



# Insight Into the Role of PGPR in Sustainable Agriculture and Environment

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A multitude of roles is played by microbes in food and agriculture that include nutrient cycling and management, organic matter decomposition and fermentation. Plant growth promoting rhizobacteria (PGPR), representing microbial groups and with ability of colonizing plant roots, influence plant growth through various indirect and direct modes in order to promote its growth and/or protect it from diseases or damage due to insect attack. Thus, PGPR research has received renewed interest worldwide. Increasing number of crop-specific PGPR are being commercialized these days. Approaches like seed-inoculation and soil application either alone or in combination with bacterial culture/product for increased nutrient availability through phosphate solubilisation, potassium solubilisation, sulfur oxidation, nitrogen fixation, iron, and copper chelation are gaining popularity. Arbuscular mycorrhizal fungi (AMF) are root fungal symbiont that improve management of abiotic stress such as phosphorus deficiency. PGPR involves roles like production of indole acetic acid (IAA), ammonia (NH<sub>3</sub>), hydrogen cyanide (HCN), catalase, etc. PGPR also improve nutrient uptake by altering the level of plant hormone that enhances root surface area by increasing its girth and shape, thereby helping in absorbing more nutrients. PGPR facilitate seed germination, seedling growth and crop yield. An array of microbes including *Pseudomonas*, *Azospirillum*, *Azotobacter*, *Klebsiella*, *Enterobacter*, *Alcaligenes*, *Arthrobacter*, *Burkholderia*, *Bacillus*, and *Serratia* enhance plant growth. Various *Pseudomonas* sp. have demonstrated significant increase in germination, seedling growth and yield in different agricultural crops, including wheat. Hence, developing a successful crop-specific PGPR formulation, the candidate should possess characteristics like high rhizosphere competence, extensive competitive saprophytic ability, growth enhancing ability, ease of mass production, broad-spectrum action, safety toward the environment and compatibility with other partnering organisms.

**Keywords:** PGPR, rhizosphere, hydrogen cyanide, indole acetic acid, nitrobacter, sulfur solubilisation, root microbiome, sustainable agriculture

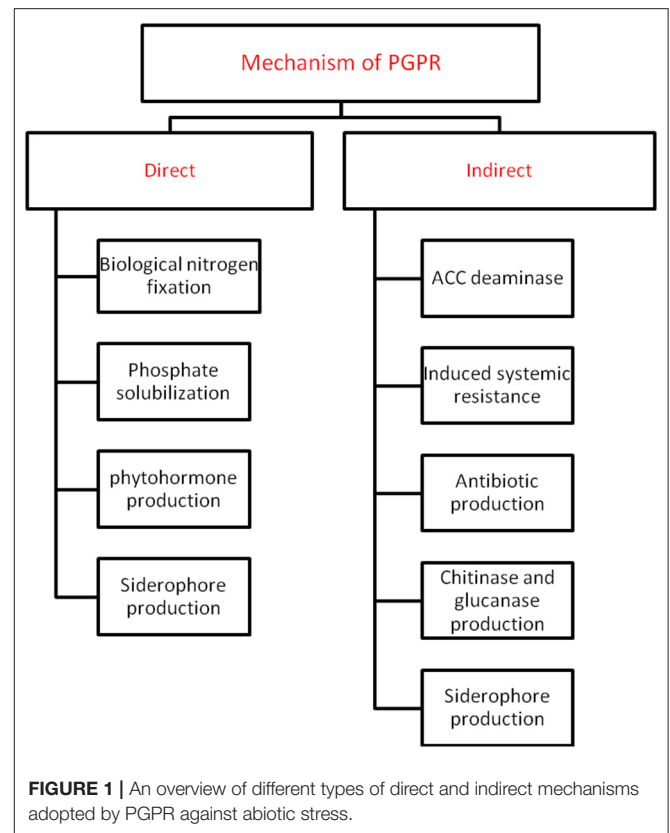
## INTRODUCTION

The twenty-first century has been witnessing rapid rise in human population along with critical issues in global agroecosystems, leading to decreased productivity and degeneration of sustainable agroecosystem. Food is a fundamental need of people that assumes a significant function in human well-being and societal advancements. While feeding the geometrically progressing human

population, required balanced value-added food to supplement a diet is significantly difficult. In contrast, there is a decrease in crop productivity, which may pose additional concern to address before long. The ever-increasing population exhibits pressure on arable land to increase crop yield, leading to indiscriminate use of chemical fertilizers, insecticides, pesticides, etc. by the farmers. Agrochemicals runoffs from such land adversely affect life on Earth through bioaccumulation and biomagnifications through the food chain. Also, the pesticides utilized to fight against plant illness affect the beneficial natural insect, soil fertility and soil microbiota adversely (Khatoon et al., 2020), and obviously additionally impact human well-being. Alongside, the soil acidity due to these strong chemicals is also altered (Slepetiene et al., 2020). Anthropogenic activities are liable to cause ecological damage and deter soil health, ultimately depleting the nonrenewable assets. It is therefore essential to adopt various environment-friendly ways. In the present circumstance, sustainable agriculture is essential as it offers the capacity to meet not only our present needs but also ensure a healthy future, something that can't be realized through the conventional harmful agrarian practices (Santoyo et al., 2017). Crop yields have been affected by a wide range of ecological destabilization emerging from complex issues (Shrivastava and Kumar, 2015). For example, salinity as a significant environmental abiotic stress is a serious global agricultural concern, turning the cultivated areas in to uncultivated region especially within the arid and semiarid zones at an estimated rate of around 1–2% annually.

