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Potential of plant growth-promoting rhizobacteria in the management of nematodes: A review

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Abstract
Over the past decade, Plant growth-promoting rhizobacteria have gained worldwide importance and acceptance for their agricultural benefits through the application of combinations of different mechanisms of action, which allows increases in crop yield. This is due to the emerging demand for reduced dependence on synthetic chemical products and to the growing necessity of sustainable agriculture within a holistic vision of development and environmental protection. There is an increasing market for biopesticides and an increase in number of microbial control studies directed towards plant-parasitic nematodes. Plant growth-promoting rhizobacteria are beneficial bacteria that colonize the rhizosphere and plant roots resulting in enhancement of plant growth or protection against certain phytonematodes. Various studies were conducted to assess myriad strains of rhizobacteria for antagonistic activity against plant-parasitic nematodes using rhizobacterial inoculants in relation to soil microbial activity and rhizosphere bacterial populations. This literature survey provides an overview of research on biological control of economically important phytonematodes using rhizobacteria.

Keywords: Plant growth-promoting rhizobacteria, Plant-parasitic nematodes, rhizosphere, biopesticides, biological control

1. Introduction
Plant-parasitic nematodes (PPN) or phytonematodes are invertebrate obligate parasite of a large number of plants. There are about 197 genera containing 4300 species of phytonematodes. The important genera of PPN include: *Meloidogyne*, root-knot nematodes; *Pratylenchus*, lesion nematode; *Heterodera* and *Globodera*, cyst nematodes; *Tylenchulus*, citrus nematode; *Xiphinema*, dagger nematode; *Radopholus*, burrowing nematode; *Rotylenchulus*, reniform nematode; *Helicotylenchus*, spiral nematode; and *Belonolamius*, sting nematode. Root-knot nematodes, *Meloidogyne* spp. have been found all over the world and are known to cause huge losses to crops of economic importance. About 90 species of root-knot nematode have been reported, but four of them, *Meloidogyne incognita*, *Meloidogyne hapla*, *Meloidogyne arenaria* and *Meloidogyne javanica*, cause most of the damage to crop plants. Other nematodes also cause damage to plants but loss varies from country to country depending upon the type of crop infested. The management of nematodes is more difficult than that of other pests because nematodes mostly inhabit the soil and usually attack the underground parts of the plants.
Development of agriculture did not just happen overnight and instantly spread to all corners of the world; it is an evolutionary process that eventually transformed plants from being independent, wild progenitors into fully dependent, domesticated cultivars with the concomitant evolution of agricultural economics. This relationship between humans, the Earth and food sources further affirms soil as the foundation of agriculture, and the vital role played by the microbes in sustaining our farmed and natural ecosystems adding importance to the study. The utilization of bacteria to stimulate plant growth in agriculture has been practiced for millennia, and more recently in human history, Hellriegel and Wilfarth [46] studied the rhizosphere root colonization and suggested the ability of soil bacteria to convert atmospheric N_2 into plant-usable forms, and the establishment of legumes on cultivated lands resulted in improved soil fertility.
Several types of microorganisms have been used to improve nutrient availability in the soil. The plant rhizosphere interacts with a large number of microorganisms that colonize in, on and around the roots of growing plants. They perform both beneficial and harmful associations with the plant roots.

These specialized bacteria that inhabit plant roots and promote plant growth positively are called plant growth-promoting rhizobacteria (PGPR). Plant growth activity of several rhizobacteria has been determined by many workers [116]. Like-wise, PGPR have been defined in different ways by different workers. Kloepper and Schroth [54] defined PGPR as soil bacteria that colonize the roots of plants following inoculation on to seed that enhance plant growth. While, Bishnoi [21] defined PGPR, a diverse group of soil bacteria, are key components of soil-plant systems, where they are engaged in an intense network of interactions in the rhizosphere, thus affecting the plant growth and yield by a number of mechanisms. PGPR (involving symbiotic and free-living) have been applied in farming practices to enhance growth and yields of legumes and nonlegume crops.

