Revitalization of plant growth promoting rhizobacteria for sustainable development in agriculture

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Abstract

The progression of life in all forms is not only dependent on agricultural and food security but also on the soil characteristics. The dynamic nature of soil is a direct manifestation of soil microbes, bio-mineralization, and synergistic co-evolution with plants. With the increase in world's population the demand for agriculture yield has increased tremendously and thereby leading to large scale production of chemical fertilizers. Since the use of fertilizers and pesticides in the agricultural fields have caused degradation of soil quality and fertility, thus the expansion of agricultural land with fertile soil is near impossible, hence researchers and scientists have sifted their attention for a safer and productive means of agricultural practices. Plant growth promoting rhizobacteria (PGPR) has been functioning as a co-evolution between plants and microbes showing antagonistic and synergistic interactions with microorganisms and the soil. Microbial revitalization using plant growth promoters had been achieved through direct and indirect approaches like bio-fertilization, invigorating root growth, rhizoremediation, disease resistance etc. Although, there are a wide variety of PGPR and its allies, their role and usages for sustainable agriculture remains controversial

and restricted. There is also variability in the performance of PGPR that may be due to various environmental factors that might affect their growth and proliferation in the plants. These gaps and limitations can be addressed through use of modern approaches and techniques such as nano-encapsulation and micro-encapsulation along with exploring multidisciplinary research that combines applications in biotechnology, nanotechnology, agro biotechnology, chemical engineering and material science and bringing together different ecological and functional biological approaches to provide new formulations and opportunities with immense potential.

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Keywords

Agriculture

Biofertilization

Nano-encapsulation

PGPR

Revitalization

Sustainable development

1. Introduction

Agriculture has been the largest financial source since the dawn of civilization. About 7.41 billion people inhabit the earth, occupying 6.38 billion hectares of earth surface, of which 1.3 billion people are directly dependent on agriculture. For sustainable agriculture maintenance soil dynamic nature is of prime importance (Paustian et al., 2016, Tscharntke et al., 2012). Agriculture Organization of the United Nations (FAO) Food

Balance Sheet 2004 shows that 99.7% of food for the earth's population comes from the terrestrial environment alone. As 79 million people are added to the world's population every year, there has been a continuous increase in the demand for food, and a simultaneous scarcity in supply (Alexandratos and Bruinsma, 2003). In India, 60.6% of land is used for agricultural purposes by half of its population to grow several forms of cereals, vegetables, and pulses. Agricultural productivity, water quality, and climate change are greatly influenced by the exchange of nutrients, energy, and carbon between soil organic matter, the soil environment, the aquatic ecosystem, and the atmosphere (Lehmann and Kleber, 2015). Soil content is regulated by a number of aspects, such as organic carbon content, moisture, nitrogen, phosphorous, and potassium content, and other biotic and abiotic factors. However, indiscriminate use of fertilizers, particularly nitrogen and phosphorus, has led to substantial pollution of soil by reducing pH and exchangeable bases; thus, making these nutrients unavailable to crops leading to loss of productivity (Gupta et al., 2015). According to the FAO, 38.47% of the world's land area is covered by agricultural land, and although 28.43% of the land is arable, only 3.13% is permanently used for crop production. The situation is further detoriated as 20–25% of land worldwide is being degraded every year and another 5–10 Mha, will be degraded each year (Abhilash et al., 2016).

As expanding agricultural land is near impossible, the unprecedented demand places serious pressure on the terrestrial ecosystem for over-production. Hence, a more scientific and improved farming technique is necessary for fulfilling the increasing demands and also maintain the fertility of the soil. Some of the current techniques involved in sustainable agriculture are sustainable management practices (Ubertino et al., 2016), agricultural intensification (Shrestha, 2016), genetically engineered crops to form nitrogen-fixing symbioses, fixing nitrogen without microbial symbionts (Mus et al., 2016, Passari et al., 2016), use of microbes or genetically engineered microbes to promote plant growth (Perez et al., 2016, Kumar, 2016) and use of bio-fertilizers (Suhag, 2016, Kamkar, 2016). In addition, many other socio-economic and scientific techniques that contribute towards sustainable development of agriculture include disease resistance, salt tolerance, drought tolerance, heavy metal stress tolerance, and better nutritional value. Use of soil microorganisms, such as bacteria, fungi, and algae, is one possible way to fulfill these desired goals (Vejan et al., 2016).

Microbes and leguminous plants in holobiant relationships through bio-mineralization and synergistic co-evolution have great potential for improving soil quality and fertility (Paredes and Lebeis, 2016, Rosenberg and Rosenberg, 2016, Agler et al., 2016). Co-evolution of soil microbes with plants is vital to respond to extreme abiotic environments, resulting in improved economic viability, soil fecundity, and environmental sustainability (Khan et al., 2016, Compant et al., 2016). Association of plants with microbes can be best explained by plant growth promoting rhizobacteria (PGPR), which show antagonistic and synergistic interactions resulting enrichment of plant growth (Rout and Callaway, 2012, Bhardwaj et al., 2014). PGPR greatly affect soil characteristics and play a vital role converting barren, poor quality land into cultivable land. Revitalization of soil quality and plants growth by PGPR had been an area actively exploited for enhanced agriculture productivity in many parts of the world (Gabriela et al., 2015). This is generally achieved through direct or indirect approaches. The direct approach involves providing the plant directly with compounds that promote plant growth. This approach is achieved through techniques such as bio-fertilization, rhizo-remediation, and plant stress control (Goswami et al., 2016). Absorption of water and nutrients from the soil is the most common environmental factor constraining growth of terrestrial plant species. PGPR as bio-fertilization improves plant growth by increasing the accessibility or uptake of nutrients from a limited soil nutrient pool. Neutralizing plant stress is another important effect of PGPR and applies to both biotic and abiotic stress. Biotic stress is a biological threat (insects, disease), whereas abiotic stress is in the form of physical (light, temperature, etc.) or chemical stress that the environment inflicts on a plant (Gabriela et al., 2015). PGPR are also indirectly involved in promoting plant growth by lessening or preventing the deleterious effects of one or more phyto-pathogenic organisms. In this case, plant growth is promoted by antibiosis, induction of systemic resistance (ISR), and competitive exclusion (Tripathi et al., 2012).

Although reports on enhancement of plants growth through PGPR are widely available, there had been paucity of information between the potential uses of PGPR for sustainable development and their present applications. Use of PGPR's area also seriously limited due to variability and inconsistency of result observed under laboratory, green house and field trails. These gaps can be filled using modern nano-biotechnological approaches and use of techniques such as nano-encapsulation and micro-encapsulation. This review highlights some of the approaches that can be adapted to implement PGPR as a tool to combat plant diseases and enhance agricultural productivity.

