Chapter 3
Plant-Growth-Promoting Rhizobacteria (PGPR)-Based Sustainable Management of Phytoparasitic Nematodes: Current Understandings and Future Challenges

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Abstract Undoubtedly, phytoparasitic nematodes cause great damage to important agricultural crops, which signifies great monetary loss. Nematicides are used to kill the plant parasitic nematodes. These chemicals have caused greater losses to our biodiversity which are untargeted leading to a great perturbation of ecosystem ecology. The impact of these chemicals on human health cannot be ignored. PGPR uses various mechanisms to manage the plant nematodes. They are also known as plant growth enhancer, phytohormone producer, siderophore producer leading to enhanced plant health. They are also helpful in the enhancement of quantum of resistance of the plants against various pathogens including plant parasitic nematodes. Inoculation of suitable rhizobacteria not only enhances the plant growth and yield characters of plants but also restrict the multiplication of pathogens and pest populations. PGPR is one of the best alternatives which could be used against plant nematodes for bringing down their population below threshold level. There are several mechanisms implicated in the management of phytoparasitic nematodes and such mechanisms have been described in the chapter.

Keywords Phytohormone · Siderophore · Plant health · Phosphate solubilisation · Enzymes

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3.1 Introduction

When we read newspapers, magazines, articles etc., there is frequent caution about the hazardous effects of chemical pesticides, including nematicides, and their consequence on the ecosystem's productivity. In order to intensify the crop produce, growers use the chemical fertilizers, pesticides, nematicides, etc. frequently without caring the catastrophic effects of such chemicals. Non-judicious use of synthetic fertilizers or pesticides causes greater reduction in biota and also offer the development of new strains of various pathogens (Ansari and Mahmood 2017b; Ansari et al. 2019; Ansari and Mahmood 2019a, b). The current situation has indeed reached at alarming stage, thus, there must be some way out to find appropriate alternatives. Biocontrol and biofertilzers are the appropriate option which may help in the protection of plant pathogens and pest making the environment more efficient and hostile. Among several biocontrol microorganisms, PGPR can ameliorate plant growth and yield by depleting pathogen population. Various mechanisms either singly or in multiple are operated for registration of good plant health. Although there are several factors which are responsible for better bacterial colonisation to the root system. These abiotic factors also play a crucial role in the establishment of beneficial phytobiomes. It has been suggested that PGPR can enhance plant growth and yield parameters (Prasad et al. 2019).

In addition, soil is the place where microbial activities, including PGPR activities are considered highly efficient. PGPR have a great potential to manage pest and pathogens effectively and are therefore considered to be an important factor in the intensification of sustainable agriculture (Ansari and Mahmood 2017a; Ansari et al. 2017a; Mahmood et al. 2019). PGPR accelerate the synthesis of various important plant-growth-promoting organic molecules, such as phytohormones, antibiotics, enzymes etc., which offer better plant health (Ansari et al. 2017a). In addition, PGPR play driving role in soil health augmentation, leading to improved plant growth, productivity and yield (Ansari et al. 2017b). Various plant pathogens, including phytoparasitic nematodes, have been found to be effectively controlled by these important microbes (Almaghrabi et al. 2013; Xiang et al. 2018; Viljoen et al. 2019). PGPR are a small portion of rhizobacteria, which can promote plant heath directly as biofertilisers or rhizoremediators or phytostimulators and stress controllers or indirectly as inhibitors of plant pathogens, including fungi, bacteria, viruses and nematodes (Lugtenberg and Kamilova 2009; Antoun 2013; Mhatre et al. 2018). PGPR are found among both Gram-negative and Gram-positive bacteria; however, Gram-negative bacteria, like pseudomonads, *Burkholderia*, *Arthrobacter*, *Serratia*, *Achromobacter*, *Rhizobium* spp., which are capable of nitrogen fixation; *Azospirillum* spp.; *Azotobacter* spp.; and *Diazotrophs* spp., show plant-growth-promoting activity (Antoun 2013). Gram-positive bacterial isolates of *Brevibacterium*, *Corynebacterium*, *Micrococcus*, *Paenibacillus*, *Sarcina*, *Bacillus* and *Pseudomonas* have also been shown to promote plant health (Antoun 2013; Kloepper et al. 2004). Among the PGPR, *Pseudomonas* spp. and *Bacillus* spp. are the two important genera that have been extensively studied (Podile and Kishore 2007). The present chapter brings the latest information on the role of PGPR on plant health amelioration, and plant parasitic nematode management. In order to provide straight information, recent studies on these aspects have been consolidated and presented in a simplified and coherent manner.

3.2 Mechanisms of PGPR

PGPR is used as alternative in the management of phytonematodes. Application of suitable strains help the plants to defend themselves from wide range of pathogens attack (Zandi and Basu 2016; Ijaz et al. 2019). PGPR enhance plant growth and yield through either direct or indirect mechanisms (Glick 1995). Direct mechanisms include different processes like phosphate solubilisation, nitrogen fixation, siderophore (iron-chelating compound) production, hydrogen cyanide (HCN), ammonia, vitamin and plant hormone (auxin, cytokinin and gibberellin) production; on the other hand, indirect mechanisms involve secondary metabolite production, which hampers soil pathogen proliferation, cell-wall-degrading enzyme synthesis, competition, induction of resistance etc., minimising the deleterious effects of pathogens (Glick et al. 1999; Prasad et al. 2019).

