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REVIEW

Biocontrol of soil borne diseases by plant growth promoting rhizobacteria

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Abstract

Biological control has received increasing interest in recent decades as one of the alternatives to chemical pesticides in the field of plant disease control, especially after the increased awareness of the dangers of pesticides to the environment in general and human health in particular, and the emergence of resistance to pesticides in some causes. Biological control is defined as any conditions or procedures in which a particular organism or substances produced from a living organism are used to reduce infection with a particular pathogen. Plant growth promoting rhizobacteria (PGPR) are able to stimulate growth and resistance against plant diseases when they are able to have a positive effect on the plant health, and then demonstrate good competitive qualities and capabilities over existing rhizosphere communities. PGPR affects plant growth improvement by fixing atmospheric nitrogen, siderophore production dissolving insoluble phosphates, and releasing hormones. In this review, we tried to focus on the potential effects of PGPR as an effective and safe technique for plant disease resistance. PGPR play a major role in plant disease resistance through induced systemic resistance (ISR), antibiotics, hydrogen cyanide, Lytic enzyme, degradation of toxins, competition for nutrients, and parasitism.

Keywords PGPR · Biocontrol · Mechanism of infection · Soil-borne diseases · Fungi · Induced systemic resistance

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Introduction

Plants throughout the world are infected by approximately 80,000 diseases, and the majority of them are described as soil-borne diseases. These diseases lead to the destruction of crops, which is considered a huge reason for world starvation, as recorded in 2015, by the hunger statistic of World Food Program (WFP) that 815 million people in the world, on average, one in nine is suffering from starvation (Ghosh et al. 2019).

The definition of soil-borne plant pathogens according to Koike et al. (2003) include pathogens that infect the plant through the soil, while Katan (2017) reported soil-borne pathogens as those pathogens present during one part of their lives at least and that can survival in soil. The structure and severity of soil borne pathogens communities differ depending on cultivar types and the plant age, nutritional status, and external stresses (Al-Hazmi et al. 1993; Ferreira et al. 2008; Krechel et al. 2002; Manici and Caputo 2009). Soil-borne pathogens have harmful effects on crops in a number of ways (Jambhulkar et al. 2015). The serious troubles caused by soil borne pathogens in crop production worldwide include sharp

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reduction in crops and drop in total yield, which leads to higher costs of product (Panth et al. 2020).

Soil is a fertile reservoir of microorganisms responsible for its main functions in universal ecosystems. The biodiversity of vegetation is directly influenced by the interaction between soil microorganisms and plants (Aislabie et al. 2013). Reynolds et al. (2003) recorded that plant–soil borne microorganisms interactions were defined as drivers of plant system composition and dynamics. Matei et al. 2017 and Weller et al. 2002 reported that soil borne microorganisms are involved in soil forming processes, making a major contribution to mess decomposition and humus formation, and the capacity of soil to control the development of plant pathogens.

Walker et al. (2003) defined rhizosphere as a zone of soil around the plant root which is directly affected by the secretions of the plant root system. Microorganisms isolated from rhizosphere of healthy pepper plants are effective not only against the pepper root rot pathogens but also have activity as biofertilizer agents (El-feky et al. 2019).

Biological control is not affective against some soil borne pathogens such as root-lesion nematodes because they frequently live within plant roots (Stirling 2014). Application of biological control against nematodes is limited, although this has been applied against potato nematodes (Palomares-Rius et al. 2014; Stirling 2014). Therefore, this review focused on factors affecting soil borne diseases, the role of PGPR in disease management and control of fungal, bacterial, viral, and nematode soil borne diseases by PGPR.

Factors affecting soil-borne diseases

Effects of abiotic factors on soil-borne diseases

Disease results from the interaction between the pathogen plant, but its severity development is affected by soil abiotic factors such as soil texture, pH, organic matter content, temperature and moisture content, and biotic components affecting the host and/or the pathogen (Alabouvette et al. 1996) including the following.

Soil temperature, moisture, texture, pH, and organic matter

Soil temperature has a major importance in pathogen growth rate, which directly affects the disease development and severity (Bouchek-Mechiche et al. 2000; Singh et al. 2005).

Soil moisture content influences disease severity as well as the opening of the lenticels, which are considered entry points for tuber infection in potato. Moisture content is increased due to heavy soils, poor irrigation drainage, and abundant rainfalls (Helias 2008).

Most fungal soil borne diseases are activated in light sandy soils, but generally clay soils are suitable for bacterial activity (Alabouvette et al. 1996; Marshall 1975). Growth of rhizoctonia is restricted at high matric potentials but spreads as a positive correlation porosity with larger pores (Harris et al. 2003). Extreme pH soils are often highly repressive to many plant pathogens and disease development (Höper and Alabouvette 1996). Plant diseases appearance and severity are affected by the quantity and quality of the organic matter in soil (Alabouvette et al. 1996).

Effects of biotic factors on the development of soil borne diseases

Inoculum sources, dissemination, survival, and density

At favorable conditions such as moisture, temperature, and soil type, bacteria can survive over winter in soil (Loria et al. 2008). Nematodes can survive and persist in soil in eggs surrounded by cysts or as juveniles in host roots (*Meloidogyne* spp.) (Wharton and Worland 2001). In the absence of resistant structures and of efficient saprophytic abilities, some pathogens need alternative hosts to survive in the absence of a main host, these frequently act as a reservoir of the pathogen (Tomlinson et al. 2005).

Finally, spores or mycelium of fungi are transported by water (rain, irrigation, and flow in soil), by soil adhering to farm equipment, or by contaminated seed (Bae et al. 2007). Moreover, some pathogens liberate mobile dissemination forms that are responsible for short distance dissemination of these pathogens (Merz and Falloon 2009).

As some diseases develop, their severity increases with increasing of inoculum density, such as black scurf (Papp et al. 2021); contrary to some diseases that decrease as increasing inoculum density, such as silver scurf (Tsror and Peretz-Alon 2005).

Cultural practices

Crop rotation

Crop rotation is a very important tactic for controlling some soil borne diseases, but it cannot control other pathogens that able to survive a long time in soil such as saprophyte or as a dormant structure in soil such as Globodera. At the same time, the application of crop rotation to avoid the main and alternative hosts is a very important agent to control soil borne pathogens (Merz and Falloon 2009; Peters et al. 2004; Samaliev et al. 1998).

Fertilization and amendments, and tillage management

Organic fertilizers, especially compost, are effective as disease suppression (Raviv 2005). Superficial tillage or no tillage resulted to disease suppression (Peters et al. 2004).

Organic farming versus conventional agriculture, and mechanisms of infection

Disease incidence severity depended mainly on the soil type (Messiha et al. 2007). Generally, organic farming is more efficient than conventional agriculture to control soil-borne diseases in the long-term (Khalil et al. 2015; van Bniggen and Termorskuizen 2003).

Cellulose is the primary barrier against biotic and abiotic stress in most plants (Locke 2002). Soil borne pathogens have different mechanisms to attack the host plant and destroy its natural walls through introduction into the roots, young buds, underground stems, stolons, tubers, or through wounds (Stevenson et al. 2001; Taylor et al. 2004), whereas other pathogens such as bacteria and fungi can be introduced by degradation of the host's cells barrier directly by mechanical and/or enzymatic degradation such as cellulases, pectinases, xylanases, and proteases, or by natural openings (stomata, lenticels, eyes) (Olivieri et al. 2004).

Finally, ecto-parasites nematodes can infect plants without penetrating the root of the host plant. On the other hand, the Endo-parasites nematodes causes diseases only when they penetrate underground parts of the host plant (Mugniéry 2007; Stevenson et al. 2001).

Control of soil borne diseases

Soil-borne pathogens are difficult to survey because soil is a complex system in which different interactions take place, especially in a short time. The importance of studying these diseases in the long term is due to the highly spread of these disease worldwide (Fiers et al. 2012).

Although chemical control is easy, quick, and highly effective, it can have harmful effects on the environment, human health, aquatic ecosystems, and minimize beneficial soil microorganisms (Attia et al. 2022). The application of biocontrol is an alternative to suppress soil borne plant pathogens through different mechanisms such as parasitism, antagonistic, competition, and induction of resistance in host plants against pathogens (Shafique et al. 2016).