Around 20% of the whole arable zone has become transformed to uncultivated region as a consequence of salinity (Rasool et al., 2013). Salinity brings about extreme change in the development and metabolism in plant (e.g., changes in plant physiology, morphology, and biochemistry) (Gupta and Huang, 2014). Drought is another abiotic stress in most aerable lands, particularly in the arid and semiarid regions affecting crop productivity (Bodner et al., 2015). Due to more serious and regular droughts owing to climate change, it is predicted that more than 50% of the arable land will have critical plant growth issues by 2050. Drought affects the crop adversely by influencing water association, photosynthetic assimilation, and supplement take-up (Osakabe et al., 2014). In present times, heavy metal contamination may pose a threat to ecology. Since these metals are hard to remove, environmentalists are worried about their harmfulness to the ecology and biological systems (Etesami, 2018). Some of these metals are needed at very low quantity for various plant metabolic processes, but at very high levels these metals affect the phytological and microbial network adversely (Ali et al., 2015). Heavy metals add to the inadequacy and irregularity of basic plant supplements (Etesami, 2018). Likewise, flood is another stress factor that affects plant productivity. All these non-biological stresses are increasing day by day due to global climatic change. Therefore, it is important to reduce environmental stress by employing ecofriendly strategies, including eco-accommodating and sustainable utilization of beneficial microbes.

Plant growth promoting rhizobacteria (PGPR) are critical players in agriculture (Etesami and Maheshwari, 2018). It helps in crop well-being by fixing nitrogen, solubilising phosphate,



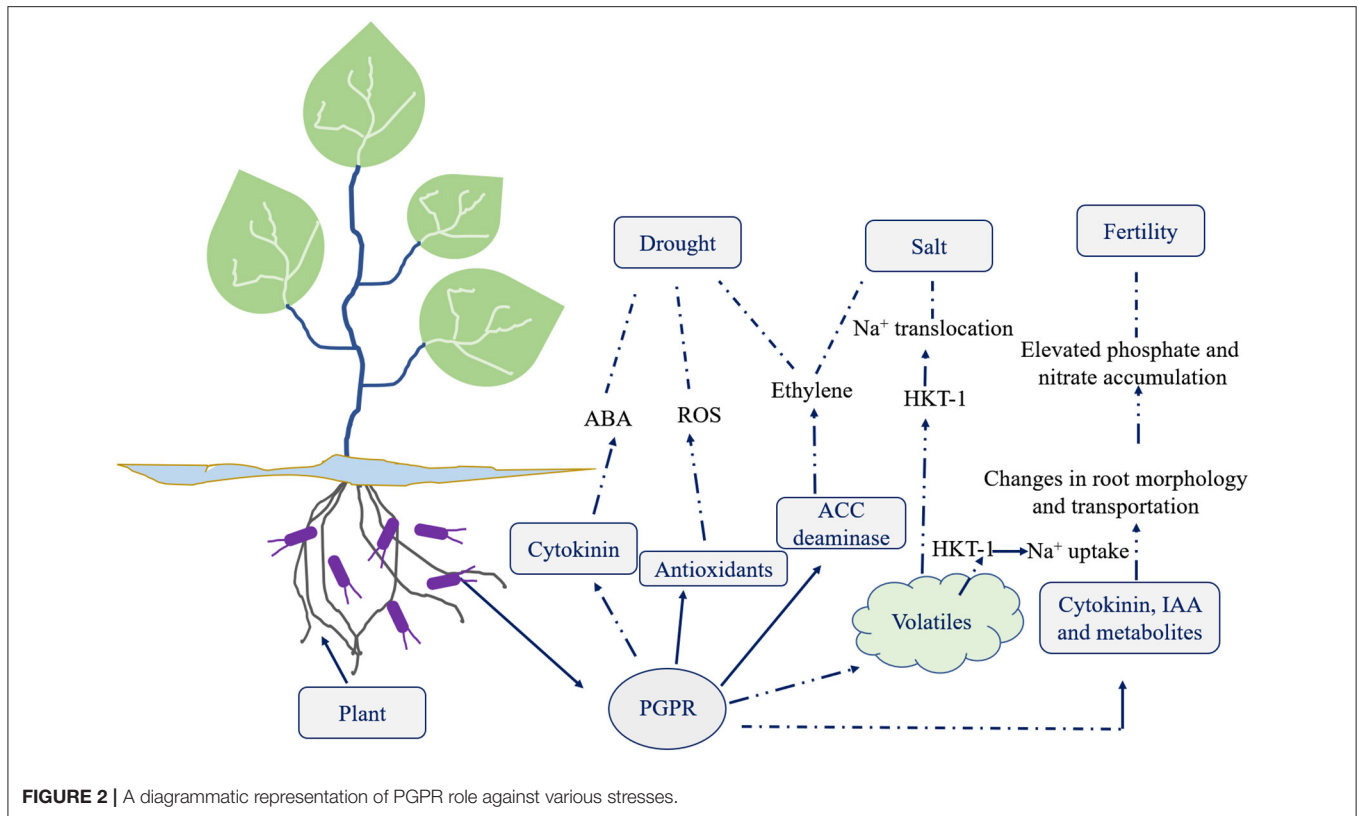
reducing heavy metals, producing phytohormones (like auxin, gibberellins, cytokinins etc.), mineralising soil organic matter, decomposing crop residue, suppressing phytopathogens, etc. (He et al., 2019). A detailed overview of the different direct and indirect mechanisms of action by plant growth promoting microbiomes is highlighted in **Figure 1**. PGPR offer critical knowledge to the agricultural and environmental biotechnology by providing several new genes and understanding of the biochemical pathways for enzymes, antibiotics, and numerous other value-based bioproducts (Backer et al., 2018). The efficacy of PGPR relies on its growth phase, the variability in soil ecology, and the species and age of plant/crop. PGPR adjust plant-soil chemistry thereby facilitating plant growth and well-being (**Table 1**). To utilize PGPR successfully, it is imperative to understand the mechanisms through which they influence and guarantee sustainable agriculture (**Figure 2**).