3.2.1 Phosphate Solubilisation

Phosphorus is a good nutrient for plants to help with its growth and developments. The phosphorus which are present in the environment is not easily accessible to the plants. Deprived inorganic phosphate (orthophosphate) in soil significantly hampers crop production (Miller et al. 2010; Wang et al. 2017). To obviate the situation, phosphate-solubilising bacteria (rhizosphere-colonising bacteria and endophytes) can help in the liberation of organic phosphates (Otieno et al. 2015). Phosphate-solubilising bacteria have been extensively studied in many cases, and it has been found that they improve plant growth and yield. Joe et al. (2016) conducted an experiment with two bacteria, *Acinetobacter* sp. and *Bacillus* sp., which were isolated from the rhizosphere of *Phyllanthus amarus*. The bacteria had shown salt tolerance and phosphate-solubilising character. Finally, they reported that the application of these two bacteria promoted vigour index, phosphorus content, the percentage of germination, plant biomass, phenolic content, and also the antioxidative activity of uninoculated control. Inagaki et al. (2015) reported the findings that the application of different phosphate-solubilising bacteria in acidic sandy soil enhanced the phosphorus content in the leaf tissue of maize. Delfim et al. (2018) indicated that the use of phosphate-solubilising bacteria *Bacillus thuringiensis* increased the availability of soil phosphorus. In brief, wheat plant was inoculated with *B. thuringiensis* at 20th day and was reinoculated 46 days after sowing. The inoculation of these phosphate-solubilising bacteria registered 11% improvement in phosphorus in the rhizosphere at Z46 (Ultisol) and 34% and 67% in aerial tissues at Z46 (Andisol and Ultisol), respectively. On the other hand, 75% enhancement of phosphorus was observed in root tissues at Z87 (Ultisol). Acid phosphatase activity, microbial biomass and root biomass were significantly increased.

3.2.2 Siderophore Production

Siderophore is a iron-chelating agents which are low in molecular weight (Chu et al. 2010; Hider and Kong 2010; Goswami et al. 2016; Ansari et al., 2017a). Iron is considered to be one of the most important elements used for the development and normal functioning of plants and a wide range of soil microorganisms. Large amount of iron is available in the soil but is not accessible form to plants due to its complex nature. These siderophores produced from PGPR assist well in the fulfilment of iron to plants by solubilising and making it available to the plants (Wandersman and Delepelaire 2004; Arora et al. 2013; Singh et al. 2017a, b). These iron-chelating agents (siderophores) contain a variety of chemical structures that can bind with metal cations (Chu et al. 2010; Hider and Kong 2010; Verma et al. 2011; Ghavami et al. 2017). PGPR have also been used in the acquisition of nitrogenase co-factors, molybdenum (Mo) and vanadium (V). Besides, siderophore production in *A. vinelandii* was tested under a variety of trace metal environments, and increased siderophore production was recorded under Fe limitation; on the other hand, under Mo limitation, only catechol-type siderophore production was found to be significantly enhanced (McRose et al. 2017). Siderophore-producing strains of bacteria possess good quantum of plant growth promotion and biocontrol features (Kumar et al. 2016, Kumar et al., 2017a,b; Bindu and Nagendra 2016). Sheirdil et al. (2019) identified some strains of PGPR through 16Sr RNA gene sequencing fatty acid profile and biolog and thereafter selected ten potential strains of PGPR on the basis of their ACC deaminase activity, siderophore production, P solubilisation and the production of indole acetic acid for the plant growth promotion of wheat. They further reported that inoculation of these PGPR significantly enhanced the plant growth and yield characters over control.

