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Plant growth promoting rhizobacteria (PGPR): A potential alternative tool for nematodes bio-control

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ABSTRACT

The increasing demand of the agricultural produce can be attained by optimizing the productivity potential and by minimizing the losses caused by notorious plant-parasitic nematode of the crops. Chemical based nematode control is an effective strategy to combat this biotic stress, but inappropriate and inadequate application of synthetic pesticides has exerted an adverse effect on bio-flora, fauna and natural enemies. Due to the environmental and regulatory pressure, use of potential biocontrol agents is the most welcomed way for nematode management by the farming community. There is an emerging market for Plant growth promoting rhizobacteria (PGPR) mediated eco-friendly biopesticides for plant-parasitic nematode biocontrol. Moreover, PGPR strains can enhance the plant growth through the production of various plant growth promoting substances. Based on the fact stated above, the present review focused on PGPR based nematodes biocontrol strategies, the direct and indirect mechanism of PGPR for nematode biocontrol and future prospect of PGPR based biocontrol agents against nematodes are discussed.

1. Introduction

Management of plant disease caused by parasitic organisms has become a challenging task to the researchers for sustainable agriculture. More than, 4000 parasitic organisms have been identified and they can be found in most major biomes. Plant parasitic organisms, uptake the water and other nutrient content from their host plants through the vascular tissues (Press and Phoenix, 2005). Among the parasitic organisms, management of nematodes is more difficult due to their inhabitation and mode of parasitism (Gillet et al., 2017). Mostly, nematodes attack underground part of the plants and cause serious yield loss. Approximately, nematode infections reduced the agriculture productivity up to 12.3% worldwide (Singh et al., 2015). Nematodes such as *Meloidogyne* sp. (Root-knot nematodes), *Heterodera* and *Globodera* sp. (cyst nematodes) and *Pratylenchus* sp. (lesion nematodes) considered as a most economically important specious due to their damage and infection level, wide host range and relationship with host plant.

Previously, various synthetic chemical nematicides such as fumigants, organophosphates and carbamates have been used to control the nematodes. Chemical nematicides increased the agricultural and economic potential in the terms of enhanced food and fibres production. On the other hand, application of chemical nematicides resulted in serious environmental rick and health impact to human (Aktar et al., 2009). Some of the chemical nematicides have started to stop their usage due to its hazardous nature to the non-targeted organisms, public health issues and environmental safety (Schneider et al., 2003). Hence, the search for alternative nonchemical, ecofriendly strategy is highly desirable for nematode control. Out of different ecofriendly approaches, plant growth promoting rhizobacterial (PGPR) strains may acts as an efficient nematode biocontrol as well as plant growth promoting agent for plant growth and yield increment. Rhizobacterial strains utilize

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amino acids, sugar and organic compounds released by plant roots for their growth and energy. In mutualism, rhizobacterial strains produced various plant growth promoting substances and biocontrol activity to support their host plant (Karthik et al., 2017). Based on the facts stated above, the present chapter focused on positive correlation of PGPR in nematode biocontrol and as well as improvement of agricultural productivity.

2. Rhizosphere – biological activities

Rhizosphere is referred to a thin layer of soil directly surrounding the root system (Zeppenfeld et al., 2017). Rhizospheric region is one the major lifeline for heterogeneous, diverse and actively metabolizing soil organisms such as free-living rhizosphere bacteria, fungi, foliar and root herbivorous insects and nematodes. In general, biodiversity and biological activities of the rhizospheric organisms are not similar across the rhizospheric environment. Higher biological activities naturally spreads about 2 mm from the root surface and differs significantly from that in the bulk soil in population, types and functions of organisms, thus, the rhizosphere is known to be a hot spot of biological activities (Mendes et al., 2013). Plant roots play a key role in rhizosphere diversity and their biological activities by providing mechanical support as well as facilitate water and nutrient uptake. Moreover, plant roots release wide variety of compounds such as amino acids, organic acids, oligosaccharides, sugar, vitamins, nucleotides, flavonoids, enzymes, hormones, volatile compounds, phenolics, mucilage, carbohydrates and various secondary metabolites, which are increase biological activities in rhizospheric region (Rohrbacher and St-Arnaud, 2016). This micro flora is a major food source for herbivores such as nematodes, springtails and mites, which, in turn, fall prey for other small carnivores such as spiders and centipedes. Saprophytes that are located in rhizospheric region decay the dead remains in rhizosphere and decompose complex molecules into simple molecules. Nutrients and waste released through decomposition process are directly utilized by host plant; because of this routine process make alive the rhizosphere.

3. Nematodes

Nematodes are the major cause of malnutrition not only by sucking blood from human being but also by taking heavy tolls from crop plants. Nematodes are the most stubborn pests of crop plants and are responsible for serious damage to almost all kinds of crops. After hatching from eggs infective juveniles penetrate and feed on the roots of growing plants, stealing nutrients from plants and exposing the roots to attack by other soil borne pathogens, thus play an important role in disease complex (Gheysen and Mitchum, 2011).

