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Fungal and bacterial nematicides in integrated nematode management strategies

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Abstract

Plant-parasitic nematodes (PPNs) pose a serious threat to quantitative and qualitative production of many economic crops worldwide. An average worldwide crop loss of 12.6% (equaled \$215.77 billion) annually has been estimated due to these nematodes for only the top 20 life-sustaining crops. Due to the growing dissatisfaction with hazards of chemical nematicides, interest in microbial control of PPNS is increasing and biological nematicides are becoming an important component of environmentally friendly management systems. Fungal and bacterial nematicides rank high among other biocontrol agents. In order to maximize their benefits, such bio-nematicides can be included in integrated nematode management (INM) programs, and ways that make them complimentary or superior to chemical nematode management methods were highlighted. This is especially important where bio-nematicides can act synergistically or additively with other agricultural inputs in integrated pest management programs. Consolidated use of bio-nematicides and other pesticides should be practiced on a wider basis. This is especially important, since there are many bio-nematicides which are or are likely to become widely available soon. Identification of research priorities for harnessing fungal and bacterial nematicides in sustainable agriculture as well as understanding of their ecology, biology, mode of action, and interaction with other agricultural inputs is still needed. Therefore, accessible fungal and bacterial nematicides with their comprehensive references and relevant information, i.e., the active ingredient, product name, type of formulation, producer, targeted nematode species and crop, and country of origin, are summarized herein.

Keywords: Nematodes, Biocontrol, Bio-nematicides, Integrated pest management, Synergism

Background

Plant-parasitic nematodes (PPNs) are considered hidden enemy of the farmers as the nematodes are subterranean in habitats and growers are unaware of losses caused by them. Much of the damage caused by nematodes goes unreported or is often confused with other causes such as fungal attack, water stress, or other physiological disorders, and by the time the disease is diagnosed, the loss to crops has already been incurred by these tiny organisms. A great loss to crops has been reported in quantitative, qualitative, and monetary terms. Abd-Elgawad and Askary (2015) reported an average worldwide crop loss of 12.6% (equaled \$215.77 billion), due to these nematodes for only the top 20

life-sustaining crops based on the 2010–2013 production figures and prices. Moreover, 14.45% (\$142.47 billion) was an average annual yield loss in the subsequent group of food or export crops. These figures are astonishing, and the authentic figure, when more crops throughout the world are considered, probably exceeds such estimations. At the same time, numerous relevant and challenging issues have been demonstrating the desperate need of human beings to provide more and better food for an over-populated world. Abd-Elgawad (2014) stressed the importance of such issues due to deregistration and banning of effective nematicides available because of environmental and health hazards, renewable manifestation of resistance-breaking nematode pathotypes on many important crops, climate change, increased adoption of intensive agriculture, and potential occurrence of quarantine nematodes. Therefore, nematode management and research should be continuously

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Table 1 Fungal and bacterial biocontrol agents used with other components in integrated nematode management

Fungus/bacterium	Integrated with	Nematode managed	Crop	Result	Reference
<i>Pasteuria penetrans</i>	Carbofuran	<i>Meloiodyne javanica</i>	Tomato	Combined application of <i>P. penetrans</i> and carbofuran reduced root galling by 50%.	Brown and Nordmeyer 1985
	Neem cake	<i>Meloiodyne incognita</i>	Tomato	<i>P. penetrans</i> in combination with neem cake was found most effective in parasitizing the nematode juveniles and adults as compared to individual treatment.	Rangaswamy et al. 2000
<i>P. penetrans</i>	Neem cake	<i>M. incognita</i>	<i>Psoralea corylifolia</i>	Nematode infection was least when <i>P. penetrans</i> and neem extract were applied in combination. Minimum number of juveniles per root system was observed.	Mehrab et al. 2013
	Neem cake	<i>M. javanica</i>	Tomato	Combined application of <i>P. penetrans</i> and neem (<i>Azadirachta indica</i>) cake reduced nematode population by 75%.	Ummaheshwari et al. 1988
<i>P. penetrans</i>	Castor cake	<i>M. incognita</i>	Chilli	Combination of castor and <i>P. penetrans</i> showed greater reduction in galling index (84.75%) and soil population (85.74%) of <i>M. incognita</i> as compared to control (<i>M. incognita</i> alone).	Chaudhary and Kaul 2013
	Nematicides	<i>M. javanica</i>	Tomato	Combined effect of <i>P. penetrans</i> with nematicides (carbofuran, aldicarb, miral, schufos, and phorate) reduced the root galling.	Ummaheshwari et al. 1987
<i>P. penetrans</i>	Carbofuran	<i>M. incognita</i>	Tomato	Combined application of <i>P. penetrans</i> and carbofuran reduced gall formation on tomato roots by 63.02%.	Somasekhar and Gill 1991
	Carbofuran	<i>Heterodera cajani</i>	Pigeonpea	The penetration to host root was minimum when <i>P. penetrans</i> was applied with carbofuran. Number of healthy cysts, eggs/cyst, and total nematode population were significantly reduced in this treatment.	Gogoi and Gill 2001
<i>P. penetrans</i>	Neem cake	<i>M. incognita</i>	Tomato	Increase in plant growth parameters and parasitism of <i>M. incognita</i> female was found when <i>P. penetrans</i> was applied in combination with neem cake.	Parvatha Reddy 1997
	Neem cake	<i>M. javanica</i>	Tomato	Combined application of <i>P. penetrans</i> and neem cake reduced root galling by 32% as compared to nematode alone treatment. The spore-encumbered juveniles were more susceptible to the effects of the neem.	Javed et al. 2008
<i>Pseudomonas fluorescens</i>	Organic manure	<i>M. incognita</i>	Tomato	<i>P. fluorescens</i> GRP3 with organic manure was the best combination for the management of <i>M. incognita</i> on tomato.	Siddiqui et al. 2001b

Table 1 Fungal and bacterial biocontrol agents used with other components in integrated nematode management (Continued)

Fungus/bacterium	Integrated with	Nematode managed	Crop	Result	Reference
<i>P. fluorescens</i>	Carbofuran	<i>Meloidogyne graminicola</i>	Rice	Combined application of <i>P. fluorescens</i> and carbofuran 3G increased plant height, root length, and grain yield and decreased nematode population by 79.34%.	Narasimhamurthy et al. 2017a
<i>P. fluorescens</i>	Neem cake (soil application)	<i>M. incognita</i>	<i>Coleus forskohlii</i>	Colus cutting dipped in 0.1% <i>P. fluorescens</i> at planting + soil application of neem cake @ 400 Kg/ha + growing marigold (<i>Tagetes erecta</i>) as intercrop uprooted and incorporated with soil at the time of earthing up (60–70 days after planting) reduced the root-knot nematode population by 72%.	Seenivasan 2007
<i>P. fluorescens</i>	Neem seed powder + carbofuran	<i>M. incognita</i>	Okra	Nematode penetration and galling was reduced by 54 and 70%, respectively, on integrated application of <i>P. fluorescens</i> , carbofuran, and neem seed powder as compared to control (nematode alone).	Sharma et al. 2008
<i>Trichoderma harzianum</i>	Neem cake	<i>M. incognita</i>	Tomato	A significant increase in plant growth and decrease in root galling and final population of <i>M. incognita</i> were observed in tomato seedlings transplanted in neem cake-amended soil incorporated with <i>T. harzianum</i> .	Rao et al. 1997a
<i>T. harzianum</i>	Neem cake Karanj cake Castor cake	<i>Tylenchulus semipenetrans</i>	Acid lime	<i>T. harzianum</i> in combination with neem (<i>Azadirachta indica</i>), karanj (<i>Pongamia pinnata</i>), and castor (<i>Ricinus communis</i>) oil cakes was effective in increasing the growth of acid lime (<i>Citrus aurantiifolia</i>) seedlings and reducing the population of <i>T. semipenetrans</i> both in soil and roots in pots.	Parvatha Reddy et al. 1996
<i>T. harzianum</i>	Carbofuran	<i>M. incognita</i>	French bean	<i>T. harzianum</i> in combination with carbofuran resulted in decreased root galling, egg masses, and nematode population in soil by 65.15% as compared to untreated control.	Gogoi and Mahanta 2013
<i>T. harzianum</i>	Carbofuran	<i>M. incognita</i>	Brinjal	Combined application of <i>T. harzianum</i> and carbofuran resulted in decreased root galling, egg masses, and nematode population in soil.	Devi et al. 2016
<i>T. harzianum</i>	Carbofuran	<i>M. incognita</i>	<i>Mentha arvensis</i>	<i>T. harzianum</i> + carbofuran resulted in lowest root galling.	Haseeb et al. 2007
<i>T. harzianum</i>	Carbofuran Neem cake	<i>M. incognita</i>	Pea	<i>T. harzianum</i> + carbofuran proved more effective than <i>T. harzianum</i> + neem cake in reducing the root galls, egg masses, and nematode population in soil.	Brahma and Borah 2016

Table 1 Fungal and bacterial biocontrol agents used with other components in integrated nematode management (Continued)