3.2.3 Plant Hormone Production

Plant hormone regulates various metabolic and biochemical reaction which are inevitable for plant growth (Waadt et al. 2015; Wani et al. 2016; Ibrahim et al. 2019). Various plant hormones affect the biochemical, physiological and various functioning of plants, including stress management. PGPR also help in the alleviation of various abiotic stresses, such as drought, salinity, heat, cold, flooding, ultraviolet radiation etc., which are common issues in the current era, and the whole world is struggling with these factors. The common phytohormones can be identified as auxin, cytokinin, ethylene, gibberellins and abscisic acid; however, some newly discovered phytohormones have also been included, such as brassinosteroids, jasmonates and strigolactones, which play a significant role in the development of stress-tolerant crop plants (Egamberdieva et al. 2017; Abd-Allah et al. 2018). Brilli et al. (2019) inoculated *Pseudomonas chlororaphis* subsp. *aureofaciens* strain M71 to tomato with the objective of assessing water tolerance level. The production of phytohormones like abscisic acid (ABA) and indoleacetic acid (IAA) was significantly enhanced, contributing a lot in shaping the leaf without alteration in photosynthesis. IAA is directly involved in cell differentiation, cell division and cell elongation of crop plants and thus is a key hormone of plant bodies (Bhardwaj et al. 2014). Maximum PGPR considerably secrete some organic compounds that are directly involved in plant growth and yield promotion leading to ameliorated plant health (Kumar et al. 2015). The amount of IAA concentration varies from species to species, strains to strains. It has been observed most of the time that *Pseudomonas* sp. is the most potent IAA producer among all genera; however, *Pseudomonas putida* is considered to be more superior in terms of production of IAA than *P. fluorescens* (Bharucha et al. 2013; Reetha et al. 2014; Kumar et al. 2015). Ethylene has an important place in the promotion of plant growth and development. The hormone can work efficiently even at very low concentrations (Abeles 1992). Ethylene concentration may effectively control plant growth and senescence (Nazar et al. 2014). Important hormones, i.e. abscisic acids (ABAs), are the molecules that are considerably involved in the alleviation of several environmental stresses and also have significant impact on plants' defence system against a wide range of plant pathogens (Alazem and Lin 2017; Davies and Zhang 1991). Two rhizobacteria, *Bacillus licheniformis* Rt4M10 and *Pseudomonas fluorescens* Rt6M10, isolated from the rhizosphere of grapevines produced ABA, IAA and gibberellins. The concentration of ABA was recorded to be higher in 45-day-old *Vitis vinifera* plants inoculated with *B. licheniformis* and *P. fluorescens* than in control plants (Salomon et al. 2014). Application of *Bacillus licheniformis* SA03 with *Chrysanthemum* plants grown under saline-alkaline conditions significantly alleviated the saline-alkaline stress leading to improved photosynthesis and biomass (Zhou et al. 2017).

3.2.4 Ammonia and Hydrogen Cyanide Production

Likewise, HCN and ammonia production is considered to be an important growth-promoting trait of strains. HCN is also considered to be involved in phytopathogen management in agroecosystems (Rijavec and Lapanje 2016). PGPR-mediated HCN production and synthesis vary considerably and depend upon the genus prevailing in the area; their efficacious nature suggest that such PGPR can be used as biological fertilisers or biocontrol in the intensification of crop production under a climate change scenario (Agbodjato et al. 2015; Rijavec and Lapanje 2016). A large number of research suggested that PGPR-producing HCN can be used for the growth promotion and yield enhancement of various horticultural crops (Rijavec and Lapanje 2016; Kumar et al. 2016). Heydari et al. (2008) isolated cyanogenic strain of *Pseudomonas fluorescence*, which exhibited biocontrol activity, leading to enhanced length of the stems and roots and enhanced germination rate in rye, wild barley and wheat. In another study, Kumar et al. (2012a,b) isolated 40 fluorescent *Pseudomonas* strains from a diverse range of soil. Among the seven strains, P1, P10, P13, P18, P21, P28 and P38, that were further selected for trial depending on their possessing of single or multiple PGPR traits, P38 was found to be a good producer of HCN. In addition, ammonia production by PGPR helps in the promotion of root and shoot elongation and the improvement of plant growth and yield performance (Marques et al. 2010). Many of the PGPR strains have been discovered so far to have both characters, i.e. production of HCN and production of ammonia. The synergistic effects of these two aspects considerably enhance the physiological and biochemical properties of plants (Agbodjato et al. 2015; Kumar et al. 2016).

3.2.5 Enzyme Production

Plant contains a wide range of enzymes, which regulate the various life cycles of plants and also help in the promotion of plant growth (Brilli et al. 2019). Samaddar et al. (2019) reported that the normal plant growth was arrested with the increased concentrations of salinity stress resulting increased stress levels, disrupted the photosynthetic variables, and also affected the antioxidant enzymatic traits in bacterial non-inoculated control plants. Further, the inoculation of *Pseudomonas* spp. considerably alleviated stress ethylene emission and exhibited enhanced plant growth and yield. In the same experiment, catalase activity was significantly higher in the *Pseudomonas* spp. inoculated plants and also neutralised the hydrogen peroxide ions formed due to oxidative stress in plants grown under salinity stress. Besides, the plant resistance against *M. javanica* infesting tomato cv. CALJN3 was improved using salicylic acid and *Pseudomonas fluorescens* CHAO. The results indicated that salicylic acid and *Pseudomonas fluorescens* CHAO elicitors induced the removal of high concentrations of toxic reactive oxygen species by scavenging antioxidant enzymes, especially that of superoxide dismutase, peroxidase and catalase. Application of these elicitors at different time schedules registered significant diminution in the number of galls, egg masses or eggs of *M. javanica* infected tomato plants over control (Nikoo et al. 2014).

