



# Plant growth promoting rhizobacteria to reduce stress and sustainable crop production

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**Abstract :** The increasing demand for crop production, with a focus on high-quality, safe, and affordable food, requires targeted efforts to meet production needs. Agriculture faces numerous challenges today, including the widespread use of chemical fertilizers and pesticides, soil fertility loss, unpredictable climate conditions, and a rise in pathogens and pests. To tackle these issues, there is a necessity to shift towards sustainable agricultural practices, embracing the use of biofertilizers, biopesticides, and the return of crop residues in lieu of conventional chemical fertilizers to restore agro-ecosystems. Taking advantage of beneficial soil microorganisms as biofertilizers presents a biological approach to sustainably intensify agriculture. Plant growth-promoting rhizobacteria (PGPR), naturally occurring soil bacteria found in the rhizospheric region of plants, play a crucial role. They stimulate growth and productivity through various direct and indirect mechanisms. Directly, PGPR contribute to soil nutrient enrichment via actions like nitrogen fixation, phosphate solubilization, siderophore production, and phytohormone production. They also enhance plant defence by initiating induced systemic resistance (ISR) against pests and pathogens. Furthermore, PGPR indirectly promote plant growth by providing useful variations to tolerate abiotic stresses, such as extreme temperatures, pH fluctuations, salinity, drought, and exposure to heavy metals and pesticides. This review provides an overview of different types of PGPR-based biofertilizers, outlines the mechanisms these microbes employ as growth promoters, and underscores their benefits. Importantly, PGPR play a supportive role in sustainable and eco-friendly agriculture, positively influencing productivity without causing adverse effects on the environment or the health of living beings.

**Keywords:** *Biofertilizer, Plant growth promoting rhizobacteria (PGPR), Plant growth, Soil health, Sustainability.*

## Introduction

In the present scenario, there is a decrease of land resources and a loss of biological diversity. By 2050, there will be about 10 billion people on the earth, putting great strain on the world's existing food resources (United Nations, 2015). Although global crop production can be augmented through agricultural intensification, which mainly relies on the use of

chemical agro-inputs like fertilizers, poses number of negative environmental effects (Vassilev et al., 2015). For instance, the nitrate contamination of ground water has been linked to excessive nitrogen fertilizers, and the eutrophication of ponds and rivers has been related to phosphate run-off in surface waters that fuels issues like global warming and climatic changes (Carmo et al., 2013). The long-term artificial fertilization by chemical means may also result in the deterioration of soil quality

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and productivity through acidification (Neog, 2018, Yan *et al.*, 2020). Imbalance in nitrogen cycling, nutritional status, physical and biological characteristics of soil, pests and disease incidence, climatic factors fluctuation and abiotic stresses are the other interlinked contributing factors for reduced agricultural productivity (Gopalakrishnan, 2015).

Towards a sustainable agricultural vision, with a gradual decrease in the use of chemical fertiliser as well as the biological and genetic potential of crop plants and microorganisms, is an effective strategy to combat the rapid environmental deterioration while ensuring high agricultural productivity and better soil health (Liu *et al.*, 2016). The exploration of eco-friendly alternatives, such as the use of biofertilisers, will not only enhance productivity but also improve soil quality and health, as well as the environment and the health of living beings. These may be defined as artificially manufactured cultures of soil microorganisms or soil inoculants to improve the fertility and productivity of soil as well as plants (Singh *et al.*, 2019). These biological agents enhance the availability of nutrients to the plants and also ameliorate the physical, chemical and biological properties of soil (Tejada *et al.*, 2016).

Microorganisms are the legacy of soil, and they improve soil fertility in their unique way through various mechanisms. In addition to being essential for the production of food and fibre and in the maintenance of global nutrient balance, soil is the core house to millions and millions of microorganisms, specifically the rhizosphere zone (Bishnoi, 2015). Rhizo refers to the roots, while spherical refers to the surrounding environment. The rhizosphere, as defined by Bowen and Rovira (1999), is a tender zone of soil surrounding a plant root, having no defined edges in the zone (about 1-3mm) where living organisms are influenced by vital root activities (root exudates and respiration) qualitatively and quantitatively. Although the root gives the plant mechanical strength and aids in nutrition and water intake, the plant roots also release certain types of chemical substances known as plant root exudates. These chemical substances influences the rhizosphere and modifies the physical and chemical properties of soil that regulates the makeup of soil microbial

communities at the root surface (Dakora and Phillips, 2002). The rhizosphere is colonized by a wide range of microbial taxa, comprising both prokaryotes (archaea, bacteria and viruses) and eukaryotes (fungi, oomycetes, nematodes, protozoa, algae, and arthropods), out of which bacteria and fungi occupies the most abundant groups (Kalam *et al.*, 2017; Buee *et al.*, 2009) showing fundamental ecological functions. The term 'rhizobacteria' implies a group of rhizospheric bacteria found in the rhizosphere that are competent in colonizing the root environment (Kloepper *et al.*, 1991). Among the most interesting plant microorganisms as biofertilizers are the plant growth-promoting rhizobacteria (PGPR) that may act as a suitable substitute for minimizing the use of chemical fertilizers in crop production (Vessey, 2003 and Atieno *et al.*, 2020). Present review discusses various mechanisms that highlights the potential of PGPR which can be used as an effective tool to achieve better soil health and sustainable development in agriculture.

