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Traditional and modern approaches of root knot nematodes management in vegetable crops: A review

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Abstract

Vegetables are the major food source for nutritional security for the teeming millions across the globe. Unfortunately, the growth and development of vegetable crops face yield reduction due to the infestation of notorious sedentary endoparasites, root-knot nematodes (RKN, *Meloidogyne* spp.). The RKN substantially harm the vegetable crops (20–100 %) culminating in huge economic losses to the growers, becoming a serious threat to the world agricultural sector. Chemical-based nematicides are effective to a certain extent but are costly, unsafe for humans and animals and subject to various regulations. Hence, it is crucial to use green and sustainable approaches for managing RKN infection. Approaches such as cultural practices, application of cover/antagonistic crops, use of organic amendments, nanoparticles (NPs) and chemical nematicides have been deployed for management of RKN. However, application of biocontrol agents is a safer, more reliable, cost-effective and promising alternative method for management of RKN. These biocontrol agents not only improve plant health but also facilitate plants to withstand various biotic stresses by inducing systemic resistance. Novel approaches, such as transgenic technologies, omics-based strategies, and integrated management of root-knot nematodes (RKNs), are receiving increasing attention.Hence, the present review focuses on the challenges associated with RKN management and provides explicit information on traditional and modern approaches of RKN management. It also emphasises sustainable biocontrol of RKN through fungi and bacteria, for food security.

Keywords: biocontrol agent; eco-friendly; integrated approaches; nematicides; root-knot nematode endoparasites

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1. Introduction

Vegetables are the major source of nutrition for the ever-increasing population across the globe. However, there are a number of biotic stresses which severely impact the production of vegetables and pose a major menace to global food security (1). Among the various biotic stresses, nematodes are the prime damaging pathogens of various crops worldwide. More than 4100 species of nematodes have been documented which includes dagger nematodes (*Xiphinema* spp.), lesion nematodes (*Pratylenchus* spp.), cyst nematodes (*Heterodera* and *Globodera* spp.) and root-knot nematodes (RKN) (*Meloidogyne* spp.). These nematodes threaten to major vegetable crops including potato, brinjal, peanut, peas, carrots, tomato and cause losses of approximately $157 billion across the globe (2, 3). Nematodes have a specific organ called a stylet which penetrates the roots of plants, delivers the effector molecules and forms the specific root galls (4) which hamper the nutrient and water uptake in infected plants (5). The nematode infected plants exhibit slow growth, poor response to fertilisers, wilting, susceptibility to other pathogens and reduced fruit yield (3, 6). The infection weakens the plant's immune mechanisms by secreting specific effector proteins, making them more vulnerable to secondary infections, culminating in substantial yield loses (2, 7). Based on the feeding habits nematodes can be divided into two groups: ectoparasites and endoparasites. Among these RKNs are most notorious endoparasites (3). Root-knot nematodes infect more than 3000 plant species (8) causing substantial damage to vegetable production and rank higher among animal pathogens which affects the world agricultural sector. They are distributed globally across diverse environmental conditions, being particularly prevalent in the tropics and subtropics, where they cause immense losses to horticultural crops (9). Four main species of RKN

(*Meloidogyne incognita* Kofoid & White, *Meloidogyne javanica* Treub, *Meloidogyne arenaria* Neal and *Meloidogyne hapla* Chitwood) severely impact the growth of infected plant and decline vegetable crop yields by 20–100 % (1, 6, 9). The RKN not only influence the yield of vegetable crops but also affects the fruit quality. *M. incognita*, *M. javanica* and *M. arenaria* are prevalent in temperate (under protected cultivation), tropical and subtropical regions while *M. hapla* is specifically found at higher altitude in tropical and temperate regions (10). Out of four RKN species affecting vegetable production, *M. incognita* is more prevalent in India trailed by *M. javanica* and *M. arenaria* while *M. hapla* has been found to infect the vegetable crops in temperate regions (11). The ever-increasing population has imposed pressure on agriculture sector for increased food production, therefore, there is an urgent need to manage RKN infection in vegetable crops for sustainable vegetable production and subsequent global food security (12, 13).

The most prevalent strategy for controlling RKN infection is application of inorganic chemicals (synthetic nematicides), however, these chemicals are costly and hazardous to the biosphere and the atmosphere (3). Moreover, the chemical based nematicides like 1,2-dibromo-3-chloropropane (DBCP), ethylene dibromide (EDB), aldicarb, 1, 3-dichloropropene + 1, 2-dichloropropane (D-D), carbofuran, methyl bromide, aldrin and dieldrin, benomyl, triazophos and trichlorfon have been banned or restricted in many nations because of their hazardous effects on humans, soil microflora, ozone layer and the atmosphere (6, 9). Hence, there is a critical need to identify alternative, eco-friendly strategies for RKN management (6, 7). Biocontrol using antagonistic bacteria (*Pseudomonas fluorescens*, *Bacillus thuringiensis*, *Bacillus amyloliquefaciens*, *Xenorhabdus bovienii*, *Pasteuria penetrans*, etc.) and fungi (*Trichoderma harzianum*, *Trichoderma viride*, *Paecilomyces lilacinus*, etc.) can be applied to control the RKN infestation (3, 4, 6, 14). These biocontrol agents restrict the RKN infestation through mechanisms such as competing for nutrients, synthesising antibiotics, toxic metabolites, volatile compounds and lytic enzymes, trapping and killing RKN juveniles or females, preventing egg hatching, altering feeding habits, inducing systemic resistance (ISR) and modifying the nematode sex ratio (5, 14), thereby providing an eco-friendly and cost-effective approach of RKN management (15). Thus, the use of beneficial fungi and plant growth promoting rhizobacteria (PGPR) enhances plant health and elicits ISR and defence systems against various pathogens. However, the exact mechanism of intricate interaction among biocontrol agents and plant for combating RKN infection is still a mystery. Recently, advanced technologies such as metabolomics offer new opportunities for developing novel biocontrol nematicides against RKN infection. This review provides comprehensive insights into the use of various fungi and bacteria-based biological control agents (BCAs) (for controlling RKN infestation), their importance, challenges and future prospects, for sustainable agriculture.

Methodology

An extensive and systematic review of the extant literature was carried out and the data under various sections on life cycle, distribution of RKN, impact on vegetable crops and management of RKN through various methods including traditional, chemical, genetic, application of bio-control agents and integrated approach were identified using various databases including PubMed, Web of Science and Google Scholar, CAB Abstracts, as well as websites such as www.sciencedirect.com, https://link.springer.com, https://www.frontiersin.org/journals. The names of the RKN, fungal bacterial and plant species mentioned in this review have been validated taxonomically using the NCBI Taxonomy Browser available at https://www.ncbi.nlm.nih.gov/Taxonomy/Browser. The literature reviewed consists of several abstracts, full-text articles, books and Ph.D. thesis. The most relevant literature contained in 150 references was selected for further examination and inclusion in this review.

Life cycle, distribution and parasitism of root-knot nematodes

Root-knot nematodes are microscopic, sexually dimorphic, sedentary, obligate endoparasites of plants (11). The males are vermiform while females are pyriform or saccate in shape. The distribution, life cycle, developmental stages, pathogenicity and survival of RKNs are largely affected by soil type, soil temperature and its moisture (abiotic and biotic factors in soil) (16). The RKNs life-cycle generally completed in 28–30 days at ideal temperature (25–30 °C), however it may extend to > 50 days in the winter season (16). The female nematode generally lays 400–500 eggs inside a gelatinous matrix that protrudes from the host root or sometimes remains embedded within it. The glycoproteinaceous gelatinous matrix protects eggs against extreme temperatures and predation. The second-stage juvenile (J2) hatches in the soil as a motile, vermiform larva capable of locating a new host and penetrating the roots. Root-knot nematode undergo four developmental molting stages (J1–J4). The eggs hatch into J1 (first stage juvenile) which transform into J2 (second stage juvenile) which is microscopic, infective and motile stage in soil (in search of suitable host). However, J2 are also able to persist in soil by utilising stored food reserves (glycogen and glycolipids) in the absence of a host (16). Post-infestation, RKNs feed on the root epidermal cells by secreting hydrolytic enzymes. These secretions stimulate the synthesis of indole-3-acetic acid (IAA) from tryptophan, triggering the formation of giant, multinucleated giant cells from pericycle cells. The cortical tissue around large cells multiplies many folds leading to the formation of larger root galls.

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These large cells contribute for the reproduction, development and also serve as food source for nematode (17). The formation of root gall in vascular tissue in host plants restricts the absorption and translocation of nutrient and water causing yield penalty to crops (6). Following infestation, the J2 stage feeds continuously for 2–3 weeks within the host plant, undergoing three rapid molts and most of juveniles transform into pyriform sedentary females. The infested plants may develop symptoms like mineral deficit, yellowing of leaf, wilting, chlorosis and occasionally death of infected plant (1). The life cycle of RKN may last for 3–4 weeks and primarily reproduce via parthenogenesis; however, males are occasionally observed but do not contribute to reproduction (11, 16). The RKNs keeps on multiplying in the soils and produces new infective second stage juvenile. Although the multiplication rate is higher under optimum conditions, RKN eggs can survive extreme environmental conditions and juveniles can survive outside the host (for several months) by utilising its stored reserve food (11, 16). Hence, RKN can survive in the soil in unfavourable conditions and infect the host plant roots when find ideal environment. The extent of infection may be very high during different seasons as the second stage juvenile remains available all times in the soil.