## RHIZOSPHERE: THE HUB FOR MICROBIAL HABITAT

Rhizosphere is characterized as the zone for various soil biological and chemical attributes and influence plant root secretions. It is the hotspot for intense interactions between the soil and the microflora (Kumar et al., 2015), impacting beneficial and or remaining negative or neutral. Their interactions affect plant growth and productivity heavily. Several microbial groups, like bacteria, fungi, protozoa, and algae coexist in

**TABLE 1** | The role of some select PGPR candidates in the rhizosphere.

Representative species	Role	Mechanism(s) involved	Participating plant(s)	Reference(s)
<i>Agrobacterium radiobacter</i>	Improves bioprotection	Antibiotics	-	Mohanram and Kumar, 2019
<i>Azotobacter chroococcum</i>	Assists in biostimulation	Production of gibberellin	Cereals	Zhang et al., 2019
<i>Azospirillum brasilense</i>	Aids in bioprotection	Siderophore	-	Lucy et al., 2004
	Biofertilisation	Phosphate solubilisation	Maize ( <i>Zea mays</i> ), Wheat ( <i>Triticum aestivum</i> L.) and Rice ( <i>Oryza sativa</i> )	
<i>Bacillus cereus</i>	Boosts bioprotection	Lipopeptides	Bean ( <i>Phaseolus vulgaris</i> )	Ongena and Jacques, 2008; Vaikundamoorthy et al., 2018; Hashami et al., 2019
		Induced and acquired systemic resistance	Tomato ( <i>S. lycopersicum</i> ) Soybean ( <i>Glycine Max</i> L.)	
	Bioremediation	Production of amylase Remediation of industrial waste	- -	
<i>Bacillus subtilis</i>	Biofertilisation	Ammonia synthesis	Maize ( <i>Zea mays</i> )	Ouhaibi-Ben Abdeljalil et al., 2016; Ait-Kaki et al., 2014; Tahir et al., 2017
	Aids in biostimulation	Through IAA and Cytokinin production	Chickpea ( <i>Cicer arietinum</i> ) Tomato ( <i>S. lycopersicum</i> L.)	
	Bioprotection	Lipopeptides Catalase production	- Cucumber ( <i>Cucumis sativus</i> )	
	Bioremediation	Degrading xenobiotics and allelochemicals	-	
<i>Enterobacter oryzae</i>	Biofertilisation	Nitrogen fixation	Mangart and Jam ( <i>Acacia acuminata</i> )	Dinnage et al., 2019
<i>Frankia casuarinae</i> , <i>F. inefficax</i> , <i>F. irregularis</i> , and <i>F. saprophytica</i>	Biostimulation	Cytokinin production	-	Nouioui et al., 2019
<i>Klebsiella pneumonia</i>	Aids biofertilisation	Nitrogen fixation	Maize ( <i>Zea mays</i> )	Kuan et al., 2016; Sharma et al., 2019
<i>Mesorhizobium loti</i>	Bioprotection	Acquired and induced systemic resistance	Peanut ( <i>Arachis hypogaea</i> )	Kaneko et al., 2000
	Biofertilisation	Nitrogen fixation	Lotus ( <i>Arabis thaliana</i> )	
<i>Methylobacterium extorquens</i>	Assists biostimulation	Cytokinin output	Arabidosis, barley, maize and soybean	Koenig et al., 2002
<i>Paenibacillus xylanexedens</i>	Facilitates bioprotection	Chitinase production	Wheat ( <i>Triticum aestivum</i> L.)	Verma et al., 2016
<i>Pseudomonas aeruginosa</i>	Assists in biofertilisation	Phosphate solubilisation	Maize ( <i>Zea mays</i> )	Hameeda et al., 2008; Ahemad and Khan, 2012; Paramanandham et al., 2017; Cheng et al., 2019; Lawrance et al., 2019
	Aids in bioprotection	Ammonia production	Field mustard ( <i>Brassica campestris</i> L.)	
		Hydrogen cyanide production	Elephant grass ( <i>Pennisetum purpureum</i> )	
	Assists in Bioremediation	Cellulase production Heavy metals uptake	Rice ( <i>O. sativa</i> ), Pea ( <i>P. sativa</i> ) Amaranthus, Tomato ( <i>Solanum lycopersicum</i> L.)	
<i>Rhizobium leguminosarum</i>	Biostimulation	Gibberellin production	Rice ( <i>O. sativa</i> L.)	Yanni et al., 2001
<i>Serratia marcescens</i>	Bioprotection	Producing siderophore, chitinase and protease	Field pumpkin ( <i>Poa pratensis</i> )	Selvakumar et al., 2008; Rathore and Gupta, 2015
<i>Staphylococcus saprophyticus</i>	Biostimulation	Manufacturing of IAA	Ornamental species	Manzoor et al., 2019
<i>Stenotrophomonas rhizophila</i>	Bioprotection	Amylase synthesis	Maize ( <i>Zea mays</i> ) and Canola ( <i>Brassica napus</i> )	Ghavami et al., 2017