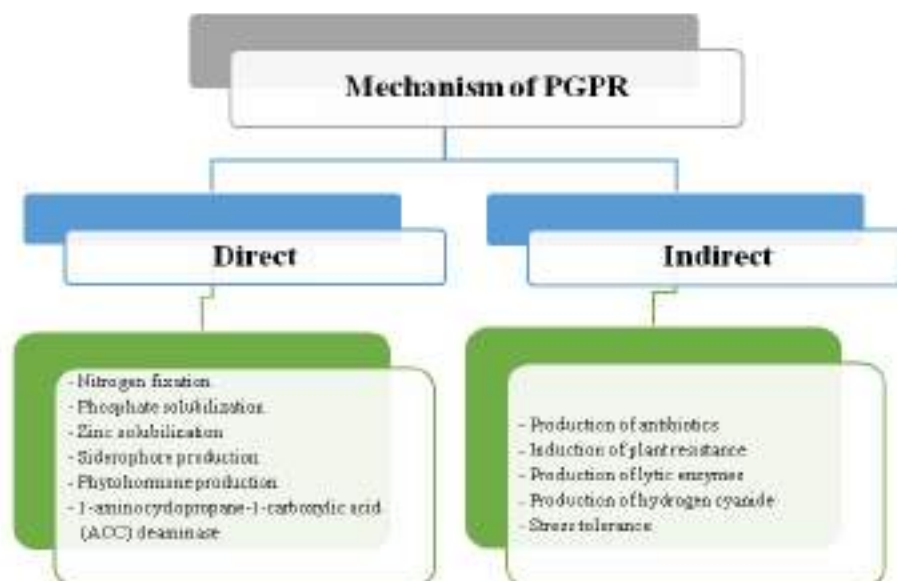
### **Plant growth promoting rhizobacteria (PGPR)**

The term plant growth promoting rhizobacteria (PGPR) was first coined by Kloepper and Schroth (1978). PGPR are generally free living, soil-borne bacteria, isolated from the rhizosphere, when applied to seed or crop augments the growth of the plant through at least one mechanism like suppression of plant disease (bioprotectants), improved nutrient acquisition (biofertilizers) or phytohormone production (biostimulants) (Kloepper *et al.*, 1980). They help in promoting growth directly by nitrogen (N<sub>2</sub>) fixation, phosphate solubilization, iron chelation and phytohormones production or indirectly by suppression of plant pathogenic organisms, induction of resistance in host plants against plant pathogens and abiotic stresses. According to their functions, these bacteria are given several names such as plant growth promoting rhizobacteria (PGPR), plant health promoting rhizobacteria (PHPR), emergence promoting rhizobacteria (EPR) and nodule promoting rhizobacteria (NPR) (Saxena and Tilak, 1994 and Podile and Dube, 1998).

Based on the nature of association with plant cell, PGPRs are further categorized as intracellular PGPR (i-PGPR) and extracellular PGPR (e-PGPR) (Gray and Smith, 2005). i-PGPR is found in the root cells generally in the nodular structure whereas e-PGPR is found in the root cortex cells rhizosphere (rhizoplane) or intracellular spaces. The i-PGPR includes the genera *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Azorhizobium*, *Mesorhizobium*, *Allorhizobium* whereas e-PGPR includes the genera *Bacillus*, *Pseudomonas*, *Erwinia*, *Caulobacter*, *Serratia*, *Arthrobacter*, *Micrococcus*, *Flavobacterium*, *Chromobacterium*, *Agrobacterium* and *Hyphomycrobium*. Beneficial effects of PGPR have been exploited in many areas including biofertilizers, microbial rhizomediation and biopesticides (Adesemoye *et al.*, 2008). In addition, recently, it has also been reported that some rhizobacteria contain an enzyme ACC-deaminase which can reduce ethylene biosynthesis in plants (Saini *et al.*, 2015). In this regard, the use of naturally occurring and environmentally safe products such as plant growth-promoting rhizobacteria (PGPR) has benefited the plants in a number of ways through direct uptake of iron, suppression of proliferation of fungal pathogens, improved N-fixation and prevention from heavy metal toxicity.

### Mechanism of action of plant growth promoting rhizobacteria

Being the dominant microbial community in the rhizosphere, PGPRs are directly or indirectly involved in plant growth promotion which eventually leads to the sustainable agricultural practices. They can act as biofertilizers that promote plants' growth and development by facilitating biotic and abiotic stress tolerance and supporting host plants' nutrition (Sagar *et al.*, 2020 and Mahadi *et al.*, 2020). Direct mechanisms of these rhizospheric microorganisms can improve plant growth by enhancing the uptake of nutrients via nitrogen fixation, phosphate solubilization, siderophore production and phytohormone (such as auxin, cytokinin, and gibberellins) production. They also improve plant defense by triggering systemic resistance induced against pests and pathogens. In addition, the indirect mechanisms of plant growth promotion such as useful variations to tolerate abiotic stresses such as extreme temperatures, pH, salinity and drought, heavy metal and pesticide pollution. The mechanisms by which bacteria can influence plant growth differ among species and strains (Castro *et al.*, 2009). The detailed mechanisms of PGPR action and their specific contribution to plant growth promotion have been reviewed comprehensively (Dutta and Podile, 2010; Bhattacharyya and Jha, 2012 and Gouda *et al.*, 2018).