Most of the research work has been focused on two major groups of plant parasitic nematodes (PPN) such as cyst (*Heterodera* and *Globodera* sp.) and root-knot nematodes (*Meloidogyne* sp.), due to their major worldwide economic impact. The cyst nematode completes their life cycle in about 30 (*Heterodera* sp.) to 60 (*Globodera* sp.) days under optimum conditions and have six stages: the egg, juvenile stages (J1, J2, J3 and J4) and the adult stage (males or females) (Williamson and Gleason, 2003). The second juvenile stage (J2) is the only stage to infect plant roots, which is vermiform, motile and find host roots using sensory organs located on their body. After finding host root it penetrates and migrates intracellularly and finally reaches for settlement in the vascular cylinder using cell wall degrading enzymes secreted from esophageal glands of the nematodes. There it induce the formation of sophisticated and metabolically active nematode feeding site (NFS) called ‘syncytium’ or ‘transfer cell’ by secreting and injecting proteins/enzymes into a host cell through its stylet (Baum et al., 2007). Large transcriptomic, metabolomics, morphological and physiological changes happens during the formation of NFS such as partial dissolution of surrounding cell walls, enlargement of nuclei, increased density of cytoplasmic organelles, accumulation of endoplasmic reticulum etc., (Hussey et al., 2002; Siddique and Grundler, 2018). After initiation of feeding site, nematodes molts to J3 then J4 and finally to adult male or female. The syncytium provides nourishment for nematode development and reproduction. The female becomes sedentary, swollen and remain attached to the roots and posterior end of the body comes out by rupturing the root cells. Males retain their vermiform shape and comes out of the roots to fertilize the protruding females. The females are generally white to yellow colour, they extracts nourishment from the syncytium to support egg production, most of the eggs were laid inside the female's body, while few cyst nematodes secrete a small amount of eggs inside gelatinous mass into the soil. After the completion of life cycle female body wall thickens to form a hard brown leathery sac known as “cyst”. Cyst acts as an initial protection for about 200–500 eggs against adverse conditions until their hatch under favourable environmental and crop conditions (Jasmer et al., 2003).

In contrast, the life cycle duration of root knot nematodes (RKN) varies from few days to several months depending on factors such as moisture, temperature, availability of a suitable host and the species of RKN. The juveniles locate and penetrate the host root using host cues and piercing action of stylet, respectively. The juvenile moves intercellularly inside the root tissues and finally reaches the vascular bundle. Then nematode injects some esophageal gland secretions for the formation of 5–7 multinucleate and metabolically active feeding cells called “giant cells” which are the result of acytokinetic mitosis (Mhatre et al., 2015; Siddique and Grundler, 2018). The J2 feeds and molts thrice to become adult male or female. Occasionally vermiform males migrate out of the roots to locate and fertilize the females, whereas, apple shaped swollen females remain sedentary inside the roots and produce eggs in a gelatinous matrix.

4. Impact of nematodes on agriculture yield and productivity

Nematodes are directly targeting the host plant root system, which obstruct the nutrient and water uptake, which leads to reduced agronomic performance, overall quality and yield of crop plants. Plant parasitic nematodes have been widely recognized as one of the potential hidden enemy responsible for huge losses in different agricultural and horticultural crops. In monitory terms, PPN's are responsible for an estimated yield loss of about $157 billion in world and $40.3 million from India, which shows an average yield loss of 12.3% (Abad et al., 2008; Singh et al., 2015).

5. Nematode management

To avoid these huge losses, nematode management is of prime importance. There are various options available for limiting this damage, including the use of crop rotation, intercropping, deep ploughing, nematicides, resistant cultivars and biological control. However, due to the formation of protective cysts, gelatinous matrix and several survival adaptations, survival in the soil without host, making crop rotation, intercropping and deep ploughing unattractive. Chemical method was very effective to control nematodes but it off-limits farmers due to its high cost, environmental issues and health hazards whereas, continuous growing of resistant cultivars on a same piece of land leads to loss of resistance due to development virulent pathotypes in due course of time. Biological control is the most effective and efficient way to overcome the nematodes stress, which also aims at safer crop protection (Timper, 2014). Biological control is defined as "A reduction of nematode populations which is accomplished through the action of living organisms other than the nematode-resistant host plant, which occurs naturally or through the manipulation of the environment or the introduction of antagonists" (Tian et al., 2007). The main aim of biological control is to reduce the populations of harmful nematodes by increasing the natural enemies in the soil. Soil is a reservoir for micro floras that are highly varied in composition and activity. Microbial flora in the rhizosphere acts as front line defence mechanism against several

Table 1
Effects of PGPR inoculation on plant parasitic nematodes biocontrol.

