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RESEARCH ARTICLE

BACTERIA AS BIOCONTROL AGENT AGAINST PLANT-PARASITIC NEMATODES

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ABSTRACT

Plant-parasitic nematodes cause serious yield loss of various agricultural crops. One strategy that has attracted the interest of researchers is the use of biocontrol agent for the management of these nematodes. As a group of biocontrol agent of plant-parasitic nematode, bacteria exhibit diverse modes of action viz. parasitizing; producing toxins, antibiotics, or enzymes; competing for nutrients; inducing systemic resistance of plants and promoting plant health. The aim of this review is to present some of the results of this work, indicating its potential and limitations.

INTRODUCTION

Plant-parasitic nematodes cause substantial yield loss (20.6%) (Sasser, 1989) to various food and fibre crops worldwide (Sasser and Freckman, 1987). Among those plant-parasitic nematodes, Root-knot nematode, Meloidogyne spp. cause yield reduction of a wide range of crops (25% - 75%), mainly in tropical and sub-tropical agricultural areas (Sasser and Carter, 1985). Worldwide estimated monetary losses per year caused by plant-parasitic nematodes are over $100 billion (Perry, 1996). Nematicide though efficient for the control of a range of nematode species, the application of nematicide is harmful to animals and humans, and may cause environmental pollution. Alternatives of chemical approaches for plant-parasitic nematode management include host resistance, crop rotation and the use of biological control agents. Microbial control can be broadly described as the use of microbial inoculums or their derived metabolites to reduce the pest populations below threshold density or to combat its disease establishment on susceptible plants. Microbial pathogens, antagonists and endophytes play a crucial role in the regulation of plant parasitic nematodes in various agro ecosystems (Mankau, 1980; Stirling,1991; Hallmann *et al.,* 1998; Kerry, 1998; Akhtar and Malik, 2000). This microorganism has evolved many simple and complicated ways for affecting particular stages of life cycle of plant-parasitic nematodes. Till now, lots of microbial strains have been screened, and many have been found to be parasitic or antagonistic to plant-parasitic nematodes. Bacteria constitute a major group of soil microorganisms that are capable of preventing infections from a wide range of nematode species including free living and parasites of plants and animals. There is a large body of literature on plant associated bacteria that have shown the capabilities to infect nematodes: *Actinomycetes, Agrobacterium Arthrobacter, Alealigenes, Aureobacterium, Azotobacter, Bacillus, Beijerinckia, Chromobacterium, Clavibacter, Clostridium, Comamonas, Corynebacterium, Curtobacterium, Desulforibtio, Enterobacter, Flavobacterium, Gluconobacter, Hydrogenophaga, Klebsiella, Methylobacterium, Pasteuria, Pseudomonas, Phyllobacterium, Phingobacterium, Rhizobium, Stenotrotrophomonas*, and *Variovorax*. Additionally, several human bacterial pathogens, such as species of *Burkholderia*, *Enterococcus*, *Staphylococcus, Serratia*, *Streptococcus* have also been reported to have antagonistic effects against nematodes (Becker *et al.,* 1988; Gokte and Swarup, 1988;Hallmann *et al.,* 1997; Neipp and Becker, 1999; Sturz *et al.,* 2000;Welbaum *et al.,* 2004; Fravel, 2005; Compant *et al.,* 2005, 2010; Rosenblueth and Martinez-Romero, 2006; Ryan *et al.,* 2008; Saharan and Nehra, 2011; Maksimov *et al.,* 2011; Bhattacharyya and Jha, 2012; Cleopas *et al.,* 2017). Bacteria used in biocontrol of plant parasitic nematodes can be categorized into two groups, parasitic bacteria and non-parasitic bacteria (Siddiqui and Mahmood, 1999). These two groups differ in their mode of action. They act synergistically on nematodes by facilitating the rhizosphere colonization and activity of microbial antagonists.