**Fig. 1: Direct and indirect mechanisms in relation to PGPR**

### *Direct promotions*

#### **Nitrogen fixation**

Nitrogen (N), a critical component of all life forms, is an essential element for plant growth. It affects the composition of nucleotides, membrane lipids, and amino acids and is an important component of chlorophyll and protein. Nitrogen being a primary limiting factor due to losses from agricultural fields such as runoff and leaching is found deficient due to various environmental factors (Kumaret *al.*, 2021). Thus, biological alternatives are favored as they resolve concerns about economics, the atmosphere, and renewable energy. Biological nitrogen fixation (BNF) provides 65% of the nitrogen presently used in agriculture, which is considered important to sustain crop production systems in future (Dakora, 2003). BNF is a process of converting atmospheric nitrogen into plant assimilable N such as ammonia through a cascade of reactions between prokaryotes and plants with the use of complex enzyme systems such as nitrogenase (Wilson and Burris, 1947). Nitrogenase is an oxygen-sensitive enzyme that can be irreversibly inactivated. The process of nitrogen fixation is accomplished through the hydrolysis of 16 ATP (energy currencies).

Nitrogen fixation can be divided into two categories:

- Nitrogen fixation through symbiotic relationships
- Nitrogen fixation through non-symbiotic relationships.

In symbiotic nitrogen fixation, bacteria undergo nitrogen fixation through inter-relationships with legume crops and meet their own needs without depending external sources (Bhattacharyya and Jha, 2012; Gopalakrishnan *et al.*, 2015). Symbiotic bacteria involved in nitrogen fixation which act as PGPR are *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, and *Mesorhizobium* with leguminous plants, *Frankia* with non-leguminous trees and shrubs (Zahra, 2001). In case of non-symbiotic bacteria which are free living nitrogen fixers, fixes nitrogen acquiring through uptake, contribute to the nitrogen account of the plants (Goswami *et al.*, 2016). Various genera, such as *Azospirillum*, *Enterobacter*, *Gluconacetobacter* and *Pseudomonas*, carry out the non-symbiotic nitrogen

fixation process by stimulating the growth of non-leguminous plants (Bhardwaj *et al.*, 2014). The quantity of the N that is fixed by the symbiotic nitrogen fixation process is thought to be more essential than the non-symbiotic nitrogen fixation process because higher amount of nitrogen is fixed symbiotically (Bohlool *et al.*, 1992).

Nitrogen fixation is mediated by a particular gene called “nif” which activate the iron proteins, contribute an electron, manufacture of the iron molybdenum cofactor, and other regulatory genes that regulate enzyme activity needed for enzyme synthesizing and operation (Reed *et al.*, 2011). For improved N-fixation, rhizobia are often applied to leguminous seeds since in the absence of specific host plant they are able to survive in the natural soil system for many years (Sanginga *et al.*, 1994). Many PGPR strains plays a major role in nitrogen fixation and make it assimilable form for the plants. Inoculating biological N-fixing PGPR in field crops boosts plant growth and productivity, assists in disease management and regulate nitrogen levels in the soil (Daman *et al.*, 2016).

Nowadays N<sub>2</sub>-fixing biofertilizers are the most common in the global market and their demand is expected to grow by a further 11.9% compounding annual growth rate (CAGR), from the current USD 2.1 billion to about USD 4.5 billion by 2026. (Markets and Markets, 2020). It has been also reported that rhizobial inoculants can reduce the annual N fertilization costs by approximately USD 29 ha<sup>-1</sup> (Herridge *et al.*, 2008). This clearly depicts the importance of N<sub>2</sub>-fixing rhizobacteria as biofertilizers. Nevertheless, there is a need to perform field trials of new strains for suitability and adaptability before application as inoculants especially for crops like cereals, vegetables, and tubers, considering they contribute to the bulk of human food.

#### **Phosphate solubilization**

Phosphorus (P) is the second most essential macronutrient after nitrogen which plays a vital role in growth and development of plants as required in various pathways of photosynthesis, respiration, energy storage and transfer etc. in the living plant cells (Mukhtar *et al.*, 2017). It exists in both inorganic (bound, fixed, or labile)

and organic (bound or non-labile) forms. The availability of P to plants is influenced by pH, compaction, moisture, aeration, temperature, texture and organic matter of soils, crop residues, extent of plant root systems and root exudate secretions and available soil microbes (Gopalakrishnan *et al.*, 2015). P accounts for about 0.2–0.8 % of the plant dry weight, however, only 0.1 % of this P is available in soil for the plants (Zhou *et al.*, 1992). Phosphate anions are extremely reactive and may be immobilized through precipitation with cations like  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{Fe}^{3+}$  and  $\text{Al}^{2+}$  depending on particular properties of a soil. On the other hand, much of this P is in mineral form and becomes slowly available to the plants (Richardson *et al.*, 2009). As a result, application of phosphatic fertilizers is a must to make up for the P lost due to the fixation of soluble phosphate by the soil constituents (specifically cations) and phosphate run off in P-loaded soils (Vikram and Hamzehzarghani, 2008).

The role of microorganisms in solubilizing inorganic phosphates in soil and making them available to plants for their growth is well known (Bhattacharya and Jain, 2000). Since P deficiency is inherent in numerous agricultural soils, such organisms are largely proposed as potential P solubilizers. Phosphate solubilizing bacteria (PSB) are the key convertor of insoluble form of phosphate in soluble form by various ways and make it available for the plants (Chen *et al.*, 2006). They convert insoluble phosphates into soluble forms by acidification, secretion of organic acids or protons, chelation and exchange reactions and production of gluconic acid and make it available to plants for its easy take up to enhance plant growth and development (Meena *et al.*, 2017; Zhu *et al.*, 2012; Mahanta *et al.*, 2014). These bacteria secrete different types of organic acids which lower the pH in the rhizosphere and thus release the phosphorus available to plants (Kaur *et al.*, 2016).