Fungus/bacterium	Integrated with	Nematode managed	Crop	Result	Reference
<i>T. harzianum</i>	Neem cake	<i>M. incognita</i>	Chick pea	Combined application of <i>T. harzianum</i> and neem cake reduced galling on chickpea roots.	Pant and Pandey 2002
<i>T. harzianum</i>	<i>Lantana camara</i>	<i>M. incognita</i>	Tomato	<i>T. harzianum + Lantana camara</i> resulted in a significant difference in the reduction of root-knot nematode population, nematode reduction rate, number of galls, and egg masses per plant.	Feyisa et al. 2015
<i>T. harzianum</i>	Neem cake + <i>P. fluorescens</i>	<i>M. incognita</i>	Briñjal	<i>T. harzianum</i> in combination with neem cake + <i>P. fluorescens</i> significantly reduced the incidence of root-knot disease of eggplant. Root galls were reduced by 81%, and yield of eggplant was enhanced by up to 70% as compared to check (nematode alone).	Singh 2013
<i>T. viride</i>	Carbofuran	<i>M. graminicola</i>	Rice	Combined application of <i>T. viride</i> and carbofuran increased plant height, root length, and grain yield and decreased nematode population by 69.17%.	Narasimhamurthy et al. 2017a
<i>T. viride</i>	<i>P. lilacinus</i> + carbofuran + mustard cake	<i>M. incognita</i>	Tomato	Integrated application of <i>T. viride</i> along with <i>P. lilacinus</i> , carbofuran, and mustard cake showed least nematode reproduction factor (0.0) as compared to untreated infested soil (1.783).	Goswami et al. 2006
<i>T. viride</i>	Compost	<i>Meloiodyne</i> spp.	Gotukola (<i>Centella asiatica</i>)	Treatments of <i>T. viride</i> + compost had significant reduction in root gall formation in Gotukola besides significant impact on plant growth that attributed to increased number of roots, leaf length, stalk length, and root length and highest fresh weight of leaves of first harvest.	Shamalie et al. 2011
<i>T. viride</i>	Neem cake	<i>M. incognita</i>	Tomato	<i>T. viride</i> in combination with either neem or castor cake was found most effective in parasitizing the egg masses of the nematode as compared to individual treatment.	Rangaswamy et al. 2000
<i>T. viride</i>	Castor cake				Ravendra et al. 2011
<i>T. viride</i>	Neem cake	<i>M. incognita</i>	Tobacco	Integrated application of <i>T. viride</i> along with neem cake significantly reduced the number of galls and egg masses on tobacco root.	Sharf et al. 2014a, b
<i>T. viride</i>	<i>P. chlamydosporia</i> + urea	<i>M. incognita</i>	Red kidney bean	<i>T. viride + P. chlamydosporia</i> + urea reduced galls and egg masses per root system.	

Table 1 Fungal and bacterial biocontrol agents used with other components in integrated nematode management (Continued)

Fungus/bacterium	Integrated with	Nematode managed	Crop	Result	Reference
<i>Paecilomyces lilacinus</i>	Neem cake + NPK (nitrogen, phosphorus, potassium)	<i>M. incognita</i>	Tomato	The antagonistic potential of <i>P. lilacinus</i> against <i>M. incognita</i> infesting tomato seedlings under nursery conditions was enhanced (53.6%) when applied in combination with neem cake and NPK.	Nagash et al. 2001
<i>P. lilacinus</i>	Neem cake Karanj leaves	<i>Heterodera zea</i>	Sweet corn	Combined application of <i>P. lilacinus</i> with neem cake and karanj leaves resulted in decline of cyst population in soil by 63.04% and 52.17%, respectively.	Baheti et al. 2017
<i>P. lilacinus</i>	Neem seed powder + dimethoate	<i>M. incognita</i>	Pigeonpea	Seed treatment with <i>P. lilacinus</i> + neem seed powder + dimethoate improved the pigeonpea yield up to 30% and suppressed the galling and nematode population up to 77%.	Askary 2008
<i>P. lilacinus</i>	Neem leaf suspension	<i>M. incognita</i>	Brinjal	<i>P. lilacinus</i> + neem leaf suspension @ 5% and 10% resulted in nematode egg parasitization by 59 and 64%, respectively, and decrease in final nematode population by 64.10 and 71.47%, respectively.	Rao et al. 1997b
<i>P. lilacinus</i>	Aldicarb	<i>M. javanica</i>	Tomato	The smallest galling index, number of galls, and nematode population were in soils treated with <i>P. lilacinus</i> in combination with aldicarb followed by <i>P. lilacinus</i> + chicken manure, <i>P. lilacinus</i> + <i>R. communis</i> , <i>P. lilacinus</i> + <i>T. minuta</i> , and <i>P. lilacinus</i> + <i>D. stramonium</i> .	Oduor-Owino 2003
<i>P. lilacinus</i>	<i>Tagetes minuta</i>				
<i>P. lilacinus</i>	<i>Datura stramonium</i>				
<i>P. lilacinus</i>	<i>Ricinus communis</i>				
<i>P. lilacinus</i>	Chicken manure	<i>M. javanica</i>	Brinjal	The highest improvement in plant growth and best protection against <i>M. javanica</i> was obtained by the integration of <i>P. lilacinus</i> with groundnut cake followed by neem cake, linseed cake, castor cake, and mahua cake.	Ashraf and Khan 2010
<i>P. lilacinus</i>	Groundnut cake				
<i>P. lilacinus</i>	Linseed cake				
<i>P. lilacinus</i>	Castor cake				
<i>P. lilacinus</i>	Mahua cake				
<i>P. lilacinus</i>	Neem cake	Soil nematodes	Pigeonpea	Damage caused by the nematodes was significantly reduced when <i>P. lilacinus</i> was added along with oil-cakes. Most effective combination of <i>P. lilacinus</i> was with neem cake.	Anver 2003
<i>P. lilacinus</i>	Mustard cake				
<i>P. lilacinus</i>	Castor cake				
<i>P. lilacinus</i>	Neem cake	<i>M. incognita</i>	Tomato	Increase in plant growth parameters and nematode egg parasitism was found when <i>P. lilacinus</i> was applied in combination with neem cake.	Parvatha Reddy et al. 1997

Table 1 Fungal and bacterial biocontrol agents used with other components in integrated nematode management (Continued)

Fungus/bacterium	Integrated with	Nematode managed	Crop	Result	Reference
<i>Pochonia chlamydosporia</i>	<i>P. fluorescens</i> + <i>T. viride</i> + carbofuran	<i>Globodera</i> spp.	Porato	Combined application of <i>P. chlamydosporia</i> along with <i>P. fluorescens</i> , <i>T. viride</i> , and carbofuran resulted in significantly higher plant growth and lower cyst nematode (<i>Globodera</i> spp.) population in soil and root. There was 70.57% increase in tuber weight and 71.93% decrease in the cyst population. A significant reduction in the population of eggs and juveniles was also noted.	Muthulakshmi et al. 2012
<i>P. chlamydosporia</i>	Carbofuran	<i>M. incognita</i>	Tomato	<i>P. chlamydosporia</i> + carbofuran resulted in maximum plant growth and minimum galls and egg masses.	Gopinatha et al. 2002
<i>P. chlamydosporia</i>	Neem cake + dazomat	<i>M. incognita</i>	Rose	Soil application of <i>P. chlamydosporia</i> + neem cake + dazomat resulted in maximum percent healthy root and flower yield and reduced the root galls.	Nagash and Jankiram 2004
<i>P. chlamydosporia</i>	Carbofuran + neem cake	<i>M. incognita</i>	Okra	Integrated application of <i>P. chlamydosporia</i> along with carbofuran and neem cake suppressed root-knot disease severity in terms of galling, egg production, and nematode population by 89%, 90%, and 81%, respectively.	Dhawan and Singh 2009
<i>P. chlamydosporia</i>	Neem cake Mustard cake	<i>M. incognita</i>	Brinjal	A significant reduction in nematode multiplication was observed when soil was treated with <i>P. chlamydosporia</i> + neem cake and <i>P. chlamydosporia</i> + mustard cake.	Parihar et al. 2015
<i>P. chlamydosporia</i>	Neem cake	<i>H. zea</i>	Sweet corn	Combined application of <i>P. chlamydosporia</i> with neem cake resulted in decline of cyst population in soil by 54.55%.	Baheti et al. 2017

refined and oriented to offer better control of PPNs in an environmentally and economically beneficial manner.

Importance of biological control of pests is growing, and this is obviously reflected by considerable venture capital in research by multinational firms and also by their acquisitions of small biotechnology corporations with microbial product portfolios (Wilson and Jackson 2013). Bio-products containing antagonists of fungi and bacteria rank high among other bio-nematicides (Askary 2015a, b; Eissa and Abd-Elgawad 2015). As such nematicides represent living systems, a number of difficulties exist to develop commercial bio-nematicidal products. Problems with their culture and formulation, variable gap between laboratory and field performance, potential negative effects on non-target or beneficial organisms, and expectations of broad-spectrum activity and quick efficacy based on practice with synthetic chemical nematicides have been addressed in details by some workers (Glare et al. 2012; Askary and Martinelli 2015). Rapid progress has been made during the past two decades in different aspects of bio-nematicidal production and use. This was especially important for the development of in vitro mass culture concerning *Pasteuria* spp. and innovative, easy-to-use formulations of numerous products. Yet, there is still a desperate need to poised these bio-nematicides as more effective and reliable products against PPNs. This trend is currently materialized in a variety of approaches, including studies on their applications, improved shelf-life, mass-culture, and interaction with other biotic and abiotic factors as well as integration of biocontrol with other management techniques.

