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Plant growth promoting rhizobacteria (PGPR) and their eco-friendly strategies for plant growth regulation: a review

Debapriya Choudhury, Santanu Tarafdar & Sikha Dutta*

Applied and Molecular Mycology and Plant Pathology Laboratory, CAS Department of Botany, The University of Burdwan, Purba Bardhaman 713 104, West Bengal, India

*Email: sikha.bu.academia@gmail.com

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Abstract

As a natural engineer, Plant Growth Promoting Rhizobacteria (PGPR) play an important role in increasing plant growth, yield and enhancing plant tolerance to stressful conditions. These beneficial bacteria take up their position in the rhizosphere, around the plants' root tissues. They may be in, or on their host tissues and help to provide nutrients to their host plants. For sustainable agriculture, PGPR transmit their extensive assistance in ecosystem management, soil structure maintenance, stress management and plant morphology and physiology modulation in an environmentally friendly manner. Plant- PGPR interactions also stimulate nutrient acquisition and accumulation, improve plant performance and enhance plants' tolerance to abiotic and biotic stresses. Beside these, PGPR are good biofertilizers and safe for our environment. Nanotechnological advances with PGPR applications are important today to increase the impact of PGPR in agriculture. Undoubtedly, PGPR concept is intimately involved with agriculture, horticulture, forestry and they are too enough to establish a vibrant environment. In this review we have focused on the versatility of PGPR-their performance and aimed to address some future prospects of PGPR as an eco-friendly tool for plant growth regulation.

Keywords

PGPR, eco-friendly, plant growth regulation, sustainable agriculture, stress management

Introduction

Soil is the core house to millions and millions of microbes, specifically rhizosphere become more precious due to rhizospheric effect. Some of these bacteria provide benefits to plant community and help plants to cope with challenging adversities (1). In the year 1978, Kopper and Schroth applied the term 'Plant growth promoting rhizobacteria' (PGPR) for beneficial rhizospheric free living bacteria (2).

PGPR are involved in improving soil composition through decomposition of crop residues, stabilization of mineral nutrients and mineralization of soil organic matter, acquisition of plant growth promoters including nutrient (biofertilizer), phosphate solvents, nitrogen fixation, nitrification and synthesis of soil organic matters (3).

PGPR maintain their host plants' health through different processes such as (i) enhancement of nutrient acquisition by host plants (ii) improvement of plant growth and crop production by producing phytohormones, siderophore and also by enriching soil nutrients (iii) promotion of nodule formation in legume and, (iv) enhancement of seedlings' emergence (4-8). Beside these, PGPR facilitate their host plants to manage different types of abiotic stresses like drought (9, 10), salinity (11, 12) and heavy metal absorption is also restricted by some metal resistant PGPR strains (13). These types of bacteria activate antioxidant signalling to reduce temperature stress (14).

PGPR tend to protect the plants against some pests and phyto-pathogens by triggering Induced Systemic Resistance (ISR) through lipopolysaccharides, flagella, homoserine lactones, acetoin and butanediol (5). From the host-PGPR interaction, the plants gain some benefits including increase in seed germination rate, yield, root growth, leaf area, chlorophyll content, protein content, nutrient content, germination percentage, root weight and root length, hydraulic activity, abiotic stress tolerance, delayed aging and biocontrol (15).

Excessive use of artificial fertilizers, herbicides, fungicides and pesticides are the major causes of environmental pollution. The demand for food is increasing rapidly due to the increase in human population. Today civilizations, industrialization, chemical fertilizers in agriculture, excessive use of pesticides are major obstacles to the survival of agriculture. Excessive use of nitrogen fertilizers produces Nitrous oxide (N_2O), a greenhouse gas that leads to global warming. The main drawback of nitrogen fertilizers is the reduction of biological nitrogen fixation. Ammonium nitrate is widely used by farmers as nitrogen fertilizer. Excess ammonium flow into the plant body meets the nitrogen requirements of the plant which reduces the symbiotic association between the plant and the microbe (16).

Reducing the use of chemical fertilizers in agriculture and reducing the burden of pollutants in the environment is possible only through the use of biofertilizer (17).

To date, various reports on PGPR- agricultural sustainability have been documented. Undoubtedly it is a highly promising tool for soil and crop management. The purpose of this review is to provide a concise overview of the PGPR and to highlight how they modify plant growth regulations in various environmental conditions.

Isolation of Plant growth promoting rhizobacteria (PGPR)

In bacteriological research, bacterial isolation is very important and the first step in separating different strains from natural mixtures. PGPR isolation can be done from rhizosphere soil sample or from root nodules. Serial dilution-spread plate is a very common, simplified and well-accepted method for isolating PGPR strains from rhizosphere soil sample. In the first step, it is important to collect soil samples that adhere to the roots. This is followed by sequential steps like, preparation of the stock solution, serial dilution of the stock solution, spread plate and incubation (18) as discussed in Fig. 1.

Endophytic bacteria can be isolated from sterilized root samples (18-21) as discussed in Fig. 2.

