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PGPR-beneficial microbes in agro forestry ecosystem

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Abstract

Plant growth promoting rhizobacteria (PGPR) are a diverse set of bacteria found in the rhizosphere, on root surfaces, and in close proximity to roots that can directly or indirectly promote the extent or quality of plant development. Rhizobacteria that promote plant growth include rhizosphere-colonizing N₂-fixing rhizobacteria that provide nitrogen to plants, as well as the well-known symbiosis of legume rhizobia. Several bacteria, including *Pseudomonas*, *Azospirillum*, *Azotobacter*, *Klebsiella*, *Enterobacter*, *Alcaligenes*, *Arthobacter*, *Burkholderia*, *Bacillus*, and *Serratia*, have been found to improve plant development in recent decades. *Rhizobium* is the most important PGPR, which is able to develop a symbiotic association with its specific host plant and increase its growth and yield by biologically fixing atmospheric nitrogen. However, the other PGPR, such as *Pseudomonas* and *Bacillus*, are able to increase plant growth and yield production by colonizing the host plant roots in a nonsymbiotic manner. PGPR's direct promotion entails either providing the plant with a plant growth promoting substance or providing the plant with a plant growth promoting substance. When PGPR inhibits the harmful effects of one or more phytopathogenic microorganisms, it indirectly promotes plant growth. In response to PGPR inoculation, significant increases in growth and yield of agronomically important crops have been recorded. Bacterial inoculants can boost plant growth and germination, improve seedling emergence, improve responses to stress, and protect plants from disease. When compared to farmed crops, the impact of PGPR on trees has received the least attention. The current review focuses on PGPR's mode of action and growth-promoting activities in trees.

Keywords: Plant growth promoting rhizobacteria, rhizosphere, nitrogen fixation, phytopathogens

Introduction

Plant Growth Promoting Rhizobacteria are symbiotic free-living soil microorganisms that live in the rhizosphere of many plant species and have a wide range of beneficial impacts on the host plant (Raza *et al.* 2016a,b) [152] through several processes such as nitrogen fixation and nodulation (Gouda *et al.* 2018; Oleńska *et al.* 2020) [78, 139]. The term "plant growth promoting rhizobacteria (PGPR)" was coined by Kloepper and Schroth (1978) [111] to describe these beneficial microbes. Furthermore, various microbial-based approaches, such as biofertilizers, biostimulants, and/or biopesticides, are currently being proposed as alternatives for increasing crop yield. Plant growth promoting rhizobacteria (PGPR) positively influence plant growth and represent promising long-term solutions for increasing plant biomass production. (Thijs and Vangronsveld 2015; Lindemann *et al.* 2016; Umesha *et al.* 2018; Liu *et al.* 2020) [186, 122, 190]. Plant health and soil fertility are highly influenced by beneficial soil microorganisms and their interactions (Jeffries *et al.* 2003) [99]. Without understanding the chemistry or the vital functions played by microorganisms, Middle Eastern farmers practised crop rotation about 6000 BC, sowing legumes and cereals alternately. Hellriegel and Wilfarth (1888) [85] researched rhizosphere root colonisation and proposed that soil microorganisms could transform atmospheric N₂ into plant-usable forms and that the introduction of legumes on cultivated areas resulted in enhanced soil fertility (Chew 2002) [45]. Plant Development Promoting Rhizobacteria is such a group of beneficial bacteria that boosts plant growth (Bajracharya 2019) [20]. The use of rhizospheric bacteria to promote plants in nutrient uptake and solubilization of fixed nutrients such as phosphorus has become more important in the paradigm of sustainable agriculture (Hayat *et al.* 2010) [92]. The plant is always associated with a well-structured and controlled colony of microbes (Turner *et al.* 2013; Chaparro *et al.* 2014; Lebeis 2014) [189, 44, 118].

Plant growth-promoting rhizobacteria (PGPR) can directly interact with plants by improving the availability of important nutrients (e.g. nitrogen, phosphorus, iron), the generation and regulation of plant-growth-related compounds (e.g. phytohormones) and the stress hormonal factors (Oleńska *et al.* 2020) [139].

The ability of PGPR to aid plant growth is critical, especially in the case of abiotic stress, when bacteria can enhance plant resilience, stress tolerance and/or even help with contaminant remediation (Bulgarelli *et al.* 2015; Smith *et al.* 2015b; Oleńska *et al.* 2020) [34, 173, 139]. PGPRs contain bacteria from the genera *Pseudomonas*, *Azospirillum*, *Azotobacter*, *Klebsiella*, *Enterobacter*, *Alcaligenes*, *Arthrobacter*, *Burkholderia*, *Pantoea*, *Bacillus*, *Serratia* and *Rhizobium*, among others (Kloepper *et al.* 1992; Fernando *et al.* 2005) [109, 64]. *Pseudomonas*, *Bacillus*, *Azospirillum*, *Agrobacterium*, *Azotobacter*, *Arthrobacter*, *Alcaligenes*, *Serratia*, *Rhizobium*, *Enterobacter*, *Burkholderia*, *Beijerinckia*, *Klebsiella*, *Clostridium*, *Vario-Vovax*, *Phyllobacterium* and *Phyllobacterium* are among the PGPR genera (Lucy, Reed & Glick 2004) [125]. *Pseudomonas* and *Bacillus* are the two most commonly reported PGPRs (Podile & Kishore 2006) [150]. Commercial applications of PGPR and their interactions with plants exist, as well as scientific applications for sustainable agriculture (Gonzalez *et al.* 2015).

