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Plant growth promoting rhizobacteria as biostimulants for plant and soil health: Current research and future challenges

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ABSTRACT

Governments, as well as growers, are working to reduce chemical uses in agricultural systems. In recent years, agricultural practices have resulted in an increase in the harmful chemical substances of rivers and underground water, as well as the salinization of soils. Solutions are therefore needed to maintain crop yield while also lowering chemical inputs such as chemical pesticides and fertilizers. One method for achieving the aforementioned desired practices is the employment of microorganisms in the soil that improve efficiency as well as nutrient uptake. The Intentional incorporation of soil microbes in crops is crucial to overcoming the challenge of boosting food production while significantly reducing pesticide usage, and environmental contamination and enhancing the productivity of natural resources. Microorganisms are capable of adapting and adjusting to the environment rather than surviving their surroundings. Plants are inhabited by microorganisms that have evolved to promote soil health through nutrient-recycling abilities. The plant growth-promoting rhizobacteria (PGPR) have been investigated since the turn of the 20th century, and their physiological mode of action is now well established. PGPR have been recognized as essential growth-promoting traits with respect to their nutrient solubilizing, disease-resistant antagonistic ability, trigger and stimulating plant immunity, colonization, and adaptivity with rhizosphere and stress response. Together, these traits make them great in assisting living organisms formidably resistant and important for improving plant and soil health. The present review deals with the role of PGPR and their significance in encouraging the growth of plants for agriculture sustainability.

1. INTRODUCTION

A global agricultural boom was sparked by the emergence of the green revolution in the second half of the 20th century. The green revolution greatly increased food yields and plant productivity by bringing in new high-yielding seed varieties and using more synthetic fertilizers, insecticides, pesticides, and other agrochemicals [1,2]. Since then, there has been a significant shift in the agricultural environment worldwide. Over the past few decades, there has been a global decline in agricultural production due to the widespread usage of synthetic agrochemicals to increase crop output, which has damaged the biological and physicochemical health of the arable soil [3]. Biological wealth is being depleted and land resources are becoming smaller in the current situation. Concurrently increasing agricultural crop yield and productivity with the production of commodities related to agriculture is necessary to meet the growing need for sustainable agriculture [4]. The aforementioned complex,

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ecological, socioeconomic, and technical issues that arise in advancing sustainable agriculture cannot be resolved in a single or simple way [5].

An efficient way to counteract the rapid environmental degradation while maintaining high agricultural productivity and improved soil health is to promote sustainable agriculture, which gradually reduces the use of synthetic agrochemicals and increases the use of materials derived from biowaste as well as the biological and genetic potential of crop plants and microorganisms [6,7]. Certain members of the soil microbial community, especially those found in the plant rhizosphere, may help plants prevent or partially overcome environmental challenges in addition to genetically modifying the crop's physiology and metabolism to increase yield [8]. The search for environmentally appropriate substitutes to lessen the negative impacts of hazardous agrochemicals resulted in the development and application of biofertilizers, biopesticides, and other microbial-based products, such as vermicompost teas and organic extracts [9]. These microbiological products are safe for the environment, non-toxic, and have the potential to be used as instruments for disease prevention and plant growth stimulation [5].

Therefore, using microbial formulations to fertilize agricultural crops could boost the biological potential and fertility of soil while reducing the harmful impacts of agrochemicals [10]. A viable alternative to reducing the use of synthetic agrochemicals in crop production is the use of effective plant growth-promoting rhizobacteria (PGPR) as biological control agents and biofertilizers [11]. The present review concisely and holistically provides deeper insights into the various aspects of PGPR, their prospects and constraints, and their significance in encouraging the growth of plants for agriculture sustainability.

2. REGULATION OF NUTRIENT UPTAKE IN PLANTS

2.1. Nitrogen Fixation (Symbiotic and Non-symbiotic)

Plant growth-promoting (PGP) microbes have the potential to serve as a viable biological source of nitrogen fixation and its mobilization in plants, hence enhancing agricultural productivity. The minority bacterial species show the ability to fix nitrogen present in the atmosphere but are generally obligate to the most common type of symbiotic relationship within legume plants that possess a special root structure (nodules with bacteroides) harbored by colonies of bacteria. This type of symbiotic relationship is most common in diazotrophs, and the process is often termed "symbiotic biological nitrogen fixation" (e.g., *Rhizobium*, *Bradyrhizobium*, *Azorhizobium, Mesorhizobium, Allorhizobium,* and *Sinorhizobium*). This type of association can be found in many nodulating crops (peas, clover, beans, and fenugreek) Dayoub *et al.* [12] or in nitrogen-fixing trees (*Dalbergia, Acacia, Albizia,* and *Leucaena*) [13]. Nodules have the ability to fix atmospheric N_2 via nitrogenase enzyme to ammonia. Symbiotic biological nitrogen fixation can also be found in some non-legume associations (*Frankia*) or stem nodulating (*Azorhizobium*) or leaf nodulating (*Klebsiella* or *Burkholderia*) plants. Non-nodulating pseudo-symbiotic nitrogen fixation occurs in plants and microbes, such as *Spirillum, Anabaena*, or *Nostoc*. Unlike symbiotic forms of association, there are some free associations of bacteria that fix N non-obligatory. A loose form of associative biological nitrogen fixation occurs when bacteria live between the soil or roots and use fixed N_2 to exchange nutrients with plants (Fig. 1). Many other PGPR known to possess N-fixing activity include *Erwinia, Acinetobacter, Alcaligenes, Pseudomonas, Ralstonia, Variovorax, Arthrobacter, Bacillus* sp., and so on. [14]. A study reported that nitrogen-fixing bacteria identified as *Stenotrophomonas maltophilia* was improved the growth of rice plant [15]. Another study reported that, inoculation of nitrogen-fixing bacterial strains namely *Azotobacter* sp., *Azospirillum* sp., *Rhizobium* sp., and *Pseudomonas* sp. improve the growth of wheat [16]. A study concluded that inoculation of N-fixing bacterial strain identified as *Erwinia rhapontici* enhances the growth and physiological parameters of amaranth [17]. A similar study concluded that inoculation of *Azotobacter beijerinckii* improve wheat growth and soil improvement in saline-alkali land, and provides a new effective strategy for improving saline-alkali soil quality and increasing crop productivity [18]. A study by, Rana *et al.* [19] reported that endophytic bacterium identified as *Rahnella aquatilis* improves the growth of wheat crops.

