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REVIEW

Antagonistic Potential of Bacterial Species against Fungal Plant Pathogens (FPP) and Their Role in Plant Growth Promotion (PGP): A Review

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ABSTRACT

Since the 19th century to date, the fungal pathogens have been involved in causing devastating diseases in plants. All types of fungal pathogens have been observed in important agricultural crops that lead to significant pre and post-harvest losses. The application of synthetic fungicide against the fungal plant pathogens (FPP) is a traditional management practice but at the same time these fungicides kill other beneficial microbes, insects, animal, and humans and are harmful to environment. The antagonistic microorganism such as bacteria are being used as an alternate strategy to control the FPP. These antagonistic species are cost-effective and eco-friendly in nature. These biocontrol bacteria have a broad mechanism against fungal pathogens present in the phyllosphere and rhizosphere of the plant. The antagonistic bacteria have different strategies against the FPP, by producing siderophore, biofilm, volatile organic compounds (VOCs), through parasitism, antibiosis, competition for limited resources and induce systemic resistance (ISR) in the host plant by activating the immune systems. The commercial bio-products synthesized by the major bacterial species *Pseudomonas syringae*, *Burkholderia cepacia*, *Streptomyces griseoviridis*, *Pseudomonas fluorescens* and *Bacillus subtilis* are used to control *Fusarium*, *Pythium*, *Rhizoctonia*, *Penicillium*, *Alternaria*, and *Geotrichum*. The commercial bio-formulations of bacteria act as both antifungal and plant growth regulators. The Plant growth-promoting rhizobacteria (PGPR) played a significant role in improving plant health by nitrogen-fixing, phosphorus solubilization, phytohormones production, minimizing soil metal contamination, and by ACC deaminase antifungal activities. Different articles are available on the specific antifungal activity of bacteria in plant diseases. Therefore, this review article has summarized the information on biocontrol activity of bacteria against the FPP and the role of PGPR in plant growth promotion. This review also provided a complete picture of scattered information regarding antifungal activities of bacteria and the role of PGPR.

KEYWORDS

Fungi; plant pathogens; synthetic fungicide; antagonism; bio-products; PGPR

1 Introduction

Bacterial species associated with the phyllo-sphere and rhizosphere soil of plants may have valuable effects on plant health by providing essential plant beneficial nutrients and Plant Growth Promoters (PGR) or by producing induction host resistance, siderophore, and antibiotics against plant pathogenic species of bacteria and fungi, respectively [1–3]. PGPR colonize the plant root to nourish the plant health. PGPR increase the nutrient supply to the plants and act as antagonist against plant pathogenic fungi at the same time [4]. The Rhizobacteria also act as shield against abiotic stress in pulses [5]. Basically, bacteria are unicellular prokaryotic microorganisms with achlorophyllous properties and having an ambient environment. Bacteria as an antagonistic played a significant role by killing and suppressing the growth of other pathogenic harmful microorganisms especially fungi that cause diseases on important agricultural crops [6,7]. The fungal pathogens cause severe infection on fruit, vegetable, and other cereal crops worldwide. The major fungal pathogens attacking fruits and vegetables are *Fusarium, Botrytis, Penicillium, Rhizoctonia, Pythium, Ascochyta, Alternaria, Leptosphaeria, Blumeria graminis, Melampsora lini*, and *Sclerotinia* [8–10]. Biological control of these fungal pathogens is an alternative to synthetic fungicide. A broad range of microorganisms such as bacteria, fungi, nematodes are being used as biocontrol agents worldwide. These biocontrol agents not only retard the growth of pathogenic target microorganisms but also improve plant health by providing nutrients through mutualistic associations. Furthermore, the application of these biocontrol agents (BCAs) is cost-effective, eco-friendly, with some more features such as these do not contaminate the water, plant product, and soil [11]. The BCAs, have different modes of action such as antibiosis, parasitism, competition, and induction of host plant resistance to control the target pathogens [3,12]. This review highlights the bacteria as biocontrol against different plant pathogenic fungi. Both the gram-negative and gram-positive bacteria are significantly used as a BCAs [13]. These biocontrol bacteria produced Siderophore and formed the biofilm against the many-targeted fungal pathogens of fruit crops [14]. Bacterial species used as antagonists belong to genera *Bacillus, Pseudomonas, Rhizobium, Stenotrophomonas, Pantoea*, and *Paenibacillus*. The antagonistic bacteria *Bacillus amyloliquefaciens* is being used to control the fungal pathogen *Botryosphaeria dothidea*, causative agent of apple ring rot [15]. The biocontrol bacteria retard the growth of fungal pathogens both *in-vivo* and *in-vitro* by producing antifungal activities. The antifungal activities of *Pseudomonas synxantha* against stone fruit fungal pathogens *Monilinia fructigena* and *M. fructicola* cause brown rot [16]. These bacteria also compete with target fungal pathogens for nutrients and space on fruit surfaces. Bio-commercial products prepared from bacterial species are being used to control many fungal and bacterial pathogens. A commercially available product Avogreen® was synthesized by *Bacillus subtilis* against a major Avocado plant disease *Cercospora* spot in South Africa [17]. Three bacterial bio-commercial products named Bio-Save® (10LP, 11LP, Blight-Ban® A506) were also synthesized by using *Pseudomonas* spp. against plant pathogenic fungal and bacterial species. Bio-Save 10LP® and 11LP® prepared from *P. syringae* strains ESC-10 and ESC-11 applied against pathogenic fungal storage pathogens of pome, potato, and citrus fruits, but the product Blight-Ban A506 used against bacterial diseases of apple and pear tree [18]. *P. syringae* strain ESC-10 and 11 was effective to control the *Helminthosporium solani* (Silver scurf of potato) and similarly, *Fusarium* spp. (Dry rot of potato) was controlled by the bio-commercial products Bio-Save 10LP® and Bio-Save 11 LP® [19]. Plant growth-promoting rhizobacteria (PGPR) are very prominent and important bacteria present in the rhizosphere. These bacteria have a vital role in plant growth promotion and to enhance soil fertility. These bacteria are also beneficial in heavy metal stress, salinity, drought and nutrient deficiency [4]. These PGPR improve plant health to combat plant diseases.