Isolation of PGPR strains from crushed root nodules has also been reported (22). Different growth media

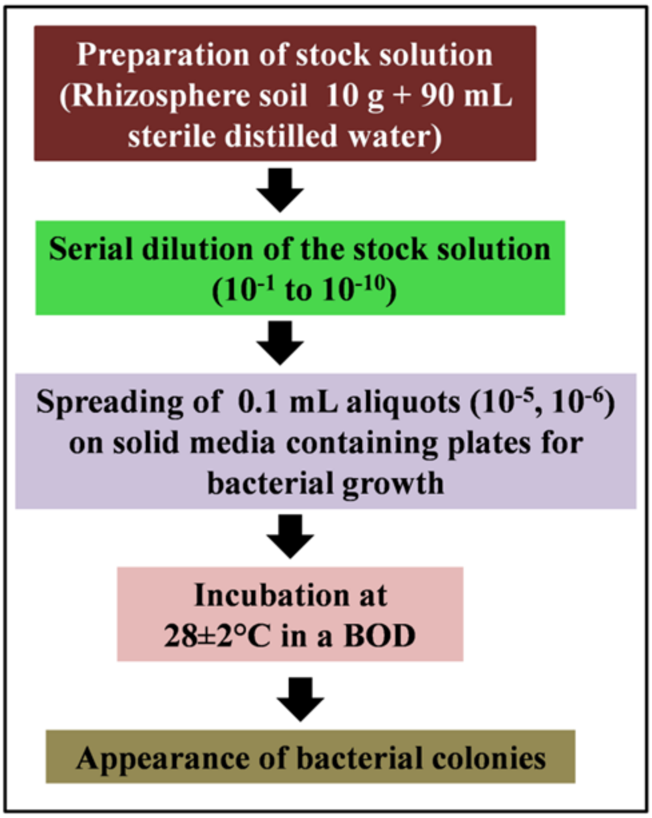

Fig. 1. Steps of serial dilution-spread plate method for isolation of PGPR from rhizosphere soil.

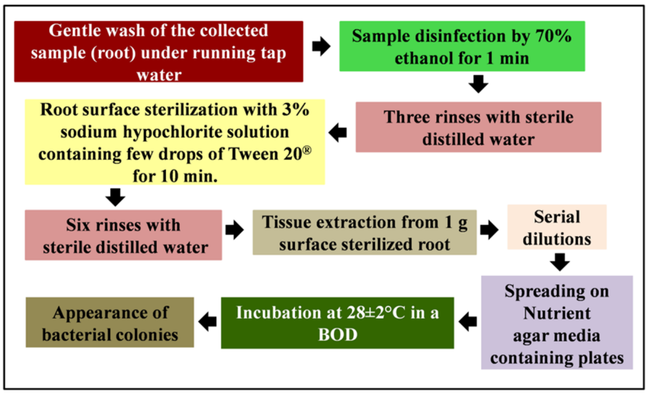

Fig. 2. Steps for isolation of endophytic bacteria from root samples.

namely Pikovskayas agar (PKV) media (18, 23), Luria–Bertani (LB) agar media (24), King B agar media (25), Tryptic soy agar media (26), Nutrient agar media (21) are used for bacterial growth.

Culture of Plant growth promoting rhizobacteria (PGPR)

Bacterial culture is basically a method that allows bacteria to multiply under controlled lab conditions. Carbohydrates, proteins and nucleic acids are important ingredients of culture media which are dissolved in water. After isolation, to maintain the purity of bacterial strains it is required to apply pure culture method (27) as presented in Fig. 3.

Sub culturing is a method where bacteria are transferred from stock culture to fresh nutritive medium. Beside solid medium, bacteria can be cultured in liquid medium or broth. Broth is liquid medium without solidifying agent (agar) containing all the important ingredients necessary for the growth of bacteria. PGPR containing broth general-

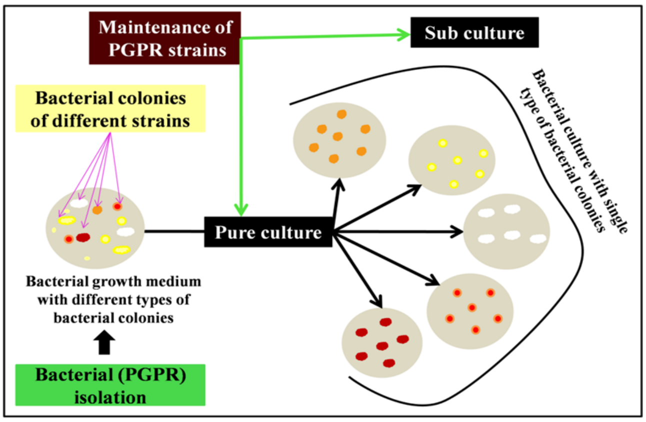

Fig. 3. Maintenance of PGPR strains (different colours represent different PGPR strains).

ly use for experimental studies including ammonia production, enzymes (Catalase, Oxidase) synthesis, EPS production, IAA production (27-29) etc.

Role of Plant growth promoting rhizobacteria (PGPR) in Plant Growth Regulation

This section is categorized into 3 main parts viz. PGPR and its types, Contributions of PGPR in plant growth regulations, Molecular responses and signalling pathways in response to Plant-PGPR interactions.