PGPRs have thepotential to promote plant growth through two pathways. First, by direct promotion of plant growth by nitrogen fixation, phosphate solubilization, potassium solubilization, phytohormone production (IAA, cytokinin, ethylene and gibberellins), and production of ACC deaminase. Second, by indirect promotion of plant growth by induced systemic resistance, production of siderophore, antibiotics, exopolysaccharides, volatile oils, lytic, and protective enzymes (Singh et al. 2019).

Two categories of PGPRs are extracellular plant growth promoting rhizobacteria (ePGPR) and intracellular plant growth promoting rhizobacteria (iPGPR). (ePGPR) may exist in the rhizosphere, on the rhizoplane, or in the spaces between the cells of the root cortex but (iPGPR) present generally inside the nodules of root host cells (Martínez-Viveros et al. 2010).

PGPR showed broad-spectrum biocontrol activity against plant diseases (Liu et al. 2017). Also, Khabbaz et al. (2019) recorded mixtures of compatible PGPR strains were effective and sustained control of a broad range of pests and diseases. Shafi et al. (2017) confirmed that *Bacillus* spp. (*B. subtilis, B. amyloliquefaciens, B. firmus* and *B. pumilus* can suppressed plant pathogens such as *Fusarium* spp., *Pythium* spp., *Aspergillus flavus*, and *Rhizoctonia solani* through competition, direct antibiosis, and induced resistance of hosts.

Also, Pertot et al. (2015) determined the potency of *Coniothyrium minitans* to inhibit *Sclerotinia sclerotiorum* and *S. trifoliorum* by production of chitinase and 1,3 glucanase, and *Gliocladium catenulatum* can inhibit the following pathogens species of *Rhizoctonia*, *Pythium, Phytophthora, Fusarium, Didymella, Botrytis, Verticillium, Alternaria, Cladosporium, Helminthosporium, Penicillium,* and *Plicaria* through toxins production.

Mycoparasitism by *Streptomyces* occurred against species of *Fusarium*, *Rhizoctonia*, *Phytophthora*, *Pythium*, *Phytomatotricum*, *Aphanomyces*, *Monosprascus*, *Armillaria*, *Sclerotinia*, *Verticillium* and *Geotrichum*. Likewise, Pertot et al. (2015) proved the inhibition capacity of *Pseudomonas* spp. against *Pythium* spp. and *Rhizoctonia solani* by production of antibiotics, siderophores, and volatiles. Also, application of *Trichoderma* sp., *Bacillus* and *Pseudomonas* have been found to be effective against root rot caused by soil borne pathogens in many crops (Shafique et al. 2016). Also, resent studies reported that plant growth promoting fungi have great ability to control Fusarium wilt disease through biochemical defense (Abd Alhakim et al. 2022; Attia et al. 2022). Finally PGPRs such as *Pseudomonas fluorescens* are very important agent against phyto-nematodes through systemic resistance induction of the host, it reduces the destructive effect resulting from these pathogens, which may include damage to up to 80% of vegetable crops, such as tomatoes (Timper et al. 2009).

Role of PGPR in disease management; detailed mechanisms

Direct mechanisms (Fig. 1)

Antibiotics production

Antibiotics production is considered one of the most effective bio-products used in bio-control of phyto-pathogens. Antibiotics are organic compounds with low molecular

weight produced by microorganisms at low concentrations to kill other pathogenic microorganisms (Saravanakumar et al. 2019).

Many antibiotics produced by various species of *Pseudomonas* such as 2, 4 diacetylphloroglucinol (DAPG), pyoluteorin, phenazine-1-carboxamide, phenazine-1-carboxylic acid, oomycin, and pyrrolnitrin exhibit antiviral, antibacterial, and antifungal properties. Moreover, *Bacillus* species produce antibiotic lipopeptides such as iturin, bacillomycin, bacilysin, surfactin, zwittermicin, and fengycin (Khabbaz et al. 2015).

Antibiotics have been shown to be particularly effective against the target pathogen *in vitro* and/or *in situ* conditions. Some strains are known to produce more than one antibiotic that can suppress/kill one or more pathogens such as *B. cereus* UW85, which produces both zwittermicin and kanosamine (Milner et al. 1996). Moreover, both phenazine and DAPG as antibiotics are produced by genetically modified *P. putida* WCS358 to decrease disease development in field-grown wheat (Glandorf et al. 2001).

Hydrogen cyanide (HCN) production

HCN is considered one of the most important compounds that can be used for suppressing phyto-pathogens. HCN is a volatile compound that could inhibits the microbial growth (Siddiqui and Shaukat 2003). Stable complexes are formed when cyanide binds with the essential elements (Cu^{2+}, Fe^{2+}, and Mn^{2+}); therefore, cyanide is considered a toxic material to most microorganisms. Most rhizobacteria have the ability to produce HCN such as *Bacillus, Pseudomonas, and Rhizobium* (Admassie et al. 2020). Rhizobacteria have HCN synthase enzyme in plasma membrane to form HCN from glycine (Blumer and Haas 2000). The mechanism of action of the toxic effect of HCN is attributed to the ability to inhibit cytochrome oxidase and electron transport, which leads to interrupting the supply of energy to the cells (Jagadeesh and Kulkarni 2003).

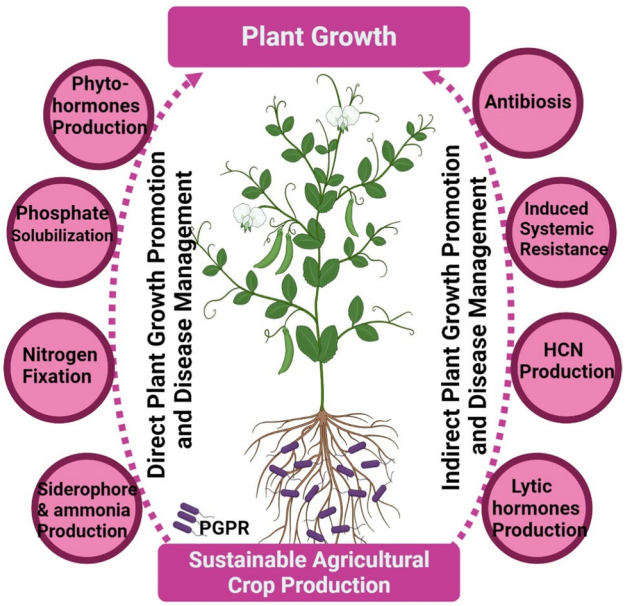

Fig. 1 Mechanism of PGPR action against plant diseases and plant growth promotion

Lytic enzyme production

PGPR are the major producers of lytic enzymes. Cell wall degrading enzymes (CWDEs) were produced at the site of the pathogen leading to openings in the cell wall and subsequent disorganization of cytoplasm of the pathogen (Jeffries 1995; Köhl et al. 2019). There are many enzymes responsible for degrading the cell wall such as chitinases, b-1,3-glucanases, and proteases (Jeffries 1995). These lytic enzymes are inducible where their production is triggered by signals after recognition of the host. Transcriptional reprogramming occurs and molecular weapons involved in prey attack and lysis, including certain CWDEs, are expressed. Lectins at the surface of the prey cell wall, surface properties, and secondary metabolites play important roles in the recognition and signaling pathways such as MAPK cascades, cAMP pathway, and G-protein signaling (Karlsson et al. 2017).

Degradation of toxins

Detoxification of pathogen toxins is an important mechanism for biological control. Many PGPR have the ability to hydrolyze toxins, such as *B. cepacia* and*dR. solanacearum,* for example, fusaric acid, which is produced by the *Fusarium species,* could be hydrolyzed (Toyoda and Utsumi 1991). Nagarajkumar et al. (2005) reported the *P. fluorescens* strain PfMDU2 could detoxify oxalic acid by *P. fluorescens* strain PfMDU2 in the biological control of sheath blight of rice caused by *R. solani*. Moreover, 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 (Fig. 1)

Siderophore production

Siderophores are low molecular weight metabolites with a high affinity for Fe^{3+}. When PGPRs recognize Fe^{3+} through a specific siderophore receptor protein, siderophores could chelate Fe^{3+} from the environment and transport the iron into microbial cells (Wilson et al. 2016).