3.2.6 Nitrogen Fixation

Nitrogen fixation is also an important phenomenon in various strains of PGPR, which contributes a lot to plant growth promotion (Prasad et al. 2019). Nitrogen although present in the atmosphere in gaseous form about 78% but not directly available to the plants and therefore needs some route through which it might be fixed. The nitrogen fixation is not uncommon among prokaryotes with strains in both bacteria and archaea (Dekas et al. 2009; Das et al. 2015). In addition, the synergistic action of *Rhizobium tropici* strain CIAT 899 and *Paenibacillus polymyxa* strain DSM 36 resulted in higher nodulation, leghaemoglobin, concentration, nitrogenase and nitrogen fixation efficiency and thereby improved the plant health status of common bean. PGPR benefits on specific nodulation were evident on accumulated plant nitrogen (Figueiredo et al. 2008). Yadegari et al. (2010) evaluated the individual and synergistic effects of *Pseudomonas fluorescens* P-93 and *Azospirillum lipoferum* S-21, as well as two highly effective *Rhizobium* strains, in relation to the improvement of plant growth and yield-contributing character. The application of PGPR and *Rhizobium* enhanced the nodulation and plant growth and yield of kidney bean.

3.3 Mechanisms of Biocontrol of Plant Pathogenic Nematodes

PGPR adopt various mechanisms to alleviate the pernicious effects of phytonematodes and avoid greater damage to the growth and yield-contributing characters of plants (Table 3.1). Amaki et al. (2019) reported that the application of *Bacillus* sp. strains AT-332 (NITE BP-1095) and AT-79 (NITE BP-1094) isolated from nature showed biocontrol activity against plant pathogenic activity, also improved the plant health. The *Bacillus* sp. strains AT-332 and AT-79 were found to be effective in the management of a wide range of plant pathogens that cause damage to plants. Ramamoorthy et al. (2001) reported that consortia of different PGPR strains resulted in improved efficacy by inducing systemic resistance against a wide range of plant pathogens. They further illustrated that seed treatment with PGPR resulted in cell wall structural modifications and physiological and biochemical changes, leading to enhanced synthesis of proteins and chemicals involved in plant defence mechanisms. In another study, microbial strains (*Pseudomonas aeruginosa* (B1), MTCC7195, and *Burkholderia gladioli* (B2), MTCC10242) were used against plant parasitic nematodes. The application of these microbial agents showed a favourable response in terms of antioxidant enhancement, which helps in the defence expression of *Lycopersicon esculentum* to alleviate oxidative stress generated under nematode infection (Khanna et al. 2019). Application of the liquid-based *B. subtilis* formulations in soil registered greater reduction in the reproduction of *M. javanica*, leading to promoted plant growth and yield of tomato plant (Lopes et al. 2019b). Turatto et al. (2018*)* evaluated anti-nematodal activity of five PGPR isolated from garlic rhizosphere. They reported that the potentiality of these PGPR arrested hatching (*Meloidogyne javanica*) and motility (*Ditylenchus* spp.). It was observed that isolates CBSAL02 (*Bacillus*) and CBSAL05 (*Pseudomonas*) significantly impaired the hatching of *M. javanica* eggs by 74% and 54.77%, respectively. Likewise, the motility of another important nematode, i.e. *Ditylenchus* spp., was reduced by 55.19% and 53.53%, respectively. In addition, various biocontrol mechanisms are well known, such as antibiosis and lytic enzyme production, and induced systemic resistance (ISR) helps in the restriction of plant pathogens (Kumar et al. 2011). PGPR possess a characteristic that can help in the acceleration of nutrient uptake and in the enhancement of the plant growth and yield attributes of

Table 3.1 PGPR-mediated plant parasitic nematode management

Country	Crops/in vitro	PPN	PGPR	Mode of action	References
China	In vitro test	*M. incognita*	*Pseudomonas putida* MCCC 1A00316	Antibiosis, some active compounds	Zhai et al. (2019)
India	*Lycopersicon esculentum*	*M. incognita*	*Pseudomonas aeruginosa* and *Burkholderia gladioli*	Antibiosis	Khanna et al. (2019)
Brazil	Tomato	*M. javanica*	*Bacillus subtilis* isolate 34	Secretion of some enzymes like protease and chitinase, lytic enzymes and phyto-hormones; siderophore production	Lopes et al. (2019a)
South Africa	Carrot	*Meloidogyne incognita*	*Bacillus firmus* T11, *Bacillus aryabhattai* A08, *Paenibacillus barcinonensis* A10, *Paenibacillus alvei* T30 and *Bacillus cereus* N10w	Production of extracellular toxic com-pounds or enzymes against nematodes	Viljoen et al. (2019)
Italy	Tomato	*Meloidogyne incognita*	*Bacillus firmus* strain 1-1582	Alteration in soil-beneficial microbial populations	d'Errico et al. (2019)
China	Tomato	*M. incognita*	*Bacillus cereus* BCM2	Increased stimulation of root exudates, which helps the plant to keep the nema-todes away	Li et al. (2019)
China	Cucumber	*Meloidogyne incognita*	*Bacillus subtilis* strain Bs-1	Production of some volatile compounds	Cao et al. (2019)
USA	Corn	*Meloidogyne incognita*	*Burkholderia renojensis*, *Streptomyces avermitilis* and *Bacillus firmus*		Aljaafri et al. (2019)
Egypt	*Solanum lycopersicum*	*Meloidogyne incognita*	*Bacillus amyloliquefaciens* subsp. plantarum SA5 and *Lysinibacillus sphaericus* Amira strain	Toxin and enzyme production	Abdel-Salam et al. (2018)
China	Tomato	*Meloidogyne incognita*	*Bacillus cereus* BCM2	Nutrient and space competition	Wang et al. (2018)