2 Control of FPP by Using Antagonistic Bacterial Species

The demand of the population for food is increasing day by day with the increase in population of the world. Every day, the scientist, researchers tried to develop new varieties for the production of high yield but after a few years, each variety becomes susceptible against various pathogens. However, various pathogenic microbes (fungi, fungi-like organisms, prokaryotes, nematodes, viruses, and virus-like pathogens) contaminate the food and are responsible for decreasing the value for human consumption [20,21]. At the early and later stages of the crop, the soil-borne fungal pathogens attack and kill the seedlings and plants. Different species of *Fusarium, Rhizoctonia*, *Pythium, Phytophthora*, *Rhizoctonia* [22,23] *Botrytis*, *Penicillium*, *Alternaria*, *Aspergillus*, *Ascochyta*, and *Colletotrichum* are examples of soil borne pathogens at different stages of host plants [24–26]. Biological control of these pathogenic microbes is necessary to control the pathogens because the biocontrol agents are cost-effective and eco-friendly [27,28]. Different bacterial species act as antagonists against FPPs (Table 1).

Table 1: Antifungal activity of bacteria against FPPs

Bacteria (Strains)	Disease	Pathogen	Host plant	References
Rahnella aquatilis (B16C), *P. fluorescens* (B8P)	Root rot	*Fusarium solani*	Faba bean	[29]
Streptomyces spp.	Rice blast	*Magnaporthe oryzae*	Rice	[30]
P. protegens (MP12)	*Botrytis* bunch rot	*B. cinerea*	Grapevine	[31]
B. mycoides *B. amyloliquefaciens* *Pseudomonas* spp.	Post-harvest disease	*C. gloeosporioides* *F. solani* *P. cinnamomi*	Avocado	[32]
Bacillus spp. *Pseudomonas* spp.	Sudden wilt disease	*Fusarium* and *Alternaria* spp.	Tobacco	[33]
B. subtilis (B1)	Wood decaying	*Lasiodiplodia theobromae*	Rubber tree	[34]
Bacillus and *Pseudomonas* spp.	Gray mould	*B. cinerea*	Table grapes	[35]
B. amyloliquefaciens *Stenotrophomonas rhizophila* *B. subtilis*	Anthracnose	*C. gloeosporioides*	Mango	[36]
Bacillus, Micrococcus, Staphylococcus and Pseudomonas spp.	Rotting	*B. cinerea* *P. expansum* *A. uvarum*	Grapes	[37]
B. amyloliquefaciens (BA17)	Gray mold	*B. cinerea*	Green bean	[38]