It was Kloepper and Schroth [54], who coined the term 'plant growth promoting rhizobacteria' for these beneficial microbes. Since then, the research on PGPR has made great strides and PGPR now represent a wide variety of soil bacteria which, when grown in association with a host plant, result in stimulation of growth of the host. The coevolution between plant and microbes can be best explained in PGPR which show antagonistic and synergistic interactions with microorganisms and soil, either directly or indirectly boosting the plant growth rate. PGPR have greatly influenced the soil characteristic and have a vital role to play in the conversion of barren and poor quality land into cultivable and fertile land that can be used for agricultural purposes. Genera of PGPR include *Pseudomonas*, *Bacillus*, *Azospirillum*, *Agrobacterium*, *Azotobacter*, *Arthrobacter*, *Alcaligenes*, *Serratia*, *Rhizobium*, *Enterobacter*, *Burkholderia*, *Beijerinckia*, *Klebsiella*, *Clostridium*, *Variovovax*, *Xanthomonas* and *Phyllobacterium*.

During the past couple of decades, considerable increase in sustainable agriculture has been noted by the use of PGPR in various parts of the world [28]. Bashan and Holguin [15] divided PGPR into two classes, biocontrol-PGPB and PGPB, but this was not accepted widely by scientists. PGPR are generally divided into two types based on their existence in and around the plant roots. These are: (i) extracellular PGPR (ePGPR); and (ii) intracellular PGPR (iPGPR). The existence of ePGPR has been found in the rhizosphere, on the rhizoplane and in the spaces between cells of the root cortex, whereas the existence of iPGPR has been found inside the roots and in the specialized nodular structures of plant roots. Though the exact mechanisms involved in growth promotion for many microbes are still unclear, various mechanisms have been suggested [164]. Bacterially mediated phytohormone production is the most likely explanation for PGPR activity in the absence of pathogens [23], while siderophore production by PGPR is considered more important for plant growth stimulation when other potentially deleterious microorganisms are present in the rhizosphere [52].

PGPR play a pivotal role in plant function by influencing plant physiology and development, either directly or indirectly. Direct stimulation includes biological nitrogen fixation, producing or changing the concentrations of phytohormones such as auxins, cytokinins, gibberellins (GA) or ethylene, solubilizing minerals like phosphorus and iron, production of siderophores and enzymes, and induction of systemic resistance [109]. The indirect stimulation of plant growth is fundamentally related to biocontrol, including antibiotic production, chelation of Fe in the rhizosphere, synthesis of extracellular enzymes to hydrolyze fungal cell wall and competition for niches within the rhizosphere [109]. Consequently, understanding soil microbial community interactions is fundamental for developing practices to manage phytonematodes.

2. Current management practices for nematodes

Chemical control was the mainstay for reducing nematode population density in most economic crops in intensive production systems throughout much the 20th century [67]. However, environmental and human health concerns reduced the availability of such control options including the use of nematicide Nemagon (active ingredient: 1, 2-dibromo- 3-chloropropane, known as DBCP) in 1979 by EPA. Many other nematicides suffered a similar fate. Cultural practices such as crop rotation in place of extended monocropping with annual crops or rotating crops with non-host crops or resistant cultivars are an economical method for nematode management. Certain nematodes exhibit a high level of specialization and has a host range which allows this nematode to be effectively managed by crop rotation. Whereas nematodes like, *Meloidogyne* spp. has a broad host range which makes rotation options very limited for its management. When both nematode types are present in the field, crop rotation options are very limited for the management of both nematodes. Planting a resistant cultivar is an effective tool for nematode management. Resistant cultivars contain genes that are combined in the host through one or multiple breeding cycles and many of these genes are quantitative. New sources of resistance will be needed for the future. Currently, there is increasing interest in the introduction of biocontrol agents for managing nematodes, partly as a response to public concerns about deleterious effect of synthetic fungicides and biological control using microbial antagonists is one potential alternative to chemical nematicides [34].