Root-knot nematodes behaviour in the soil is largely influenced by abiotic and biotic factors in soil (16). For instance, temperature and moisture are the major factors which govern the RKN infection but other factors like physical and chemical composition of soil, antagonistic flora and fauna and stage of host plants also influence the extent of infection. Distribution of RKN, their life cycle, developmental stages, pathogenicity and survival are largely affected by soil type, soil temperature and its moisture. Compared to clayey soils, sandy and sandy loam soils with 50 % or more sand content are the most suitable for RKNs, as infective juvenile locomotion and root penetration are facilitated in coarse-textured soils. RKNs need moisture (40–60 %, below field capacity) for their survival and locomotion, however when moisture level is higher, the hatching of eggs is inhibited and the J2 stage fails to survive due to hypoxia (11). Three common species of RKN, *M. incognita*, *M. arenaria and M. javanica*, require temperatures of 18–30 °C (18) for survival and multiplication and hence these species are more predominant in tropics and subtropics area of the globe. However, *M. hapla* is distributed commonly in temperate and sub temperate areas (temperature 0–15 °C or above). Thus, the optimum temperature (25–30 °C) and moist soil are most suitable for infection, juvenile movement, gall formation and fast multiplication of RKN (18). Highest population of RKNs and severe damage in vegetable crops has been observed in northern plains during warm wet summers as optimum condition for growth and development are available during this season (19). Hence, the *M. hapla* resides only in temperate area while the other three species are distributed across plains under a wide range of climatic conditions. Therefore, the distribution, life cycle and infection capacity of RKN is chiefly governed by temperature and soil environment (1, 19).

Management of root-knot nematodes

The polyphagous nature, specialised survival mechanisms and high reproductive potential of RKNs render their management exceptionally challenging once the RKN infection gets established in the field (1). Moreover, management of RKN is not ecologically and economically sound-as their eradication is not possible, hence, the concept of "living with nematodes" (20) and the development of sustainable management practices are widely accepted among nematologists (1). Therefore, this section reviews the diverse strategies used for RKN management in vegetables crops with specific emphasis on biocontrol strategy (Fig. 1).

Root-knot nematodes management via cultural/physical practices

Management of RKN by employing cultural practices is one of the most common approaches to RKN infection as various biotic and abiotic factors of soil environment specifically controls the nematode behaviour (1). For instance, physio-chemical make-up of soil, soil humidity, soil heat and microbial composition of soil significantly govern RKN behaviour and its interaction with host plants. Hence, the alteration in soil environment using various management practices also alters the nematode pathogenesis. Therefore, various cultural practices like crop-rotation and fallowing, trap crops, cover crops and antagonistic crops, demolition of crop residues, weed management, deep summer ploughing, sanitation and soil solarisation plays crucial role in RKN management.

Crop rotation/fallowing/intercropping

Crop rotation involves alternating susceptible host crops (tomato, potato etc.) with non-host crops (mustard, wheat, maize, garlic, onion etc.). The crop rotation deprives the RKN from finding the right host which leads to famishment and disruption of its life cycle (1, 21). Crop alternation with non-host plants like garlic, onion, mustard, sesame, wheat etc. decreases the RKN population in infected field, as these crops may release certain allelopathic chemicals in the rhizosphere which prevent the RKN infection (22, 23). Hence, crop rotation could be an option for managing the RKN infection in vegetable crops. For instance, it was reported that an "okra-brinjal-okra" cropping sequence increased field RKN infestation, whereas "okra-cucumber-mustard" and "okra-cowpea-cabbage" sequences significantly reduced it (24). Recently, it was observed that “tomato-mustard-tomato” and “tomato-marigold-tomato” rotations effectively countered *M. incognita* infestation and increased tomato yield (23). Crop rotation can be efficiently used along with fallowing

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where the infected field is left as it is. Leaving infected fields fallow for 2–3 years reduces RKN populations by depriving the nematodes of hosts required to complete their life cycle (22). However, these methods mainly depend on the careful selection of nonhost crops, season of fallowing and RKN infection capability to infect nonhost crops. Moreover, fallowing the fields for 2–3 years may cause economic losses to growers.

Plantation of trap, antagonistic and cover crops

Root-knot nematodes infection is generally controlled by application of chemical nematicides. However, they might be hazardous to both human and soil micro flora. Therefore, alternate strategies like plantation of RKN suppressive crops (considered as cover/trap/antagonistic crops) provide sustainable control of RKN infection (1). Trap crops are extremely susceptible crops which are grown in RKN infected field and disrupt the RKN life cycle, interfering with their reproduction, egg hatching and larval development (22). Moreover, these crops do not allow their roots to be food of RKN, famish them out and reduce their population. Sometimes these crops develop additional structures or functions which trap the RKN and eliminate by digesting them. For instance, *Crotalaria spectabilis*, Venus flytraps (*Dionaea muscipula*) and bladderworts (*Utricularia* spp.) have been evaluated as trap crop against RKN infection (1, 22). Mustard and marigold have also been recently used as trap crops for *M. incoginita* in tomato crops (23). However, the success of this strategy solely depends upon the extent of RKN infection, time of sowing and later destruction of infected crop (23).

Antagonistic crops release certain bio-chemicals from their roots which are detrimental to RKN. These crops are used as inter crops, cover crops or as rotation crop with RKN susceptible plants. Some crops like mustard, sesame, marigold and asparagus (*Asparagus officinalis*) release nematotoxic compounds from their roots and are well known for their antagonistic properties against RKN (1). Out of the above-mentioned crops, marigold releases polythienyls compounds which are toxic to RKN and hence it is considered as the most suitable RKN suppressive crops. It has been observed that the marigold intercropping significantly reduced the RKN population in tomato, okra, brinjal by 36.2, 53.5 and 72.9 %, respectively and decreased root galls formation by 45.4, 40.1 respectively and 86.2 %, respectively (25).

Cover crops are grown in RKN infected fields between the farming of main crops. These crops improve the soil health by preventing soil erosion, recycle the nutrients, add organic amendments and restrict the growth of insects, weeds and pathogens including RKN. For instance, many crops like jack bean, castor bean, *Crotalaria*, velvet bean, cereals, castor, sorghum-sudan, marigold and grasses have been used as cover crops for controlling RKN infection (26, 27). Because RKNs have limited mobility and migrate only short distances, non-host cover crops are utilised to reduce soil populations through starvation and allowed main crop to grow with less RKN infection (1). Moreover, when cover crops are grown as green manure, they release some nematotoxic compounds which significantly suppress RKN populations in infected fields. However, trap, antagonistic and cover crops need to be selected carefully for RKN management.

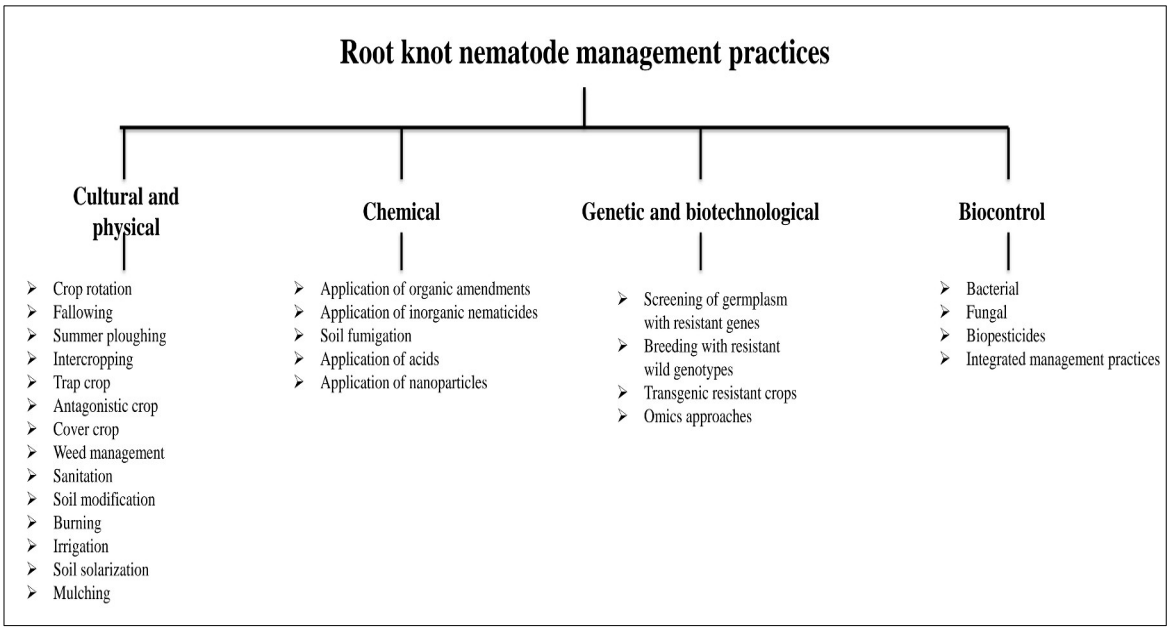


Fig. 1. Various practices used for the management of root-knot nematodes (RKNs).