2. Plant growth promoting rhizobacteria

Plants have always been in a symbiotic relationship with soil microbes (bacteria and fungus) during their growth and development. The symbiotic free-living soil microorganisms inhabiting the rhizosphere of many plant species and have diverse beneficial effects on the host plant (Raza et al., 2016a, Raza et al., 2016b) through different mechanisms such as nitrogen fixation and nodulation are generally referred to as Plant Growth Promoting Rhizobacteria (PGPR) (Fig. 1). They tend to defend the health of plants in an eco-friendly manner (Akhtar et al., 2012). PGPR and their interactions with plants are exploited commercially and have scientific applications for sustainable agriculture (Gonzalez et al., 2015). Applications of these associations have been investigated in oat, canola, soy, potato, maize, peas, tomato, lentil, barley, wheat, radicchio, and cucumber (Gray and Smith, 2005).

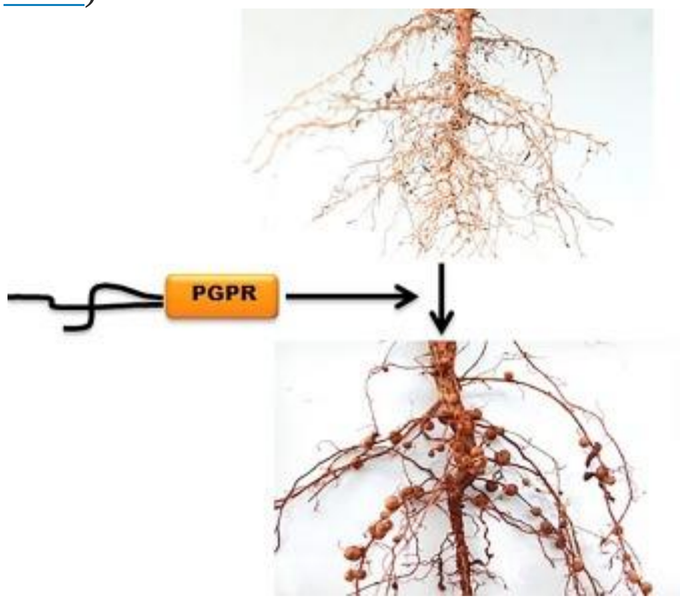

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Fig. 1. Location of the plant growth promoting rhizobacteria in plant roots.

PGPR are involved in various biotic activities of the soil ecosystem to make it dynamic for turnover and sustainable for crop production (Gupta et al., 2015). They competitively colonize plant roots system and enhance plant growth by different mechanisms, including phosphate solubilization (Ahemad and Khan, 2012) nitrogen fixation (Glick, 2012), production of indole-3-acetic acid (IAA), siderophores (Jahanian et al., 2012), 1-amino-cyclopropane-1-carboxylate (ACC) deaminase, and hydrogen cyanate (Liu et al., 2016); degradation of environmental pollutants, and production of hormones and antibiotics or lytic enzymes (Xie et al., 2016). In addition, some PGPR may also infer more specific plant growth-promoting traits, such as heavy metal detoxifying activities, salinity tolerance, and biological control of phytopathogens and insects (Egamberdieva and Lugtenberg, 2014).

2.1. Rhizosphere

Rhizosphere also known as the microbe storehouse is the soil zone surrounding the plant roots where the biological and chemical features of the soil are influenced by the roots. Bacteria in the rhizosphere may be symbiotic or non-symbiotic, which is determined by whether their mode of action is directly beneficial to the plant or not (Kundan et al., 2015). The root system, which serves as anchorage and for uptake of water and nutrients, is a chemical factory where phenolic compounds are synthesized and released to simultaneously arbitrate numerous underground interactions. The compounds released by plant roots act as chemical attractants for a huge number of heterogeneous microbial communities. The composition of these compounds depends upon the physiological status and species of plants and microorganisms (Kang et al., 2010).

Three different components make up the rhizosphere: the rhizosphere (soil), the rhizoplane, and the root itself. Among them, the rhizosphere is the soil zone regulated by roots through release of substrates and that affects microbial activity. The rhizoplane is the root surface that strongly binds soil particles, and the root is colonized by microorganisms (Barea et al., 2005). The concentration of bacteria in the rhizosphere is approximately 10–1000 times higher than in bulk soil, but less than that in a laboratory medium. To maintain their beneficial effects in the root environment, bacteria must compete well with other rhizosphere microbes for nutrients secreted by the root. The interactions between the plant and the rhizosphere are essential to procure water and nutrients from soil and the interactions are beneficial to the plants and the soil-borne microorganisms.

2.2. Different forms of PGPR

PGPR can be classified into two main type namely extracellular plant growth promoting rhizobacteria (ePGPR) and intracellular plant growth promoting rhizobacteria (iPGPR) (Viveros et al., 2010). ePGPR inhabit the rhizosphere (on the rhizoplane) or in the spaces between the cells of the root cortex, whereas iPGPR mainly inhabit inside the specialized nodular structures of root cells. The bacterial genera included as ePGPR are *Azotobacter*, *Serratia*, Azospirillum, *Bacillus*, *Caulobacter*, *Chromobacterium*, *Agrobacterium*, *Erwinia*, *Flavobacterium*, *Arthrobacter*, *Micrococcous*, *Pseudomonas*, and *Burkholderia*. The endophytic microbes belonging to iPGPR include *Allorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, and *Rhizobium*, as well as *Frankia* species, which can fix atmospheric nitrogen specifically for higher plants (Bhattacharyya and Jha, 2012).

3. Role of PGPR as a plant growth enhancer

PGPR enhance plant growth due to specific traits (Table 1) (Gupta et al., 2015). PGPR enhance plant growth through direct and indirect mechanisms, which involve enhancing plant physiology and resistance to different phytopathogens through various modes and actions (Zakry et al., 2012). These include nutrient fixation, neutralizing biotic and abiotic stress, and producing volatile organic compounds (VOCs) and enzymes to prevent disease. However, the mode of action of different types of PGPR varies according to the type of host plant (Fig. 2) (Garcia et al., 2015). They are also influenced by a number of biotic factors (plant genotypes, plant developmental stages, plant defense mechanisms, other members of the microbial community) and abiotic factors (soil composition, soil management and climatic conditions) (Vacheron et al., 2013).