Mechanism of PGPR action

Plant roots release a wide range of organic nutrients (organic acids, phytosiderophores, sugars, vitamins, amino acids, nucleosides, mucilage) and signals that attract microbial communities, particularly those that can metabolise and grow in this microbial habitat (Ahemad and Kibret 2014; Hasan *et al.* 2014) [6]. Three distinct traits describe the PGPR:

1. They must be able to colonise the root.
2. They must be able to survive and multiply in microhabitats associated with the root surface, in competition with other microbiota, for at least the time required to express their plant promotion/protection activities.
3. They must promote plant growth (Bishnoi, 2015) [33].

The rhizospheric soil bacteria that surround the plant root compete for this nutritional benefit and as a result, have an impact on the plant's growth, yield and defence mechanisms, either as free-living microbes or in a mutualistic connection with the plant root (endophytic/epiphytic) (Vejan *et al.* 2016) [199]. Rhizobacteria have an impact on plant development. When reintroduced by plant inoculation in a soil harbouring competitive microflora, about 2-5% of rhizobacteria have a good influence on plant development and are referred to as plant growth-promoting rhizobacteria (PGPR). The direct mechanism (Table 1), which directly encourages plant development in a direct form, is the most common method of action for PGPR. Nitrogen fixation, phytohormone synthesis, phosphate solubilization and increased iron availability are all part of this plant growth promotion mechanism. By removing pathogens or triggering plant defensive responses, PGPR can indirectly boost plant growth.

Many PGPR have many mechanisms of action (Narasimhan *et al.* 2003; Gupta and Dikshit 2010; Haymer 2015; Thijs *et al.* 2016; Delshadi *et al.* 2017) [136, 82, 93, 184, 51]. In the absence of pathogens, bacterially mediated phytohormone production is the most likely explanation for PGPR activity (Tien, Gaskins & Hubbell 1979) [187], whereas siderophore production by PGPR is thought to be more important for plant growth stimulation when other potentially deleterious microorganisms are present in the rhizosphere (Kloepper, Leong, Teintze, & Schroth 1980) [108]. PGPR influence plant physiology and development, either directly or indirectly (Table 2) and hence play an important role in plant function. Direct stimulation includes biological nitrogen fixation

(Zahran 2001) [204], the production or alteration of phytohormones such as auxins, cytokinins, gibberellins (GA) (Vacheron *et al.* 2013; Tien *et al.* 1979) [191, 187] or ethylene (Glick, Karaturovic, & Newell 1995) [76], the solubilization of minerals such as phosphorus and iron. The manufacture of antibiotics, chelation of Fe in the rhizosphere, synthesis of extracellular enzymes to hydrolyze fungal cell walls and competition for niches within the rhizosphere are all examples of indirect plant growth promotion (Van Loon 2007) [194]. *Pseudomonas fluorescens* and *Bacillus subtilis*, in particular, are frequently explored as the most promising candidates for indirect stimulation (Damayanti, Pardede, & Mubarik 2007) [49]. Experimental evidence reveals that plant growth stimulation is the consequence of many pathways that may be triggered simultaneously, suggesting that PGPR may use more than one method to boost plant growth (Martínez-Viveros, Jorquera, Crowley, Gajardo, & Mora 2010) [130]. Several plant growth promoting (PGP) mechanisms of PGPR, according to Podile and Kishore (2006) [150], include root hair modification and increased branches, improved seed germination, increased leaf area per plant, release of certain phytohormones, increased nutrient and water uptake by plants, increased biomass of plants with more vigour growth, and better carbohydrate accumulation, all of which contribute to plant growth. Glick (2003) [74], on the other hand, divides bacterial supported plant development into three categories: plant hormone synthesis (Dobbelaere, Vanderleyden, and Okon 2003) [54], bacterial assisted enhanced nutrient uptake by plants and biological control of plant diseases (Saravanakumar *et al.* 2008) [162]. Dey *et al.* (2004) [52] suggest the need of exploring other mechanisms of plant growth promotion by PGPR apart from the list already studied. Listing all the explored and investigated mechanisms of PGPR, following can be included:

- a) Solubilization and mineralization of nutrients notably phosphorus (Richardson 2001; Banerjee and Yesmin 2006) [156, 22].
- b) Nitrogen fixation through symbiosis and asymbiosis (Kennedy, Choudhury and Kecskes 2004) [105].
- c) Release of certain plant hormones such as gibberellic acid and cytokinins (Dey *et al.* 2004) [52], indole acetic acid (Patten and Glick 2002) [145] and abscisic acid (Dobbelaere, Vanderleyden and Okon 2003) [54].
- d) Production of 1-aminocyclopropane-1-carboxylate (ACC)-deaminase helping to lower ethylene level in roots this increasing length and vigor of roots (Penrose and Glick 2001) [148].
- e) Antagonism toward plant pathogens by producing substances such as cyanides and antibiotics (Glick and Pasternak 2003) [74].
- f) Increasing the availability of nutrients specifically of iron through chelating by producing siderophores (Glick and Pasternak 2003) [74].
- g) Tolerance against several abiotic stresses such as oxidative (Štajner *et al.* 1995) [175] and drought stress (Alvarez, Sueldo and Barassi 1996) [9].
- h) Water soluble vitamin production including biotin, niacin, thiamine and riboflavin (Revillas *et al.* 2000) [155].
- i) Detoxification of heavy metals (Ma *et al.* 2011) [126].
- j) Tolerance of salinity (Tank and Saraf 2010) [182].
- k) Biological control of pests and insects (Russo *et al.* 2008) [159].

