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Role of Plant Growth Promoting Rhizobacteria in Sustainable Agriculture: A Review

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Abstract: ***Deterioration of soil and land degradation has adversely affected food production. The last few decades have seen a lot of research on the role of soil microorganisms – the plant growth producing rhizobacteria (PGPR) in increasing the sustainability of agriculture so much so that soil microbes are now being proclaimed as a cornerstone of the next green revolution. These microbes can provide protection against biotic stresses of some pathogenic microbes and also increase tolerance for abiotic stresses such as drought, salinity and heavy metal toxicity thus promoting increased yield. This review is an attempt to study the current knowledge on the use of soil bacteria to mitigate biotic and abiotic stress factors of plants and the challenges involved in putting this knowledge into practical use for improvement in crop yield.***

Keywords: plant growth promoting rhizobacteria, PGPR, sustainable agriculture, biofertilizers

1. Background

The soil ecosystem is in state of delicate equilibrium between the soil nutrients and the biomass. Agricultural produce is directly related to soil quality which is regulated by a number of factors: organic carbon content, moisture, nitrogen, phosphorous, potassium content; contaminants in soil and water and also the soil microbiome which include bacteria and fungi. Indiscriminate use of agrochemicals has led to severe pollution of biosphere leading to alteration of soil microbiota and loss of productivity. [1]

These chemicals have changed the nature of the soil in terms of pH, salinity and hardening of soil resulting in soil degradation and poor crop production. Use of chemical fertilizers has also altered the soil microbiota resulting in added stress on plants. With ever increasing population and consistently increasing demand for food and animal feed, the world is looking for a way forward. The Food and Agricultural Organization stresses upon sustainable agricultural practices to increase food production and conserve agricultural land and deplores the state of depleting forest cover. Some of these methods include efforts at reducing soil erosion by reducing tillage and use of cover crops: improving soil nutrition by increasing the content of organic matter in the soil in the form of animal manure and compost; and phytoremediation to tackle the problem of heavy metal contamination of soil. [2]

In this context the last few decades have seen a lot of research on the role of soil microorganisms – the plant growth producing rhizobacteria (PGPR) in increasing the sustainability of agriculture so much so that soil microbes are now being proclaimed as a cornerstone of the next green revolution. These microbes can provide protection against biotic stresses of some pathogenic microbes and also increase tolerance for abiotic stresses such as drought, salinity and heavy metal toxicity thus promoting increased yield. [3] Although the use of microbial inoculants has a long history beginning in early 20th century when rhizobial inoculants from legumes were used to improve soil fertility [4], many more strains of rhizobacteria are being promoted as biofertilizers based on the recent research in this field. This review is an attempt to study the current knowledge on the use of soil bacteria to mitigate biotic and abiotic stress factors of plants and the challenges involved in putting this knowledge into practical use for improvement in crop yield. Literature relevant to the topic was extensively searched for the purpose of writing this review.

2. What are Plant Growth Promoting Rhizobacteria (PGPR)?

Dense populations of microorganisms colonize the root zone of plants and the narrow area of soil around them called the rhizosphere which is a more attractive habitat than bulk soil because of the organic carbon provided by plant roots through their secretions and the surface cells. Rhizobacteria respond to root exudates by means of chemotaxis; and in such scenario, competent bacteria tend to modulate their metabolism towards optimizing nutrient acquisition. Some of these symbiotic bacteria can exist in a mutualistic relationship with plants colonizing the roots for nutrition and at the same time promoting plant growth through a multitude of mechanisms. [5]

PGPR can be classified into exracelluar plant growth promoting rhizobacteria (ePGPR) and intracellular plant growth promoting rhizobacteria (iPGPR). The ePGPR exist in the rhizosphere while the iPGPR are generally located in the specialized nodular structures on the roots. *Agrobacterium, arthrobacter, Aztobacter, Azospirillum, Bacillus, Burkholderia, Caulobacter, Chromobacterium, Erwinia, Flavobacterium,Micrococcus, Pseudomonas, and Serratia* belong to ePGPR. The iPGPR belong to the family of Rhizobiaceae and include *Allorhizobium, Azorhizobium, Bradyrhizobium, Mesorhizobium, Rhizobium and Frankia* species. [6]

3. Mechanism of action

PGPR increase the sustainability of plants by enhancing the physiological functions of plants and making them resistant to various phytopathogens and adverse physical and chemical conditions. This is achieved through certain direct methods that improve plant nutrition and vigour and also through some indirect mechanisms that help plants to mitigate stress. These mechanisms have been briefly described in the following passages. Figure 1 summarizes the various biotic and abiotic stresses and the role of PGPR in alleviating these stresses.