**FIGURE 2** | A diagrammatic representation of PGPR role against various stresses.

the rhizosphere. Of all these, the bacteria that promote plant growth are the most abundant (Bahadur et al., 2017). Growth promoting bacteria in general and rhizobacteria in particular exhibit extensive interaction in rhizospheric zone. Giving an extraordinary environment inside the rhizosphere, plant releases many compounds as root exudates that is high in sugars, amino acids, organic acids, flavonoids, proteins, and fatty acids. Such root exudates are usually low molecular weight compounds, non-metabolically released. The exudates act as signals either to repel various microbial pathogens or to gather beneficial microbes owing to the physiological status, plant species, and the microflora (Ahmed et al., 2019). The exudates may also act as rhizospheric messenger molecules between plant root and rhizobacterial organisms (Lucini et al., 2019), thus are significant growth triggers for soil microbes that assume a crucial role in advancing plant development and in mobilizing protection against phytopathogens. Along with root exudates, plants also release additional components like metabolically released or secreted compounds, lysates released from moribund cells during autolysis, and mucilage (a plant polysaccharide) in the rhizospheric zone. All such secretions act as chemoattractants for rhizospheric microflora. Few PGPR can enter the root, setting up endophytic association (Wozniak et al., 2019 and Papik et al., 2020). Some of them overcome the endodermis barrier, rising above from root cortex to vascular systems, developing as endophytes (inside leaves, stem, and other organs). The degree of host plant endophytic relationship mirrors the capacity of these microbes to adapt to different explicit biological specialties. Such

bacteria-plant relationships can be derived for crop well-being and productivity.

## PGPR AND ABIOTIC STRESS

Any unfavorable environmental condition that may affect the functional diversity of microbes and also the physicochemical properties of soil can dictate abiotic stress. Numerous drastic conditions including heavy metal toxicity, salinity, drought, and flooding affecting the plant microbiome and the surrounding ecology are abiotic stress.

### Heavy Metals

Hyper-aggregation of noxious metals like Hg, As, Cd, and Pb in soil result in plant stress, and extraordinarily diminish crop productivity. Such metal aggregations directly influence soil pH and its texture, thereby hampering crop growth by imparting negative consequences on a few biological processes (Hamid et al., 2021). Majority of the microbes, particularly the heterotrophs, receive food through carbonaceous forms from the host plant through the symbiotic association. Thus, there is a decrease in the effect of pollutants on plants added by the help of these (Zafar-ul-Hye et al., 2013). Though PGPR helps in plant growth and productivity, it also improves soil properties through various mechanisms to regulate soil metal contaminants (Table 2). Some peculiar binding metal peptides are associated with metal chelation or accumulation. Transformation mechanisms by PGPR, like

**TABLE 2** | Heavy metals bioremediation by PGPR.

PGPR	Participating plant	Metal(s)	Cultivation condition	Role of PGPR	References
<i>Brevundimonas Diminuta</i> , <i>Alcaligenes faecalis</i>	<i>Scripus Mucronatus</i>	Mercury	Green house	<ul style="list-style-type: none"> <li>• Increased phytoremediation</li> <li>• Decrease in toxicity of soil</li> </ul>	Mishra et al., 2016
<i>Bacillus</i> , <i>Staphylococcus</i> , <i>Aerococcus</i>	<i>Prosopis juliflora</i> , <i>Lolium mltiflorum</i>	Chromium, Cadmium, Copper, Lead and Zinc	Green house condition	<ul style="list-style-type: none"> <li>• Improve the efficiency of Phytoremediation</li> <li>• Tolerate high conc. of Chromium.</li> </ul>	Wani and Khan, 2012
<i>Rhizobium</i> sp., <i>Microbacterium</i> sp.	<i>Pisum sativum</i>	Chromium (VI)	Glasshouse conditions	<ul style="list-style-type: none"> <li>• Improve in concentration of nitrogen in the plants</li> <li>• Decreased Chromium toxicity</li> </ul>	Mishra et al., 2016
<i>Bacillus megaterium</i>	<i>Brassica napus</i>	Lead	Under field conditions	<ul style="list-style-type: none"> <li>• Decrease in Soil pollution</li> <li>• Total dry-matter yield of plants</li> </ul>	Reichman, 2014
<i>Bradyrhizobium japonicum</i> CB1809	<i>Helianthus annuus</i> and <i>Triticuma estivum</i>	Arsenic	Pot studies	<ul style="list-style-type: none"> <li>• Excess of plant biomass</li> <li>• Growth in conditions of high arsenic concentration</li> </ul>	Yavar et al., 2014
<i>Mesorhizobium huakuii</i> subsp. <i>rengei</i> B3	Tomato <i>Astragalus sinicus</i>	Cadmium	Hydroponics	<ul style="list-style-type: none"> <li>• Expression of PCSAt gene increased ability of cells to bind Cd2</li> </ul>	Sriprang et al., 2003
<i>Bacillus subtilis</i> SJ-101	<i>Brassica juncea</i>	Nickel	Pot experiments in growth chamber	<ul style="list-style-type: none"> <li>• Facilitated the accumulation of Nickel.</li> </ul>	Zaidi et al., 2006
<i>Azotobacter chroococcum</i> HKN-5, <i>Bacillus megaterium</i> HKP-1, <i>B. mucilaginosus</i> HKK-1	<i>Brassica juncea</i>	Lead, zinc	Pot experiments in greenhouse	<ul style="list-style-type: none"> <li>• Stimulated plant growth</li> <li>• Protected plant from metal toxicity</li> </ul>	Wu et al., 2006

metal bioaccumulation, biosorption, precipitation, oxidation, and reduction of metal in enzymatic pathway, decreases the toxic effect of heavy metal ions (Sharma and Archana, 2016).

