

Review

Plant Growth Promoting Bacteria (PGPB)—A Versatile Tool for Plant Health Management

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Submitted: 21.01.2019 | Accepted: 29.03.2019 | Published: 03.06.2019

Abstract Plant growth-promoting bacteria (PGPB) include bacteria isolated from rhizosphere, phyllosphere, marine, rock surface, and from different ecosystems. PGPB enhance plant growth by promoting nitrogen fixation, phosphorus solubilization, and production of phytohormones such as indole acetic acid (IAA), gibberellins, polyamines, nitric oxide, and stress-mitigating enzyme viz., 1-aminocyclopropane-1-carboxylate deaminase. Further, they protect plant health through the synthesis of antibiotics and hydrolytic enzymes and induction of resistance in plants. Conspicuously, the mixtures of PGPB strains have been reported for their synergistic action in enhancing plant growth and protection. Due to their wide range of properties in maintaining crop health, PGPB can be an integral component in sustainable crop production practices. The effect of PGPB has been demonstrated successfully against many plant diseases and pests affecting crop cultivation. PGPB are also used in wastewater treatment and soil conservation. The current review discusses the mechanisms of action of PGPB and their usefulness in pest and disease management practices.

Keywords biofertilizer; plant disease; induced resistance; rhizobacteria; mode of action; biocontrol

How to cite Khabbaz, S.E.; Ladhakshmi, D.; Babu, M.; Kandan, A.; Ramamoorthy, V.; Saravanakumar, D.; Al-Mughrabi, T.; Kandasamy, S. Plant Growth Promoting Bacteria (PGPB)—A Versatile Tool for Plant Health Management. *Can. J. Pestic. Pest Manag.* **2019**, *1*(1), 1–25; doi:10.34195/can.j.ppm.2019.05.001.

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Introduction

Global demand for food, feed, and fuel from agricultural crops is increasing at a rapid pace. The world population is anticipated to reach 9.1 billion in 2050 from current the population of 7.3 billion [1]. Crop loss due to pests and diseases is a major concern and constant threat to food production worldwide. Farmers are becoming more and more dependent on agrochemicals as a relatively reliable method of crop protection. Over the years, the continuous application of synthetic chemicals has caused great concerns for the health of humans and the environment. The indiscriminate use of chemical inputs has led to several negative effects, i.e., persistence of toxic residues in groundwater; development of resistance in pathogens to the applied chemicals; and elimination of beneficial non-target organisms from the environment, affecting the ecological balance [2–4]. Consequently, it has been proposed, nowadays, that a revival of the principles and practices followed in olden day agriculture could ensure safe food production and sustain agriculture by preserving the health of natural resources such as soil, water, and environment. The increased awareness of consumers regarding the negative effects of chemical inputs has also led to the demand for safe agricultural produce. Therefore, it is necessary to develop safe and environment friendly agricultural practices to meet the demand of consumers. In this context, crop health management using plant growth promoting bacteria (PGPB) has been studied as an alternative or integrated approach to reduce the use of toxic pesticides in the control of pests and diseases in crop production [5–8]. PGPB are associated with many plant species and well-known for their ability to enhance crop growth through the production of phytohormones [9,10]. The characteristics of PGPB are quite conspicuous. They are naturally occurring non-pathogenic bacteria that enhance plant growth through their excellent root-colonizing ability [11,12]; production of growth-promoting substances such as indole-3-acetic acid (IAA), gibberellic acid (GA_3), and 1-aminocyclopropane-1-carboxylate deaminase [13]; and activation of plant defense mechanisms [14–17]. These bacteria are also used for wastewater treatment [9], to reduce soil erosion, and to restore marine mangroves. The most widely studied group of PGPB is rhizobacteria, that associate with plant growth promotion and disease control and are most commonly known as plant growth promoting rhizobacteria (PGPR) [18]. This review focuses on recent advances in the research and potential of PGPB in the management of plant health (Figure 1), mainly elucidating the (i) mode of action of PGPB in suppressing plant disease and promoting plant growth; (ii) exploring the role of PGPB in the control of pathogens, nematodes, and insect pests in crops; and (iii) the success and intricacies in the development of bioformulations for the control of pests and diseases.

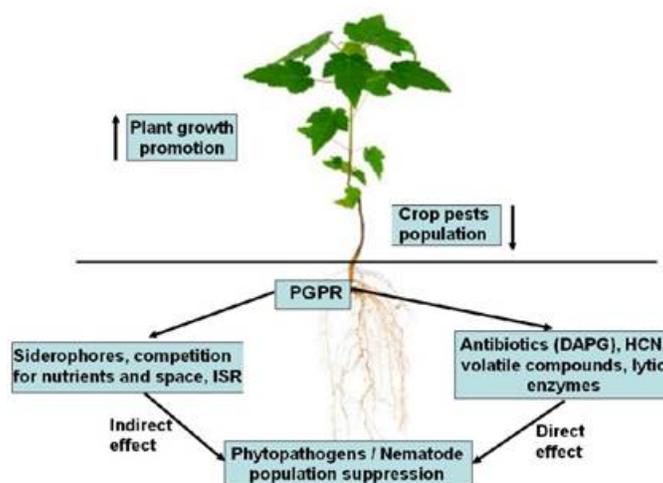


Figure 1. Schematic representation of mode of action of plant growth-promoting bacteria (PGPB) in the management of plant health.

Important genera of PGPB

PGPB can be classified into three categories. The first category belongs to free-living bacteria that specifically interact with plants under suitable conditions. The second category lives in rhizospheric soil zones adjacent to roots or phyllospheric zone; i.e., epidermis of plant leaves. The third category forms stable associations with certain tissues and organs of plants known as endophytic bacteria [19].