3 Biocontrol Potential of Lactic Acid Bacteria against the FPP

Lactic acid bacteria (LAB) are gram-positive bacteria with some salient features such as non-sporulation, fastidious, rod shape, and catalase-negative. Due to safe food bio-preservation status, the LAB was used as a biocontrol agent against many fungal and bacterial pathogens [39]. In food industries, LAB produced anti-microbial compounds (e.g., anti-fungal and anti-bacterial) for the preservation of food during packaging and storing. Various types of antifungal compounds [Proteinaceous, Lactic acid, 4-hydroxyphenyl acetic acid, Benzoic acid, Pitocin TV35b, Sodium acetate, cyclo (Phe-OH-Pro, Mevalonolactone, Phenyl-lactate, Phenolic compound, Propionic acid, Diketopiperazines, and 2-hydroxy-4-methylpentanoic acid)] are produced by these bacteria to kill fungal pathogens. The antifungal activities of two Lactic acid bacteria named Plantarum UFG 121 and Plantarum UFG 108 have been observed against the fungal pathogens *Aspergillus flavus, A. niger, P. chrysogenum, P. roqueforti*, and *F. culmorum* [40]. The LAB inhibited the growth of these fungal pathogens by producing different organic compounds. The antifungal compounds produced by LAB were isolated and reported from different sources such as; *Lactobacillus Plantarum* was reported from grass silage [41], isolated from a wax gourd [42], and *Pediococcus pentosaceus* from maize [43]. The LAB strain 58 and 13 retarded the spore germination on fruit surface by *P. expansum* [44]. The LAB produced antifungal metabolites include cyclic dipeptides, biosurfactants, phenyl-lactic, and reuterin. The *L. plantarum* strain (LR14) inhibited the hyphal and spore germination of four fungi; A. *niger*, *Mucor racemosus*, *Rhizopus stolonifer*, and *P. chrysanthemum* by using antifungal peptides [45]. Post-harvest application by coating the grapes with *Lactococcus. plantarum* controlled the fruit decay by *B. cinerea* in storage [46]. PFL9 and PFR77 isolates of LAB inhibited the spore germination and delayed the infection caused by *Alternaria alternata*, *Orynespora cassiicola*, and *Phomopsis varsoniana* on pomegranate fruit [20]. The four LAB named *L. plantarum*, *L. paracasei, L. hilgardii* and *L. lactis* retarded the growth of *F. oxysporum* and promoted the plant growth in tomato plant [47]. *In-vitro*, these LABs reduced the disease incidence from 55–76% indicating that LAB is a good biocontrol agent against soil-borne pathogenic fungi [48].

4 Mechanism of Action Used by Bacteria against Fungal Pathogenic Species

Bacteria follow two major antagonistic modes of action (direct and indirect) against pathogenic fungi. During the direct mode of action, the bacteria parasitize the targeted pathogen through parasitism while during the indirect method the bacteria activate the systemic resistance of the host plant and also produce antibiotic substances to suppress the growth of opposite pathogens [13]. There are more antagonistic modes of action (Siderophore production, competition for nutrients and space, production of volatile organic compounds, biofilm formation on the fruit surface, and quorum sensing) applied by the bacteria to suppress the growth of FPP (Fig. 1).

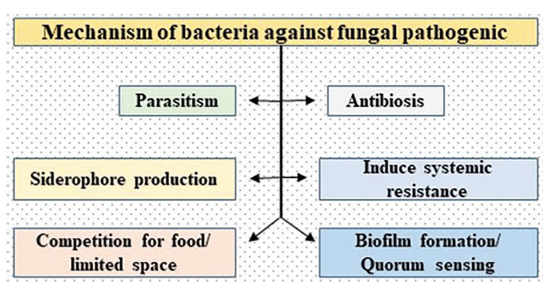

Figure 1: Mechanism of bacteria against fungal plant pathogens

4.1 Siderophore Production

Micronutrients are essential elements for the development of any microorganism. Among all the micronutrients the iron (Fe^{2+}) is very important for the growth of microorganisms. Bacteria utilize iron for energy purposes and body development. Iron is oxidized from Fe^{2+} to Fe^{3+} in the presence of water and oxygen [2]. These complex molecules secluded during siderophore production, by using these molecules bacteria with functional categories, are: 1) Catolate phenate 2) Pyridoxines 3) Carboxylates and

4) Hydroxamates. The produced siderophore has the ability to inhibit the hyphal and mycelial growth of target pathogens in a medium plate and repel the pathogenic fungi from the host plant surface [49]. Siderophore production by *Pseudomonas aeruginosa* FP6 was compared in two mediums (Succinate medium and King's B medium) [50]. The siderophore production is high in succinate medium as compared to King's B medium. This siderophore production strain was also tested against two fungal pathogens of the chili plant *Colletotrichum gloeosporioides* and *Rhizoctonia solani* under controlled conditions. Siderophore production by *Pseudomonas* strains SPs9 inhibited the growth of *F. oxysporum* causing wilt in chili plant [51]. *P. protegens* MP12 had the ability to produce siderophore with antifungal activity against the fungal pathogen of grapevine *B. cinerea* [31].