Table 1. Plant growth promoting rhizobacteria and their application in plant growth and development.

Name of Microbe	Source/Host plant	Uses	References
Achromobacter xylosoxidans	*Vigna radiata*	Influence plant homeostasis	Ma et al. (2009)
Azospirillium brasilence	*Festuca arundinacea*	Increase plant tolerance to polycyclic aromatic hydrocarbons	Orlandini et al. (2014)
Azospirillium lipoferum	*Triticum aestivum*	Promote development of root system	Belimov et al. (2004)
Azospirillum brasilence	*Saccharum officinarum*	Alter plant root architecture by increasing the formation of lateral and adventitious roots and root hairs	Orlandini et al. (2014)
Azospirillum brasilence and *Bradyrhizobium japonicum*	*Zea mays, Glycine max*	Synthesize indole acetic acid in concentrations that are adequate to induce morphological changes and promote growth	Orlandini et al. (2014)
Azotobacter chroococcum	*Brassica juncia*	Stimulated plant growth	Narozna et al. (2014), Orlandini et al. (2014)
Azotobacter chroococcum	*Triticuma estivum*	Phosphate solubilization	Bhattacharyya and Jha (2012), Damir et al. (2011)
Azotobacter aceae	*Fagopyrum esculentum*	Nitrogen fixation	Bhattacharyya and Jha (2012)

Name of Microbe	**Source/Host plant**	**Uses**	**References**
Bacillus amyloliquefaciens	*Solanum lycopersicum*	Prevent tomato molt virus	Oteino et al. (2015)
Bacillus circulans, Cladosporium herbarum	*Vigna radiata*	Phosphate solubilization	Oteino et al. (2015)
Bacillus licheniformis	*Piper nigrum*	Protection from *Myzus persicae*	Kumar et al. (2015)
Bacillus megaterium	*Camellia sinensis*	Phosphate solubilization	Stefanescu (2015)
Bacillus megaterium var. phosphaticum	*Cucumis sativus*	Phosphate solubilization	Stefanescu (2015)
Bacillus mucilaginosus	*Piper nigrum, Cucumis sativus*	Improve potassium intake capacity	Liu et al. (2012)
Bacillus subtilis	*Brassica juncia*	Facilitate Nickel accumulation	Prathap and Ranjitha (2015), Oyedele et al. (2014)
Bacillus subtilis	*Hordeum vulgare*	Prevent powdery mildew	Prathap and Ranjitha (2015), Oyedele et al. (2014)
Bacillus subtilis	*Gossypium hirsutum*	Prevent from *Meloidogyne incognita* and *M. arenaria*	Prathap and Ranjitha (2015), Oyedele et al. (2014)
Bradyrhizobium japonicum, Pseudomonas chlororaphis,	*Glycine max*	Phosphate solubilization	Rathore (2015)

Name of Microbe	Source/Host plant	Uses	References
Pseudomonas putida			
Burkholderia spp.	Most of the fruit plants	Help inducemore ethylene production	Islam et al. (2016)
Enterobacter agglomerans	*Solanum lycopersicum*	Phosphate solubilization	Oteino et al. (2015)
Flavomonas orizihabitans INR	*Cucumis sativus*	Prevent stripped cucumber beetle	Oteino et al. (2015), Bhattacharyya and Jha (2012)
Herbaspirillum seropedicae	*Oryza sativa*	Enhanc production of gibberellins	Araujo et al. (2009)
Methylobacterium mesophilicum	*Oryza sativum, Eucalyptus globulus*	Influenc N-Acyl-homoserine lactone	Sanderset al. (2000)
Paenibacillus polymyxa	*Phaseolus vulgaris*	Alleviate adverse effects of drought stress and maintain plant growth	Ngumbi and Kloepper (2016)
Paenibacillus polymyxa	*Sesamum indicum*	Prevent fungal disease	Ngumbi and Kloepper (2016)
Pencillium sp.	*Triticum aestivum*	Prevent till disease	Richa et al. (2013)
Pseudomonas aeruginosa	*Cicer arietinum*	Positively stimulate potassium and phosphorus uptake	Ahemad and Kibret (2014)
Pseudomonas aeruginosa,	*Vigna*	Prevent root knot	Ngumbi and Kloepper

Name of Microbe	Source/Host plant	Uses	References
Bacillus subtilis	*radiate*	formation	(2016), Ahemad and Kibret (2014)
Pseudomonas cepacia	*Cucumis sativus*	Prevent pathogens in *Pythium ultimum*	Montano et al. (2014)
Pseudomonas cepacia	*Phaseolus vulgaris*	Prevent *Sclerotium rolfsii*	Montano et al. (2014)
Pseudomonas cepacia	*Gossypium hirsutum*	Help fightthe*Rhizoctonia solani* virus	Montano et al. (2014)
Pseudomonas fluorescens	*Medicago sativa*	Increase metabolism, sequestercadmium from solution and degradetrichloroethylene	Ramadan et al. (2016)
Pseudomonas fluorescens	*Triticum aestivum Hordeum vulgare*	Help prevent *Fusarium culmorum*	Santoro et al. (2016)
Pseudomonas fluorescens	*Phaseolus vulgaris*	Prevent halo blight	Ramadan et al. (2016)
Pseudomonas fluorescens	*Gossypium hirsutum*	Help cease damping off of cotton	Ramadan et al. (2016), Santoro et al. (2016)
Pseudomonas gladioli	*Gossypium hirsutum*	Inferred resistance against *Helicoverpa armigera* virus	Ross et al. (1995)
Pseudomonas putida	*Arabidopsis*	Improve utilization of plant secondary	Ahemad and Khan

Name of Microbe	Source/Host plant	Uses	References
	thaliana	metabolites	(2012)
Pseudomonas putida, Serratia marcescens	*Cucumis sativus*	Prevent cucumber anthracnose	Ahemad and Khan (2012), Rathore (2015)
Pseudomonas sp.	*Dianthus caryophyllus*	Prevent *Fusarium* wilt	Rathore, (2015), Ahemad and Khan (2012)
Rhizobium leguminosarum	*Phaseolus vulgaris*	Phosphate solubilization	Ahemad and Kibret (2014)