### Induced Systemic Tolerance (IST) in Metal Stress

Induced systemic resistance induces abiotic stress tolerance toward metals. The genetic basis of the process is well-known (Hobman and Crossman, 2015; Wheaton et al., 2015). Contaminating metals in the rhizosphere hinders plant nutrient uptake resulting in a delayed plant growth (Lal et al., 2018). This could be addressed by inoculating PGPR having metal resistance ability. PGPR can effectively stimulate IST against abiotic stress in plants. IAA delivering PGPR managed heavy metal stress while improving nitrogen fixation and other growth conditions (Guo et al., 2020). *Cellulosimicrobium* reportedly enhanced the flowering period under chromium (Cr<sup>6+</sup>) stress (Karthik and Arulselvi, 2017). The isolated and characterized Cr<sup>6+</sup> resistant bacteria could also dissolve phosphate, produce ammonia, and secrete enzymes like lipase and amylase in the rhizosphere of *Phaseolus vulgaris*. Factors responsible to activate IST in host plants are recognized as similar to those of induced systemic resistance (ISR). ISR induction correlates with factors like bacterial external membrane lipopolysaccharides, biosurfactants, siderophores, volatile organic compounds, and other microbial metabolites. Studies show that gibberellic acid (GA) eased metal toxicity by reducing Cd<sup>2+</sup> absorption (Zhu et al., 2012). Rhizobacteria also possess a metal rejection mechanism to protect the delicate cell parts from heavy metals, changing their cell wall and membrane.

### Siderophores in Metal Sequestration

Siderophores are microbial metabolites that form trace metal complexes. These are organic compounds of lower molecular weight having a good iron affinity. Microbes produce these in iron-deficient condition. Microbially released siderophores perceivably resist metal stress efficiently. Microbial siderophores formed tie up with metal ions making the limited metal ion bioavailable. *Streptomyces* siderophores assimilated iron and diminished Cd<sup>2+</sup> retention (Dimkpa et al., 2009a). Bacterial siderophore reduced the oxidative stress minimizing the toxic impact of metals and accelerating plant biomass growth (Dimkpa et al., 2009b).

### Biosurfactants in Metal Reduction

Amphiphilic composite biosurfactants found primarily on the microbial cell surface. They enhance trace metal tolerance and help in ousting soil metal. Because of the amphiphilic nature, these hold together more closely to noxious metals (Gupta and Kumar, 2017), by showing an undeviating connection between biosurfactants and trace metals. This binding nature of biosurfactants with heavy metal helps reduce its concentration in soil (Lal et al., 2018).

### Impact of Organic and Inorganic Acids in Heavy Metal Reduction

PGPR produce many low molecular weights natural (organic) acids, like oxalic and citric acids (Archana et al., 2012), which



demonstrably reduce metal stress in farming. These form less-toxic metal complexes and facilitate plant growth in metal-contaminated soils. These complexes (e.g., metallic oxalate crystal) enhance resistance in plants by reducing the adverse cytological effects of the native metal ions by inactivating them (Gao et al., 2010). Inorganic acids by PGPR could decrease metal stress through precipitation. Microbial organic acid is perceived to have a solid limit in chelating heavy metals (Gadd, 2010). Insolubilizing and immobilizing heavy metals is either instantaneous *via* the enzymatic action (Pagnanelli et al., 2010), or through the circuit with the aid of bacterial oxidation of Fe, or through involvement of microbial inorganic acids like H<sub>2</sub>S, H<sub>2</sub>CO<sub>3</sub> and H<sub>3</sub>PO<sub>4</sub> (Zhou et al., 2013).

### Bacterial EPS in Metal Reduction

Extracellular polymeric substances (EPS) are heavy molecular weight homo- or hetero-polysaccharides microbial polymers (Staudt et al., 2004). It binds to bacterial cell surface, present internally as a capsule or is secreted externally. Extracellular polysaccharides such as lipopolysaccharides, polysaccharides, dissolvable peptides, and glycoprotein released by rhizospheric bacteria (Hassan et al., 2017) have a significant number of anion-restricting locales that help in evacuation or recuperation of heavy metals from the rhizosphere through biosorption (Mishra et al., 2017). Due to the composition, it assumes a pivotal job in heavy metal decontamination by diminishing their availability in soil and plant systems (Rajkumar et al., 2012).

### Salinity

Salinity conditions are detrimental for agro-economy. The primary reason for the salinity issue is attributed to the accumulating salts due to the use of agrichemicals over long (Rengasamy, 2002). There is alternation in plant homeostasis in salt-stressed region in the soil, leading to nutritional imbalance. Being sessile, plants can't run and escape from the situation, but rather struggle and acclimatize to it. Studies identify the significance of PGPR to boost growth and productivity in salt-stressed plant for sustainable agriculture (Venkateswarlu et al., 2008).

### Halotolerance by Scavenging (ROS)

The reactive oxygen species (ROS) like O<sub>2</sub><sup>-</sup>, O<sub>2</sub>, and H<sub>2</sub>O<sub>2</sub> is formed under salinity stress significantly damaging the cell, known as oxidative stress. An enzymatic and nonenzymatic protective antioxidant system is activated to neutralize such toxicity by managing the H<sub>2</sub>O<sub>2</sub> level (Bharti and Barnawal, 2019). Enzymes like catalase and ascorbate peroxidase and non-enzymatic components like ascorbate routinely regulate the ROS levels (Kapoor et al., 2015). Along with ROS production, the salt-stressed plant is hypohydrated. PGPR capable to produce the enzymatic and non-enzymatic components help the plant to survive under salt stress. ROS-responsive signaling and regulatory genes of PGPR are beneficial (Miller et al., 2010). By boosting the antioxidants and polyamines, some PGPR mitigate the increased soil salinity, elevating the photosynthetic performance (Radhakrishnan and Baek, 2017).