PGPR and its types

Plant growth promoting rhizobacteria are important groups of beneficial rhizosphere bacteria that contribute a mutulistic relationship with plants. These provide an eco-friendly safeguarding policy for the plants (30). PGPR maintain the existence of plants by promoting their growth and acting as biocontrol agents (31, 32) and regulate agro-ecological natural equilibrium by increasing productivity with a low chemical assimilation (33). Some common plant growth promoting rhizobacteria and their host plants are reported (Table 1).

Table 1. Plant growth promoting rhizobacteria (PGPR) and their host plants (4, 15, 31, 34-44)

PGPR	Host plants
Rhizobium leguminosum	*Phaseolus vulgaris*
Pseudomonas cepacia	*Phaseolus vulgaris*
	Gossypium hirsutum
	Cucumis sativus
Pseudomonas sp.	*Dianthus caryophyllus*
Pseudomonas fluorescens	*Phaseolus vulgaris*
	Triticum aestivum
	Hordeum vulgare
Azotobacter chroococcum	*Brassica juncia*
	Triticuma aestivum
Azospirillum brasilence	*Saccharum officinarum*
	Zea mays
Bradyrhizobium japonicum	*Glycine max*
Achromobacter xylosoxidans	*Vigna radiata*
Bacillus subtilis	*Hordeum vulgare*
	Gossypium hirsutum
	Brassica juncia
Methylobacterium mesophilicum	*Eucalyptus globulus*
	Oryza sativum
Serratia sp.	*Zea mays*
Acinetobacter sp.	*Zea mays*

Plant growth promoting rhizobacteria colonize in rhizosphere region including root surface, or superficial intercellular space of host root, and frequently they form root nodules. As endophyte they also remain in apoplastic region of host plants (45). Broadly PGPR are categorized into two prime groups as presented in Fig. 4. These are represented as iPGPR: Intracellular plant growth promoting rhizobacteria and ePGPR: Extracellular plant growth promoting rhizobacteria (46).

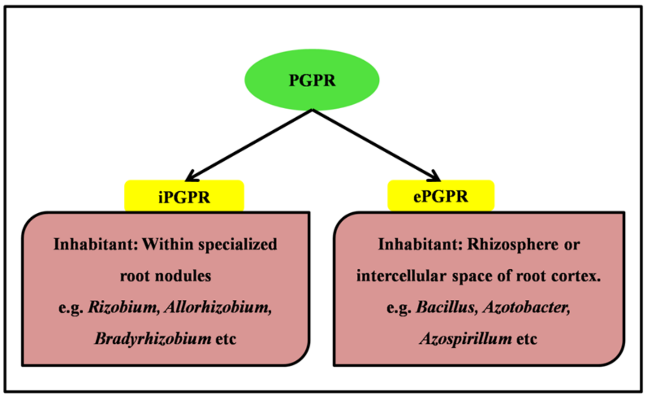

Fig. 4. Types of PGPR on the basis of their inhabitants (iPGPR and ePGPR indicate intracellular and extracellular Plant Growth Promoting Rhizobacteria respectively).

Mechanisms by which PGPR stimulate plant growth are categorized into biofertilizers, phytostimulators and biopesticides or biocontrol agents (45, 47).

Biofertilizers

Mechanisms like biological nitrogen fixation, ammonia production, phosphate solubilization are covered in this section. PGPR enhance the supply of primary nutrients to the plant body through these processes and stimulate plant growth.

Phytostimulators

This section covers some PGPR mechanisms, such as the production of phytohormones (auxin, cytokinin and gibberellin) and the reduction of ethylene concentration.

Biopesticides or biocontrol agents

Some of the important PGPR mechanisms like competitive exclusion, acquired and induced systemic resistance, production of fungal wall degrading enzymes and production of antibiotics (siderophores, Hydrogen cyanide and antifungal metabolites) are included within this category.

Contributions of PGPR in Plant Growth regulations

The starting letters 'PGP' of PGPR directly indicate its promising role in plant growth promotion. Plant growth means plant's overall growth including plant biomass, yield and key regulators (48). PGPR help plants to perform proper physiological functions trough photosynthesis, nitrogen metabolism, ammonia production, phytohormone production and regulation, mineral solubilization, metal chelating (49-56) as discussed in Fig. 5.

From ecological point of view PGPR are good biofertilizer (2) and maintain soil fertility by recycling the soil nutrients (57). Agricultural sustainability directly depends upon soil texture quality. A sustainable agricultural system