Table 1: Direct mechanisms and PGPR (Verma *et al.* 2019)

Mechanism	PGPR	Crops	References
Nitrogen fixation	Symbiotic	<i>Rhizobium</i> and allied genera	Lucas-Garcia <i>et al.</i> (2004) ^[124] , Vargas <i>et al.</i> (2010) ^[197] , Laranjo <i>et al.</i> (2014) ^[116] and Abd-Alla <i>et al.</i> (2017) ^[1]
		<i>Frankia</i>	Crannell <i>et al.</i> (1994) ^[48] , Santi <i>et al.</i> (2013) ^[161] , Diagne <i>et al.</i> (2013) ^[53] and Ballhorn <i>et al.</i> (2017) ^[21]
	Free-living	Cyanobacteria, <i>Azotobacter</i> , <i>Azospirillum</i> , <i>Beijerinckia</i>	Steenhoudt and Vanderleyden (2000) ^[176] , Cassán <i>et al.</i> (2009) ^[39] and Shariatmadari <i>et al.</i> (2013) ^[166]
Phosphate solubilisation	<i>Pseudomonas</i> , <i>Bacillus</i> , <i>Rhizobium</i>	<i>Stevia rebaudiana</i>	Mamta <i>et al.</i> (2010) ^[130] , Schoebitz <i>et al.</i> (2013) ^[163] and Oteino <i>et al.</i> (2015) ^[141]
Iron sequestration	<i>Alcaligenes</i> , <i>Pseudomonas</i> , <i>Bacillus</i>	Pigeon pea	Gamit and Tank (2014) ^[68]
Zinc solubilisation	<i>Burkholderia</i> , <i>Pseudomonas</i> , <i>Bacillus</i>	Maize, rice	Goteti <i>et al.</i> (2013) ^[77] , Vaid <i>et al.</i> (2014) ^[192] and Sunithakumari <i>et al.</i> (2016) ^[178]
Potassium solubilisation	<i>Bacillus</i> , <i>Pseudomonas</i>	<i>Pinus canariensis</i> , <i>Cucumis sativus</i>	Bagyalakshmi <i>et al.</i> (2012) ^[19] , Parmar and Sindhu (2013) ^[143] and Prajapati and Modi (2016) ^[151]
Phytohormone production	<i>Bacillus</i> , <i>Rhizobium</i> , <i>Pseudomonas</i>	Chick pea, onion	Khare and Arora (2010) ^[106] , Reetha <i>et al.</i> (2014) ^[154] and Pandya and Desai (2014) ^[142]

Table 2: Indirect mechanism of PGPR (Deka *et al.* 2015) ^[52]

Mechanism	Effect	References
Plant growth regulator production	Biomass (aerial part and root)	Gutierrez Manero <i>et al.</i> (1996) ^[83]
Flowering		Gutierrez Manero <i>et al.</i> (2001) ^[84]
Ethylene synthesis inhibition	Root length	Glick <i>et al.</i> (1994) ^[73]
Induction of systemic resistance	Health	Van Loon <i>et al.</i> (1998) ^[193]
Root permeability increase	Biomass and nutrient absorption	Sumner (1990) ^[177]
Organic matter mineralization (nitrogen, sulfur, phosphorus)	Biomass and nutrient content	Liu <i>et al.</i> (1995) ^[123]
Mycorrhizal fungus association	Biomass and phosphorus content	Germida and Walley (1996) ^[70]
Insect pest control	Health	Zehnder <i>et al.</i> (1997) ^[207]

Interactions between PGPR and conifers have been studied in the genera *Araucaria*, *Picea* (spruce), *Pinus*, *Pseudotsuga* (Douglas fir) and *Tsuga* (hemlock) by number of workers (Bent *et al.* 2001; Brunetta *et al.* 2007; Vasconcellos and Cardoso 2009; Singh *et al.* 2010) ^[28, 33, 198, 171]. The best-studied PGPR belong to *Arthrobacter*, *Curtobacterium*, *Bacillus*, *Burkholderia*, *Chryseobacterium*, *Enterobacter*, *Paeni Bacillus*, *Phosphoro Bacillus*, *Pseudomonas*, *Staphylococcus*, *Serratia* and *Streptomyces* (Enebak *et al.* 1998; Garcia *et al.* 2004; Barriuso *et al.* 2005) ^[63, 69, 25]. An extensive screening of PGPR in conifers was carried out by Barriuso *et al.* (2005) ^[25] in the rhizosphere of *Pinus pinea* and *Pinus pinaster*, when these were colonized by ectomycorrhizal fungus (EMF) *Lactarius deliciosus*. Earlier, growth promotion of *P. pinea* by PGPR was reported by Garcia *et al.* (2004) ^[69].

PGPR and plant growth regulation

Plant growth regulators (PGRs) are phytohormones that are generated in certain organs of the plant and then translocated to other regions, where they trigger unique biochemical, physiological and morphological roles in plant growth and development (Hayat *et al.* 2012) ^[91]. Auxins, gibberellins, cytokinins, ethylene and abscisic acid are five well-known phytohormones and soil microorganisms, particularly rhizosphere bacteria, are potential producers of these hormones (Patten and Glick 1996; Arshad and Frankenberger 1998) ^[144, 16]. By managing and modifying phytohormones and growth regulators, PGPR promotes drought-stressed plant growth (Bresson *et al.* 2014) ^[32]. Gibberellins and cytokinins promote plant development while ET and abscisic acid prevent it (Taiz and Zeiger 2010) ^[180]. In both symbiotic and

