



Efficacy of Beneficial Microbes in Sustainable Management of Plant Parasitic Nematodes: A Review

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Authors' contributions

This work was carried out in collaboration among all authors. Authors RGM and ZS, conceived and designed the manuscript. Authors RGM and MBM wrote the manuscript and performed bibliographic search. Authors ZS and RGM performed critical reading of the manuscript together. Authors YZ and LT edited the manuscript. All authors agreed the submission of this manuscript.

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ABSTRACT

The soil inhabits many microbes, including plant parasitic nematodes. Plant parasitic nematodes are reported to cause substantial damage to crops which results in yield and economic losses. Chemical control is the most widely used method to control plant parasitic nematodes. However, the consequences of synthetic chemicals are detrimental to human health, animals, and the environment and face so many strict regulatory measures. Synthetic chemicals are also not reliable with their inability to provide long-term protection. Many studies have shown that the use of beneficial fungi and bacteria has the potential to prevent and suppress plant parasitic nematodes while keeping the environment safe. Several experiments have demonstrated that bioproducts of microbial origin are cheap, safe, and provide long-lasting biocontrol effects against pathogens both in vitro and field conditions. Therefore, this review aims to discuss mechanisms that beneficial

microbes and their products use to successfully suppress plant parasitic nematodes. The review also explains the importance of using commercial bionematicides in the sustainable management of plant parasitic nematodes. The existing challenges that are limiting the full application of beneficial microbes, and what needs to be done to fully utilize biocontrol agents in the management of plant parasitic nematodes have also been discussed. To the best of our knowledge, this review has come at the right time to give researchers and plant growers more options when several synthetic chemical nematicides are being banned by regulatory authorities due to their hazardous effects.

Keywords: Biocontrol; beneficial microbes; chemical control; plant parasitic nematode.

1. INTRODUCTION

Microbes such as bacteria, fungi, viruses, and nematodes are found in the environment and influence how other living organisms operate and respond to changing environmental patterns. Plants interact with various microbes, and these interactions have positive or negative impacts on either organism. Notably, beneficial microbes help plants acquire nutrients, produce growth promoting traits and enhance defense against pathogens and pests [1-2]. On the other hand, harmful microbes are responsible for causing physical injuries and diseases in plants, thus reducing yield and production [3].

The soil which forms part of the environment inhabits many microbes, including plant parasitic nematodes. It is known that nematodes are found in abundance in the soil, estimated at 100g of the bulk of soil containing 2000-4000 nematodes [4-5]. Most of the nematodes are obligate. Hence there must be a living plant tissue present to feed on to reproduce, grow and survive [6]. Recent taxonomy studies show over 25,000 species of nematodes though this number is still increasing with the progress of research and discovery of new species [7-8]. The majority of plant-parasitic nematodes feed on roots although some nematodes feed on leaves and other upper parts of a plant [9]. In general, depending on their feeding style, nematodes are classified as endoparasites for those that penetrate the host root to feed; and ectoparasites for those that feed externally by inserting their mouth stylet into the root cells [10]. Some plant parasitic nematodes are sedentary while others are migratory; that is, they move through the soil looking for plant roots [11]. The migration of nematodes is controlled by signaling communication. After that, they begin to inject their nematode effectors into the plant that later controls the genetic system of the host plant [6], [12].

Nematodes have been reported as beneficial organisms in some cases [13-14]. However, if poorly managed, plant parasite nematodes can cause substantial damage to crops which results in yield and economic losses [15-16]. The annual yield loss caused by the plant parasitic nematode is estimated at 8.8% in developed countries and 14.6% in tropical and sub-tropical climates [17], [18]. In vegetables only, damage by pathogenic nematodes can reach as high as 30% [19]. In addition to causing direct damage to crops, plant pathogenic nematodes have been reported to accelerate diseases such as vesicular wilt and bacteria wilt [17], [20].

Most of the plant parasitic nematodes feed on roots. As a result, their symptoms may not appear in aboveground plant parts. This makes nematodes difficult to diagnose and reduces crop yield without plants showing any noticeable aboveground symptoms [17], [21]. The other challenge is that most of the efforts to control plant pathogens, pests, and weeds have focused on the aboveground regions of plants such as stems, leaves, flowers, and fruits [22]. This makes prevention and control of plant parasitic nematodes so difficult as they are not integrated when controlling other pre-existing pathogens and pests.

There are so many ways that have been employed to control nematodes and improve crop yields that include chemical control [23], biological control [24], genetic control through genetic engineering of resistant varieties [19] and cultural control [25] such as crop rotation [26] and use of cover crops [27], [28]. Chemical control is the most widely used method by growers to control plant parasitic nematodes in their fields. However, the consequences of synthetic chemicals have been detrimental to human health, animals, and environmental quality, resulting in agricultural and natural resource pollution [19]. Chemicals are also not reliable as they are unable to provide long-term

protection and face so many strict regulatory measures [27], [29]. As a result, researchers are working on finding the best alternative that will help to achieve sustainable management of plant parasitic nematodes.