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 called siderophore-mediated suppression of plant pathogens, where PGPR can be selected for biological control through competition for iron with pathogens that produce lesser amounts of siderophores with lower affinity for iron (Khabbaz et al. 2015; Lugtenberg and Kamilova 2009).

This mechanism has been investigated in particular for isolates of *Pseudomonas* spp., where pathogen populations in rhizospheres are reduced due to the presence of siderophores, which leads to a decrease of iron around the pathogen (Raaijmakers and Mazzola 2012; Wilson et al. 2016).

As a cell component, iron deficiency results in growth inhibition, decreased DNA and RNA 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 (Leong 1986).

Induced systemic resistance (ISR)

Application of PGPR was shown to trigger a plant-mediated resistance in the vegetative part above ground (Wei et al. 1991) in many plant species, including potato, tomato, bean, tobacco, radish, and cucumber (Van Loon et al. 1998). Phenotypically PGPR-mediated ISR resembles pathogen resistance enhancement in which non-infected parts of a previously infected plant can overcome the next infection, referred to as systemic acquired resistance (SAR) (Ross 1961).

The main difference between ISR and SAR are first ISR is promoted by nonpathogenic PGPR, while SAR is enhanced systemically after inoculation with pathogens. Second, ISRs include lipopolysaccharides and salicylic acid (SA). Whereas some of the rhizobacteria have activate resistance through the SA-dependent SAR mechanisms, but others mechanisms require jasmonic acid and ethylene perception. SAR is accompanied by the induction of pathogenesis related proteins (PR) (Van Loon et al. 1998).

ISR presented many different changes as follows: (1) encouragement of epidermal and cell walls and deposition of newly formed barriers beyond infection sites, including lignin, callose, and phenolics; (2) enhancement enzyme activity such as polyphenol oxidase, peroxidase, chitinase, and phenylalanine ammonia lyase; (3) promote phytoalexin production; and (4) improve expression of stress-related genes (Timmusk and Wagner 1999). However, these changes may be present singly or in combination (Steijl et al. 1999). Protection from diseases by biocontrol and its consistency in the field are generally not sufficient to compete with conventional methods of disease control. Moreover, the combination of ISR and SAR that results in an improve protection against specific bacterial pathogens (van Wees et al. 2000) offers great potential to integrate both forms of induced resistance in agricultural practices.

Root colonization

Rhizosphere colonization is important not only as the first step in pathogenesis of soil borne microorganisms but also is crucial in the application of microorganisms for beneficial purposes (Lugtenberg et al. 2001). PGPR generally improves plant growth by colonizing the root system and pre-empting the establishment of or suppressing deleterious rhizosphere microorganisms (Schroth and Hancock 1982).

PGPR must be able to compete with the indigenous microorganisms and efficiently colonize the rhizosphere of the plants to be protected. Colonization is widely believed to be essential for biocontrol (Parke 1991; Weller and Cook 1983), and a biocontrol agent should grow and colonize the root surface. Colonization or even initial population size of the biocontrol agent has been significantly correlated with disease suppression (Parke 1991). Cell surface characteristics influence the attachment of bacteria to roots, which may be necessary for colonization. Certain mutants that affect accumulation of secondary metabolites also influence colonization of roots in the field (Mazzola et al. 1992).

Analysis of mutants indicates that prototrophy for amino acids and vitamin B1, rapid growth rate, utilization of organic acids and lipopolysaccharide properties contribute to colonization (Lugtenberg et al. 2001). A variety of bacterial traits and specific genes contribute to colonization but only few have been identified (Benizri et al. 2001; Lugtenberg et al. 2001).

These include motility, chemotaxis to seed and use specific components of root exudates, production of pili or fimbriae, production of specific cell surface components, ability of protein secretion, and quorum sensing (Lugtenberg et al. 2001). Competition of introduced bacteria with indigenous microorganisms already present in the soil and rhizosphere of the developing plant is another important aspect for root colonization.

Formulation

PGPRs make up the largest amount of the bio-pesticide market, predicted to attain USD 1.67 billion by 2022 (Arthurs and Dara 2019). Although PGPRs are very effective as control agent against broad spectrum of many plant diseases *in vitro*, they have very low commercial availability as *in vivo* application due to the difficulties in handling, and care is important at all steps from production till end use not only to maintain the microbial activity after loading but also to improving efficacy (Shaikh and Sayyed 2015).

Good commercial formulate, as shown in Fig. 2, are mainly characterized by long shelf life. It should not be harmful to plants, it should be well dissolved in water, should release the bacteria after dissolving in water, low cost, more effective than agrochemicals and the carriers must be cheap, live in and tolerate adverse condition, and readily available for formulation development (Nakkeeran et al. 2006; Shaikh and Sayyed 2015).

The first step for establishment of effective formulation is the production of a PGPR strain in huge amounts. This needs the selection of a proper, cheap, and easily available medium. Mass production is achieved through liquid, semisolid, and solid state fermentation techniques (Shaikh and Sayyed 2015).

Types of formulations

There are two forms, dry powder (solid) and liquid suspensions. In dry powder (solid) carrier used may be talc, peat, lignite, vermiculate, kaolinite (Gupta 2005). The powder is normally spray-dried or lyophilized biomass with practically no free moisture for the growth of bacteria but this method can be used for spore forming microbes by freeze-drying or air-drying. In moist powder, culture organisms that do not form a mat of biomass can easily be formulated into a moist powder, and granular formulations usually contain metabolically active microbes for spraying, seed coating, or direct into the soil (Shaikh and Sayyed 2015).

Liquid formulation carrier based allows adding a sufficient amount of nutrients, cell protectants, and inducers responsible for cell/spore/cyst formulation, thus ensuring a longer shelf life than dry powder (Brar et al. 2012).

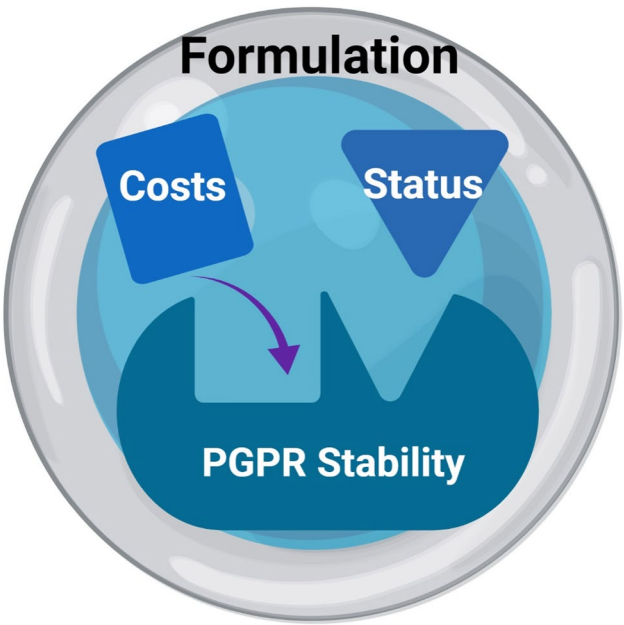

Fig. 2 Factors affecting PGBR formulation

Control of fungal soil-borne diseases by PGPR

Fungal pathogens cause serious damage diseases on many vital crops. The host-ranges of fungi widely differ, more than any other plant pathogens. Some of them are narrowly specialized to closely related plants, whereas other pathogens are have a broad spectrum of plant hosts, for example, oomycetes attack five crops – potato, maize, rice, wheat, and soybean (Newman and Derbyshire 2020).

More than 19,000 fungal pathogens can infect and may partially or completely destroy crops worldwide and may remain dormant until favorable conditions, and they are easily dispersed by different mechanisms such as insects, wind, water, and soil (Jain et al. 2019). Fungal pathogens are the main destructive and distributed plant pathogen, as they represent about 80% of crops diseases that cause serious crops and economic inhibition (Dayarathne et al. 2020).

