases and pests, hence decreasing the need for pesticides that may otherwise endanger human health and non-target organisms in crop systems. Biocontrol is achieved through antagonistic interactions which involve competition for colonization sites or nutrients and the production of antimicrobial compounds by the PGPR (Singh & Sachdev, 2018). These will in turn inhibit the pathogen/pest thereby promoting plant growth (Johansson et al., 2004). The bacterial isolate *P. chlororaphis* PCL1391 was reported in a study to inhibit the growth of root pathogen *Fusarium oxysporum* by effectively colonizing tomato roots and releasing a wide range of antifungal compounds, including phenazine-1-carboxamide (PCN), hydrogen cyanide, chitinases, and proteases (Johansson et al., 2004). Hence efficient colonization of the root can confer on a bacterium biocontrol property. Another biocontrol strain *Pseudomonas fluorescens* 2P24 uses quorum sensing (QS) and antibiosis for inhibiting plant pathogens (Singh & Sachdev, 2018).

The present paper provides an extensive summary on the phenomenon of root colonization by microorganisms, particularly plant growth-promoting rhizobacteria (PGPR), and its consequential influence on plant growth. It elaborates on the mechanisms of root colonization, such as chemotaxis, adhesion, biofilm formation, and signalling molecules, which facilitate a symbiotic relationship between plants and microbes. The review highlights diverse ways in which PGPR can boost plant growth, including nutrient transfer, growth hormone production, biocontrol, and stress tolerance. Comprehending these interactions has significant implications for sustainable agriculture and plant protection, as the utilization of PGPR and other beneficial microbes can effectively reduce the dependence on chemical fertilizers and pesticides while simultaneously enhancing plant resistance to environmental stressors. Nevertheless, the paper acknowledges the prevailing challenges, such as the variable effectiveness and compatibility of PGPR, which requires further scientific research on molecular mechanisms, signalling molecules, and long-term effects on soil health and plant fitness to advance agricultural applications.

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