2.2. Solubilization of Phosphorous

Soil phosphorous is present in organic form as the biomass of partially degraded organic matter of living organisms as in humus and other components [20]. Alternatively, it is present as inorganic complexes of insoluble Fe, Ca, Al ions, and mineral phosphates such as silicate. A fair fraction of P is non-labile to plants and this insoluble P has higher accessibility than the other reserves to plants. The inorganic form of phosphate present in the soil that is available to plants is HPO_4^{2-} and $H_2PO_4^-$ [1]. Whereas organic phosphate (such as nucleic acids and phosphoglycerates) are inositol phosphate esters, which are dephosphorylated by the action of microbial phosphatases. Organic P is hydrolyzed as inorganic P and inositol during the phosphatase reaction [21]. Various microorganisms release this enzyme, such as *Bacillus, Pseudomonas, Rhizobium, Flavobacterium, Arthrobacter Erwinia, Beijerinckia, Escherichia, Serratia, Microbacterium, Burkholderia, Staphylococcus, Micrococcus, Penicillium, Mucor, Aspergillus, Rhizopus,* and *Meyerozyma* [22,23]. Most symbiotic, non-symbiotic, and mycorrhizal associations can solubilize P around roots. Enzymes involved in P hydrolysis include organophosphate hydrolysis enzymes (phosphomonoesterases such as phytases, phosphodiesterases, phosphotriesterases, polyphosphates, pyrophosphatase) [24–26] which are produced by microorganisms in acidic or basic soil type. Plants also produced some phosphomonoesterases from root exudates. Transformation of phosphate [inorganic P form: (acidic soil: $FePO_4$. $2H_2O$, $AlPO_4.2H_2O$; alkaline soil: tricalcium phosphate, dicalcium phosphate, hydroxyapatite, and fluorapatite); organic form: (inositol phosphate, nucleotides, phospho-proteins, sugar-phosphate, phytate, and phytin)] to make it bioavailable in the form of soluble phosphate for plants [27,28]. With the secretion of organic acids from microorganisms and the release of hydroxyl or carboxyl ions, there is a reduction in pH (acidification) and a release of P around the microbial cells. The release of organic acids, i.e., succinate, gluconate, citrate, oxalate, tartrate, acetate, and so on, causes acidification. A study reported that, P- solubilizing bacterial strains identified as *Pseudomonas fluorescens, Pseudomonas putida, Enterobacter* sp*., Bacillus megaterium, Bacillus firmus,* and *Pantoea agglomerans* were evaluated on maize crops. The result of this study revealed that inoculation of P-solubilizing strains improves fresh and dry shoot weight, root weight, and P-nutrition uptake in mailze plant [29]. Another study revealed that, inoculation of P-solubilizing bacterial strains identified as *Pseudomonas moraviensis, Bacillus halotolerans, Enterobacter hormaechei*, and *Pseudomonas frederiksbergensis* enhances the growth of wheat crop [31]. A study concluded that, bacterial strain namely *Pseudomonas azotoformans* was isolated from soil in Southern Algeria, and inoculation of this strain improved seed germination percentage, shoot and root length, and fresh and dry weights as compared to uninoculated control [32]. Another study concluded that, inoculation of P-solubilizng bacteria namely *Bacillus thuringiensis* enhance growth and physiological parameters of sweet pepper [33]. Jiao *et al.* [34] reported that, inoculation of phosphorus