3. Biological control of plant-parasitic nematodes

3.1 Definition of biological control

Biological control of nematodes is defined as the reduction in nematode population density through the action of living organisms other than nematode-resistant plant cultivars, which occur naturally or through the manipulation of the environment or the introduction of antagonists [102]. In recent years, biological control agents for plant-parasitic nematode management have attracted more attention, the market for biopesticides is growing, and the interest in microbial control research is increasing.

3.2 Mechanisms of biological control

Mechanisms of biological control acting through antagonistic micro-organisms would have to act directly on the pathogen (antagonism) or through the intermediate agency of the host [12]. Two main mechanisms identified are antagonism (antibiosis, competition for nutrients or niche exclusion and siderophore-mediated suppression) and induced resistance (systemic acquired resistance or SAR and induced systemic resistance or ISR) of biological control of plant pathogens [55]. The most vulnerable stages of plant-parasitic nematodes to manage with biological control are the egg and second-stage juvenile stages. These life stages exist outside of the plant in the water film on soil particles which allows the antagonistic micro-organisms the opportunity to come in contact, infect and parasitize the nematodes. If these two stages of the plant-parasitic nematodes are controlled, the life cycle of the nematodes will be interrupted and result in reduced population density of the nematode thus successful management.

3.3 Antagonists

Biological control studies on PPN have switched from the survey and empirical tests to quantitative experimentation and basic research on the modes of action, host specificity and epidemiology of selected organisms. Biological control is achieved through mechanisms such as parasitism, competition and antibiosis which adversely affect the survival and reproduction of nematodes. The main antagonists used for nematode biocontrol are fungi and bacteria. Chen [30] and Stirling [103] summarized the possible fungi and bacteria for nematode biocontrol including nematode-trapping fungi, endoparasitic fungi, cyst and egg parasites, bacteria such as *Pasteuria* as a hyperparasite of nematodes, predatory and endomopathogenic nematodes and microarthropods, plant growth-promoting rhizobacteria and endophytes. Chen and Dickson [31] reported detailed information on fungal antagonist of nematodes. Other antagonists such as viruses, mites, collembola, turbellarians, oligochaetes and protozoans may reduce nematode population density but are limited on their efficacy [103]. There are many species of soil bacteria which are reported to promote plant growth by producing growth regulators, inducing root exudation and enhancing the availability of nutrients to plant besides control of soil borne plant pathogenic fungi. In this review, we focus on plant growth-promoting rhizobacteria (PGPR) as biological control agents for plant-parasitic nematodes.

4. Plant Growth-promoting Rhizobacteria (PGPR)

Bacteria that colonize roots effectively are termed "Rhizobacteria". Root colonization is the process where bacteria survive on seeds, multiply in spermosphere in response to seed exudates rich in carbohydrates and amino acids, attach on to the root surfaces and colonize the developing root system. Thus, colonization of roots is an active process and not a transitory relation between bacteria and roots in the soil. PGPR are free-living bacteria that colonize plant roots, and cause unapparent and symptomatic infections when applied to seeds or crops, enhance the growth of the plant or reduce the damage from soil-borne plant pathogens. PGPR induces spectrum of resistance against pest and diseases in wide range of crops apart from enhancing crop productivity. Antoun [7]; Lugtenberg & Kamilova [58] classified PGPR as biofertilizers (increasing the availability of nutrients to plant), phytostimulators (plant growth promoting, usually by the production of phytohormones), rhizoremediators (degrading organic pollutants) and biopesticides (controlling diseases, mainly by the production of antibiotics and antifungal metabolites). Several research groups have randomly screened rhizosphere bacteria for antagonistic activity against nematodes [17]. Isolates of *Agrobacterium radiobacter*, *Bacillus subtilis*, *Pseudomonas* spp. that are familiar as antagonists of soil borne bacterial and fungal diseases of plants, also have potential as biological control agents for nematodes. Rhizobacteria-nematodes interactions have been extensively considered to manage plant-parasitic nematodes [79].