Parasitic bacteria: *Pasteuria* spp., an obligate, endospore-forming, actinomycetes bacterium, can colonize more than 300

nematode species, including the majority of important PPNs and free-living nematodes (Mankau, 1980; Sayre and Starr, 1988; De Leij *et al.,* 1992; Sikora, 1992; De-Channer, 1997; Cho *et al.,* 2000; Preston *et al.,* 2003). Parasites of the genus *Pasteuria* have a similar life cycle in different hosts, which begins with bacterial spores attaching to nematode juveniles as they move in the soil (Viaene *et al.,* 2006). These spores later germinate, form germ tubes that penetrate the developing juvenile and the germ tubes form primary colonies in the pseudocoelom (Chen and Dickson, 1998). Many daughter colonies that are formed from vegetative micro colonies form sporangia from which endospores are latter formed. The parasitized nematode survives but its fecundity will be greatly reduced with female adults containing as much as two million spores that are released into the soil (Sayre and Wergin,1977; Kerry, 1987; Tian *et al.,* 2007). A single spore binding to the body wall of a J_2 may be enough to cause infection and propagation of the parasite (Preston *et al.,* 2003). There are four described species of *Pasteuria* and several undescribed species, viz., *P. ramose, P. penetrans, P. thornei, P. Nishizawae.* The most common and widespread species, *Pasteuria penetrans*, is mainly parasitic on *Meloidogyne* spp., while *Pasteuria thornei* parasitise lesion nematodes, *Pratylenchus* spp., and *Pasteuria nishizawae* infects cyst nematodes, *Heterodera* spp. and *Globodera* spp.; *Pasteuria usgae* infects *Belonolaimus* spp. (Sayre and Starr, 1988; Viaene *et al.,* 2006). *Pasteuria penetrans* significantly reduced galling caused by *Meloidogyne arenaria* in tomato (Cho *et al.,* 2000). *Pasteuria penetrans* also reduced gall and egg mass in eggplant and soybean (Sharma and Vivaldi, 199). Generally, populations of this bacterium are only efficient parasites of the nematode species from which they originated. Similar studies on *M. arenaria* also resulted in reduction of root galling and overwintering juvenile populations over two subsequent seasons (Chen *et al.,* 1996). Some of the key characteristics that make *P. penetrans* a successful biocontrol candidate are its ability to limit nematode reproduction, reduce infectivity of spore-bearing juveniles, and persist in soil for long periods and its resistance to desiccation and extreme temperatures (Siddiqui and Mahmood, 1999).

Following the successful development of mass propagation methods of some *Pasteuria* isolates, a biocontrol product has since been commercialized for the control of soybean cyst nematodes (Wilson and Jackson, 2013). However, challenges still remain on the management of the broader community of plant parasitic nematodes because *Pasteuria* spp. has narrow host ranges. Many other *Pasteuria* species are known to infect nematodes like *Pasteuria thornei* infects *Pasteuria usgae* infects *Belonolaimus* spp., and *Pasteuria nishizawae* parasitizes. Their capacity to act as biological control agents is influenced by soil physical properties. The number of *Pasteuria* endospores available to infect nematodes is markedly influenced by soil textural properties such as macroporosity, microporosity and aggregate stability, and this probably explains why the parasite is an effective control agent in some situations but not in others (Mateille *et al.,* 2010).Although the use of *P. penetrans* to control RKN is promising, its inability to grow outside its hosts and its host specificity limits its commercial application as an effective biocontrol agent (Jatala, 1986; Kerry, 1987; Becker *et al.,* 1988).

Non parasitic bacteria: Some of these bacteria inhabit the rhizosphere, while others establish endophytic populations in specific ecological niches within the root (Hallmann *et al.,* 1997; Kloepper *et al.,* 1999; Compant *et al.,* 2010). However, regardless of their location, all are able to directly or indirectly promote plant growth. In many cases they suppress pathogens or other detrimental organisms by producing antibiotics, siderophores or lytic enzymes; by detoxifying or degrading pathogen virulence factors; or by inducing systemic resistance to pathogens (Compant *et al.,* 2005).