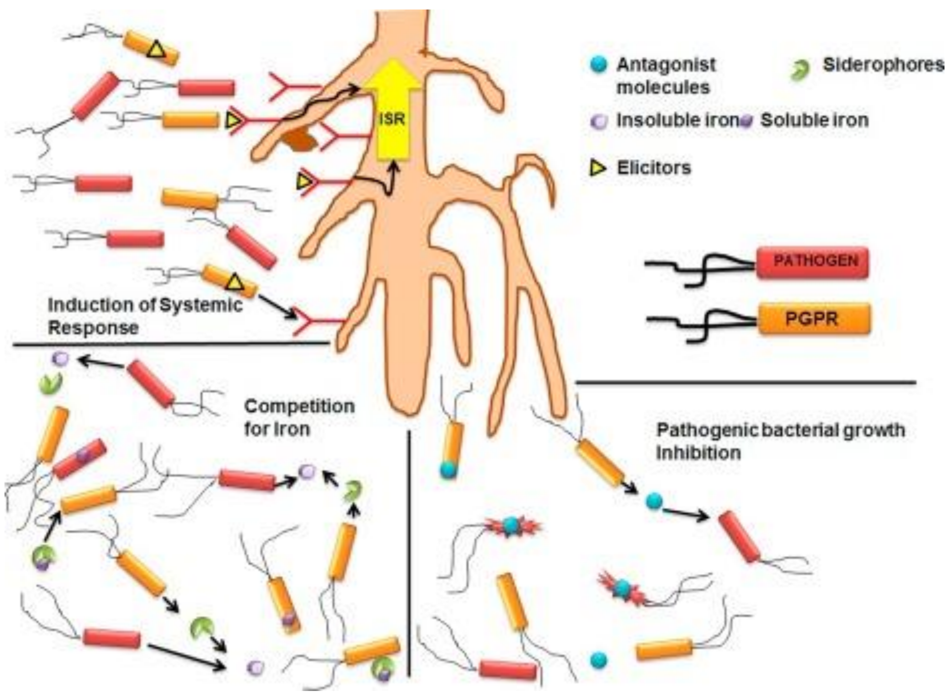

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Fig. 2. Different forms of plant growth promoting rhizobacteria in plants. ISR: Induction of Systemic Response.

3.1. Direct mechanisms

PGPR can directly facilitates the growth and development of plants through mechanisms such as nutrient uptake or increases nutrient availability by nitrogen fixation, mineralization of organic compounds, solubilization of mineral nutrients, and production of phytohormones (Bhardwaj et al., 2014).These mechanisms affect plant growth activity directly and vary according to the microbial strain and the plant species. Direct enrichment of mineral uptake occurs due to increases in individual ion fluxes at the root surface in the presence of PGPR.

3.1.1. Nutrient fixation

PGPR act as direct growth enhancers to plants, as they have the tendency to increase the accessibility and concentration of nutrients by fixing or locking their supply for plant growth and productivity (Kumar, 2016). Plants absorb nitrogen from the soil in the form of nitrate (NO^{3-}) and ammonium (NH^{4+}), which are essential nutrients for growth. Nitrate is usually the predominant form of available nitrogen in aerobic soils where nitrification occurs and is absorbed by the plant (Xu et al., 2012). Some PGPR have the ability to solubilize phosphate, resulting in an increased number of phosphate ions available in the soil, which can be easily taken up by plants (Paredes and Lebeis, 2016). *Kocuria* Turkanensis 2M4 isolated from the soil rhizosphere acts as a phosphate solubilizer, a siderophore producer, and an IAA producer for many different plant species (Goswami et al., 2014). Other microbes such as *Klebsiella* sp. Br1, *Klebsiella pneumoniae* Fr1, Bacillus pumilus S1r1, *Acinetobacter* sp. S3r2, and *Bacillus subtilis* UPMB10 have the capacity to fix atmospheric N_2, delay N remobilization, and area potential source for nutrient fixation.

3.1.2. Nitrogen fixation

Biological nitrogen fixation is an astounding process that accounts for approximately two-thirds of the nitrogen fixed globally. This biological process is carried out either by symbiotic or non-symbiotic interactions between microbes and plants (Shridhar, 2012). Symbiotic PGPR, which are most frequently reported to fix atmospheric N_2 in soil, include strains of *Rhizobium* sp., *Azoarcus* sp., *Beijerinckia* sp., *Pantoea agglomerans*, and *K. pneumoniae* (Ahemad and Kibret, 2014). Inoculating a combination of rhizobacterial species into soil improves its quality and enhances nodule formation. N_2 fixation is carried out a by a particular gene called *nif*, which along with other structural genes is involved in activating the iron protein, donating electrons, biosynthesizing the iron molybdenum cofactor, and many other regulatory genes mandatory for the synthesis and activity of the enzyme (Reed et al., 2011). Inoculation of biological N_2-fixing PGPR on crops and crop fields revitalizes growth promoting activity, disease management, and maintains the nitrogen level in agricultural soil (Damam et al., 2016).

3.1.3. Phosphate solubilization

Phosphorus is the second most essential nutrient required by plants in adequate quantities for optimum growth. It plays an important role in almost all major metabolic processes, including energy transfer, signal transduction, respiration, macromolecular biosynthesis, and photosynthesis (Anand et al., 2016). However, 95–99% of phosphorus present is in insoluble, immobilized, or precipitated forms; therefore, it is difficult for plants to absorb it. Plants absorb phosphate only as monobasic ($H_2PO_4^-$) and dibasic (HPO_4^{-2}) ions. Solubilization and mineralization of phosphorus by phosphate-solubilizing bacteria is an important trait that can be achieved by PGPR. The low molecular weight organic acids synthesized by various soil bacteria solubilize inorganic phosphorus (Sharma et al., 2013). Phosphate solubilizing PGPR are included in the genera *Arthrobacter*, *Bacillus*, Beijerinckia, Burkholderia, Enterobacter, Micr obacterium *Pseudomonas*, *Erwinia*, Rhizobium, *Mesorhizobium*, *Flavobacterium*, Rhodococcus, and *Serratia* and have attracted the attention of agriculturists as soil inoculate improve plant growth and yield (Oteino et al., 2015). Among them, *Mesorhizobium ciceri* and *Mesorhizobium mediterraneum*, which are isolated from chickpea nodules, are good phosphate solubilizers (Parmar and Sindhu, 2013). Although these microbes solubilize phosphorus resulting in increased soil fertility, studies regarding their use as a bio-fertilizer are limited.

3.1.4. Potassium solubilization

Potassium is the third major essential macronutrient for plant growth. As more than 90% of potassium exists in the form of insoluble rock and silicate minerals, the concentration of soluble potassium is usually very low in soil (Parmar and Sindhu, 2013). Potassium deficiency has become a major constraint in crop production. Without adequate potassium, plants have poorly developed roots, low seed production, slow growth rate, and a lower yield. It is essential to find an alternative endemic source of potassium for maintaining potassium status and plant uptake in soils for sustaining crop production (Kumar and Dubey, 2012).