4.1 Mode of action

Plant-parasitic nematodes are attacked by a number of microorganisms present in the rhizosphere. These microorganisms in association with the plant rhizosphere have a profound effect on the nematode populations, influencing both the dynamics of nematodes and the dynamics of a large number of antagonistic organisms and parasites present in the rhizosphere. As the present options to control infective stages are unlikely to result in total population control, effective natural enemies that are active at this stage must be capable of reducing nematode populations at least to densities below the economic threshold level. More and more PGPR have been identified as pathogens of plant-parasitic nematodes and have shown suppression effects on nematode pest populations (Table 1). Although the uses and benefits of PGPR-based inoculants are becoming better understood, little is known about the mechanisms by which PGPR induce suppressiveness to plant pathogens, specifically nematodes. For example: Do PGPR suppress soil nematodes via root colonization or through increasing soil microbial activity? Do inoculants that contain multiple strains of PGPR increase soil microbial activity or affect nematode suppression more than inoculants containing one or two strains? PGPR may induce plant growth promotion by direct or indirect modes of action [16]. The mechanism involved in PGPR-mediated plant growth promotion is directly by production of plant growth regulators (auxins, cytokinins, gibberellins) and facilitation of the uptake of nutrients (nitrogen fixation, solubilization of phosphorus). The indirect promotion of plant growth occurs when PGPR lessen or prevent the deleterious effects of plant pathogens on plants by production of inhibitory substances (antibiotics, antifungal metabolites, iron-chelating siderophores, cell wall-degrading enzymes and competition for sites on roots) or by increasing the natural resistance of the host (induced systemic resistance).

The most important species of *Bacillus* genus are known to produce cytotoxins and other toxins, which are responsible for their toxicity against nematodes [117]. The effect of PGPR may be due to colonization of roots and biocontrol activity against nematodes and other pathogens. Several workers have demonstrated the mode of action of *P. fluorescens*, it increased the production of antibiotics, inhibiting early root penetration of phytonematodes by alteration of specific root exudates such as polysaccharides and amino acids which modify nematode behaviour [100]. The significant reduction in root-knot infection caused by *Meloidogyne incognita* has been reported in tomato plants [25]. The direct antagonism by different species of *Bacillus* has been reported by many workers [57, 115] and this may elicit ISR that results in reduction in disease severity by a broad range of pathogens and growth promotion under field conditions [53]. Shanthi and Rajendran [81] reported that *P. fluorescens* and *B. subtilis* induce systemic resistance in banana plants against lesion nematode. Saharan and Nehra [78] in a critical review discussed various PGPR, their mechanisms and multiple effects on various types of plants such as ornamentals, forest crops, vegetables, fruit crops and other agricultural crops. Beneduzi *et al*. [18] demonstrated that rhizobacteria ISR in plants resembles pathogen-induced SAR that rendered uninfected plants more resistant to pathogens in many plant species. They further suggested that PGPR induce resistance through the salicylic acid-dependent SAR pathway, or require jasmonic acid and ethylene perception from the plant for ISR. Rhizobacteria, *Pseudomonas* and *Bacillus* species, are well known for their antagonistic effects and for their potential to trigger ISR. The antagonistic activities of PGPR might be due to synthesis of hydrolytic enzymes, competition for nutrients and suitable colonization of niches on the root surfaces. The regulation of plant ethylene level through ACC-deaminase enzyme can act to modulate the levels of ethylene in response to stress imposed by the infection, production of siderophores, antibiotics and phytohormones. Antagonistic activities of PGPR have also been found due to release of ACC-

deaminase, degradation of Quorum sensing, indole-3 acetic acid and cytokinins signalling [110].