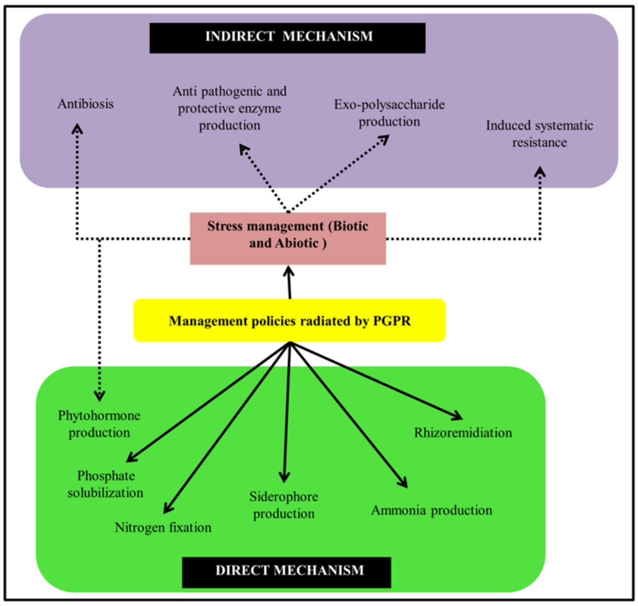

Fig. 5. Policies raised by PGPR to regulate plants' internal activities (all the solid and dotted lines indicate the management policies by PGPR, where dotted lines are exclusive for indicating stress related management).

can reimpose our daily lives by raising a large financial support (58). At present day it is impossible to imagine a sustainable crop production without involvement of beneficial microbes (59). They colonize in plant root area, and also improve the productivity (60). PGPR can show their performance versatility (45). Some PGPR with their performances are documented (Table 2).

gen uptake throughout whole plant body (44). In addition to nitrogen fixation, PGPR conduct a 5-step reaction as sketched in Fig. 6 to complete the nitrogen cycle on Earth.

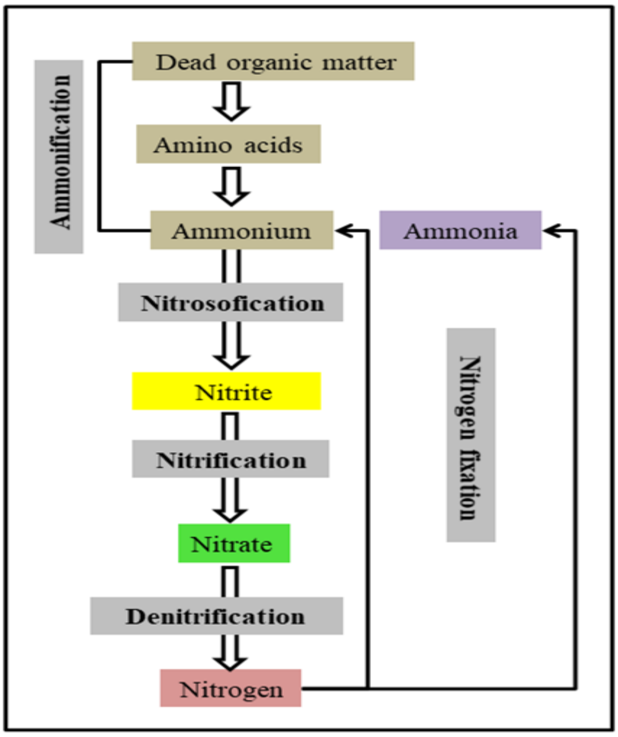

Fig. 6. PGPR involvements in Nitrogen cycle (where Ammonification, Nitrosofication, Nitrification, Denitrification and Nitrogen fixation indicate intermediate steps).

Table 2. Plant growth promoting rhizobacteria (PGPR) and their applications (4, 6, 23, 44, 61-95)

TYPE OF FUNCTIONS		PGPR
Nitrogen fixation		*Bacillus tequilensis*, *Pseudomonas aeruginosa*, *Klebsiella* sp., *Azotobacter* spp, *Azospirillum*, *Enterobacter cloacae*, *Bacillus drentensis*, *Rhizobium*, *Bacillus pumilus* Sol-1, *Alcaligenes* sp. Mal-4, *Providencia vermicola* Ama-2, *Brevundimonas* Kro13, *Kluyvera ascorbata* SUD165, *Pseudomonas putida*, *Ochrobactrum*, *Bacillus megaterium*, *Bacillus mycoides*
Phosphate solubilization		*Bradyrhizobium*, *Bacillus tequilensis*, *Pseudomons*, *Azotobacter*, *Azospirillum brasilense*, *Azospirillum amazonense*, *Agrobacterium*
Siderophore production		*Rhizobium ciceri*, *Bradyrhizobium japonicum*, *Kluyvera ascorbata*, *Pseudomonas fluorescens*, *Pseudomonas putida*, *Mesorhizobium ciceri*, *Azotobacter Chroococcum*, *Serratia marcescens*, *Proteus vulgaris*, *Paenibacillus polymyxa*, *Pseudomonas aeruginosa* 4EA, *Klebsiella* sp., *Azotobacter vinelandii*, *Bacillus megaterium*, *Bacillus subtilis*, *Pantoeaallii* and *Rhizobium radiobacter*
Phytohormone production	IAA	*Bradyrhizobium*, *Rhizobium*, *Azotobacter chroococcum*, *Bacillus*, *Pseudomons*, *Azotobacter*, *Azospirillum*, *Bradyrhizobium japonicum*, *Sphingomonas* sp., *Mycobacterium* sp., *Bacillus* sp., *Rhodococcus* sp., *Cellulomonas* sp., *Pseudomonas* sp., *Pseudomonas fluorescence*, *Brevibacillus* sp., *Klebsiella oxytoca*, *Burkholderia*, *Enterobacter* sp., *Rahnella aquatilis*, *Bacillus tequilensis*, *Bacillus subtilis*, *Phyllobacterium*, *Agrobacterium*
	Cytokinin	*Rhizobium leguminosarum*, *Azotobacter chroococcum*
	ABA	*Bacillus subtilis*
	GA	*Achromobacter xylosoxidans*, *Gluconobacter diazotrophicus*, *Acinetobacter calcoaceticus*, *Rhizobia*, *Azotobacter* sp., *Bacillus* sp., *Azotobacter chroococcum*, *Serratia nematodiphila*