The ability of PGPR to solubilize potassium rock by producing and secreting organic acids has being widely investigated. Potassium solubilizing PGPR, such as *Acidothiobacillus* sp., *Bacillus edaphicus*, *Ferrooxidans* sp., *Bacillus mucilaginosus*, *Pseudomonas* sp., *Burkholderia* sp., and *Paenibacillus* sp., ha ve been reported to release potassium in accessible form from potassium-bearing minerals in soils (Liu et al., 2012). Thus, applying potassium-solubilizing PGPR as biofertilizer to improve agriculture can reduce the use of agrochemicals and support eco-friendly crop production (Fig. 3) (Setiawati and Mutmainnah, 2016).

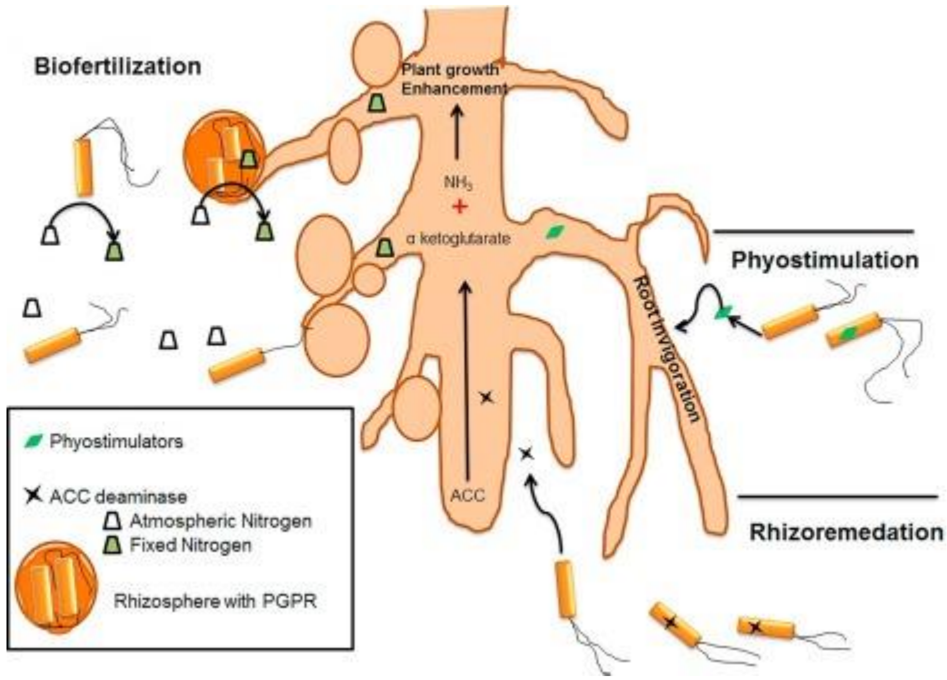

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Fig. 3. Role of plant growth promoting rhizobacteria in different applications in the plants.

3.1.5. Phytohormone production

Phytohormones or plant growth regulators are organic substances, which at low concentrations (<1 mM), promote, inhibit, or modify growth and development of plants (Damam et al., 2016). Ironically, production of these phytohormones can also be induced by certain microbes, such as PGPR, in plants. Common groups of phytohormones include gibberellins, cytokinins, abscisic acid, ethylene, brassino steroids, and auxins that the root cell can proliferate by overproducing lateral roots and root hairs with a consecutive increase in nutrient and water uptake (Sureshbabu et al., 2016). Plant growth regulators are also called exogenous plant hormones, as they can be applied exogenouslyas extracted hormones or synthetic analogues to plants or plant tissues. Phytohormones are categorized based on their site of action.

(a)

Root invigoration

Root invigoration includes several hormone-mediated pathways intersecting with pathways that perceive and respond to external environmental signals (Jung et al., 2013). Production of these hormones can be occasionally induced by certain microbes, such as *Pseudomonas putida*, *Enterobacter asburiae*, *Pseudomonas aeruginosa*, *Paenibacillus polymyxa*, Stenotrophomonas maltophilia, *Mesorhizobium ciceri*, *Klebsiella oxytoca*, *Azotobacter* chroococcum, and *Rhizobium leguminosarum*, which are regarded as PGPR. Hormones such as auxins, gibberellins, kinetin, and ethylene are specifically produced by these microbes and play an important role in root invigoration (Fig. 3) (Ahemad and Kibret, 2014).

(b)

Shoot invigoration

Cytokinins, gibberellins, and auxins also play an important role as plant growth hormones that control virtually all aspects of growth and development in higher plants. Skoog and Miller, 1957 confirmed that higher concentrations of cytokinins act as a positive regulator in shoot development rather than root development. Some of the major cytokinins are i6Ade [6-(3-methyl-2-butenylamino) purine], *trans*-zeatin [6-(4-hydroxy-3-methyl-*trans*-2-butenylamino) purine], *cis*-zeatin [6-(4-hydroxy-3-methyl-*cis*-2-butenylamino) purine], and dihydrozeatin [6-(4-hydroxy-3-methyl-butylamino) purine] (Murai, 2014). Regulation of the production of such plant hormones by microbes could be a vital step to revolutionize crop production and improve desired qualities (Fig. 3). Microbes that induce production of hormones also play an important role in shoot invigoration, which is generally seen in PGPR, such as *Rhizobium* *leguminosarum*, *Pantoea agglomerans*, *Rhodospirillum rubrum*, *Pseudomonas fluorescens*, *Bacillus subtilis*, *Paenibacillus polymyxa*, *Pseudomonas* sp., and *Azotobacter* sp. (Prathap and Ranjitha, 2015).

3.1.6. Siderophore production

Siderophores are small organic molecules produced by microorganisms under iron-limiting conditions that enhance iron uptake capacity. Research on siderophores has drawn much attention in the last 10 years due to their unique characteristics to extract iron metal ions (Saha et al., 2016). *Pseudomonas* sp., as PGPR, utilizes the siderophores produced by other microbes present in the rhizosphere for fulfilling their ions requirement (Fig. 2). More specifically, *Pseudomonas putida* utilize heterologous siderophores produced by other microorganisms to enhance the level of iron available in the natural habitat (Rathore, 2015). A potent siderophore, such as the ferric-siderophore complex, plays an important role in iron uptake by plants in the presence of other metals, such as nickel and cadmium (Beneduzi et al., 2012). As PGPR can produce siderophores, they are a major asset providing the plant with the required amount of iron. Research regarding the ability of siderophores to increase iron uptake capacity of plants is however very limited, and considerable research are further required in the context.