Phosphate Solubilizing Bacteria (PSB) involved in P solubilization and mineralization act principally by acid phosphatases, catalysing the hydrolysis of phosphoric esters, is an important feature that is found in PGPR (Glick, 2012). Another mechanism of phosphate solubilization is by phytase

production, since organic P can constitute between 30 to 50% of the total P of the soil, a high content of which corresponds to phytate. This organic P is mainly mineralized by acid phosphatases, C-P lyase, D-glycerophosphate, phosphor hydrolases, phosphonoacetate hydrolase, and phytase making it accessible to plants (Turner *et al.*, 2003). Rhizobia, including *R. leguminosarum*, *R. meliloti*, *M. mediterraneum*, *Bradyrhizobium* sp. and *B. japonicum* are the common potential phosphate solubilizers (Vessey, 2003; Egamberdiyeva *et al.*, 2004; Rodrigues *et al.*, 2006). The phosphate solubilizing PGPR belonging to genera *Bacillus*, *Pseudomonas*, *Arthrobacter* and *Streptomyces* have gained much attention as it promotes plant growth and yield (Hamdali *et al.*, 2012; Jog *et al.*, 2014). The two species form chickpea nodules; *Mesorhizobium ciceri* and *Mesorhizobium mediterraneum* potentially can be considered among best P solubilizers (Parmar *et al.*, 2013). Backer *et al.* (2018) reported that inoculating the plants with PGPR can be an effective strategy to enhance the crop growth and yield through improving colonization of rhizosphere. The use of P solubilizing biofertilizers as bioinoculants can open up a new horizon for sustaining soil P levels and by large, sustainable crop production (Rizvi *et al.*, 2021).

### Zinc solubilization

Zinc (Zn) is a micronutrient crucial for plants, playing a role in regulating the production of various proteins, activating enzymes, and serving both catalytic and structural functions in plant metabolism at concentrations as low as 5-100 mg kg<sup>-1</sup> (Rana *et al.*, 2012). Plants predominantly absorb zinc as a divalent cation ( $\text{Zn}^{2+}$ ), but in calcareous and high pH soils, it is taken up as a monovalent cation  $\text{Zn}(\text{OH})^+$  (Meena *et al.*, 2017). Despite its significance in plant growth and metabolism, zinc deficiency is widespread in most arable lands, primarily due to nutrient depletion caused by crop harvesting (Cakmak *et al.*, 2017). To address zinc deficiency, chemical zinc fertilizers are commonly used to supplement these deficits. However, their high cost and limited conversion into a readily usable form for plants pose challenges (Montalvo *et al.*, 2016).

Recent literature highlights advancements in

rhizobacterial zinc solubilization (Joshi *et al.*, 2013; Kamran *et al.*, 2017; Perumal *et al.*, 2019), suggesting that the field application of zinc-solubilizing bacteria (ZSB) in crop plants can enhance zinc uptake, subsequently improving plant growth and yields. These bacteria employ various mechanisms for solubilization, including acidification. These microbes produce organic acids in the soil, which sequester zinc cations and reduce the pH of the surrounding soil (Alexander, 1997). Additionally, the anions produced can chelate zinc, enhancing its solubility (Jones and Darrah, 1994). Various strains like *Trichoderma* sp., *Providencia* sp., *Anabaena* sp., *Calothrix* sp., etc., have demonstrated significant zinc solubilization, resulting in the growth promotion and increased productivity of different plants, including wheat (Rana *et al.*, 2012; Santiago *et al.*, 2011).

Research by Naz *et al.* (2016) revealed that species like *Pseudomonas*, *Azotobacter*, *Azospirillum*, and *Rhizobium* significantly enhance zinc uptake in wheat. Similarly, Sharma *et al.* (2012) investigated 134 bacilli from the soybean (*G. max*) rhizosphere for zinc solubilization and found that the isolates substantially increased zinc concentration in inoculated crops compared to un-inoculated ones. Reports also exist on zinc-solubilizing abilities and increased zinc uptake following inoculation of wheat by *Pseudomonads* (Joshi *et al.*, 2013), maize by *Bacillus* (Hussain *et al.*, 2015), and wheat and rice by various ZSB (Perumal *et al.*, 2019).

### Siderophore production

Iron (Fe), being a transition metal ion and an essential micronutrient crucial for the growth and metabolism of all living organisms. It plays a vital role in electron transport chain, oxidation–reduction reactions, detoxification of oxygen radicals, synthesis of DNA precursors and in several other biochemical processes (Hider and Kong, 2010). It exists either in the divalent (ferrous or  $\text{Fe}^{2+}$ ) or trivalent (ferric or  $\text{Fe}^{3+}$ ) states which is determined by the pH and Eh (redox potential) of the soil and the availability of other minerals (e.g., sulphur is required to produce  $\text{FeS}_2$  or pyrite) (Bodek *et al.*, 1988). Although these are present

in the soil in larger amounts as it is 4<sup>th</sup> most abundant element on the Earth, but are usually found unavailable to the plants or microbes for their uptake due to their insoluble complex forms (Ma *et al.*, 2016). Fe under aerobic environments occurs in the form of insoluble hydroxides and oxyhydroxides that are unavailable to both plants and microbes (Rajkumar *et al.*, 2010). At neutral and alkaline pH, the Fe becomes insoluble under oxidized conditions which necessitate special mechanisms for Fe acquisition in most organisms.