PGPB mainly include *Agrobacterium radiobacter*, *Acinetobacter* spp., *Arthrobacter* spp., *Azospirillum brasilense*, *Azospirillum lipoferum*, *Azotobacter chroococcum*, *Bacillus fimus*, *Bacillus licheniformis*, *B. cereus*, *Bacillus megaterium*, *Bacillus mucilaginosus*, *Bacillus pumilus*, *Bacillus subtilis*, *Bacillus amyloliquefaciens*, *Delftia acidovorans*, *Paenobacillus macerans*, *Pantoea agglomerans*, *Pseudomonas chlororaphis*, *Pseudomonas fluorescens*, *Pseudomonas solanacearum*, *Pseudomonas syringae*, *Serratia entomophila*, *Streptomyces griseoviridis*, *Streptomyces lydicus*, and *Rhizobia* spp. [7,13].

Mode of action of PGPB

PGPB stimulate plant growth through a variety of mechanisms that include improvement of plant nutrition, secretion of unique enzymes and regulation of phytohormones, and suppression of disease-causing organisms. A spate of studies suggests that the plant growth stimulation by PGPB is a net result of the simultaneous and synergistic action of multiple mechanisms. The different modes of action of PGPB will be discussed in this review.

Plant growth promotion

The mechanism of plant growth promotion by PGPB includes biological nitrogen fixation (BNF), synthesis of phytohormones (IAA, GA₃, and cytokinin), abiotic stress relief, inhibition of plant ethylene synthesis, increased availability of micro and macronutrients (phosphorus and iron), and production of volatile compounds.

Biological nitrogen fixation

PGPB have the property of fixing atmospheric nitrogen by inducing the formation of paranodules in non-legumes. The bacteria produce a unique enzyme, nitrogenase, which converts the atmospheric nitrogen to ammonia. Nitrogen-fixing diazotrophic bacteria, such as *Gluconacetobacter diazotrophicus* PAL5, *Herbaspirillum rubrisubalbicans* M4 and *Azospirillum brasilense* SP7 improve the total nitrogen uptake in sugarcane plants [20]. Application of *Pseudomonas fluorescens* caused a significant increase in the uptake of nitrogen (N) and potassium (K) in black pepper [21]. Application of *Bacillus* sp. strains OSU-142, RC-07, and M-13, *Paenibacillus polymyxa* RC-05, *Pseudomonas putida* RC-06, and *Rhodobacter capsulatus* RC-04 showed increase in uptake percentage of N and P in sugar beet under field conditions [22]. Kalagudi et al. [23] reported that strains of *Azospirillum* exhibited colonization in paranodules. Competition between pathogenic and saprophytic microorganisms for organic materials released from the roots reduces the growth and pathogenic activity of pathogens [24]. In general, the root exudates of the plants support the enhanced proliferation of rhizosphere microflora. The exudates contain mainly low molecular organic compounds, such as sugars, amino acids, and organic acids [25]. The root exudates enhance microbial activity and, therefore, increase the rate of nitrogen mineralization in the soil [26] Application of 100 mL broth culture of *Bacillus* and *Azospirillum* to 45-day-old tissue culture plants of *Musa*, along with 33% nitrogen fertilizer, increased shoot and root growth under greenhouse conditions. The plants also showed an increase in bunch yield and finger weight [27]. In PGPB, the property of biological nitrogen fixation as a biofertilizer has proven its

benefit. Therefore, the exploitation of PGPB could reduce the nitrogenous application of synthetic fertilizers and help maintain the soil health.

Phytohormones

PGPB are known to produce IAA, cytokinins, gibberellins, and ethylene stress-mediating enzymes like ACC deaminase. They synthesize IAA using tryptophan as a precursor [28]. PGPB belonging to *Azospirillum*, *Aeromonas*, *Azotobacter*, *Bacillus*, *Paenibacillus*, *Burkholderia*, *Enterobacter*, *Pantoea*, *Pseudomonas*, and *Rhizobium* genera have been reported to produce IAA. Inoculation with IAA-producing PGPR has stimulated seed germination, accelerated root growth and modified the architecture of the root system, and increased the root biomass [16,17,29–31]. Vessey [32] has explicitly reviewed the production of this hormone by PGPR and its implication in biofertilization for plant growth promotion. Application of either *Bacillus* or selected strains of *P. fluorescens* resulted in enhanced plant height, tiller numbers (3–4 fold), and grain yield due to the production of IAA and GA3 like phytohormones [33]. Shao et al. [31] demonstrated the involvement of genes *patB*, *yclC*, and *dhaS* in plant growth promotion and biosynthesis of IAA in *Bacillus amyloliquefaciens* SQR9.

ACC deaminase

ACC deaminase produced by PGPB acts on 1-aminocyclopropane-1-carboxylic acid (ACC), an immediate ethylene precursor in higher plants, and degrades this compound into α -ketobutyrate and ammonium [13,34–36]. Decreased ethylene levels allow the plant to be more resistant to a wide variety of environmental stresses. Rhizosphere bacteria with ACC deaminase activity have been reported in *Achromobacter* [37], *Azospirillum* [38,39], *Bacillus* [40], *Enterobacter* [41], *Pseudomonas* [13,42], and *Rhizobium* species [43]. The use of PGPR possessing ACC deaminase in mitigating flooding, salinity, drought, and pathogenic stresses has been demonstrated in several studies [13,44,45].

Phosphorus Solubilization

Phosphorus is a key nutrient that stimulates growth and development of roots and makes plants more resistant to drought. The introduction of *Bacillus megaterium* biovar *phosphaticum* in the rhizosphere of rice helps in increasing the availability of ‘P’ from insoluble sources of soil-bound phosphates [46]. *Enterobacter asburiae* PSI-3, a phosphate-solubilizing microorganism isolated from rhizosphere of pigeon pea, secretes glucuronic acid to dissolve poorly soluble mineral phosphates [47]. Gram-negative bacteria communicate through Acyl homoserine lactones (AHLs) [28]. Application of *Bradyrhizobium* prior to sowing increases the nitrogen, available phosphorus, and potassium in the soil [48]. The high P uptake was facilitated by *B. amyloliquefaciens* FZB24 from soils rich in phosphorous, and this promoted plant growth in wheat plants [10].