nonsymbiotic roots, phytohormones are known to mediate processes such as plant cell expansion, division, and extension. Among these hormones, auxins have received the greatest attention, with indole-3-acetic acid (IAA) being the most common and well-studied. IAA is known to drive both short-term (e.g., cell elongation) and long-term (e.g., cell division and differentiation) responses in agricultural plants (Govindasamy *et al.* 2010) ^[79]. Root-associated microbes, such as symbiotic or endophytic bacteria, play an important role in the production of plant growth hormones (phytohormones), which affect seed germination, root system development for better nutrient uptake, vascular tissue development/elaboration, shoot elongation, flowering and overall plant growth (Sgroy *et al.* 2009) ^[165]. Hormone levels in plants can be controlled by microbe-produced plant growth regulators, which have effects similar to exogenous plant phytohormonal treatments (Egamberdieva, 2009; Turan *et al.* 2014) ^[58, 188]. Microbe-produced phytohormones like auxins and cytokinins are similar to plant-produced phytohormones in that they regulate plant hormone levels, regulating photosynthetic processes to promote plant growth and development and activating pathogen defence responses (Backer *et al.* 2018) ^[18]. Auxins are a category of hormones that help plants grow and develop. Indole Acetic Acid (IAA) is the most frequent and physiologically active phytohormone in plants, and it regulates gene expression by upregulating and downregulating it. IAA is produced by plant shoot apical meristems as free/diffusible auxins and is detected in practically all plant tissues (Maheshwari *et al.* 2015) ^[127]. More than 80% of rhizospheric bacteria have been found to be capable of synthesising and releasing auxins. *Aeromonas*, *Azotobacter*, *Bacillus*, *Brady Rhizobium*, *Burkholderia*,

Enterobacter, *Meso Rhizobium*, *Pseudomonas*, *Rhizobium* and *Sino Rhizobium* all produce IAA, which is produced by a variety of bacterial genera including *Aeromonas*, *Azotobacter*, *Bacillus*, *Brady Rhizobium*, *Burkholderia*, *Enterobacter*, *Meso Rhizobium* (Ahmad *et al.* 2008; Celloto *et al.* 2012; Sharma *et al.* 2016; Çakmakçı *et al.* 2020) [7, 41, 168, 35]. A single bacterial strain can create IAA via many pathways in some situations. These biosynthesis routes can be independent of or dependent on tryptophan, a key IAA precursor molecule (Kashyap *et al.* 2019) [104], with mechanisms sourced from degraded roots or bacterial cell exudates (Spaepen *et al.* 2007; Egamberdieva *et al.* 2017) [174, 59]. The capacity of rhizospheric beneficial bacteria to manufacture IAA under salinity stress conditions could be critical for balancing and controlling IAA levels in the roots, resulting in enhanced plant responses to salinity stress (Egamberdieva *et al.* 2015) [60]. Microbe-produced IAA has recently been shown to boost root and shoot biomass output in water-stressed situations (Kumar *et al.* 2019). Many PGPR-produced phytohormones, including indole lactic acid (ILA), indole-3-butyric acid (IBA), indole-3-propionic acid (IPA), indole-3-pyruvic acid (IPA), 2,4-dichlorophenoxy acetic acid (2,4-D) and 2-methyl-4-chlorophenoxy acetic acid (MCPA) and tryptophol (TOL), can control various physiological processes (Ijaz *et al.* 2019; Swarnalakshmi *et al.* 2020) [97, 179]. PGPR with the ability to produce plant growth-regulating hormones, like auxins and cytokines, were tested on *P. contorta* (lodgepole pine) (Bent *et al.* 2002) [29].

Cytokinins are a type of hormone that affects plant growth and development by regulating physiological processes such as seed germination, cell division, apical dominance, root and shoot growth, flower and fruit production, leaf senescence, pathogen interactions and nutrient mobilisation and assimilation (Egamberdieva *et al.* 2015; Akhtar *et al.* 2020) [60, 8]. It has been observed that cytokinin, either alone or in combination with other phytohormones like auxin and abscisic acid, can enhance the growth of salt-stressed plants while also improving tolerance via modifying gene expression (Kang *et al.* 2012; Kunikowska *et al.* 2013) [102]. PGPR such *Arthrobacter*, *Bacillus*, *Azospirillum* and *Pseudomonas* have been shown to manufacture cytokinins, which have been shown to have beneficial effects on the root system. Plant

growth and development are aided by cytokinin-producing PGPR, which are also powerful biocontrol agents against a variety of diseases (Naz *et al.* 2009; Maheshwari *et al.* 2015) [138, 127]. Plants and plant-associated microbes are known to have more than 30 growth-promoting cytokinin chemicals that are produced at varied quantities (Hayat *et al.* 2012; Amara *et al.* 2015) [91, 11]. In the past two decades, several studies have reported the effects of cytokinin producing PGPR on root system architecture, plant growth and tolerance to biotic and abiotic stresses including drought (Arkhipova *et al.* 2007; Dodd *et al.* 2010; Egamberdieva *et al.* 2015) [15, 55, 60], salinity (Naz *et al.* 2009; Cordero *et al.* 2018) [138, 47], bacterial pathogens (Naseem *et al.* 2014) [137], fungal pathogens (Mishra *et al.* 2018) [132] and insect pests (Giron and Glevarec 2014; Zhang *et al.* 2019) [72, 208].

Alexandre *et al.* 2021 reported that Arbuscular Mycorrhizal Fungi (*Rhizophagus clarus*) and Rhizobacteria (*Bacillus subtilis*) can improve the clonal propagation and development of Teak for Commercial Plantings. Aditya (2009) [5] reported on co-inoculation effects of nitrogen fixing and phosphate solubilizing microorganisms on teak (*Tectona grandis*) and Indian redwood (*Chukrasia tubularis*) that the effect of nitrogen fixing *Azotobacter* and phosphate solubilizing *Bacillus megaterium* on the growth of two trees; Teak (*Tectona grandis*) and Indian redwood (*Chukrasia tubularis*) were tested under nursery condition. Seed priming with beneficial micro-organisms including fungi and bacteria (*Trichoderma*, *Pseudomonas*, *Bacillus*, *Rhizobia* etc.) ameliorates a good sort of biotic, abiotic and physiological stresses to seed and seedlings (Sharma *et al.* 2015) [169]. PGPR had a wide range of impact on conifers (Table 3). These biological seed treatments may provide an alternate to chemical control of the pests and diseases and also increase the plant growth. Seed bioprimering allows the bacteria to enter/adhere the seeds and also acclimatization of bacteria within the prevalent conditions (Mahmood *et al.* 2016) [128]. PGPR are a good range of root colonizing bacteria which may produce IAA like compounds (Kandoliya and Vakharia 2013) [101], enhance plant growth by increasing seed emergence, plant growth and crop yield (Kloepper 1992) [109].