Atmospheric nitrogen fixation

Nitrogen is one of the major constituents of plant cells which present in DNA, RNA, protein, amino acid etc. Eukaryotic plants rely entirely on symbiotic microbes for biological nitrogen fixation because they do not have the ability to break the triple bond between two nitrogen atoms. Some plant growth promoting bacteria namely *Klebsiella* sp., *Acinetobacter* sp., *Bacillus pumilus* (44), *Azotobacter* spp. (4), *Burkholderia* (96), *Psedomonas* (62) have been reported to show atmospheric nitrogen fixing ability. PGPR with atmospheric nitrogen fixing ability can raise the nitro-

Atmospheric nitrogen fixing PGPR show versatility in their performance including disease management, crop growth promotion in addition with the nitrogen maintenance in agricultural land (58). *Bacillus tequilensis* also shows positive response in atmospheric nitrogen fixation in soil though this is a potent phosphate biofertilizer (23).

Ammonia production

Ammonia (NH_3) is the first stable product of nitrogen fixation which can fulfill the nitrogen demand in plant body. As an important nutrient source it is frequently used in agricultural field to improve the crop productivity though it shows detrimental effect above its optimum level (96, 97). Ammonia producing PGPR are included in the genera *Bacillus*, *Psedomonas*, *Serratia* (43).

Phosphate solubilization

Plants need phosphate for growth, maturation and function. Usually inorganic phosphate is soluble in nature. Chemical fertilizer contains inorganic phosphate but it becomes immobilize and inaccessible to plants (98). Phosphate solubilizing bacteria are the key convertor of insoluble form of phosphate in soluble form and make it useable for plants (99). Some PGPR can apply this management policy have been mentioned (Table 2). Phosphate solubilizing PGPR also improve plant growth and yield (100). A synergistic efficiency of phosphate solubilisation is found in the combine application of bacteria instead of individual (101).

Phytohormone production

Phytohormones are organic compounds which are key players in plant growth, development and maintenance of plants' cellular activities even under environmental stress conditions (6, 102). Phytohormones such as Auxin, Cytokinin, Gibberellin are involved in the growth and development of the plants (48), are reported to be produced by many PGPR (103-105). Among the various types of natural Auxin produced by plant growth promoting rhizobacteria, IAA is important one (6). Auxin producing PGPR can activate Auxin responsive genes that promote plant growth (106) and induce root length (107) and biomass also (108). It has been documented in previous studies that PGPR which are able to produce Auxin, also involve in hormonal changes, and also regulate some defense genes, wall related genes at transcriptional level (109). Some strains of PGPR have been shown to promote plant shoot growth by eliciting Gibberellins production (110). *Achromobacter xylosoxidans, Gluconobacter diazotrophicus, Acinetobacter calcoaceticus, Rhizobia, Azotobacter* spp., *Bacillus* sp., *Herbaspirillum seropedicae* and *Azospirillum* spp. are some Gibberellic acid producing PGPR (94). Increment in Cytokinin concentration with plant growth has been found after *Bacillus subtilis* inoculation in lettuce plant (111). On the other hand, PGPR showed a down regulating effect on ethylene concentration (16) as shown in Fig. 7.

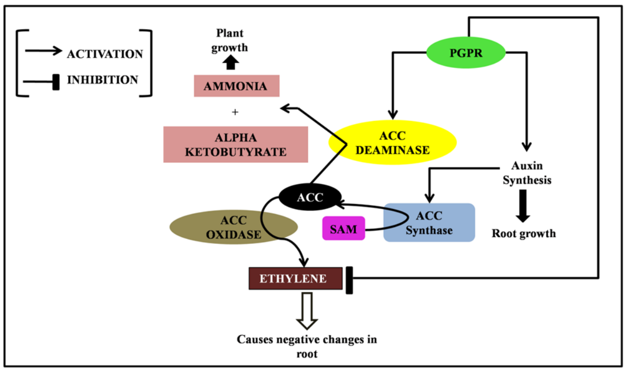

Fig 7. Regulation of Auxin-Ethylene biosynthesis by PGPR in response to stress (where ACC and SAM indicate 1-Aminocyclopropane-1-Carboxylic acid and S-Adenosyl-L-methionine respectively).