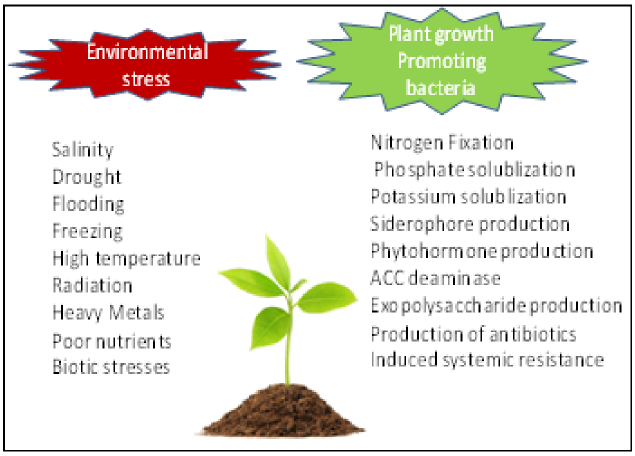

Figure 1: Role of plant Growth promoting bacteria (PGPR) in helping plants to combat biotic and abiotic environmental stresses

Nitrogen fixation

Nitrogen is the most important nutrient for plant growth and vitality. PGPR fix atmospheric nitrogen by a process called Biological Nitrogen Fixation (BNF) with the help of an enzyme called dinitrogenase reductase which helps to convert inert nitrogen gas N_2 into ammonia gas (NH_3) - a biologically utilizable form. The energy required for this process is derived from the organic carbon derived from the host plant. Some of these bacteria such as those from the family of rhizobiaceae form symbiosis with leguminous plants (e.g. rhizobia) and non-leguminous trees. They infect and establish symbiotic relationship with the roots of leguminous plants resulting in the formation of the nodules wherein the rhizobia colonize as intracellular symbionts. This has been documented by many researchers including Giordano and Hirsch (2004) in sweet clover-*Sinorhizobium meliloti* interaction. [7]

Over the last two decades, the role of some other nitrogen fixing free living bacteria and archaebacteria called diazotrophs in providing biologically utilizable nitrogen to plants has been explored. Commercial inoculants of *Azoarcus* sp., *Burkholderia* sp., *Gluconacetobacter* sp., *Diazotrophicus* sp., *Herbaspirillum* sp., *Azotobacter* sp., *Bacillus polymyxa*, and especially *Azospirillum* sp. have been used to increase nitrogen content of soil.[8] Thus PGPR represent an economically beneficial and a sustainable alternative to chemical fertilizers.

Phosphorus Solublization

Phosphorus is the second important growth limiting plant nutrient after nitrogen. Although it is abundantly available in the soil, most of it is in insoluble organic or inorganic compound form. PGPR convert insoluble phosphorus to a soluble bio-available form. The inorganic phosphorus present in the soil in form of apatite is solublized by phosphate solubilizing microorganisms (PSMs) by the action of organic acids or H^+ ions.[10] Rijavec and Lapanje have proposed that HCN secreted by PGPR helps in increasing P availability.[11] Also, the extracellular enzymes secreted by these bacteria release phosphorus by substrate degradation of the soil biomass constituted by dead and decaying organic matter converting it into soluble dibasic (HPO_4^{2-}) and monobasic ($H_2PO_4^{1-}$) phosphates [9]. In India strains of PSMs *Pseudomonas striata*, *B. Polymyxa*, and *B. megaterium* are being used commercially to reduce phosphate fertilizer requirements by up to 75%. [12]

Potassium Solublization:

Potassium is the third essential macronutrient required for plant growth. Most of the potassium exists in nature in the form of insoluble rock and silicate minerals. Hence, the concentration of soluble potassium is generally very low in soil.

The organic acids secreted by PGPR can solubilize potassium, making it available for uptake by plants. Potassium solubilizing PGPR, such as *Acidothiobacillus* sp., *Bacillus edaphicus*, *Ferrooxidans* sp., *Bacillus mucilaginosus*, *Pseudomonas* sp., *Burkholderia* sp., and *Paenibacillus* sp., have been reported to release potassium in accessible form from potassium-bearing minerals in soils. [13]

Siderophore production:

PGPR have an ability to produce low molecular weight metal chelating compounds called siderophores which can chelate iron to form Fe^{3+} complexes. These are water-soluble molecules that can be found in extracellular and intracellular locations. Plants can assimilate iron from bacterial siderophores either by the direct uptake of siderophore-Fe complexes, or by ligand exchange reaction and utilize them for growth in conditions of limited iron availability.[14] Another means for increasing the concentration of available iron is through solubilization by organic acids produced by PGPR. A formulation of the Fe mobilizing bacteria, *Acidithiobacillus ferrooxidans* developed by AgriLife (India) is being used commercially.[12] Similarly strains of Zn-mobilizing bacteria are being used to increase Zn uptake, and increased productivity of several crops, including rice, wheat and soybean.[15,16] Research has shown that siderophores can also form stable complexes with other heavy metals such as Aluminium, Cadmium, Copper, Galium, Lead and Zinc. This increases the solubility of the metal, thus enhancing their uptake and mobilization. [17]