Disease suppression

Disease suppression is proposed to be due to direct and indirect mechanisms (Figure 1). The direct mechanisms include the production of antibiotics [16,17,49], lytic enzymes [50], hydrogen cyanide (HCN) [16,17,51], volatile compounds [16,17,52], and degradation of pathogen-derived toxins [53]. The indirect mechanisms include production of siderophores [54], competition for nutrients and space [55], and induction of systemic resistance [6,56].

Direct mechanisms

Antibiotics Antibiotics are low molecular weight heterogeneous group of organic chemical compounds produced by microorganisms. Antibiotics have the property of inhibiting growth and metabolism of other microorganisms at low concentrations [7,57]. Species of *Pseudomonas* have been primarily reported for producing of phenazine-1-carboxylic acid, phenazine-1-carboxamide, 2,4 diacetylphloroglucinol (DAPG), oomycin, pyoluteorin, and pyrrolnitrin. However, a few *Pseudomonas* species have also reported for the production of aerugine, azomycin, butyrolactones, cepaciamide A, kanosamine, rhamnolipids, pseudomonic acid, karalicin, viscosinamide, 2,3-deepoxy-2,3-dedihydrorhizoxin (DDR), exhibiting antifungal, antibacterial, and antiviral properties. Similarly, *Bacillus* species produce antibiotic lipopeptides such as iturin, bacillomycin, bacilysin, fengycin, surfactin, and zwittermixin [7,16,17]. These antibiotic compounds have antiviral, antifungal, and antibacterial activities. Of the various antibiotics, DAPG induces the expression of its own biosynthetic gene by acting as an intracellular signaling compound. It has also been demonstrated that two non-related *Pseudomonas* spp. could signal to each other in the production of 2,4-DAPG in the suppression of plant pathogens [58]. Keel et al. [59] illustrated the importance of 2,4-diacetylphloroglucinol (DAPG) produced by *Pseudomonas fluorescens* against root diseases.

Pseudomonas fluorescens strain 2-79 is antagonistic to *G. graminis* var. *tritici* by the production of antibiotic phenazine-1-carboxylic acid (PCA) in wheat [60]. Fluorescent pseudomonads are a group of bacteria that produce 2,4-DAPG, phenazine, pyrrolnitrin, and pyoluteorin, and were found to be effective in the biological control of *Pythium* infection in alfalfa seedlings [61]. The other reported antibiotic from pseudomonads is phenazine-1-carboxamide [62]. The pyrrolnitrin of *Pseudomonas* and *Burkholderia* has exhibited a broad range of antifungal activity against Basidiomycetes, Ascomycetes, and Deuteromycetes fungi, including *Rhizoctonia solani*, *Botrytis cinerea*, *Verticilliumdahliae*, and *Sclerotiniasclerotiorum* [63].

Some of the biocontrol strains are known to have more than one antibiotic, which can suppress one or more pathogens. *Bacillus cereus* strain UW85 produces both zwittermixin and kanosamine [64]. Genetically modified *Pseudomonas putida* WCS358r strains produce both phenazine and DAPG, and suppress disease development in field-grown wheat [65]. *Pseudomonas fluorescens* strain CHA0 produces the antifungal metabolites 2,4-diacetylphloroglucinol (DAPG), pyoluteorin (PLT), and pyrrolnitrin (PRN), which are major determinants of its disease-suppressive ability [66]. The availability of carbon source determines the production of antibiotics in rhizobacteria. Interestingly, the availability of glucose has stimulated the production of DAPG while repressing pyoluteorin in *P. fluorescens* strain CHA0. However, the expression of pyoluteorin was observed in *P. fluorescens* strain CHA0 after the depletion of glucose [67]. This has indicated that the carbon source and environment also influence the production of antibiotics in PGPB.

Hydrogen cyanide (HCN) HCN production has been reported for its critical role in the suppression of plant pathogens [16,17,51]. The role of HCN in the suppression of plant pathogens was reported by several researchers in various crops. Meena et al. [68] compared the HCN production by several strains of *P. fluorescens* and their efficacy in controlling root rot of groundnut caused by *Macrophomina phaseolina*. It was proposed that HCN could kill the pathogen by inhibiting electron transport and interrupting the supply of energy to the cells [69]. *P. fluorescens* strain CHA0, possessing the property of HCN has suppressed *F. oxysporum* f.sp. *radicis-lycopersici* in tomato, despite the production of fusaric acid by the pathogen [70]. Ramettee et al. [71] reported that HCN is a wide-spectrum antimicrobial compound involved in the control of root diseases produced by rhizosphere-based fluorescent pseudomonads.

Lytic enzymes PGPB have been reported as major producers of lytic enzymes. It is reported that lytic enzymes degrade chitin and glucan in the cell wall of target fungi which disrupts the osmotic strength of cellular membranes [24]. Several studies have reported that the production of chitinases could be increased by addition of chitin in the growing conditions [72]. It has reported that chitinase of *Serratia plymuthica* C48 suppressed *Botrytis cinerea* through the inhibition of germ tube elongation and spore germination [73]. Radjacommare et al. [74] reported

an increased chitinase activity in *Pseudomonas*-treated rice plants challenged with *Rhizoctonia solani*, along with the expression of 28 and 38 kDa chitinases. Cell wall lytic activity of *Paenibacillus* sp. 300 and *Streptomyces* sp. 385 was also demonstrated against *F. oxysporum* f. sp. *cucumerinum* [75]. Velazhahan et al. [76] reported a significant association between the level of chitinase production and the disease-suppressing potential of *P. fluorescens*.

Volatile compounds Volatile organic compounds secreted by PGPB work as initiators of plant growth promotion and defense responses in plants [16,17]. Pharmacological application of 2,3-butanediol induced growth promotion and disease resistance, while bacterial mutants blocked in 2,3-butanediol and acetoin synthesis were devoid of growth promotion and induced resistance capacities [77]. *Pseudomonas fluorescens* A6 has been reported to produce a new and unique antifungal compound not found in other *Pseudomonas* strains. The spectroscopic analysis showed that this molecule is a cyclic peptide containing three or four amino acids [78]. Activation of the induced systemic resistance (ISR) pathway in *Arabidopsis* seedlings primed with *B. subtilis* GBO3 and *B. amyloliquefaciens* IN937a revealed that volatiles have been responsible for the induction of defense against *Erwinia carotovora* subsp. *carotovora* [79].