Hydrogen cyanide (HCN) production

Hydrolysis of cyanogenic compound and Ethylene biosynthesis are some common pathways of cyanide production for plants. Plants detoxify most of it by a special enzyme β cyanoalanine (99). Depending upon its concentration hydrogen cyanide exerts positive impact on plants. At a low concentration it regulates plant metabolic processes as a signaling molecule whereas it shows its anti herbivore activity at high concentration (112). In the agriculture system HCN is commonly used as a biocontrol agent, and it is a good metal chelator also (113). In a Pea - *Pythium* pathosystem HCN has been reported as biocontrol trait for pseudomonads (114). As potent biofertilizer HCN producing PGPR promote plant vegetative growth, and yield also (113). PGPR which are characterised with of HCN and ammonia production can exert synergistic effect on plant growth and plant metabolite modulation (43). The concentration of HCN produced by PGPR under *in vitro* condition is unable to relate to the geochemical processes instead of biocontrol hypothesis (112).

Siderophore production

These are small, iron chelating low molecular weight secondary metabolites secreted by nearly all bacterial species (115-117). These are categorised on the basis of chemical nature of their iron-chelating group which may be α-hydroxyl-carboxylate, catechol, hydroxamate, or mixed types (116). As a scavenger they scavenge iron from environment and make mineral (115). Siderophores transport Fe^{3+} ions and transport them across cell membranes (118). Siderophore producing microbes are considered as an efficient PGPR which show multifunctional potentiality in plant growth promotion (119), and also put down diseases (120). *Pseudomonas putida* enhances the level of iron content in the natural habitat utilizing heterologous siderophores produced by other microorganisms (34).

Rhizoremediation

At present era it is very urgent to reduce the pollution level to keep away all of the organisms from its cope. Contaminated soil and water is a big problem for agricultural sustainability. Combine effect of phytoremediation and bioaugmentation regulate rhizoremediation (58). Phytoremediation is a promising approach by which plants can extract metals from contaminated soil (121). Biological waste treatment by adding cultured microorganisms is known as bio-augmentation (122). Genetically engineered *Pseudomonas fluorescens*, *Pseudomonas aeruginosa* and certain *Bacillus* sp. are some examples of PGPR having rhizoremediation property (123). PGPR participate in this remediation process by removing organic contaminants, or by applying certain processes such as phytoextraction, rhizofitration, phytostabilization and phytovolatilization (57) to treat heavy metals (121) and lower the contamination levels.

Stress tolerance

The devastating impact of environmental stress on crop yield is a serious problem at present scenario. Now it is very urgent to adopt some eco-friendly management policies to secure our agricultural system. Environmental stress may be caused by abiotic factors, or some biotic agents like, fungi, bacteria, nematodes, herbivores, oomycetes etc (124). Worldwide major losses in crop field can be accomplished by abiotic mediators including salinity, floods, drought, radiation, high temperature, extreme cold, heavy metals etc (16, 124). Any kind of stress ultimately converts to oxidative stress and increases the production of some free radicals such as H_2O_2, O^{2-}, $\cdot N{=}O$, ClO^-, and OH^- which are considered as Reactive Oxygen Species (ROS) having the capacity to damage plants membrane lipids, proteins and nucleic acids (125). PGPR are some key agents which protect plants from multiple stresses (60) through some management policies (Table 3).

Table 3. Plant growth promoting rhizobacteria (PGPR) management policies to protect plant from stress effects (2, 31, 58, 126-129)

Management strategies	PGPR
Protective enzymes production	*Pseudomonas fluorescens* LPK2, *Sinorhizobium fredii* KCC5, *Trichoderma* sp., *Bacillus subtilis*, *Variovorax paradoxus* 5C-2 , *Pseudomonas fluorescens* biotype G, *Enterobacter* sp., *Stenotrophomonas maltophilia*, *Bacillus cepacia*, *Bacillus licheniformis*, *Bacillus cereus*, *Bacillus circulans* and *Bacillus thuringiensis*
Disease resistance antibiosis	*Pseudomonas* sp., *Bacillus* sp., *Pseudomonas fluorescens* and *Pseudomonas aeruginosa*
Volatile organic compounds secretion	*Pseudomonas*, *Bacillus*, *Arthrobacter*, *Stenotrophomonas* and *Serratia*, *Bacillus megaterium* BOFC15
Exopolysaccharides secretion	*Rhizobium leguminosarum*, *Azotobacter vinelandii*, *Bacillus drentensis*, *Enterobacter cloacae*, *Agrobacterium* sp., *Xanthomonas* sp., *Rhizobium* sp., *Bradyrhizobium* sp., *Pseudomonas putida*, *Bacillus subtilis* and *Azospirillum brasilense*

and sustain host plants growth, and yield acting as protective barrier against biotic and abiotic type of stress conditions (58). EPS producing PGPR strains enhance plant growth by avoiding water stress (55) and also stimulate the production of enzymatic antioxidant such as Superoxide dismutase (SOD), Catalase (CAT) and Peroxidase (POD) to detoxify ROS (129, 136). Some PGPR showing stress-tolerance capabilities have been listed (Table 4).