India	Gerbera	*Meloidogyne incognita*	*Bacillus subtilis strain* Bbv 57 (KF718836)	Antibiosis, enzyme production	Ramyabharathi et al. (2018)
China	Wheat cv. Aikang 58	*Heterodera avenae*	*B. cereus* XZ 24-2-1, *B. cereus* XZ-33-3, *B. weihenstephanensis* MH-58-60-01 and *B. thuringiensis* MH 032-003	Excretion of hydrolytic enzymes	Ahmed et al. (2018)
Egypt	Tomato	*Meloidogyne incognita*	*Bacillus thuringiensis* and *Bacillus subtilis*	Production of metabolites	Khalil and El-Naby (2018)
Korea	Tomato	*Meloidogyne* spp.	*Pseudomonas chlororaphis* O6	HCN production	Kang et al. (2018)
China	In vitro	*Meloidogyne incognita*	*Pseudomonas putida* 1A00316	Volatile organic compounds	Zhai et al. (2018)
Brazil	In vitro	*Meloidogyne javanica* and *Ditylenchus* spp.	Rhizobacteria (CBSAL02, CBSAL05, CBSAL14, CBSAL18 and CBSAL21)	Production of toxic metabolites, secondary metabolites and extracellular enzymes	Turatto et al. (2018)
Iran	Tomato	*Meloidogyne javanica*	*Paenibacillus polymyxa* (Prazmowski) Ash et al. (NCIM 2188), *Bacillus subtilis* (Ehrenberg) Cohn (MCC 0067), *Pseudomonas striata* Chester (NCIM 2847) and *P. fluorescens* (Flugge) Migula (333-S)	Production of toxic metabolites	Sohrabi et al. (2018)
Iran	Pistachio	*Meloidogyne incognita*	*Pseudomonas fluorescens strains* VUPF5, VUPF52; *Bacillus cereus* strain PRC95; and *Bacillus subtilis* strain PRC96	Development of ISR	Zeynadini-Riseh et al. (2018)

plants, leading to reduced multiplication of plant pathogens (Kloepper and Schroth 1981; Liu et al. 2016). Moreover, PGPR also assist in plant growth promotion by acting as biofertilisers, rhizoremediators, phytostimulators and stress alleviators and also restrict the reproduction of a wide range of plant pathogens like fungi, bacteria, viruses and plant parasitic nematodes (Antoun 2013; Lugtenberg and Kamilova 2009). Important PGPR like fluorescent and non-fluorescent pseudomonads, *Arthrobacter*, *Burkholderia*, *Achromobacter*, *Rhizobium* spp., *Serratia*, which are capable of nitrogen fixation; *Azospirillum* spp.; *Azotobacter* spp.; and *Diazotrophs* spp. (Antoun 2013). Various isolates of *Brevibacterium*, *Corynebacterium*, *Micrococcus*, *Paenibacillus*, *Sarcina*, *Bacillus* and *Pseudomonas* have also shown plant-growth-promoting activities (Antoun 2013; Kloepper et al. 2004). However, a wide range of bacterial genera are found to be plant growth enhancers; *Bacillus* and *Pseudomonas* spp. are the predominant genera that are currently being exploited at a large scale (Podile and Kishore 2007).