Rhizobacteria: Bacteria that colonize the rhizosphere are commonly referred to as rhizobacteria. Kloepper and Schroth (1978) coined the term 'Plant Growth Promoting Rhizobacteria' (PGPR) for rhizobacteria capable of enhancing plant growth. PGPR represent all beneficial rhizobacteria which are naturally occurring, free-living soil bacteria that are able to colonize roots and enhance plant growth when added to seeds and roots (O'Sullivan and O'Gara, 1992; Sikora and Hoffmann-Hergarten 1993; Ramazan *et al.,* 2018). Plant health promoting Rhizobacteria (PHPR) are those bacteria that stimulate plant growth by limiting plant pathogens or parasites (Sikora, 1988; Weller and Thomashow,1993; Sikora. and Hoffmann-Hergarten, 1993; Castaneda-Alvarez and Aballay, 2016). *Pseudomonas* is among the most effective rhizospheric bacteria which ameliorate plant growth by restricting the parasitic root pathogens (Oostendorp and Sikora, 1989) through the production of biologically active substances or the conversion of unavailable minerals and organic compounds into forms that are available to plants (Siddiqui and Mahmood, 1999). They also play an important role in decomposition, biodegradation and the carbon and nitrogen cycles and improve seed germination, root development, mineral nutrition, water utilization (Weller, 1988). *Bacillus* spp. also have an important role in plant growth promotion by enhancing the biosynthesis of plant hormones, gibberellic acid (GA3) and indole-3-acetic acid (IAA) that have a close relation with plant nutrient availability. Higher level of plant growth-promoting hormones (GA3 and IAA) and defense-related enzymes such as peroxidase (PO), polyphenol oxidase (PPO) and superoxide dismutase were detected in *B. subtilis* OTPB1 treated plants compared with non-treated plants (Chowdappa *et al.,* 2013; Cleopas *et al.,* 2017).

Endophytic bacteria: Bacteria that reside in the internal tissues of living plants without causing any negative effects, have been found in every plant species and recognized as potential sources of novel natural products (Guo *et al.,* 2008). Endophytic bacteria can form a range of different relationships including symbiotic, mutualistic, commensalistic and trophobiotic. Endophytic microorganisms have an important role in host protection as they are associated with beneficial effects such as plant growth promotion and bio control potential against plant parasitic nematodes (Hallmann *et al.,* 1998; Sturz *et al.,* 2000; Jonathan and Umamaheswari, 2006). Endophytes colonize the same root tissues as sedentary plant-parasitic nematodes as (i) there is a continuum of root associated organisms from the rhizosphere to the rhizoplane or to the epidermis to the cortex (Kloepper *et al.,* 1992); and (ii) endophytic bacteria in roots are mostly derived from the rhizosphere (Compant *et al.,* 2010). Therefore, this association of endophytic bacteria with nematodes throughout the nematode life cycle makes these bacteria excellent candidates for biocontrol strategies. Most research on the interaction of endophytic bacteria with nematodes has been conducted on root knot nematode, *Meloidogyne* spp.(Mekete *et al.,* 2009), but the association of cyst nematodes, *Globodera rostochiensis*

is also of great interest (Hallmann *et al.,* 2001, Siddiqui *et al.,* 2000 ; Ali *et al.,* 2002). Bacterial antagonists, *Rhizobium etli* G12 leads to a reduction in the number of juveniles that penetrate the root and ultimately the number of galls and egg-masses production in *M.incognita* (Martinuz *et al.,* 2013).Nine endophytic bacteria were listed and investigated for biological control of nematodes by Sikora *et al.,* (2007).Most endophytes appear to originate from the rhizosphere or phyllosphere; however, some may be transmitted through the seed. Endophytic bacteria have the potential to remove soil contaminants by enhancing phyto remediation and may play a role in soil fertility through phosphate solubilization and nitrogen fixation (Ryan *et al.,* 2008).

Mode of action of nonparasitic bacteria: Potential targets of nonparasitic bacteria are nematode eggs, juveniles in the soil and sedentary adults on the host roots. Thus the antagonists affect egg hatching, movement of the juveniles through the soil and their attraction and orientation to the host roots, recognition of host tissue and feeding sites, penetration of root tissues (Neipp and Becker 1999).The mechanism by which antagonistic bacteria inhibit plant-parasitic nematodes have been put forth by Sikora and Hoffmann-Hergarten, 1993; Hallmann 2001; Siddiqui *et al.,* 2001.

- Production of antibiotics (metabolic products), enzyme, toxins that kill, inhibited or repelled nematode.
- Degradation of the root exudates that the nematode relies on for host location and to stimulate egg hatch.
- Induction of systemic acquired resistance (SAR).