It was proposed that the majority of PGPR activate ISR through jasmonate and ethylene signals. On the other hand, salicylic acid (SA) accumulation is associated with the pathway of systemic acquired resistance (SAR) [80]. The fluorescent pseudomonads produce salicylic acid, which aids in the synthesis of substances like phytoalexins, lignins, phenols, and several PR proteins. Production of salicylic acid, jasmonic acid, and ethylene are involved in signal transduction and induce the ISR in plant systems [16,17,81].

Degradation of toxins Another mechanism of biological control is the detoxification of pathogen toxins. Several microorganisms, including strains of *B. cepacia* and *Ralstonia solanacearum*, can hydrolyze fusaric acid, a phytotoxin produced by various *Fusarium* species [82]. Nagarajkumar et al. [83] demonstrated the involvement of oxalic acid detoxification by *P. fluorescens* strain PfMDU2 in the biological control of sheath blight of rice caused by *R. solani*. Seed treatment, followed by soil application of rice with *P. fluorescens* strain, PfMDU2, carrying an oxalic acid detoxifying gene in plasmid, reduced the severity of sheath blight by 75% compared with the control.

Indirect mechanisms

Siderophores Siderophores are low molecular weight metabolites with a high affinity for Fe^{3+} . They chelate Fe^{3+} from the environment and transport the iron into microbial cells after being recognized by a specific siderophore receptor protein [84]. The presence of siderophore-producing organisms in close vicinity to plant roots is known to protect the plant from pathogenic organisms by chelating the available iron and making it unavailable to pathogens. This phenomenon is referred to as the siderophore-mediated suppression of plant pathogens [16,17,85]. It was reported that PGPR acquire ferric ions more competitively through production of siderophores under iron-limiting conditions. Conspicuously, the siderophore affinity for sequestering iron from the environment is stronger in PGPB than the pathogenic fungi, ultimately leading to a dearth of iron. This causes a disruption in pathogenic fungal cells, affecting their further growth and infection of plants [86]. Being a cell component, iron deficiency results in growth inhibition, decreased RNA and DNA synthesis, a reduction in sporulation, changes in morphology, and alterations in the energy required for the tricarboxylic acid cycle (TCA), electron transport chain, and oxidative phosphorylation [87]. In vitro antagonistic activity of *Pseudomonas* sp. is based on competition for nutrients [55]. *P. fluorescens* and *P. putida* produce siderophores and control soft rot of potato caused by *E. carotovora*. Pseudobactin is the siderophore produced by *P. fluorescens* that controls take-all disease in wheat and barley caused by *Gaeumannomyces* var. *tritici*. Pyoverdinin-type pseudobactin siderophores produced by *P. fluorescens* strains induce ISR [88]. Application of *P. fluorescens* WCS374r and *P. putida* WCS358r inhibits the mycelial growth of *Botrytis cinerea* in *Eucalyptus urophylla* by producing siderophores such as pseudobactin and pseudomonine [89]. Several bacterial traits, including flagella, siderophores, and lipopolysaccharides, have been proposed to trigger ISR. However, there is no clear evidence for an overall ISR signal activated by one single specific trait of bacteria [90,91].

Competition Competition for space and nutrients is believed to be a basic principle for the suppression of phytopathogens by PGPR [92]. The metabolites of plant root systems have served as an excellent carbon source for active and competitive colonization of PGPR in the rhizosphere [93]. The signal transactions between plant and PGPR, and motility of flagella, have further increased the affinity of PGPR in the rhizosphere [94]. The presence of amino acids, organic acids, and sugars in root exudates act as microbial attractants [5]. It is also interesting to note that the competency of PGPR depends on their potential to take advantage of a favorable environment or adaptability to newer conditions. The degree of chemotactic response varies among different strains of *Azospirillum* [95]. PGPR may possess a unique sense towards chemo-attractants. Rhizobacteria exhibit greater chemotactic responses towards root exudates of rice than the ones from non-rhizospheres [96].

Induced resistance Systemic acquired resistance (SAR) develops when plants successfully activate their own defense mechanisms in response to primary infection by a pathogen. The hypersensitive reaction is manifested as a local necrotic lesion of brown and desiccated tissue. Similar to SAR, ISR is effective against fungal, bacterial, and viral pathogens that are induced by PGPR. ISR differs from SAR in that PGPR do not cause visible symptoms on the host plant [14]. A major difference between these two induced pathways is the involvement of salicylic acid, jasmonic acid, and ethylene signals [80]. The fluorescent pseudomonads produce salicylic acid that aids in the synthesis of substances such as phytoalexins, lignins, phenols, and several pathogenesis-related (PR) proteins.

PGPR-mediated ISR was first reported against *Fusarium* wilt and *Colletotrichum* leaf spot in carnation and cucumber, respectively [97,98]. The activation of different sets of genes was attributed to the sensitivity of plants to phytohormones, volatiles, and lipopolysaccharides produced by the PGPR [99]. PGPR-mediated resistance strengthens the cell wall and changes the metabolic responses and physiology of plants, which results in the higher accumulation of defense-related enzymes against biotic and abiotic stresses [56,100,101]. The strengthening of cortical cells of root was reported in tomato plants upon priming with endophytic bacteria *P. fluorescens* WCS417 [102]. Similarly, the greater deposition of phenolics in the exodermis and cortical cell layers was reported in grapevine upon inoculation with *Burkholderia phytofirmans* PsJN [103]. The biochemical and physiological changes include the expression of pathogenesis-related enzymes and proteins [100,104].