3.1.7. Exopolysaccharide production

Exopolysaccharides (EPSs) are high molecular weight, biodegradable polymers that are formed of monosaccharide residues and their derivatives and biosynthesized by a wide range of bacteria, algae, and plants (Sanlibaba and Cakmak, 2016). EPSs play a central role maintaining water potential, aggregating soil particles, ensuring obligate contact between plant roots and rhizobacteria, sustaining the host under conditions of stress (saline soil, dry weather, or water logging) or pathogenesis and thus are directly responsible for plant growth and crop production (Pawar et al., 2016). EPS producing PGPR, such as *Rhizobium leguminosarum*, *Azotobacter vinelandii*, *Bacillus drentensis*, *Enterobacter cloacae*, *Agrobacterium* sp., *Xanthomonas* sp., and *Rhizobium* sp., have an important role increasing soil fertility and contributing to sustainable agriculture (Mahmood et al., 2016).

3.1.8. Bio-fixation of atmospheric nitrogen

Bio-fixation of atmospheric nitrogen is part of a mutualistic or non-mutualistic relationship in which plants provide a niche and fixed carbon to microbes in exchange for fixed nitrogen. In either case, atmospheric nitrogen is fixed to the soil resulting in enhanced availability (Kuan et al., 2016). This relationship between plants and PGPR of the genera *Azospirillum*, *Klebsiella*, *Burkholderia*, *Bacillus*, and *Pseudomonas* has been widely studied (Islam et al.2016). However, such processes are restricted mainly to legumes in agricultural systems but there is considerable interest in exploring whether similar symbioses or non-symbioses can develop in non-legumes, which produce the bulk of human food and enrich soil fertility.

3.1.9. Rhizoremediation

Contaminated soil and water is a major problem for all organisms worldwide. Adversity due to pollution in the biosphere is diverse depending on the nature of the pollution. Pollution can be alleviated by bioremediation, which is a process or technique in which living organisms or their products are used naturally or artificially to remediate/destroy or immobilize pollutants in the environment (Uqab et al., 2016). Although it is time consuming, bioremediation is one of the most cost-effective means of remediating soil and water pollution. Various bioremediation techniques are available, including bio-pile, landfarming, phytoremediation, bio-slurry, and bioventing, and all of them can be used to degrade pollutants at contaminated sites. However, application of these techniques is unidirectional and need be further associated with each other to overcome such limitations (Hassan et al., 2016). One such experimental approach is rhizoremediation, which is the combination of phytoremediation and bio-augmentation. The process of extracting metals from contaminated soil using plants (phytoextraction), and their remediation is known as phytoremediation (Fig. 3) (Hamzah et al., 2016). Bio-augmentation is the use of added microorganisms to “reinforce” biological waste treatment so that they can effectively reduce the contaminant load by transforming the waste into less dangerous compounds (Herrero and Stuckey, 2015). The symbiotic and non-symbiotic relationships between microbes and plants, which are best explained by PGPR, make it a unique candidate for rhizoremediation. At present, studies using PGPR as tools for rhizoremediation are restricted to a few microbial species, such as *Pseudomonas aeruginosa*, genetically engineered *Pseudomonas fluorescens*, and certain *Bacillus* species (Kuiper et al., 2004). Further exploration of PGPR and their application as bioremediators is needed for large scale removal of pollutants in forms of heavy metals or other impurities from soil and water sources.

3.2. Indirect mechanisms

Indirect mechanisms involve the process through which PGPR prevent or neutralize the deleterious effects of phytopathogens on plants by producing repressive substances that increase natural resistance of the host (Singh and Jha, 2015). This mechanism can also be defined as a process that helps plants grow actively under environmental stress (abiotic stress) or protect plants from infections (biotic stress) (Akhgar et al. 2014). The contribution of PGPR in this mechanism includes production of hydrolytic enzymes (chitinases, cellulases, proteases, etc.), various antibiotics in response to plant pathogen or disease resistance, induction of systematic resistance against various pathogen and pests, production of siderophores, VOCs, EPSs, etc. (Nivya, 2015, Gupta et al., 2014).

3.2.1. Stress management

Stress is defined as any factor that has a negative effect on plant growth (Foyer et al., 2016). Stress of any kind increases the formation of reactive oxygen species (ROS) such as H_2O_2, O^{2-}, and OH^- radicals. Excess ROS production causes oxidative stress, which damages plants by oxidizing photosynthetic pigments, membrane lipids, proteins, and nucleic acids. Plants are frequently subjected to various environmental stresses and have developed specific response mechanisms (Ramegowda and Senthil-Kumarb, 2015). Over the past few decades, the understanding of the molecular mechanisms implicated in abiotic and biotic stress tolerance has been reached through various studies (Tripathi et al., 2015, Tripathi et al., 2016, Pontigo et al., 2017, Singh et al., 2017, Tripathi et al., 2017). Some of the examples of active PGPR participation and their role in stress management in plants are discussed below.

(a)

Abiotic stress tolerance

Abiotic stress (high wind, extreme temperature, drought, salinity, floods etc.) have a high negative impact on survival, biomass production, and production of staple food crops by up to 70%, which threatens food security worldwide. Aridity stress imparted by drought, salinity, and high temperature is the most dominant abiotic stress limiting plant growth and productivity (Vejan et al., 2016). Tolerance to this stress is multigenic and quantifiable in nature, and includes accumulation of certain stress metabolites, such as poly-sugars, proline, glycine-betaine, abscisic acid, and upregulation in the synthesis of enzymatic and non-enzymatic antioxidants, as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase, ascorbic acid, α-tocopherol, and glutathione (Agami et al., 2016). Apart from these, several other strategies that alleviate the degree of cellular damage caused by water stress and improve crop tolerance include exogenous application of PGPR in compatible osmolytes, such as proline, glycine-betaine, trehalose, etc., which has gained considerable attention formitigating the effect of stress.

The use of PGPR in plant abiotic stress management has been comprehensively studied through bacterial strains, such as *Pseudomonas putida* and *Pseudomonas fluorescens* that neutralize the toxic effect of cadmium pollution on barley plants due to their ability to scavenge cadmium ions from soil (Baharlouei et al., 2011). Moreover, improved leaf water status, particularly under salinity and other abiotic stress conditions, has also been reported as an effect of PGPR (Ahmad et al., 2013, Naveed et al., 2014). The establishment of a correlation between PGPR and drought resistance has been reported in several crops, including soybean, chickpea, and wheat (Ngumbi and Kloepper, 2016). Enhanced salinity stress tolerance in okra through ROS-scavenging enzymes and improved water-use efficiency, which is initiated by PGPR, has also been reported by Habib et al., 2016.