The objective of this review article is to highlight the current knowledge of the biological control potential of

fungal and bacterial agents in attempt to include them in effective integrated nematode management (INM) programs. Also, research priorities and perceived factors for harnessing fungal and bacterial nematicides in sustainable agriculture were identified.

Fungal and bacterial interaction with other inputs

The most studied and promising groups among the nematode-antagonistic organisms are the nematophagous fungi and bacteria (Askary and Martinelli 2015). The two groups include many species. These bio-nematicides are frequently applied to sites and ecosystems that routinely receive other inputs including chemical pesticides, surfactants (e.g. wetting agents), fertilizers, mineral nutrition, and soil amendments which may interact with bio-active ingredients targeting PPNs. Fungal and bacterial biocontrol agents used with other components in INM are listed in Table 1. Basically, such biocontrol agents (BCA) are living systems sensitive to biotic and abiotic factors that result from inputs, especially in the soil rhizosphere. Thus, BCA should be compatible with them to maximize their benefits. In this respect, we propose that bio-nematicides should not be used as direct competitors with chemical nematicides for several reasons. Bio-nematicides fall behind chemical nematicides in traits prized by growers: price, performance, handling, distribution, and ease of both storage and use. Hence, our suggestion is especially important where bio-nematicides can act synergistically or additively with such inputs in INM programs. Positive results have been demonstrated (Table 1). For example, shoot dry weight of tomato had better ($P \leq 0.05$) increase, when *Pseudomonas fluorescens* GRP3 was combined with organic manure for the management of *Meloidogyne*

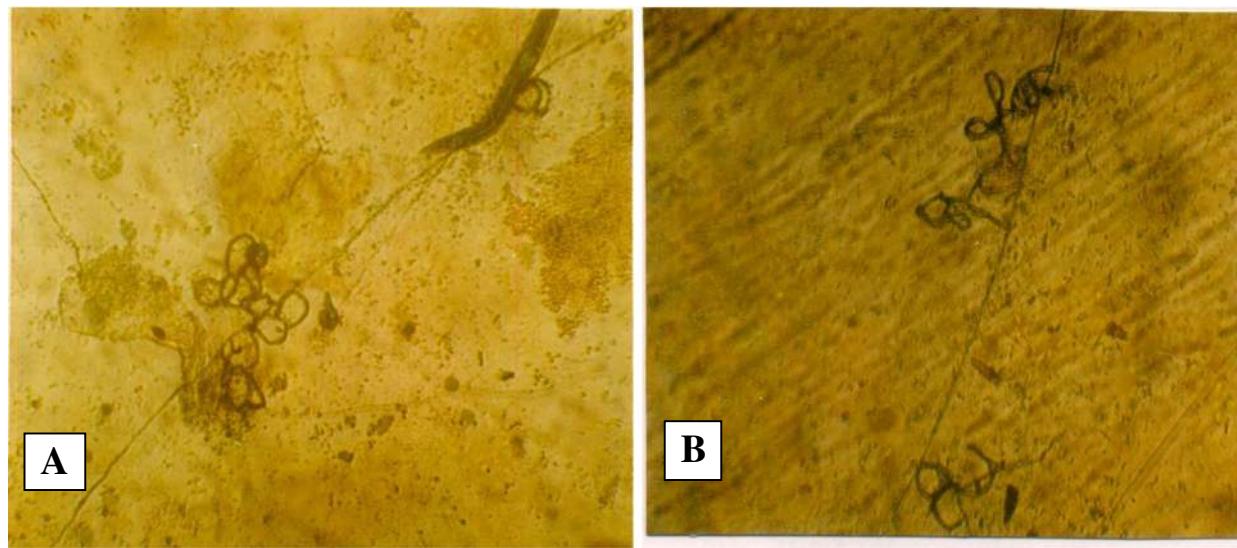


Fig. 1 *Monacrosporium megalosporum*. **a** A portion of hypha showing entangled nematode with adhesive net, the lower portion showing arched or circular hyphal meshes. **b** A portion of hypha with adhesive network

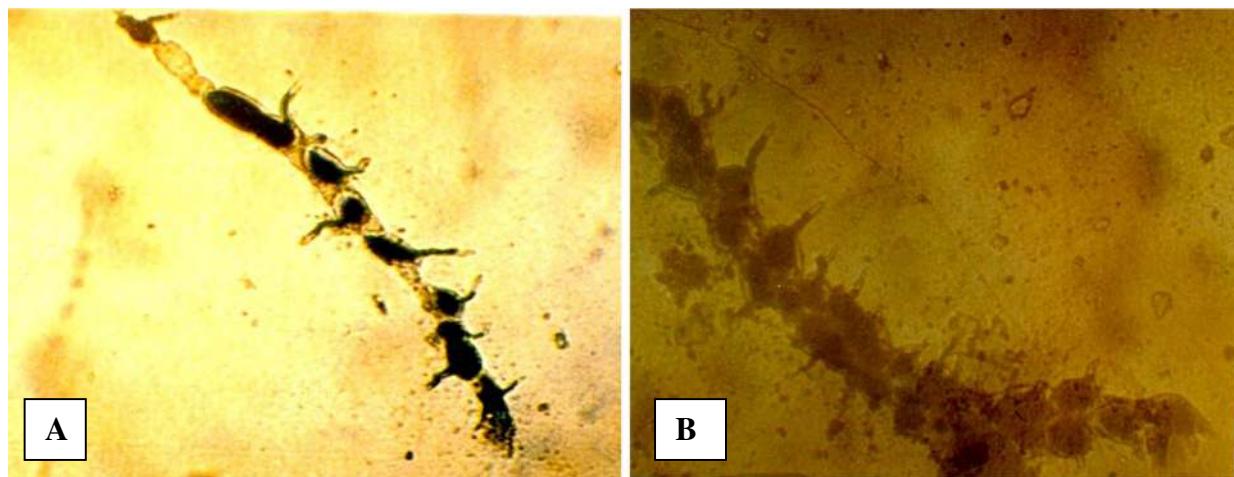


Fig. 2 *Catenaria anguillulae*. **a** Chain of mature and immature sporangium. **b** Double chain of mature and immature sporangium on nematode cadaver

incognita than using either *P. fluorescens* or organic manure alone (Siddiqui et al. 2001b). New tactics for synergistically or even additively incorporating BCA with favorable inputs should be tried further and broadly disseminated for real and better penetration of markets and developed BCA. A similar plan was recently put forward for insecticides too (Stevens and Lewis 2017).

We should also highlight and get use of approaches where bio-nematicides can be included in INM programs in ways that make them complimentary or superior to chemical pest management methods. In this respect, endospores formed by bacterial genera *Bacillus*, *Clostridium*, and *Pasteuria* are tolerant to exposures for most agrochemicals. Such endospore-forming bacteria are both the most heat-resistant form of life and highly resistant to desiccation and chemical destruction; these endospores have a prolonged shelf life (more than a year) and can also be applied to seeds several days before planting. They can be used along with inorganic and organic fertilizers, microelements, and several fungicides, herbicides, and pesticides; they can often be tank-mixed. Abd-Elgawad and Vagelas (2015) focused on widening this approach since a tank mix of one or more inputs with a bio-nematicide can save time and money. Also, bio-nematicides can also be used in rotation with such chemicals as pesticides to delay pest resistance by breaking pressure from a single mode of action. Clearly, consolidated use of bio-nematicides and other pesticides should be practiced on a wider basis. In this vein, only few companies are actively fostering the concerted use of bio-nematicides and chemical pesticide, e.g., the product VOTiVO™ and PONCHO®/VOTiVO™ mix, which is based on *Bacillus firmus* against PPNs, combined with a synthetic insecticide, Poncho1, as a seed treatment (Anonymous 2018).