In a Fe-deficient environment, microorganisms have evolved specialized mechanisms for the assimilations of iron, including production of Fe chelating compounds, known as siderophores (Saini *et al.*, 2015). The term 'Siderophore' was first coined in 1973 and defined as low molecular weight (500- 1000 Da) compounds that have the tendency to bind ferric iron with an extremely high affinity and thus makes the iron available for plants (Bindu and Nagendra, 2016). These compounds are produced in response to iron deficiency which normally occurs in neutral to alkaline soils, due to low Fe solubility at elevated pH (Sharma and Johri 2003). Siderophores produced by biofertilizers make it available to plants by converting into soluble and chelating from available complex organic or inorganic iron (Meena *et al.*, 2017). These are classified by the presence of ligands that chelate the  $\text{Fe}^{3+}$  iron. These include the catecholates, hydroxamates and carboxylates (Louden *et al.*, 2011). The strategy of microbial-origin siderophores in plant growth is unclear, in a low Fe environment, plant growth promotion (PGP) is thought to involve one of the following mechanisms (Kumar *et al.*, 2021):

- i. Microbial-origin siderophores having a high redox potential migrate from  $\text{Fe}^{2+}$  of iron to a plant's transport system by the apoplastic pathway.
- ii. Microbial-origin siderophores from soil chelate Fe and exchange ligands with plant origin siderophores (based on concentration, pH, and redox potential), the Fe free plant-origin siderophores bind with receptor protein for the first time. The membrane receptor and the  $\text{Fe}^{3+}$  siderophore transporter are the common

transporter for high affinity microbial acquisition of Fe (Neilands, 1981; Crowley *et al.*, 1991). To overcome the Fe limitation, bacteria release siderophores to scavenge Fe from these mineral phases by formation of soluble Fe complexes that can be taken up by active transport mechanisms (Saharan and Nehra, 2011). As a result, the secretion of siderophore by bacteria provide plants with Fe which enhances the plant growth directly by increasing the availability of iron in the soil surrounding the roots (Krewulak and Vogel, 2008; Vejan *et al.*, 2016).

The secretion of Fe siderophore complex by bacteria and its absorption by the plants to quench Fe thirst in calcareous and alkaline soil is a direct mechanism (Sharma and Johri, 2003), whereas chelation of soluble Fe by microbial siderophores result in shift in rhizospheric communities (Bano and Musarrat, 2003), being an indirect mechanism. PGPR, being a valuable asset has the ability to capture Fe through the siderophores and make it available to plants appears to be the most effective technique for meeting their Fe intake demand (Sayed *et al.*, 2013). In recent years, considerable interest has been paid to rhizobacteria, which are aggressive root colonizers and produce siderophores (Roy and Chakrabarty, 2000; Khandelwal *et al.*, 2002; Goswami *et al.*, 2014). Rathore (2014) has also reported that *Pseudomonasputida* enhanced the level of iron content in the natural habitat by utilizing heterologous siderophores produced by other microorganisms. Besides microbial Fe nutrition, siderophores can also form stable complex with heavy metals such as Al, Cd, Cu etc. that relieves the plants from heavy metal stress (Neubauer *et al.*, 2000). Many siderophores also play a very important role in microbial infection and shown to be a possible biocontrol agent for preventing plant diseases (Gouda *et al.*, 2018). Previous studies of Venkat *et al.*, 2017; Bindu and Nagendra, 2016 have showed prominent role of different siderophore producing microbial strains in growth promotion and bio-control activity. Thus, Siderophore producing microbes can be considered and should be given more

attention as an efficient PGPR which shows multifunctional potentiality in plant growth promotion (by various ways Sayyed *et al.*, 2004 and Aloo *et al.*, 2019).

### Phytohormone production

Phytohormones, also known as plant growth regulators are the organic compounds that stimulate promote, inhibit, or change plant growth and development at small proportions (<1 mM) (Damam *et al.*, 2016). These include indole-3-acetic (IAA) acid (auxin), cytokinins, gibberellins and abscisic acid. It regulates growth and development of plants by various physiological and metabolic activities like cell division, stem elongation, inhibition, root growth, activation of bud and development of branch, promotion or delay in leaf senescence, chlorophyll production etc (Meena *et al.*, 2017; Wong *et al.*, 2015).

*Indole-3-acetic acid (IAA)*: IAA is the member of the group of phytohormones and quantitatively the most abundant type of auxin that accelerates plant growth and development by improving root/shoot growth and seedling vigour (Gopalkrishnan *et al.*, 2015). This phytohormone auxin is a key regulator of many aspects of plant growth and development, including cell division, differentiation and vascular bundle formation and an essential hormone for nodule formation (Woodward and Bartel, 2005). Indole acetic acid (IAA) is a part of auxin and main precursor of cell division and elongation that influence growth of stem (Hayat *et al.*, 2010). Although plants are able to synthesize IAA themselves, 80% of the bacteria isolated from the rhizosphere can produce IAA (Patten and Glick, 1996).

In order to produce IAA, the bacteria use tryptophan as precursor (Asghar *et al.*, 2004). The release of tryptophan in root exudates may result in its conversion into IAA by rhizospheric microbes (Kravchenko *et al.*, 2004). The indole-3- acetamide (IAM) pathway is considered the most favoured pathway in bacteria (Patten and Glick 2002). The salient ones are *Aeromonas*, *Bacillus*, *Azotobacter*, *Burkholderia*, *Enterobacter*, *Pseudomonas* and *Rhizobium* genera (Swain *et al.*, 2007; Ahmad *et al.*, 2008). On inoculation of *R. leguminosarum* bv. *viciae*, 60-fold increase in IAA was reported in the

nodules of vetch roots (Camerini *et al.*, 2008). On inoculation of plants with PGPR, a change in root architecture is observed, mainly as an increase in root hairs and lateral roots and shortening of the root length. Also, rhizobacterial IAA loosens the plant cell wall and hence, facilitates an enhanced amount of root exudation that provides additional nutrients to support the growth of rhizosphere bacteria (Glick, 2012). Many researchers have also reported the *in vitro* IAA production, in *A. caulinodans*, *B. japonicum*, *B. elkanii*, *R. japonicum*, *R. leguminosarum*, *R. lupine*, *R. meliloti*, *R. phaseoli*, *R. trifolii* and *Sinorhizobium* spp. (Afzal and Bano, 2008; Biswas *et al.*, 2000; Boiero *et al.*, 2007; Chandra *et al.*, 2007; Senthilkumar *et al.*, 2009), *Pseudomonas aeruginosa* (Khare and Arora, 2010), *Acetobacter diazotrophicus* L1 (Patil *et al.*, 2011).