Liu et al. (2012) reported that dual inoculations of *Glomus versiforme* and *G. mosseae* and *Bacillus polymyxa* and *Bacillus* sp. exhibited greater management of *Meloidogyne incognita* and promoted the plant growth and yield productivity of *Lycopersicon esculentum*, which might be due to the stimulation of plant-growth-promoting molecules by the rhizobacteria, helping in the reduction of nematode infections. Anwar-ul-Haq et al. (2011) assessed the effectiveness of *Bacillus* spp., *Azotobacter* spp., *Pseudomonas putida* and *P. fluorescens* against *Meloidogyne incognita* infection on tomato root cultivar 'Money Maker' in the green house at 30 ± 4 °C. Tomato plants treated with *P. fluorescens* considerably reduced nematode-related parameters, leading to ameliorated plant growth and yield. PGPR such as *P. putida* and *Bacillus* spp. also enhanced the plant-growth and yield-related performances of the tomato plants. Siddiqui and Singh (2005) conducted experiments with the objective of assessing fly ash amendments at different dose levels, i.e. 0, 20 and 40% + soil, and *Pseudomonas striata* and a nodule-forming bacteria, *Rhizobium* sp., against the reproduction of *Meloidogyne incognita* infecting pea. The inoculation of second-stage juveniles of *M. incognita* reduced the rate of transpiration as well as plant growth and yield attributes of pea. On the other hand, the inoculation of *Rhizobium* sp. and *P. striata* improved transpiration from first week onwards with or without nematode-inoculated plants. Moreover, the addition of 40% fly ash registered considerable reduction in nematode multiplication. However, the highest reduction in nematode population was recorded in the *Rhizobium* sp. inoculated plants as it caused greater pernicious effect on galling and nematode multiplication than *P. striata*. The inoculation of both rhizobacteria registered highest improvement in the reduction of nematode population as compared to their individual effects, which suggested that both organisms have a synergistic role in the management of plant nematodes. This study also elaborated that both PGPR had the ability to release some nematotoxic compounds, which became lethal to nematodes life cycle. Khan et al. (2016) described that the inoculation of *Pseudomonas aeruginosa*, *P. fluorescens*, *P. stutzeri* and *P. striata* enhanced root nodulation and reduced the *Meloidogyne incognita* infesting mungbean. The application of rhizobacteria such as *Pseudomonas aeruginosa*, *P. fluorescens*, *P. stutzeri* and *P. striata* improved the plant growth and yield characters of mungbean and also reduced nematode-related parameters such as galling, egg masses and fecundity, which might be due to the production of siderophores, HCN, IAA and NH_3. Pankaj et al. (2010) reported that *Gluconacetobacter diazotrophicus* Co99–70, *Bacillus* sp. RKB-91 and *Pseudomonas* sp. RKP-33 potentially controlled the severity of *Meloidogyne graminicola* of rice cv. Basmati-370. Seed inoculation with *G. diazotrophicus* Co99-70 was found to be highly effective in the diminution of galling and in lowering nematode multiplication. Restriction in the multiplication of root-knot nematodes was found to be due to antibiosis against nematodes and volatile fatty acids produced by *G. diazotrophicus*. These bacteria also promoted the root and shoot growth of seedlings. These organic molecules may also reduce egg hatching ability by intervening in embryogenesis. Padgham and Sikora (2007) evaluated the performance of *Bacillus megaterium*, which was isolated from a rice-growing region of Taiwan. Root dip and soil-drenching methods successfully impaired nematode-related variables (*Meloidogyne graminicola*) and enhanced crop health. *Bacillus megaterium* possesses endospore-forming ability, which creates a conducive environment for the biological control of *Meloidogyne graminicola*. It was further justified that the dry spores of *Bacillus* could be applied directly through seed treatments as these bacteria quickly colonise the roots and help in the enhancement of plant growth. Huang et al. (2010) conducted an in vitro test followed by pot experiments and reported that *Bacillus megaterium* YMF3.25 inhibited the egg hatching and reduced the infection of *Meloidogyne incognita* through the production of various organic compounds that are nematicidal in nature. After gas chromatography-mass spectrometry (GCMS), benzeneacetaldehyde, 2-nonanone, decanal, 2-undecanone and dimethyl disulphide were found to be nematostatic to the juveniles and eggs at the concentration of 0.5 mmol. In addition, some organic compounds such as nonane; phenylethanone; 3,5-dimethoxy-toluene; phenol; 2,3-dimethyl-butanedinitrile; and 1-ethenyl-4-methoxy-benzene also exhibited nematicidal activities. Chen et al. (2000) reported that some organics were incorporated into soil with or without fumigants (methyl bromide). Three weeks later, *Meloidogyne hapla*, *Bacillus thuringiensis*, *Paecilomyces marquandii* and *Streptomyces costaricanus* were inoculated to soil individually. *B. thuringiensis* plus *S. costaricanus* inoculated plants enhanced lettuce head weight in unfumigated organic soil. All other amendments were also found to be effective against *M. hapla*, which reduced root galling in soil treated with or without fumigants. In this trial, the organic residue might be the carbon source for the proliferation of biocontrol microorganisms, which reduced the nematode population. The organic compounds released after the decomposition of the organic matter was also considered to be the reason behind nematode population reduction.

Mendoza et al. (2008) elaborated the mode of action of antagonist bacteria *Bacillus firmus* against *Meloidogyne incognita*. Significant rates of paralysis and mortality were detected after the incubation of three nematode species in low concentrations of pure culture filtrates following the removal of the bacterial cells. The same culture filtrates also significantly reduced the hatching of *Meloidogyne incognita*. Pure bacterial cell suspensions added to sand also reduced the survival of