PGPR strains	Agriculture crops	Nematodes	Reference
Bacillus subtilis	Tomato	*Rotylenchulus reniformis*	Niknam and Dhawan (2001)
Azotobacter chroococcum	Tomato	*Meloidogyne incognita*	Chahal and Chahal (2003)
	Brinjal	*Meloidogyne javanica*	Bansal and Verma (2002)
Pseudomonads stutzeri	Turmeric	*Meloidogyne incognita*	Seenivasan et al. (2001)
Pseudomonads fluorescens + oil cakes	Citrus	*Tylenchulus semipenetrans*	Reddy et al. (2000)
	Carrot	*Rotylenchulus reniformis*	Rao and Shylaja (2004)
	Okra	*Meloidogyne incognita*	Devi and Dutta (2002)
Pseudomonads fluorescens	Bean	*Meloidogyne javanica*	Tabatabaei and Saeedizadeh (2017)
and *Rhizobium leguminosarum*			
Bacillus subtilis	–	*Meloidogyne incognita*	Adam et al. (2014)
Pseudomonads putida, Pseudomonads fluorescens, Serratia marcescens, Bacillus	Tomato	*Meloidogyne incognita*	Almaghrabi et al. (2013)
amyloliquefaciens, Bacillus subtilis and *Bacillus cereus*			
Pseudomonads fluorescens	Banana	*Meloidogyne javanica*	Rodrıguez-Romero et al. (2008)
Azotobacter chroochoccum and			
Azospirillum sp.		*Meloidogyne incognita*	Sharma and Mishra (2003)
Bacillus isolates		*Meloidogyne incognita, Heterodera cajani*	Siddiqui and Shakeel (2007)
Paenibacillus macerans		*Meloidogyne exigua*	Oliveira et al. (2009)
Pseudomonads fluorescent		*Heterodera cruciferae*	Aksoy and Mennan (2004)
Bacillus sp.	Tomato and pepper	*Meloidogyne incognita*	Kokalis-Burelle et al. (2002)
Bacillus velezensis and *Bacillus mojavensis*	Soybean	*Heterodera glycines*	Xiang et al. (2017)
Paenibacillus polymyxa and *Paenibacillus lentimorbus*	Tomato	*Meloidogyne incognita*	Son et al. (2009)
Bacillus subtilis, Paenibacillus polymyxa and *Burkholderia cepacia*	Tomato	*Meloidogyne incognita*	Siddiqui and Akhtar (2009)
Bacillus sp., Azotobacter sp., Pseudomonads putida and *Pseudomonads fluorescens*	Tomato	*Meloidogyne incognita*	Anwar-ul-Haq et al. (2011)
Bacillus consortium	Papaya	*Meloidogyne incognita*	Jaizme-Vega et al. (2006)
Different PGPR consortium	Tomato	*Meloidogyne* sp.	Alfianny et al. (2017)
Bacillus firmus	Corn, cotton, sorghum,	*Heterodera* sp.,	Bayer Crop Science (2016b)
	soybean, sugar beet	*Meloidogyne* sp. and *Pratylenchus* sp.	
Pasteuria sp.	Cotton	*Rotylenchus reniformi*	Schmidt et al. (2010)
Pseudomonas putida and			
Pseudomonas alcaligenes	Chickpea	*Meloidogyne incognita*	Akhtar and Siddiqui (2009)
Pseudomonas alcaligenes and			
Bacillus pumilus		*Meloidogyne incognita*	Akhtar and Siddiqui (2008)
Bacillus amyloliquefaciens	Tomato	*Meloidogyne incognita*	Burkett-Cadena et al. (2008)
Rhizobium etli	Tomato	*Meloidogyne incognita*	Reimann et al. (2008)
Pseudomonas oryzihabitans	Potato	*Globodera rostochiensis*	Andreoglou et al. (2003)
Rhizobium etli	Potato	*Globodera pallida*	Reitz et al. (2000)
Rhizobacterial strains	–	*Mesocriconema xenoplax*	Mota et al. (2017)
Bacillus, Enterobacter and			
Pseudomonas	–	*Meloidogyne incognita*	El-Sayed et al. (2014)
Bacillus sp.	Yellow melon	*Meloidogyne incognita*	Medeiros et al. (2009)
Bacillus sp. and *Lysobacter* sp.	Tomato	*Meloidogyne incognita*	Zhou et al. (2016)
Bacillus subtilis	carrot	*Meloidogyne incognita*	Rao et al. (2017)
Bacillus tequilensis and *Bacillus flexus*	Basil	*Meloidogyne incognita*	Tiwari et al. (2017)
Pseudomonas protegens	–	*Nacobbus aberrans*	Lax et al. (2013)
Paenibacillus polymyxa, Bacillus megaterium and *Bacillus circulans*	Tomato	*Meloidogyne incognita*	El-Hadad et al. (2011)
Nitrogen fixing bacteria	Banana	*Meloidogyne incognita* and *Radopholus similis*	Aggangan et al. (2013)
Streptomyces sp.	Eggplants	*Meloidogyne incognita*	Rashad et al. (2015)
Streptomyces sp.	–	*Meloidogyne incognita*	Ruanpanun et al. (2010)
Bacillus subtilis,			
Pseudomonas fluorescens, Pseudomonads stutzeri and *Paenibacillus polymyxa*	chickpea	*Meloidogyne incognita*	Khan et al. (2012)
Stenotrophomonas maltophilia,B. mycoides and *Pseudomonas* sp.	Potato	*Paratrichodorus pachydermus* and *Trichodorus primitivus*	Insunza et al. (2002)
Bacillus subtilis	Banana	*Meloidogyne incognita*, *Pratylenchuscoffeae*, *Radopholus similis* and *Helicotylenchus multicinctus*	Jonathan and Umamaheswari (2006)
Pseudomonas aeruginosa	Mungbean	*Meloidogyne* sp.	Siddiqui et al. (2001)
Pseudomonas aeruginosa and *Bacillus subtilis*	Tomato	*Meloidogyne javanica*	Siddiqui (2002)
B. thuringiensis	–	*Meloidogyne incognita*	Dhawan et al. (2004)
Pseudomonas striata and *Rhizobium* sp.	Pea	*Meloidogyne* sp.	Siddiqui and Singh (2005)
Pseudomonas fluorescence	Mungbean	*Heterodera cajani*	Latha et al. (2000)
Pseudomonas fluorescens	Tomato	*Meloidogyne javanica*	Eltayeb (2017)
Pseudomonas fluorescens	Castor and Cotton	*Rotylenchulus reniformis*	Poornima (2015a)
Pseudomonas fluorescens	Tomato	*Meloidogyne incognita*	Poornima (2015b)
Pseudomonas fluorescens	Banana	*Helicotylenchus Multicinctus*	Selvaraj et al. (2014)
Different PGPR strains	Grapevines	*Meloidogyne ethiopica*	Aballay et al. (2013)

(*continued on next page*)

Table 1 (*continued*)

PGPR strains	Agriculture crops	Nematodes	Reference
Consortium: *Pseudomonads fluorescens* (Pf 128) and *Bacillus subtilis* (Bbv 57)	Tomato	*Meloidogyne incognita*	Meena et al. (2012)
Bacillus polymyxa +VAM	Tomato	*Meloidogyne incognita*	Liu et al. (2012)
Pseudomonas fluorescens	Jasmine	*Meloidogyne incognita*	Seenivasan and Poornima (2010)
Methylobacterium fujisawaense	–	*Meloidogyne incognita*	Prabhu et al. (2009)
Pseudomonas fluorescens	Okra	*Meloidogyne incognita*	Veronika and Khan (2015)
Pseudomonas fluorescens and *B. Subtilis*	Rice	*Meloidogyne graminicola*	Priya (2015)

pathogens and can be exploited as ideal bio-control agents (Mendes et al., 2013). Use of such bio-friendly organisms helps to maintain ecological balance and achieve pollution free environment. After establishment, bio-agent remains effective in soil for long periods and in due course of time it leads to the concept of “suppressive soils” where the population of PPNs are being suppressed by these soil dwelling microorganisms naturally (Trudgill et al., 2000).