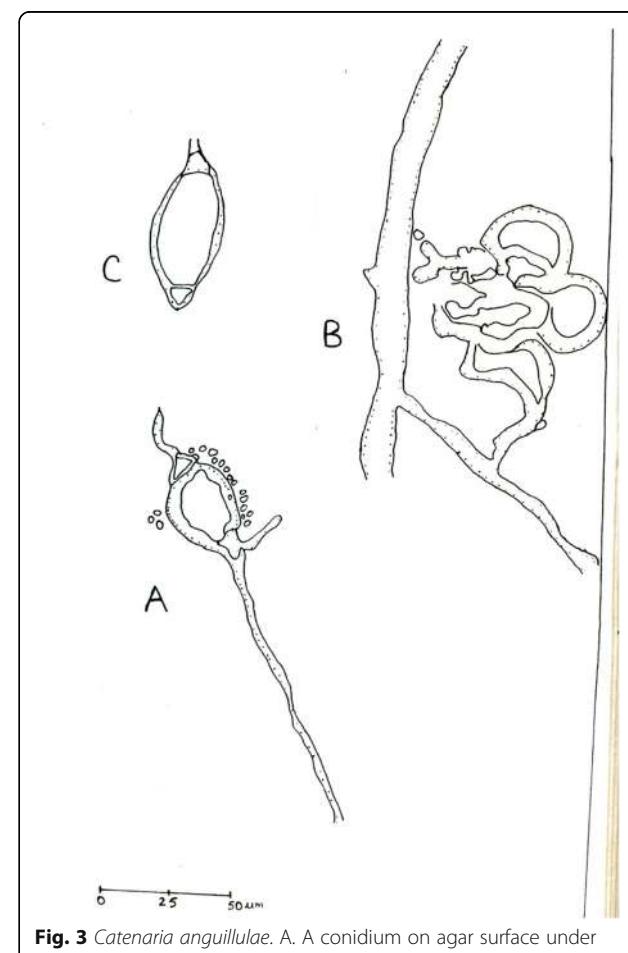


Fig. 3 *Catenaria anguillulae*. **A**. A conidium on agar surface under germination. **B**. A portion of hypha with adhesive network. **C**. Detached conidium

Mode of action of fungal and bacterial nematicides

Fungi group may be divided into nematode-trapping, endo-parasitic, egg- and female-parasitic, and toxin-producing fungi (Askary 1996; Jansson et al. 1997). For example, for the nematode-trapping fungus, entangled nematode with adhesive network of *Monacrosporium megalospororum* hypha is illustrated (Fig. 1). *Catenaria anguillulae*, an endoparasitic fungus, is a member of the Chytridiomycota, the only major group of true (chitin-walled) fungi that produce motile spores, termed zoospores (Deacon 2018). This fungus is often found as a facultative (non-

specialized) parasite of nematodes and other small organisms. Phase-contrast microscopy was used to show the single and double chain of mature and immature fungal sporangium on parasitized nematodes (Fig. 2). It can be grown easily on culture media and different parts, under germination, of the fungus grown on agar surface (Fig. 3). Based on their modes of action, the nematophagous bacteria can also be broadly grouped into parasitic bacteria and non-parasitic rhizobacteria. Eissa and Abd-Elgawad (2015) adopted the following categories of nematophagous bacteria: obligate parasitic bacteria,

Table 2 Modes of action of fungal and bacterial biocontrol agents against phytonematodes (Askary and Martinelli 2015)

	Mode of action
Fungus	
<i>Aspergillus niger</i>	It is an egg parasite and induces systemic resistance against plant-parasitic nematodes. The fungus coming in contact with a cyst or an egg mass begins to grow rapidly. It colonizes the eggs where larval formation has not been completed, thus providing early protection to the growing plants against nematodes.
<i>Paecilomyces lilacinus</i>	It is mainly egg parasite. The fungus produces antibiotics viz, leucinostatin and lilacin and enzymes such as protease and chitinase. Protease has nematicidal activity, causes degradation of the eggshell, and inhibits hatching. Chitinase breaks down the eggshell making the route for the fungus to pass through. The decomposition of chitin releases ammonia, which is toxic to second-stage juveniles of root-knot nematode (RKN). Its hypha enters the vulva and anus of RKN females. The fungus penetrates the egg and develops profusely inside and over the eggs, completely inhibiting juvenile development. The infected eggs swell and buckle. As penetration continues, the vitelline layer of the egg splits into three bands and a large number of vacuoles; lipid layer disappears at this stage. The developing juvenile inside the egg is destroyed by the rapidly growing hyphae. Many conidiophores are produced and the hypha moves to the adjacent eggs.
<i>Trichoderma harzianum</i>	Secretes many lytic enzymes like chitinase, glucanases, and proteases which help parasitism of <i>Meloidogyne</i> and <i>Globodera</i> eggs. The chitin layer is dissolved through enzymatic activity. The hyphae of <i>T. harzianum</i> penetrate the eggs and juvenile cuticle, proliferate within the organism, and produce toxic metabolites.
<i>T. viride</i>	Produce antibiotics like trichodermin, dermadin, trichoviridin, and sesquiterpene heptalic acid which are involved in the suppression of nematodes.
<i>Pochonia chlamydosporia</i>	Parasitizes the eggs and adult females of plant-parasitic nematodes. The root-knot and cyst nematodes are the primary hosts of this fungus, but it is also known to parasitize citrus, burrowing, and reniform nematodes. The fungus enters the nematode cysts either through natural openings or it may directly penetrate the wall of the cyst. It forms a branched mycelia network when in close contact with the smooth eggshell. The fungus produces an appressorium that adheres to the eggshell by mucigens and from which an infection peg develops and penetrates the eggshell. Penetration also occurs from lateral branches of the mycelium. This results in disintegration of the eggshell's vitelline layer and also partial dissolution of the chitin and lipid layers, possibly due to the activity of exoenzymes. Egg hatching is inhibited due to toxins secreted by the fungus.
Bacteria	
<i>Pasteuria penetrans</i>	Bacterial spores are attached to the nematode's body and germinate forming a germ tube that penetrates the body cuticle. Vegetative mycelial colonies eventually fill the body with a large number of endospores.
<i>Pseudomonas fluorescens</i>	Produce antibiotics viz, phenazines, tropolone, pyrrolnitrin, pyocyanin, and 2,4-diacetylphloroglucinol which have suppressive effect on plant-parasitic nematodes.
<i>Bacillus firmus</i>	Enzymatic action, degradation of root exudates, root-protection, and the production of a phytohormone.
<i>B. thuringiensis</i>	Nematicidal toxins found in families of <i>B. thuringiensis</i> proteins.
<i>B. subtilis</i>	The genes are encoding surfactin and iturin synthesis as antibiotics.

opportunistic parasitic bacteria, rhizobacteria, cry protein-forming bacteria, endophytic bacteria, and symbiotic bacteria.

Several nematicides have been banned due to their health and environmental hazards; therefore, the

merits and demerits of potential biological control agents with different modes of action against PPNs should be continuously researched for more details about their virulence mechanisms. The modes of action for common fungal and bacterial nematicides are

Table 3 List of commercial products of fungal biocontrol agents used in the nematode management (data are collected by the authors and based on Askary and Martinelli (2015))

Fungus	Product	Formulation	Company/institution	Country
<i>Aspergillus niger</i>	Kalisena	Soluble (liquid) concentrate	Cadila Pharmaceutical Limited	India
<i>A. niger</i>	Kalisena	Suspension concentrate for direct application	Cadila Pharmaceutical Limited	India
<i>A. niger</i>	Beej Bandhu	Wettable powder	–	India
<i>A. niger</i>	Pusa Mrida	Wettable powder	–	India
<i>A. niger</i>	Kalasipahi	Capsule	–	India
<i>Pochonia chlamydosporia</i>	KlamiC®	Granulate	Rothamsted Research and Centro Nacional de Sanidad Agropecuaria	UK, Cuba
<i>P. chlamydosporia</i>	PcMR-1 strain	Liquid	Clamitec, Myco solutions, Lda	Portugal
<i>P. chlamydosporia</i>	Xianchongbike	Liquid	Laboratory for Conservation and Utilization of Bio-resources, Yunnan University	China
<i>P. chlamydosporia</i>	IPP-21	–	–	Italy
<i>Purpureocillium lilacinus</i>	BIOACT®WG	Water-dispersible granulate	Bayer Crop Science	USA
<i>P. lilacinus</i>	BIOACT®WP	Water-dispersible powder	Bayer Crop Science	USA
<i>P. lilacinus</i>	PL Gold	Wettable powder	BASF Worldwide, Becker Underwood	South Africa
<i>P. lilacinus</i>	Stanes Bio Nematon	Liquid or powder	Imported from T. Stanes and Company Limited, India, by Gaara company, Egypt	India and Egypt
<i>P. lilacinus</i>	PL 251	Water-dispersible granulate	Biological Control Products	South Africa
<i>P. lilacinus</i>	BIOCON	Wettable powder	Asiatic Technologies Incorporation	Philippines
<i>P. lilacinus</i>	Shakti Paecil	Wettable powder	Shakti Biotech	India
<i>P. lilacinus</i>	PAECILO®	Wettable powder	Agri Life	India
<i>P. lilacinus</i>	Paecilon	Liquid	Enpro Bio Sciences Private Limited	India
<i>P. lilacinus</i>	Nematofree	Wettable powder	International Panaacea Limited	India
<i>P. lilacinus</i>	Gmax bioguard	Talc based carrier	Greenmax Agro Tech	India
<i>P. lilacinus</i>	Yorker	Wettable powder	Agriland Biotech	India
<i>P. lilacinus</i>	Miexianning	Talc based carrier	Agricultural Institute, Yunan Academy of Tobacco Science	China
<i>P. lilacinus</i>	PI Plus® (<i>P. lilacinus</i> strain 251)	Wettable powder	Biological Control Products	South Africa
<i>P. lilacinus</i>	Melocon®WG	Water-dispersible granulate	Prophyta GmbH Certis	Germany, USA
<i>Trichoderma harzianum</i>	Romulus	Wettable powder	DagutatBiolab	South Africa
<i>T. harzianum</i>	ECOSOM®	Wettable powder	Agri Life	India
<i>T. harzianum</i>	Trichobiol	Wettable powder	Control Biologico Integrado; Mora Jaramillo Arturo Orlando—Biocontrol	Columbia
<i>T. harzianum</i>	Commander Fungicide	Wettable powder	H.T.C Impex Private Limited	India
<i>T. viride</i>	Trifesol	Wettable powder	Biocultivos Agricultura Sostenible	Columbia