Production of antibiotics (metabolic products), enzyme, toxins that kill, inhibited or repelled nematode: Metabolites produced by some bacteria, especially *Bacillus* spp., *Pseudomonas* spp. and *Burkholderia* spp. interfere with nematode behaviour, feeding and reproduction, thereby reducing penetration and damage in plants (Sikora and Hoffmann-Hergarten, 1992; Meyer *et al.,* 2000; Viaene *et al.,* 2006). Exuded metabolites reduce hatch and attraction and/or degradation of specific root exudates which control nematode behavior and alter the nematode-plant recognition process or create a hostile environment for nematodes in the rhizosphere (Sikora and Hoffmann-Hergarten, 1993; Mankau, 1995; Siddiqui and Shahid 2003). *Bacillus* species synthesize various types of lipopeptides with specific activities against plant pathogens which give them a unique importance in agriculture. The metabolites produced by *Bacillus* spp. are amphiphilic and surfactant lipopeptides mainly bacitracin, circulins, polymyxins, tyrocidins and surfactin (Brandbury, 1986). Gong *et al.,* (2015) reported those lipopeptides as bacillomycins, iturins and mycosubtilin. Most of the metabolites are produced at the onset of sporulation (Mankau, 1995).Those by-products of *Bacillus* spp. inhibit egg hatching, reduce juvenile survival and/or kill nematodes directly, reduce root penetration and migration (Oostendorp and Sikora, 1989;Racke and Sikora, 1992; Sikora and Hoffmann-Hergarten, 1992; Oka *et al.,* 1993; Meyer, 2003; Padgham and Sikora, 2007;Tian *et al.,* 2007;Lian *et al.,* 2007; Zhang *et al.,* 2012; Adam *et al.,* 2014).The crude metabolites produced by strains of *B. cereus, B. megaterium, B. pumilus, B. subtilis, B. thuringenisis, Enterobacter asburiae, E. cloacae* and *Paenibacillus macerans* caused high mortality in J_2 of *Meloidogyne* spp.(Spiegel *et al.,* 1991; Devidas and Rehberger, 1992; Nagesh *et al.,* 2005; Padgham and Sikora.,2007;Huang *et al.,* 2009; Ying *et al.,* 2010;Lee *et al.,* 2016). Siddiqui *et al.,* (2006) have reported production of metabolites, including HCN and 2, 4-diacetylphloroglucinol (DAPG) by *Pseudomonas fluorescens* strains CHA0. Production of antimicrobial compounds including Phl and Plt by *P. fluorescens* plays a crucial role in the suppression of root-knot nematode. The ability of *P. fluorescens* strain F113 to produce diacetylphloroglucinol (DAPG) was responsible for the increased hatching ability and the reduction in juvenile mobility of *Globodera rostochiensis*. Similar effects on egg hatchability and juvenile mobility of *G. rostochiensis* were obtained *in vitro* in the presence of synthetic DAPG (Cronin *et al.,* 1997). *Pseudomonas chlororaphis* O6 induce mortality in J_2 of root-knot nematodes and inhibit egg hatch (Lee *et al*.2011;Nandi *et al.,* 2015;Kang *et al.,* 2018). B. cereus S2 can produce some secondary metabolites, sphinganine and phytosphingosine, that cause a robust of reactive oxygen (ROS) in the intestinal tract of nematode thereby induce oxidative injury, cell apoptosis and cell necrosis on the reproductive area of Meloidogyne incognita and Caenorhabditis elegans and destroy the internal structure of nematode, therefore make lethal effect on nematode as well as suppress nematode reproduction(Gao *et al.,* 2016). Corynebacterium paurometabolu inhibits nematode egg hatching by producing hydrogen sulphide (Mena and Pimentel, 2002). Siddiqui and Ehteshamul-Haque, (2000), Insunza *et al.,* (2002) and Siddiqui *et al.,* (2003) showed that endophytic bacteria produced specific metabolites, which can inhibit hatch of eggs and the mobility of the second-stage juveniles of nematodes.