Biocontrol of nematodes can be achieved mainly by fungal and bacterial antagonists. The fungal antagonists of nematodes consists of a variety of microorganisms which includes nematode-trapping fungi, endo-parasitic fungi, toxin producing fungi, vesicular-*Arbuscular mycorrhiza* (VAM) and parasites of sedentary nematode, females and eggs (Tranier et al., 2014). Whereas, the bacterial antagonists consist of mainly three groups *viz.*, epiphytic, endophytic and endoparasitic bacteria. Bacteria achieve biological control through the mechanisms like parasitism, competition and antibiosis (Abd-Elgawad and Kabeil, 2012).

6. Plant growth promoting rhizobacteria (PGPR)

The soil surrounding the plant roots “rhizosphere” harbours many species of bacteria, which promotes plant growth by producing plant growth regulators and enhancing the availability of nutrients besides inducing resistance in plants which provides front line defence against soil borne plant pathogens. These bacteria are grouped as plant growth-promoting rhizobacteria (PGPR). PGPR is a diverse group of free-living soil bacteria that colonize rhizosphere and contribute to plant growth promotion which in turn increase the yield of agriculture crops (Kumar et al., 2016). Diverse soil microorganisms such as *Acinetobacter* sp., *Alcaligenes* sp., *Azospirillum* sp., *Agrobacterium* sp., *Arthrobacter* sp., *Azotobacter* sp., *Bacillus* sp., *Burkholderia* sp., *Bradyrhizobium* sp., *Cellulosimicrobium* sp., *Enterobacter* sp., *Erwinia* sp., *Frankia* sp., *Flavobacterium* sp., *Klebsiella* sp., *Microbacterium* sp., *Proteus* sp., *Pseudomonas* sp., *Rhizobium* sp., *Serratia* sp. and *Xanthomonas* sp. are the basic constituents of rhizosphere flora and exhibit successful rhizosphere colonization (Bhattacharyya and Jha, 2012; Tailor and Joshi, 2014; Karthik et al., 2016; Teymouri et al., 2016). Among the rhizobacterial genera, *Azospirillum*, *Pseudomonas* and *Bacillus* are the widely explored commercial rhizosphere-colonizing microorganisms. The success in use of these rhizospheric bacteria for beneficial purposes such as phytostimulation, biofertilization, phytoremediation and biocontrol depends on their colonization in rhizosphere. Rhizospheric microorganisms have the ability to enhance the plant growth by production of various plant growths promoting substances and eliminating phytopathogens/nematodes, which has been discussed clearly in following sections. PGPR were also reported to be the potential agent to reduce damage caused by plant parasitic nematodes and the interaction was studied extensively for the efficient management of plant parasitic nematodes (Tabatabaei and Saeedizadeh, 2017; Rashad et al., 2015).

Pseudomonas sp. and *Bacillus* sp., belongs to aerobic endospore-forming bacterial group are the dominant antagonists of PPN's from rhizosphere. Several strains of *Bacillus* can suppress nematodes and promotes the plant growth. In addition, a direct antagonism was also reported by *Bacillus* sp. towards PPN's *viz.*, *Meloidogyne, Heterodera* and *Rotylenchulus* (Siddiqui and Mahmood, 1999; Kokalis-Burelle et al., 2002; Li et al., 2005). The rhizospheric strains of *Pseudomonas* also exhibit pathogenic mechanisms against PPN's (Kerry, 2000; Siddiqui et al., 2005). Studies were made to understand the mechanisms involved in the reduction of PPN populations during *Pseudomonas*-PPN's interaction through the production of antibiotics and induced systemic resistance (ISR) (Siddiqui and Shaukat, 2003). Along with these two major antagonists, several other rhizobacteria were also reported as antagonists of PPN's includes the members of the genera such as *Agrobacterium, Actinomycetes, Arthrobacter, Aureobacterium, Alcaligenes, Azotobacter, Azospirillum, Bacillus, Beijerinckia, Burkholderia, Bradyrhizobium, Chromobacterium, Clostridium, Clavibacter, Comamonas, Curtobacterium, Corynebacterium, Desulforibtio, Desifovibri, Enterobacter, Gluconobacter, Hydrogenophaga, Flavobacterium, Klebsiella, Phyllobacterium, Methylobacterium, Phingobacterium, Pseudomonas, Serratia, Rhizobium, Streptomyces, Stenotrotrophomonas,* and *Variovorax* (Tian et al., 2007; Siddiqui and Mahmood, 1999; Wani, 2015). PGPR strains when used as microbial inoculants have shown plant growth promotion as well as nematicidal activity are represented in Table 1. Their utilization can be helpful in both attaining substantial increase in plant growth and suppression of nematodes. Therefore, PGPR plays significant role in the development of sustainable agriculture system and is one of the major components in integrated nematode management (Abd-Elgawad and Kabeil, 2012).