**Cytokinin:** Cytokinin's are a class of phytohormones which are known to promote cell divisions, cell enlargement and tissue expansion in certain plant parts (Werner *et al.*, 2003). Cytokinin plays a crucial role, from seed germination to leaf and plant senescence, including photosynthesis and respiration (Salisbury and Ross, 1992; Arshad and Frankenberger, 1993). It is also documented that 90% of rhizospheric microorganisms are capable of releasing cytokinins and about 30% growth promoting compounds of the cytokinin group has been identified from the microbial origin (Nieto and Frankenberger, 1990). Cytokinin production has been reported in various PGPR, like *Arthrobacter giacomelloi*, *Azospirillum brasilense*, *Bradyrhizobium japonicum*, *Bacillus licheniformis*, *P. fluorescens* and *Paenibacillus polymyxa* (Timmusk *et al.*, 1999; Per-rig *et al.*, 2007). *Rhizobium* strains are also reported as the potent producers of cytokinins (Senthilkumar *et al.*, 2009).

**Gibberellins:** Gibberellins are a class of phytohormones commonly associated with modifying plant morphology by the extension of plant tissue, particularly stem tissue (Salisbury, 1994). The hormone is responsible in several plants developmental processes, such as cell division and elongation, stem elongation and leaf expansion, fruit setting, increase fruit size and number of buds and break down the tuber dormancy and delay of senescence in many organs of

different range of plant species (MacMillan, 2002). Many PGP microbes are reported to produce gibberellins (Dobbelaere *et al.*, 2003; Frankenberger and Arshad, 1995) including *Rhizobium*, *S. meliloti* (Boiero *et al.*, 2007), *Flavobacterium*, *Micrococcus*, *Agrobacterium*, *Clostridium* (Tsakelova *et al.*, 2006; Hayat *et al.*, 2010).

**Abscisic Acid:** Abscisic acid plays an important role in water-stressed environment (arid and semi-arid climate) where it helps in combating the stress through stomatal closure of leaves. The transport of abscisic acid can occur both in xylem and phloem tissues and can also be translocated through parenchyma cells. However, the movement of abscisic acid in plants does not exhibit polarity like auxins (Walton and Li, 1995). Various studies have reported to stimulate the stomatal closure, shoot growth inhibition, induce seeds to store proteins and in dormancy, induce gene transcription for proteinase inhibitors and thereby provide pathogen defense and counteracts with gibberellins (Davies 1995; Mauseth 1991). It has also been reported that the *Rhizobium* sp., *B. japonicum* and *Azospirillum* sp. can produce abscisic acid (Dangar and Basu, 1987; Boiero *et al.*, 2007).

**1-aminocyclopropane-1-carboxylic acid (ACC) deaminase - Ethylene** is well known as a plant growth regulator and has also been recognized as a stress hormone (Saleem *et al.*, 2007). Ethylene plays a crucial role in the growth and development of plants, however, has different effects on plant growth depending on its concentration in root tissues. At higher concentrations, it can be detrimental, as it induces defoliation and cellular processes that lead to inhibition of stem and root growth as well as premature senescence, all of which lead to reduced crop performance (Li *et al.*, 2005; Bhattacharyya and Jha, 2012). Under different environmental stress conditions, such as salinity, drought, water logging, radiation, heavy metals and pathogenicity, the endogenous level of ethylene is significantly increased which negatively affects the overall plant growth. At this condition, the plant responds by synthesizing 1- aminocyclopropane-1-carboxylate (ACC), which is the precursor for ethylene (Glick *et al.*, 2007).

ACC deaminase is a member of a large group of enzymes that utilizes vitamin B<sub>6</sub> and considered to be under tryptophan synthase family. PGPR like Rhizobia has the ability to uptake ACC and convert it into alpha-ketobutyrate and ammonia (Arshad *et al.*, 2007) and thereby lower the level of ethylene in the plant (Penrose *et al.*, 2001). This is used as a source of carbon and nitrogen. The destruction of ethylene is done by PGPR via the enzyme ACC deaminase which diminishes or prevents the detrimental effects of the higher ethylene levels (Glick *et al.*, 1998). Rhizobacteria with ACC-deaminase activity are found to belong to genera *Azospirillum* (Li *et al.*, 2005), *Achromobacter* (Govindasamy *et al.*, 2008), *Bacillus* (Ghosh *et al.*, 2003), *Enterobacter* (Li and Glick, 2001), *Pseudomonas* (Govindasamy *et al.*, 2008) and *Rhizobium* (Duan *et al.*, 2009) Hence, on inoculation of rhizobia producing ACC deaminase, the plant ethylene levels are lowered and result in longer roots providing relief from stresses, such as heavy metals, pathogens, drought, radiation, salinity, etc. Strains, such as *R. leguminosarum* bv. *viciae*, *R. hedysari*, *R. japonicum*, *R. gallicum*, had been known to produce ACC deaminase (Duan *et al.*, 2009; Hafeez *et al.*, 2008). In 1998, Glick and co-workers have demonstrated a model explaining the mechanism of how the ACC-deaminase containing PGPR can lower the plant ethylene levels and in turn can stimulate plant growth. According to this model, PGPR get attaches either to the seed surface or roots of the developing plant, in response to tryptophan and other amino acids produced by the seeds, and thus results in the synthesis of the auxin (IAA) (Patten and Glick, 2002). IAA producing bacteria are reported to produce high levels of ACC and known to inhibit ethylene levels (Glick, 2014) which together with the plant produced IAA, is responsible for the rapid transformation of S-adenosyl-L-methionine into ACC (Li *et al.*, 2000). Inoculation of plants with PGPR having ACC-deaminase had shown to promote root elongation, shoot growth, enhanced rhizobial nodulation and minerals uptake (Glick, 2012).