Many researchers have highlighted the potential of beneficial microbes to prevent and suppress the plant parasitic nematodes as part of biological control methods. The presence of beneficial microbes and their metabolites are enough to sustainably suppress or restrict the growth of plant parasitic nematodes [30]. In another research, rhizosphere microbiomes modulated by pre-crops were found to suppress plant parasitic nematodes and assist plants in developing immunity against plant parasitic nematodes [31]. In marine environments, cyanobacteria, have been explored and reported to have novel bioactive compounds that could be used to suppress plant parasitic nematodes [32], [33].

Having looked at the importance of beneficial microbes and their formulated products to human health, environment as well as their effectiveness [15], [34], [35]; there is a lot that needs to be done to ensure full application of these bioproducts as the best alternative to synthetic chemicals pesticides. Therefore, this review discusses mechanisms that beneficial microbes and their products use to suppress the presence of plant parasitic nematodes. The review will also explain the importance of using commercial bioproducts with nematocidal activities rather than synthetic chemical nematicides in the sustainable management of plant parasitic nematodes. The existing challenges and opportunities associated with the application of microorganisms' biocontrol products in the management of plant parasitic nematodes, will also be discussed.

2. BENEFICIAL MICROBES AS BIOCONTROL AGENTS FOR PLANT PARASITIC NEMATODES

2.1 Beneficial Fungi and Plant Parasitic Nematodes

In the last decades, the molecular and physiological mechanisms of beneficial fungi to suppress the presence of plant parasitic nematodes have well been documented [36–39]. Beneficial fungi such as *Trichoderma* spp, mycorrhizal fungi, *Syncephalastrum racemosum*

and endophytes qualify them as biological control agents against nematodes by acting as resistance inducers, secrete lytic enzymes, parasitism, antibiosis and paralyzing the plant parasites [40–43]. Some fungi also compete with plant parasitic nematodes for space and resources, providing nutrients and water uptake to plants [44]. Other fungal species induce plant resistance to nematodes through activation of hormone-mediated plant defense mechanisms [36], [42]. The presence of *Dactylella oviparasitica*, *Fusarium* sp. and *Fusarium oxysporum* fungi has shown to be effective in soil suppressiveness to destroy nematode cysts and eggs [45]. Research has shown that fungi such as *Hirsutella* spp. penetrate the nematode by producing conidia that adhere to the cuticle, digest, and kill nematodes before they even invade the roots of plants on target [46], [47].

In addition, the alteration of the transport of chemical defense components through the synthesis of secondary plant metabolites and different enzymes contribute to plant defenses. *Aspergillus niger* F22 fungus inhibited egg hatching by 95.6% within a week and killed second-stage juveniles by 100% within 24hours after treatment in vitro. After conducting organic acid analysis and gas chromatography-mass spectroscopy (GC-MS), the research found that the fungal strain was able to exhibit oxalic acids with nematocidal activity against plant parasitic nematode. While in the field, the results also show that the formulated bioproduct from fungal strain F22 had reduced the gall formation by more than 58.8% on the watermelon roots compared to the untreated, and reduced disease incidence more than the chemical nematicide Sunchungtan [48]. Other known fungi and their mechanisms to prevent and control plant parasitic nematodes include the following:

2.1.1 Nematode trapping fungi

This is a group of fungi that live as both saprophytes and parasites. The fungi act as traps that capture, infect, kill and digest nematodes [49]. There are approximately 200 species of nematode trapping fungi. Sometimes there is a mutual relationship between nematodes and other microbes, including nematodes trapping fungi. For instance, nematodes provide nutrition such as nitrogen for other microorganisms [47], [50]. Nematode trapping fungi act against plant parasitic nematodes by secreting a nematocidal substance that kills the nematodes [24]. There

are several processes involved in the trapping process that led to nematode suppression. The processes were better documented by [51] in their published review article in which *Arthrobotrytis oligospora* was used as a model fungus that traps nematodes by using adhesive networks. The trapping process includes the following stages in order: attraction, recognition, trap formation, adhesion, penetration, and digestion. The molecular and morphological mechanism that underlines the ability of fungi to function as biocontrol agents against plant parasitic nematodes [52] have so far been well understood includes the taxonomy, ecology, and physiological activities [50], [53], [54]. The other nematode-trapping fungi include *Dactylellina* with adhesive knobs and nonconstricting rings, *Drechlerella* with structural constricting rings, and *Mortierella* that acts by using adhesive hyphae [5]. Because of their effectiveness in controlling plant parasitic nematodes, nematode trapping fungi form one of the tools that need to be incorporated in the sustainable management of plant parasitic nematodes. However, because it requires growers and researchers to have technical knowledge and skills to implement this method, there is a need to improve awareness that will include all stakeholders involved in managing plant parasitic nematodes.

2.1.2 Endoparasitic fungi

This is a group of fungi that acts on plant parasitic nematodes by using adhesive conidia and zoospores. Endoparasitic fungi such as *Drechmeria conospora*, *Esteya vermicola*, *Haptocillium*, *Hirsutella* and *Catenaria*. *E. vermicola* were studied and found to produce volatiles and adhesive conidia that attract, infect and increase nematodes mortality rates [55], [56]. *Drechmeria conospora* causes diseases and kills plant parasitic nematodes by not only producing various zoospores but also secretes more than 13 bioactive metabolites such as 4(S)-butoxy-3-(butoxymethyl)-2-hydroxycyclopent-2-en-1-one and 5-hydroxymethylfuran-2-carboxylic acid that are more toxic to the *Meloidogyne incognita* nematode and negatively affect hatching of its eggs [57].