Table 3: The most studied PGPR in conifers, their mode of action, the host plants (Cardoso *et al.* 2011)

Action	PGPR	Effects on plants	Conifer species	References
Hormones	<i>Bacillus</i> sp. <i>Pseudomonas fluorescens</i> M20; <i>P. fluorescens</i> BSP53a; <i>P. polymyxa</i> L6; <i>Chryseobacterium balustinum</i> ;	Root length; shoot dry weight; root weight; seed germination	<i>Pinus pinaster</i> ; <i>P. pinea</i> ; <i>P. roxburghii</i>	Barriuso <i>et al.</i> (2005) [25]; Bent <i>et al.</i> (2001) [29]; Dubeikovskiy <i>et al.</i> (1993) [56]; Singh <i>et al.</i> (2008, 2010) [172]
Siderophores	<i>Arthrobacter oxydans</i> <i>Bacillus</i> sp <i>Pseudomonas fluorescens</i> ; <i>Staphylococcus</i> sp;	Root length; shoot dry weight; root weight; seed	<i>P. pinaster</i> ; <i>P. pinea</i> ;	Barriuso <i>et al.</i> (2005) [25]; Singh <i>et al.</i> (2008, 2010) [172]
Phosphate solubilization	<i>Arthrobacter oxydans</i> <i>Curtobacterium</i> sp.; <i>Burkholderia</i> sp.; <i>Staphylococcus</i> sp.; <i>Pseudomonas fluorescens</i>	Germination Shoot height and dry Mass	<i>P. roxburghii</i> <i>P. pinaster</i> ; <i>P. pinea</i> ; <i>P. halepensis</i> ; <i>P. roxburghii</i>	Barriuso <i>et al.</i> (2005) [25]; Rincón <i>et al.</i> (2008) [157]; Singh <i>et al.</i> (2008, 2010) [172]
MHB	<i>B. cereus</i> ; <i>B. sphaericus</i> ; <i>P. fluorescens</i> ; <i>Streptomyces</i> sp.	Root length; Shoot length; No. leaves initiated; Shoot dry weight; Root dry weight	<i>P. sylvestris</i> ; <i>P. contorta</i> ; <i>P. taeda</i> ; <i>P. elliotii</i> ; <i>Pseudotsuga menziesii</i> ;	Bending <i>et al.</i> (2002) [27]; Frey-Klett <i>et al.</i> (1999) [67]; Schrey <i>et al.</i> (2005) [164]
Induced systemic resistance	<i>Streptomyces</i> sp. <i>P. fluorescens</i> ; <i>Chryseobacterium balustinum</i> ; <i>Enterobacter intermedius</i> ; <i>Phosphorobacillus latus</i>	Root length; shoot dry weight; root weight; neck root diameter; stem length; Incorporation of thymidine and leucine	<i>Picea abies</i> <i>Picea abies</i> <i>P. pinea</i> ;	Lehr <i>et al.</i> (2008) [120] Garcia <i>et al.</i> (2004) [69]
Antagonism	<i>B. subtilis</i> ;	–	<i>P. roxburghii</i>	Singh <i>et al.</i> (2008, 2010) [172]

ACC degradation	<i>P. aeruginosa</i> <i>Staphylococcus</i> sp.	–	<i>P. pinaster</i> ; <i>P. pinea</i>	Barriuso <i>et al.</i> (2005) [25]
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PGPR and Nitrogen fixation

Nitrogen is a fundamental requirement for the synthesis of nucleic acids, proteins, and other organic nitrogenous substances in all forms of life. Despite the fact that the atmosphere contains roughly 78 percent nitrogen, it is very inert and unavailable to growing plants. The process of biological N₂ fixation (BNF), in which nitrogen-fixing bacteria convert elemental nitrogen into ammonia utilising a complicated enzyme system known as nitrogenase, converts atmospheric N₂ into plant-usable forms (Kim & Rees 1994) [107].

Nitrogen fixing organisms are generally categorized as

1. Symbiotic N₂-fixing bacteria including members of the family rhizobiaceae (*Rhizobium*, *SinoRhizobium*, *Brady Rhizobium*, *Meso Rhizobium* and *Azo Rhizobium*, collectively termed rhizobia) which forms symbiosis with leguminous plants (Zahran 2001) [204] and nonleguminous trees (e.g. *Frankia*).
2. Non-symbiotic (free living, associative and endophytes) nitrogen fixing forms such as cyanobacteria (*Anabaena*, *Nostoc*), *Azospirillum*, *Azotobacter* and *Azocarus*, etc.

(Bhattacharyya & Jha, 2012) [30]. In the rhizobia legume symbiosis, the signalling pathways (Long 2001), evolutionary history (Henson, Watson, & Barnum 2004) [94] and molecular features affecting host specificity (Young, Mutch, Ashford, Zeze & Mutch 2003) have all been reviewed. BNF contributes 106 metric tonnes per year globally, with symbiotic nitrogen fixation accounting for 80% and free-living nitrogen fixation accounting for the remaining 20%. As a result, BNF represents a cost-effective and environmentally friendly alternative to the current agricultural practise of using high doses of chemical fertilisers (Adesemoye, Torbert, & Kloepper 2009) [4].