4.2 Competition for Food and Limited Space

Biocontrol bacteria have the ability to (1) colonize in scratched fruit to ingest the food (Carbon source) for their existence, and (2) restrict the carbohydrates tendency for the target fungus by decreasing its germination rate and consequently reduce its invasion capability on the host surfaces [52]. An *in-vitro* study showed that in the presence of a biocontrol agent the fungal pathogen slowed down the utilization of sucrose, glucose, and fructose [53]. Other bacterial species belonging to the genera *Pseudomonas, Bacillus*, and *Pantoea* also acted as a biocontrol agent against infectious fungi due to their colonization of all food resources under controlled conditions. *In-vitro* and *in-vivo* research was conducted to measure the incidence and severity of fungal pathogens on the bell pepper plant [54]. The biocontrol bacteria (*Arthrobacter Pseudomonas* spp.) was used to inhibit the growth of the fungal pathogens *B. cinerea* (cause of gray mold) and *A. alternate* (cause of *Alternia* rot on bell pepper). The biocontrol bacteria compete for nutrients with fungal pathogens on the fruit surface.

4.3 Parasitism

The biocontrol bacterial species secrete chitinases, glucanases, and protease enzymes for the degradation of the fungi cell wall [3]. In a simple way, the cell wall degradation is impossible because of chitin present an insoluble form and designed by N-Acetyl glucosamine which is interlinked with β1-4 that provide support to the cell wall. In addition, β1-3 glucan is one of the essential components in which several other components were covalently associated and gave mechanical stability as well as integrity to the fungal cell wall. As antagonistic agents, the bacteria need diverse antifungal enzymes to degrade the cell wall of pathogenic fungi [55]. Glucan is an antifungal enzyme which is secreted by a few antagonistic bacterial species to hydrolyze the glucans present in the fungal cell wall by two noteworthy mechanisms. In first, the bacteria secrete exo-1,3 glucanases that had the capability to hydrolyze the concerned glucans by successive integration of glucose particles with some non-reducer residues. Secondly, the bacteria secrete endo-1,3 glucanases [56,57]. To breakdown the chitin of the fungal cell wall, the antagonistic bacteria secreted chitinases for the hydrolyzation of chitin. Non-splitting N-Acetyl glucosamines were found with β1,4 linkages by following these two mechanisms: 1) NAG residues successively segmented by exo-chitinase, and 2) aleatory sites concerned with polymer chain activated by the endo-chitinase. The species of *Pseudomonas* and *Bacillus* were found to be a good biocontrol agent by secreting antifungal enzymes against fungal pathogens. The antifungal activities of different *Bacillus* strains (EPP21, EPP32, EPP49, EPP65, EPP74, and EPP100) have been recorded against the fungal pathogens *R. solani, S. rolfsii*, and *F. solani* of the pearl millet plant [58]. These antagonistic bacterial strains inhibited the growth of fungal targeted pathogens and also improved the plant health and provided systemic resistance by producing IAA. *Bacillus safensis* produced two antifungal compounds named iturin A2 and iturin A6 against the rice blast pathogen *Magnaporthe oryzae*. In dual culture plate, the iturin A2 inhibited the spore and hyphal germination of the mention fungal pathogen [59]. *B. subtilis* strain (DZSY21) produced antifungal volatile compounds (2-Methylbutyric acid and isopentyl acetate) *in-vitro* that inhibited the mycelial growth and sporulation of the fungus *Curvularia lunata* causing brown leaf spot on maize [60].

4.4 Biofilm Formation and Quorum Sensing

Biofilm formation is an effective antimicrobial property of bacteria on fruit surface against pathogenic fungi. This biocontrol mechanism of bacterial species assists its adherence, colonization as well as multiplication on fruit lesions against target pathogens [61]. Bacteria use it as a biocontrol agent forming micro-colonies around the lesion of fruits and protect them from harmful pathogens. The existence of these micro-colonies is measured by using the quorum sensing with concerned regulators (farnesol, phenethyl alcohol, and tyrosol) [62,63]. Through this quorum-sensing, the bacterial species interlink with each other and adapt themselves according to their environment during protection [64]. However, the biocontrol mechanism of this biofilm formation by the bacteria is not fully understood. The biocontrol of *F. oxysporum* through the bacteria *B. amyloliquefaciens* strain W19 with OF (organic fertilizer) reduced the effect of the target fungal pathogen and formed a thick biofilm formation on the soil against the pathogen. The biofilm is formed by lipopeptide. On the fruit surface, the formation of bacteria micro-colonies also competed for food and space. The species of the genus *Bacillus* as compared to other genera (*Micrococcus*, *Brevibacillus*, *Pseudomonas*, and *Curtobacterium*) had more antifungal antagonistic potential on grapes fruit surfaces against the fungal pathogens *B. cinerea, P. expansum*, and *A. uvarum* [37]. Surfactin, an antifungal compound, produced by *Pseudomonas* and *Bacillus*, also formed biofilm against many fungal and other pathogenic microbes on the fruits and soil surfaces [65]. Under controlled conditions, *B. velezensis* (QST713) triggered the surfactin and fengycin related genes (surFF and fenA) to control the fungal pathogen [66].