2.1.3 Egg and female parasitic fungi

This is a group of fungi with special modifications and acts against female plant parasitic nematodes and their eggs [58]. Generally, fungal species such as *Dactylella*, *Trichoderma* *Purpureocillium*, and *Pochonia* act by producing toxins against plant parasitic nematodes,

activating the induced systemic resistance, producing zoospores and appressoria depending on the specific species [59–61]. *Pochonia chlamydosporia*, a soil and plant-growth-promoting and biocontrol fungus has a mechanism to parasitize eggs and kill female plant parasitic nematodes. The whole genome of this fungus shows genes that are associated with the synthesis of hydrolytic enzymes and other genes responsible for biocontrol against plant parasites and pathogens [62]. Basidiomycetes have also been reported to invade and parasitize eggs of nematodes. In an association where *Deladenus siricidicola* parasitic nematode depends on *Amylostereum areolatum* fungi to provide nutrition, it turns out that fungal hyphae start invading and killing nematode eggs [53]. This shows how effective the egg and female parasitic fungi can be to sustainably control the developmental stages of nematodes and adults' parasitic nematodes in plant production.

2.2 Beneficial Bacteria and Plant Parasitic Nematodes

Plant growth promoting and biocontrol bacteria influence both plants and other microbial communities [63]. The beneficial bacteria control and suppress the presence of plant pathogenic nematodes by reducing egg masses and killing nematodes directly, competition for space and nutrition, antibiosis production, activating plant induced systemic resistance, regulation of nematode behaviors, and altering nematode-host recognition [64–68]. Recently, several beneficial bacteria with nematocidal activities have well been studied and documented [69]. Therefore, this review has focused on only the most widely used beneficial bacterial species with nematocidal activities as shown in Table 1. Different bacteria species have similar and different mechanisms, but all offer antagonism against plant parasitic nematode. The following sections will discuss examples of beneficial bacteria, their mechanisms, and research progress for suppression of plant parasitic nematodes.

Pasteuria spp. is a common bacterium of parasitic nature that associates with plant parasitic nematodes. The most *Pasteuria* groups are *Pasteuria penetrans sensu stricto* and *Pasteuria thornei* that parasitizes root-knot nematodes *Meloidogyne* spp and *Pratylenchus brachyurus* respectively. Usually, *Pasteuria* spp. bacteria parasitize females and second-stage juveniles of nematodes [70]. This bacterium

suppresses migratory stages of sedentary parasitic nematodes by limiting their movement toward the roots then attaches spores on nematode surfaces. *Pasteuria* spp. also penetrates the nematode and localizes with a high density inside the pseudocoelom thus affecting embryogenetic processes and impairing host reproduction [4]. Recently, this bacteria spp. has been isolated from the soils that offer suppressiveness against root-knot nematodes and has been used as a candidate for biocontrol against plant parasitic pathogens [71], [72].

Streptomyces spp. This is the main group of actinomycetes reportedly to exhibit nematocidal activity that interrupts and eliminates growth stages and adult plant parasitic nematodes while enhancing the growth and development of plants [30], [74]. *Streptomyces* strain KPS-E004 and KPS-A032 gives significant control over root-knot *Meloidogyne incognita* when inoculated individually as well as in combination in chilli plants. The inoculation by the two strains also improves the chilli plant's growth performance by more than 75% compared to uninoculated plants [75]. In addition, it was found that there was a lower number of eggs, second-stage juveniles, and galls per plant. *Microbacterium*, *Brevundimonas*, *Acinetobacter*, and *Sphingopyxis* were investigated and found to exhibit antagonistic effects that reduced the number of hatched eggs, reduced second-stage juveniles root invasion, reduced motility, and increased mortality of second-stage juveniles [79].

Bacillus spp. isolates were examined for their ability to suppress plant parasitic nematodes. It was discovered that five of 70 bacterial isolates from the root zone of crops and goat pasture were able to kill second-stage juvenile in vitro within 24 hours. Three out of the five selected isolates caused more than 80% mortality rate within 24 hours and a reduction in root-knot galling and several nematode eggs [76]. *Bacillus methylotrophicus* R2-2 and *Lysobacter antibiolicus* strain 13-6 were studied for their potential to control root-knot nematode *Meloidogyne incognita* in tomatoes. Both strains were found to significantly reduce the root-knot disease incidence and severity more than the synthetic chemicals abamectin and carbofuran both in the greenhouse and fields [77]. These results show that bacteria with antagonistic effects are better biocontrol candidates alternating the chemical control method [90]. There are several mechanisms that beneficial

bacteria use is preventing and controlling plant parasitic nematodes. Some of these mechanisms are highlighted in Table 1. However, the description of mechanisms has been given in the following sections and include the following:

2.2.1 Volatile organic compounds (VOCs)

Bacterial volatile organic compounds are low molecular weight compounds that promote the growth of plants and suppress pathogens, insects, and nematodes [91], [92]. Beneficial bacteria such as *Arthrobacter nicotianae*, *Bacillus* spp., and *Bacillus amyloliquefaciens* increase the level of volatiles such as terpenoids, esters, alkanes, alcohols, alkenes, and ketones that acts by inactivating and suppressing the plant pathogens and parasites [31], [93], [94]. Bacterial strains such as *Wautersiella fausenii*, *Proteus hauseri*, *Achmobacter xylooxidans*, *Arthrobacter nicotianae* and *Pseudochrobactrum saccharolyticum* were tested for their ability to produce volatile organic compounds. The results show that 53 volatile organic compounds that include aldehydes, ketones, alkyls, alcohols, alkenes esters, alkynes, acids, ethers, and other phenolic compounds were produced. After that, 19 of these volatile organic compounds demonstrated high activity to suppress nematodes more than the commercial nematocide, dimethyl disulfide used as a positive control [95]. Another study assesses the effect of volatile organic compounds that were produced by 200 isolates of rhizosphere bacteria. The results showed that 82.5% of the isolates produced more than 20% nematocidal organic compounds against *Panagrellus redivivus* and *Buesaphelenchus xylophilus*. In the same study, 22 isolates were able to completely suppress *P.redivivus*, while seven isolates showed 100% suppression of *B.xylophilus* [96]. In another research, it was found that more than 99% of *M.graminicola* nematodes were dead in just three days after being exposed to the volatile compounds produced by *Bacillus* sp., *Paenibacillus* sp., and *Xanthomonas* [80]. In addition, more nematodes were present in citrus rootstock treatments that were infested with root weevils than non-infested citrus rootstocks. These nematodes were attracted by the volatiles that was secreted from the rootstock's wounds caused by the weevils as a response to the attack [22]. Based on these previous studies, the use of volatile organic compounds producing bacteria cannot be underestimated although more research is needed to demonstrate how the volatile organic compounds can be used at the farm level by farmers.

Table 1. The most common bacterial species effective in the management of plant parasitic nematodes

Common beneficial bacteria species	Mode of Action	Stage of plant parasitic nematodes	Reference
<i>Pasteuria</i> spp.	Parasitism	Migratory stages of nematodes, adult nematodes	[4]; [70], [71], [72] [73]
<i>Streptomyces</i> spp.	induced systemic resistance, Volatile organic compound, lytic enzymes, antibiotics	Eggs, growth stages, and adult nematodes	[30], [74]; [75]
<i>Bacillus</i> spp.	Volatile organic compound, lytic enzymes, antibiotics, induced systemic resistance, plant growth promotion, crystal proteins	Eggs, growth stages, and adult nematodes	[76]; [77]; [78]
<i>Brevundimonas</i> spp.	induced systemic resistance, Volatile organic compound, lytic enzymes, antibiotics,	growth stages, and adult nematodes	[79]
<i>Xanthomonas</i> spp.	Volatile organic compound, lytic enzymes, antibiotics	growth stages, and adult nematodes	[80]
<i>Pseudomonas</i> spp.	ACC deaminase, Volatile organic compound, lytic enzymes, antibiotics, induced systemic resistance	Eggs, growth stages, and adult nematodes	[81] [82] [83] [84]; [85]
<i>Rhizobium</i> spp. (<i>Rhizobium etli</i> G12)	plant growth promotion, induced systemic resistance	adult nematodes	[86] [87]
<i>Azobacter chroococcum</i>	Volatile organic compound, lytic enzymes, antibiotics	adult nematodes, growth stages	[88] [89]

2.2.2 Induced systemic resistance (ISR)

This refers to the enhanced plant defense response that results when an agent such as parasites and pathogens stimulates the plant immune system and provides non-specific protection against a broad range of plant enemies [97], [98]. Several research studies show that beneficial bacteria such as rhizobacteria have influenced plant-induced resistance against different pathogens. This process is achieved by modifying and strengthening structural cell walls, accumulation of phenolic compounds, and changes in the physiological processes through the synthesis of biochemical compounds such as salicylic acids, siderophores, jasmonic acid, and other metabolites that up-regulate defense reactions within the plant tissues [70], [99]. *Bacillus amyloliquefaciens*, such as *B. amyloliquefaciens* FZB42 have complete genomes that consist of genes associated with the synthesis and production of antimicrobial metabolic compounds that do not directly act on suppression of plant parasitic nematodes but activate plant defense mechanisms [66], [68]. For example, enzymes phenol, peroxidase, polyphenol oxidase, phenyl ammonia lyase, chitinase, and super oxide dismutase produced by *Pseudomonas fluorescens* Pf1 were noted to induce systematic resistance in rice plants against rice root-knot nematode [100]. In another study, root-knot nematode *Meloidogyne incognita* root infection was found to be effectively reduced by the induced systemic resistance stimulated by the presence of *R. etli* G12 endophytic strain [87].