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Weed management and sanitation

The RKN infection can be easily transmitted from propagules produced through vegetative part of infected plants (28). In this regard, sanitation is a critical strategy to prevent the infection of RKN in vegetable crops from infected area to new fields (1). Therefore, it is important to obtain RKN free plant propagules from authentic sources. The weed management in infected fields is also a compulsory practice to manage the RKN load in soil. Certain weeds, such as *Solanum nigrum*, *Chenopodium album* and *Tithonia rotundifolia*, serve as alternative hosts of RKN for the reproduction and completion of their life cycle (29). Hence, weed removal and their destruction play an important role for minimising the RKN load in infected field. Crop residue can also be source of RKN infection and can provide shelter and protection to RKN during harsh conditions. Thus, it is important to remove and destroy the crop residue of infected crops after harvesting. The agricultural tools and machineries can also spread RKN infection in uninfected plants therefore, it is also important to clean them after use.

Summer ploughing

Natural heating of soil from sunlight during summers can be useful to manage the RKN load in infected field. Deep plowing of infested fields three to four times followed by exposure to solar heat is highly effective against RKNs, as it exposes the RKN, their eggs and larva to high temperature which cause dehydration and destruction of RKN in soil. It has been observed that the deep ploughing and fallowing in summer seasons efficiently decreases the *M. incognita* in brinjal (30). Another study reported that deep ploughing (10 and 20 cm) followed by fallowing of infected field for 2 months was found very effective for RKN management and the above practice significantly reduced the RKN population by 78.2–92.3 % respectively in infected field at the time of plantation of tomato (31). Soil solarisation can also be used to improve the efficiency of summer ploughing where polythene mulching traps retained more heat compared to direct exposure of soil. However, these methods are labour intensive, season dependent and require careful monitoring.

Root-knot nematode management via physical methods

Among the various methods available, soil solarisation is a primary physical method that is highly effective for controlling RKN infection in vegetable crops as the activity, survival, growth and pathogenesis of RKN depends upon the specific temperature ranges (1). Physical methods can be employed either individually or with chemical and cultural methods. In soil solarisation, soil is shielded/mulched with polythene sheets (transparent) so as to trap the solar heat during summer season which significantly heats up the moist soil and results in increased mortality of nematodes (or making them susceptible to nematode antagonists). The exposure period of solarisation must be sufficient to penetrate the solar heat into deep soil layers (32). The exposure period ranging from 2–9 weeks have been found to be effective for RKN destruction, however, various factors like soil properties (structure, texture, moisture content and chemical composition), cropping sequence, temperature sensitivity of organism of interest, size and nature of polythene sheet used for covering the soil are key factors for the success of solarisation (33). The transparent polythene sheet was found more effective than the black sheets and 50–100 µm thickness of polythene sheet was found as optimum for solarisation (34). Another study observed that soil solarisation for 3–4 weeks reduces the root galls while improved the plants growth parameters and fruit yield in eggplant (32). Hence, soil solarisation by trapping natural solar heat can be employed for management of RKN infection in field condition and in green/net house cultivation. However, the cost of polythene sheet, duration of solar exposure and soil structure are key constrains in this strategy.

Root-knot nematode management via chemical methods

Application of organic amendments in soil

Organic amendments have been traditionally applied in field to improve the soil organic carbon (SOC) content, soil fertility, biological activity, texture and nutrients. However, it has been found that the use of organic mixtures/amendments can also be employed in soil for managing RKN infection (35). Basically, organic amendments may include industrial wastes, plant products, animal and poultry waste (organic manures), vermi-composts, plant wastes and extracts, green manures, etc. (28). These amendments stimulate soil biological processes by triggering the proliferation of microbial antagonists, predators or parasites. Upon decomposition, they release nematicidal compounds and improve the soil's nutrient-holding capacity, thereby enhancing plant vigour and tolerance to RKN infection (1, 35). Various studies have been conducted using diverse organic amendments in infected field for countering RKN infection (36, 37). For instance, in a study, it was described that the application of leaf extract of *Lantana camara* in eggplants significantly paralysed the RKN juveniles after 12 hr of application and even resulted in mortality of 96 % juveniles (38). Sunhemp (*Crotolaria juncea*) organic amendment was also found as effective RKN suppressive agent and significantly reduced the RKN infestation in roots of brinjal (37). Furthermore, a mixture of wild spinach powder, Mexican poppy, wild eggplant and trailing eclipta were reported to be quite effective for RKN suppression in tomato plants (39). The oil cakes and organic manure derived from plants have also been widely applied for management of RKN infection and reduction of RKN load in soil (1). Similarly, vermicompost, farm yard manure and poultry manure have been found to suppress the RKN population in soil (36). However, the combination of organic amendments, their quantity, carbon to nitrogen (C : N) ratio and period of application are critical for their efficacy against RKN infection. Moreover, it has been evidenced that the C : N ratio plays an important role in microbial degradation, N uptake and N content of

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amendments is directly linked to RKN management in RKN infected field (40). Generally, organic amendments (like animal manures, oil cakes and green manures) which have lower C : N ratios release ammonia during the decomposition in soil and are more nematotoxic (40, 41). However, the lower C : N ratios may show toxic effects on the plants. Another study described the importance of C : N ratio of organic amendment and reported that C : N ratio could avoid phytotoxicity in plants and exhibit more nematicidal properties (41). Thus, it is necessary to apply the organic amendments in suitable combinations to improve the nematicidal properties and avoid phytotoxicity.

Root-knot nematode management via inorganic compound as nematicides

This chemical approach is traditionally the most common method of RKN management where mixtures of inorganic compounds have been used as nematicides to control the RKN infection in vegetable crops. Earlier 1, 3-dichloropropene and 1, 2-dichloropropane mixture (D-D mixture), methyl bromide and ethylene dibromide were used as nematicides however, due to their hazardous effect on non-target organisms, environment and human health, these fumigant nematicides have been phased out and the infection of RKN is still an intensifying problem (1, 6, 42). Nematicides control the RKN infection by killing RKN, preventing egg hatching, host penetration and by altering the moulting process (1). Currently, only limited chemicals like carbofuran (3 % CG), dazomet and fluopyram (34.48 % w/w SC) are registered as potent chemicals for the control of RKN in vegetable crops. However, inorganic nematicides are costly, toxic, hazardous to humans, environment (ozone and the atmosphere) and are not a perfect solution to the problem of RKN (6).

Application of nanoparticles

Recently, the synthesis of nanoparticles (NPs) via application of eco-friendly approaches and their employment in biological field have gained much attention. Due to their small size, NPs penetrate tissues efficiently and act as potent nematicidal agents. An earlier study demonstrated that silver oxide (Ag_2O), silicon (Si) and titanium oxide (TiO_2) NPs were reportedly nemato-toxic to RKN (*M. incognita*) during *in vivo* and *in vitro* studies on tomato (43). It has also been evidenced that the spray of zinc oxide (ZnO) NPs distorted the shapes of second stage juveniles and reduces the egg hatching by 60 % in lentil plants (44). Many reports concluded that the application of Ag NP is an effective remedy for countering infection of RKN (45, 46). Silver NPs have been found quite effective against *M. incognita* as their application at 800, 400 and 200 mg dm^{-3} cause 100 % mortality of J2 (43, 47). Similarly, another study also treated *M. incognita* with silver NPs and observed that 99 % of RKN inactivation after 6 hr of treatment (45). The gold NPs have also been used for the management of RKN infection and it has been observed that gold NPs effectively reduced the RKN infection. For example, a previous experiment studied the role of gold NPs in managing RKN in tomato (48). They reported that direct exposure of *M. incognita* J2 to gold NPs significantly reduced the RKN population (100 % mortality of J2) and improved the growth of tomato plants. Recently, an experiment also studied role of gold (Au), silver (Ag) and platinum (Pt) NPs on RKN and found that these NPs significantly reduced nematode survival and reproduction under laboratory conditions (49). Out of three NPs applied, Ag NPs were most effective against nematodes with 100 % mortality. Hence, NPs can be applied in vegetable crops to control the nematodes, however, this method is expensive, labour intensive and depend upon the efficacy of NPs.