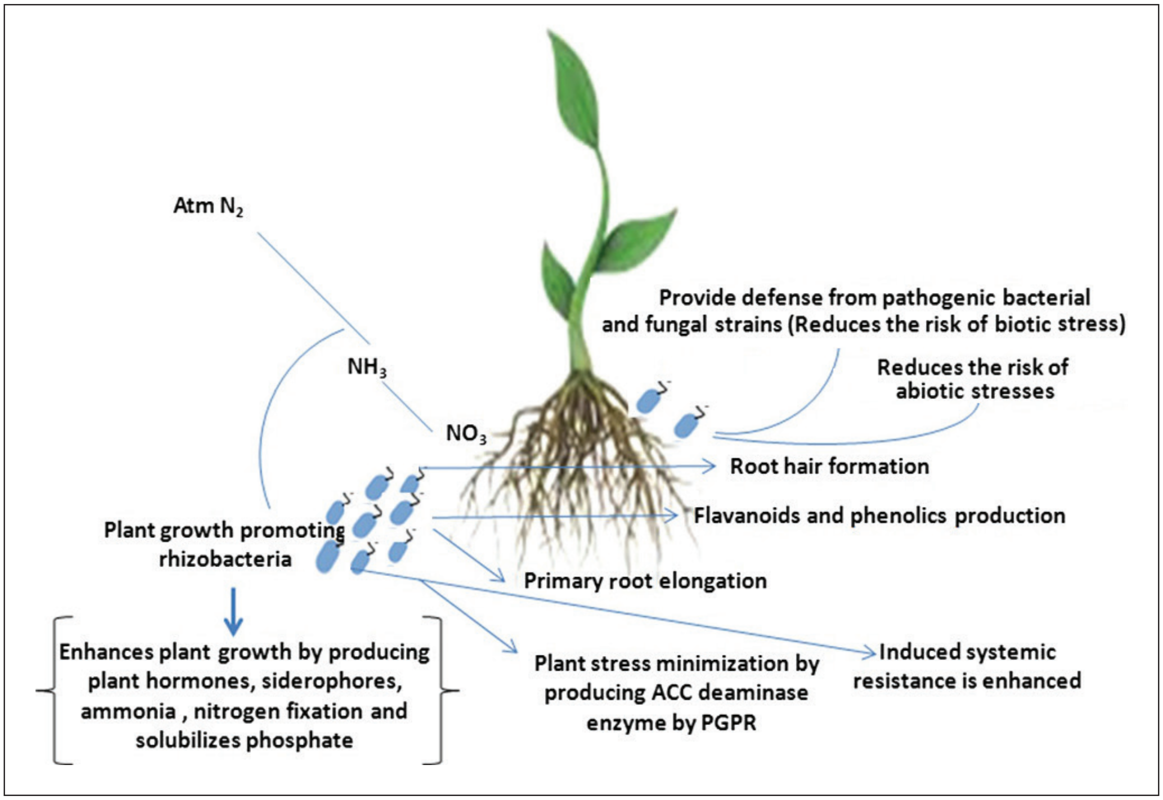

Figure 1. The mode of action used by PGPR toward growth promotion in plants adopted from Rai *et al.* [30].

solubilizing bacterial sp. namely *Pseudomonas migulae*, *Pseudomonas poae*, and *Pseudomonas extremaustralis* showed the highest soil N, P, and K content, leaf N, P, and K content and biomass as compare to control.

2.3. Potassium Solubilization

Potassium is one of the crucial nutrients required by plants in large amounts. It is present in mineral forms such as mica, feldspar, biotite, muscovite, illite, and orthoclase. PGPR plays a vital role in making avail potassium for plants [35]. Plants release different exudates that provide nutrients as well as stimulate root-colonizing bacteria and these bacteria interact with surrounding regions for nutrient sequestration. Its availability in soil is in the form of a solution, exchangeable and non-exchangeable ions, and mineral rocks. K is present as insoluble minerals rocks (silicate rocks (e.g., orthoclases), muscovite, biotite, microcline, feldspar, illite, and mica (e.g., biotite and muscovite) in soil and it is solubilized by many bacteria through organic acid action which dissolves the rock minerals, thereby increasing chelating mineral ions [36]. Chelation and ligand formation by the release of acid ions increase mineral release from rocks. Low pH increases soil acidification, enhanced chelation of cations that bound with K due to organic acid produced by bacteria provides dissolution, the release of various minerals, and the polysaccharide layer production [37,38]. Different microbes that play a role in K solubilization include *Paenibacillus sp., Bacillus sp. viz B. megaterium, B. edaphicus, B. circulans, and B. mucilaginosus, Burkholderia, Pseudomonas* are some PGPR that solubilizes potassium [39]. A study reported that inoculation of K-solubilizing bacterial strain identified as *Klebsiella oxytoca* improve maize plant height, shoot biomass, root biomass, root length, plant K uptake, grain starch, protein, oil content as well as photosynthetic rate, transpiration rate, and water use efficiency compared to control [40]. Another study reported that, bacterial strain isolated from rhizosphere of wheat and identified as *Bacillus pumilus*, *Bacillus simplex,* and *B. megaterium*. The study revealed that inoculation of this strain enhances growth and yield over control [41]. A study documented that, inoculation of *B. megaterium* improve the growth and physiological parameters of wheat plant [42]. Gandhi *et al.* [43] reported that bacterial strains identified as *Bacillus fungorum, B. paramycoides*, and *Pseudomonas aeruginosa* enhances growth of wheat. Kaur *et al.* [7] reported that inoculation of K solubilizing bacterium namely *Pseudomonas gessardii* (51.3±1.7 mg/ml) improves the growth and physiological parameters of eggplant (*Solanum melongena* L.).

2.4. Phytohormone Production

PGPR can produce some phytohormones (auxin, ethylene, cytokinin, gibberellin, and abscisic acid) that are essentially needed by plants for their growth and maturity [44]. Phytohormones regulate plant physiology through chemical signaling in response to environmental changes favoring seed germination, branching, flowering, fruiting, and leaf senescence. They are required by plants in a very low concentration, i.e., less than 1 mM. PGPR produces secondary metabolites product that regulate gene expression in living organisms, vegetative, as well as reproductive growth of plants and their responses to stress, are endogenous signaling mechanisms of phytohormones [45]. Microorganisms provide these endogenous phytohormones through rhizospheric or phyllosphere interaction with plants, relieving and altering the hormone balance with variations in environmental conditions. Phytohormones produced by such rhizobacteria often activate the signaling of other hormones [viz., jasmonic acid (JA), salicylic acid (SA), brassinosteroids, and nitric oxide] available in plants in a cascade [46]. Hence, rhizobacteria can indirectly stimulate plants to adjust levels of various phytohormones that are exclusively present in their systems. Under nutrient-deprived conditions, the use of PGPR with high phytohormone production is an ideal biofertilizer in agriculture to increase the yield of different crops [47]. A study reported that inoculation of indole acetic acid-producing bacterial strain identified as *Streptomyces hydrogenans* DH16 significantly enhanced seed germination, shoot length, root length, fresh and dry weights, and lateral root of *Pisum sativum* [48]. Another study reported that inoculation of PGP bacteria identified as *Priestia aryabhattai* and *P. frederiksbergensis* produce gibberellin and IAA effectively promoted the germination of mallow and broccoli plants under saline conditions [49]. A study documented that, IAA producing *Pseudomonas* sp. and *Sphingobium* sp. were isolated from *Ceanothus velutinus* plant and inoculation of both of isolates improves the growth of *Arabidopsis thaliana* [50].