7. Mechanism of PGPR in nematode suppression

The rhizobacteria exhibits different mode of actions in the rhizosphere to suppress plant parasitic nematodes. The mechanism of nematode suppression can be categorized manly in two major headings *viz.*, direct antagonism by producing enzymes, toxins and other metabolic products and indirect effect by regulating nematode behaviour, altering root diffusates and inducing the production of repellents by host that adversely affects the host recognition, alteration the nematode feeding site development or sex ratio inside the root tissue, promoting plant growth, competing for essential nutrients and inducing systemic resistance (Siddiqui and Mahmood, 1999; El-Nagdiand Youssef, 2004).

7.1. Direct antagonism

7.1.1. Antibiosis

Antibiotics are low molecular weight organic compounds produced by microorganisms. It plays an important role in the biocontrol of several pests by means of competition and parasitism (Raguchander et al., 2011). Antibiosis is an important phenomenon in disease suppression by fluorescent pseudomonads. Most rhizobacteria act against PPN's by producing toxins, metabolic by-products and enzymes. This helps in inhibition of nematode hatching, development, survival and reproduction (Siddiqui and Mahmood, 1999). The ammonia produced at the time of decomposition of nitrogenous organic materials by ammonifying bacteria, is toxic to nematodes and helps in reduction of nematode populations. It is additionally reported that *P. fluorescens* produce secondary metabolites like 2–4-diacetylphloroglucinol which reduced the population of cyst nematodes (Siddiqui andShaukat, 2003). Whereas, some rhizobacteria was found to produce compounds like hydrogen cynamide, which kills deleterious organisms from the

rhizosphere and helps to create a favourable environment for better plant growth (Tian et al., 2007). Rose et al. (2012) also found that the presence of *P. fluorescens* is responsible for reduction in nematodes growth rate and found most effective when combined with neem cake. In a study, three genera of PGPR *Azospirillium*, *Azotobacter*, *Rizobium* and a mycorrhizal genus *Glomus* sp. have been reported to lessen the root galling caused by *M. javanica* in chickpea significantly (Siddiqui and Mahmood, 2001).

7.1.2. Production of lytic enzymes

Enhancement of growth through activity of enzymes is another mechanism of PGPR by producing certain enzymes such as chitinases, peroxidase, phenylalanine ammonia lyase, dehydrogenase, lipases, β-glucanase, proteases, phosphatises etc. *Corynebacterium paurometabolu* was found to produce hydrogen sulphide and chitinase, which inhibit nematode egg hatching (Mena and Pimentel, 2002). Three bacterial isolates *viz.*, *Stenotrophomonas maltophilia, B. mycoides* and *Pseudomonas* sp. from the roots of nematicidal plants showed 56 – 74% reduction in the *Tricodorid* nematode population in potato. Further, these bacteria were characterized for phenol oxidation and antifungal activity with production of hydrolytic enzymes and HCN (Insunza et al., 2002). Study to evaluate the effect of 16 potential PGPR isolated from roots of grapevines, seven isolates viz., *S. marcescens, Pantoea agglomerans, C. acidovorans, Sphingobacterium spiritivorum, A. piechaudii, B. mycoides* and *S. plymuthica* proved effective in inhibiting damage and reproduction of the *M. ethiopica*. The secondary metabolites of all strains showed significant hatching inhibition of the *M. ethiopica* and among the isolates *B. megaterium* and *P. putida* were found most effective (Aballay et al., 2013).

7.1.3. Induced Systemic Resistance (ISR)

Induced resistance is the enhanced plant defence ability, which is acquired after appropriate stimulation against broad spectrum pests and diseases. The increased defence response due to an inducing agent after pathogen infection is called induced systemic resistance (ISR) or systemic acquired resistance (SAR) (Van-Loon, 2000) (Fig. 1). The ISR can be induced by rhizobacteria, whereas the resistance induced by other pathogens is called SAR. This induced resistance provides non-specific protection against wide range of pathogens *viz.*, fungi, bacteria, nematodes, viruses and insect pests (Beneduzi et al., 2012). There are several defence enzymes that have been associated with systemic resistance include phenylalanine ammonia lyase (PAL), polyphenol oxidase (PPO), peroxidase (PO), superoxide dismutase (SOD), lipoxygenase (LOX), catalase (CAT), chitinase, ascorbate peroxidase (APX), β-1,3-glucanase and proteinase inhibitors (Pokhare et al., 2012; Mhatre et al., 2017). These enzymes initiate the induction of resistance by producing phytoalexin and phenolic compounds (Viswanathan et al., 2003).

Several studies demonstrated that rhizobacteria reduce nematodes severity by inducing plant systemic resistance (Ramamoorthy et al., 2001; Pieterse et al., 2002). This induced resistance is achieved by mechanical and physical strengthening of cell wall by means of cell wall thickening, callose deposition and phenolic compound accumulation or by synthesis of several biochemical compounds up-regulated in defence reaction *viz.*, PR proteins, phytoalexin, lipopolysaccharides (LPS's), siderophores, salicylic acid (SA), jasmonic acid (JA), PO, chitinase and other secondary metabolites (Siddiqui and Mahmood, 1999; Ramamoorthy et al., 2001). In contrast, Siddiqui and Shaukat (2004) found that induced systemic resistance by *P. fluorescence* is independent of salicylic acid accumulation in tomato roots.

In a study, the infection of potato cyst nematode and root knot nematode was effectively reduced by *R. etli* by inducing systemic resistance (Hallmann et al., 2001). The role of lipopolysaccharides of *R. etli* as an inducing agent of systemic resistance was studied by Reitz et al. (2000) and found to have direct role in suppressing the recognition and penetration of *G. pallida* and *M. incognita* juveniles (Reitz et al., 2000; Mahdy et al., 2001). Meena et al. (2012) recorded the highest enzymatic activity with lowest nematode population in tomato when treated with consortium of PGPR formulation (*P. fluorescens,* Pf128 + *B. subtilis*, Bbv 57). This shows the potential role of PGPR in inducing systemic resistance against nematodes by activating and accumulating defence enzymes viz., PO, PPO and PAL.