4.2 Commercialization of PGPR

Different stages in the process of commercialization include isolation of antagonist strains, screening, pot tests and field efficacy, mass production and formulation development, fermentation methods, formulation viability, toxicology, industrial linkages and quality control. The success and commercialization of PGPR strains depend on the linkages between the scientific organizations and industries. Since the discovery of rhizobia in 1886 [46], *Rhizobium* inoculants have been commercially produced worldwide, mainly in the developed countries. In 1897, a bacteriological fertilizer based on *B. subtilis* was marketed for inoculation of cereals under the proprietary name Alinit by Bayer AG [50]. During the early 1950s, research findings from China, Russia and several other western countries further prompted the potential use of microbes to be explored for plant disease management and opened new vistas to use PGPR as an alternative to chemical pesticides for the management of soilborne pathogens [51]. Owing to the potential of PGPR, the first commercial product of *B. subtilis* was introduced during 1985 by Gustafson, Inc. (Plano, Texas) in the United States and the strains of *B. subtilis* A-13, GB03, GB07 were sold for the management of soilborne pathogens under the trade names of Quantum, Kodiak and Epic, respectively [22]. In the United States, 60-75% of cotton, peanut, soya bean, corn, vegetables and small grain crops are now treated with commercial products of *B. subtilis* for the management of soilborne pathogens [65]. PGPR have been largely applied in 48 different crops over 3.35 million ha in China [112] and productivity gains as high as 23% in sweet potatoes and 22.5% in potatoes were reported in addition to 85.5% and 80.3%, reduction levels of disease caused by *Xanthomonas oryzae* and *Glomerella cingulata*, respectively. Some of the important PGPR strains along with their commercial products used for combating various diseases in crops as formulated by Chet and Chernin [33] and Glick *et al*. [39] are listed in Table 2.

Among several PGPR strains, Bacillus-based products gained momentum for commercialization since *Bacillus* spp. produce endospores which can tolerate extremes of conditions such as temperature, pH and exposure to pesticides and fertilizers [10]. During mid-1990s in the United States, *B. subtilis* started to be used as seed dressing, with registration in more than seven crops and application to more than 2 million ha [10]. Eighteen different commercial products of *Bacillus* origin are now used in China to mitigate soilborne diseases, applied to an area of 20 million ha of different crop plants [32, 50], 25 million ha of soya beans inoculated with *B. japonicum* in South America and approximately 500,000 ha of wheat and maize inoculated with commercial *Azospirillum* inoculants in Argentina and Mexico [38]. Recently, in India, the PGPR use has increased considerably due to more awareness about the farming practices and now more than 40 stakeholders from different provinces have registered for mass production of PGPR with Central Insecticide Board, Faridabad, Haryana in collaboration with Tamil Nadu Agricultural University, Coimbatore, India [76].

Despite the promising results in lab and greenhouse studies, the field results show lack of consistency and there exist variation in responses from site to site, year to year and for different crops under consideration. The reason for this inconsistency can be attributed to the fact that the experiments are conducted under controlled conditions in the lab and greenhouse settings, whereas the field studies are influenced by a myriad of biotic and abiotic factors. The inherent heterogeneity of the soil is one of the main obstacle, where introduced bacteria sometimes cannot find an empty niche in the soil. These inoculated bacteria have to compete with the often better adapted native microflora for nutrients and space. They cannot withstand this severe competition with the indigenous microflora and as a result shortly after inoculation into the soil, the bacterial population declines rapidly. A threshold number of cells is essential to obtain the intended positive plant response, for example, 10e6-10e7 cells/plant for the *A. brasilense* and this number too varies among different species [13]. Thus in order to exhibit their positive impact on plant growth, these PGPR must survive and multiply in microhabitats associated with the root surface, in competition with other microbiota, at least for the time needed to express their plant promotion/protection activities.

The factors which govern the success of inoculation are (1) the effectiveness of the introduced bacterial strain in terms of colonization, (2) competence with the indigenous microflora, (3) the species and variety of plant can also be a determining factor since different plant species or cultivars produce different types of root exudates, which also influence the activity of the inoculated microorganisms and also serve as substrates for the formation of biologically active substances [19]. So, more research in PGPR need to be diverted towards colonization, about their ecology, survival and activity in the plant rhizosphere. Besides this, reproducibility of the effects of microbial inoculants needs to be tested across a wide range of soil types and environmental conditions. Also, when used in conventional agriculture, the microorganisms must also be compatible with the chemical fertilizers and also withstand the pesticides which are commonly used on seeds or foliage to deter the diseases. Thus, a thorough understanding of the mechanisms utilized by the PGPR is imperative to utilize their full potential in the agriculture system and the advent of new and powerful technologies for studying co-operative microbial interactions in the rhizosphere guarantees a greater understanding of these processes and will facilitate their successful application in the field.