Plant systems need a signal or stimuli to activate defense pathways and secondary metabolites. Application of PGPR activates the defense genes, enhances plant growth, and plays an important role in plant protection. The phenylpropanoid pathway products, such as phenolics and lignin, which were induced in Pf-1 treated plants, showed enhanced resistance to several pests and plant pathogens [105]. Induction of phenylpropanoid metabolism was observed after the application of Pf-1 and FP-7 by increasing the levels of peroxidase (PO), polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL), phenol, and lignin activity [106]. PAL is the first enzyme in the metabolic pathway leading to the production of phytoalexin, phenolic substances, and the formation of lignin with the help of peroxidases. Increased activity of peroxidases by the application of rhizobacteria has been reported in different plants, viz., rice [107], tomato [108], groundnut [109], cotton [110], banana [111], tea [56], and mango [72]. *P. fluorescens* Pf-1 treated cowpea plants showed enhanced activity of the enzymes PO and PAL [112].

Application of *P. fluorescens* in black pepper increased levels of peroxidase (PO), phenylalanine ammonia lyase (PAL), and polyphenol oxidase (PPO) against the pathogen *Phytophthora capsici*, and induced systemic protection by reducing disease incidence [113]. Application of *P. fluorescens* and *Bacillus subtilis* inhibit rice seedborne pathogens, such as *Helminthosporium oryzae*, and stack burn caused by *Trichoconis padwickii*, and increasing the phenol, PO, and PPO contents, and enhancing disease resistance [114]. Application of *P. chlororaphis* and *B. subtilis* reduced the damping off in chili by inducing the phenylpropanoid pathway and production of phenolics, and triggered defense-related enzymes such as PAL, PO, and PPO [115]. Application of *P. fluorescens* strains Pf-1 and MMP on cotton leaves reduced the development of bacterial blight and increased the activity level of peroxidase (PO) against bacterial blight [116]. The recent review by Mhlongo et al. [117] examined using a metabolomics approach in understanding the induced resistance and defense responses of plants primed with PGPR against various stresses.

PGPR in crop management

Plant growth promotion

Greenhouse studies showed that the application of *Bacillus* sp. RAB9 and *Bacillus pumilus* increased the total dry matter (TDM) by increasing the root dry matter (RDM), shoot dry matter (SDM), and growth rate of micropropagated *Musa* sp. [118]. Beneficial bacteria are capable of increasing the growth and vigor in several agriculturally important crops, including black pepper [119]. Treatment of wheat seed with *B. subtilis* (Embr.144), *Curtobacterium pusillum* (Embr.9769), and *Pantoea agglomerans* (Embr.1494) resulted in a significant increase in seed germination and yield, and the suggested mechanism may be production of hydrocyanic acid, siderophores, and induction of resistance [120]. Wet seed treatment with *P. fluorescens* Pf-1 significantly increased the seed germination and seedling vigor of cotton [116]. Seed treatment with *P. fluorescens* resulted in better germination, establishment, and growth of the seedlings of rice [121], and offered protection against rice sheath blight. Pepper cuttings treated with *P. fluorescens* resulted in enhanced plant vigor [122]. Verma et al. [123] stated that application of various strains of PGPR and *Rhizobium* on various crops enhanced the uptake of nutrients along with the reduction in disease incidence. Application of a mixture of *P. fluorescens* isolates (Pf32, Pf93) and *B. subtilis* (B49) to seed, soil, and foliage significantly reduced the bacterial blight incidence in cotton plants. In addition, it increased plant height, number of branches, and number of bolls under field conditions and, thereby, a maximum yield was recorded compared to the untreated control [124].

Maize seed priming with *Azotobacter* led to recording the highest grain yield, maximum number of kernels per ear, grain yield, and dry matter accumulation [125]. Treatment of lettuce seeds with *B. amyloliquefaciens* strain EXTN-1 showed enhanced growth and quality by pathogen suppression through oxidative burst, lignification, and the expression of pathogenesis-related proteins [126].

Management of plant diseases

PGPB treatment has been reported to be effective in managing fungal, bacterial and viral diseases of several crops. Application of PGPR is becoming a major component in the integrated management of plant diseases. Studies on the biocontrol activity of numerous PGPR showed that PGPR act against many soilborne pathogens, viz., *Aphanomyces* sp., *Pythium* sp., *Fusarium* sp., *Gaeumannomyces graminis*, *Phytophthora* sp., *Sclerotium rolfsii*, and *Thielaviopsis basicola* [16,17,127,128]. Among the different strains of *P. fluorescens*, Pf-1 (TNAU-B-RS) strain isolated from black gram showed broad-spectrum activity in suppressing several pathogens (fungi, bacteria, and viruses) which attack major crops, including rice, sorghum, sugarcane, tomato, banana, hot pepper, cotton, legumes, mango, tea, cabbage, cauliflower, and brinjal, by inducing ISR. In plants, Pf-1 treatment activates the genes encoding pathogenesis-related (PR) proteins and genes involved in the phenylpropanoid pathway [105]. Application of PGPR has been found to be effective against blast caused by *P. grisea*, sheath blight caused by *Rhizoctonia solani*, sheath rot caused by *Sarocladium oryzae* [107], bacterial blight (*Xanthomonas oryzae* pv. *oryzae*) [116,124], tungro disease (RTV) of rice [129], and *Fusarium* wilt in tomato [130,131].

Similarly, the application of *Pseudomonas putida* 89B-27 and *Serratia marcescens* 90-166 was reported to be effective in controlling wilt disease in cucumber plants [132]. Anandraj et al. [133] reported that the application of *P. fluorescens* IISR-6 and *Bacillus* IISR-51 reduced the incidence of foot rot caused by *Phytophthora capsici* in black pepper. Joseph et al. [134] reported that, in coconut, application of *P. fluorescens* strain PS1 resulted in a 50% reduction in leaf rot disease caused by *C. gloeosporioides*, *Fusarium* sp., and *Exserohilum rostratum*. Under in vitro conditions, *P. fluorescens* strain P 11 showed 65%–80% inhibition against vanilla pathogens, including *Colletotricum gloeosporioides*, *Sclerotium rolfsii*, *Fusarium oxysporum*, *F. semitectum*, and *Verticillium* sp. [135]. Capsule rot of cardamom caused by *Phytophthora meadii* was also reduced by spraying *P. fluorescens* culture filtrate

where the bacterium colonized the panicles and caused lysis of hyphae or zoospores [136]. Application of *Pantoea agglomerans* strain IC1270 reduced citrus green mold caused by *Penicillium digitatum* [137].