Table 4 Biocontrol agents of fungal species targeting nematodes on economic crops

Fungus	Nematode managed	Crop	Reference
<i>Aspergillus niger</i>	<i>Meloidogyne incognita</i>	Mung bean	Bhat and Wani 2012
<i>A. niger</i>	<i>Meloidogyne</i> spp.	Tomato	Li et al., 2011
<i>A. niger</i>	<i>Meloidogyne javanica</i>	Tomato	Zareen et al. 2001
<i>A. niger</i>	<i>M. javanica</i>	Pigeonpea	Askary 2012
<i>A. niger</i>	<i>Meloidogyne arenaria</i>	Tomato	Mokbel et al. 2009
<i>A. niger</i>	<i>M. incognita</i>	Okra	Sharma et al. 2005
<i>A. niger</i>	<i>Meloidogyne</i> spp.	Tomato	Singh et al. 1991
<i>A. niger</i>	<i>Meloidogyne</i> spp.	Tomato	Khan et al. 1984
<i>A. niger</i>	<i>M. incognita</i>	Brinjal	Goswami and Singh 2002
<i>A. niger</i>	<i>M. javanica</i>	Chickpea	Hussain et al. 2001
<i>Paecilomyces lilacinus</i>	<i>Meloidogyne graminicola</i>	Rice	Narasimhamurthy et al. 2017a, b
<i>P. lilacinus</i>	<i>M. incognita</i>	Black gram	Kumar et al. 2017
<i>P. lilacinus</i>	<i>M. incognita</i>	Chrysanthemum	Nagesh et al. 2003
<i>P. lilacinus</i>	<i>M. incognita</i>	Banana	Devrajan and Rajendran 2002
<i>P. lilacinus</i>	<i>M. incognita</i>	Okra	Saikia and Roy 1994
<i>P. lilacinus</i>	<i>M. incognita</i>	Okra	Davide and Zorilla 1986
<i>P. lilacinus</i>	<i>M. incognita</i>	Okra	Simon and Pandey 2010
<i>P. lilacinus</i>	<i>M. incognita</i>	Tobacco	Ramakrishnan and Nagesh 2011
<i>P. lilacinus</i>	<i>M. javanica</i>	Tomato	Ganaie and Khan 2010
<i>P. lilacinus</i>	<i>M. javanica</i>	Tomato	Maheswari and Mani 1989
<i>P. lilacinus</i>	<i>M. incognita</i>	<i>Pittosporum tobira</i> (mock orange)	Baidoo et al. 2017
<i>P. lilacinus</i>	<i>Rotylenchulus reniformis</i>	Tomato	Walters and Barker 1994
<i>P. lilacinus</i>	<i>R. reniformis</i>	Chickpea	Ashraf and Khan 2008
<i>P. lilacinus</i>	<i>M. incognita</i>	Cardamom	Eapen and Venugopal 1995
<i>P. lilacinus</i>	<i>Heterodera cajani</i>	Pigeonpea	Siddiqui and Mahmood 1995
<i>P. lilacinus</i>	<i>Radopholus similis</i>	Banana	Mendoza et al. 2004
<i>P. lilacinus</i>	<i>M. javanica</i>	Tomato	Khan et al. 2006
	<i>Rotylenchulus similis</i>	Banana	
	<i>Heterodera avenae</i>	Barley	
<i>P. lilacinus</i>	<i>M. incognita</i>	Tomato	Oclarit and Cumagun 2009
<i>P. lilacinus</i>	<i>M. incognita</i>	Tomato	Khan and Goswami 2000
<i>P. lilacinus</i>	<i>R. similis</i>	Betelvine	Sosamma et al. 1994
<i>P. lilacinus</i>	<i>R. similis</i>	Arecanut	Sudha et al. 2000
<i>P. lilacinus</i>	<i>M. incognita</i>	Tomato	Candanedo-Lay et al. 1982
<i>P. lilacinus</i>	<i>M. incognita</i>	Tomato	Roman and Rodriguez-Marcano 1985
<i>P. lilacinus</i>	<i>Meloidogyne</i> spp.	Lettuce	Prakob et al. 2009
<i>P. lilacinus</i>	<i>M. incognita</i>	Tobacco	Ramakrishnan and Rao 2013
<i>P. lilacinus</i>	<i>M. javanica</i>	Tomato	Khan and Esfahani 1990
<i>P. lilacinus</i>	<i>M. javanica</i>	Pumpkin, Guar, Chili, Watermelon	Perveen et al. 1998
<i>P. lilacinus</i>	<i>Tylenchulus semipenetrans</i>	<i>Citrus Jambhiri</i>	Deka et al. 2002
<i>P. lilacinus</i>	<i>M. incognita</i>	Tomato	Goswami and Mittal 2004
<i>P. lilacinus</i>	<i>M. incognita</i>	Bitter gourd	Bhat et al. 2009
<i>P. lilacinus</i>	<i>M. incognita</i>	Brinjal	Nisha and Sheela 2016
<i>P. lilacinus</i>	<i>M. incognita</i>	Okra, Tomato	Walia et al. 1999

Table 4 Biocontrol agents of fungal species targeting nematodes on economic crops (Continued)

Fungus	Nematode managed	Crop	Reference
<i>P. lilacinus</i>	<i>T. semipenetrans</i>	Citrus (KhasiMandarin)	Mahanta et al. 2016
<i>P. lilacinus</i>	<i>T. semipenetrans</i>	Citrus (KhasiMandarin)	Manzoor et al. 2002
<i>P. lilacinus</i>	<i>M. incognita</i>	Tomato	Cabanillas and Barker 1989
<i>P. lilacinus</i>	<i>M. incognita</i>	Tomato	Khalil et al. 2012a
<i>P. lilacinus</i>	<i>M. incognita</i>	Tomato	Khalil et al. 2012b
<i>P. lilacinus</i>	<i>M. incognita</i>	Tomato	Amin 2000
<i>P. lilacinus</i>	<i>M. incognita</i>	Tomato	Cabanillas et al. 1989
<i>P. lilacinus</i>	<i>M. incognita</i>	Okra	Thakur and Devi 2007
<i>P. lilacinus</i>	<i>H. cajani</i>	Pigeonpea	Siddiqui et al. 1998
<i>P. lilacinus</i>	<i>M. javanica</i>	Tobacco	Hewlett et al. 1988
<i>P. lilacinus</i>	<i>M. javanica</i>	Tomato	Esfahani and Pour 2006
<i>P. lilacinus</i>	<i>M. incognita acrita</i>	Potato	Jatala et al. 1979
	<i>Globodera pallida</i>		
<i>P. lilacinus</i>	<i>M. incognita</i>	Potato	Jatala et al., 1980
<i>P. lilacinus</i>	<i>M. javanica</i>	Pigeonpea	Askary 2012
<i>P. lilacinus</i>	<i>M. incognita</i>	Banana	Jonathan and Rajendran 2000
<i>P. lilacinus</i>	<i>M. incognita</i>	Betelvine	Jonathan et al. 1995
<i>P. lilacinus</i>	<i>M. incognita</i>	Cowpea	Hasan 2004
<i>P. lilacinus</i>	<i>M. incognita</i>	Okra	Dhawan et al. 2004
<i>P. lilacinus</i>	<i>M. incognita</i>	Betelvine	Bhatt et al. 2002a
<i>P. lilacinus</i>	<i>R. reniformis</i>	Tomato	Parvatha Reddy and Khan 1988
<i>P. lilacinus</i>	<i>R. reniformis</i>	Chickpea	Anver and Alam 1999
<i>P. lilacinus</i>	<i>R. reniformis</i>	Pigeonpea	Anver and Alam, 1997
<i>P. lilacinus</i>	<i>M. javanica</i>	Broad bean, Okra	Zareen et al. 1999
<i>P. lilacinus</i>	<i>M. arenaria</i>	Brinjal	Sivakumar et al. 1993
<i>P. lilacinus</i>	<i>M. incognita</i>	French bean	Santin 2008
<i>Pochonia chlamydosporia</i>	<i>M. incognita</i>	Tomato	Silva et al. 2017
<i>P. chlamydosporia</i>	<i>M. javanica</i>	Lettuce	Viggiano et al. 2015
<i>P. chlamydosporia</i>	<i>M. javanica</i>	Tomato and Pepper	Tzortzakis 2007
<i>P. chlamydosporia</i>	<i>M. incognita</i>	Tomato	De Leij et al. 1992
<i>P. chlamydosporia</i>	<i>M. javanica</i>	Broad bean, Okra	Zareen et al. 1999
<i>P. chlamydosporia</i>	<i>Heterodera schachtii</i>	Sugar beet	Ebrahim et al. 2008
<i>P. chlamydosporia</i>	<i>M. incognita</i>	Brinjal	Parihar et al. 2015
<i>P. chlamydosporia</i>	<i>M. incognita</i>	Bell pepper	Rao et al. 2004
<i>P. chlamydosporia</i>	<i>M. incognita</i>	Tomato	Sankaranarayanan et al. 2000
<i>P. chlamydosporia</i>	<i>H. cajani</i>	Pigeonpea	Siddiqui and Mahmood 1995
<i>P. chlamydosporia</i>	<i>Heterodera avenae</i>	Wheat	Bhardwaj and Trivedi 1996
<i>P. chlamydosporia</i>	<i>Meloidogyne hapla</i>	Tomato	De Leij et al. 1993
<i>P. chlamydosporia</i>	<i>M. javanica</i>	Lettuce and Tomato	Verdejo-Lucas et al. 2003
<i>P. chlamydosporia</i>	<i>M. incognita</i>	Okra	Kumar and Jain 2010a
<i>P. chlamydosporia</i>	<i>M. incognita</i>	Okra	Dhawan and Singh 2010
<i>P. chlamydosporia</i>	<i>M. javanica</i>	Tomato	Siddiqui and Ehteshamul-Haque 2000
<i>P. chlamydosporia</i>	<i>M. incognita</i>	Pigeonpea	Askary, 2008
<i>P. chlamydosporia</i>	<i>M. incognita</i>	Common bean	Sharf et al. 2014a