Biological inoculants have gained popularity in recent years for sustainable crop production in various parts of the world, and biological nitrogen fixation is a key source of N input in agricultural soils, especially those in arid regions. The cyanobacteria *Rhizobium*, *Azo Rhizobium*, *Brady Rhizobium*, *Sino Rhizobium*, *Allo Rhizobium*, *Meso Rhizobium* and *Frankia* are symbiotic nitrogen-fixing bacteria (Paul and Clark 1996) [146]. The mechanisms of *Rhizobium*-legumes symbiotic N₂ fixation have been extensively researched. *Frankia*'s symbiosis with non-leguminous actinorhizal plants is also being studied these days. The principal N₂-fixation mechanism, the symbiotic system, plays a critical role in enhancing the fertility and maximising production of low-N soils.

Biological N₂-fixed by the *Rhizobium*-legume symbiosis can also benefit cereals grown in intercrops or crops cycled with legumes. The grasses in many natural grassland systems utilise nitrogen fixed by their legume counterparts to meet their nitrogen needs, and the protein provided as a result of this connection improves the fodder quality for animal production (Paynel *et al.* 2001) [147]. Rhizobia as PGPR can contribute to growth promotion in non-legume species in addition to symbiotic N₂ fixation in legumes (Höflich *et al.* 2000) [95]. Rhizobia naturally produce molecules that promote crop growth (auxins, abscisic acids, cytokinins, riboflavin, lumichrome, lipo-chitooligosaccharides and vitamins) to act as PGPR, and their colonisation and infection of cereal roots

would be expected to increase vigour and grain yield (Matiru and Dakora 2004) [131]. *Rhizobium*'s other PGPR roles include phytohormone production (Arshad and Frankenberger 1998) [16], inorganic phosphorus solubilization (Chabot *et al.* 1996) [42], siderophore release (Plessner *et al.* 1993; Jadhav *et al.* 1994) [149, 98] and antagonism against plant pathogenic bacteria (Ehteshamul-Haque and Ghaffar 1993) [62].

PGPR and phosphorus solubilisation

Phosphorus (P) is one of the most important macronutrients for plant growth and development and insufficient P availability to crop plants is a global problem. P availability reduces crop output on 30-40% of the world's arable land (Vance, Uhde-Stone, & Allan 2003) [195]. PSBs (phosphate solubilizing bacteria) may play a key role in providing phosphate to plants in a more environmentally friendly and long-term manner. Mineral forms such as apatite, hydroxyapatite and oxyapatite, as well as organic forms such as inositol phosphate (soil phytate), phosphomonoesters, phosphodiester and phosphotriesters, are found in soil. Phosphate-solubilizing bacteria (PSB) are one of the most essential bacterial physiological features in soil biogeochemical cycles (Jeffries, Gianinazzi, Perotto, Turnau, & Barea 2003) [99], as well as in plant growth promotion by PGPR.

Bacillus, *Rhizobium*, and *Pseudomonas* bacteria have been found to be the most effective phosphate solubilizing bacteria (Banerjee *et al.* 2010) [23]. The most common PSB bacteria include *Azotobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Pseudomonas*, *Rhizobium* and *Serratia* (Bhattacharyya & Jha, 2012) [30]. *Azotobacter chroococcum*, *Bacillus circulans*, *Cladosporium herbarum*, *BradyRhizobium japonicum*, *Enterobacter agglomerans*, *Pseudomonas chlororaphis*, *Pseudomonas putida* and *Rhizobium leguminosarum* are some examples of widely reported P-solubilizing microbial species intimately associated with a wide range of agricultural crops (Antoun, Beauchamp, Goussard, Chabot, & Lalande 1998; Cattelan, Hartel, & Fuhrmann 1999; Chabot, Beauchamp, Kloepper, & Antoun 1998) [14, 40, 43]. There have also been cases of phosphate solubilization by *Azotobacter*, a non-symbiotic nitrogen fixer (Kumar *et al.* 2001) [113]. *Rhizobium* (e.g., *Rhizobium/Brady Rhizobium*) phosphate-solubilizing activity is linked to the synthesis of 2-ketogluconic acid, implying that the organism's phosphate-solubilizing activity is solely attributable to its capacity to lower medium p^H (Halder and Chakrabarty 1993) [87]. The ability to dissolve phosphate also depends on the type of nitrogen source utilised in the media, with more solubilization in the presence of ammonium salts than in the presence of nitrate. This is thought to be due to protons being extruded to compensate for ammonium uptake, resulting in a lower extracellular p^H (Roos 1984) [158]. The action of low molecular weight organic acids generated by diverse soil bacteria typically results in the solubilization of inorganic phosphorus (Zaidi, Khan, Ahemad & Oves 2009) [206]. In contrast, organic phosphorus is mineralized through the production of a variety of phosphatases that catalyse the hydrolysis of phosphoric esters (Glick, 2012). Phosphate solubilization and mineralization can coexist in the same bacterial strain (Tao, Tian, Cai, & Xie 2008). Phosphorus solubilizing bacteria not only provide P to plants, but they

also help them grow by increasing the efficiency of BNF and increasing the availability of other trace elements (Tao, Tian, Cai, & Xie 2008) such as iron, zinc. The possibility of enhancing P uptake of crops by inoculation with P-solubilizing strains of PGPR presents a promising approach towards recovering the reservoirs of insoluble phosphorus from the soil and thus minimizing the external application of phosphate fertilizers to the soil.