2.5. Siderophores Formation

Siderophores (Fe-celating agents) are "iron bearing" <10,000 Da low molecular weight molecules comprising ligands specific for Fe. Siderophores can be divided into catecholate type, hydroxamates type, and carboxylate type based on ligands chelating the ferric ion and several varieties of bacterial siderophores combine the various functional groups [51]. Secretion of siderophores nearby efficient PGPR ensures solubilization of iron through siderophore-iron complex formation. As Fe (III) attaches to ligands due to higher affinity, it is scavenged by these low molecular weight compounds and reduced to Fe (II) inside both microbial and plant cells. This ensures the bioavailability of iron to a wide range of bacteria and fungi that secrete siderophores [52]. After the utilization of this siderophore-Fe, the siderophore is returned to the surface of the cell. Plants utilize the advantage to take up the siderophore for their own Fe requirement [53]. Microorganisms use an active transport mechanism to recognize ferric-siderophores via membrane receptor complex. The ability of soil microorganisms to produce siderophores is vital for plant growth. A study reported that, PGP bacteria identified as *Gluconacetobacter diazotrophicus* and *Azospirillum brasilense* contribute to the iron nutrition of strawberry plants through siderophores production [54]. Another study reported that, siderophore producing bacteria namely, *Pseudomonas fluorescence* improve growth of Alfalfa by alleviating cadmium stress [55]. A study documented that, inoculation of siderophore producing bacterium identified as *Bacillus subtilis* improves growth, yield and iron content of groundnut [56]. Syed *et al.* [57] documented that siderophore producing *Trichoderm*a spp. and *P. fluorescence* enhnace the growth, biochemical features and yield attributes of chickpea by lowering Cd uptake. A study found, efficient siderophores producer and identied as *Serratia* sp. EU-C1RK1 (69.16±0.71 psu). The study revealed that, inoculation of this bacterium enhance growth and nutrient uptake of oats (*Avena sativa* L.) [6].

3. STRESS TOLERANCE MECHANISMS

3.1. 1-Aminocyclopropane-1-carboxylate (ACC) Deaminase Production

The gaseous hormone ethylene (ET) is produced by all higher plants, while some bacteria, fungi, and other species can also synthesise it. Since ethylene is a gaseous plant hormone, it can be passively diffused across plant tissues quickly and without the aid of certain transporters [58]. Even at very low concentrations, typically less than 1.0 ppm (i.e., 1.0 μl^{-1}), ET can cause plant reactions. Even in the absence of stress, ET has been found to be active at concentrations as low as 0.05 µl/l. This is significant because ethylene is produced in a wide variety of amounts depending on the environmental conditions [59]. ET can cause seed germination, plant root elongation, development of leaf and root primordia in stems and roots, and the start of flowering at low concentrations. The enzyme S-adenosyl-methionine (SAM) synthetase, also referred to as AdoMet-synthetase, catalyses the synthesis of SAM from the combination of methionine and adenosine triphosphate, which is the first step in the synthesis of ethylene in plants. The enzyme ACC synthase then converts SAM to ACC. Furthermore, the enzyme ACC oxidase transforms the ACC into ethylene [60]. This process produces a number of other products besides ethylene, such as the volatile substances carbon dioxide and hydrogen cyanide. Plants that have been studied have been shown to have several copies of the ACC synthase and ACC oxidase genes. Several stresses, such as flooding, metal contamination of the soil, plant injuries, and elevated salt levels in the soil, cause the transcription of several of the ACC synthase genes [61].

Agrobacterium, Azospirillum, Rhizobium, Methylobacterium, Alcaligenes, Bacillus, Rhodococcus, Burkholderia, Enterobacter, Sinorhizobium, Pseudomonas, Ralstonia, and *Variovorax* are among the many PGP microorganisms that have been found to possess the ACC deaminase trait [62]. ACC deaminase-containing rhizobacteria have been shown to improve salt tolerance, which in turn encourages rice plant development under salt stress [63]. The inoculation of rhizobacterial strains that generated ACC deaminase improved maize growth and yield at all assessed salinity levels [64]. The application of three ACC-producing microbial consortiums, including *Ochrobactrum pseudogrignonense*, *B. subtilis*, and *Pseudomonas* sp., significantly increased the dry weight of the treated plants, length of the roots and shoots, and the percentage of seeds that germinated [65]. A study concluded that, ACC deaminase producing rhizobacterial strain namely *Enterobacter cloacae*, *Serratia ficaria* and *Burkholderia phytofirmans* were used as consortia and single-strain inoculations. The results showed that inoculation of these strain improves growth and yield of wheat (*Triticum aestivum*) [66]. According to a study by Khan and Singh [67] reported that, inoculation of ACC deaminase-producing *Pseudomonas* sp. augment drought stress tolerance and nutrient status of wheat. Another study revealed that, a salt-tolerant endophytic bacterium namely *Bacillus altitudinis* NKA32 with ACC deaminase activity modulates physiochemical mechanisms in rice for adaptation in the saline ecosystem [68].