Fungi are a more abundant soil borne pathogen than bacteria. There are an estimated 8,000 fungal species that cause diseases in plants (see Table 1). Most of them attack roots leading to completely or partially destroyed plants and crops by yellowing root rot, wilting, stunting, dieback, stem collar, and crown rot. Some common fungi include: *Rhizoctonia*, *Fusarium*, *Alternaria Pythium*, *Phytophthora*, *Cylindrocladium*, *Sclerotinia,* and *Sclerotium* (Abdelaziz et al. 2021; Ghosh et al. 2019; Hashem et al. 2021). *Rhizoctonia solani* is considered a major soil-borne plant pathogenic fungus that causes different diseases in solanaceous crops resulting in annual crop loss (20–40%) worldwide (Ghosh et al. 2017).

Islam et al. (2012) recorded the potency of *Bacillus* spp., *Pseudomonas* spp., *and Streptomyces* spp. as biological control agents. Application of PGPR have several possible mechanisms against fugal soil borne diseases, including the production of fungi toxic metabolites such as siderophores production, HCN, fungal cell wall degrading enzymes, competition for essential nutrients such as space, antagonism as deform the morphology of mycelium, suppressing the mycelia growth and break down fungal cell walls, plant growth promotion by plant growth regulators as IAA, auxins, cytokinins, riboflavin, and vitamins. Also, hormonal interactions and nutrient uptake and induction of the defense responses in plants via ethylene and JA-dependent pathways (see Table 1 and Fig. 3) (Gowtham et al. 2016).

Where the last mechanism is considered one of the most promising strategies for crop safeguard, in this strategy, there are no direct effects on the pathogen but the natural defenses system in plant is activated, which is called a systemic acquired resistance (Goel and Paul 2015; Walters and Fountaine 2009).

Table 1 Control of fungal plant pathogens by PGBR

Disease	Causative pathogen	Host	PGPR	Mechanism of action	References
Black scurf and stem canker	*Rhizoctonia solani*	Potato	*Bacillus* sp.	deform the morphology of mycelium	(Ben Khedher et al. 2015; Calvo et al. 2010)
Rhizoctonia wilt	*Rhizocto nia sp*	Tomato and potato	*Delftia lacustris Bacillus subtilis* and *Bacillus cereus*	suppressing the mycelia growth and released volatile inhibitory compounds	(Janahiraman et al. 2016; Montealegre et al. 2003)
Verticillium wilt	*Verticillium dahlia* and *Verticillium alboatrum*	Potato, pepper, and tomato	*Paenibacillus alvei* K165, *Pseudomonas* sp., and *Bacillus*	Root colonization, Enhancement of resistance,	(Angelopoulou et al. 2014, López-Escudero and Mercado-Blanco 2011, Sharma and Nowak 1998)
Early blight	*Alternaria solani*	Potato and tomato	*A.xylosoxidansB. subtilis* (B1) and *L. fusiformis* (L2)	ISR	(Attia et al. 2020; Chowdappa et al. 2013)
Phytophthora crown rot and Pink rot	*Phytophthora erythroseptica*	Potato	*Bacillus subtilis, Pseudomonas stutzeri, maltophilia Stenotrophomonas* and *B. amyloliquefaciens*	pathogen suppression by hormonal interactions and nutrient uptake or and enhancement of ISR	(Islam et al. 2012; Schnider-Keel et al. 2000)
Late blight	*Phytophthora infestans*	Potato, pepper, and tomato	*Bacillus megaterium, Pseudomonas, Rahnella, Serrati* and *Bacillus subtilis*	suppression of the disease and induces resistance production broad spectrum antifungal Antibiotics production -fungal cell-wall-degrading enzymes	(Daayf et al. 2003; Jung and Kim 2003; Lamsal et al. 2013; Larousse et al. 2017; Pieterse et al. 1998; Yan et al. 2002)
Foot rot	*Phytophthora capsici*	Potato, tomato, and black pepper	*Bacillus vallismortis* EXTN-EXTN-1	ISR	(Thanh et al. 2009)
Black dot and anthracnose	*Colletotrichum*	Potato, pepper, and tomato	*Bacillus amyloliquefaciens*	induced systemic resistance	(Jetiyanon et al. 2003)
Root rot and charcoal rot	*Macrophomina phaseolina*	Pepper	*Pseudomonas fluorescens, Bacillus subtilis* and *P. aeruginosa*	producing a variety of microbial metabolites	(Yu et al. 2011) (Fiers et al. 2012) and (El-Gamal et al. 2016)
Root rots	*Rhizoctonia solani* and *Fusarium solani*	Potato, pepper, and tomato	*Delftia lacustris, Bacillus subtilis* and *Bacillus cereus*	suppressing the mycelia growth and released volatile inhibitory compounds	(Montealegre et al. 2003) and (Janahiraman et al. 2016)
White mold	*Sclerotinia sclerotinium*	Potato and tomato	*Streptomycetes* sp.,	Chitinase production	(Jetiyanon et al. 2003)

Table 1 (continued)

Disease	Causative pathogen	Host	PGPR	Mechanism of action	References
Fusarium wilt	*Fusarium sp*	Potato, tomato, and pepper	*Streptomyces, Bacillus megaterium* var *phosphaticum, Glomus intraradices* and *Glomus macrocarpus*	break down fungal cell walls, siderophore and IAA production, stimulate plant defense system	(Abed et al. 2019), (Castillo et al. 2016), (Khan et al. 2018) and (Jehlička et al. 2019)
	Fusarium oxysporum	Tomato	*Bacillus* sp.	Root colonization -Siderophores production -HCN -fungal cell wall degrading enzymes	(Gowtham et al. 2016)
	Fusarium oxysporum	Potato, tomato, and black pepper	*Bacillus vallismortis* EXTN-1 (EXTN-1),	ISR	(Thanh et al. 2009)
Dry rot	*Fusarium roseum*	Potato	*Bacillius cereus, B. lentimorbus, B. cepacia* and *B. licheniformis*	produce inhibitory volatile substances and complex lytic chitinase and antagonism	(Parke and Gurian-Sherman 2001), (Sadfi et al. 2001) and (Recep et al. 2009)
Damping off	*Pythium* and *Rhizoctonia solani*	Potato, tomato, and pepper	*Bacillus* sp., *Streptomyces* sp., *P. putida*, *Paenibacillus* sp., and *Pseudomonas fluorescens*	competition and antibiosis, producing high levels of enzymes, metabolites, siderophores and enhanced phenolic compounds and PR-proteins accumulation	(Elad 1996), (Ramamoorthy et al. 2002), (Gravel et al. 2005), (Jayaraj et al. 2007) (Liu et al. 2017)
Silver scurf	*Helminthosporium solani*	Potato	*P. putida*, and *Rhizobium etli* G12	Induced systemic resistance by Lipopolysaccharide	(Martinez et al. 2002) and (Reitz et al. 2000)

Systemic acquired resistance is associated with the production of endogenous elicitor by the plant such as accumulation of salicylic acid, indole acetic acid (IAA), abscisic acid (ABA), jasmonic acid (JA), and several lipo-peptides such as bacillomycin, mycosubtilin, surfactin, iturin, and fengycin, also stimulate plant defense systems through different molecular pathways at the transcriptional level and induction of enzymes chitinase, β-1,3-glucanase, peroxidase, and polyphenol oxidase (Abbasi et al. 2019; Angelopoulou et al. 2014; Attia et al. 2020).

The most vital characteristic of the members of *Bacillus* spp. is endospore former, which helps the durability of bacteria in nature and can last for perhaps millions of years (Zimina et al. 2016). These bacteria can produce ethanol, H_2, acetone, acetic, formic, lactic, and succinic acids by fermentation of glucose. Especially *Bacillus subtilis* YM 10–20 can produce anti-fungal compounds (Chitarra et al. 2003).

Sansinenea and Ortiz (2011) recorded that antifungal metabolites of *Bacillus species* are resistant to temperature and pH changes and do not lose their antifungal activities. *Bacillus megaterium* KL39, a biocontrol agent, produces an antifungal active against a broad range of plant pathogenic fungi (Jung and Kim 2003).

Also, Li et al. (2014) recorded that *Bacillus amyloliquefaciens* strain SQR9 showed activities against a broad spectrum of fungal soil borne pathogens such as *Fusarium solani, Sclerotinia sclerotiorum, Verticillium dahliaekleb, Phytophthora parasitica,* and *Fusarium oxysporum* by the production of different antifungal compounds.