PGPR in phytoremediation

Plant and microbe interactions are used in green technology to improve contaminated soil. Phytoremediation is a cost-effective, ecologically friendly, solar-powered soil remediation method that depends on plants' ability to intercept, take up, accumulate, sequester, stabilise, or translocate pollutants. Abiotic and biotic factors such as soil pH, soil components, nutrient availability, plant selection and kind of contaminants all influence phytoremediation (Thijs *et al.* 2016) [184]. It has recently been discovered that the effectiveness rate of phytoremediation is significantly dependent on the plant microbiome (Hou *et al.* 2019) [101]. When PGPR are introduced to a contaminated site, they boost the ability of plants to store heavy metals, recycle nutrients, maintain soil structure, detoxify pollutants, and manage diseases and pests; PGPR also reduces metal toxicity by modifying their bioavailability in plants. Root exudates such as free amino acids, proteins, carbohydrates, alcohols, vitamins, and hormones, which are significant sources of sustenance for microbes, are provided by the plants (Tak *et al.* 2013) [189]. Researchers have described a biological application of PGPR for heavy metal phytoremediation and salt-impacted soil phytoremediation (Nakkeeran *et al.* 2006; Barea 2015; Le Mire *et al.* 2016) [141, 24, 122]. Plant-microbiome interactions are currently being explored as part of a metaorganism strategy to determine the most promising strategies to improve phytoremediation success rates.

The role of

- a) Plant host selection.
- b) Root exudates.
- c) Investigation of single or microbial consortium *in situ*.
- d) Molecular study of PGPR strains are all combined in the PGPR-based metaorganism approach (Thijs *et al.* 2016) [184].

PGPR for biocontrol

Through antibiosis, parasitism, competition for resources and space in the vicinity of plant roots, and/or activation of host defence responses, PGPR indirectly aids plant growth by suppressing harmful bacteria that restrict plant growth or root diseases (Podile and Kishore 2006) [150]. *Bacillus subtilis* strains are the most extensively utilised PGPR because of their disease-fighting and antibiotic-producing capacities (Kokalis-Burelle *et al.* 2006) [112]. *Fluorescent pseudomonads* are also known to reduce soil-borne fungal diseases by creating antifungal compounds and sequestering iron in the rhizosphere by releasing iron-chelating siderophores, making it unavailable to other species (Dwivedi and Johri 2003) [57]. Suppression of deleterious microorganisms by PGPR is mainly by parasitism, by competing for available nutrients, production of enzymes or toxins and inducing resistance by activating plant defence response against pathogens (Podile and Kishore 2006) [150]. *Fluorescent pseudomonads* attach themselves to plant roots and absorb available nutrients, reducing the nutrients available for disease growth (Walsh *et*

al. 2001) [201]. For pathogen eradication, PGPR competes for resources with native rhizosphere microorganisms. Siderophore synthesis by PGPR sequesters the majority of available Fe³⁺ in the rhizosphere, forcing pathogens to become iron-deficient and is hence a key contributor to pathogen suppression (O'Sullivan and O'Gara 1992) [140]. The PGPR synthesises hydrolytic enzymes, enhances nutrient competition, regulates the level of the plant hormone ethylene via the ACC-deaminase enzyme and creates siderophores to protect the rhizosphere from plant diseases (Kumari *et al.* 2016; Anand *et al.* 2016) [114, 12]. There are numerous examples of PGPR being used to effectively control soil-borne illnesses (Haas and Defago 2005) [86].

PGPR and biotic stress tolerance

Drought, salinity, high and low temperatures, heavy metal toxicity, and nutrient deficiency are all examples of extreme environmental conditions that can cause significant annual reductions in overall crop production, yield and quality worldwide as climate change risks arise (Acquaah 2009; Awasthi *et al.* 2014; Shrivastava and Kumar 2015) [3, 17, 170]. Living organisms, such as bacteria, viruses, fungi, insects and nematodes, cause biotic stress in plants (Hamid *et al.* 2021) [88]. The accumulation of specific solutes, such as proline, sugars, polyamines, betaines, polyhydric alcohols and other amino acids, results in PGPR-mediated plant osmolytes homeostasis, which plays a key role in maintaining turgor-driven cellular swelling to withstand osmotic stress caused by drought and high soil salinity (Vurukonda *et al.* 2016) [200]. PGPR releases osmolytes that function in tandem with those produced by plants to improve plant growth and development and so maintain plant health (Sandhya *et al.* 2010; Vardharajula *et al.* 2011) [160, 196]. Another study found that using a combination of PGPR, compost, and mineral fertiliser resulted in increased amounts of soluble sugar and proline, which improved wheat's capacity to retain membrane stability, chlorophyll content and water potential under stress (Kanwal *et al.* 2017) [103].

PGPR in seed priming

Soaking seeds in bacterial solution activates physiological processes in the seed, preventing plumule and radicle development until the seeds are exposed to temperature and oxygen after being sowed (Anita *et al.* 2013) [13]. Even before sowing, PGPR continue to replicate in the seed and proliferate in the spermosphere (Taylor and Harman 1990) [183]. Seed biopriming is being studied because it allows endophytic bacteria to enter the sidewalls while avoiding the harmful effects of high temperatures. The use of a biopriming treatment may help to promote faster and more even germination, as well as improved plant growth (Moeinzadeh *et al.* 2010) [133]. In crops such as carrot (Jensen *et al.* 2004) [100], sweet corn (Callan, Mathre and Miller 1990, 1991) [37] and tomato (Callan, Mathre and Miller 1990, 1991) [37], biopriming using rhizospheric bacteria has been documented (Harman and Taylor 1988; Legro and Satter 1995; Warren and Bennett 1999) [89, 119, 202]. When it comes to the efficacy and survivability of biological agents, priming has been shown to be advantageous and to improve plant growth and yield (Harman, Taylor and Stasz 1989; Callan, Mathre and Miller 1990, 1991; Warren and Bennett 1999) [90, 37, 202]. Seed priming with PGPR results in better germination and seedling establishment (Anita *et al.* 2013) [13]. When combined with bacterial coating, bio-osmopriming can