Molecular responses and signalling pathways in response to Plant-PGPR interactions

Plant microbe signalling exerts phyto-beneficial roles including crop biomass, nutrient uptake and metabolite up-regulation. Some important traits sustain plants under

As anti-phytopathogenic agents (130) PGPR produce some cell wall degrading enzyme such as β-1, 3-glucanase, ACC deaminase and chitinase and neutralize pathogens (126). *Burkholderia*, is an ACC deaminase secreting genus has been reported to increase the growth of tomato seedlings by limiting ethylene levels (131). ACC deaminase also reduces the ethylene induced negative changes in the roots (132) as presented in Fig. 7**.** Various types of plant-microbe interactions are essential for regulating the local and systemic types of plant defence mechanism which help to increase the chances of survivability of the plants living in stress affected area (131). PGPR defeat plants in dehydration by improving plants water use efficiency (WUE) and water absorption through roots (133)**.** Induced systemic resistance (ISR) is a modern approach in agricultural research, inspired by non pathogenic microbes and involved in control of numerous diseases (58). VOCs producing PGPR show their potentiality in plant growth, in plant pathogen control and also in ISR induction (134). Involvement of VOCs produced by *Bacillus subtilis* in hormonal regulation, plant growth development, photosynthesis and phytohormone induction with alleviation of ethylene level have been reported (134). Hormonal regulation plays central role in stress management (135). PGPR change the levels of endogenous phytohormone within wheat seedlings and enhance the ability to overcome the stress like salt and drought (136). *B. subtilis* resists drought stress elevating the levels of Abscisic acid (137). IAA producing bacteria help plants to defend against water deficit condition (138) by increasing root growth and/or enhancing the formation of lateral roots and roots hairs in various plant species (60). In this context EPS secretion is one of the prime characterizations of PGPR which are high molecular weight, biodegradable polymers

Table 4. Stress responsive Plant growth promoting rhizobacteria (PGPR) (127, 129, 139)

Type of		PGPR
ABIOTIC STRESS	Salinity	*Azospirillum brasilense*, *Pseudomonas syringae*, *Pseudomonas fluorescens*
	Drought	*Achromobacter pechaudii*, *Azospirillum brasilense*, *Acinetobacter* sp., *Pseudomonas* sp., *Pseudomonas fluorescens* biotype G, *Bacillus subtilis* and *Azospirillum brasilense*
	Temperature	*Burkholderia phytofirman*, *Aeromonas hydrophila*, *Serratia liquefaciens*, *Pseudomonas* sp. (strain AKM-P6) and *Pseudomonas putida* (strain AKM-P7)
	Heavy	*Pseudomonas putida* (Pb and Cd resistence), *Brevibacillus* sp. (Zn resistance)
BIOTIC STRESS		*Paenibacillus Polymyxa* (strains B2, B3, B4), *Paenibacillus favisporus* (strain BKB30), *Bacillus amyloliquefaciens* (strain HYD-B17), *Bacillus licheniformis* (strain HYTAPB18),

biotic and abiotic types of stress (140). Advanced bioinformatic studies indicate reciprocal gene regulation between bacteria and their host plants during colonization and post colonization also (141). Phyto-beneficial proteins have been reported to induce in sorghum roots after PGPR inoculation (141). Some phyto-beneficial proteins deal with DNA regulation including Phosphodiesterase, sulfatase, Carbohydrate kinases (FGGY_C) whereas some of these are stress relieving in nature such as HSP70 (141). The important protein family Carbohydrate kinases (FGGY _C) are involved in the production of carbohydrates and control plant biomass (141). PGPR enhance photo pigment contents in Basil leaves under water stressed condition (142), and maintain photosynthesis to manage plant biomass and survivability. Induction of photosynthetic rate, plant biomass, and photosynthetic pigments such as chlorophyll content, carotenoids under salt stress after inoculation of PGPR have been reported (143). Carotenoids are belonging to C_{40} tetraterpene family, this report also supports the fact that the biosynthesis of terpene is somehow regulated by PGPR. Phosphodiesterase is one of the key players involved in DNA–protein crosslink repair mechanism in plants (141) and cellular homeostasis maintains by HSP70 (141). PGPR regulate phenylalanine concentration in tomato (144). Phenylalanine is an important product of shikimic acid pathway, regulates biosynthesis of phenolic compounds. One of the important phenolic compounds is flavonoids which are non enzymatic antioxidant, synthesized from an extended part of shikimic acid pathway, more specifically from phenyl propanoid acetate pathway. PGPR enhance flavonoid biosynthesis genes (145) and also trigger the core pathway of phenolics biosynthesis by upregulating the key enzyme PAL in Chickpea (146) as shown in Fig. 8.