2.2.3 Production of lytic enzymes and antibiotics

Many lytic enzymes that are produced by various beneficial bacteria species include chitinases, lipases cellulases, glucanases, collagenases, chitosanase pectinases and proteases. These lytic enzymes act on the eggs, juveniles, and adult nematodes by lysis and paralyzing them [101-104]. Some bacteria species produce antibiotics that act directly or indirectly on the developmental stages and adult plant parasitic nematodes. The antibiotics include but are not limited to surfactin, iturins, acteriocins, fengycin, and bacteriocins that are normally produced by some strains of *Bacillus subtilis* and *Bacillus amyloliquefaciens* [103-105]. Fluorescent *Pseudomonads* spp. has been reported to produce 2,4-diacetylphloroglucinol that act on the various nematodes such as *Meloidogyne*

javanica, *Meloidogyne graminicola* and eggs and juveniles of *Globodera rostochiensis* [106–108].

2.2.4 Production of 1-Aminocyclopropane-1-Carboxylate (ACC) Deaminase

Some beneficial bacteria synthesize 1-Aminocyclopropane-1-Carboxylate deaminase that adheres ACC, the precursor of ethylene in a plant. The bacteria have genomes with genes responsible for the production of ACC that enhance plant resistance to biotic and abiotic stresses [82]. In plants, ACC deaminase controls the overproduction of ethylene produced by plant that would otherwise cause a deleterious effect on plant growth [109], [110]. A good example has been demonstrated by the production of ACC deaminase by PGPB *P. putida* UW4 in controlling wilt disease of *Pinus pinaster* caused by pinewood nematode *Bursaphelenchus xylophilus*. When the seedlings of *Pinus pinaster* were inoculated with strain UW4 and its mutant AcdS (without ACC deaminase gene) in the presence of the nematode, symptoms of pine wilt disease were reduced in treatments that were inoculated with wild type *P. putida* UW4, whereas seedlings infested with the mutant, displays symptoms of PWD though *P. putida* UW4 strain did not show any nematocidal effects when tested in vitro. Further results showed that seedlings inoculated with *P. putida* UW4 were less colonized by the nematodes compared with those inoculated with mutant strain [82]. These results show that *P. putida* UW4 strain had an indirect influence in activating the plant defenses against the nematode through ACC deaminase.

2.2.5 Plant growth promotion bacteria (PGPB)

Plants attacked by parasitic nematodes experience pressure to receive and obtain the required nutrition and other growth factors. As such, plant growth promotion bacteria relieve the plants from such kind of stress. Research reports have indicated that plant growth promoting bacteria can improve yield even in plants that have been affected by plant parasitic nematodes [66], [111] [110] Plant growth promoting bacteria is responsible for nitrogen fixation [113], [114], solubilization of phosphorous and potassium [115], iron [116], zinc and synthesize auxins such as ethylene, abscisic acid cytokinin, jasmonic acid, gibberellins and Indo-3-acetic acid [117] that are needed by plants not only for growth and survival but also as part of bio-management of pathogens and parasitic nematodes [118]. However, thorough management and control of

plant parasitic nematodes does not only depend on plant growth promotion activity by the beneficial bacteria but includes metabolic by-products, enzymes, and toxins that these bacterial strains produce [119]. *Bacillus aryabhatai* KMT-4 was screened for the ability to suppress root-knot nematode and improve growth. The in vitro results shows that the bacterium was able to reduce egg hatching, mobility and kills *Meloidogyne javanica* nematodes. During the pot experiment, the bacteria were able to reduce eggs by 73% and plant root galls by 80% compared to the chemically treated and untreated plants. Among the mechanisms, the bacterial strain was able to exhibit plant growth promoting traits such as indo-3-acetic acid (IAA), siderophores, ammonia, hydrogen cyanide, chitinase, and secondary metabolites with nematocidal activity and contributed to the suppression of nematodes [120]. Six rhizosphere bacterial isolates were studied for their ability to suppress and kill plant parasitic nematodes in the laboratory and greenhouse. These isolates were *Paenibacillus amylolyticus*, *Brevibacillus agri*, *Gluconobacter frateurii*, *Beijerinckia mobilis*, *Achromobacter aloeverae* and *Pseudomonas stutzeri*. All these bacterial strains exhibit nematocidal activities that result in a 100% nematode mortality rate. The strains were also able to demonstrate the production of lytic enzymes and other plant-growth- promoting and biocontrol traits that were suggested to play a role in nematode suppression [34].

2.2.6 Hydrogen cyanide (HCN)

Research has also proved the nematicide effect that hydrogen cyanide has on plant parasitic nematodes [121]. For example, *Pseudomonas chlororaphis* PA23 strain exhibited hydrogen cyanide and other compounds that were able to kill *Caenorhabditis elegans* nematodes. Furthermore, the hydrogen cyanide produced by PA23 strain could assisted the bacteria to sense the availability of *C.elegans* nematodes and act as the repellent mechanism [122]. These qualities are of significance in sustainable management of plant parasitic nematodes. *Pseudomonas fluorescens* strain CHAo could produce hydrogen cyanide that acts against the root-knot nematode *Meloidogyne javanica*. The hydrogen cyanide produced shows nematocidal ability by causing mortality of *Meloidogyne javanica* and inhibited egg hatching in vitro. Further results show that Strain CHAo exhibited

greater biocontrol potential by suppressing nematode populations and galling in tomato roots that were grown in soil inoculated with eggs or juvenile. CHAo bacterial strain significantly reduced nematode root penetration [78]. Hydrogen cyanide produced by *Pseudomonas chlororaphis* 06 had nematocidal activity against *Meloidogyne hapla* nematode by reducing the number of galls on tomato plants and kills juveniles both in vitro and in plants [123]. *P. fluorescens* and *P. putida* were able to produce secondary metabolites, which included hydrogen cyanide that plays a role in causing mortality in wheat cyst nematode *Heterodera avenae* and inhibited hatching of nematode eggs [83].