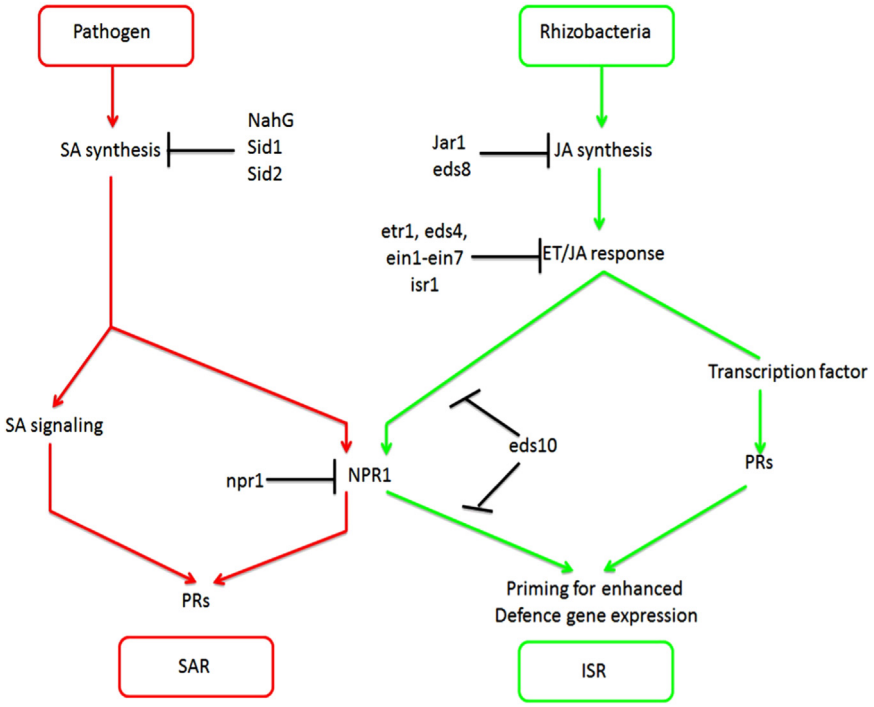

Fig. 1. Schematic representation of the pathogen- induced systemic acquired resistance (SAR) and rhizobacteria-mediated induced systemic resistance (ISR) signal transduction in plants (Pieterse et al., 2002).

7.2. Indirect effects

PGPR facilitates plant growth by production of phytohormones (auxins, cytokines, ethylene, abscisic acid and other plant growth regulator compounds) and siderophores, improvement of nutrient uptake/availability to plants by nitrogen fixation, phosphate solubilization, organic compounds mineralization, which helps to promote plant growth by help to cope up with nematodes stress.

7.2.1. Phytohormone production

Majority of the rhizobacterial strains are able to produce plant growth promoting substances, which regulate the growth and development of plant. PGPR produce several phytohormones/plant growth regulators such as auxins (indole acetic acid, indole butyric acid and phenylacetic acid), cytokines (isopentenyl adenosine, isopentenyl adenine riboside, trans-zeatin ribose and zeatin), gibberellic acid, abscisic acid, ethylene, polyamines, brassinosteroids, jasmonates, salicyclic acid, strigolactones and other plant growth regulator compounds (Gopalakrishnan et al., 2015), which are directly influence plant growth and metabolisms. Among the phytohormones, indole acidic acid is the most common phytohormone. Phytohormones produced by PGPR believed to play an important role in plant growth promotion and plant-bacterial interactions. Main role of microbial phytohormones is the enhancement of plant growth by stimulates cell division and elongation, tissue expansion and indicative beneficial effects on plant growth and yield (Karthik et al., 2016; Khan et al., 2009). Moreover, microbial indole acetic acid increases the lateral and adventitious rooting leading to improved mineral and nutrient uptake (Arora et al., 2013; Shaikh and Saraf, 2016). Previous research reports highlighted that may PGPR strains produce either single phytohormone or multiple phytohormones (Karthik and Arulselvi, 2017). It has been suggested that phytohormones synthesized by PGPR's may prevent the deleterious effects of various environmental stresses (Glick, 2010). Inoculation of phytohormones producing PGPR to field by seed application results in enhanced plant growth and nematode biocontrol (Khan et al., 2012). For instance, phytohormones producing *Streptomyces* strains increase the growth of eggplants by potentially reducing the number of galls and nematode egg mass (Rashad et al., 2015). Similarly, Ruanpanun et al. (2010) reported the nematicidal activity of phytohormone producing *Streptomyces* sp. Therefore, any direct influence on phytohormones production by bacteria may in turn affects their phyto-stimulating efficiency.

7.2.2. Nitrogen fixation

Nitrogen is an important macronutrient for plant growth and development, which is involved photosynthesis, building material in protein synthesis and major component in nucleic acids in the form of nitrogenous bases. Agriculture soil contains limited quantity of nitrogen due to regular nitrogen loss. However, plants unable to utilize atmospheric nitrogen directly. In this circumstance, PGPR plays a key role in nitrogen fixation and nutrient supplementation. These nitrogen-fixing microorganisms classified into two different groups like symbiotic and free living nitrogen-fixing microorganisms (Gopalakrishnan et al., 2017). Nitrogen fixing PGPR strains with nematicidal activity plays an important role in sustainable agriculture, which provides nitrogen source as well as nematode free environment to the host plant. Interestingly, Aggangan et al. (2013) reported that inoculation of nitrogen fixing bacteria significantly promote the banana growth by suppressing the population *Meloidogyne incognita* and *Radopholus similis*. Similarly, El-Hadad et al. (2011) also reported the plant growth promotion and nematicidal activity of nitrogen fixing microorganism *Paenibacillus polymyxa*. Recently, El-Sayed et al. (2014) reported the nematode biocontrol activity of nitrogen fixing PGPR strains. Some PGPR genera such as *Rhizobium, Bradyrhizobium, Sinorhizobium, Mesorhizobium* and *Frankia* have the ability to fix atmospheric nitrogen and provide it to plants and helps in plant growth promotion (Zahran, 2001; Vessey, 2003; Arora et al., 2012; Gaby and Buckley, 2012; Dash et al., 2017).