R. similis in bioassays by 41% over the control. The mode of action responsible for nematode paralysis and mortality was therefore demonstrated to be closely associated with the production of bioactive compounds (secondary metabolites) by the bacteria. Mashela and Nthangeni (2002) evaluated the effectiveness of *Ricinus communis* with and without *Bacillus* species for the suppression of *Meloidogyne incognita*. Application of organic materials and *Bacillus* suppressed nematode population, which might be due to enhanced concentrations of chemicals during microbial decomposition or enhanced nematophagous microbial populations. Ricin, a compound isolated from *Ricinus communis*, could also be the possible reason behind the considerable reduction of nematode population. Serfoji et al. (2010) conducted a glasshouse experiment for the effectiveness of *Glomus aggregatum* and *Bacillus coagulans* against the *Meloidogyne incognita* infesting tomato cv. Pusa Ruby. *G. aggregatum* alone and in combination with *B. coagulans* exhibited maximum plant biomass of tomato cv. Pusa Ruby and decreased root-knot nematode population, which might be due to increased beneficial microbial population. Xiong et al. (2015) reported the biocontrol effectiveness of *Bacillus firmus* YBf-10 against *Meloidogyne incognita*. Results further revealed that the inoculation of *B. firmus* YBf-10 caused lethal activity, inhibition of egg hatch and mortality of *M. incognita*. In addition, pot trials revealed that soil drenching with YBf-10 considerably controlled nematode reproduction by efficiently reducing the damage by *M. incognita* to tomato plants. Nematode-related parameters such as root galls, egg masses and total nematode population were found to be significantly checked, which might be due to the secondary metabolites produced by YBf-10 leading to improved plant growth and yield attributes. Kavitha et al. (2007) conducted an experiment to assess the effectiveness of some biocontrol microorganisms such as *Pseudomonas fluorescens*, *Bacillus subtilis* and *Trichoderma viride* against *Meloidogyne incognita* infesting tropical sugar beet cv. Indus. 2.5 kg/ha of biocontrol was applied and compared with carbofuran (1 kg a.i./ha). The application of these antagonists improved the plant growth and yield performance of sugar beet and also caused greater reduction in nematode population over control. *P. fluorescens* registered maximum improvement in the plant growth and yield variables of sugar beet. Besides, some well-studied plant defence enzymes, such as peroxidase, polyphenol oxidase and phenylalanine ammonia-lyase, were found to be increased, being higher in plants treated with *P. fluorescens*, followed by *T. viride* and *B. subtilis*, which might be due to the induction of resistance to plant nematodes by the crop plants. Moreover, a study published in the *Journal of Phytopathology* in 2015 reported that *B. pumilus* L1 produced protease and chitinase enzymes, which were found to be nematostatic as they inhibited second-stage juveniles. Hatching and mortality rate were correspondingly increased with increasing concentrations of crude enzymes and time, which might be due to the partial destruction of the eggshell and juvenile body. The pot experiment also demonstrated that the application of a biocontrol agent to potted soil caused significant reduction in the number of galls and egg masses of *M. arenaria*, leading to enhanced plant growth of tomato, which could be due to the presence of certain plant-growth-promoting molecules (Lee and Kim 2016). Moghaddam et al. (2014) reported that two strains of *Bacillus pumilus*, ToIrFT-KC806241 and

ToIrMA-KC806242, were isolated and characterised from tomato fields through morphological and molecular-based techniques. The inoculation of ToIr-MA against *M. javanica* considerably reduced nematode-related parameters such as the number of galls and eggs. ToIr-MA had the ability to produce proteolytic enzymes, which might be the source of the suppression of egg hatching. Siddiqui et al. (2007) used some biocontrol PGPR, such as *Pseudomonas putida*, *P. alcaligenes*, *Paenibacillus polymyxa*, *Bacillus pumilus* and *Rhizobium* sp. for the management of *Meloidogyne javanica* on lentil. It was seen that *Pseudomonas putida* registered greater suppression on the egg hatching and penetration of *M. javanica*, followed by other rhizobacteria like *P. alcaligenes*, *P. polymyxa* and *B. pumilus*, leading to improved plant growth and yield-related characters. Interestingly, the plant growth character was found to be considerably improved. In nematode-inoculated plant, *Rhizobium* sp. of lentil strain was the agent that registered the highest improvement in the plant's health as compared to other PGPR. Combinatorial effect of *Rhizobium* sp. with any other PGPR caused a considerable reduction in nematode galling and egg masses. Highest reduction was recorded in *Rhizobium* plus *P. putida* inoculated-plant which might be due to production of siderophores and other nematostatic organic molecules by the rhizobacteria as per analysis performed with the help of SDS-PAGE. Tong-Jian et al. (2013) tested the effectiveness of *Bacillus cereus* X5 against *Meloidogyne* sp. in vitro by examining the mortality and egg hatching of second-stage juveniles. The biofumigation of the *Meloidogyne* sp. infested soil with some organic additives such as chicken manure, pig manure and rice straw alone or in combination with *B. cereus* X5 was also found to show great nematicidal activity. The application of bio-organics like *B. thuringiensis* BTG or *T. harzianum* SQR-T037 enhanced the plant's biomass and reduced nematode galling and population. *B. cereus* X5 also exhibited great quantum of effectiveness in the management of root-knot nematodes, which might be due to the production of nematicidal compounds, and the production of plant-growth-promoting molecules could be reason behind enhanced plant growth and yield. Mahdy et al. (2000) tested the biocontrol potentiality of *Bacillus cereus* S18 against three species of root-knot nematodes, *Meloidogyne incognita*, *M. javanica* and *M. arenaria*, infesting tomato. A drastic reduction trend line of galls and the number of egg masses was recorded after the treatment of the plants with *Bacillus cereus* S18, which might be due to the congestion in embryogenesis, egg hatching, mortality etc., leading to improved plant growth and yield attributes of tomato. Siddiqui and Mahmood (2001) assessed the effectiveness of *Pseudomonas fluorescens*, *Azotobacter chroococcum* and *Azospirillum brasilense*, singly as well as in combination with *Rhizobium* sp. and *Glomus mosseae*, for the plant growth promotion of *Cicer arietinum*. All rhizobacteria and plant symbionts significantly enhanced the plant growth and yield characters of chickpea on one hand, while on the other hand, the application of these microorganisms drastically reduced the root galls, egg masses and reproducing ability of *Meloidogyne javanica*, which might be due to the release of some toxic chemicals inhibitory to nematodes. Oyekanmi et al. (2007) reported that the inoculation of soybean plants with *Glomus mosseae* (200 spores/plant), *Bradyrhizobium japonicum* (10^6 cells/plant) and *Trichoderma pseudokoningii*