Table 4 Biocontrol agents of fungal species targeting nematodes on economic crops (Continued)

Fungus	Nematode managed	Crop	Reference
<i>P. chlamydosporia</i>	<i>M. incognita</i>	Brinjal	Rao et al. 2003
<i>P. chlamydosporia</i>	<i>M. incognita</i>	Brinjal	Dhawan et al. 2008
<i>P. chlamydosporia</i>	<i>R. reniformis</i>	Cotton	Wang et al. 2005
<i>P. chlamydosporia</i>	<i>M. hapla</i>	Lettuce	Viaene and Abawi 2000
<i>P. chlamydosporia</i>	<i>M. incognita</i>	Lettuce and Tomato	Van Damme et al. 2005
<i>P. chlamydosporia</i>	<i>H. cajani</i>	Pigeonpea	Kumar and Prabhu 2008
<i>Trichoderma harzianum</i>	<i>M. javanica</i>	Tomato	Feyisa et al. 2016
<i>T. harzianum</i>	<i>H. cajani</i>	Pigeonpea	Kumar and Prabhu 2008
<i>T. harzianum</i>	<i>M. javanica</i>	Tomato	Naserinasab et al. 2011
<i>T. harzianum</i>	<i>Meloidogyne</i> spp.	Cardamom	Anonymous 1995
<i>T. harzianum</i>	<i>M. incognita</i>	Chickpea	Hemlata et al. 2002
<i>T. harzianum</i>	<i>M. incognita</i>	Chickpea	Pant and Pandey 2002
<i>T. harzianum</i>	<i>M. incognita</i>	Pea	Brahma and Borah 2016
<i>T. harzianum</i>	<i>M. arenaria</i>	Maize	Windham et al. 1989
<i>T. harzianum</i>	<i>M. incognita</i>	Brinjal	Devi et al. 2016
<i>T. harzianum</i>	<i>M. incognita</i>	Cardamom	Eapen and Venugopal 1995
<i>T. harzianum</i>	<i>H. cajani</i>	Pigeonpea	Siddiqui and Mahmood 1996
<i>T. harzianum</i>	<i>M. incognita</i>	French bean	Gogoi and Mahanta 2013
<i>T. harzianum</i>	<i>M. incognita</i>	Brinjal	Kumar and Chand 2015
<i>T. harzianum</i>	<i>M. incognita</i>	Green gram	Deori and Borah 2016
<i>T. harzianum</i>	<i>M. incognita</i>	Pigeonpea	Askary 2008
<i>T. harzianum</i>	<i>M. incognita</i>	Tomato	Kumar and Khanna 2006
<i>T. harzianum</i>	<i>M. javanica</i>	Tomato	Sharon et al. 2001
<i>T. harzianum</i>	<i>M. incognita</i>	Brinjal	Rao et al. 1998
<i>T. harzianum</i>	<i>M. graminicola</i>	Paddy	Pathak and Kumar 2003
<i>T. harzianum</i>	<i>M. incognita</i>	Green gram	Singh and Mahanta 2013
<i>T. harzianum</i>	<i>M. javanica</i>	Tomato	Jamshidnejad et al. 2013
<i>T. harzianum</i>	<i>Meloidogyne</i> spp.	Tomato	Khattak and Khattak 2011
<i>T. harzianum, T. viride</i>	<i>M. incognita</i>	Okra	Kumar and Jain 2010b
<i>T. harzianum, T. viride</i>	<i>M. incognita</i>	Okra	Prasad and Anes 2008
<i>T. harzianum, T. viride</i>	<i>M. javanica</i>	Tomato	Al-Hazmi and Javeed 2016
<i>T. harzianum, T. viride</i>	<i>M. incognita</i>	Tomato	Dababat et al. 2006
<i>T. harzianum, T. viride</i>	<i>M. incognita</i>	Tomato	Devi and Sharma 2002
<i>T. harzianum, T. virens</i>	<i>M. graminicola</i>	Rice	Pathak et al. 2005
<i>T. harzianum, T. viride</i>	<i>M. incognita</i>	Tomato	Dababat and Sikora 2007
<i>T. harzianum, T. viride</i>	<i>M. javanica</i>	Mung bean, Okra	Siddiqui et al. 2001a
<i>T. harzianum, T. viride</i>	<i>Meloidogyne</i> spp.	Roundleaf fountain Palm	Jegathambigai et al. 2011
<i>T. harzianum, T. viride</i>	<i>M. javanica</i>	Brinjal	Bokhari 2009
	<i>R. reniformis</i>		
<i>T. viride</i>	<i>M. incognita</i>	Mulberry	Muthulakshmi et al. 2010
<i>T. viride</i>	<i>M. incognita</i>	Tomato	Goswami and Mittal 2004
<i>T. viride</i>	<i>M. incognita</i>	Soybean	Devi and Hassan 2002
<i>T. viride</i>	<i>M. incognita</i>	Chickpea	Pandey et al. 2003
<i>T. viride</i>	<i>Helicotylenchus multicinctus</i>	Banana	Jonathan et al. 2004

Table 4 Biocontrol agents of fungal species targeting nematodes on economic crops (Continued)

Fungus	Nematode managed	Crop	Reference
<i>T. viride</i>	<i>M. incognita</i>	Okra	Chatali et al. 2003
<i>T. viride</i>	<i>Pratylenchus thornei</i>	Chickpea	Dwivedi et al. 2008
<i>T. viride</i>	<i>M. incognita</i>	Cucumber	Krishnaveni and Subramanian 2004
<i>T. viride</i>	<i>M. incognita</i>	Tomato	Rangaswamy et al. 2000
<i>T. viride</i>	<i>M. incognita</i>	Mulberry	Muthulakshmi and Devrajan 2015
<i>T. viride</i>	<i>M. incognita</i>	Betelvine	Bhatt et al. 2002b
<i>T. viride</i>	<i>M. graminicola</i>	Rice	Priya 2015
<i>T. viride</i>	<i>M. incognita</i>	Green gram	Umamaheswari et al. 2004
<i>T. viride</i>	<i>M. incognita</i>	Sugar beet	Kavitha et al. 2007
<i>T. viride</i>	<i>M. incognita</i>	Cowpea	Kumar et al. 2011
	<i>R. reniformis</i>		
<i>T. virens</i>	<i>M. incognita</i>	Bell pepper	Meyer et al. 2001
<i>Trichoderma</i> spp.	<i>M. incognita</i>	Common bean	Santin 2008

summarized in Table 2. Predatory and egg-parasitic fungi, as well as the parasitic bacteria *Pasteuria* spp., were the most studied due to their PPN control potential, ease of laboratory production, and adaptation capability under different agricultural systems. Such bioagents, with different action mechanisms, can play a significant role in PPN management. They have a determined specificity against certain species or even stages of PPNs (Askary and Martinelli 2015). Hence, by considering and identifying such a specificity, PPN management can be targeted successfully. Clearly, sometimes, there is a significant difference in the effectiveness of a definite biocontrol agent against the same PPN species. Possible explanations for these differences include loss of virulence during the in vitro culture process or during formulation, or environmental factors occurring in the field (Crow et al. 2011). Also, current investigations of such mechanisms may lack in the exactitude of the applied parameter. Biochemical measures may be more accurate than others. Korayem et al. (1993) examined the effects of the plant extracts of *Artemisia absinthium*, *Citrullus colocynthis*, *Punica granatum*, *Ricinus communis*, and *Thymus vulgaris* on motility of *Helicotylenchus dihystera* and *Meloidogyne incognita* and the reversibility of the movement inhibition, the egg-hatching inhibition of *M. incognita*, and the inhibition of acetylcholinesterase (AChEs) of *H. dihystera*. Surprisingly, AChE inhibition by extracts of *P. granatum*, *T. vulgaris*, and *A. absinthium* were more than that by oxamyl, which was reported as a strong inhibitor for AChE (Opperman and Chang 1990). Likewise, detail information is required regarding the modes of action of many bio-nematicides in terms of their effect on nematode acetylcholinesterase inhibition.