#### *Indirect growth promotions*

There are many indirect ways through which PGPR promotes plant growth with their biocontrol properties and induction of systemic resistance against phytopathogens and insect pests. Indirect mechanisms can be defined as the process by which PGPR prevents/neutralizes the harmful effects of phytopathogens on plants, by creating repressive substances that enhances the host's natural resistance (Singh and Jha, 2015). The indirect mechanism includes:

1. The production of antibiotics such as 2,4-diacetyl phloroglucinol (DAPG), kanosamine, phenazine-1-carboxylic acid, neomycin A, pyrrolnitrin, pyocyanin and viscosinamide. As mentioned above, DAPG due to its broad spectrum antibacterial, antifungal and anti-helminthic activity is considered more important.
2. The production of low molecular weight metabolites such as hydrocyanic acid (HCN) which inhibits electron transport and hence disruption of energy supply to the cells.
3. The production of hydrolytic enzymes (chitinases,  $\beta$ -1, 3 glucanase, cellulases, proteases and lipase which lyse the pathogenic fungal and bacterial cell walls)
4. It induces systemic resistance in plants by any of the metabolites (Reddy, 2013; Hafeez *et al.*, 2006; Narayanasamy, 2008).

#### **Production of Antibiotics**

Biocontrol is a process through which a living organism limits the growth or propagation of undesired organisms or pathogens (Gopalkrishnan *et al.*, 2015). For plant growth promoting (PGP) microbes, antibiosis is one of the most effective biocontrol mechanism by which PGPR employ to prevent proliferation of phytopathogens (Jeyanthi and Kanimozhi, 2018).

Antibiotics are the heterogeneous group of low molecular weight organic compounds that are deleterious to the growth or metabolic activities of other

microorganisms (Duffy, 2003). A total of six classes of antibiotic compounds are related with the biocontrol mechanism of the plants *viz.*, phenazines, phloroglucinols, pyoluteorin, pyrrolnitrin, cyclic lipopeptides (all of which are diffusible) and hydrogen cyanide (HCN)- which is volatile (Haas and Defago, 2005). The main mechanism of action is to inhibit the cell wall synthesis of pathogen, influence membrane structures of cells and inhibit the formation of initiation complexes on the small subunit of the ribosome (Maksimov *et al.*, 2011). As a result, the release of antibiotics permits these PGPR species to compete effectively by killing the pathogens affecting the plants antibiotics (Bardin *et al.*, 2004; Chandra *et al.*, 2007). However, overuse of antibiotic-producing PGPR strains can also cause pathogenic strains to become resistant (Kenneth *et al.*, 2019). Antibiotics like polyenes, macrolides, aminoglycosides, nucleosides, and benzoquinones have been discovered in PGP microbes. The antibiotics are majorly produced by *Actinobacteria* as total number of microbial bioactive molecules since the year 2012 was near to 33,500; where *Actinobacteria* accounts 41 % producing 13,700 from the total (Berdy, 2012). Various microbes present under PGPR biofertilizers such as *Pseudomonas* sp. *Bacillus* sp. *Streptomyces* sp. etc. have the tendency to produce compounds like 2,4-diacetylphloroglucinol (DAPG),  $\beta$ -1-3-glucanase, chitinases, antibiotics amphisin, HCN, phenazine, oomycin A, tropolone, pyoluteorin, tensin, pyrrolnitrin, and cyclic lipopeptides (Singh *et al.*, 2019; Bhattacharyya and Jha, 2012). These substances have antibiotic, antibacterial, antifungal, antiviral, antihelminthic, antimicrobial, antioxidant and antitumor qualities.

### Induction of plant resistance

In addition to enhancing mineral uptake and improving general plant physiology, rhizospheric inoculants can also strengthen plant defense systems, through making plant resistant to a various phytopathogens (Martinez-Viveros *et al.*, 2010). The use of PGP strains are reported to trigger the resistance of plants against the pathogens (Ramamoorthy *et al.*, 2001), and this phenomenon is known as induced

systemic resistance (ISR). Induced resistance is a physiological state in which the crop plant's defensive efficacy is ameliorated as a result of biological or chemical means, which helps protect plant tissues that were not exposed to the initial attack from future attacks (Van Loon *et al.*, 1998). On the basis of the nature of the elicitor and the involved regulatory pathways, induced resistance can be differentiated into two forms *viz.* systemic acquired resistance (SAR) and induced systemic resistance (ISR) (Choudhary *et al.*, 2007).