PGPR produces antioxidants like catalase, and neutralizes ROS-mediated oxidative stress. Improved performance of SOD in salt-stressed plants inoculated with PGPR assumes a critical role in superoxide scavenging.

### Halotolerance by Decreasing Ethylene Level

Ethylene, a gaseous hormone, helps in controlling and regulating plant growth (Fahad et al., 2015). Usually, two ethylene peaks measured in plant tissues, the first usually being smaller than the second. First peak is seen when the plant is subjected to stress, and the second peak shows up after a couple of hours. A quick ethylene antecedent is 1-aminocyclopropane-1-carboxylate (ACC). Some PGPR produce ACC deaminase that protects plants from ethylene stress. ACC deaminase in plants breaks apart ACC to form  $\alpha$ -ketobutyrate and ammonia, consequently reducing the ethylene level. As a sink for ACC, PGPR formulation with active ACC deaminase decreases plant ethylene levels (Glick, 2014). In comparison to the control without microbial inoculations, seedlings treated with ACC deaminase-containing bacteria decreased ethylene in plants exposed to salt stress (Barnawal et al., 2017), thus an effective method to mitigate salt stress to an extent.

### Drought

Drought is a leading factor that hinders worldwide agricultural productivity. It is believed to have played down the national cereal production by 9–10% (Lesk et al., 2016). The capacity of a plant to sustain and endure during drought situation is its drought resistance. Solutions to increase abiotic stress tolerance like drought in plants enabling its growth meeting food needs under restricted accessibility of water resources need to be established (Mancosu et al., 2015). Abscisic acid (ABA) improves drought tolerance owing to a few responsible active signaling genes like DSM2, Os-NAP, and OsNAC5. These genes facilitate an increase in the yield during drought (Goswami and Suresh, 2020).

### Improving Root System for Water Uptake

An increased number of rootlets with lesser diameter with greater depth in the root system is a novel approach to sustain plant productivity in drought conditions (Ngumbi and Kloepper, 2016) as it allows draft-stressed plants to enhance the hydraulic conductance by raising the area of contact with the available water in soil with an increase in volume (Comas et al., 2013). It is suggested that modifications in the root architecture caused by bacteria maximizes the total area of the root resulting in improved nutrient and water absorption facilitating the overall growth (Timmusk et al., 2014). Comprehensive studies are needed to understand the underlying mechanism. Naik et al. (2020) has reported the root elongation property of a nano formulation (SomRE) to overcome abiotic stress without any adverse effect on the soil microbiota.

### Facilitating Shoot Growth

Decreased accessible leaf surface to restrict evaporative loss is an adoptive mechanism in plants to address drought stress which may stunt shoot growth (Skirycz and Inzé, 2010).

Treating such plants with PGPR improves shoot growth; plants inoculated with successful PGPR strains may retain close-to-average shoot growth in drought stress, resulting in enhanced crop productivity.

### Relative Water Content

Perhaps a better approach to evaluate plant water status is measure its relative water content (RWC) in leaf as it is involved in tissue metabolic activity. A reduced RWC indicates turgor deficiency that restricts cellular development and diminished plant growth (Ngumbi and Kloepper, 2016). Maximizing RWC could significantly enhance drought tolerance. PGPR-treated plants reportedly managed RWC better compared to the non-treated plants. Dodd et al. (2010) found that better RWC could be a consequence of change in the physiological activity like stomatal closure. Grover et al. (2014) reported 24% enhancement RWC in drought-stressed sorghum plants inoculated with *Bacillus* sp. strain KB 129.

### Osmotic Adjustment in Drought Tolerance

Osmotic modification is a major adaptation strategy in plants that allow them to tackle drought-stress (Farooq et al., 2009). Proteins, enzymes, cell organelles, and membrane are safe from oxidative destruction (Huang et al., 2014). Osmotic adaptation in drought stress is the active accumulation of inorganic and organic compatible solutes (Kiani et al., 2007). The solutes include ammonium compounds like sucrose, non-protein amino acids like proline, betaine, glycine, polyols like mannitol, inorganic ions like calcium, and organic acids like malate. They preserve cell turgor and reduce water demand while maintaining the water content.

Proline is a fundamental osmolyte in plants experiencing drought-stress (Huang et al., 2014). Proline also helps stabilize subcellular structures like proteins and membranes, scavenge free radicals and buffer the capacity for cellular redox (Hayat et al., 2012). Critical studies suggest that plants with higher proline levels can withstand dry season (Lum et al., 2014). PGPR inoculation helps increase proline levels in plants. A combined three PGPR strains (*Bacillus cereus* AR156, *B. subtilis* SM21, and *Serratia* sp. XY21) enhanced proline concentration 3–4-folds in cucumber leaves compared to the control (Wang et al., 2012). The high proline level protected cucumber plants from excess drying. PGPR application increased concentrations of dissolvable sugar and free amino acids in maize (Bano et al., 2013). Additional free amino acids and dissolvable sugars alongside proline are essential for withstanding conditions of extreme drought.