Table 1: Reported PGPR involved in pathogenesis against nematodes

PGPR	Plants	Plant parasitic nematodes	Mode of action	References
Bacillus thuringiensis	-	*Meloidogyne* sp.	Biocontrol (nematicidal property)	Prasad *et al*., 1972
B. subtilis, *B. Pumilus*	-	Root-knot and cyst nematodes	Biocide	Gokte and Swarup, 1988
Pseudomonas sp., *Bacillus* sp.	-	*Meloidogyne* spp.	Biocontrol (nematicidal)	Becker *et al*., 1988
Pseudomonas sp., *Bacillus* sp.	Sugarbeet	*Heterodera schachtii*	Biocontrol	Oostendorp and Sikora, 1989,1990
B. penetrans, *P. chitinolytica*	Lentil, pea and other plants	*M. javanica*, *Meloidogyne* sp., plant-parasitic nematodes	Growth promoting/biocontrol	Stirling, 1984; Chanway *et al*., 1989; Oka *et al*., 1993
B. polymyxa	Spruce seedlings	Plant-parasitic nematodes	Growth promoting/biocontrol	Chanway and Holl, 1993
P. fluorescens, *Rhizobium* sp.	Rice, cucurbits and other plants	Plant-parasitic nematodes, *Hirschmanniella oryzae*, *M. incognita*	Biocontrol	Kloepper and Scroth, 1978; Kloepper, 1993; Hallmann *et al*., 1995; Swarnakumari, 1996; Swarnakumari and Lakshmanan, 1999; Swarnakumari *et al*., 1999
Brevundimonas vesicularis, *Serratia marcescens*, *P. fluorescens*, *Burkholderia cepacia*, *Phyllobacter rubiacerum*,	Cotton	*M. incognita*	Colonize galled tissues and acts as biocontrol	Quadt-Hallmann *et al*., 1997; Hallmann *et al*., 1998, 1999
B. thuringiensis, *Bacillus* spp., *Rhizobium etli*, *B.cereus*	Brinjal, potato and other crops	*Meloidogyne* spp., *Globodera pallida*, *M. incognita*	Beta-exotoxin, nematicidal, lipopolysaccharides, biocontrol	Rai and Rana, 1979; Carneiro *et al*., 1998; Mahdy *et al*.,2000
Azospirillum spp., *B. thuringiensis*	Banana, tomato, pepper, cotton and wheat	Nematodes and *Radopholus similis*	Biocontrol	Mena *et al*., 1997; Bashan, 1998
Rhizobacteria, *B. sphaericus*	Potato	*Globodera* sp.	Induce resistance/biocontrol	Hasky-Gunther *et al*., 1998
B. thuringiensis, *Streptomyces* sp.	Lettuce	*M. hapla*	Biocontrol	Chen *et al*., 2000
Bacillus spp., *Rhizobium* sp.	Tomato and other plants	*M. incognita*, other root-knot nematodes	Biocontrol	Martinez-Ochoa, 2000; Munif *et al*., 2000
Bacillus spp.	Tomato, brinjal	*M. incognita*, *Meloidogyne* sp.	Systemic resistance, biocontrol	Weller, 1988; Munif *et al*., 2000
Rhizobium etli, *P. fluorescens*	Beans, Arabidopsis thaliana, potatoes, cucumber	*M. incognita*	Decreased root galling and acts as biocontrol agent	Hallmann *et al*., 1998, 2001
P. aeruginosa, *P. fluorescens*	Tomato, mung bean, soybean	*M. incognita*, *Meloidogyne javanica*	Root colonization and acts as biocontrol	Siddiqui and Ehteshamul-Haque, 2000a, 2001; Siddiqui and Shaukat, 2003a,b
Pseudomonas sp.	-	Plant nematodes	*In vitro* nematicidal activity	Ali *et al*., 2002
P. fluorescens, *Pseudomonas* spp.	Mustard, soybean, tomato	Plant parasitic nematodes, *Rotylenchulus reniformis*	Auxin, nematicidal activity, induce resistance	Asghar *et al*., 2002; Niknam and Dhawan, 2002
P. fluorescens, *B. thuringiensis*	Pigeon pea	*Radopholus similis*, *P. coffeae* and *Helicotylenchus multicinctus*, *M. incognita*	Inhibitory on egg hatching and nematode multiplication	Shanthi *et al*., 2003; Dhawan *et al*., 2004
Bacillus spp., *Pseudomonas* spp.	Banana, potato	Plant parasitic nematodes, *Heterodera* sp.	Biocontrol	Aksoy and Mennan, 2004; Jaizme-Vega *et al*., 2004
P. aeruginosa, *Bacillus* sp., *Pseudomonas* sp.	Tomato, crop plants	*M. incognita*	Biocontrol	Siddiqui, 2004; From *et al*., 2005; Li *et al*., 2005
B. subtilis, *Pasteuria penetrans*	Banana, tomato	Plant parasitic nematodes	Biocontrol	Jonathan *et al*., 2000; Jonathan and Umamaheshwari, 2006
B. subtilis, *P. fluorescens*	Banana, grapevine	*Pratylenchus* sp., *M. incognita*	Induce systemic resistance, biocontrol	Shanthi *et al*., 1998, 2003; Shanthi and Rajandran, 2006; Van Loon, 2007
Rhizobium sp.	Wheat	Plant parasitic nematodes	Biocontrol	Afzal and Bano, 2008
Rhizobium sp., *P. striata*	Wheat, chickpea	Plant parasitic nematodes	Biocontrol	Afzal and Bano, 2008; Akhtar and Siddiqui, 2008, 2009
Pseudomonas sp., *A. brasiliense*, *Bacillus* spp., *Rhizobium* sp., *B. Subtilis*	Tomato, pigeonpea, lentil, pea, chickpea, citrus	*Meloidogyne* spp., plant parasitic nematodes	Biocontrol, plant growth promoting	Siddiqui and Mahmood, 1995a, b, 2001b; Siddiqui, 2004; Siddiqui *et al*., 2005; Siddiqui and Shakeel,