3.2. Induced Systemic Response

Plants trigger a response against microorganisms irrespective of whether they are pathogenic or beneficial. Systemic acquired resistance (SAR) is related to pathogenic microorganisms, whereas induced systemic resistance is related to beneficial ones [69]. The SA mediated pathway is triggered SAR in infected sites via signaling molecules, sometimes causing necrosis in plants. While ethylene and jasmonate pathways respond to induce systemic response (ISR), helping plants overcome pathogens. In ISR, bacterial flagellar and lipoproteins, lipopolysaccharides, pyoverdine, O-side chains, and signaling molecules all play a role in the triggering mechanism [70]. Hence, PGPR used in different crops provides an indirect defense strategy against many plant pathogens.

ISR is a fascinating phenomenon orchestrated by certain PGPR that involves the activation of a plant's innate defense mechanisms against a wide spectrum of pathogens. PGPR initiates ISR through several interconnected processes. Firstly, they prime the plant, essentially preparing it to respond more effectively to potential threats. This priming involves molecular and biochemical changes that act like an immune memory system [71]. PGPR also releases signaling molecules, such as SA, JA, and ET, which serve as messengers to alert the plant of looming pathogen dangers. These signals activate various defense pathways, including SAR, a well-documented defense mechanism involving the production of antimicrobial compounds and pathogenesis-related proteins [72]. ISR also involves in the enhancement of secondary metabolites production with antimicrobial properties and the reinforcement of physical barriers like cell walls. PGPR plays a role in regulating plant hormones and improving nutrient uptake, ultimately contributing to a more robust and resilient plant defense system. Furthermore, PGPR microbial competition in the root zone can effectively outcompete pathogenic microorganisms, reducing the risk of pathogen colonization [73]. PGPR-induced ISR is a complex and multifaceted process that fortifies plants against a multitude of potential threats, fostering healthier and more resilient crops while minimizing the need for chemical pesticides.

Plant defense mechanisms that are induced by ISR include cell wall reinforcement Ahn *et al.* [74], the production of secondary metabolites Choudhary *et al.* [75], and the accumulation of defense-related enzymes (chitinases, glucanase, peroxidase, phenylalanine ammonia lyase, and polyphenol oxidase) [23]. Beneficial rhizobacteria can be used to bioprime plants, giving them systemic resistance to a variety of plant diseases, such as bacteria, viruses, and fungi. Additionally, data from a variety of fields and cannabis trials has validated PGPR's role as ISR mediators against a few insects and nematodes [76,77], hence, they can be applied for potential control. PGPR that are ISR mediators include *B. subtilis*, *B. amyloliquefaciens*, *B. cereus*, *B. pasteurii*, *B. sphaericus*, *B. mycoides*, *B.* pumilus, Rhizobium leguminosarum, *P. fluorescence*, *P. putida*, Serratia marcescens Bhattacharyya and Jha [23] and endophytic Actinobacteria Jacob and Sudini [78].

3.3. Microbial Volatile Organic Compounds (VOCs)

Many bacteria secrete different types of small organic compounds (molecular weight <300 g mol^{-1}), which are small and volatile (gaseous) in nature. These molecules interact between bacteria and plants and stimulate phytohormone signaling and ISR, strengthen defense against phytopathogens, and stimulate photosynthesis. VOCs include compounds with functional groups ketones, aldehydes, terpenes, sulfides, fatty acids, and indoles. VOCs produced by microbes are effective in plant microbes signaling against pathogenic ones. These compounds exist in both solid and liquid states in soil pores, re-volatilized in organic matter or minerals surface, thus promoting their absorption by plants [79]. These VOCs are able to trigger other phytohormones within plants. VOCs assist bacteria in different roles such as the production of different biocontrol compounds, iron acquisition, phytohormones, ISR triggering, and induction of growth [80].

A study concluded that proline and chlorophyll content increased and root Na^+ buildup decreased in soybeans (*Glycine max*) exposed to 100 mM NaCl thanks to a putative VOC mix produced from *Pseudomonas simiae* AU. The increase of RuBisCO long-chain proteins (photosynthesis) and vegetative storage proteins (Na+ homeostasis) in exposed soybean seedlings was validated by protein expression analysis [81]. *In vitro* (150 mM NaCl/15 mM $CaCl_2$) and in soil (200 mM NaCl/20 mM $CaCl_2$), *Paraburkholderia phytofirman*s PsJN VOCs have been shown to promote plant development and induce salt tolerance. The rosette area, fresh weight, and primary root length of *Arabidopsis* plants were all greater than those of the control plants, and exposure to VOCs demonstrated the growth-promoting effects of direct bacterial inoculation in parallel. In order to simulate the effects of VOCs, the plants were exposed to a mixture of 2-undecanone, 7-hexanol, and 3-methylbutanol molecules [82].

3.4. Biofilms

The colonized population of microorganisms around the rhizosphere coordinates their action to survive and multiply themselves around a habitat [44,83,84]. Bacteria use quorum sensing (QS) to survive different habitats by secreting signaling molecules to counteract pathogens in inhabitat plants. Rhizobacteria are capable of developing biofilms in response to Acyl-homoserine lactones [85]. QS is involved in forming dense films called biofilms; these films are frequently involved in inhabiting the neighbor territory, keeping them alive in stresses, i.e., drought, as well as low nutrients [86]. In symbiosis, the formation of biofilm is essential for root colonization and even involved in nodulation, as seen in *Glycine max* cv Osumi. Biofilm-active compounds such as surfactants are involved in biocontrol agents against pathogens [87]. Biofilm is present with different biomolecules like proteins, lipids, nucleic acids, and humic substances other than polysaccharides [88]. Effective colonization of roots by PGPR contributes more biofilm for layers around roots; these layers trap the nutrients and hence are beneficial during stress to plants and protect against phytopathogens [89].