4.5 Induced Systemic Resistance

Induction of host plant resistance can also be generated by antagonistic bacterial species against FPP through activating the different chemical and biochemical reactions (such as a change in protein profiling structure, change in tissue structure, and change in PR genes) inside the host plant [67]. Induce systemic resistance (ISR) produced by biocontrol bacteria activate the immune systems of the host plant that were triggered through the production of ROS (Reactive Oxygen Species) and by closing the stomata [68]. An experiment conducted to control the black rot disease of grapes, caused by *Aspergillus* spp. through an ISR in grapes fruit [69]. The application of *B. subtilis* OTPB1 induced systemic resistance against *A. solani* and *P. infactent* in tomato plants. Production of IAA and gibberellic acid by biocontrol bacteria promoted root and shoot growth of tomato plants, and at the same time controlled the associated pathogens [70]. *Bacillus* species produced ISR in cotton plants against charcoal root pathogens. The application of two *Bacillus* species, *B. subtilis* IAGS174 and *B. megatherium*, combined with Benzothiadiazide activated defense biochemical reactions related to enzymes and phenolic compounds production [71]. Endophyte bacteria *Bacillus*, *Stenotrophomonas*, and *Lysinibacillus* determined ISR in tomato plants against collar rot diseases caused by *Sclerotium rolfsii*. These bacterial species protected the plant cell wall by providing strengthening through lignification, lipid peroxidation, and suberization [72].

4.6 Antibiosis

Antimicrobial metabolites of bacterial species, also known as secondary metabolites, are low molecular weight and have been proved lethal against other plant pathogenic microbes [73]. Three main antibiotics, iturin, trichothecene and pyyrrolnitrin have been emitted by the bacteria *B. subtilis*, *Myrothecium roridum*, and *Pseudomonas cepacia*, respectively, to control fungal diseases [74]. Antibiotics proved to be effective at low concentrations associated with the chemical groups alcohols, esters, aldehydes, terpenes, ketones, sulfur compounds, and lactones. Due to their volatile ability in the environment, they travelled unrestricted distances in solid and in liquid media as well as gas complexes, having a great advantageous effect as BCA. Currently, researchers are paying attention to produce commercial products related to volatile metabolism. Bio fumigation of fruits was possible via microorganisms able to emit VOCs in a locked and protected chamber that was verified as an alternative good source to control some important phytopathogens [75]. The genus *Bacillus* as BCA, produced some secondary metabolites against some major fungal pathogens [76]. The two species that secrete volatile compounds are suggested to be good BCA, which includes *Brevibacillus breves, that* emits fengycin and iturin A, and *B. subtilis*, that emits gramicidin. Both bacterial species were suggested to be good BCA which prevented the growth of FPPs [77]. Some antifungal activities of bacteria have been documented in Table 2.

Table 2: Recent antifungal activities of bacteria and their mode of action

Mechanism	Bacteria (strain)	Target pathogen	Disease	Host crop	References
Parasitism, Biofilm formation	*B. cereus*	*A. solani*	Early blight	Tomato	[78]
Antibiotics, Siderophore	*Bacillus* and *Pseudomonas* spp.	*S. rolfsii*	southern blight	*Dendrobium officinale* medicinal plant	[79]
Siderophore	*Bacillus* and *Pseudomonas* spp.	*C. falcatum*	Red rot	Sugarcane	[80]
Antibiotic	*B. velezensis*	*B. cinerea*	Grey mold	Grapes	[81]
Competition, parasitism	*Streptomyces albidoflavus (*OsiLf-2)	*Magnaporthe oryzae*	Rice blast	Rice	[82]
Induce systemic resistance	*Mesorhizobium* spp.	*F. oxysporum*	*Fusarium wilt*	Chickpea	[83]
Induce systemic resistance	*A. xylosoxidans* *B. subtilis* *L. fusiformis*	*A. solani*	Early blight	Tomato	[84]