Available products of fungal and bacterial biocontrol agents used against PPNs

In the past three decades, research workers have prepared different types of formulation of bionematicides that have been commercialized in the world market. Lists of some available fungal (Tables 3 and 4) and bacterial (Tables 5 and 6) nematicides, which indicate relevant information in terms of the active ingredient, product name, type of formulation, producer, targeted nematode species, crop, and country, are presented. There are also cottage industries, which use cheap labor to produce other unavailable microbial products mainly for domestic markets. These products of developing countries, especially in Asia, Africa, and Latin America, might be cost-effective and efficacious against PPNs. However, they have not usually undergone the strict and cost rules of registration schemes required in North America and Europe (Wilson and Jackson 2013). There are also some unpublished products sold on market, but their sell scale is either small, local, and/or has not been approved by the government, while other products are in the pipeline. Therefore, a globally standard procedure for approval by governments, especially for non-registered, available bio-nematicides, was suggested.

Due to their ability to manage a wide range of PPN species, some BCA have been formulated in a commercial product to control different PPN species effectively via a single natural product rather than multiple chemical products (Askary and Martinelli 2015). Coating seeds with biopesticides is an inexpensive option that allows targeted delivery and potentially enhances rhizosphere colonization, but this delivery option requires

Table 5 List of commercial products of bacterial biocontrol agents used in the management of plant-parasitic nematodes

Bacterium	Product name	Company/institution	Country
<i>Pasteuria penetrans</i>	Econem	Nematech Pasteuria Bioscience	Japan USA
<i>P. nishizawai</i>	Clariva PN	Syngenta	Brazil
<i>P. usage</i> (or <i>P. penetrans</i>)	Econem	Bayer CropScience	Multi-national
<i>Pseudomonas fluorescens</i>	SHEATHGUARD (or Sud ozone)	Agriland Biotech	India
<i>Bacillus cereus</i> (CM-1c strain) and <i>Bacillus subtilis</i> (CM-5 strain)	BioStart™ Defensor	Bio-Cat Microbials	USA
<i>Bacillus thuringiensis</i>	Avid 0.15EC (or abamectin)	Syngenta	Multinational
<i>Bacillus subtilis</i>	Stanes Sting	Imported from T. Stanes and Company Limited, India, by Gaara company, Egypt	India and Egypt
<i>B. licheniformis</i> <i>B. subtilis</i>	Quartzo	FMC Química do Brasil Ltda.	Brazil
<i>B. licheniformis</i> <i>B. subtilis</i>	Nemix C	FMC Química do Brasil Ltda.	Brazil
<i>B. licheniformis</i> strain FMCH001(DSM32154) <i>B. subtilis</i> strain FMCH002 (DSM32155)	Presense	FMC Química do Brasil Ltda.	Brazil
<i>B. firmus</i>	1. Bionem-WP 2. BioSafe-WP 3. Chancellor	Agro Green	Israel
<i>B. firmus</i> strain GB-126	VOTIVO®WP	Bayer Crop Science	Germany
<i>B. methylotrophicus</i>	Onix	Laboratorio de Bio Controle Farroupilha S.A.	Brazil
<i>B. subtilis</i>	Pathway Consortia®	Pathway Holdings	USA
<i>B. chitosporus</i> , <i>B. laterosporus</i> , <i>B. licheniformis</i> (mixture)	BioStart® BioStart™	Bio-Cat Rincon-Vitova	USA
<i>B. amyloliquefaciens</i>	Nemacontrol	Simbiose Indústria e Comércio de Fertilizantes e Insumos	Brazil
<i>Bacillus</i> sp., <i>Pseudomonas</i> sp., <i>Rhizobacterium</i> sp., <i>Rhizobium</i> sp.	Micronema	Agricultural Research Centre	Egypt
<i>B. cereus</i>	Xian Mie	XinYi Zhong Kai Agro- Chemical industry CO., Ltd.	China
<i>Bacillus</i> spp.	Nemix	Chr. Hansen	Brazil
<i>Burkholderia cepacia</i>	Deny Blue circle	Stine Microbial Products	USA
<i>Serratia marcescens</i> produces volatile metabolites toxic to and other PPNs	Nemaless	Agricultural Research Centre	Egypt

improved efficacy of coating materials and technology or better formulation. Microbial seed treatment is used for disease control, PPN management, and also for insect control (Glare et al. 2012). Improved seed supply systems that reduce the storage period are required if this delivery mechanism is to become more familiar with BCA. Such multiple effects should be further investigated then materialized commercially.

Different formulations of the same pesticide may generally differ in their toxicity to target organisms. Owing to the continuous introduction of novel active ingredients, carriers, and formulations in different market segments and differences in susceptibility and reaction of bacterial species to nematicide formulations,

comprehensive information about different aspects of relevant modules should be available to stakeholders and updated continuously. Current issues in experimentations of biological control agents and their applications against PPNs to maximize their benefits have been recently reviewed (Abd-Elgawad, 2016).

Future prospects

It should be clear that the use of bio-nematicides is not limited to beneficial BCA, but they should involve the use of their genes and/or products, such as metabolites, that reduce the negative effects of PPNs and promote positive responses by the growing plant. Furthermore,

Table 6 List of bacterial biocontrol agents against phytonematodes infesting agricultural crops

Bacterium	Nematode managed	Crop	Reference
<i>Pasteuria penetrans</i>	<i>Meloidogyne incognita</i>	Tomato, cucumber	Kokalis-Burelle 2015
	<i>Meloidogyne arenaria</i>	Snapdragon	
<i>P. penetrans</i>	<i>M. arenaria</i>	Tomato, oriental melon	Cho et al. 2000
<i>P. penetrans</i>	<i>Meloidogyne</i> spp.	Brinjal, mung bean	Zaki and Maqbool 1990
<i>P. penetrans</i>	<i>Heterodera cajani</i>	Cowpea	Singh and Dhawan 1994, 1996, 1999
<i>P. penetrans</i>	<i>Meloidogyne</i> spp.	Sugarcane	Spaull 1984
<i>P. penetrans</i>	<i>M. incognita</i>	Tobacco, soybean, hairy vetch	Brown et al. 1985
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	Vargas et al. 1992
<i>P. penetrans</i>	<i>M. incognita</i>	Kiwi	Verdejo-Lucas 1992
	<i>M. arenaria</i>		
	<i>Meloidogyne hapla</i>		
<i>P. penetrans</i>	<i>Xiphinema diversicaudatum</i>	Peach	Ciancio 1995
<i>P. penetrans</i>	<i>M. arenaria</i>	Peanut	Chen et al. 1996, Chen et al. 1997
<i>P. penetrans</i>	<i>M. javanica</i>	Chickpea	Sharma 1992
<i>P. penetrans</i>	<i>M. javanica</i>	Tomato	Maheswari and Mani 1989
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	Mankau and Prasad 1972
	<i>M. javanica</i>		
	<i>Pratylenchus scribneri</i>		
<i>P. penetrans</i>	<i>M. javanica</i>	Tomato	Stirling 1984
		Grape	
<i>P. penetrans</i>	<i>M. arenaria</i>	Peanut, rye, and vetch	Oostendorp et al. 1991
<i>P. penetrans</i>	<i>M. acronea</i>	Tomato	Page and Bridge 1985
<i>P. penetrans</i>	<i>M. incognita</i>	Banana, tomato	Jonathan et al. 2000
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	Chand and Gill 2002
<i>P. penetrans</i>	<i>M. javanica</i>	Tomato	Daudi et al. 1990
<i>P. penetrans</i>	<i>M. javanica</i>	Tomato	Daudi and Gowen 1992
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	De Channer 1989
<i>P. penetrans</i>	<i>M. incognita</i>	Tobacco, soybean, tomato, hairy vetch, pepper	Dube and Smart 1987
<i>P. penetrans</i>	<i>M. graminicola</i>	Tomato	Duponnois et al. 1997
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	Weibelzahl-Fulton et al. 1996
	<i>M. javanica</i>		
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	Adiko and Gowen, 1994
<i>P. penetrans</i>	<i>M. incognita</i>	Brinjal, tomato, wheat	Ahmed 1990
<i>P. penetrans</i>	<i>M. graminicola</i>	Rice	Thakur and Walia 2016
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	Ahmed et al. 1994
<i>P. penetrans</i>	<i>H. avenae</i>	Wheat	Bhattacharya and Swarup 1988
<i>P. penetrans</i>	<i>M. javanica</i>	Tomato	Walia 1994
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	De Leij et al. 1992
<i>P. penetrans</i>	<i>Pratylenchus penetrans</i>	Tomato	Somasekhar and Gill 1991
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	Amin 2000
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	Rangaswamy et al. 2000
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	Sekhar and Gill 1991
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	Ravichandra and Reddy 2008