These antifungal metabolites vary according to pathogen such as the following lipopolysaccharide bacillomycin against *Fusarium oxysporum*; fengycin produced against *Verticillium dahliaekleb, Fusarium oxysporum, Fusarium solani*, and *Phytophthora parasitica*; Surfactin against *Sclerotinia sclerotiorum, Rhi-zoctonia solani*, and *Fusarium solani* but bacillibactin effective against *Fusarium solani, Sclerotinia sclerotiorum Verticillium dahliaekleb, rhizotonia solani, Phytophthora parasitica* and *Fusarium oxysporum*.

Also, many researchers proved the activity of *Bacillus* against root rot and damping caused by *Rhizoctonia solani* by various antibiotics such as iturin A, surfactin, plipastatin, bacilysin, mycobacillin, and mycosubtilin (Maget-Dana and Peypoux 1994; Sengupta et al. 1971; Walker and Abraham 1970).

Akram and Anjum (2011) recorded the ability of *B. fortis* 162 and *B. subtilus* 174 against *Fusarium* wilt of tomato through induction of systemic resistance in tomato plants, increasing the level of phenyl ammonia lyase (PAL), PPO, and PO and significantly reduced tomato *Fusarium* wilt severity.

In addition, Nain et al. (2012) recorded the activity of *Bacillus species* through acetyl-CoA carboxylase (ACC) deaminization activity, phosphorous solubilization ability, fungicidal, IAA production, and ammonia production activity. Which resulted to significantly enhanced seed germination, fresh and dry weight, leaf area, root and shoot length, and increasing yield.

Pseudomonas spp. have distinctive characteristics that make them a vital biocontrol agent, such as colonization and proliferation inside the plant, competition with other microorganisms, adaptation to stresses, and they produce a wide spectrum of active biological metabolites such as antibiotics, Siderophores, volatile compounds, and growth stimulant compounds (Stockwell and Stack 2007).

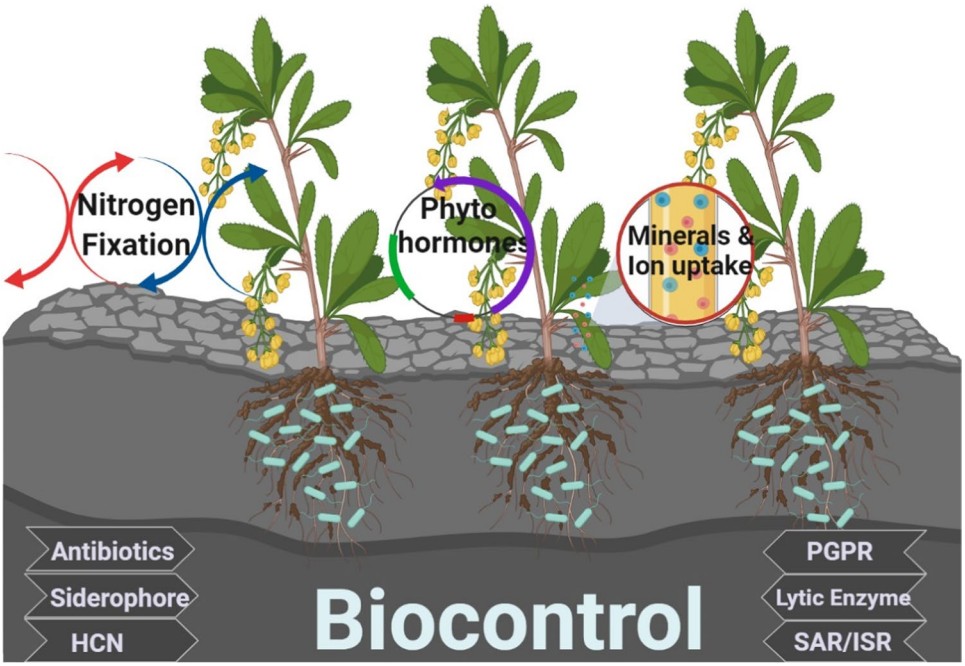

Fig. 3 Biocontrol of fungal plant diseases by PGBR and other important factors

Pseudomonas fluoresces are reported to have antagonistic activity toward soil-borne plant pathogens (Ali Siddiqui and Ehteshamul-Haque 2001) through production of certain antibiotics (Raaijmakers et al. 2002) such as 2, 4-diacetylphloroglucinol (Raaijmakers and Weller 1998) and siderophores (De Meyer and Höfte 1997).

Weller (2007) reported the potency of *Pseudomonads* as biocontrol and growth promoting agents. *Pseudomonas* sp. produce secondary metabolites such as 2, 4-diacetylphloroglucinol, lipopeptides, phenazines, pyrrolnitrine, pyochelin, and hydrogen cyanide, which have an inhibitory effect *in vitro* as in field conditions against root diseases when introduced into the seed or soil treatments (Haas and Defago 2005, Reddy et al. 2009; Siddiqui and Shaukat 2003). Also, *Pseudomonas fluorescence* have extracellular diffusible pigments such as pyoverdin, pyochelin, and ferripyoverdin, which may illustrate their potential to control seed- and soil-borne pathogenic fungi and oomycetes (Keel et al. 1992).

Pseudomonas produce indole acetic acid (IAA), which helps to enhancement plant growth by increasing root length, cell division, and cell enlargement by increasing absorption of water and nutrients also enhancing the capacity to anchor to the soil (Salisbury 1994). *Pseudomonas fluorescens* can produce cytokinins, which promote cell divisions and cell enlargement (García de Salamone et al. 2001).

Another mechanism to inhibition of phytopathogens by *Pseudomonas* spp. is production of siderophores during iron starvation (Geels and Schippers 1983). Also *Pseudomonas* spp. can produce pyoluteorin, pyrrolnitrin, phenazines, cyanide, 2, 4-diacetylphloroglucinol (Compant et al. 2005), and enzymes that can destroy fungal cells, i.e. cellulose, chitinase, proteases, and beta-glucanase (Hernández-León et al. 2015).

Another mechanism of PGPR is detoxification of virulence factors where *Burkholderia cepacia* has potency to hydrolyze fusaric acid, a phytotoxin produced by *Fusarium species* by controlling the sensing capacity of pathogens by inducting auto inducer signals and thus arresting the expression of virulence factor (Compant et al. 2005).

Bacillus subtilis spp. strains have shown antifungal activity against *Fusarium oxysporum* (Yuan et al. 2013), *Puccinia striiformis* (Reiss and Jorgensen 2017), *Rhizoctonia solani* (Asaka and Shoda 1996), and *Pythium aphanidermatum* (Leclère et al. 2005). Based on the above research and experiences, *Bacillus species* such as *B. amyloliquefaciens*, *B. licheniformis*, *B. pumilus,* and *B. subtilis* are available in the market as bio-fungicide formulations as excellent control agents against plant fungal diseases (Pérez-García et al. 2011).

Finally, the scarcity of information about some fugal soil-borne diseases is probably because these diseases are present in isolated zones such as Phoma leaf spot, Rosellinia rot, and Thecaphora smut (Fiers et al. 2012).

Control of bacterial soil-borne diseases by PGPR

Plant pathogenic bacteria are widely spread over the world representing approximately 7100 plant pathogens that belong to *Erwinia, Xanthomonas*, *Agrobacterium*, *Pseudomonas*, *Ralstonia*, and *Pectobacterium* (Aguilar-Marcelino et al. 2020; Mansfield et al. 2012). Bacterial plant pathogens cause serious crop losses throughout the world (Krueger 2004).

There are many bacterial plant pathogens that have a broad crops range worldwide, including *Pseudomonas syringae* (infected crops ranging from potato to banana, olive, phaseolicola, and tomato), *Ralstonia solanacearum* (infected crops ranging from tobacco, potato, eggplant, tomato, and banana), *Agrobacterium tumefaciens*, *Xanthomonas,* and *Erwinia amylovora* (Mansfield et al. 2012). Bacterial diseases are one of the most important biotic stresses of plant crop production (Campos and Ortiz 2020).