Phytohormone production:

Plants can adapt themselves to environmental stresses through changes in root morphology which are mediated through phytohormones especially Indole Acetic Acid (IAA). Plant auxins in appropriate concentrations can modulate root configuration in terms of cell elongation resulting in enhanced root length and growth of lateral roots. Further, PGPR such as *Pseudomonas putida*, *Enterobacter asburiae*, *Pseudomonas aeruginosa*, *Paenibacillus polymyxa*, Stenotrophomonas maltophilia, *Mesorhizobium ciceri*, *Klebsiella oxytoca*, *Azotobacter* chroococcum, and *Rhizobium leguminosarum* can also produce as well as influence the production of phytohormones such as auxins, cytokinins, gibberellins and ethylene by the plants. This can influence modifications in root growth in response to stress factors within soil. [18] Examples are positive response of pea (Phaseolus vulgaris) to salt stressed soil in presence of Azospirillum brasilense and response of wheat (T. aestivum) to drought stress in presence of Azospirillum.[19,20] Some strains of PGPR can secrete large amounts of gibberellins which can enhance plant shoot growth.[21]

Production of 1-Aminocyclopropane-1-carboxylate (ACC) deaminase

Ethylene is a “stress hormone” that is increasingly produced by plants during conditions of biotic and abiotic stress. It is a growth regulator - excess of ethylene affects the plant growth by inducing defoliation and other cellular processes that can reduce crop yield.[8] PGPR can produce ACC deaminase which can lyse ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC) into ammonia and 2- oxobutanate thus regulating the levels of ethylene. Many studies have demonstrated that plants inoculated with such PGPR showed increased stress tolerance [22].

Other Biocontrol Activities in response to abiotic stress:

Zhou et al demonstrated that PGPR *Bacillus megaterium* BOFC15 secretes a polyamine, spermidine that induces polyamine production in *Arabidopsis*. The inoculated plants showed higher drought tolerance and an increase in biomass, through a favourable root architecture and elevated photosynthetic capacity.[24] Kumar et al demonstrated that tobacco plant inoculated with *Paenibacillus lentimorbus* showed enhanced growth and decreased virulence of cucumber mosaic virus. They proposed that this effect was mediated through the production of HCN by the rhizobacterium.[25]

Massalha et al have discussed the role of lumichrome and riboflavin secreted by PGPR in accelerating the growth of leaves and height of the plants resulting in improved production of biomass.[26] Similarly lipo-chitooligosaccharides and thuricin 17 are known to increase plant growth especially when plants are growing under conditions of stress.[27] Similarly, PGPR also help plants to grow in presence of stress of flooding. Etesami et al have demonstrated this in case of Rice (*Oryza sativa*) seedlings inoculated with REN1 strain of *Pseudomonas fluorescens* that produces ACC deaminase. The seedlings responded with increase in length of roots.[28] Kang et al demonstrated that *Serratia nematodiphila* increases pepper (*Capsicum annum*) growth under conditions of low temperature.[29]

Role of PGPR against biotic stressors of plants:

Biotic stress is caused by different pathogens, such as bacteria, viruses, fungi, nematodes, protists, insects, and viroids. This results in a significant reduction in agricultural yield. Plants inoculated by soaking their roots or seeds overnight in cultures of PGPR exhibit enormous resistance to different forms of biotic stress.[30] For example *Pseudomonas* species has been shown to produce a wide variety of antifungal antibiotics such as phenazines, phenazine-1-carboxylic acid, phenazine-1-carbxamide, pyrrolnitrin, pyoluteorin, oomycin A, cepaciamide A, ecomycins, viscosinamide, butyrolactones and pyocyanin; bacterial antibiotics such as pseudomonic acid and azomycin; antitumor antibiotics such as FR901463 and cepafungins and antiviral antibiotics such as Karalicine.[31] PGPR are facilitators of induced systemic resistance (ISR) in many plants. They help in activation of a huge number of defense enzymes, such as chitinase, β-1, 3-glucanase, phenylalanine ammonia lyase, polyphenol oxidase, peroxidase, lipoxygenase and sulphur oxide dismutase. ISR involves jasmonic acid and ethylene signaling within the plant. These hormones enhance the host plant’s defense responses.[32] Forexample, Zebelo et al reported that cotton (*Gossypium hirsutum*) plants inoculated with *Bacillus* spp. exhibited increased gossypol and jasmonic acid secretion which reduced larval feeding by *Spodoptera exigua*.[33]