				2007; Siddiqui and Akhtar, 2008, 2009a; Siddiqui and Fatui, 2009; Shamseldin *et. al*., 2010
Serratia marcescens, *P. fluorescens*, *Pseudomonas* sp., *Bacillus* spp.	Crop plants, tomato, chickpea	Plant parasitic nematodes, *M. incognita*, *Meloidogyne* spp.	Biocontrol, nematicidal activity	Siddiqui and Mahmood, 1997, 1999; Siddiqui, 2006; Mohamed *et al*., 2009; Elyousr *et al*., 2010
Pseudomonas spp., *Bacillus* spp.	Crop plants	Plant parasitic nematodes and other pathogens	Release of hydrolytic enzymes, root colonization, production of antibiotics	Raajimakers *et al*., 2010; Maksimov *et al*., 2011
Pseudomonas spp., *Bacillus* spp., *Azotobacter* sp.	Tomato	*M. incognita*	Plant growth, biocontrol	Anwar-ul-Haque *et al*.., 2011
Pseudomonas spp., *Bacillus* spp., *Azotobacter* spp., *Burkholderia* sp., *Serratia* sp.	Crop plants, black gram	Plant parasitic nematodes, *M. incognita*	Biocontrol	Akhtar *et al*., 2012; Bhat *et al*., 2012
P. fluorescens, *P. aeruginosa*	Pigeonpea	*Pratylenchus loosi*	Biocontrol due to protease activity	Rahanandeh *et al*., 2012
Paenibacillus spp.	-	*Meloidogyne* spp.		Bakengesa, 2016
Bacillus spp.	-	*H. glycines*, *M. incognita*	Biocontrol	Xiang *et al*., 2017a; Xiang *et al*., 2017b
P. fluorescens, *Rhizobium leguminosarum*	Chickpea,bean, lentil,pea, tomato	*M. javanica*	Biocontrol, plant growth promoting	Saeedizadeh, 2016; Tabatabaei and Saeedizadeh, 2017
B. pumilus, *Paenibacillus costume*, *Mycobacterium immunogenum*	Tomato	*M. incognita*	Biocontrol	Cetintas *et al*., 2018