Root-knot nematode management via genetics-based methods

This method is based on the application of breeding and genetic manipulation of plants for development of RKN resistant varieties. Identifying resistance sources in wild genotypes and introgressing them into commercial cultivars is the most reliable method for development of RKN resistant varieties (1). Genetic engineering can be used as powerful tool in the field of nematology for the development of RKN resistant varieties, however, it is a prerequisite to screen the wild relatives and existing germplasm lines to identify sources of RKN resistance. Several studies suggested that the many wild genotypes have the natural resistance against RKN (50, 51). Initially, the resistant against RKN was reported in wild tomato (*Solanum peruvianum*) in the 1940s and afterwards *Mi*-1 gene (a dominant resistance gene) was discovered in a tomato (*Solanum lycopersicum*) x *S*. *peruvianum* population (52). Later, RKN resistance *Mi* gene was discovered in wild *S. peruvianum* which provide resistance against three important species RKN (*M. arenaria*, *M. incognita* and *M. javanica*) and other RKN resistance genes such as *Mi-3*, *Mi-2*, *Mi-5*, *Mi-4*, *Mi-7*, *Mi-6*, *Mi-8* and *Mi-9* have been discovered in other *Solanam* spp. (50, 51, 53, 54). Many molecular markers based on PCR technology (CAPS, RAPD and SCAR) have also been identified for screening of *Mi* gene (53, 55, 56) for screening of resistant genotypes or marker-assisted selection (MAS). The *Mi* genes reported in the tomato impart natural resistance against various diseases. These genes belong to NBS-LRR gene family (nucleotide binding site- leucine rich repeat) and confer resistance against RKNs (51). In successive studies several isozyme markers (Aps-1, Rex-1 and DNA markers) have also been developed and successfully used for introduction of *Mi* gene to tomato (57). A heat stable *Mi-9* gene was identified in the wild tomato (*Solanum arcanum*) which can be used for production of RKN resilient solanaceous varieties (53). Moreover, screening of wild eggplant genotypes revealed that wild eggplant (*Solanum aculeatissimum*) consists of a heat stable gene *SacMi* like *Mi* gene and one wild eggplant (*Solanum torvum*) has been reported as highly resistant against RKN infestation (58). Hence, the introduction of resistant gene via breeding can be used for transferring resistance gene to host plants. Conventional breeding requires careful screening,

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crossing and selection of desired characters which is difficult, labour intensive and time consuming in case RKN and various other root pathogens. However, these technical difficulties can be minimised using marker-assisted selection. The marker assisted selection can serve as a tool to fasten the introduction of gene through breeding, however, the breeding programme takes long time to introgress the gene from the donor to the host plant.

Protease enzymes are essential for RKN for digestion of protein to amino acids and for fresh protein synthesis. Therefore, mechanism which can block the RKN proteases can be used to develop effective technique against RKN parasitism. This technique was initially established in transgenic potato against the infection of golden cyst nematode (59). Recently, a modified rice cystatin (OC-I1D86) gene in expressing in a transgenic eggplant line provide significant resistant against RKN. Moreover, in the recent past several genes (*Mi-1.2*, *Cry6A*, *Phyto cysteine protinase inhibitor gene* (*CeCPI*), *CeCPI* and *fungal chitinase (PjCHI-1),* Protease gene (*Mi-cpl-1*), *Remusatia vivipara* (*rvl1*) and *Sclerotium rolfsii* (*srl1*) lectin genes) have also been inserted in the transgenic tomato to cope up with problem of *Meloidogyne* infection. To date, RKN-resistant transgenic lines remain confined to research stages and their commercial release has been hindered by ethical, health and regulatory concerns regarding edible crops. Moreover, transgenic plants/crops that are edible (fruits and vegetable) cannot be released easily as a variety due to ethical, health and environmental issues.

RNA interference (RNAi) is other recent technique which can be used to develop RKN resistant varieties by modification at molecular level. RNA interference studies on *Caenorhabditis elegans*, a free-living nematode has paved the path of development of strategies against RKN infection (60). Further, a host made integrase (dsRNA) gene silencing in tobacco to counter RKN infection (*M. incognita*) has been successfully demonstrated (61). Another study developed technique for production of resistant tomato genotype against RKN (*M. incognita*) and tomato leaf curl virus using the RNAi technology (62). Later, a previous study have demonstrated the success of RNAi technique against RKN infection in several crops (63). Though RNAi is a new and reliable strategy to combat the problem of RKN infection but, it is still in its infancy. Hence, it needs focused research and inputs so as to develop RNAi-based RKN resistant vegetable crops.

Root-knot nematode management via application of bio-control agents

Microbes are important constituents of soil environment which maintain the soil health and also manage various plant diseases by targeting soil-borne pathogens (11). Biocontrol is the approach where helpful organisms and their derivatives are used to control pathogens, support plant growth and significantly enhance the crop production. These biocontrol agents are competitive growers which prevent the growth of pathogens without any negative impact on environment. These biocontrol agents can stay in soil for longer periods and control the disease by various mechanisms, like:

Parasitism: The nematophagous fungi and bacteria pierce the cuticle of RKN, destruct them via enzymatic action and use RKN as their food for nutrients;

Competition: Competition for primary resources like food, space, water, nutrient and intraspecific and interspecific competition impacted the activity, reproduction and movement of nematodes;

Induced systemic resistance: Biocontrol agents like fungi and bacteria triggers the systemic signalling in plant which induced the systemic resistance in plant. This process produces the systemic signalling in plants which shield the plant against various pathogens and allowed plants to withstand against RKN infection;

Antibiotics: Biocontrol agents release certain secondary metabolites into the soil which are nematicidal, can act as antibiotics and destruct the RKN and their infectious stage via allelochemicals damage;

Plant growth improvement: Biocontrol agents encourage the plant development by enhancing nutrient uptake, their sequestration and solubilisation (Fig. 2). Hence, biocontrol agents help plants to grow better and allow plants to withstand RKN infection (11).

Various antagonistic microorganisms against RKNs have been reported in cultivated soils across the world which have been distributed in diverse environmental and climatic conditions. Various fungi and bacteria can act as RKN antagonists and need to be explored for their nematicidal and suppressive effect as an effective method of RKN management. Biocontrol agents use various direct or indirect methods like secretion of secondary metabolite, toxins, extra cellular enzymes, volatiles compounds to kill RKN and induces systemic resistance via activation of defence dependent gene to suppress RKN (7, 64). Moreover, fungal biocontrol agents release bioactive compounds having strong nematicidal properties by activating defence dependent gene and plant growth promoting rhizobacteria directly compete with RKN for food and space (3, 12). The efficacy of antagonist BCAs may also be impacted by various abiotic and biotic factors (1). Hence, many efforts have been tried to increase the efficacy of antagonist BCAs against RKN by utilisation of organic amendments (40, 65). These organic amendments provide favourable conditions and act as substrate for growth and development to RKN antagonists bacterium. For instance, in many studies it has been reported that application of organic amendments like plant seed cake (jojoba, neem, olive, mustard and karanja seed cakes), vermi-compost and farmyard manure (FYM) along with RKN antagonist bacterium significantly enhance the biocontrol efficacy against RKN infection (65, 66). The details of mechanisms and various bacteria and fungi used RKN biocontrol agents are discussed below:

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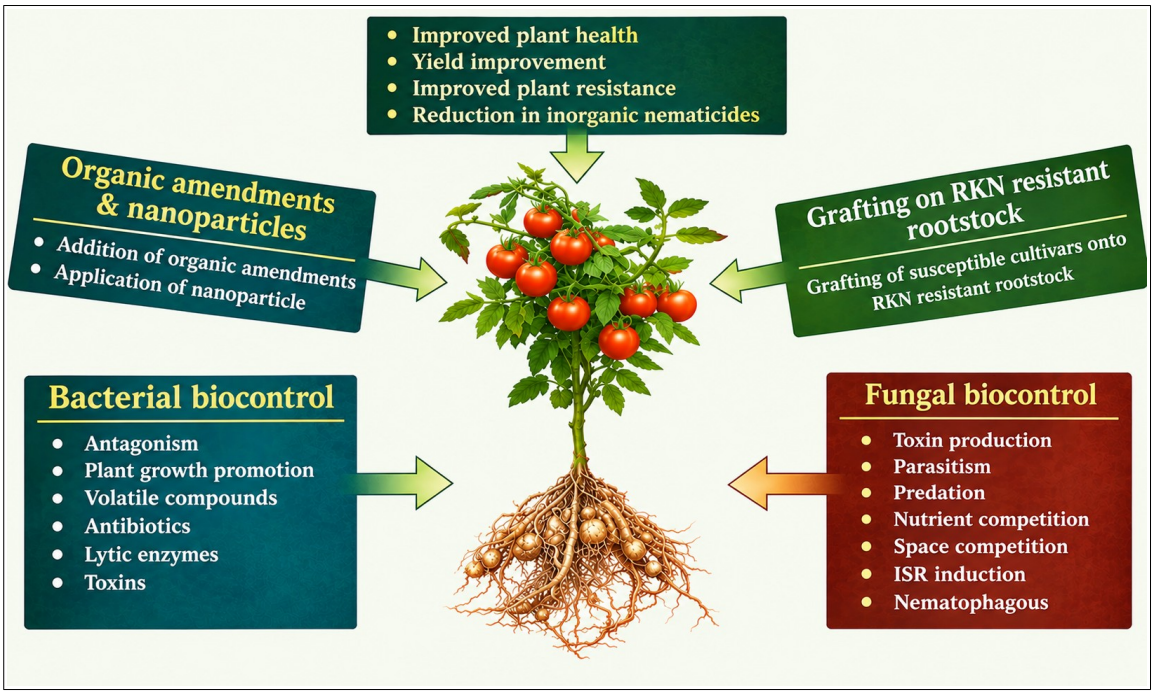


Fig. 2. Mechanisms of biocontrol of root knot nematodes (RKNs) via application of bacterial and fungal agents.