(b)

Biotic stress tolerance

Biotic stress is caused by different pathogens, such as bacteria, viruses, fungi, nematodes, protists, insects, and viroids, and results in a significant reduction in agricultural yield (Haggag et al., 2015). Global food production suffers a loss of about 15% worldwide mainly due to phytopathogens (Strange and Scott, 2005). Stress is a major challenge to crop yield and thereby encourages breeding of resistant crops due to the vast economic loss. Biotic stress has adverse impacts on plants, including co-evolution, population dynamics, ecosystem nutrient cycling, natural habitat ecology, and horticultural plant health (Gusain et al., 2015). Such problems could be solved by using PGPR, such as *Paenibacillus polymyxa* strains B2, B3, B4, *Bacillus amyloliquefaciens* strain HYD-B17, *B. licheniformis* strain HYTAPB18, *B. thuringiensis* strain HYDGRFB19, *P. favisporus* strain BKB30, and *B. subtilis* strain RMPB44. Plants inoculated by soaking their roots or seeds overnight in cultures of PGPR exhibit enormous resistance to different forms of biotic stress (Ngumbi and Kloepper, 2016).

3.2.2. Disease resistance antibiosis

Utilization of microbial antagonists against plant pathogens in agricultural crops has been suggested as a substitute for chemical pesticides. PGPR, like *Bacillus* spp. and *Pseudomonas* sp., play a major role inhibiting pathogenic microorganisms by producing antibiotics. The production of antibiotics by PGPR against several plant pathogens has become one of the most effective and most studied bio-control mechanism sover the past two decades (Fig. 2) (Ulloa-Ogaz et al., 2015).

Most *Pseudomonas* species produces a wide variety of antifungal antibiotics (phenazines, phenazine-1-carboxylic acid, phenazine-1-carboxamide, pyrrolnitrin, pyoluteorin, 2,4diacetylphloroglucinol, rhamnolipids, oomycin A, cepaciamide A, ecomycins, viscosinamide, butyrolactones, N-butylbenzene sulfonamide, pyocyanin), bacterial antibiotics (pseudomonic acid andazomycin), antitumor antibiotics (FR901463 and cepafungins) and antiviral antibiotics (Karalicine) (Ramadan et al., 2016). *Bacillus* sp. also produces a wide variety of antifungal and antibacterial antibiotics. Such antibiotics are mainly derived from ribosomal and non-ribosomal sources. The ribosomal originating antibiotics include subtilosin A, subtilintas A, sublancin and those of the non-ribosomal origin include chlorotetain bacilysin, mycobacillin, rhizocticins, difficidin, and bacillaene etc. *Bacillus* sp. also produces a wide variety of lipopeptide antibiotics, such as surfactin, iturins, and bacillomycin etc. (Wang et al., 2015). The antibiotics are further grouped into volatile and non-volatile compounds. The volatile antibiotics include alcohols, aldehydes, ketones, sulfides, hydrogen cyanide, etc., and the non-volatile antibiotics are polyketides, cyclic lipopeptides, aminopolyols, phenylpyrrole, heterocyclic nitrogenous compounds etc. (Fouzia et al., 2015).

3.2.3. Induced systemic resistance

Induced systemic resistance (ISR) is defined as a physiological state of improved defensive capacity evoked in response to a particular environmental stimulus. PGPR induces systemic resistance in many plants against several environmental stressors (Prathap and Ranjitha, 2015). Signals are produced and a defense mechanism is activated *via* the vascular system during pathogenic invasion which results in the activation ofa huge number of defense enzymes, such as chitinase, β-1, 3-glucanase, phenylalanine ammonia lyase, polyphenol oxidase, peroxidase, lipoxygenase, SOD, CAT, and APX along with some proteinase inhibitors (Fig. 2). ISR is not specific against a particular pathogen but it helps the plant to control numerous diseases (Kamal et al., 2014). ISR involves ethylene hormone signaling within the plant and helps to induce the defense responses of a host plant against a variety of plant pathogens. A variety of individual bacterial components induce ISR, such as lipopolysaccharides, cyclic lipopeptides, siderophores, 2, 4-diacetylphloroglucinol, homoserine lactones, and volatiles, like 2, 3-butanediol and acetoin (Berendsen et al., 2015). Although the vast majority of PGPR induce ISR in plants, and their use could revolutionize agriculture, basic research on utilizing PGPR and uses of modern tools and techniques to support plants from laboratory to field has been lacking till date.

3.2.4. Production of protective enzymes

PGPR promote plant growth by producing metabolites that control phytopathogenic agents (Meena et al., 2016). PGPR produce enzymes such as β-1,3-glucanase, ACC-deaminase, and chitinase, which are generally involved in lysing cell walls and neutralizing pathogens (Goswami et al., 2016). Most of the fungal cell wall components are comprised of β-1,4-N-acetyl-glucoseamine and chitin; hence, β-1,3-glucanase- and chitinase-producing bacteria control their growth. *Pseudomonas fluorescens* LPK2 and *Sinorhizobium fredii* KCC5 produce beta-glucanases and chitinase causing *fusarium* wilt by *Fusarium oxysporum* and *Fusarium udum* (Ramadan et al.2016). *Phytophthora capsici* and *Rhizoctonia solani*, regarded as the most catastrophic crop pathogens in the world, are also inhibited by PGPR (Islam et al., 2016).

3.2.5. Production of VOCs

VOCs that are produced by bio-control strains promote plant growth, inhibit bacterial and fungal pathogens and nematodes, and induce systemic resistance in plants against phytopathogens (Raza et al., 2016a, Raza et al., 2016b). Particular bacterial species from diverse genera, including *Pseudomonas*, *Bacillus*, *Arthrobacter*, *Stenotrophomonas*, and *Serratia* produce VOCs thatimpact plant growth. 2, 3-Butanediol and acetoin produced by *Bacillus*spp. are the most effective VOCs for inhibiting fungal growth and improving plant growth (Santoro et al., 2016). It has been reported that bacterial VOCs are determinants for eliciting plant ISR (Sharifi and Ryu, 2016). The VOCs from PGPR strains directly or indirectly mediate increased disease resistance, abiotic stress tolerance, and plant biomass. VOC emissionsare a common characteristic of a wide variety of soil microorganisms and include cyclohexane, 2-(benzyloxy)ethanamine, benzene, methyl, decane, 1-(N-phenylcarbamyl)-2-morpholinocyclohexene, dodecane, benzene(1-methylnonadecyl), 1-chlorooctadecane, tetradecane, 2,6,10-trimethyl, dotriacontane and 11-decyldocosane, although the quantity and identity of the VOCs emitted vary among species (Kanchiswamy et al., 2015).