5 Success Stories of Bacterial Bio-Products against FPPs

To date, numbers of bio commercial products, prepared from antagonistic bacteria, are available in the market to protect the economically important crops from plant pathogenic fungi [85]. Commercially available bio-products can be applied in the field pre-harvest and post-harvest. During soil application of these bacterial commercial products, a few disadvantages have been noticed such as not all the products are suitable for all types of soils. Soil pH and moisture also affect the product solubility whereas, clay contents retard the adherences of products. Other bacteria, already present in the soil, were a hindrance to the progression of the biocontrol agent. Soil application of these biocontrol agents enhanced the competition between fungal and bacterial pathogens. Antagonistic bacteria utilized more the nutrients, minerals, competed for carbon sources, and colonized efficiently around the roots side which gave protection against pathogenic microbes [86]. Pre-harvest application of biocontrol agents in the phyllospheric part of plants also reduced the fungal infection by suppressing them. Premature fruit application of bacterial biocontrol agents restricted the many fungal pathogens such as *Botrytis*, *Penicillium*, *Colletotrichum*, *Aspergillus*, and *Fusarium* species [87]. An experiment was conducted to control the two pathogenic fungi *P. italicum* and *P. digitatum* by application of a commercial pre-harvest bacterial product [45]. The pre-harvest application successfully suppressed the growth of fungal pathogens as compared to the control. The pre-harvest application of bacterial products also reduced the fungal infections in mango, banana, and citrus fruits [88]. Different bacterial bio-products were suitable to control the post-harvest fungal pathogens and are commercially available in the market to date. The application of these products as single or combined with other products produced effective results in controlling the postharvest fungal pathogens [89]. Bacterial species belonging to the genera *Pseudomonas*, *Bacillus*, *Enterobacter*, and *Burkholderia* are being used to prepare commercial bio-products. The commercial products had broad-spectrum mechanisms to control the targeted pathogens by producing different volatile metabolites, production of antifungal enzymes and by activating systemic resistance in host plants [35,90]. Commercial biocontrol agents such as *B. thuringiensis*, *Pantoea agglomerans*, *Serratia plymuthica, B. subtilis*, and *Enterobacter cloacae* have already expressed their antifungal activities against different post-harvest fungal pathogens. Some of the commercially available bio-products have been tabulated as success stories in Table 3.

Table 3: Commercial antifungal bio-products of bacteria [91]

Product (country)	Company	Bacteria (strain)	Target pathogen	Host crop
Companion® (USA)	Growth Products, NY	*B. subtilis* (GB03)	*Fusarium, Pythium*, and *Rhizocotonia* spp.	Peas, barley and wheat
Intercept TM (USA)	STC & Fairfield, IA	*Pseudomonas cepacia*	*Fusarium, Pythium*, and *Rhizocotonia* spp.	Maiz, cotton and vegetable
AtEze® (USA)	ESS Inc., CA	*P. chlororaphis*	*Pythium* and *Rhizocotonia* spp.	Vegetable crops
Bio-Save® (USA)	Eco Science Corp. FL	*Psudomonas syringae* (ESC-100)	*Botrytis, Pencillium*, and *Geotrichum* species	Citrus and pome fruit
Deny® (USA)	SMP, Shwanee, KS	*Burkholderia cepacia*	*Fusarium, Pythium*, and *Rhizocotonia* spp.	Cotton, Peas, Sorghum, Wheat and bean
Subtilex® (USA)	BU & Ames, IA	*Bacillus subtilis (*MB 1600)	*Fusarium, Pythium*, and *Rhizocotonia* spp.	Vegetables crops
Mycostop® (Finland)	KA & Oy	*S. griseoverdis*	*A. brassicicola*	Crucifers
Biocoat® (Netherland)	S&G seed	*P. flourescens* (WCS374r)	*Fusarium oxysporium*	Cotton, tomato, pepper
Epic® Kodaik (USA)	Gustafasn, TX	*B. subtilis*	*Alternaria, Fusarium, Pythium*, and *Rhizocotonia* spp.	Legumes and Cotton crops