Table 6 List of bacterial biocontrol agents against phytonematodes infesting agricultural crops (Continued)

Bacterium	Nematode managed	Crop	Reference
<i>P. penetrans</i>	<i>M. javanica</i>	Tomato	Ciancio and Bourjate 1995
<i>P. penetrans</i>	<i>M. javanica</i>	Grape	Walker and Watchtel 1989
<i>P. penetrans</i>	<i>M. javanica</i>	Tomato	Jayaraj and Mani 1988
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	Brown and Smart 1985
<i>P. penetrans</i>	<i>M. incognita</i>	Tomato	Singh et al. 2008
<i>P. penetrans</i>	<i>M. incognita</i>	Cherry tomato	Kasumimoto et al. 1993
<i>P. penetrans</i>	<i>M. javanica</i>	Tomato	Walia and Dalal 1994
<i>P. penetrans</i>	<i>M. javanica</i>	Brinjal	Kumar et al. 2005a, b
<i>P. penetrans</i>	<i>M. javanica</i>	Okra, chickpea	Vikram and Walia 2015
<i>P. penetrans</i>	<i>M. javanica</i>	Tomato	Vikram and Walia 2014
<i>Pseudomonas fluorescens</i>	<i>M. graminicola</i>	Rice	Narasimhamurthy et al. 2017a
<i>P. fluorescens</i>	<i>M. graminicola</i>	Rice	Narasimhamurthy et al. 2017b
<i>P. fluorescens</i>	<i>M. incognita</i>	Field pea	Siddiqui et al. 2009
<i>P. fluorescens</i>	<i>M. graminicola</i>	Rice	Seenivasan et al. 2012
<i>P. fluorescens</i>	<i>M. incognita</i>	Tomato	Santhi and Sivakumar 1995
<i>P. fluorescens</i>	<i>H. cajani</i>	Pigeonpea	Siddiqui et al. 1998
<i>P. fluorescens</i>	<i>M. incognita</i>	Okra	Devi and Dutta 2002
<i>P. fluorescens</i>	<i>M. incognita</i>	Bell pepper	Rao et al. 2004
<i>P. fluorescens</i>	<i>M. incognita</i>	Tomato, brinjal	Anita and Rajendran 2002
<i>P. fluorescens</i>	<i>M. incognita</i>	Cowpea	Nama and Sharma 2017
<i>P. fluorescens</i>	<i>M. incognita</i>	Chilli	Wahla et al. 2012
<i>P. fluorescens</i>	<i>M. incognita</i>	Tomato	Siddiqui et al. 2001b
<i>P. fluorescens</i>	<i>Radopholus similis</i>	Banana	Aalten et al. 1998
	<i>Meloidogyne</i> spp.		
<i>P. fluorescens</i>	<i>M. javanica</i>	Tomato	Eltayeb 2017
<i>P. fluorescens</i>	<i>M. incognita</i>	Tomato	Singh and Siddiqui 2010
<i>Pseudomonas</i> sp.	<i>M. incognita</i>	Black pepper	Devapriyanga et al. 2012
<i>P. fluorescens</i>	<i>M. incognita</i>	Mulberry	Muthulakshmi et al. 2010
<i>P. fluorescens</i>	<i>M. incognita</i>	Papaya	Rao 2007
<i>Pseudomonas</i> sp.	<i>Globodera rostochiensis</i>	Potato	Trifonova et al. 2014
<i>P. fluorescens</i>	<i>M. incognita</i>	Maize	Ashoub and Amara 2010
<i>P. fluorescens</i>	<i>Hirschmanniella gracilis</i>	Rice	Seenivasan and Lakshmanan 2002
<i>P. fluorescens</i>	<i>M. incognita</i>	Okra	Kumar and Jain 2010b
<i>P. fluorescens</i>	<i>M. arenaria</i>	Groundnut	Kalaiarasan et al. 2010
<i>P. fluorescens</i>	<i>M. incognita</i>	Banana	Sandeep 2004
<i>P. fluorescens</i>	<i>M. javanica</i>	Tomato	Verma 2009
<i>P. fluorescens</i>	<i>Aphelenchoides besseyi</i>	Tuberose	Pathak and Khan 2010
<i>P. fluorescens</i>	<i>M. incognita</i>	Cowpea	Kumar et al. 2011
	<i>Rotylenchulus reniformis</i>		
<i>P. fluorescens</i>	<i>M. incognita</i>	Banana	Jonathan et al. 2006
<i>P. fluorescens</i>	<i>R. similis</i>	Banana	Kumar et al. 2008
<i>P. fluorescens</i>	<i>R. similis</i>	Banana	Senthilkumar et al. 2008
<i>P. fluorescens</i>	<i>Helicotylenchus multicinctus</i>	Banana	Jonathan et al. 2004
<i>P. fluorescens</i>	<i>M. javanica</i>	Tomato	Siddiqui and Shaukat 2003

Table 6 List of bacterial biocontrol agents against phytonematodes infesting agricultural crops (Continued)

Bacterium	Nematode managed	Crop	Reference
<i>P. fluorescens</i>	<i>R. reniformis</i>	Cotton	Jayakumar et al. 2004
<i>P. fluorescens</i>	<i>R. reniformis</i>	Cotton	Jayakumar et al. 2002
<i>P. fluorescens</i>	<i>M. incognita</i>	Cotton, cucumber	Hallmann et al. 1998
<i>P. fluorescens</i>	<i>M. incognita</i>	Tomato	Hanna et al. 1999
<i>P. fluorescens</i>	<i>Hirschmanniella gracilis</i>	Rice	Ramakrishnan et al. 1998
<i>P. fluorescens</i>	<i>Tylenchulus semipenetrans</i>	Citrus	Santhi et al. 1999
<i>P. fluorescens</i>	<i>M. incognita</i>	Black pepper	Eapen et al. 1996
<i>P. fluorescens</i>	<i>M. incognita</i>	Grapevine	Shanthi et al. 1998
<i>P. fluorescens</i>	<i>M. incognita</i>	Tomato	Khalil et al. 2012b
<i>P. fluorescens</i>	<i>M. incognita</i>	Cucumber	Krishnaveni and Subramanian 2004
<i>P. fluorescens</i>	<i>M. incognita</i>	Sugar beet	Kavitha et al. 2007
<i>P. fluorescens</i>	<i>M. incognita</i>	Okra	Sharma et al. 2008
<i>P. fluorescens</i>	<i>Pratylenchus thornei</i>	Chickpea	Dwivedi et al. 2008
<i>P. fluorescens</i>	<i>M. incognita</i>	Black gram	Akhtar et al. 2012
<i>P. fluorescens</i>	<i>Globodera</i> spp.	Potato	Mani et al. 1998
<i>P. fluorescens</i>	<i>H. cajani</i>	<i>Sesamum indicum</i>	Kumar et al. 2005a, b
<i>P. fluorescens</i>	<i>M. incognita</i>	Tomato	Jothi et al. 2003
<i>P. fluorescens</i>	<i>M. graminicola</i>	Rice	Anita and Samiyappan 2012
<i>P. fluorescens</i>	<i>M. graminicola</i>	Rice	Priya 2015
<i>P. fluorescens</i>	<i>M. incognita</i>	Jasmine	Seenivasan and Poornima 2010
<i>P. fluorescens</i>	<i>M. incognita</i>	Mulberry	Muthulakshmi and Devrajan 2015
<i>P. fluorescens</i>	<i>M. incognita</i>	Tomato	Abo-Elyousr et al. 2010
<i>Pseudomonas</i> sp.	<i>M. incognita</i>	Okra	Vettrivelkalai et al. 2010

many products of fungi or bacteria used as soil conditioners, plant growth promoters, or plant strengtheners are not considered as bio-nematicides even though such outputs may increase plants' ability to tolerate nematode attack (Wilson and Jackson 2013).

It goes without saying that the most successful product should be accepted by growers/end users. In order to achieve satisfaction of such users, more research, especially on the biology, ecology, interaction with other agricultural inputs, and mode of action of these fungal and bacterial biocontrol agents are needed when used as nematicides. Admittedly, such research priorities may call for further development of specialized techniques and realization of growers by merits and demerits of biocontrol agents. The end users should be adequately taught to optimize and adapt to suit their needs for sustainable and environmentally friendly PPN management tactics. Such information is essential for a realistic appraisal of the impact of molecular techniques to enhance their biocontrol potential and monitor their survival and efficacy aiming at developing advanced strategies for PPN control.

Conclusions

We have evaluated the different strategies of using fungi and bacteria in integrated management of plant-parasitic nematodes. This is a hot issue of present and future research. However, due to the wide versatility of this area, we consolidated uses of bio-nematicides and other pesticides which should be practiced on a wider basis; bio-nematicides can act synergistically or additively with other agricultural inputs in integrated pest management programs. Our presentation as a professional review article and meta-analysis study indicated research priorities for utilizing fungal and bacterial nematicides in sustainable agriculture.

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Availability of data and materials

The data sets supporting the conclusions of this article are included within the article.

Authors' contributions

Both authors read and approved the final manuscript. They contributed according to the order of authors.

Ethics approval and consent to participate

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