3.5. Phytopathogens Biocontrol

The biocontrol of plant disease is an important characteristic of rhizobacteria. They provide host plants with benefits such as growth promotion and disease control. PGPR inhibits the growth of pathogenic bacteria, nematodes, fungi, and oomycetes via antagonism and suppresses diseases. Their proliferation and colonization steps are important in the biocontrol of the root system [90]. Biocontrol agents secreted by PGPR include 2,4-diacetyl phloroglucinol, fengycin, surfactin, phenazine, pyrrolnitrin, hydrogen cyanide, pyoluteorin, mycosubtilin, and antifungal cyclic lipopeptides [91]. Lytic enzymes, i.e., cellulases, chitinases, proteases, as well as glucanases, help bacteria in lysis and degradation of the cell wall in many fungi [92–94]. Phytopathogenic bacteria often induce virulence with increased population density, thus increasing their autoinducer secretion through QS [44,95]. This communication is interrupted by the degradation of autoinducers through enzymes produced by PGPR that help interrupt phytopathogenic QS [96] (Table 1).

4. BIOTECHNOLOGICAL APPLICATIONS OF PGPR

4.1. Agricultural

Biofertilizers are the foundation of organic farming and they contain viable or dormant cells of efficient strains of bacteria, fungi, and algae that fix nitrogen, phosphate, potassium, and zinc, or that break down cellulosic materials [115,116]. Applying these microorganisms to seed, soil, or compost aims to boost their population and accelerate microbial activity, which increases the amount of nutrients available for plant uptake [1]. Although they do not contain any nutrients, they do help plants by releasing macronutrients and micronutrients. Furthermore, there are several direct ways that biofertilizers promote plant growth. By fixing atmospheric nitrogen both alongside and independently of plant roots, biofertilizers solubilize insoluble phosphates and other minerals, greatly increasing soil productivity. Apart from their functions, a range of bacteria and fungi can help promote plant growth by secreting hormones that directly stimulate plant growth, including gibberellins, auxin, cytokinin, abscisic acid, and indole acetic acid [117]. Plants and the majority of the beneficial microorganisms used as biofertilizers including bacteria, fungi, and

Table 1. Mechanism and action of PGPR.

Disease	Phytopathogen	PGPR used for biocontrol	Mechanism of action	Reference
Fusarium wilt	*Fusarium oxysporum*	*Bacillus* sp., *Azotobacter chroococcum*, *Serratia marcescens, Stenotrophomonas maltophilia*	It produces antimicrobial compounds, competes for nutrients and space, and induces systemic resistance in plants.	[97]
Late blight	*Phytophthora infestans*	*Aureobasidium pullulans*	Produces antifungal metabolites and induces plant defense mechanisms.	[98]
Root rot	*Fusarium oxysporum* and *Ralstonia solanacearum*	*Bacillus subtilis*	Mycoparasitism - attacks and kills fungal pathogens	[99]
Downy mildew	*Pseudoperenospora cubensis*	*Achromobacter* sp., *Streptomyces* sp., *Bacillus licheniformis*	Produces antifungal compounds and competes for space on plant surfaces.	[100]
Powdery mildew	*Podosphaera xanthii*	*Bacillus* spp., *Serratia marcescens*, *Trichoderma* sp.	Induction of systemic resistance	[101]
Citrus canker	*Xanthomonas citri*	*Bacillus thuringiensis*, *B. altitudinis*	Produces antimicrobial peptides	[102]
Bacterial spot	*Xanthomonas axonopodis* pv. *passiflora*	*Bacillus* sp.	Increased defense enzymes	[103]
Damping off	*Pythium aphanidermatum*	*Bacillus pumilus*, *Paenibacillus glucanolyticus*, *Pseudomonas indica*	Antagonists released VOCs that inhibited pathogen growth	[104]
Gray mold	*Botrytis cinerea*	*Bacillus velezensis*	broad-spectrum antagonistic activity	[105]
Fusarium wilt	*Fusarium oxysporum*	*Bacillus cereus*	Resistance and competition to phytopathogen	[106]
Root-rot and damping-off	*Sclerotiorum rolfsii*	*Bacillus* sp.	Antimicrobial activity against pathogen	[107]
Rhizome rot	*Rhizoctonia solani, Fusarium solani, Schizophyllum commune, Macrophomina phaseolina, Fusarium graminearum*	*Bacillus* sp., *Pseudomonas* sp.	Phytopathogenic activity is caused by the synergism of microbes and the production of antifungal compounds like HCN	[108]
Bacterial panicle blight	*Burkholderia glumae*	*Bacillus glumae and B. velezensis*	Competition	[109]
Bacterial canker	*Clavibacter michiganensis*	*Bacillus cereus*	Resistance to pathogen through induced systemic resistance	[110]
Southern blight	*Sclerotium rolfsii*	*Stenotrophomonas maltophilia*, *Bacillus subtilis*	Bacteria colonized plant roots and protected plants	[111]
Sudden Decline Syndrome	*Fusarium solani*	*Streptomyces polychromogenes*, *S. coeruleoprunus*	Volatile antifungal metabolites inhibited pathogen	[9]
Stem rot	*Sclerotinia sclerotiorum*	*Trichoderma. atroviride*, *T. koningiopsis*, *Serratia proteamaculans*, *s Ochrobactrum anthropi*	Possible suppression of pathogen by synergetic action	[112]
Grapevine trunk disease(s)	*Diplodia mutila, Neopestalotiopsis vitis, Neoscytalidium dimidiatum, and Trichothecium roseum*	*Pseudomonas koreensis*	Potential inhibition by volatile antimicrobial compounds	[113]
White Rot	*Sclerotinia sclerotiorum*	*Bacillus* sp.,	Antibiosis capacity of bacteria	[114]