Root-knot nematode management through application of bacterial biocontrol agents

Bacteria are one of the important elements of soil biotic community and have great potential as biocontrol agent for suppressing nematodes in plant rhizosphere (67). Bacterial biocontrol agents use various strategies like antagonism, plant growth promotion, direct inhibition by production of volatile compounds, antibiotics, lytic enzymes and toxins and impact the RKN growth and development via parasitism and colonisation (1, 2, 3, 68). *Pasteuria penetrans* is one of the most studied endospore-forming gram positive obligate parasitic bacteria, broadly found in cultivated soils across the globe and its efficacy against RKN infestation in various vegetable crops has been widely explored (69). This bacterium destroys the RKNs by attaching directly to its cuticles through adhesive endospores and multiplying in body of RKN (70). The parasitism is accomplished by the attachment of bacterial spores to juvenile RKN (J2), multiplication of bacteria in the body of RKN by using its resources, destruction of the reproductive system of female causing sterility and finally altering the life cycle of RKN (71). However, many factors like large scale mass production of bacterium, quantity of endospores present in soil, irrigation practices, soil texture, porosity and soil structure highly impact the efficacy and commercial application of this bacterium against RKN infection (1).

Plant growth promoting rhizobacteria are generally reported abundantly around the root zone of plant and their mechanisms of action like ISR, nutrients competiveness, plant growth promotion and antibiosis have been potentially exploited as antagonists against RKN (1). *Pseudomonas fluorescens* and *Bacillus* spp. (like *Bacillus subtilis*) are the most explored antagonist bacterium species among the PGPR which have been used as biocontrol agent and exhibited significant RKN suppressive efficacy in vegetable crops (65). Plant growth promoting rhizobacteria manage the RKN by employing various indirect methods such as, alteration in the plant microbiome, induction of plant internal systemic resistance, nitrogen fixation, alteration in hormones, siderophore production and nutrient solubilisation (3, 5). Plant growth promoting rhizobacteria stimulate the production of IAA to boost plant development, increase tolerance against RKN by impacting the production of an array of growth promoting compounds (N-acyl-homoserine lactones, lipopolysaccharides, siderophores, exopolysaccharides, etc.), enzymes (phenylalanine ammonia-lyase, ascorbate peroxidase, chitinase, β-1,3-glucanase, catalase, superoxide dismutase, polyphenol oxidase and lipoxygenase) in plants (64, 72) and also reduces the extent of RKN infection by colonising the plant roots. For instance, the exogenous treatment of salicylic acid and colonisation by *P. fluorescens* strains effectively induces the internal immunity of tomato against RKN *M. javanica* (12). Similarly, endophytic bacteria have also been reported as beneficial against RKN infection in vegetable crops (3). For example, *Bacillus cereus* BCM2 colonising the roots of tomato significantly reduces the damage of RKN *M. incognita* infection by controlling J2 infestation (73). Similarly, it has been observed that the RKN infection, gall formation and egg masses production can be reduced by using endophytic bacteria like *Bacillus megaterium*, *Bacillus licheniformis*, *Bacillus mycoides*, *B. thuringiensis*, *Bacillus pumilus* (74). The bacterial genera belonging to plant growth

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promoting bacteria (PGPB) (*Bacillus*, *Pseudomonas* and *Serratia*) exhibited a significant biocontrol efficacy against nematodes since last two decades and have significant effect on nematode population density in soil (2, 74). These bacteria manage the RKN by direct mechanism wherein the RKN antagonist bacterium produces various nematicidal compounds and enzymes (like collagenases, proteases, lipases, chitinases etc.) to constrain the growth and development of RKN at various life stages (12). For instance, in previous studies it has been reported that the crystals protein (Cry) from *B. thuringiensis* destroyed the vital organs of RKN while many enzymes (such as cellulases, glucanases and pectinases) produced by *Serratia marcescens* effectively control the infection of nematodes (75). Likewise, *Pseudomonas* spp. produces nemato-toxic compounds like 2,4-diacetyl phloroglucinol (DAPG) which constrain the egg hatching and motility of juvenile nematodes while other nematotoxic compounds, such as bacillomycin D, surfactin, fengycins, bacteriocins and lipopeptides produced by *Bacillus* spp., considerably repress the infection of RKN *M. incognita* (64, 76). Interestingly, it has been also observed that the nemato-toxins released by *Photorhabdus* and *Xenorhabdus* spp. effectively suppressed the endoparasitic nematodes found in roots (77). Moreover, the *Bacillus* spp. and *Pseudomonas* spp. produces certain nemato-toxins (hydrogen cyanide and hydrogen sulfide) which have high nematicidal properties against nematodes (12, 78). Furthermore, *Bacillus atrophaeus* also produces certain volatile compound like 2-undecanone (2-UD) and dimethyl disulfide (DMDS) which exhibited high nemato-toxic properties against RKN (2, 7). Likewise, four potent nematicidal volatile compounds (acetaldehyde, ethylbenzene, dimethyl disulfide and 2-butanone) produced by deep-sea bacterium *Virgibacillus dokdonensis* showed various controlling mechanisms like direct contact-killing, fumigation, prevention of egg-hatching, attraction and repellence against juvenile of RKN (79).

The various strains *Bacillus* have been widely reported for the synthesising array of VOCs and secondary metabolites which exhibited robust nemato-toxic properties against nematodes (15, 76). Nematicidal properties of *Bacillus cereus* 09B18 and *Bacillus subtilis* OKB105 culture filtrates have been evaluated previously with 95 % efficacy against juveniles of nematodes *Heterodera filipjevi* and *M. javanica* (80, 81). Several studies reported that the bacterial strains like *Serratia plymuthica* M24T3, *B. subtilis* OKB105 and *Bacillus amyloliquefaciens* B3 have the strong nemato-toxic properties and caused varying degree of mortality (65–100 %) in nematodes when applied as biocontrol agent (76, 82). *Bacillus thuringiensis* strains inhibit the nematodes through Cry protein synthesis while *Serratia proteamaculans* Sneb 851 also exhibited strong nemato-toxic property against *M. incognita* (83, 84). Moreover, many *Bacillus* spp. strains are identified to produce VOCs with potent nemato-toxic properties. For instance, volatile compounds like 2-UD, DMDS and methyl isovalerate (MIV) produced by *B. atrophaeus* GBSC56 exhibited high nematicidal properties (up to 90 %), triggered internal systemic resistance against *M. incognita* and also promoted the plant health in greenhouse environments (2). However, previous observation showed that the PGPBs exhibited positive impact on growth of plant rather suppressing the nematodes in field and green house conditions (7, 76). Hence, based on previous reports different bacteria deploy different mechanisms which can be utilised for management of RKN, however, extensive research and explorations are required for discovery of novel nemato-toxic chemicals for sustainable agriculture production. The different bacterial species used for RKN management in vegetable crops have been summarised in Table 1.