2.2.7 Cry protein mediated infection

Crystal proteins (Cry proteins) produced by specific bacteria species are toxic and act against insects, pathogens, and parasites, including plant parasitic nematodes. The widely used Cry protein-producing bacteria is *Bacillus thuringiensis*. The use of *Bacillus thuringiensis* has been noted to be the most successful method to control plant parasitic nematodes [124]. According to [125], there are Cry 5, Cry6 and Cry55 Cry6, Cry12, Cry13, Cry 14, Cry21, and Cry55 Cry proteins species that are responsible for completely suppressing the presence of plant parasitic nematodes by killing juveniles and retarding their growth, causing abnormal mortality, intestine lysis by using lytic pores and inhibiting the plant parasitic nematodes brood size [125], [126]. Recently, researchers have sequenced the whole genome of *Bacillus thuringiensis* strain DB27 and identified three cry-like genes of Cry 21 family with nematocidal activity [127]. The Cry6A and Cry5B were found to be successfully promote nematocidal toxicity of *Bacillus thuringiensis* against the plant pathogenic nematodes [124]. Other crystal-forming bacteria such as *Bacillus sphaericus*, *Bacillus thuringiensis* kurstaki and *bacillus thuringiensis* israelensis were also reported in various research reports to show nematocidal effects on eggs and larva of the *Trichostrongylus colubriformis* nematode [73]. The capacity and mechanisms of bacteria that produce Cry proteins offering nematocidal activity provide another step forward to sustainable management of nematodes. However, more research and formulations of Cry bacteria are needed so that the products and their use are accessible by many growers at all levels.

Table 2. Summary of major metabolites of beneficial bacteria to suppress plant parasitic nematodes

Mechanisms	Name of Biocompound	Beneficial Bacteria	Stage of Plant Parasitic Nematodes	References
Volatile Organic Compounds	Aldehydes	<i>Bacillus</i> spp.,	eggs, juveniles, adult nematodes	[80]
	Ketones	<i>Paenibacillus</i> spp.,	eggs, juveniles, adult nematodes	[80]
	Alkyls	<i>Xanthomonas</i> spp.	eggs, juveniles, adult nematodes	[80]
	Alcohols	<i>Wautersiella fausonii</i> , <i>Proteus</i>	eggs, juveniles, adult nematodes	[95]
	alkenes esters	<i>hauseri Achmobacter xylooxidans</i>		
	alkynes	<i>Arthrobacter nicotianae</i> and		
	terpenoid	<i>Pseudochrobactrum</i>		
	ethers	<i>saccharolyticum</i>		
	phenolic compounds			
Lytic Enzymes	Lipases	<i>Rahnella aquatilis</i>	juveniles	[128]
	Proteases	<i>Bacillus megaterium</i>	eggs and juveniles	[129]
		<i>Lysobacter capsica</i> YS1215	eggs and juveniles	[130]
		<i>Brevibacillus laterosporus</i> G4	juveniles	[63], [131], [132]
		<i>Pseudomonas fluorencens</i> CHA0	eggs, juveniles, nematode adults	[133]
	Collagenases	<i>Bacillus cereus</i>	juveniles	[134]
		<i>Bacillus thuringiensis</i> FB833T	adults and Juveniles	[135]
	Chitinases	<i>Lysobacter capsica</i> YS1215	Eggs and juveniles	[136] [137]
	Gelatinases	<i>Lysobacter capsica</i> YS1215	juveniles	[130], [136]
Cellulases and pectinases	<i>Pseudomonas</i> spp.	eggs, juveniles and adult nematode	[101]	
Glucanases	<i>Pseudomonas</i> spp.	eggs, juveniles and adult nematode	[101]	
Complex chitosanases	<i>Bacillus cereus</i>	juveniles	[102], [135]	
Antibiotics	Surfactin, fengycin, polyketides, acteriocins, bacteriocins, iturins	<i>Bacillus subtilis</i> , <i>Bacillus amyloliquefaciens</i> FZB42	Eggs, juveniles, adult nematodes	[68], [100], [103]–[105]
	Mersacidin	<i>Bacillus</i> spp.	juveniles,	[108]
	2,4-diacetylphloroglucinol (DAPG)	<i>Pseudomonas</i> spp.	Eggs, juveniles, adult nematodes	[106], [108], [138], [139]
Toxic Compounds	Hydrogen Cyanide (HCN)	<i>Bacillus</i> spp.	eggs, juveniles, adult nematode	[101]
		<i>Pseudomonas</i> spp.	eggs, juveniles, female nematodes	[83], [101], [121]
		<i>Pseudomonas fluorescens</i> CHA0	Juveniles	[78]
		<i>Pseudomonas Chlororaphis</i> PA23	eggs, juveniles, adult nematodes	[122]
		<i>Pseudomonas aeruginosa</i>	Juveniles	[140]
	<i>Pseudomonas Chlororaphis</i> O6	Juveniles	[123], [141]	

Mechanisms	Name of Biocompound	Beneficial Bacteria	Stage of Plant Parasitic Nematodes	References
	Crystal Proteins	<i>Bacillus thuringiensis</i> <i>Bacillus thuringiensis</i> YBT-1518 <i>Bacillus sphaericus</i> , <i>Bacillus thuringiensis</i> kurstaki and <i>Bacillus thuringiensis</i> israelensis	juveniles, adult nematode juveniles, adult nematodes eggs, juveniles	[125], [142] [126] [73].