Bacillus spp. can synthesize various molecules that are toxic to nematodes. *Bacillus thuringiensis* (*Bt*) the ideal biopesticide, known to specifically kill caterpillars and beetles is also reported to target nematode populations. B. thuringiensis shows nematicidal activity towards M. incognita and Heterodera glycines by producing crystal inclusions (Cry proteins), a toxic proteins during sporulation (Noel, 1990; Zukerman *et al.,* 1993;Leyns *et al.,* 1995).Currently, three families of Cry proteins have been found to exhibit potent activities against the juveniles of nematodes (Cry5, Cry12, Cry13, Cry14, and Cry21 in the Cry5 family, Cry6 in the Cry6 family, and Cry55 in the Cry55 family) (Waele *et al.,* 1995; Dhawan *et al.,* 2004).Prasad *et al.,* (1972) and Chen *et al.,* (2000) reported that populations of *Meloidogyne incognita and M.hapla* were significantly reduced by treatment with *B. thuringiensis* var. *thuringiensis. Bacillus nematocida* B16, using a Torjan horse mechanism lures nematodes to their death. It is reported to be highly nematicidal against the nematode *Panagrellus redivivus.* This bacterium secrets benzaldehyde and 2-heptanone, as volatile organic compounds to attract nematodes. After the nematode has consumed it as food, it secretes a range of extracellular proteases which lyses the intestinal tissues, eventually killing it (Huang *et al.,* 2005a). *B. firmus* is suggested the involvement of toxins which is effective against *Meloidogyne* spp., *Ditylenchus dipsaci* (Mendoza *et al.* 2008), *Rodopholus similis* (Mendoza *et al.,* 2008), *Heterodera* spp., *Tylenchulus semipenetrans*, *Xiphinema index* (Keren-Zur *et al.,* 2000).*Pseudomonas aeruginosa* and *Bacillus subtilis* are reported to be highly nematicidal against *Meloidogyne javanica* by producing toxin (Siddiqui,2002). *Pseudomonas fluorescens* Pf1 and *Bacillus subtilis* BSt are reported to be highly nematicidal against *Rotylenchulus renifomis* by producing toxin (Niknam and Dhawan, 2002a, 2002b). Qaiser *et al.,* (2017) identified Cyclo (d-Pro-l-Leu) produced by *Bacillus amyloliquefaciens* Y1 as a nematicide for control of *M. incognita.* Franco *et al.,* (2007)

and Qin *et al.,* (2011) reported one bacterial group of actinobacteria, which are known to produce bioactive compounds, trigger induced systemic resistance, and also have the capacity to colonize roots. Bacteria that degrade soil amendments (degrades chitin) release nematicidal compounds (ammonia) to kill most nematodes in soil (Spiegel *et al.,* 1991). *Bacillus* species are capable of producing enzymes like chitinase and β-1, 3-glucanase having a very strong lytic activity (Tian *et al.,* 2000; Li *et al.,* 2002; Ha *et al.,* 2014; Castaneda-Alvarez and Aballay ,2016). Chitinase produced by *Paenibacillus illinoisis* KJA-424 caused the lysis of *M. incognita* eggshell and resulted in the inhibition of egg hatching *in vitro* (Jung *et al.,* 2002; Khan *et al.,* 2008). The wide distribution of cuticle-degrading proteases in *Bacillus* strains with nematicidal activity suggested that these enzymes likely play an important role in bacteria-nematode plant environment interactions and that they may serve as important nematicidal factors in balancing nematode populations in the soil. *B. subtilis* produce hydrolytic enzyme such as protease, lipases, b-gluconase and cellulase which are responsible for nematode mortality (Miller and Sands 1977;Chantawannakul *et al.,* 2002;Qiuhong *et al.,* 2006; Tian *et al.,* 2007).*Bacillus pumilus* L1 produce both protease and chitinase, 2-methylbutyric Acid besides promoted tomato plant growth when infested by *M.arenaria* (Wei *et al.,* 2010; Lee and Kim, 2015; Lee *et al.,* 2016). Huang *et al.,* (2005b) reported that *Brevibacillus laterosporus* G4 without parasporal crystals having extracellular protease can infect nematodes. *Pseudomonas fluorescens* can synthesize enzymes that can monitor the level of plant hormones and limit the available iron via siderophores (Glick, 1995 ;VanLoon *et al*. 1998; Siddiqui *et al.,* 2005). The use of ACC deaminase-producing plant growth promoting bacteria, *Pseudomonas putida* UW4 has been shown to be a useful strategy to reduce the damage due to *Bursaphelenchus xylophilus* (Nascimento *et al.,* 2013).