Table 1. Reports on bacterial species used as biocontrol agent against infection of root knot nematodes in vegetable crops

Name of bacterial biocontrol agent used	Type of RKN managed	Crop	Symptoms of disease managed / results obtained	References
Bacillus thuringiensis	*Meloidogyne incognita*	Tomato (*Solanum lycopersicum* L.)	Reduced RKN population by 80.5 %.	85
Pseudomonas putida,*Pseudomonas fluorescens*, *Serratia marcescens*, *Bacillus amyloliquefaciens*, *Bacillus subtilis* and *Bacillus cereus*			Application of bacterial agents improved plant growth and reduced nematode infection in tomato.	86
Pseudomonas jessenii and *Pseudomonas synxantha*	*M. incognita*	Tomato	Application of bacterial agents (more than 75 % concentration) leads to 100 % mortality of second stage juvenile (J2)	87
Pseudomonas protegens	*M. incognita*	Tomato	Application of bacterial agent resulted in 87.76 % mortality of J2 after 24 h of treatment and reduced root gall index by 30.67 % in comparison to control (49.33 %).	88

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Serratia plymuthica	*M. incognita*	Tomato	Application of bacterial agent resulted in 92.67 % mortality of J2 after 24 h of treatment and reduced root gall index by 38.67 % in comparison to control (49.33 %).	
Bacillus cereus (Accession no. MT626659) *and* *B. megaterium* (Accession no. MT626661)	*M. incognita*	Tomato and Brinjal	Inhibited 96 % egg hatching and caused 85–89 % mortality of J2. Reduced nematode populations (up to 93 %), eggs and galls in tomato and brinjal in greenhouse conditions.	89
Bacillus subtilis, *Bacillus pumilus*, *Bacillus megaterium* and *Bacillus cereus*	*M. incognita*	Tomato	Application of four bacterial agents viz. *B. subtilis*, *B. pumilus*, *B. megaterium* and *B. cereus* reduced the root galls by 91.95, 84.21, 83.70 and 81.8 % respectively after 75 days of inoculation.	90
Bacillus subtilis CRB7	*M. incognita*	Tomato	Reduced root gall formation (37.0–85.8 %) in tomato under protected cultivation.	91
Pseudomonas fluorescens	*M. incognita*	Grafted Tomato	Reduced root galls, egg masses and nematode population compare to control.	6
Bacillus subtilis and *B. pumilus*	*M. incognita*	Eggplant (*Solanum melongena* L.)	Application of bacterial agent significantly reduced the root galls, egg masses and J2 in tomato.	92
Pseudomonas fluorescens and Bacillus subtilis	*M. incognita*	Eggplant (Brinjal)	Application of *Bacillus subtilis* enhanced the plant growth in brinjal and reduced the nematode population in soil by 70.64 % and in root by 44.73 % compare to control.	93
Bacillus subtilis and Pseudomonas fluorescens	*Meloidogyne javanica*	Eggplant (Brinjal)	Reduced nematode infection and gall formation in brinjal.	94
Bacillus cereus strain Bc-cm103	*M. incognita*	Cucumber	Significantly reduced the root galls, egg hatching and caused 100 % mortality of J2.	95
Bacillus pumilus strain S1-10	*M. incognita*	Ginger	Repelled and suppressed J2 and reduced 79 % egg hatching and 71 % nematodes population under greenhouse.	96

RKN: root-knot nematode.

Management of root-knot nematode through application of fungal bio-control agents

The use of fungal BCAs is a major topic of interest for pathologists and entomologists for development of effective methods of RKN management in infected field (97). Helpful fungi can be used for management of RKN in vegetable crops and these fungi have array of biocontrol mechanisms which can be applied to manage the RKN at various phases of their developmental cycle (3). Depending on the mechanism of countering RKN these fungi can be categorised into different groups (97). Nematode trapping fungi are those fungi which trap the RKN by forming specific assemblies like constricting rings, knobs and sticky nets/webs to immobilise and consume RKN (13, 98). For example, two fungal antagonists *Monacrosporium* spp. and *Arthrobotrys* spp. forms sticky nets and constricting rings respectively to trap the nematodes (99). The trapping mechanism of these fungi involved the interaction between the carbohydrate released by the nematode cuticle and lectin released by the fungal agents (1). Many reports suggested that these trapping fungi effectively predate the RKN *M. incognita* and *M. javanica* infesting vegetable crops (98, 99). However, limited availability in soil and specific affinity to certain nematode species of these trapping fungi limit their application in RKN management. Parasitic fungi are RKN antagonist group of fungi (*Pochonia chlamydosporia*, *Paecilomyces lilacinus*, *Dactylella oviparasitica*, *Cladosporium oxysporum* and *Nematophthora gynophila*) which have been observed as female and egg parasites (100). The inactive stages of RKN (obese females and eggs) are highly susceptible to parasitisation and colonisation of fungi. The parasitic fungi infect the RKN by inserting fungal hyphae through cuticle gelatinous matrix of eggs and females. Finally, these fungi engulf the eggs and females with help of

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mycelial network and there by control the population of RKN (1). For instance, *P. lilacinus* is a commercially available parasitic fungal biocontrol agent which is reported as highly nemato-toxic against RKN like *M. javanica* and *M. incognita* and available with diverse trade names for management of RKN in various vegetable crops like brinjal and tomato (6, 29). Similarly, the conidia of *Purpureocillium lilacinum* target the eggs of RKN, enters in them and prevents the egg hatching (101). In some studies, it has been observed that the application of like *Pochonia rubescens*, *Paecilomyces lilacinus* and *Pochonia chlamydosporia* (facultative parasitic fungi) targeted the immobilised stages of nematodes (adult female, eggs and cysts) and effectively managed the nematode infection (4, 6). While application of some endophytic fungi (like *Acremonium sclerotigenum*) observed to increases the mortality of J2s (95–99 %), reduces the egg hatching and decreases the RKN infection in infected crops (102). Fungi reduce the RKN load in infected area by various mechanisms. Like some fungi like *Arthrobotrys* and *Dactylella* (predatory fungi) and *Nematophthora* and *Hirsutella* (parasitic fungi) penetrate in RKN, capture them by forming specific structures, feed on them and proliferate in their bodies while some fungi like *Pleurotus ostreatus* immobilised the nematodes, penetrated their cuticles with hyphae and are finally killed (5, 12, 75, 98). Some fungi indirectly reduce the RKN population by accumulating in the roots of plant and compete with RKN for food and shelter while many fungi release the specific compounds which controls the nematode population by targeting non-motile stages, preventing the egg hatching and blocking the attraction of RKN juvenile towards plant roots. For instance, secondary metabolites produced by *Trichoderma* spp. have potent nemato-toxic effect on RKN. These chemicals restrict the biological function of RKN impact their growth and reproduction and also directly kills them (98). Some useful endophytic fungi like arbuscular mycorrhizae fungi (AMF) colonise the plants roots and activate internal systemic response (ISR) and SA-mediated responses against RKN by triggering genes related to defence and plant antioxidant enzymes (103, 104). These *Trichoderma* spp. are filamentous fungi (*T. viride*, *T. harzianum*) which are available in market for the remediation of RKN in vegetable crops (6, 105). It has been observed in previous study that the *Trichoderma* species prevented the entry of nematodes in plant roots by parasitising the infectious juveniles and supports the plant health and crops yield (98). *Trichoderma* strain TH has been significantly reducing the RKN infection in tomatoes by decreasing leakage of electrolyte malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) while increasing the production of salicylic acid (SA), jasmonic acid (JA), flavonoids, lignin, phenols and cellulose (106). Similarly, *T. harzianum* reduces the RKN (*M. incognita*) infection by 61.88 % in tomato and reduces root gall index, egg masses and nematode number in brinjal while *P. chlamydosporia* M10.43.2 reduces the female reproduction (14.7–27.6 %) and RKN infection (32–43 %) by triggering the systemic resistance in tomatoes (107, 108). Hence, fungal biocontrol proposes various environment-friendly strategies like defence-triggering, trapping, antagonistic behaviour, parasitism, nematicidal and secretion of secondary metabolite which not only reduces the RKN population but also offer better crop yield, soil health and reduces the dependency on inorganic nematicides (6). Further research is required towards limitations associated with their field application, environmental variability, competition with indigenous soil microorganisms, development of potent fungal biocontrol agents with higher nemato-toxic property and their commercial application in RKN infected fields. The different fungi identified as biocontrol of different RKN in vegetable crops are summarised in Table 2.

Development of nematicides from bio-control agents (bacteria and fungi)

Development of nemato-toxins from bacterial and fungal BCAs is another dimension of their application for ecofriendly and sustainable management of RKN (3). The nematicides developed from BCAs not only control the RKN infection but also reduce dependency on inorganic chemicals, maintain soil well-being, contribute to integrated pest management and sustainable crop cultivation (6, 12, 75, 98). Hence, the present section highlights the key nematicides developed from bacteria and fungi for management of nematode infection.

Nematicides derived from bacteria

Bacteria like rhizosphere bacteria, *Pseudomonas* spp. and *Bacillus* spp. releases certain lytic enzymes and antimicrobial compounds which are potent nemato-toxic against RKN (3, 7). Rhizobacteria releases various hydrolytic enzymes (like protease, chitinase, cellulase, keratinase, glucanases, lipase, etc.) which hydrolyses the important chemical constituents of nematodes (eggshell and exoskeleton) and disturb the metabolism and development of nematodes (5, 72). For instance, protease enzymes degrade the body structure of nematodes by disrupting the peptide linkage of glucose-protein molecules while chitinases act on chitin matrix of the eggshell, hydrolyse its polymeric linkages and leading to premature egg hatching (4). It has also been observed that the nematicidal property of antagonistic bacteria and nematophagous fungus depend on the activity of extracellular enzymes released by them. These extracellular enzymes hydrolyse the collagen component in cuticle layer and kills the nematodes. Recently, a study isolated a protease enzyme from *Bacillus cereus* (NJSZ-13) which degraded the nematode cuticle and exhibited high nematicidal property against nematodes (123). Collagenase isolated from the strains of *Brevibacterium frigoritolerans* FB37BR and *P. fluorescens* FP805PU exhibited strong nemato-toxic property against nematodes

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(123). Moreover, it has been also observed that the lipid layer in nematode eggshell prevents moisture loss and protects nematodes in unfavorable conditions. Hence, disrupting this lipid layer may lead to exposure of nematode body to extreme conditions. Therefore, the bacterial strains of *B. amyloliquefaciens* and *B. thuringiensis* which showed strong lipase activity exhibited potential nematicidal property (84, 124). Similarly, hydrolytic enzymes (like pectinases, amylase, glucanases, chitinase and cellulases) isolated from different *Pseudomonas* spp. highly impacted the *M. incognita* and along with secondary metabolites exhibited strong nemato-toxic property against RKN (125, 126).