3. BIOCONTROL OF THE PLANT PARASITIC NEMATODES USING BIOPRODUCTS OF MICROBIAL ORIGIN

Many synthetic chemicals of non-organic origin are banned in many countries. These chemicals include barbofuran, carbosulfan, ethylene dibromide, and chloropicrin [120]. To achieve sustainable agriculture, researchers are formulating beneficial microbiomes and their metabolites into biopesticide useful in plant production [143]. Some microbes genetically modified to produce toxins and be species-specific and non-pathogenic to other useful organisms [144]. Bioproducts are safer because they are naturally biodegradable, display different modes of action, and have less toxicity to living organisms and the whole environment. Furthermore, bioproducts sources are available in abundance in nature making them fit for achieving sustainable agriculture [35], [145], [146].

Several microbes and their metabolites have been formulated into useful biopesticides with nematocidal effects such as Majestene from 94.5% heat-killed *Burkholderia* sp. strain A396, MeloCon WG made from 6% *Paecilomyces lilacinus* strain PL251 [147]. Recently, bioproducts with nematocidal effect formulated from *Trichoderma album* (Biozeid®), *Aschophyllum nodosum* (Algaefol®), *Bacillus megaterium* (Bioarc®) and *Trichoderma harzianum* (Plant Guard®) were tested for their efficacy in controlling root-knot nematode, *Meloidogyne incognita* for tomatoes. The results show a reduction of root galls and juveniles of the soil nematodes while promoting tomato growth [23]. *Purpureocillium lilacinum* (strain251) (BioAct) WG and Velum with fluopyram; biological control and chemical control methods respectively, were used to evaluate their management efficacy against *Meloidogyne incognita* in tomatoes. The results show that when used as a single treatment, BioAct controlled the nematode population throughout the growing season while Velum had only better results against *M. incognita* at only the planting stage [148].

Bacillus firmus strain 11582 was commercially formulated and tested for its efficacy to control root-knot *Meloidogyne incognite* in tomatoes. The bioformulation was either used alone or in combination with a synthetic chemical nematocidal oxamyl or fosthiAZE. When used alone, the bioformulation suppressed population levels of

nematodes and fungal infections (caused by *Pseudopyrenochaeta lycopersici*) in tomatoes, especially during the second crop cycle. In contrast, the combination of bioformulation and chemicals resulted in the lowest root galling to all the treatments and improved yield of tomatoes [149]. *Bacillus firmus* was formulated into a commercial bioproduct (BioNem) and has widely been used in the control of devastating root-knot nematode *Meloidogyne incognite*. The BioNem is effective in inhibiting mobility, reducing gall formation, number of eggs, and nematode populations while improving yield performance of crops [111]. These research results show that formulated bioproducts from beneficial microbes could be the best effective method if integrated into sustainable management of plant parasitic nematodes. Some of the important bioproducts with nematocidal effects from bacteria have well been explained and documented in reviews by [68], [94], [150].

4. CHALLENGES AND OPPORTUNITIES IN SUSTAINABLE PREVENTION AND CONTROL OF PLANT PARASITIC NEMATODES

Plant parasitic nematodes have more complex biology and are very difficult to work with because they have different specific developmental stages that exist only inside the roots, are not easy to culture and some species are more diverse. Furthermore, very few plant parasitic nematodes have been studied, with more attention being on those that are most damaging to plants, such as *Meloidogyne* sp., *Globodera* sp., and *Heterodera* sp [18]. The use of advanced cellular, molecular and biotechnological tools that include the application of metabolomics techniques such as nuclear magnetic resonance and mass spectrometry is forming one way of dealing with biological challenges. The availability of complete genome sequences will help in extending knowledge of the biology and genetics of various microbes that exhibit biocontrol effects against plant parasitic nematodes.