7.2.3. Phosphate and potassium solubilization

Phosphate is another major nutrient source for plant growth, after nitrogen. Phosphate plays several key roles in plant growth such as nucleic acid composition, protein synthesis, cell division, development of new tissues and associated with complex energy transformation (Gopalakrishnan et al., 2015; Oves et al., 2013). On the other hand, availability of phosphate compounds in agricultural sites in the form of insoluble state. PGPR from soil employs to convert unavailable forms of phosphorus to available form by chelation, production of organic acid and acidification (Gulati et al., 2010), thereby influence the host plant growth and nutrient availability. Several PGPRs genera as such as *Arthrobacter, Bacillus, Beijerinckia, Burkholderia, Enterobacter, Erwinia, Flavobacterium, Microbacterium, Pseudomonas, Rhizobium, Rhodococcus* and *Serratia* are previously reported as phosphate solubilizers (Zaidi et al., 2009; Sharma et al., 2013; Ahemad et al., 2009; Oves et al., 2009). Guang-Can et al. (2008) reported that bacterial strains *B. cereus*, *B. megaterium*, *B. caryophylli*, *P. cichorii* and *P. syringae* are possess both phosphate solubilization and mineralization capacity, thereby increase the bioavailability of phosphate. Inoculation of phosphate solubilizing *Mesorhizobium mediterraneum* strain enhanced the growth of chickpea and barley (Peix et al., 2001). Inoculation of phosphate solubilizing microorganism influence the plant growth by nutrient facilitation and nematicidal activity. In agreement with this, El-Hadad et al. (2011) documented that inoculation of phosphate solubilizing bacteria *B. megaterium* increased the shoot length, shoot and root dry weight and N, P, K content of tomato plant and reduced the rhizospheric population of *M. incognita*.

Potassium is an important macronutrient for plant after nitrogen and phosphate. In plant growth, potassium plays the crucial role in biochemical and physiological functions (Zhang and Kong, 2014). However, maximum quantities of potassium containing minerals (muscovite, orthoclase, biotite, feldspar, illite, mica) are present in the soil as a fixed form, which is not easily utilized by the plant. Similar to phosphate solubilizing bacteria, some rhizospheric microorganisms solubilize insoluble potassium to release potassium in accessible form for plant growth and yield. Potassium solubilizing PGPR's involved various mechanisms such as excreting of organic acid, chelation, reduction, complexolysis, exchange and acidolysis for potassium solubilization (Meena et al., 2016). Various microbial genera such as *Acidothiobacillus ferrooxidans, B. edaphicus, B. mucilaginosus, Burkholderia, Paenibacillus* sp. and *Pseudomonas* sp. involved in potassium solubilization (Han and Lee, 2006). El-Hadad et al. (2011) also documented the positive effect of potassium solubilizing bacterial inoculation on tomato plant growth and nematicidal activity.

7.2.4. Siderophores and ammonia production

Iron is an essential element for living organisms for may biological processes such as respiration, electron transport, photosynthesis, co-factor for many enzymes, etc., (Aguado-Santacruz et al., 2012). Under aerobic atmosphere, iron exists in an insoluble from in soil, which is not available easily for living organisms. At low iron bioavailability environmental condition, PGPR have evolved specific mechanisms to chelate insoluble form iron by the production of low molecular weight siderophores (Dell'mour et al., 2012). A large number of PGPR including *Aeromonas, Azadirachta, Azospirillum, Azotobacter, Bacillus, Burkholderia, Enterobacter, Pseudomonas, Rhizobium, Serratia* and *Streptomyces* sp. helps in production of siderophores, which transport iron into plant cells aiming better growth promotion (Cornelis, 2010; Sujatha and Ammani, 2013). Siderophores production and nematicidal activity of *Streptomyces* sp. was reported by Ruanpanun et al. (2010). Similarly, El-Sayed et al. (2014) have reported the multifarious plant growth promoting activities of *Bacillus* sp., *Enterobacter* sp. and *Pseudomonas* sp. along with nematicidal activity.