considerably improve the uniformity of germination and plant growth features. When uniform germination and superior stand establishment choices are taken into account, biopriming is the preferred strategy. Biopriming has been practised and explained in a variety of ways by various researchers (Callan, Mathre and Miller 1991; Bennett, Mead, and Whipps 2009; Moeinzadeh *et al.* 2010) [36, 27, 133]. There are many methods for explaining biopriming, which differ in the temperature and length of time the seeds are soaked (Gholami, Shahsavani and Nezarat 2009; Abuamsha, Salman, and Ehlers 2011) [71, 2]. Some of the researchers have also surface disinfected the seeds before soaking into the bacterial

suspension (Sharifi, Khavazi and Gholipouri 2011; Firuzsalari, Mirshekari and Khochebagh 2012) [167, 65]. Biopriming of *Abies hickelii* and *A. religiosa* with *Pseudomonas fluorescens* alongside hydropriming has shown a rise within the germination percentage up to 91.45% in *A. hickelii* and 68% during *A. religiosa* (Rodriguez *et al.* 2015). Alwathnani *et al.* (2012) [10] demonstrated the antagonistic effect of *Trichoderma harzianum* and *Trichoderma viride* against *Fusarium oxysporum* as inhibition of radial growth of pathogen. Bio priming with *Pseudomonas fluorescens* improved flooding tolerance in Sandal (*Santalum album*) seedlings. (Chitra *et al.* 2021) [46]

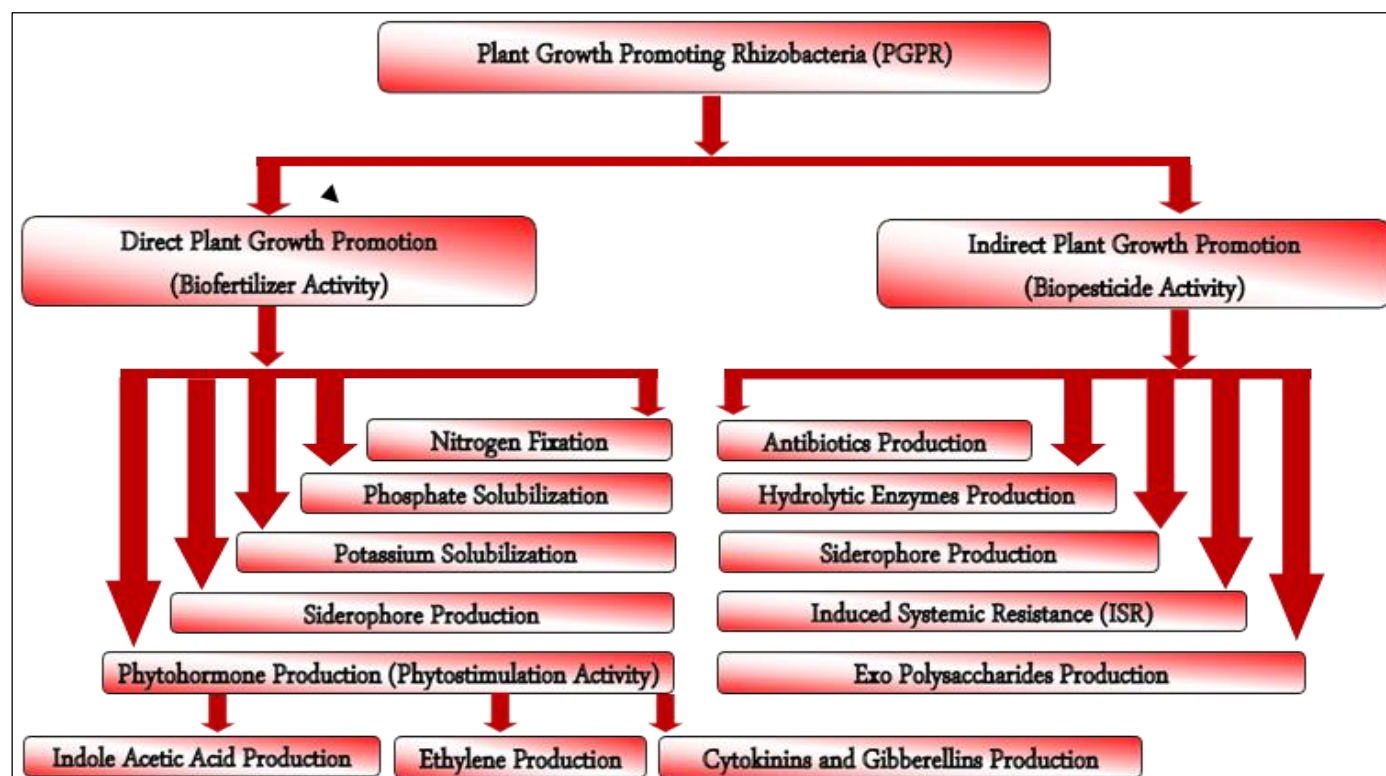


Fig 1: Mode of action of Plant Growth Promoting Rhizobacteria (Gupta *et al.* 2015) [81]

Conclusion

Recently, studies on PGPR have attained more significant and scientific attention. PGPR plays an essential role in helping plants to establish and grow in nutrient deficient conditions. Considering the good impact of PGPR in terms of biofertilization, biocontrol, and bioremediation, all of which exert a positive influence on crop productivity and ecosystem functioning, encouragement should be given to its implementation in agriculture. Several PGPR stains are being commercialized for various crops in agriculture and these are widely used. By exploiting the PGPR from forest ecosystem, it is possible to develop microbiome and these can be well utilized for plantations trees and also for agriculture crops, since forest is a source of diversified microbes, flora and fauna, which can be well exploited for the natural sources.

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