6 Role of Plant Growth Promoting Rhizobacteria (PGPR)

A huge diversity of soil-borne microorganisms associated with plant roots provide nutrients to plants, while in response to the nutrient supply, plants reversely provide shelter for the survival of these microbes [92]. This mutualistic mechanism is supported by both of these species; without this mechanism the survival of both species would not be possible [93]. Finally, the bacterial species, present in the rhizosphere and associated with roots of different crops, provide nutrients to the plants by colonization around the roots and the root surface, converting N_2 into Ammonia (NH_3), and then to nitrite (NO_2^-) and nitrate (NO_3^-). These beneficial bacteria secrete some hormones that promote plant growth, and also act as biocontrol agents against plant pathogenic microbes [94]. The rhizospheric beneficial bacteria have been categorized into two groups 1) PGPRs and, 2) Endophyte bacteria. PGPR species belong to multiple genera such as *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Azospirilum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, and *Erwinia* which exist in the rhizospheric soil, and they perform multiple functions to promote plant growth [95]. The role of PGPR is shown in Fig. 2. In this figure, the PGPRs were categorized on functional bases such as (a) Biofertilizers (enhance the availability of nutrients in the soil) (b) Biopesticides (secretion of specific lytic enzymes to control plant pathogens) (c) Phytostimulators (produce phytohormones to enhance plant growth) and, (d) Rhizomediators (balanced the accessible pollutants with metal solubilizations). The members of Endophytic bacteria belong to the genera *Allorrhizobium*, *Azorhizobium*, *Bradyrhizobiom*, *Mesorhizobium*, and *Rhizobium* [96]. The mechanism of plant growth-promoting by PGPRs is still unknown; however, the researchers continue their efforts since the last 30 years to identify the mechanisms.

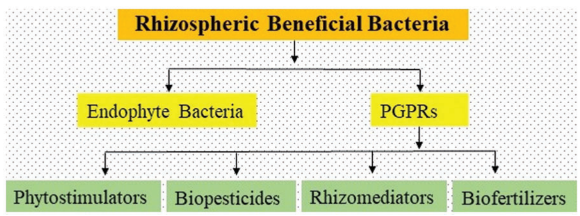

Figure 2: Role of plant growth promoting bacteria and their antifungal activities

6.1 Nitrogen Fixation by PGPRs

Two types of bacteria have been reported to convert atmospheric nitrogen into nitrite and nitrate, and then the plant species utilize the atmospheric nitrogen. The first types of bacteria were interlinked with plant roots symbiotically with the resulting formation of nodules [97]. The second type of bacteria were free-living bacteria. These free-living bacteria fully participated in NF (nitrogen fixation), e.g., *Azotobacter*, *Paenibacillus*, *Bacillus*, *Azospirilum*, *Burkholderia*, and *Herbaspirillum*. The free-living bacteria converted 20–30 kg/ha of nitrogen per year [98]. Mixed application of the NF bacteria *A. brasilense, Sinorhizobium americanum*, and *Rhizobium phaseoli* in maize crop increased crop yield with increases in root and shoot lengths [99]. *Cedecea davisae* RS3 as a PGRP also increased crop yield of chickpea by nitrogen fixation and with production of IAA [100].

6.2 Solubilization of Phosphorus (P)

Phosphorus (P) has a vital role in the development of living cells and plant tissues [101]. The plant takes up P in the forms of mono-phosphate and dibasic phosphate [102]. The beneficial bacterial species (PGPR) produced some specific enzymes (phytase and phosphatase), which are used in the solubilization of P into the phosphate form; this process is also known as mineralization [103]. PGPRs synthesize and release some specific acids that act like chelators to control Ca cations; these cations have the ability to convert soluble phosphate into an insoluble form. Therefore, it is concluded that the PGPRs are recognized as good and primary mediators of phosphate solubilization [104].

6.3 Phytohormone Production

The phytohormones (auxins, cytokinins, gibberellins, abscisic acid, and ethylene) produced by PGPRs have a chief role in the development of important agricultural crops. These phytohormones are used by the plant for the development of body parts such as excessive cell division and cell enlargement, and extension of roots and shoots [105,106]. During the production of these types of hormones, the PGPRs develop a symbiotic association with plant roots. The phytohormones, auxin, synthesize the IAA that promote root and plant growth by improving the branch size, number, and weight. For the production of IAA, the PGPRs utilize the L-tryptophan from plant roots. However, the proper mechanism of IAA production by this process is still unknown. The gibberellic acid produced by the bacterial species *A. diazotrophicus, Rhizobium meliloti, Herbaspirillum seropedicae, Bacillus* spp., and *Azospirilum* spp. is used for the development of flowering, seed germination, fruit set, and stem elongation. Cytokinins are synthesized by important bacterial species such as *Pseudomonas*, *Bacillus*, *Azospirilum*, *Xanthomonas*, *Klebsiella*, and *Proteus* [95].