From laboratory to the farm - role of PGPR in sustainable agriculture:

The need for sustainable increase in crop yield, the knowledge and experience regarding harmful effects associated with the use of chemical fertilizers, and pesticides, and the incremental knowledge gained from research on the role of soil microflora and PGPR as biofertilizers and biocontrol agents has opened new vistas. However, performance of PGPR in field conditions is variable. Plants control the colonization of microbes in the rhizosphere through a variety of signaling molecules such as jasmonic acid, salicylic acid, flavanoids, terpenes and phenolic compounds secreted in the root exudates. These compounds vary not only with the plant genotype but are also affected by the various stages of plant growth as well as weather conditions, soil characteristics and activity of the indigenous microbial flora of the soil.[26] Hence, microorganisms that show promise in the laboratory may not exhibit key characteristics for widespread colonization in sustainable and productive agricultural systems. Similarly, attempts to introduce rhizobacteria as biocontrol agents have often failed because of problem of their instability in long-term culture.[34] Hence, current research is focused on understanding the mechanisms that govern microbial colonization in diverse soil communities and varied climatic conditions.

Curating PGPR from plant associated environments:

Large scale isolate collections have been generated from the roots and shoots of various plants and genome sequencing of a large subset of these collections has been done from grapevine, potato, Arabidopsis and sugarcane. The aim is to provide a rich screening tool for PGPR traits that could be readily detected in genomes.[35] Thus research on PGPR has moved from laboratory to ecological systems and development of superior PGPR strains with improved traits is possible by using genetic manipulations.[36]

Diversification of inoculum:

Complex inocula, rather than single strains, can provide plants with stronger disease resistance and growth promotion, for example, use of microbial consortium improved arsenic sequestration efficiency of the hyper-accumulator fern *Pteris vittata*, tripling its phytoremediation efficiency.[37] Consortia can be constituted by PGPR of closely related strains thus enhancing the niche breadth of a particular trait. They can also consist of distantly related strains that provide PGP via different mechanisms – thus they contribute to an overall additive effect.[38] However, effect of consortia can be worse than single strains. For example, increasing strain richness within the biocontrol species *Pseudomonas fluorescens*, can cause community collapse and subsequent loss of plant protection.[39]

Biofertilization using biofilms:
Most formulations of PGPR inoculants have bacteria in the free–floating planktonic growth. It has been seen that survival of free bacterial cells in soil is poor resulting in poor colonization of rhizosphere by the desired PGPR. On the other hand immobilization of cells in biofilms prolongs cell survival by allowing greater interaction of the bacteria and their metabolites with the plants. Biofilms contain sessile bacterial growth embedded in a matrix of substances; mainly exo-polysaccharides, proteins and DNA thus increasing the intimacy of contact between the bacteria and the plant.[40] Galelli et al demonstrated that Bacillus subtilis subsp. spizizenii showed increased PGP activity in Lactuca sativa when in biofilm resulting in significant increase in biomass of the plants.[41]

Adding biochar to the soil:
It has been found that biochar can influence soil pH, organic matter content, cation exchange capacity of the soil making it favourable for growth of bacterial inoculants. It also increases water retention and oxygen tension within the soil, preventing overgrowth of fungal predators but promoting growth of arbuscular mycorrhizal fungi.[42]

Despite these technological advances, the path for large scale use of PGPR as biofertilizers and biocontrol agents is still ridden with hurdles. A lot needs to be done to integrate microbiome-based plant breeding for heritable PGPR community in farmlands.[43] At the same time bioremediation processes need to continue to improve the quality of soil and overcome the damage caused by chemical contaminants. Soil specific bio-inoculants are required to overcome environmental constraints. Farmers need to be trained in the use of these bio-innoculants and and their use has to properly monitored for any setbacks in terms of crop yields as this might discourage their usage.

4. Conclusion

Although the use of PGPRs as inoculants is centuries old, this has been largely focussed on legumes and cereals. The promising applicability of PGPR in sustainable agricultural processes is exciting but there are some major hurdles that need to be addressed to increase their efficacy. Further research is needed to isolate desired plant specific rhizobacteria from natural biomes. However, practical utility of new technological advances does have its own incubation period and we need to invest time and patience with close monitoring to look for the effects of new interventions. Combining bioremediation with plant growth promotion would be a beneficial approach in addressing this global agriculture problem. We need to ensure that this is approached in a systematic and thorough manner.

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