SAR can be triggered by exposing the plant to virulent, avirulent, and non-pathogenic microbes and involves the accumulation of pathogenesis-related proteins like chitinase and glucanase along with salicylic acid. However, ISR does not does not involve the accumulation of pathogenesis-related proteins or salicylic acid, while, depends on pathways involving jasmonate or ethylene pathway and thus inducing the host plant's defense response against a variety of plant pathogens (Yan *et al.*, 2002; Glick, 2012). Lactones, lipopolysaccharide, siderophores, acetoin, and butanediol are some of the structural components of the bacterial cell that can cause ISR (Doornbos *et al.*, 2012). Several rhizobial species are reported to ISR in plants by producing bio-stimulatory agents including *R. etli*, *R. leguminosarum* bv. *phaseoli* and *R. leguminosarum* bv. *trifolii* (Mishra *et al.*, 2006; Peng *et al.*, 2002).

### Production of lytic enzymes

PGP microbes promote plant growth by the secretion of lytic enzymes that regulate phytopathogenic agents. PGPR produces enzymes such as glucanases, proteases, chitinases, and lipases, which aid in the destruction of pathogen cell walls (Neeraja *et al.*, 2010). The fungal cell wall is made up of chitin and beta 1-4 N-acetylglucosamine, and the PGPR bacteria produces enzymes called beta 1-3 glucanase and chitinase that either digest the enzymes or deform components of cell wall of fungal pathogens. Ramadan *et al.* (2016) also reported that the species *Fusarium oxysporum* and *F. udum* causes fusarium wilt by producing enzymes such as chitinase and beta-glucanases, which are produced by PGPR such as *Pseudomonas fluorescence* LPK2.

### Production of Hydrogen cyanide (HCN)

Hydrogen cyanide (HCN) is a biocontrol agent and is one of the important chemical molecules produced by PGPR that help in the inhibition of plant pathogens (Mahmood *et al.*, 2016; Mukhtar *et al.*, 2017). HCN is a volatile, secondary metabolite that suppresses the development of pathogens by negatively affecting their growth and development (Meena *et al.*, 2017). In the agriculture system, HCN is commonly used as a biocontrol agent, and it helps in chelating the metal ions and in phosphate solubilization (Rijavec and Lapanje, 2016). Production of HCN by *Pseudomonas*, *Rhizobium*, *Bacillus*, *Alcaligenes*, and *Aeromonas* enhances the effectiveness of antifungal activity of these bacteria (Meena *et al.*, 2017; Bahadur *et al.*, 2017). It acts as a source of nitrogen to their host plant and root and shoots elongation, biomass improvement and thus boost productivity of maize (Marques *et al.*, 2010).

### Stress tolerance

The benefits of PGPR such as increased growth and development of plants has been discussed above, however, PGP microbes under stress condition act as stress relievers. Abiotic stresses commonly seen are drought, extremes of temperature, soil salinity, acidity, alkalinity and heavy metals issues which results in severe yield loss. The formation of free radicals and highly reactive oxygen species increases the response to many types of stress (Yan *et al.*, 2020). In a study conducted by Mrabet *et al.*, 2005, the indigenous and native microbes were found more effective and competitive as they are well adapted to the local environments. PGPRs depicts a number of mechanisms in mitigating stress-induced negative effects on physiological and biochemical processes of plant (Saharan and Nehra, 2011). PGPR also aids in the neutralisation of adverse effects on plants by scavenging the cadmium (Cd) on that causes the problem (Sharma *et al.*, 2021). PGPR acts as good scavengers which aid in strengthening resistance to abiotic stress by creating ROS - Scavenging enzyme (Habib *et al.*, 2016). Nadeem *et al.* (2016) also reported the PGPR strains such as *Paenibacillus polymyxa* B2, B3, B4, *Bacillus*

*thuringiensis*, and *Bacillus subtilis* RMPB44 can help with the issues like ecosystem nutrient cycling, co-evolution, and plant health of specifically horticultural plants etc.

Rhizobia also employs certain key tolerance mechanism/pathways against certain stress factor such as abiotic stresses, heavy metals and pesticides which can be considered as the major constraints for sustainable agriculture. These mechanisms ultimately help rhizobia to execute their beneficial PGP traits under the stress conditions. There are number of reviews on tolerance and nodulating capacity of *Rhizobium* and *Bradyrhizobium* to soil acidity, salinity, alkalinity, temperature extremes and osmotic stress conditions (Graham, 1992; Kulkarni and Nautiyal, 2000).

### Conclusion

The escalating concerns tied to the use of chemical fertilizers in agriculture, particularly their long-term impacts on the environment, soil, and human health, are pressing issues. The predominant challenge facing us in the 21st century is to innovate and adopt sustainable agricultural practices. To accomplish this, leveraging scientific knowledge to understand the interplay between soil, microbes, and their influence on plant growth is crucial.

There's a growing interest in harnessing both native and non-native beneficial PGP (Plant Growth-Promoting) microorganisms. These microorganisms offer a range of advantages, such as promoting plant growth, bolstering defence against diseases, and enhancing survival under stress conditions. Importantly, this approach ensures soil health, human safety in consuming crops, and environmental protection.

To move towards sustainability, a shift in behaviour is essential. This includes responsible consumption of natural resources and minimizing the use of chemical fertilizers to boost productivity. Although the utilization of these bio-resources is currently limited globally, the outcomes are promising, and efforts can be made to enhance their efficiency.

Through intensified research and development,

collaboration among researchers, agricultural institutions, and universities can accelerate the progress of biofertilizers. This, in turn, can facilitate widespread adoption among farmers, contributing significantly to sustainable agricultural productivity. Addressing regulatory issues related to operations, policy development, and social acceptance of biofertilizer products is crucial to unlocking their full potential in sustainable agriculture.

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