6.4 Role of ACC (1-aminocyclopropane-1-carboxylic acid) Activity of Bacteria

The PGPRs play an important role to compensate for this situation by their ACC deaminase production ability [95]. The bacteria synthesize an enzyme (ACC synthetase) and this enzyme convert the S-adenosylmethionine (SAM) to 1-aminocyclopropane-1-carboxylic acid (ACC), resulting in the production of indole acetic acid which is helpful for plant development [107]. This ACC deaminase is also used for the conversion of nitrogen into ammonia in the rhizospheric soil of the plant. The ACC deaminase antifungal activity of rhizospheric bacteria was used to control the fungal pathogen *Fusarium culmorum, the* causal agent of the seedling blight of wheat [108]. The ACC activity of *P. fluorescence* promoted the excessive modulation in an alpha crop [109].

6.5 Minimize the Rhizospheric Metal Contamination

Excessive application of synthetic chemicals/fertilizers in soil has a bad impact on both soil and plant health [110]. The beneficial microorganisms available in the rhizosphere become weaker and are suppressed due to more applications of trace metals like cobalt, magnesium, zinc, iron, chromium, selenium, and copper [111]. The PGPRs not only improve plant health, but also maintain the toxicity effects of metals [112]. The biofertilizer of the bacteria *Paenibacillus* sp. reduced the effect of cadmium in cotton plants by improving plant health through an increase in height, weight, chlorophyll contents, and root length [113]. The biofertilizer application of *E. aerogenes* reduced the cadmium contamination in rice plants and increased root and shoot lengths with more chlorophyll production [114].

6.6 Production of Volatile Metabolites or Volatile Organic Compounds

The volatile organic compounds (VOC) emitted by the PGRPs, are used to control phytopathogens and at the same time, these bacteria promote plant growth by ISR [115]. The bacterial species belong to different genera producing VOCs like acetoin and 2, 3-Butanediol, produced by members of the genus *Bacillus* [116]. The species of the genus *Bacillus*, *Stenotrophomonas*, *Pseudomonas*, *Serratia*, and *Arthrobacter* mostly suppressed the growth of FPPs by producing antifungal VOCs. These VOCs produce resistance in the host plant against a variety of pathogenic microbes and abiotic stresses by the activation of both ISR and SAR [117]. A number of PGPRs are soil borne bacterial species and they synthesize and emit VOCs in the soil such as tetradecane, dodecane, cyclohexane, benzene, 1-(N-phenylcarbamyl)-2-morpholinocyclohexene, methyl, dotriacontane, decane, 2-(benzyloxy) ethanamine, benzene(1-methylnonadecyl), 11-decyldocosane, 2,6,10-trimethyl, and 1-chlorooctadecane [118,119]. The different PGPRs and their roles in plant growth are presented in Table 4.

Table 4: Examples of PGPRs and their role in plant development

Bacteria (strain)	Host plant	Function	References
B. subtilis (Q3) *Paenibacillus* (Q6)	Cotton	Phosphorus solubilization and promotion of plant growth	[120]
A. poferum *B. megaterium* *R. radiobacter*	Black soybean	P. solubilization and promotion of plant growth with reducing crop maturity	[121]
B. amyloliquefaciens *M. extorquens*	Maize	Nitrogen fixation	[99]
Rhizobium spp. (R1, R2, R3 and R4)	Soybean	P. solubilization Siderophore production IAA production	[122]
A. brasilense	Wheat	Nitrogen fixation Promotion of plant growth	[123]
B. amyloliquefaciens (Bk7) *Alc. faecalis* (P1)	Rice	Antifungal activity Promotion of plant growth	[124]
Bacillus spp. *Pseudomonas putida*	Tomato	Antifungal activity Promotion of plant growth	[125]
B. subtilis *P. aeruginosa* *S. aureus*	Tomato	Antifungal activity	[126]
B. circulans	Mung bean	P. solubilization	[127]
B. subtilis	Barley	Antifungal activity	[128]
Paenibacillus polymyxa	Sesame	Antifungal activity	[129]
S. thermocarboxydus (BPSAC147)	Tomato	Growth potential Increase photosynthetic and antifungal activities	[130]

7 Conclusion and Future Prospective

By using bacteria as an effective biocontrol agent we can improve our soil fertility, plant health and crop production. These multitalented biocontrol agents improved seed health by coating it before sowing, and afterwards the soil was made more beneficial for cropping. A few previous studies reported by many researchers showed that the mixing of biocontrol agents with artificially prepared pesticides improved plant health and stimulated many genes in host plants against infectious plant pathogens. The application of biocontrol agents is cost-effective and ecofriendly. We should need to understand the biochemistry of biopesticides and increase them by better ways. Bacterial biopesticide chemistry is still not fully understood and explains the need of future research.

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