### PGPR and Plant Growth Substances

Externally applied chemical growth regulators and various phytohormones like cytokinins, abscisic acid, gibberellins, auxins, and ethylene facilitate plant growth and development. Jasmonic acids (JAs) reportedly play an important role in drought tolerance in plants. Its exogenous utilization enhances the formation of various antioxidants to withstand drought. Antioxidants' influence has been highlighted in crops including in Desi chickpea cultivated under drought stress. The expression pattern of the jasmonate signaling pathway gene (MYC2) is

significantly outlined (Domenico et al., 2012). PGPR encourage growth of drought-stressed plants (Bresson et al., 2014) by controlling and adjusting the phytohormones and growth regulators. Plant growth is encouraged by gibberellins and cytokinins and inhibited by ET and abscisic acid (Taiz and Zeiger, 2010). Drought stress increases the levels of growth inhibitors. Studies have highlighted that SomRE (an organic root growth promoter) help to transport nutrients to the upper portion of plant for their growth and development. SomRE contains vulcanine and borrelina that help in root elongation (Naik et al., 2020).

### Flood

Reports indicate the effect of rhizobacteria on plant physiology when exposed to flooding (Ravanbakhsh et al., 2017). Studies reveal that plant roots associated with bacterial population impact in regulating ethylene. Such exchange of gas reduces during flooding, resulting in rapid accumulation of inside plant. Accumulated ethylene regulates the traits related to flood adaptation (Sasidharan and Voeselek, 2015). Ravanbakhsh et al. (2017) highlighted the role of *R. palustris* in ACC deaminase production which led to a reduction in the ethylene levels. ACC level rises during flood (low oxygen condition) attributed to the action of both ACC synthase and ACC oxidase genes. High ACC concentration accumulated in the root is reduced by ACC deaminase which helps ACC to diffuse out of the roots. This mechanism helps reduce ethylene levels during and after flooding. Any disturbance in the ethylene signaling pathway leads to a drastic reduction in the responses to flood situations (Ravanbakhsh et al., 2017).

## PGPR AND BIOTIC STRESS

Biotic stress in plants is brought about by living forms, particularly bacteria, viruses, fungi, insects, and nematodes. Such stress interferes directly with host nutrients causing plant death. Both pre- and post-harvest loss occurs due to biotic stress. Although few microbes participate in the biological control of pathogens, yet PGPR is known to create protection from many diseases following various mechanisms including bacteriocin, antibiosis, volatile organic compound (VOC) production, and lysis through the extracellular enzyme (Hamid et al., 2021). The microbial stimulants are seen to be effective in the suppression of a variety of plant-pathogen which ultimately leads to sound development in the harvest.

### Bacteriocin

Bacteriocins (bacterial toxins against bacteria) are peptide secretions with narrow-spectrum antimicrobial activity. Bacteriocins are produced by Gram-negative (e.g., colicin) as well as Gram-positive (e.g., nisin) bacteria (Zimina et al., 2020). These toxins are very specific in their action and eliminate competitor bacterial species (Rooney et al., 2020). Bacteriocins have shown promising results under *in vitro* conditions against bacterial spot disease in tomatoes (Príncipe et al., 2018).

## Antibiosis

Antibiotics produced by PGPR are more efficient than others due to their antimicrobial, insecticidal, antiviral, phytotoxic, cytotoxic, and anthelmintic properties (Fernando et al., 2018). Numerous species of *Pseudomonas* produce a wide scope of antifungal antibiotics, including 2,4-diacetylphloroglucinol (2,4-DAPG), butyrolactones, rhamnolipids, N-butylbenzene sulfonamide (Ramadan et al., 2016). *Bacillus* species also excrete a large variety of antibiotics, including bacilysin, bacillaene, mycobaccillin, etc. Additionally, they produce various lipopeptide biosurfactants e.g., bacillomycin with antibiotic activity (Wang et al., 2015).

## VOC Production

PGPR secretes numerous Volatile Organic Compound (VOC), which are biocontrol specialists for certain nematodes and microorganisms. Some illustrations of VOC are benzene, cyclohexane, tetradecane, 2-(benzyloxy)-1-ethanamine. HCN is one of the VOC (delivered by rhizospheric microbes) having the capacity in the biocontrol of some phytopathogens (Kanchiswamy et al., 2015). HCN of *Pseudomonas* sp. can hinder some pathogenic growths (Hamid et al., 2021). Likewise, VOCs emitted by *Bacillus* spp. are successful inhibitors of fungus (Santoro et al., 2016). Along with the role of biological control, VOC plays role in pollinator attraction through communication signals (Liu and Brettell, 2019).

## Lysis via Extracellular Enzyme

Lytic compounds produced by PGPR give another powerful system to infectious microbes. Extracellular enzyme of rhizobacteria (chitinase and  $\beta$ -1,3- glucanase) are associated with lysis of cell wall (Goswami et al., 2016). As the fungal cell wall is mostly made out of chitin and  $\beta$ -1,4-N-acetyl-glucosamine, Chitinase and  $\beta$ -1,3-glucanase of rhizobacteria can degrade them and act as are strong antifungals. For instance, *P. fluorescens* LPK2 and *S. fredii* KCC5 discharge  $\beta$ -glucanases and chitinases help in under-expression of the wilts which is brought about by *Fusarium udum* and *F. oxysporum* (Ramadan et al., 2016). Microbes show insecticidal action which has been accounted for protease, lipase, and chitinolytic activity (Rakshiya et al., 2016). PGPR with ACC deaminase action moreover assumes a vital part taking all things together sorts of stresses, including biocontrol.