A spate of studies suggests the efficacy of PGPB in managing bacterial plant diseases. *P. putida* 89B-61 and *B. pumilus* SE 34 induce ISR against tomato bacterial wilt caused by *Ralstonia solanacearum* [138]. Angular leaf spot caused by *Pseudomonas syringae* pv. *lachrymans* was reduced by the application of *Flavimonas oryzae* strain INR-5, *S. marcescens* strain 90-166, and *Bacillus pumilus* [139]. Treating tomato seedlings with *Bacillus amyloliquefaciens* strain EXTN-1 against *Ralstonia solanacearum* led to oxidative burst, lignification, and expression of PR genes, thereby suppressing disease incidence [140]. In melon, application of *Bacillus* strain RAB9 and MEN2 reduced the incidence of bacterial fruit blotch disease caused by *Acidovorax avenae* subsp. *citrulli*. Aflatoxin contamination in groundnut was reduced by reducing the disease incidence of *A. flavus* in groundnut by application of Pf-2 and *Bacillus* sp. [141].

Though viral diseases cannot be managed by conventional plant protection measures, PGPB offers protection against viral infection, to a certain extent, by inducing systemic resistance.

Cucumber mosaic virus (CMV) infected plants showed delayed symptoms by seed treatment with *P. fluorescens* strain 89b-27 and *S. marcescens* strain 90-166 [142]. *P. fluorescens* strain CHA0 induced ISR against tobacco necrosis virus (TNV) [143]. Nallathambi et al. [144] reported that application of desert isolates CIAH-111, CIAH-196, and CIAH-311 reduced the incidence of virus diseases in watermelon. *Bacillus pumilus* strain SE34 and *Bacillus amyloliquefaciens* strain 937a reduced CMV incidence in tomato [145] by inducing systemic resistance. Application of Pfl reduced TSMV the number of local lesions in cowpea through the increased induction of PO, PPO, and PAL [112].

The efficacy of PGPB isolates are determined by their rhizosphere competency. Application of PGPR has been hampered by inconsistent performance in field tests [146], which is usually attributed to their poor rhizosphere competence [5]. Rhizosphere competence of biocontrol agents is mainly determined by the efficacy of root colonization and their ability to survive and proliferate, along with the development of roots in the rhizosphere region.

Management of plant nematodes

The reported species of bacteria for the management of nematodes are *Agrobacterium* sp., *Arthrobacter* sp., *Azotobacter* sp., *Clostridium* sp., *Desulfovibrio* sp., *Serratia* sp., *Burkholderia* sp., *Azospirillum* sp., *Bacillus* sp., *Chromobacterium* sp., and *Corynebacterium* sp. [147]. Seven to ten percent of the bacteria from the rhizosphere of sugar beet, tomato, and potato plants showed greater antagonistic activity against root-knot and cyst nematodes [148].

The exotoxins of rhizobacteria have showed greater nematocidal activity against eggs and juveniles of root-knot nematode under in vitro conditions [149]. Seed treatment and soil application of *P. fluorescens* Pfl reduced the incidence of soil and root nematode *Rotylenchulus reniformis* in cotton [150]. Root-knot nematode *Meloidogyne javanica* was managed by the application of native isolates of *Diazotrophicus* PAL-5, *Herbaspirillum rubrisubalbicans* M4, and *Azospirillum brasilense* sp. 7 in sugarcane [20].

Khan et al. [151] reported that the culture filtrates of *Cyanobacterium* and *Microleus lacustris* have nematocidal activity on egg hatching and larval mortality. Dipping of fresh vine cuttings in solutions of the rhizobacterial strains IISR 853, IISR 865, IISR 528, and IISR 658, and further application of 10 mL in the root zone, reduces the incidence of *Radopholus similis* in black pepper [152]. In banana, soil application of *P. fluorescens* led to minimum root populations of *Radopholus similis*, *Pratylenchus coffeae*, and *Helicotylenchus multicinctus* being recorded [153]. The recent review from Mhatre et al. [154] focused on the use of PGPR as a biocontrol for nematodes, and proposed PGPR as an alternative to chemical control.

Management of crop pests

Cotton plants treated with *P. gladioli* reduced the growth of *Helicoverpa armigera* by increasing polyphenol and terpenoid content [155]. Reports showed that *B. pumilus* strain INR-7 and *S. marcescens* strain 90-166 had induced systemic resistance against cucumber beetle, *Diabrotica undecimpunctata* [156]. *Azospirillum*-inoculated sorghum crop had a lower incidence of shoot fly (*Atherigona soccata*) due to the increased activity of PAL, which led to the increased production of total phenol [157]. Application of *Bacillus amyloliquefaciens* strain 937a, *B. subtilis* 937b, and *B. pumilus* SE 35 resulted in reduced incidence of *Bemisia argentifolii* by reducing the population of crawlers, nymphs, and pupae [158]. Application of *P. fluorescens* Pf1 and FP7 against leaf folders in rice increased the occurrence of natural enemies [159]. *Pseudomonas fluorescens* strains showed antagonism toward coconut eriophyid mite (CEM) *Aceria guerreronis*, which is a very serious problem in coconut [160]. The lack of a delivery system for coconut has become a major constraint in coconut gardens. Mathew and Sivaprasad [135] used honeybees or ants for the transportation of *P. fluorescens* in coconut plantations. Application of a consortium of *P. fluorescens* strains and *Beauveria bassiana* isolates as a single bioformulation effectively reduced the incidence of leaf folder (*Cnaphalocrocis medinalis*) insects and sheath blight (*Rhizoctonia solani*) disease in rice plants [161]. Recently, it was reported that the combination of PGPR with entomopathogenic fungus effectively reduced the incidence of fruit borer and *Fusarium* wilt in tomato [131].