Additionally, some bacteria also produce Cry proteins which exhibited strong nemato-toxic property against nematodes. For instance, *B. thuringiensis* releases many Cry proteins which damage the intestinal lining of nematodes, impact pore development and detrimental to cell (64, 84). Many bacteria also release effective secondary metabolites which exhibit potent nemato toxic property against nematodes. For example, *B. cereus* produces a chemical sphingosine (unsaturated hydrocarbon chain amino alcohol) which causes severe oxidative damage and shows high nemato toxic property against RKN (127). A thermostable metabolite thuringiensin, has been produced by *B. thuringiensis* which disturbs the RNA formation by competing with adenosine triphosphate (ATP) for binding sites. This process is closely related to carbamate insecticide aldicarb used against nematodes. Moreover, these *B. thuringiensis* strains also synthesise trans-aconitic acid which disturbs the tricarboxylic acid (TCA) cycle by inhibiting the aconitase (128, 129). Bacteria also produce several volatile compounds which exhibit strong nematicidal activity against nematodes. For instance, *Bacillus* spp. produces volatile compounds 2-nonanone and 2-UD. Out of these two compounds application of 2-nonanone disturbs the integrity of nematodes intestine and pharynx, however the complete mechanism of action of this compound is still to be investigated (130). Likewise, *P. fluorescens* releases 2,4-diacetyl phloroglucinol (2,4-DAPG) and hydrogen cyanide that disturb the mitochondrial lining, inhibits mitochondrial cytochrome oxidase and also decreases the eggs hatching in different RKN (4, 78, 129). It has been observed that the prokaryotic bacteria (actinomycetes) produce various compounds which showed remarkable antimicrobial potential towards many pathogens (12, 64, 84). For example, *Streptomyces avermitilis* produce a macrocyclic lactone compound avermectin B1 which is generally applied to constrain insects and parasites. It disturbs the glutamate-gated chloride channel receptors and exhibited strong nemato-toxic activity against *M. incognita* and other nematodes (131). Similarly, Milbemectin isolated from *Streptomyces hygroscopicus* is similar to avermectin and showed strong nematotoxic property against nematodes while spectinabilin extracted from *Streptomyces spectabilis* exhibited potent nematotoxic property against nematodes (129, 132). Likewise, a compound Spinosad extracted from *Saccharopolyspora* spp. inhibit nicotinic acetylcholine and gamma-aminobutyric acid receptors, disrupt neural activity, paralysed nematodes and exhibited potent nematotoxic property to counter infection of *M. incognita* (4).

Table 2. Different fungal species used as biocontrol agent against infection of root knot nematodes in vegetable crops

Name of fungal biocontrol agent used	Type of RKN managed	Crop	Symptoms of disease managed /results obtained	References
Aspergillus terreus	*M. incognita*	Tomato	Reduced egg hatching and egg masses by 73 and 76 % respectively.	109
Aspergillus strictum	*M. incognita*	Tomato	Reduced egg hatching and egg masses by 68 and 71 % respectively.	
Purpureocillium lilacinus	*M. incognita*	Tomato	Reduced RKN disease symptoms by 76.24 %.	85
Acremonium implicatum	*M. incognita*	Tomato	Reduced root galls/plant by 60 %.	110
Lecanicillium muscarium R. Zare and W. Gams 2001	*M. incognita*	Tomato	Application of fungal agent promoted the plant growth and reduced the RKN population.	111
Purpureocillium lilacinus	*Meloidogyne spp.*	Tomato	Reduced egg masses of RKN by 85 %.	112
Aspergillus japonicus ZW1Saito1906	*M. incognita*	Tomato	Depleted the root galls /plant and egg masses by 47.3 and 51.8 respectively.	113
Arthrobotrys oligospora Fresen1850	*M. incognita*	Tomato	Reduced nematode population, root galls/plant and promoted growth of plant	114
Trichoderma harzianum	*M. javanica*	Tomato	Reduced egg hatching and exhibited strong nematicidal activity	115

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Pochonia chlamydosporia, Purpuricillium lilacinum	*Meloidogyne* spp.	Tomato	Application of *Pochonia chlamydosporia* and *Purpuricillium lilacinum* at 2 % reduced egg hatching by 9.57 and 11.43 %, respectively.	116
Trichoderma viride and Paecilomyces lilacinus	*M. incognita*	Grafted Tomato	*Application of fungal biocontrol agents reduced root galls, egg masses and nematode population in grafted tomato plants*	6
Purpureocillium lilacinum	*M. incognita*	Eggplant	*P. lilacinum* significantly reduced the egg hatching, J2 survival and also reduced the RKN population and the number of galls	101
Trichoderma harzianum and Pochonia chlamydosporium	*M. incognita*	Eggplant	Application of *Trichoderma harzianum* and *Pochonia chlamydosporium* significantly reduced the egg hatching by 77.60 and 53.0 % and J2 mortality by 82.0 and 70.20 % respectively	117
Pochonia chlamydosporium	*M. javanica*	Eggplant	*Application of P. chlamydosporia* in eggplant significantly inhibited egg hatching and second-stage juveniles and also reduced the number of galls, egg masses and the nematode population.	118
Trichoderma harzianum ITCC-6796, T. longibrachiatum ITCC-7437, T. viride ITCC-6889,	*M. incognita*	Cucumber	*T. viride* and *T. harzianum* reduced root galls by 66 and 61 % respectively	119
Pochonia chlamydosporia	*M. incognita*	Cucumber	Application of biocontrol agent reduced egg masses and nematode population	120
Biocult (a.i. Glomus species +Trichoderma asperellum Lieckf and Nirenberg)	*M. enterolobii*	Cowpea	Application of fungal biocontrol reduced nematode eggs, J2 in root and J2 in soil by 80, 84 and 53 % respectively	121
Purpureocillium lilacinus	*M. incognita*	Capsicum (*Capsicum annuum* L.)	Application of fungal agent reduced the egg masses, RKN population and root gall index by 60.15, 61.10 and 48.72 % respectively.	122

RKN: root-knot nematode.

Nematicides derived from fungi

Many studies have revealed that fungal species like *Nematoctonus*, *Arthrobotrys*, *Pochonia*, *Pleurotus*, *Trichoderma* produces various chemicals like secondary metabolites, volatile compounds, lytic enzymes and toxins which exhibit strong nemato-toxic property and can be used as novel nematicides (12, 133). For instance, the application of a compounds phomalactone extracted from *Nigrospora* spp., demonstrated potent nemato-toxic property against *M. incognita* and successfully counter the infection of J2 of RKN (*M. incognita*) in tomato when applied at a concentration of 500 mg/L (4). Similarly, secondary metabolite aurovertin D derived from *Pochonia chlamydosporia* also exhibited strong nemato-toxic property against RKN (134). The application of thermolide and hypocrellin A isolated from fungal species *Talaromyces thermophilia* and *Shiraia bambusicola* also exhibited strong nematotoxic property against nematodes and caused up to 50 % mortality in nematodes (129, 135). Another metabolite flavipin isolated from *Chaetomium globosum* exhibited strong nematicidal property against RKN by increasing membrane permeability, blocking ATP synthesis and preventing protein synthesis (4). Some of the compounds isolated from fungus may also induces stress in nematodes by triggering the mitochondrial death pathway and have strong nematicidal activity (136, 137). For instance, it has been observed that depsipeptide beauvericin synthesised by *Beauveria bassiana* induces severe oxidative stress by initiating mitochondrial death process and showed strong nematotoxic effect against *M. incognita* (129, 137).

Hence, many compounds have been produced by bacterial and fungal agents which have been used for managing the various nematodes. However, the documentation, function and mechanism of action of several secondary metabolites are still to be explored, restraining our knowledge about molecular targets of these bioactive compounds. These limitations constrain the potential use of these compounds as nematicide. The novel techniques like biotechnological approaches, omics and molecular docking are required to be explored to study these compounds in targeted manner for development of novel nematicides, for effective management of nematodes and sustainable agriculture production.