The use of some beneficial microorganisms has faced criticism on their efficacy to control plant parasitic nematodes. For example, the use of some fungi has been debatable in some studies. The application of *Fusarium oxysporum* to suppress nematode is still debatable and speculative because in some studies the strategy was unsuccessful [151]. There are also fungal species that do not show high activity to control

Biocontrol of Plant parasitic nematodes

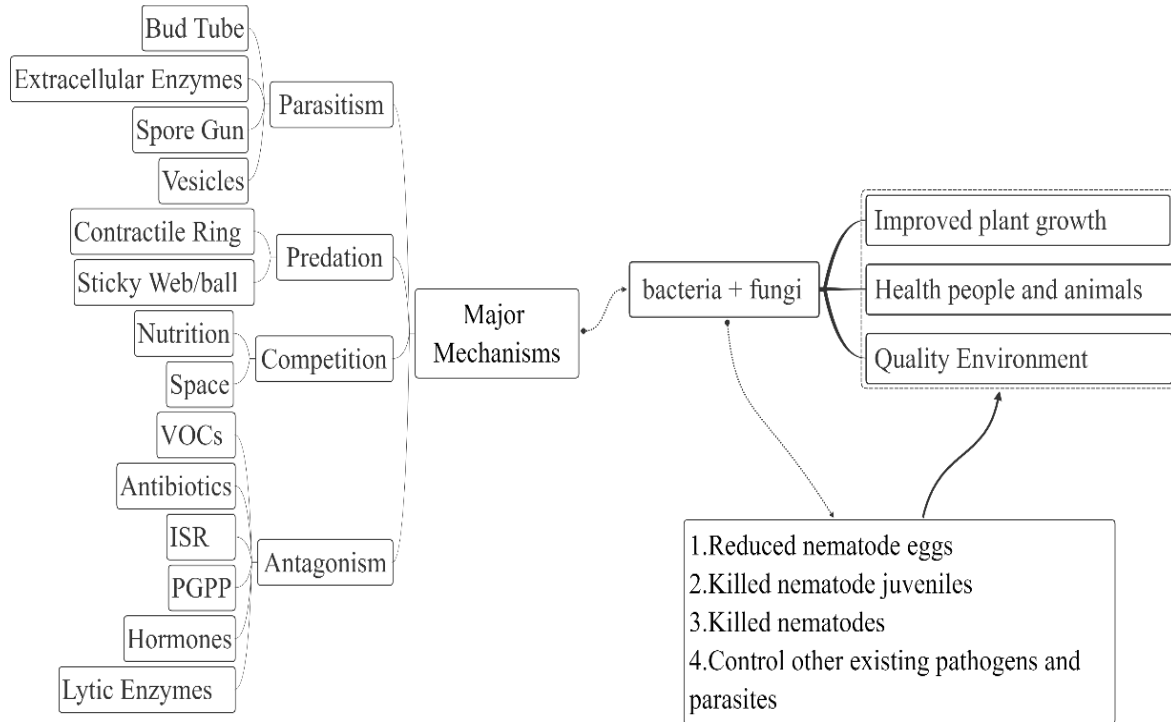


Fig. 1. the summary of major mechanisms of beneficial bacteria and fungi against plant parasitic nematodes and their impact on plant growth, people and environment

plant parasitic nematodes when used in combination or the presence of other beneficial microorganisms. For example, Burkholderia cepacia and Trichoderma virens were studied for their ability to suppress Meloidogyne incognita on Bell pepper. The results show that when used individually, Burkholderia cepacia and Trichoderma virens reduced the number of eggs and second-stage juveniles, whereas when combined, their efficacy to control Meloidogyne incognita was not detectable [152]. However, based on these reports, more research is needed to verify this scientific and practical scenario if sustainable management of plant parasitic nematodes is to be achieved.

There have been poor formulation levels of most of the beneficial microbes into bioproducts. In addition, several farmers have been reporting the slow effectiveness of bioproducts as compared with synthetic chemicals. Another challenge is that beneficial microbes are easily affected by biotic and abiotic factors thus influencing their efficacy to control the targeted enemy. In

addition, it is challenging for some farmers to determine the right dose at a given time [144]. This challenge has resulted in the lower utilization of biocontrol agents. However, the key to successful science and use of bioproducts is being able to identify and detect, as with nematocidal plants [153], the potential defense mechanisms that microorganisms use. In addition, determining the chemistry behind various microbial and bioproducts, the required dose, and environmental conditions will assist in the successful use of biocontrol agent and products in the sustainable management of plant parasitic nematodes.

5. CONCLUSION

Plant parasite nematodes can cause substantial damage to crops which can result in yield and economic losses. Chemical control, which is the most widely used method by growers, has detrimental effects on humans and the environment hence faces more restrictions from regulatory authorities. Researchers are working

on finding the best alternatives that will help to sustainably manage plant parasitic nematodes using beneficial microbes and their bio-products. Bioproducts have proven to be cheap, safe to humans and animals, environmentally friendly, reliable, and effective in controlling plant pathogens and parasites. Despite the challenges that come with complexity in the biology of plant parasitic nematodes, this review has demonstrated that the availability of advanced molecular and biotechnological tools is furthering our knowledge in genomics of microbes and plant parasitic nematodes. Furthermore, research on the use of biological control agents needs to be made to foster their successful application in the sustainable management of plant parasitic nematodes. Therefore, researchers and growers need to work together so that other challenges that hinder the full utilization of biocontrol agents in the management of plant parasitic nematodes have been resolved.

DISCLAIMER

Authors have declared that no competing interests exist. The products used for this research are commonly and predominantly use products in our area of research. There is absolutely no conflict of interest between the authors and producers of the products because we do not intend to use these products as an avenue for any litigation but for the advancement of knowledge. Also, the research was not funded by the producing company.

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COMPETING INTERESTS

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