Management of abiotic stress

Abiotic factors, such as low and high temperature, salinity, drought, flood, and heavy metals, affect the normal growth of plants and cause yield losses of up to 82%, depending on the crop. PGPR play a vital role in alleviating the abiotic stress of crops. Applications of PGPR strains help salt-stressed plants to combat the stress situation. Sorghum plants inoculated with *Azospirillum* had more water content, higher water potential, and lower canopy temperature, and were less drought-stressed than uninoculated plants. Cultivation of papaya in a nutrient-deprived soil in the semidesert area of Mexico, demonstrated that the association of rhizobacteria plays an important role in the survival of plants by fixing mineral nutrients [28]. Isolation of bacteria associated with plant roots of cactus growing in rocks without soil indicated the presence of *P. fluorescens* and *Bacillus* sp. From the utilization of minerals, it was evident that PGPR play a role in the rock weathering and survival of plants in desert areas [162]. Chia-Hui Hu and Kloepper [163] reported that tomato seedlings treated with *B. amyloliquefaciens* IN-937a, *B. pumilus* INR-7, and *B. subtilis* GB-03 tolerate high temperatures up to 45 °C, where PGPR appeared to dampen heat stress and minimize the classic heat shock response. Further, the induction of abiotic stress-related enzymes and accumulation of proline have been demonstrated as a potential mechanism used by PGPR strains in mitigating drought stress in green gram plants [101].

Under stressful conditions, ethylene, an important phytohormone, is overproduced and causes senescence. PGPR containing ACC deaminase can hydrolyze ACC, the immediate precursor of ethylene, and reduce the deleterious effects of salt stress-induced ethylene production. Inoculation of PGPR on trace metal-contaminated soils plays an important role in phytoremediation and reduced the deleterious effects of heavy metals. Some reports are demonstrating that *Pseudomonas putida* is tolerant to a number of heavy metals at higher levels [164,165].

Genetic improvement of PGPR

Genetic engineering of PGPR strains manipulated with potential plant growth promotion and antagonistic genes could enhance the efficacy against biotic and abiotic stresses that affect crop production. De Meyer and Hofte [166] found that SA produced by *P. aeruginosa* 7NSK2 was important in the induction of systemic resistance against *B. cinerea* in bean. Maurhofer et al. [167] introduced SA biosynthetic genes *pchBA* from *P. aeruginosa* PAO1 into *P. fluorescens* strain P3 (which does not produce SA) under the control of a constitutive kanamycin promoter.

The *pchA* gene product is an isochorismate synthase, converting chorismate to isochorismate, and the *pchB* gene product is an isochorismate pyruvate lyase catalyzing the formation of SA from isochorismate. Introduction of *pchBA* into *P. fluorescens* strain P3 enhanced the capability to produce more SA and, thereby, induce greater resistance against necrosis virus. *Pseudomonas putida* has shown improved efficacy against soilborne pathogens after the mobilization of phenazine and phloroglucinol biosynthetic gene loci [168]. The mobilization of *phzH* gene from *P. chlororaphis* to *P. fluorescens* and *P. aureofaciens* strains that possess PCA has increased their efficacy in controlling root rot in tomato [169].

Formulations, shelf life of PGPB and commercial products

Commercial formulations of PGPR, along with suitable carriers, are used to improve crop health and to protect plants from various pests and diseases under field conditions. Organic or non-organic carriers protect the bacteria from desiccation and death of cells, thereby increasing the survival rate [170,171]. Carriers such as peat, turf, wheat bran, talc, lignite, kaolinite, pyrophyllite, zeolite, montmorillonite, alginate, pressmud, sawdust, and vermiculite, etc., are used for formulation [16,17,128]. In addition, the efficacy of the formulation is enhanced by the use of additives [172]. Food base plus compost tea (FBCT) and food base plus preservative (FBP) have performed well in enhancing the growth of tomato and cucumber plants. Formulations without stickers (adhesives) are associated with poor adhesion of bacteria to seeds. A comparison between carboxymethyl cellulose (CMC) and gum Arabic showed that CMC was a better adhesive for retaining the shelf life of the formulations [173].

Efficient biocontrol agents are expected to have long shelf life without losing their efficacy. Shelf life of the PGPR in carrier material is considered to be a critical factor in commercial production. In general, viability of PGPR in various bioformulations has been better at low temperatures compared to high temperatures [174]. The talc-based formulation of *P. fluorescens* isolated from the rhizosphere of different crops has been developed and tested for its efficacy against various diseases [56,175]. The methods of application include seed treatment [176], seedling root dip [177], soil application [178], and foliar application [179]. Effective biological control depends on the methods and strategies for introducing and maintaining population levels and activities of these organisms in association with crops and plants [180]. Manikandan et al. [130] reported that *Pseudomonas* strain Pfl in talc formulations survived for up to 90 days at 10^8 cfu/mL. There was a significant increase in the population of bacteria for up to three months, which lead to increased root and shoot numbers and weight of the pods in groundnut [181]. Survival of bacteria varied between 45 days to 12 months in talc-based formulations [182]. To maintain the efficacy and reliability of the biological control agents, a number of resistance inducers were tested alone and in combination with *P. fluorescens* isolates. Among the various compounds tested, soil drenching and seed treatment of DL- β -aminobutyric acid (BABA) and γ -amino butyric acid increased the effectiveness of *P. fluorescens* against charcoal rot in chickpea caused by *Macrophomina phaseolina* [183].