Degradation of the root exudates that the nematode relies on for host location: Plant growth-promoting rhizobacteria may interfere with host identification through receptor blockage on the roots or by modifying root exudates of the host plant, thus hindering the attraction, hatching or penetration behaviour of the nematodes (Oostendorp and Sikora 1986;Becker *et al.,* 1988; Oostendorp and Sikora 1990; Spiegel *et al.,* 1991; Sikora, 1992; Sikora and Hoffmann-Hergarten, 1993; Siddiqui and Mahmood, 1999). Franken *et al.,* (1990) demonstrated that attraction of the cyst nematode, *Globodera pallida* to sugar beet tubers was reduced following tuber treatment with *Agrobacterium radiobacter*. Host recognition was controlled by the interaction between root surface lectin and nematode cuticular carbohydrate. PHPR may induce biological control by binding lectins which are required in host recognition. *B. subtilis* was reported to promote plant growth by producing growth regulators, including root exudation and enhancing the availability of nutrients to plants besides control of soil-borne pathogens (Weller, 1988). These characteristics make these species good candidates for use as seed inoculants and root dips for biological control of soil-borne plant pathogens. *Bacillus sphaericus* and *Agrobacterium radiobacter* have been shown to reduce hatching of two species of cyst nematodes (Oostendorp and Sikora, 1989; Racke and Sikora, 1992).Among plant growth-promoting rhizobacteria *Pseudomonas putida, Pseudomonas aeruginosa, Bacillus subtilis* caused greater inhibitory effect on the hatching and penetration of *M. javanica* (Siddiqui,2002; Siddiqui *et al.,* 2007).Inhibition of *Criconemella xenoplax* egg hatch by *Pseudomonas aureofaciens* was observed by Wescott and Kluepfel (1993). *P. fluorescens* strain CHA0 and its GM derivative CHA0/pME3424 caused mortality of *M. javanica* juveniles *in vitro* and reduced nematode penetration in mung bean roots under glasshouse conditions(Siddiqui, 2005; Bakker *et al.,* 1991;Gamliel and Katan, 1993) *Bacillus* spp., *Pseudomonas* spp. and *Telluria chitinolytica* have been shown to inhibit penetration of nematodes into the roots thereby reducing root galling (Becker *et al.,* 1988; Oostendorp and Sikora, 1990). Root and soil populations of the rice root nematode, *Hirschmanniella oryzae,* were reduced following the application of *P. fluorescens* as a seed treatment (Swarnakumari *et al.,* 1999). Application of *P. chitinolytica* reduced the penetration rate of juveniles of root-knot nematodes in tomato (Spiegel *et al.,* 1991). Fewer galls and egg masses of *M. incognita* were observed following treatment of tomato roots with *P. fluorescens* strain PF1 (Santhi and Shivakumar, 1995).

Induction of systemic acquired resistance (SAR): Induced resistance (both ISR and SAR) has been documented for plant-parasitic nematodes. When a pathogen attacks a plant, the non-infected plant tissues acquire an ability to resist the subsequent attack; this type of broad spectrum and long-term ability of plants is known as systemic acquired resistance (SAR). The ability of plants to develop ISR in response to root colonization by non-pathogenic bacteria depends on the interactions between the colonizing rhizobacterium and host plant (Van Loon *et al.,* 1998; Pieterse *et al.,* 2002). The onset of systemic acquired resistance (SAR) is characterized by expression of genes for pathogenesis-related proteins such as chitinase and peroxidase (Jonathan and Umamaheswari, 2006; Ramamamurthy *et al*. 2001; Jeunn *et al.,* 2004; Siddiqui and Shaukat, 2002; Mohamed and Hammad, 2003). PPO, POD and PAL are important defense enzymes of plants, which are positively correlated with the plant systemic resistance against pathogens. Enzymes induced by systemic resistance cannot directly induce nematode mortality; rather, they cause abnormal females and as a result lower nematode fecundity. Treatment with *P. fluorescens* induced the activity of peroxidase, polyphenol oxidase, phenylalanine ammonia lyase, catalase and chitinase in tomato against *M. incognita* (Wei *et al.,* 1996; Pieterse *et al.,* 2002), Anita *et al.,* 2004); Mohamed and Hassabo, 2005). Andress *et al*. (2008) found that POX increased in the roots of a resistant line of wheat H-93-8 compared with the susceptible line in response to cereal cyst nematode, *Heterodera avenae*. The Cre2 gene (resistance gene) in this line inhibited reproduction of this nematode. POX catalyzes the formation of lignin through polymerization of phenols. Siddiqui and Shaukat (2002) found that secondary metabolite 2-4 diacetylphloroglucinal producing *P. fluorescens* strain CHA0 induced systemic resistance against root-knot nematode in tomato. *P. fluorescens* induced ISR against *M. javanica* (Siddiqui and Shaukat, 2004) and *Heterodera schachtii*, and also reduced early root penetration (Oostendrop and Sikora, 1990). Sikora (1988) demonstrated that *Bacillus subtilis* induced systemic protection against *M. incognita* in cotton. *B. subtilis* GB03 originate volatile compounds that regulate ethylene biosynthesis enzymes, as well as ethylene biosynthesis related genes (ERF1, GST2, and CHIB). It also regulated jasminic acid- and SA-mediated defense mechanism (Ryu *et al.,* 2004). Salicylic acid (SA) production by bacteria acts as an endogenous signal for the activation of certain plant defense responses after pathogen attack. *Bacillus sphaericus* B43 and *Rhizobium etli* G12 triggered ISR against potato cyst