Table 2: Commercial products based on different PGPR strains

PGPR	Products	Crop
Agrobacterium radiobacter	Diegall, Galltrol-A, Nogall, Norbac 84 C	Fruit, nut, ornamental nursery stock and trees
Azospirillum brasilense	Azo-Green	Turf and forage crops
Bacillus cereus	Pixplus	Cotton
Bacillus pumilus	Sonata ASO, Ballard	Oak trees, nurseries and landscapes
Bacillus subtilis	Epic, HiStick N/T, Kodiak, Rhizo-Plus, Serenade, Subtilex	Barley, beans, cotton, legumes peanut, pea, rice and soybean
B. subtilis	Companion	Horticultural crops and turf
Bacillus amyloliquefaciens GB99	Quantum 4000	Broccoli, cabbage, cantaloupe, cauliflower, celery, cucumber, lettuce, ornamentals, peppers, tomato and watermelon
Burlkholderia cepacia	Blue Circle, Deny, Intercept	Alfalfa, barley, beans, clover, cotton, maize, peas, sorghum, vegetables and wheat
Pseudomonas auerofaciens	BioJect, Spot-less	Turf and other crops
Pseudomonas sp. + Azospirillum	BioJect	Turf and other crops
Pseudomonas chloroaphis	AtEze	Ornamentals and vegetables
P. chloroaphis	Cedomon	Barley, oats, wheat and other cereals
Pseudomonas fluorescens	BlightBan A506, Conquer, Victus	Almond, apple, cherry, mushroom, peach, pear, potato, strawberry and tomato
Pseudomonas syringae	Bio-save10	Citrus and pome fruit
Streptomyces griseovirdis K61	Mycostop	Field, ornamental and vegetable crops

Conclusion A ND Future Prospects

The agricultural production depends on complex biological equilibrium in soil, which will ultimately aid in modifying agro-ecosystems and obtaining more favorable conditions for plant growth and health. Beneficial microbial communities, such as PGPR promotes soil ecosystem health that contributes to suppression of nematodes and other pests. Similarly, the presence of PGPR in the rhizosphere may also protect the host root from damage caused by pathogens. With the evolving of molecular biology, biotechnology and bioinformatics, new techniques and studies will provide more guidance for the development of more effective strategies for biological control of PPN. The world's biggest agricultural companies are trying to expand their business in crop protection especially in biological control products. Thus, future success of industries producing microbial inoculants, especially PGPRs, will depend on innovative business management, product marketing, extension education and extensive research. Further optimization is required for better fermentation and formulation processes of effective PGPR strains to be helpful in the biological control of PPN responsible for causing considerable economic losses to crop plants. With the progress of agriculture towards sustainability, microbes as biocontrol agents will find immense potential for its use in future farming.

However, we should be realistic with cautions. Only a few commercial biocontrol products from the rhizobacteria with nematicidal potentials have been developed and used in the agriculture system. Most of the work has been done in pots or under controlled conditions and therefore to ascertain the potentiality of PGPR, extensive studies are needed under field conditions. Currently, biological control agents are not replacing nematicides. The development of biocontrol agents is often unpredictable and too variable for large-scale implementation. Concerted efforts will be required to demonstrate the benefits of the PGPR biocontrol agents to the farmers so that the eco-friendly agents can be popularized. Unless end users are convinced by the benefits of the biocontrol PGPRs by conducting trials of their own, the success stories will remain in the research laboratories only.

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