(6.8×10^7 spores/plant) caused greater reduction in *Meloidogyne incognita* population and enhanced plant growth and yield characters. The application of these microorganisms solely, dually or in consortium registered greater improvement in plant health, and the microorganisms were assumed to be working synergistically. The inoculation of these microbes also proved to be antagonistic to root-knot nematodes as there were reduced root galls, egg masses and other nematode-related parameters, which might be due to the combinatorial application of these microorganisms. Different cultivar response to root-knot nematodes were the robust reason behind the poor reproduction of nematodes.

Bhat et al. (2012) reported that *Meloidogyne incognita* race-1 inoculation hampered the growth, nodulation, the nitrogen contents of root and shoot as well as leghaemoglobin, bacteroid and nitrogenase activity, exhibiting poor plant health of blackgram. However, the application of *Bradyrhizobium* inhibited *Meloidogyne incognita* race-1 activity because in the treated plant, there were lesser number of galls and egg masses, which might be due to the inhibition of egg hatching and secondary infection. Saikia et al. (2013) reported that the rhizobacteria *Bacillus megaterium* (ATCC No. 14581) and *Pseudomonas fluorescens* (ATCC No. 13525), fungi *Trichoderma viride* (MTCC No. 167) and *Paecilomyces lilacinus* (PDBC PL55) and plant symbiont *Glomus intraradices* registered greater management of *M. incognita* infesting *Withania somnifera* cv. Poshita. Except plant symbiont (*G. fasciculatum*), all rhizospheric microbes exhibited greater reduction in nematode population, which might be due to various reasons like competition, hyperparasitism, induced resistance etc. Rhizobacteria generally produces some organic molecules, such as phenolic compounds, organic acids and secondary metabolites, which have already been proven to be nematostatic, resulting in the enhancement of plant growth and yield characters. Tian et al. (2014) reported the effectiveness of endophytic bacterium *Sinorhizobium fredii* Sneb183 against soybean cyst nematodes (*Heterodera glycines*). The inoculation of *Sinorhizobium fredii* Sneb183 inhibited the penetration of juveniles and their further development inside the roots of soybean, which might be due to change in root exudates or the production of toxic chemicals. Reimann et al. (2008) reported that the inoculation of *Rhizobium etli* G12 to tomato plants resulted in induced resistance against *Meloidogyne incognita*. The application of *R. etli* accelerated the colonisation of *Glomus intraradices* on tomato. In addition, the application of these two microorganisms significantly reduced nematode penetration and stopped the reproduction of *Meloidogyne incognita*. However, the sole application of both beneficial microorganisms registered greater enhancement in plant growth and reduced nematode development and population, and their combinatorial application significantly enhanced the rate of reduction in nematode multiplication, which might be due to the reduced rate of secondary infection. Ugwuoke and Eze (2010) reported that the inoculation of *Glomus geosporum* and *Rhizobium* (IRJ 21774) registered a significant increase in the root nodulation of *Vigna unguiculata* L. Walp). The inoculation of these microorganisms also reduced root gallings and other nematode-related parameters, leading to enhanced plant growth and yield parameters.

3.4 Conclusions and Future Prospects

A concluding remark could be drawn here that PGPR could be an alternative approach in the management of phytoparasitic nematodes. PGPR are the currently available option, which can be potentially isolated from a diverse range of soil and exploited for the purpose. Suitable and putative strains of PGPR, like *Rhizobium*, *Pseudomonas*, *Bacillus* etc., can be commercialised at a large scale. The biopesticides extracted from these biocontrol bacteria could also be used in the management of various soil-borne plant pathogens and pests, including phytonematodes. The application of PGPR not only improves soil health but also provides a good source of nutrition to plants by obviating phytonematode stress. A single mechanism is not the reason behind the biocontrol of these plant parasitic nematodes. Multiple mechanisms are operated simultaneously, which help in the reduction of nematode population and thereby enhance plant health. However, significant research has been conducted that advocated that PGPR could be exploited, commercialised and used at a large scale for the betterment of agroecosystems. However, a major hurdle in the commercialisation of these PGPR might be the isolation and identification of suitable strains. Identification of potential strains and their proper exploitation will be an option in the 'next generation agriculture'. Potent strain selection could be done through genomics and metagenomics studies, which will indeed unravel many hidden facts about the biomanagement of these phytonematodes.

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