nematode by reducing the juvenile penetration of the roots on the responder side when the bacteria were applied as an inducer to the other half of root system (Hasky- Gunther *et al.,* 1998; Reitz *et al.,* 2000). These two bacteria also caused ISR against *M. incognita* on tomato by reducing the J_2 penetration on the responder root side (Ongena and Jacques, 2008; Siahpoush *et al.,* 2011; Adam *et al.,* 2014).*B. sphaericus* strain B43 was investigated for the induced resistance against *Globodera pallida* in potato roots by split root system. It was observed that, both living and heat-killed bacterial cell effectively reduced the incidence of *G. pallida* in potato roots (Hasky-Gunther *et al.,* 1998). Kloepper *et al.,* (2004) and Xia *et al.,* (2011) investigated the elicitation abilities of *B. subtilis*, *B. cereus*, *B.amyloliquefaciens*, *B.pasteurii*, *B. sphaericus*, *B. pumilus* and *B. mycoides* for induced resistance in tomato, muskmelon, bell pepper, sugar beet, watermelon, tobacco, *Arabidopsis* sp., loblolly pine, cucumber, and green kuang futsoi and long cayenne pepper against various pathogenic diseases including root-knot nematodes under green house and field conditions. Gao *et al.,* (2016) and Hu *et al.,* (2017) also observed that *B. cereus* induce systemic resistance in tomato infested by *M.incognita*.

Mass-production, formulations and application methods: Inoculum quality, mass-production and formulation methods of antagonistic microorganisms have been crucial point for commercialization. Another major challenge is the low yield of the active desirable compound obtained from the cultures (Yu *et al.,* 2010). Genetic engineering technology which identifies the regulatory gene/s in the biosynthesis pathway of the active compound can lead to increase production of the bioactive compounds (Radic and Strukelj, 2012). Stable growth and development of biological agent under field conditions is a major problem due to adverse environmental conditions. The formulation that can enhance the shelf-life of bacterial product during storage, transportation and also during field application is also important. Formulations that are compatible with the delivery of microbial agents through drip irrigation systems may also enable precise application and reductions in inoculums rates. Procedures have been defined for risk assessments of biological control agents released into the environment (Kiewnick *et al.,* 2004) and some studies have been done on the impact of releases on the rhizosphere microbial community (O'Flaherty *et al.,* 2003).The application of rhizosphere bacteria as seed treatments (Oostendorp and Sikora, 1989) and endophytic fungi as bare root dips (Pinochet *et al.,* 1998) or in tissue cultured plantlets (Sikora,2001) or in row treatments provide an opportunity for the large scale use of biological control.

Conclusion

Rigorous laboratory and field screening activities have discovered several microorganisms for the development of biopesticides. The main considerations for the practical adoption of biological control agents are the exposition of their mode of action, development of such formulation that can be used with other pesticides with synergetic effect, stability under field application, and perfect demonstration of cost benefit ratio. Increased understanding of the molecular basis of the various pathogenic/antagonistic mechanisms of the bacteria could potentially enhance their value as effective biological control agents. Understanding the ecological basis of the interactions among these co-applied biocontrol agents will greatly help in maximizing their performance. The primary obstacle in commercializing a biocontrol agent for usage by farmers is the inconsistent field performance. Since, biocontrol agents have to act in soil in presence of different factors like adaphic conditions, weather, and soil inhabiting microbes, which may have synergistic or antagonistic effect on their activity. Rational management decision can be made only by analyzing the interactions that occurring naturally among host plant, nematode target, soil microbial control agent and environment. Ultimately, lots of commercial products based on bacteria are likely to be developed, and they will be marketed on the basis that they promote plant growth or reduce nematode population and other soil borne pathogens.

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