4. Future prospects and perspective

PGPR has been enhancing the agriculture productivity through different mechanisms and processes. However, there is variability in the performance of PGPR that may be due to various environmental factors that may affect their growth and exert their effects on plant. The environmental factors include climate, weather conditions, soil characteristics or the composition or activity of the indigenous microbial flora of the soil (Gupta et al., 2015). There are also numerous forms of other boitic and abiotic factors in form of weeds, pathogens, herbicides etc. that limits the effects of PGPR on plants resulting in poor productivity. With the introduction and application of modern tools and techniques such as nanomaterials, biosensors, nano-fertilizers and development in the fields of biotechnology and nanotechnology, the agriculture sector has acquire a boost during the recent decades.

Soil is the richest medium of natural nanoparticles, both as primary particles and agglomerates/aggregates. Nano agriculture is intended to infuse nanotechnology, biotechnology and other disciplines of science into agricultural sciences in order to transform traditional farming practices to precision agriculture that ensure food security to the growing population of the country (Subramanian and Tarafdar, 2011). The expansion of new nanodevices (biosensors, enzyme encapsulation) and nanomaterials (nanotubes, nanowires, fullerene derivatives and quantum dots) with the surfacing of nanotechnology announces probable narrative application in the field of agriculture and life sciences (Dixshit et al., 2013). Their unique size-dependent properties make these materials superior and indispensable in many areas sustainable agriculture development. Nanoparticles in plant pathology targets specific agricultural problems in plant-pathogen interactions and provide new ways for crop protection. This includes early detection of biotic stresses and their management, enhancing input use efficiencies and self-life of perishables (fruits, flowers and vegetables etc.). PGPR (*Pseudomonas fluorescens*, *Bacillus subtilis*, *Paenibacillus* elgii, and *Pseudomonas putida*) treated with gold, aluminium and silver coated nanoparticles have been reported not only to significantly increase the plant growth, but also to inhibit the growth of harmful fungal parasite within rhizosphere, thus acting as potential nano-biofertilizers. The nano bio-fertilizers can be encapsulated by micro-encapulation and used to control the release of the fertilizer into the target cell without any unintened loss. Increased adhesion of beneficial bacteria on to the roots of oilseed rape and protected the plants against infection fungal pathogens through Titania nanoparticles were experimentally proven by Mishra and Kumar, (2009). Rate of seed germination in different monocots and dicots have also be documented to be improved by pre-treatment with ZnO nanoparticles (Mishra and Kumar, 2009). In present scenario, the context of nano bio-fertilizers offers a great opportunity to develop eco-friendly compounds that can be easily replacable in place of chemical pesticides (Caraglia et al., 2011). Nanoencapsulation and microencapsulation of insecticides, fungicides or nematicides are helpful in producing a formulation which offers effective control of pests while preventing residue in soil. Encapsulated herbicide molecules such as pentimethalin and metalachlor with polymers such as poly styrene sulphonate (PSS) and poly alylamine hydrochloride (PAH) break open only under moist condition and thus can be easily controlled. These encapsulated herbicides have sustained release of active ingredients that ensure effective weed control (Kanimozhi and Chinnamuthu, 2012). Moreover, these have thermal and hydro stability. Such encapsulated insecticides, fungicides and nematicides may help in producing formulations effective to control pests.

Development of smart biosensors for detection of nutrients and contaminants have a huge impact on precision farming that can makes use of computers, global positioning system (GPS), remote sensing devices to measure highly localized environmental conditions, utilizing resources with maximum efficiency and identifying the nature and location of problems. Precision farming has been a long desired goal to minimize input (i.e. fertilizer, pesticides, herbicides, etc.) and maximize output (i.e. crop yields) through monitoring environmental variables and applying targeted action. Nano scale Zeolites which are naturally occurring crystalline aluminum silicates, can also play significant role by improving the water retention capacity of sandy soil and increase porosity in clay soils (Srilatha, 2011, Subramanian and Tarafdar, 2011, Vacheron et al., 2013, Trivedi and Hemantaranjan, 2014). Bioremediation too has emerged as a potential tool to clean up the metal-contaminated/polluted environment. Reducing the bioavailability of metal contaminants in the rhizosphere (phytostabilization) as well as improving plant establishment, growth, and health could significantly speed up the plant growth and indeed its productivity (Ma et al., 2011).

Development of superior or novel PGPR strains by improving above traits can be possible using genetic manipulations. These PGPR-biotechnologies can be exploited as a low-input, sustainable and environment-friendly technology for the management of plant stresses. Currently, nanobased products and technology for agricultural growth are practices in some of the developed countries like USA, China, Germany, France, Japan, Switzerland, and South Korea. In India, large scale implementation of such products are still confined to selected biotechnological products such as Golden rice, BT cotton, BT Brinjal, Cucumber, seedless bananas, Flavr Savr tomatoes etc. and therefore requires major upliftment to satisfy the needs of the growing population.

5. Conclusion

Agriculture and soil have been carrying the burden of sustaining mankind on planet earth. Indiscriminate exploitation of resources has limited the productive and humans are looking for alternative sources for fulfillment of their livelihood needs. PGPR plays an important role in enhancing plant growth; remediating and managing contaminated and degraded wastelands and eutrophied water bodies; and controlling pesticide pollution, nitrogen, and phosphorous runoff. However, over-dependence of the human population on chemical fertilizers and pesticides has led to the circulation of life-threatening chemicals, which are not only hazardous for human consumption but can also disturb the ecological balance. Moreover, they have entered the food chain through different sources. Such changes can alter plant–microbe interactions by modifying microbial biology and biogeochemical cycles. Application of modern tools and techniques for enhancement of PGPR can serve as key in sustainable agriculture by improving soil fertility, plant tolerance, crop productivity, and maintaining a balanced nutrient cycling. Further studies on selecting suitable rhizosphere microbes and producing microbial communities along with exploring multidisciplinary research that combines applications in biotechnology, nanotechnology, agro biotechnology, chemical engineering and material science and bringing together different ecological and functional biological approaches can provide new formulations and opportunities with immense potential.

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