Mansfield et al. (2012) ranked the top ten plant pathogenic bacteria as the follows: *Pseudomonas syringae*, *Ralstonia solanacearum*, *Agrobacteruim tumefaciens*, *Xanthomonas* sp., *Erwinia* sp., *Dickeya* sp., *Xylella* sp., *Pectobacterium* sp. and *pseudomonas* sp. Plant bacterial diseases symptoms often appear as leaf spots, specks, wilts, blights, rots, cankers, scabs, and galls accompanied mostly by the production of toxins or enzymes that lead to host-plant break down and death (Ellis et al. 2008).

Ralstonia solanacearum is considered one of the most dangerous soil borne pathogens because *R. solanacearum* has a wide host range of more than 200 species in 50 families, especially solanaceous crops such as potato, pepper, eggplant, and tomato, and it causes yield reduction up to 90 to 100% (Kipgen and Bora 2017; Yanti et al. 2022). Moreover, in potato alone, *R. solanacearum* led to worldwide annual crop loss estimated at US$ 1 billion (Tomlinson et al. 2005).

Commercially, fewer biological control products for bacterial diseases of plants are available than for fungal diseases and often a combination of more than one biological control agent is used (Arwiyanto 2014). The application of PGPRs as biological control agents against plant disease in most agricultural crops such as *Agrobacterium* sp., *Klebsiella* sp., *Burkholderia* sp., *Azotobacter* sp., *Bacillus* sp., *Pseudomonas* sp., *Enterobacter* sp., *Rhizobium* sp., and *Serratia* sp. was studied by (Mishra and Arora 2018; Sindhu and Dadarwal 2001).

Rai et al. (2017) recorded the application of *Pseudomonas protegens* against *R. solanacearum* through different pathways and the production of antimicrobial metabolites such as diacetyl phloroglucinol, pyoluteorin, pyrrolnitrin, and HCN. *B. subtilis* ATCC6633 can produce bacteriocin, which can inhibit the germination of *Clostridium* sp. that causes soft rot of potato (Chatterjee et al. 2005).

Rajer et al. (2017) illustrated the potency of *Bacillus* sp. against *Clavibacter michiganensis* through production of volatile compounds that have antimicrobial activity such as benzaldehyde, nonanal, benzothiazole and acetophenone and against *Xanthomonas axonopodis* by production of bacillaene, bacillibactin, butirosin, bacilysin, carotenoid, difficidin, fengycin, haloduracine alpha, ladderane, lichenysin, microcin, plipasain, and surfactin.

Bacillus sp. have broad spectrum activity against plant bacterial diseases such as common scab, ring rot, bacterial wilt, bacterial speck, and bacterial spot by different mechanisms; first, through competition mechanism because *Bacillus* sp. have a potency to replicate rapidly, resistant to adverse environmental conditions such as *Bacillus* sp. produces endospores resistant to UV light and heat, which allows them to survive in harsh environmental conditions (Raaijmakers et al. 2002); second, *B. subtilis* can produce volatile compounds that play a vital role in plant growth enhancement and activation of induced systemic resistance (ISR) in host plants (Compant et al. 2005).

Banerjee et al. (2017) proved that *B. cereus* IB311 has good bio-controlling activity because it is safe, cost effective, and has a positive impact on the agricultural field. Sharga and Lyon (1998) reported that *Bacillus subtilis* Bs 107 had complete activity *in vivo* against *E. carotovora* subsp. carotovora and *E. carotovora* subsp. atroseptica.

Lactic acid bacteria (LAB) act as effective bio-fertilizers and bio-stimulants, improving nutrient availability, minimal biotic and abiotic stresses, and directly stimulate plant growth (Hamed et al. 2011; Lamont et al. 2017; Shrestha et al. 2014).

Shrestha et al. (2009) showed that LABs can suppress soil borne bacterial pathogens and improve plant growth such as bacterial spot in pepper and tomato as well as bacterial wilt (*R. solanacearum*) in pepper. LAB act as biological control of pathogenic bacteria through different microorganisms as they produce one or more antimicrobial metabolites, such as organic acids, mainly lactic and acetic acids, carbon dioxide, diacetyl, hydroxide peroxide, and other antimicrobial peptides such as bacteriocins (Arena et al. 2016; Cortés-Zavaleta et al. 2014; Herreros et al. 2005; Reis et al. 2012; Tharmaraj and Shah 2009).

Organic acids diffuse through the cytoplasmic membrane of pathogens in their hydrophobic form and then reduce intracellular pH and stop metabolic activities which generally restricts growth of pathogenic bacteria. Also, hydrogen peroxide, which is produced and accumulated by LAB in the presence of oxygen, has a toxic effect on bacterial pathogens, especially that they cannot produce catalase enzymes (Dalié et al. 2010; Reis et al. 2012). Also, LAB may overcome pathogens by pre-emptively colonizing plant tissues (Tsuda et al. 2016), which creates competition for nutrients and space, or by induction defense responses of hosts toward the pathogen (Konappa et al. 2016).

PGPRs have potency to enhance plant growth under field conditions by solubilizing precipitated phosphates to host plants, through many ways such as synthesis of organic acids or protons (Richardson et al. 2009; Verma et al. 2001), chelation, and substitution reactions (Hameeda et al. 2008). PGPRs can also promote nodulation, nitrogen uptake, growth and yield (Sekar and Kandavel 2010).

Some PGPR strains have another mechanism to control pathogens by inhibition of virulence factor by secretion protein molecules that detoxify the pathogens toxins (see Table 2) (Compant et al. 2005).

Many strains of *Streptomyces* spp. produce antibacterial metabolites or antibiotics, which are active against several plant pathogens. In addition, *Streptomyces* sp. have the potential to significantly reduce the severity of potato scab caused by *Streptomyces scabies* (Liu et al. 1995; Ryan et al. 2004).

P. fluorescens has the capacity to control potato soft rot disease caused by *Pectobacterium atrosepticum* and *Dickeya* spp. through inhibition of enzymes that hydrolysis the tuber wall (Jafra et al. 2006; Kastelein et al. 1999). Also, *Pseudomonas* spp. and *Bacillus* spp. have great potency against potato diseases (Kempe and Sequeira 1983).

Furthermore, *Pseudomonas* sp. 23S, has antagonistic activity against *Clavibacter michiganensis* subsp. *in vitro* and *in vivo* in addition to application as plant growth promoting agents. This antagonistic activity is explained by different mechanisms through its ability to induce ISR in infected tomato plants and reduce the severity of bacterial canker disease caused by this fungus, as well as to its ability as a PGPR agent.

The activity of *Pseudomonas* sp. 23S against *C. michiganensis* depends on several factors; first, the best time for treatment with *Pseudomonas* sp. is five days before pathogen attack; second, the method of inoculation, where stem inoculation is more effective; and finally, age of plants, where young tomato plants are more sensitive (Takishita et al. 2018).

Shrestha et al. (2014) recorded three strains of *Bacillus* that have antibacterial potency against bacterial leaf spot of tomato and pepper of *Xanthomonas vesicatoria* in the greenhouse and field, which showed decreased bacterial leaf spot severity when inoculated with the three *Bacillus* strains.

Recently, Principe et al. (2018) demonstrated that application of *P. fuorescens* SF4c, after 12 h of infection of tomato plants with *Xanthomonas vesicatoria,* resulted in reduction of the spot disease symptoms on tomato fruit because *P. fuorescens* can produce tailocins.

More recently Marin et al. (2019) reported that *Bacillus* and *Pseudomonas* have potential biological activity for different species of *Xanthomonas* sp. singly, but the combination of several strains have more potency against *Xanthomonas* sp.