cyanobacteria have symbiotic interactions. In India, a wide variety of commercial biofertilizer formulas are currently accessible. The interactions between various microorganisms and agricultural plants are being leveraged to create biofertilizers [1]. A study concluded that a nitrogen-fixing bacterial strain identified as *Rahnella* sp was inoculated on *Aegilops kotschyi* and inoculation of this bacterium improve growth and physiological parameters [118]. In an another study concluded that, endophytic nitrogen-fixing bacterium identified as *R. aquatilis* from cereal crops and inoculation of bacterial strain improve growth of wheat crop (*Triticum aestivum* L.) [19].

The infinite variety and complexity of plant diseases has led to the development of pesticides. Unfortunately, a variety of environmental problems including phytopathogen resistance have resulted from the continued usage of these herbicides [5]. Biopesticides are frequently employed to control a variety of pests, including insects and illnesses. They are produced using natural resources such as microorganisms, plants, animals, and particular minerals [119]. As of early 2013, there were over 400 registered biopesticide active ingredients and over 1,250 active biopesticide products. Sustainable organic farming operations need to use environmentally friendly pest and disease management practices along with balanced nutritional supplements to improve the quality and quantity of agricultural outputs [120]. To control pests in an eco-friendly way, a form of pesticide known as a biopesticide employs natural substances or microorganisms. It is common practice to utilize biopesticides and their byproducts to control a wide variety of pests. Their purpose is to protect crops from various pests, rodents, bacteria, and viruse [5]. *Trichoderma*, NPV, *Bacillus thuringensis*, and neem-based insecticides are the most widely developed and used biopesticides in India [121]. The quantity of microorganisms and plant and insect derivatives used as the active ingredient for the control of diseases, insects, and pests, as well as their beneficial benefits, have been reported worldwide in organic crop production. A study documented that, *Paenibacillus alvei* and *Lysinabacillus fusiformis* act as biocontrol agent against *Phytophthora capsici* [122]. A study revealed that, inoculation of *S. marcescens* inhibiting the growth of *Pythium aphanidermatum* [123].

4.2. Environmental

Soil metal contamination is a major problem because of the increasing number of impacted locations worldwide as well as the detrimental consequences that metals have on the environment and human health. Because metals are harmful and non-biodegradable, it is imperative to clean up the hundreds of contaminated sites worldwide and stop more metal pollution [124]. Traditional restoration methods, which rely on physical and chemical methods, are often expensive, impractical, and cause secondary environmental issues. In light of this, microbe-aided phytoremediation has grown in popularity due to its low cost, lack of negative environmental effects, and significant recent developments [125]. Microorganisms are essential to the recovery of natural ecosystems and are a fundamental part of them. Actually, for plants to survive metal toxicity and thrive in these harsh environments, plant-microbe interactions in metal-contaminated soil are crucial. Therefore, improving our understanding of this intricate relationship is crucial to the advancement of phytoremediation. Microbes are therefore crucial to the restoration of function and biodiversity in an ecosystem.

The ability of the microbial cells to create and detect signal molecules allows them to spread out as a biofilm across the root surface and begin functioning in unison once a particular population density is attained [85]. QS is the name given to this particular phenomenon. Microbes are very beneficial, essential for plant nutrition, and able to mitigate the negative effects of metals. Certain rhizosphere bacteria are able to directly handle organic and inorganic contaminants by taking advantage of their natural degrading processes, such as volatilization, transformation, and rhizo-degradation [126]. Metal complexation, EPS sequestration, volatilization, efflux, impermeability to metals, Hg(II) reduction to Hg(0), and enzymatic detoxification discharged from cells are some of the resistance mechanisms displayed by bacteria [127]. Additionally, bacterial plasmids contain resistance genes for a number of toxic-heavy metals and metalloids. PGP microorganisms can lessen a number of limiting factors for phytoremediation technologies, such as metal solubility, pollution level, and soil chemistry. A study revealed that, *Trichoderma harzianum* have showing tolerance in Cd-polluted soil and enhanced growth of barley [128]. Another study revelaed that, combine application of *Bacillus mycoides* and rock phosphate enhance growth of wheat by alleviating heavy metal stress [129].

5. COMMERCIAL APPLICATION OF PGPR

Marketing and commercialization are PGPR primary and most important tasks for success. Before entering the farming field, meticulous management techniques, adequate study, market analysis, and survey, are necessary to produce the right microbial inoculation in a laboratory. The particular crop and the climate at the time of commercial availability determine which microbial isolate is best [130]. For example, if a certain crop is susceptible to fungi, the selection process may be based on the microorganisms' particular antagonistic activity against the fungus. The performance of microorganisms is significantly influenced by the climatic conditions of their surroundings. Microbes in the laboratory are exposed to various biotic and abiotic stimuli in order to force them to combat natural environmental conditions, taking into account the climatic setting [131]. A nation's ecological zone combines the soil, climate, and temperature characteristics of a particular area. The process of creating novel microbial consortia for various ecological zones based on different crops is quite intricate and challenging. Climate factors such as rising temperatures may cause severe drought, which would impact PGPR performance in addition to crop growth and development [132]. Since native microorganisms are not naturally formed from locally rhizospheric soils, their performance has not yet been determined, and as a result, commercial inoculation may not be successful. Climate conditions can alter a plant's physiology and disrupt root exudation, which can lead to alterations in the plant's growth and development [133].