In *Solanum*, enhancement of photochemical efficiency after *Bacillus* inoculation has been reported, and this makes plant to cope with abiotic stresses such as salt, drought and heavy metal (146). Flavonoids are 15 C plant phenolics involve in pigmentation, pollination, antimicrobiosis and UV protection. Side by side this flavonoid enhancement positively correlates with non pathogenic defence management or ISR: Induced Systematic Response. PGPR regulate some biochemical signalling involved in nitrogen fixation. Nitrogenase is the multi-subunit oxygen

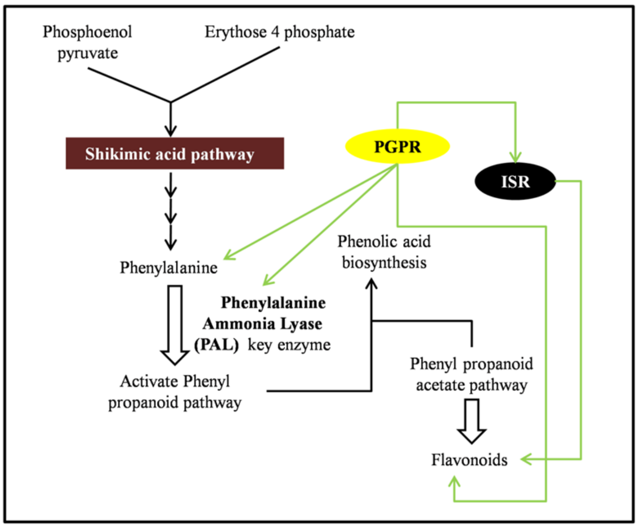

Fig. 8. Phenolic compounds-PGPR-ISR interrelationship (where, ISR represents Induced Systematic Resistance. Black arrows are indicators of sequential biochemical steps and green lines indicate the routs for induction of plant defence triggered by PGPR).

liable key enzyme for Nitrogen fixation, present in prokaryotes. Nitrogenase activity has been presented in Fig. 9.

Nitrogenase reductase, the small component of Nitrogenase enzyme is anchored by nifH. It has been confirmed that *Bacillus* promotes nifH gene expression in sugarcane varieties (65). Signalling system of some defence responsive enzymatic antioxidants such as CAT, GPx and SOD are regulated by plant growth promoting rhizobacteria under environmental adverse situations (147). Phytohormonal regulation is triggered by activation of ACC deaminase, the main enzyme of stress regulation that is shown in Fig. 7.

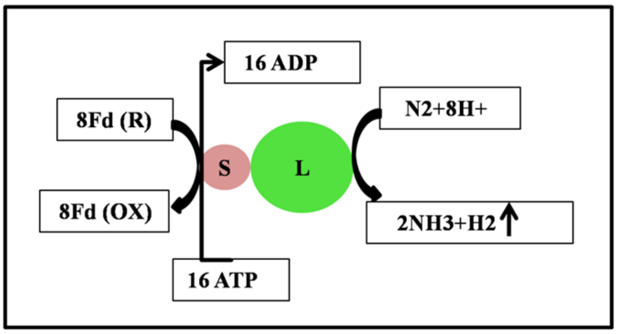

Fig. 9. Schematic presentation of Nitrogenase activity (where S and L represent Small and Large subunit respectively. Fd (R) indicates Reduced Ferredoxin and Fd (OX) indicates Oxidized Ferredoxin).

Conclusion

Agriculture is the only way to fulfill food demand worldwide. But unfortunately it is closely involved in the production of chemical pollutants. The use of chemical fertilizers, pesticides and insecticides by farmers has been increased to meet the growing food demand to feed booming population worldwide. They increase crop yields but reduce soil quality, which ultimately disturbs the ecosystem.

Environmentally PGPR are very good. They provide promising assistance in crop management and maintenance of soil ecosystems in terms of biofertilization, bioremediation, pest management, disease management, biocontrol and stress tolerance. They have also been shown to maintain plant cellular homeostasis in adverse environmental conditions.

In the current situation, it is very important to increase crop production by keeping the ecosystem sustainable. There is no doubt that PGPR are sufficient to increase global agricultural production in an environmentally sound way. Nanotechnology is a potent tool in this regard. Although it is difficult to incorporate nanotechnology into agriculture, it is efficient enough to promote global environmental and agricultural sustainability.

Future Prospects

PGPR are capable to manage plants' internal activities, plant growth and productivity even under adverse environmental conditions and also participate in contaminated soil management. But the effects of PGPR are gradually diminishing due to some abiotic and biotic factors. PGPR are lost in a large percentage in the conventional method of their application as biofertilizer (16).

Therefore, advanced technology needs to be improved to increase the use of PGPR in the agricultural system. Nanotechnology is a potential tool for improving PGPR services in agriculture (16). Nowadays, in agricultural revolution, nanoagriculture is a potential tool. In nanoagriculture, nanofertizers improve crop production efficiently by assisting plants in efficient nutrients uptake, monitoring plant growth, enhancing food quality, protecting plants, detecting plant diseases, increasing food production and reducing waste (16, 148). Nanoencapsulation technology is a potential method to extend PGPR service life (16). The application of nanotechnology in agriculture and environmental sustainability is not easy, so more research is needed to make it more convenient. In addition, much effort is required to obtain information on particular steps regulated by PGPR in plant biochemical pathways.

Overall, there has been a lot of work in PGPR over the decades, but the application of nanotechnology in PGPR-agricultural systems requires a lot of work that will play an important role in sustainable agriculture without harming the ecosystems.

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Authors contributions

The main concept of the review was provided by SD. Literature study was done by DC. The whole work was discussed by both Authors and finally DC prepared the manuscript. ST helped DC to prepare the figures according to the prescribed format.

Compliance with ethical standards

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