Plant growth promoting substances from PGPR strains directly

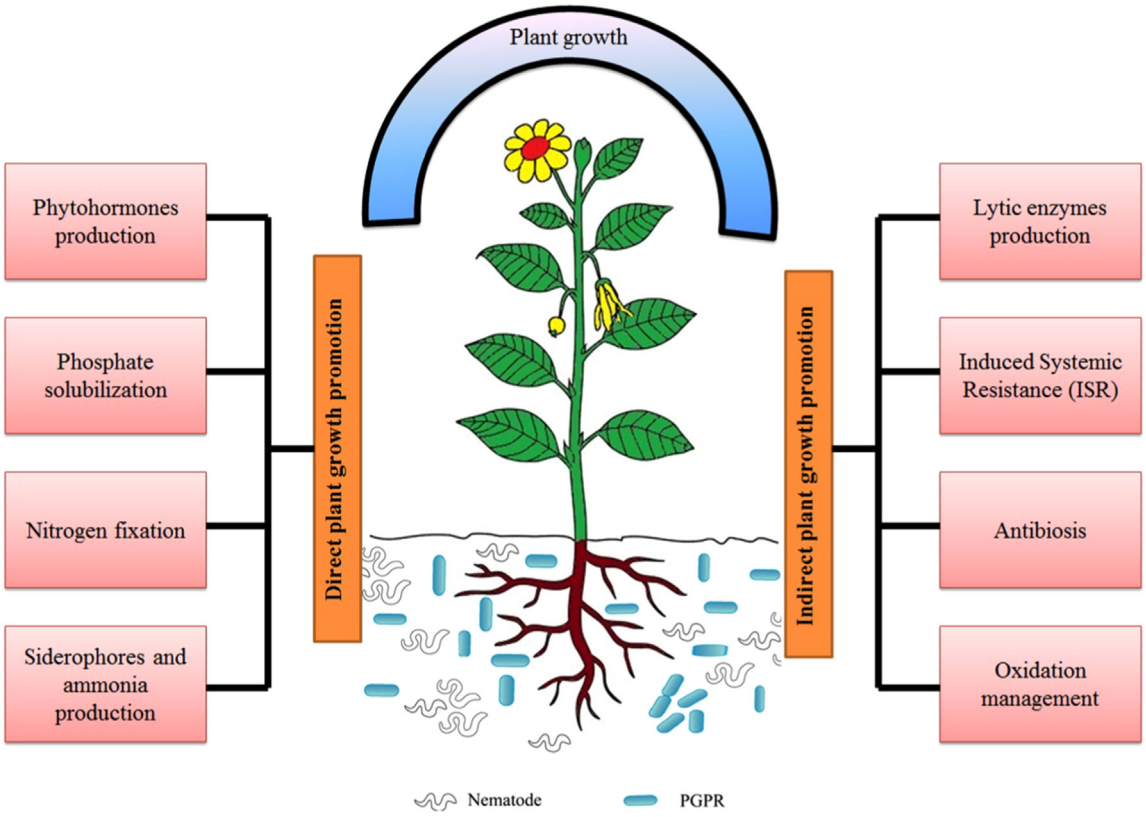

Fig. 2. Schematic diagram represent the plant growth promoting and nematicidal activity of PGPR.

influence their host plant growth by inducing the cell division, tissue development, physiological and biochemical metabolisms. However, these PGPR strains provide additional support to the host plant to cope up with nematode infection. Over all plant growth promoting and nematode biocontrol mechanisms of PGPR has been highlighted in Fig. 2.

8. Commercialization of PGPR

The success of PGPR commercialization is the outcome of the collaboration between interdisciplinary scientific organizations and private industries and its extension to the stakeholders (Tabassum et al., 2017). The economical and viable market, consistent and broad spectrum action, safety and stability, longer shelf life, low investment costs and easy availability of career materials are the requisites for the commercial success of any PGPR strains. The following PGPR based bionematicidal products were already been commercialized in market:

"**Deny**"→*B. cepacia* based commercial biocontrol formulation inhibit egg hatching and mobility of nematode juveniles (Meyer and Roberts, 2002).
"**BioYieldTM** and **GustafsonLLC**"→ *Paenobacillus macerans* and *B. amyloliquefaciens* based commercial transplant mix for management of nematodes in tomato, strawberry and bell pepper, from USA (Meyer, 2003).
"**BioNem**"→ *B. firmus* based product from Israel, for control of root knot and other nematodes. The pre-plant application of BioNem significantly reduced nematode populations as well as root infestation by nematodes in several vegetable crops and herbs resulting in an overall yield improvement (Giannakou and Prophetou-Athanasiadou, 2004). Table 2 highlights some commercial available PGPR formulations in India.

Table 2
Products commercially available in India.

Organism	Formulation name/type	Use
Pseudomonas fluorescens	1% WP, 1% AS	Nematicide
Bacillus subtilis	1% WP, 1% AS	Nematicide
Pseudomonas fluorescens	Arka Plant Growth Booster	Plant growth promoter
Pseudomonas fluorescens + *Trichoderma harzianum*	Arka Plant Growth Enhancer and Yield Promoter	Plant growth and yield promoter

9. Future prospects

Enhanced production with better crop protection and improved soil fertility in an eco-friendly manner is the need of hour. Better understanding of the rhizosphere population and their colonization are the prerequisites for proper exploitation of efficient PGPR strains for sustainable agriculture. Combination of molecular and biotechnological tools along with classical approaches will aid in better understanding of rhizosphere biology to improve the efficiency of an integrated nematode management strategy. Further, genetic engineering tools can be used for improving the biocontrol efficiency of PGPR by over expressing several different anti-phyto-pathogen traits synergistically for efficient pest management. The consortium of effective bacterial strains can be explored at its full potential for reducing the harmful impact of different biotic stresses on plant growth. More attention should be given for commercialization PGPR based biopesticides. Future research on optimizing growth conditions, consistent and broad-spectrum action, safety, stability and longer shelf life of PGPR products are indispensible for commercialization success of PGPR.

10. Conclusion

The Green Revolution enhanced global agricultural production and triggered the use of synthetic chemical fertilizers for improving productivity and better crop protection. Excessive use of agrochemicals has become a major threat to human health and the environmental safety; hence, many chemicals have been banned worldwide. Meeting the food demands of escalating populations is a major challenge and this can be fulfilled by increasing productivity of crop by adopting proper crop protection and production measures. These conditions can be achieved with a single but multifaceted strategy i.e. the use of PGPR, which aims at safer crop protection, improved soil fertility, enhanced plant growth and leads to sustainable agriculture. This strategy has wide acceptance worldwide as one of the safe method of pest control and plant growth promotion. With the improvement in PGPR technology by the use of genetic engineering, consortium application and other developments will ensure the stability in production and productivity of the agro-ecosystems, thus leading to an ideal and sustainable agricultural.

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