Table 2 Biocontrol of bacterial plant pathogens by PGPR

Disease	Causative pathogen	Host	PGPR	Mechanism of action	References
Soft rot	*Erwenia carotovora* and *Clostridium* spp.	Potato	*Pseudomonas* sp.	siderophores production and induce ISR	(Leeman et al. 1996)
Common scab	*Streptomyces scabies*	Potato	*Bacillus subtilis*, and *Pseudomonas species*	affect the soil microbial community and Enzyme production	(Singhai et al. 2011; Wang et al. 2019)
Bacterial Blackleg and Tuber Soft Rot	*Pectobacterium* and *Dickeya*	Potato	*Lactobacillus* sp., and *Pseudomonas* sp.	Antagonists siderophores, antibiotics and surfactants producing	(Arseneault et al. 2016; Compant et al. 2005; Raoul des Essarts et al. 2016; Tomihama et al. 2016; Tsuda et al. 2016)
Ring Rot	*Clavibacter michiganensis*	Potato	*Bacillus subtilis* FA26	Production of volatile organic compounds	(Rajer et al. 2017)
Bacterial wilt or Brown rot or southern bacterial wilt	*Ralstonia solanacearum*	Potato, tomato and black pepper	*Pseudomonas, Streptomyces*, *Serratia,* and *Bacillus cereus*	ISR and plant growth promotion, antibiotic production, enzyme production, competition and antagonists	(Aguk et al. 2018; Álvarez and Biosca 2017; Chamedjeu et al. 2019; Guo et al. 2004; Mahmoud 2007; Thanh et al. 2009)
Bacterial speck	*Pseudomonassyringae*	Tomato	*Azospirillium brasilense*, *Bacillus*, and Paenibacillus sp.	Secondary metabolites production	(Bashan and De-Bashan 2002; Liu et al. 2017)
Bacterial spot	*Xanthomonas axonopodis*	Tomato and pepper	*Bacillus* and *Paenibacillus* sp.	Secondary metabolites production	(Liu et al. 2017)

The *Bacillus subtilis* QST 713 strain is commercially available against *Xanthomonas* sp. that cause bacterial spot in tomato, peppers, eggplants, and potatoes (Pritchard et al. 2016). *Dickeya* sp. causes bacterial soft rot, which is the major destructive diseases of potato (*Solanum tuberosum*) grown worldwide (Czajkowski et al. 2015; Pritchard et al. 2016). *Dickeya* potato soft rot disease is difficult to control because the pathogen is able to spread via water, survive on field weeds and plant debris (Gardan 2005).

Serratia plymuthica A30 has antagonistic activity against *Dickeya* spp. *in vitro* and *in vivo* (Hadizadeh et al. 2019). More recent reports suggest another strategy to control the potato soft rot and blackleg diseases using a combination of biocontrol strains (Krzyzanowska et al. 2019, Raoul des Essarts et al. 2016).

Several studies have shown that *Bacillus, Serratia, Pseudomonas, Lactobacillus, Delftia, Ochrobactrum,* and *Rhodococcus* could be used as biocontrol agents against potato soft rot disease by various mechanisms such as competition, inhibition, or by ISR in potato plants (Czajkowski et al. 2011; Diallo et al. 2011; Jafra et al. 2006).

Biocontrol of nematode diseases by PGPR

Nematodes are plant pathogens that spread in different areas on corps such as wheat, barley, and oats and attack more than 50% of major European cereal-growing areas (Subbotin et al. 2003). Root-knot nematodes attack a wide range of vegetables, including cucumber, mint, beans, cucurbits, and peach (Tariq-Khan et al. 2017). Nematodes are the major biotic agents on crops that attack all plant crops and cause billions of dollars in crop losses annually (Bozbuga et al. 2018).

Nematodes diseases are one of the most destructive biotic stresses of crop production in world agriculture causing economic losses estimated up to 12.3% to 20% of plant crops worldwide (Koenning et al. 1999; Singh et al. 2015). The global economic losses due to nematode attacks are estimated to be about $157 billion every year (Singh et al. 2015). Nematodes act as vectors for some plant viral diseases (Brown et al. 2004). Nematodes are directly targeting the root system of the host plant, which obstructs the water and nutrient uptake, resulting in reduction of agronomic performance, and seriously effects the quality and yield of crop plants (Singh et al. 2015).

There are various ways available for limiting this damage, such as to use resistant cultivars, nematicides, crop rotation, and biological control. Unfortunately these practice are not always effective because nematodes are capable of forming protective cysts, gelatinous matrix, and surviving in the soil without a host. Finally, biological control is the most effective and efficient way to overcome the nematodes (Timper 2014).

The main mechanism of biological control is competition by reduction of the populations of nematodes by increasing

Table 3 Control of nematodes plant pathogens by PGPR

Disease	Causative pathogen	Host	PGPR	Mechanism of action	References
Trichodorid nematodes density	*Trichodorid nematodes*	Potato	*Stenotrophomonas maltophilia, B. mycoides* and *Pseudomonas* sp.	Antifungal activity by hydrolytic enzymes production, HCN, and phenol oxidation	(Insunza et al. 2002)
Nematode root galls	*Meloidogyne incognita*	Potato, pepper, and tomato	*Rhizobium etli, Serratia, Desulfovibrio, Bacillus, Agrobacterium, Clostridium, Pseudomonas, Alcaligenes,* and Streptomyce	Antagonists and induced systemic resistance (ISR)	(Chowdhury et al. 2015; Kerry 2000; Siddiqui and Mahmood 1999; Wolfgang et al. 2019)
Root-knot nematode	*Meloidogyne* spp.	Potato and tomato	*Bacillus subtilis*	Activating ISR	(Adam et al. 2014)
Root-lesion nematode	*Pratylenchus* sp.	Potato	*Microbacterium esteraromaticum, Pseudomonas chlororaphis, Kocuria varians, K. kristinae*, and *Tsukamurella paurometabola*	High level of mortality	(Sturz and Kimpinski 2004)
Potato cyst nematode	*Globodera pallida, Globodera*	Potato	*Pseudomonas fluorescens*	Competition, production of siderophores, and alteration of specific root exudates such as polysaccharides and amino acids	(Jacobs and Crump 2003, Kavitha et al. 2007; Tobin et al. 2008)

the natural enemies in the soil. Soil is a reservoir for micro floras that are highly varied in composition and activity (Mendes et al. 2013). Use of biological control agents helps to maintain ecological balance as is safe for the environment. Also biological agents remain effective in soil for long periods (see Table 3 and Fig. 4) (Trudgill et al. 2000).

Control of nematodes is very difficult because of their inhabitation and parasitism mode (Gillet et al. 2017). PGPRs reduce nematodes severity by inducing plant systemic resistance, which is achieved by mechanical and physical strengthening of the plant cell wall by cellulose precipitation and phenolic accumulation or by synthesis of biochemical metabolites (Pieterse et al. 2002; Ramamoorthy et al. 2001), or by mutualism with plant host (Karthik et al. 2017), or by competition, production of siderophores, and alteration of specific root exudates such as polysaccharides and amino acids (Jacobs and Crump 2003, Kavitha et al. 2007; Negi et al. 2011; Tobin et al. 2008).

Several PGPR were also reported as antagonists of plant parasitic nematodes, including the members of the genera such as *Bacillus, Rhizobium, Pseudomonas, Klebsiella, Phyllobacterium, Methylobacterium, Agrobacterium, Beijerinckia, Actinomycetes, Bradyrhizobium, Arthrobacter, Aureobacterium, Corynebacterium, Desifovibri, Alcaligenes, Streptomyces Azotobacter, Azospirillum, Stenotrotrophomonas, Curtobacterium Hydrogenophaga, Serratia, Desulforibtio, Burkholderia, Comamonas, Chromobacterium, Gluconobacter, Clostridium, Clavibacter, Enterobacter, Phingobacterium, Flavobacterium*, and *Variovorax* (Siddiqui and Mahmood 1999; Tian et al. 2007; Wani et al. 2015).

Almaghrabi et al. (2013) and Siddiqui and Akhtar (2009) reported that *Pseudomonads putida*, *Serratia marcescens, Pseudomonads fluorescens, Bacillus subtilis, Bacillus amyloliquefaciens, Bacillus cereus, Paenibacillus polymyxa*, and *Burkholderia cepacia* have potency against *Meloidogyne incognita* that infected tomato plants. Also, *Bacillus subtilis* was applied as a biological control against *Rotylenchulus reniformis* and *Azotobacter chroococcum* against *Meloidogyne incognita* (Chahal and Chahal 2003; Niknam and Dhawan 2001). *Stenotrophomonas maltophilia*, *B. mycoides*, and *Pseudomonas* sp. were used against *Paratrichodorus pachydermus* and *Trichodorus primitivus*; also in addition, *Pseudomonas oryzihabitans* and *Rhizobium etli* against *Globodera* that infected potato (Insunza et al. 2002; Reitz et al. 2000).