## CO-METABOLISM OF PGPR

As a part of the metabolic cooperation with plants, it is suggested that plants provide amino acids, sugars, organic acids, and other carbon sources to microbes dwelling in the rhizospheric region (Jones et al., 2009). This niche is valuable to explore metabolic associations between plants and rhizomicrobes (Jacoby and Kopriva, 2019). Rhizospheric microbial metabolites are considered crucial in ecological success. Various rhizomicrobes that share this habitat have important ecological roles based on their substrate uptake patterns (Ghoul and Mitri, 2016). The idea of niche differentiation can be based on different rhizomicrobial strains coexisting in the same niche exhibiting partitioned metabolism. If two strains have similar substrate

uptake pattern then the fittest survives, leading to competitive exclusion of the strain that is less fit (Jacoby and Kopriva, 2019). Often a rhizobacteria strain functions in a way that it excretes a novel metabolite that was not a part of the native root. This leads to the formation of a new niche that could be inhabited by cross-feeding strains (Ponomarova et al., 2017). When ample amount of sugar is added, soil microbes quickly proliferate giving a notion that there is carbon limitation in the growth of microbes (Blagodatskaya and Kuzyakov, 2013). Thus, it is attributed that plants contain ample amount of carbon that diffuse to outside through multiple metabolic pathways.

Even though carbon fixation occurs primarily through respiration, carbon is released by plants through rhizospheric deposition (Pausch and Kuzyakov, 2018). While rhizomicrobes provide metabolites to plants, the plant rhizodeposits provide a range of metabolites offering huge opportunities both to attract and inhibit specific microbial strains (Chagas et al., 2018). Rhizomicrobes provide nitrogen, phosphorus and iron to plants in utilizable forms that are crucial for growth. Rhizomicrobes provide plants with phytohormones like ACC deaminase, cytokinin, and indole-3-acetic acid which aid in its growth and development (Kumar et al., 2019). Thus, such cometabolism allows a healthy symbiotic relationship between the plants and rhizomicrobes.

## CRITERIA TO SELECT SUITABLE PGPR CANDIDATE

For the development of a successful PGPR formulation, the rhizobacterial species should possess the following characteristics (Jeyarajan and Nakkeeran, 2000):

- Should be enhancing plant growth
- Should be amenable for mass multiplication
- Should possess high rhizospheric competence
- Should have high competitive saprophytic ability
- Should demonstrate broader activity spectrum
- Should be ecologically compatible to other inhabiting rhizobacteria
- Ability to tolerate abiotic (thermal, desiccation, radiations, and oxidizing agents) stress
- Should be environmentally safe.

## PGPR AS BIOFERTILISER

Biofertilisers are the live formulation of beneficial microbes which assists in the availability of nutrients by their biological activity and builds up soil health and thus soil microflora. So, the main component of this biofertiliser is plant growth promoting microbes (PGPM). This PGPM can be categorized into three major groups, i.e., Arbuscular mycorrhizal organisms (AMF), plant development advancing rhizobacteria (PGPR), and nitrogen-fixing rhizobia (Vejan et al., 2016), which are considered to be helpful for plant development and nourishment. Nonetheless, it has been accounted for that PGPR has been utilized worldwide as biofertilizers, adding to expanded yields and soil quality. Subsequently, with likely PGPR commitment,



it could prompt sustainable agribusiness. Such biofertilizers are available in both solid and liquid forms, and liquid formulations are found to be more effective. Liquid formulations are primarily of three types, i.e., root inoculation, seed inoculation and soil inoculation (Lopes et al., 2021). Upon applying *Burkholderia phytofirmans* biofertiliser to Ryegrass root, seed, and soil, soil inoculation method was most efficient in improving the production of plant biomass, phytoremediation and hydrocarbon degradation (Afzal et al., 2013).

## CHALLENGES WITH PGPR

One constraint in using PGPR is their property of natural variation. It is difficult to predict the response of an organism in field conditions (unlike in controlled laboratory environment). Another challenge is that PGPR are living in nature and they must be able to propagate artificially and mass produced in an optimized manner with regard to their viability and biological activity until field application. Like *Rhizobium*, PGPR bacteria will not live in soil for long, and over time cultivators will need to reinoculate to restore their population.

## CONCLUSION AND FUTURE PROSPECTS

Crop yield is affected by a wide range of ecological concern emerging from complex natural conditions. It is important to address environmental (abiotic) stress through ecofriendly strategies. A way to accomplish eco-accommodative sustainable agriculture is utilizing the beneficial microbes. PGPR help soil and crop well-being through various ways. For microbes, rhizosphere, where soil and microfauna have extreme intense

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interactions, is a hotspot. Among all, plant growth promoting bacteria are most abundant in the rhizosphere. PGPR improve soil properties through various mechanisms regulating soil contaminations. PGPR help to adapt to abiotic stresses like salinity, drought, flood stress, and also to the biotic stresses. Additionally, PGPR also helps plants to adapt to flood stress. Rhizosphere and PGPR rhizomicrobiome cometabolise, the former as the source of nutrients for the rhizomicrobes and the rhizomicrobe biotransform nitrogen, phosphorus and iron converting them into more utilizable forms for the plants. Understanding the genetics in PGPR investigation and engineering it is a more promising futuristic approach, which shall provide overexpression of the desired traits in the participating strain. As microbes behave differently in the laboratory and field conditions, there is also a need to propagate PGPR in field conditions for them to regain their biological activity and viability.

## AUTHOR CONTRIBUTIONS

PM has contributed to the first drafting and formatting of the manuscript. PKS outlined the manuscript and has designed the figures. DC has helped in preparing table and figure for the manuscript. SM and RP have developed the skeleton for the manuscript along with editing and other valuable scientific inputs. All authors contributed to the article and approved the submitted version.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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