A plant growth activator is a commercial product designed to stimulate plant growth and is found as a powder formulation containing a microbial community of over 40 strains of predominantly *Bacillus* sp. Several commercial products containing PGPR have so far been marketed. Among them, *Bacillus*-based products have achieved successful commercialization due to their ability to produce endospores that resist adverse environment conditions, including changes in temperature and pH, as well as pesticides and fertilizers. Owing to the potentiality of *Bacillus* spp., 18 different commercial products of *Bacillus* origin from China were reported to mitigate soilborne diseases [184]. Formulations are available in simple mixtures of 2–3 strains, or may contain 30–40 strains. Examples are Lawn Booster, Plant Growth Activator (PGA), Equity and Naturize, SuperBio[®], Soil Builder and Super bio[®], health start[®], Healthy TurfTH, and PHC BioPak[®] [172]. Maksimov et al. [19] compiled the available information on the formulations of *Azospirillum* sp., *Bacillus pumilus*, *B. subtilis*, *Paecilomyces* sp., *Pseudomonas* sp., *Serratia* sp., *Streptomyces* sp., *Trichoderma harzianum*, and *Penicillium vermiculatum*, along with their trade names, diseases which that had efficacy against, and manufacturer details.

Performance of non-native PGPB isolates

Streptomyces roseoflavus MB-97 isolated from the Chinese Bohai sea was used as a biocontrol agent against root rot pathogens *Fusarium* sp. and *Rhizoctonia* sp. Results showed that 50% of the disease incidence was reduced in soybean plants [185]. Cultivation of papaya in a nutrient-deprived soil in the semidesert area of Mexico demonstrated association with rhizobacteria plays an important role in the survival of plants by fixing mineral nutrients [28]. It has been demonstrated that *Pseudomonas fluorescens* isolated from *Lotus corniculatus* enhances the nitrogen-fixing capacity in alfalfa plants and reduces the incidence of *Pythium* damping off [186]. Isolation of bacteria associated with the roots of cactus growing in rocks without soil revealed the presence of *P. fluorescens* and *Bacillus* sp., wherein they play a role in rock weathering, fixing minerals for their own survival and, also, assisting in the survival of plants in desert areas [162]. Chia-Hui Hu and Kloepper [163] reported that treating tomato seedlings with *B. amyloliquefaciens* IN-937a, *B. pumilus* INR-7, and *B. subtilis* GB-03 tolerated high temperatures up to 45 °C, where PGPR minimized the heat shock response. *Azospirillum brasilense* is capable of promoting many growth characteristics of the unicellular microalgae *Chlorella vulgaris*, which is commonly used for tertiary wastewater treatment. Valderrama et al. [187] reported that co-immobilization of microorganisms (microalgae and PGPR) in small beads eliminates higher percentages of N and P, when compared with *C. vulgaris* alone. *Pseudomonas putida* also plays a role in removing the heavy metal chromium [188,189]. This technique represents a simple, reproducible, and cheap method for removing chromium compared to conventional methods. Association of *Vibrio* sp. with mangrove plant roots produce AHLs (acyl homoserine lactones) and suggests that these molecules probably play a major role in coordinating the physiological and genetic changes required for proliferation and for changing the surrounding environment [190].

Endophytic PGPB

Bacteria associated with plants are able to penetrate and colonize the plant endophytically. It is believed that the endophytic bacteria experience a comparatively protective and uniform environment inside the plants when compared to the rhizosphere. Endophytic bacteria have systemic movement inside plants and have an advantage in being able to restrict pathogen entry into the vascular stele [191]. Endophytic organisms play a key role in plant survival and fitness by increasing nutrient acquisition and disease suppression [192]. Two endophytic strains of *Rhizobium leguminosarum*, RPE-2 and RPE-3, were found to significantly increase plant biomass, chlorophyll content, root growth, and leaf area [193]. Endophytic PGPR *Pseudomonas* species enhance resistance against *Verticillium* wilt for up to five weeks [194]. Cucumber seed treatment with *Serratia plymuthica* antagonistic to *Pythiummultimum* showed antagonistic action and colonization in the cortex, endodermis, and vascular stele, and restricted growth in the epidermis. Deposition of callose-enriched wall opposition was observed at the site of pathogen penetration. *P. fluorescens* CICA-90 colonized internal and external roots, and stem tissues showed antagonistic activity against bacterial ring rot caused by *Clavibacter michiganensis* subsp. *sepadonicus* [195]. Jha et al. [196] reported that rice plants treated with a mixture of *Pseudomonas pseudoalcaligenes* and *B. pumilus* decreased proline concentrations in a situation of salinity stress, when compared to control treatment, and concluded that the mixture of endophytic and rhizospheric bacteria could be used against salinity stress.

Conclusions and future directions

Of the numerous genera of PGPB, *Pseudomonas* and *Bacillus* genera have been intensively studied for their antagonistic activity and ability to activate ISR against various pests and diseases. In-depth studies on the mechanisms of PGPB have opened new means in designing strategies for improving the efficacy of biocontrol agents. The recent developments in the identification of antimicrobial compounds and genes responsible for encoding

antibiotics have helped researchers to screen and select elite strains for the control of targeted pathogens and genetic improvement of specific strains of PGPB. At the same time, this knowledge could also be used to develop a super consortium with multiple modes of action for the control of pests and diseases. In addition, PGPB could serve as a source of various growth-promoting and disease-resistance elements for the genetic engineering of crops against pests and diseases. The characterization of PGPB strains from different ecosystems could also be helpful in assessing the suppressive potential of soil against various pathogens, including nematodes. Besides pests and disease control, PGPB have great potential as biofertilizers and in mitigating abiotic stresses in plants. Therefore, PGPB could be a versatile tool for the management of plant health in the era of sustainable agriculture.

Nevertheless, the success of PGPB in the management of plant health relies mainly on their survival in the introduced ecosystem. Therefore, research should be more focused on the development of formulations which could enhance survival capacity and maintain shelf life under stressful environmental conditions. A combination of endophytes and PGPR could have a more pronounced growth-enhancing effect on host plants in addition to disease resistance. Therefore, efforts should be directed towards the development of products containing multiple mixtures of compatible PGPB strains for effective and sustained control of a broad range of pests and diseases.

Author Contributions: All authors participated substantially in this work.

Funding: This research received no external funding.

Conflicts of Interest: The authors declare no conflict of interest.

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