Control of viral diseases by PGPR

Plant viral diseases are considered one of the major crops pathogens worldwide that can attack allium crops such as garlic, onion, shallot, and leek (Lefeuvre et al. 2019; Mansouri et al. 2021). Viral plant pathogens are classified as specialist viruses that attack one or a few related crops and generalist viruses that have several different hosts that may be in different families (Kumar et al. 2020).

Diseases caused by viruses generally appear on the foliar level as leaf deformation, mosaic, ruckle, necrosis, dwarfing, and rolling. Only some viruses at underground systems such as tobacco rattle virus, potato mop-top virus, potato virus Y, and tobacco necrosis virus can destroy tubers of potatoes (Fiers et al. 2012). (Gaffney et al. 1993) proved the potency of the *P. fluoresces* strain CHA0 against viral

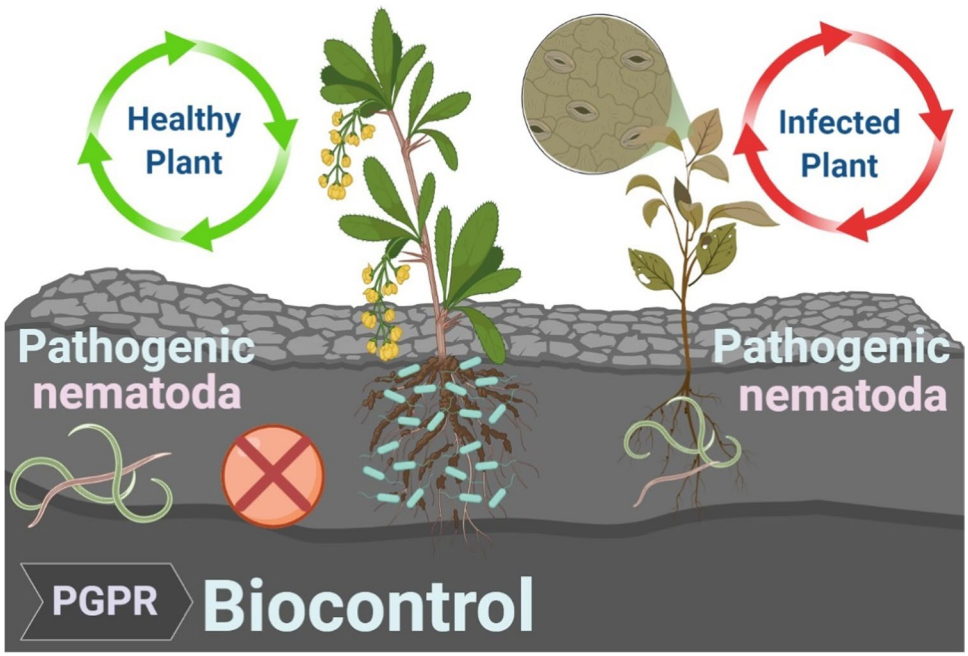

Fig. 4 Effect of plant pathogenic nematodes on plants and the biocontrol by PGPR

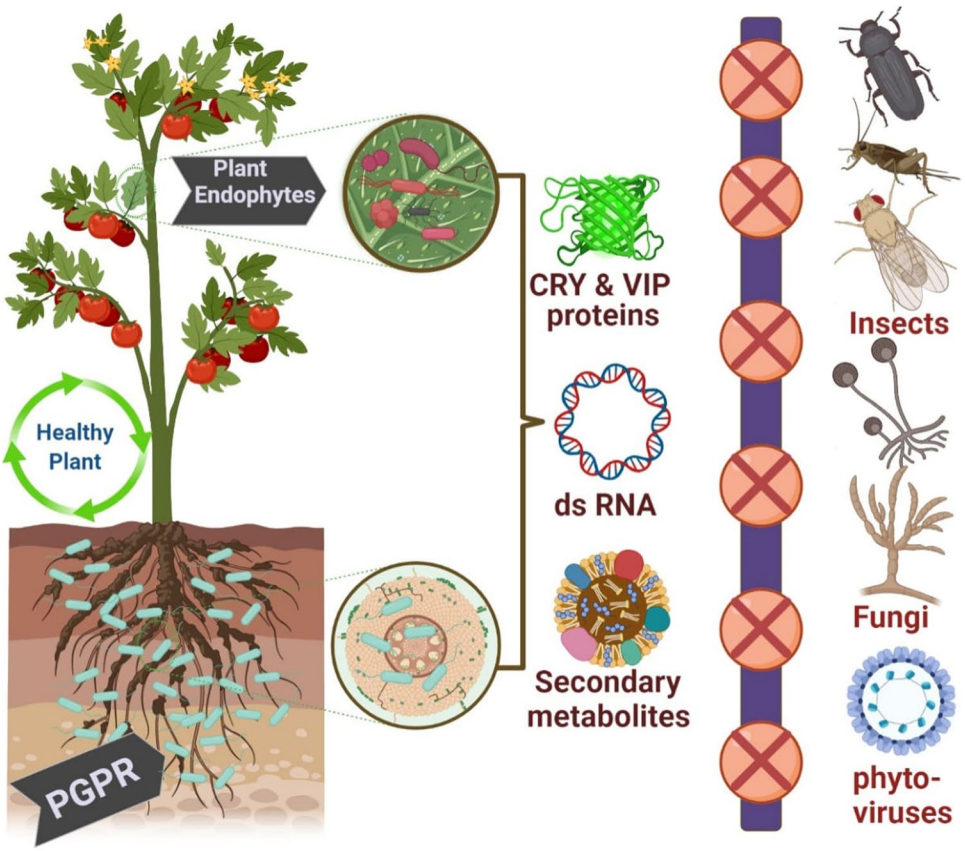

Fig. 5 Action mechanism of PGBR, and plant endophytes on plant pathogenic viruses, insects, and soil-born fungi through creation of specific proteins, nucleic acids, and secondary metabolites

pathogens not only by induction accumulation of salicylic acid, which plays an important role in signal transduction of systemic resistance, but also systemic acquired resistance proteins induction (see Fig. 5).

Moreover, Maurhofer et al. (1998) recorded that the *P. aeruginosa* PAO1 could improve induced systemic resistance in tobacco against tobacco necrosis virus by induction of SA biosynthesis genes. Currently, endophytic fungi are promising smart biological control against plant pathogens as well as promotion of healthy plants through the induction of the systemic resistance of plants against diseases. Systemic resistance was achieved by reducing the percent of disease severity, increasing the content of photosynthetic pigments, the total carbohydrates, total soluble proteins, and phenols, as shown in Fig. 5.

Conclusion

Plant growth promoting rhizobacteria (PGPR) is one of the most promised strategies against many plant pathogens. Scientists tended to apply PGPR as safe eco-friendly inducers to control a wide range of different plant pathogens such as fungi, bacteria, viruses, insects, and nematodes. The defense mechanisms of PGPR against plant pathogens may include production of antibiotic, hydrocyanic acid (HCN), Siderophores, lytic enzymes, and degradation of toxins. The role of PGPR is not only to inhibit the plant pathogens but also to activate and stimulate the systemic resistance in the plant.PGPR can improve plant health through stimulating the production of substances responsible for physiological defense as phenols, proline, antioxidant enzymes, salicylic acid, jasmonic acid, and production of a group of pathogeneses related proteins. PGPR can also, building plant structural defense components such as lignin, cellulose, and surface waxes. Therefore, the application of PGPR is considered a promising safe bio-effective strategy to control plant diseases instead of harmful chemical methods.

Authors' contributions AMA, AHH, GSE, and MSA suggested the research topic, investigated the article, planned the research methodology, and wrote the original draft. GSE drew the figures. AMA, AHH, GSE, DAE, SS, DHMA, and MSA participated in data representation and article revising and editing. All authors read and approved the final article.

Data availability The datasets supporting the conclusions of this article are included within the article and its additional files.

Declarations

Ethical approval Not applicable.

Informed consent Not applicable.

Conflicts of interest The authors declare that they have no conflict of interest.

Research involving human participation and/or animals Not applicable.

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