In terms of their desirable traits and colonization capabilities in specific stressful environments, PGPR may be well-known for its positive effects on plant growth and development. Understanding the disease control mechanism, growth promotion features, and resistance to biotic and abiotic variables can help predict the performance of microbial inoculants in different climatic situations [134,135]. The identification and isolation of niche-specific microorganisms with superior microbial features is required to attain maximal microbial efficiency. The needs of the crop are given high consideration while marketing microbial inoculation. Therefore, no single microbial strain is capable of performing well for every crop and in every climate. The primary and most important processes in commercialization include field surveying farmers' fields, isolating particular microbial strains with particular characteristics, choosing an appropriate carrier material, and injection technique [72].

Furthermore, commercial businesses favor microorganisms that have no negative effects on the environment or people. The laws governing the selection and screening process for commercial marketing should be regulated by the government [136]. Neglected non-targeted consequences, such as the replacement of natural species, could be another significant problem. Hypovirulent strains may become pathogenic, poisonous, or allergic. Before the widespread acceptance, registration, and implementation of PGPR for the management of pests and diseases, the aforementioned safety concerns must be addressed [137].

6. ROLE OF PGPR IN AGRICULTURE: PROMISE VERSUS BOTTLENECKS

The rising expense of agrochemicals and societal need for green technology is driving up demand for microbial inoculants. There has been a reported 12% annual growth in the global market for biostimulants [138]. Some PGPB, such as *Burkholderia, Pseudomonas, Rhizobium, Azospirillum, Azotobacter, Bacillus*, and *Serratia* sp., have been used to produce commercial products on a large scale [139]. However, different nations have varied laws governing the use of microbial inoculants in agricultural techniques [140]. The shelf-life, dependability, and uniformity of microbial inoculants in agricultural settings are the primary constraints. The shelf life of gram-negative bacteria is less than that of spore-forming gram-positive bacteria. It was suggested that super-inoculants with all the desired characteristics be used [141]. According to reports, some of the PGPB are opportunistic human pathogens such *Burkholderia cepacia* and *Pseudomonas aeruginosa* [142,143], which provide dangers to humans and the environment that should be appropriately addressed prior to their commercial production. Enhancements are required for the creation of novel nanoparticle-based carriers, more effective PGP rhizobacterial consortia, and application device optimization. Further problem is that plants are home to a variety of human infections, many of which have been shown positive effects on plant health by boosting plant growth [144–146]. More research is needed to address the issue of possibly harmful microorganisms in sustainable agriculture. The rhizosphere of plants is designed to make it easier for beneficial microorganisms to colonize than for harmful ones [147]. The biosafety of PGPB products is now being reevaluated in the United States, Europe, and other nations. Through changes in rhizosphere biology, resource availability, and biogeochemical cycling, climate change can influence the relationship between plants and microbes [148]. Once the shortcomings pertaining to long-term impacts on soil microbial populations, farmer acceptance, economic sustainability, and governmental regulations are resolved, PGPB's full potential will be achieved.

7. CONCLUSION

In addition to being essential to a country's survival, the agriculture sector helps it meet the demands of its expanding population and generate revenue for exports. The agroindustry has seen a number of technological advancements since the green revolution, which has improved crop yield but also caused environmental issues. The rising use of biological inoculants rather than agrochemicals for sustainable agriculture worldwide during the past ten years has unavoidably brought about a revolution. Maintaining the integrity of our planet's health and appropriate biogeochemical cycling, as well as the general growth and increased productivity of crop plants, depends on the triad of interactions between the bioinoculant microorganism, resident soil microbiota, and host plant. Growing concerns about food safety and the necessity to regulate the quality of food production to meet shifting customer demands are predicted to cause farmers to turn to organic farming and embrace sustainable agricultural methods. In order to find environmentally suitable substitutes for harmful chemicals, it is necessary to take into account the three important "Ps": people, prosperity, and the planet. To achieve the intended results and win over the confidence of farmers, who are the true stakeholders in agriculture, this microbial product-based technology must first undergo extensive research and development. Authentication, strain enhancement, and commercial production quantification are the main research issues that require further attention. As environmentally sustainable crop development alternatives, governments and federal agencies ought to encourage the use of biofertilizers and biopesticides. Entrepreneurs ought to contribute more to the biofertilizer sector and support new businesses financially. Furthermore, widespread public education is necessary to inform farmers and consumers alike of the benefits of employing microbe-based biopesticides and fertilizers in order to ensure a more environmentally friendly future.

8. AUTHOR CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agree to be accountable for all aspects of the work. All the authors are eligible to be an author as per the International Committee of Medical Journal Editors (ICMJE) requirements/guidelines.

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This study does not involve experiments on animals or human subjects.

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13. USE OF ARTIFICIAL INTELLIGENCE (AI)-ASSISTED TECHNOLOGY

The authors declares that they have not used artificial intelligence (AI)-tools for writing and editing of the manuscript, and no images were manipulated using AI.

14. DATA AVAILABILITY

All the data is available with the authors and shall be provided upon request.

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