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Omics approaches for biocontrol of root-knot nematode

To mitigate the pathogens attacks, plants have evolved complex interactions between rhizosphere and soil microbes which is governed by a series of processes like the release of signalling messengers from roots and soil microbes (bacteria and fungi) (3, 68, 126, 137). This complex interaction mechanism compelled the scientific community for discovery of new antimicrobial agents. However, the mechanism of interaction between microbes and plants under nematodes infection has not been much explored (3). The previous studies mostly rely on microbial regulation of RKN using fungal and bacterial agents, however, limited investigations have been conducted on omics approaches (137, 138). Omics approaches involved the exploration of genomics and biochemical profiling for discovering novel nematotoxins for mitigating RKN infection (3, 126).

Metagenomics offers advanced technologies such as next generation sequencing (NGS), which can increase our knowledge regarding mechanisms and biodiversity of rhizospheric microbial communities (3). Studies exhibited that approximately 103–104 taxonomic units of microbiome exists/gram of soil which shows that enough nematode antagonistic microbial agents are present in rhizosphere (12, 139). Next generation sequencing can be applied to identify the unknown microbial taxa for mitigating RKN infection and effective cure of pathogens (140, 141). This technology not only explores newer BCAs but also offers to explore the interaction of microbes with nematodes (126, 141). Exploration of genomics not only improve our knowledge regarding genome of microbial agents but also enhance our understanding regarding their biology, evolution, pathogenicity against RKN and DNA sequence responsible for antagonistic property (3, 141).

Metagenomics research allows discovery of novel microbes and provides deep knowledge of microbial exchanges in root zone and soil which is very important for discovering newer multispecies microbial combinations for effective mitigation of nematodes (2, 126). Moreover, functional metagenomics also permits identification of novel genes in microbes responsible for production of nematotoxic bioactive compounds using recombinant DNA technology (5, 142). Additionally, novel microbes responsible for nematodes suppression in soil and rhizosphere can be studied using recent microbial techniques (12, 142). Hence, application of metagenomics in biocontrol investigation on nematodes shall transform the management of nematodes and promote sustainable agriculture.

Other important omics approaches like transcriptomics and proteomics allows insight of molecular interaction between microbial agents and nematodes. Transcriptomic studies allow discovery of new genes and provide detailed understanding regarding gene expression at the time BCAs and nematode interaction, down regulation and upregulation of DNA sequences responsible for nematotoxic activity, pathways for nematode control, development of targeted nematode biocontrol approaches and responses of BCAs to various natural stresses that impact their efficiency of countering nematodes infection (143, 144). Proteomic studies allow the understanding regarding expression of proteins by biocontrol agents at the time of their dealings with nematodes. Analysis of differential protein expression provides assessment of nematotoxic activity and discovery of proteins responsible for nematodes destruction (64, 145).

Study of proteomics can be applied to understand the intricate molecular process of nematode destruction by exploring the protein-protein signalling between nematodes and microbes and can also identify the bioactive proteins (like enzymes, nematicidal toxins, antimicrobial peptides) released by microbes to control nematodes which can be used to develop novel bionematicide (3, 138). Moreover, newly established technique of meta-proteomics protocols, such as metabolite, protein and lipid extraction (MPLEx) allow to simultaneously isolate of proteins, lipids and metabolites, facilitating the detection of newer peptides and proteins accountable for nematode destruction (138, 146). Hence, transcriptomics and proteomics are appreciable techniques which provides in-depth knowledge of complex signalling between nematode and BCAs and allows the researchers to discover novel and more efficient biocontrol strategies for management nematodes in the agriculture sector.

Metabolomics plays important role in discovery of novel nematicides from microbes responsible for biocontrol of nematodes. In metabolomics, advanced techniques like nuclear magnetic resonance (NMR), liquid chromatography-mass spectrometry (LC-MS), gas chromatography-mass spectrometry (GC-MS) and computational tools are used to study and analyse bio-compounds of BCAs at particular times and under different conditions (2, 13, 145, 147). It allows the study of numerous metabolites responsible for stress response and signalling and more sensitive tool than transcriptomics or proteomics to understand the metabolic processes accountable for morphological responses (126, 148). For instance, it has been observed in several studies that *Pseudomonas* spp. produce various secondary metabolites (hydrogen cyanide, phenazines, pyrrolnitrin etc.) with high nematotoxic properties for mitigation of nematode through mechanisms like disturbing respiration, reproduction, cuticle and membranes integrity (149, 150). Hence, metabolomics-based research allows to identify the unexplored metabolites produced by rhizospheric microbes which can produce novel nematotoxic compounds.

The omics technologies provide better opportunity for developing potent nematicides.

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However, the potential of omics technologies still required to explored for their practical application. Moreover, genome sequencing, data storage, data integration, bioinformatics analysis and cost of omics discoveries are major constraint in the application of omics technologies and their field-level applications are still under progression.

Integrated approach root-knot nematode management

From above discussion it has been clearly evident that none of the approaches alone is sufficient to eradicate the nematode infection from infected filed and each individual approach have their own limitation. Moreover, soil biotic and abiotic factors largely impact the potential of every RKN management approach. Therefore, the concept of integrated management practice is a viable alternative for effective management of RKN in infected fields. Integrated management practice ensures the synergism of two or more approaches together to reduce the RKN infection below the threshold level to get maximum production and minimum disturbance to natural microbial environment. Recently, grafting of susceptible tomato cultivar on RKN resilient eggplant rootstock along with three BCAs (*P. lilacinus*, *T. viride* and *Pseudomonas fluorescence*) was used as an integrated approach to control the RKN in tomato (6). In this study it was observed that the use of BCA *P. lilacinus* at 4 g/kg soil along with grafted tomato plants effectively counter the RKN infection and declined RKN parameters like root galls, egg masses and final nematode population by 84.65, 95.7 and 82.12 %, respectively. The grafted tomato plants inoculated with *P. lilacinus* showed better growth than control. Previous studies have revealed that application of two or more approach is more effective for the management RKN infection than the individual approach. For instance, treatment of seed okra with *P. fluorescens* and use of FYM with biocontrol agents, *P. lilacinus* and *P. fluorescens* reduced the RKN population by 82.4 % (36). Similarly, seed treatment of carrot with *B. subtilis* IIHR BS-2 followed by use of vermi-compost combined with *B. subtilis* IIHR BS-2 in soil reduced the RKN population by 69.3 % (65). Hence, the integrated nematode management (INM) strategy can be used for management of RKN infection in vegetable crops without disturbing the natural microflora of rhizosphere. However, the combination of two or more techniques requires standardisation for field application.

Key challenge in root-knot nematode management

Root-knot nematode management is quite challenging due to their complex biology, diversity and complex interactions between environment, microbe and host plants (12, 126, 142). It is also quite difficult to find effective biocontrol agents due to their wide host range and influence of environment factors (like temperature, pH, moisture content, soil texture and soil type) on nematicidal activity of BCAs (3, 12). Moreover, high cost of production, varying field efficacy, survival in soil for prolonged periods, short formulation shelf-life, registration of biocontrol products and authorisation from regulatory bodies, public acceptance, market adoption and biosafety are some of the major key challenges in adoption of biocontrol strategy for RKN management (68, 129). The use of biotechnological and omics approaches provides both opportunities and challenges in the development of biocontrol of RKN (68, 140). These techniques are labour intensive and costly. Moreover, complex life cycle of nematodes, specific interaction between microbes and plants, study of structure and abundance of secondary metabolites and protein, differential gene expression, effectiveness under dynamic field conditions are key challenges for biotechnological and omics approaches (126, 142). Therefore, combination of ecological features and data from all omics approaches need to be studied in detail for insight knowledge of nematodes biology, microbial interactions and biocontrol mechanisms (126, 142). Hence, addressing these key aspects will pave the way for more efficient and sustainable management of nematode infection in agricultural systems.

4. Conclusion and future prospects

Root-knot nematode are one of the most significant plant parasitic nematodes hampering the vegetable production worldwide. Due to health and environmental hazards, the fumigant nematicides have been banned in most of the countries, which has intensified the problem of RKN infection and these notorious endoparasites have become major constraints in sustainable cultivation of vegetables in protected cultivation and in open field. Due to specific survival mechanism, high reproductive potential, polyphagous nature and countrywide distribution of RKN, their management is quite difficult in vegetable cultivation, leading to high economic losses. Moreover, due to unawareness of RKN infestation, limited adoption of phytosanitary measures and use of infected planting material RKN infection spreads to new areas in protected and open field vegetable cultivation. Therefore, in the current scenario it is important to create awareness among the farmers and academicians regarding RKN infection and its management through traditional and modern approaches. In the present review, we have tried to comprehend the importance of RKN infection in vegetable crops and its management through traditional approaches like cultural methods, sanitation, soil solarisation, prevention, summer ploughing, nematode suppressive crops, application of organic amendment, application of biocontrol agents (bacterial and fungal), bacterial and fungal based nematicides and modern approaches (biotechnological approaches and omics approaches). Application of biocontrol agents (fungal and bacterial) individually or as consortia provides environment friendly and effective management of RKN.

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However, each individual method has its own limitation, therefore, INM approach using more than one approach together can be more beneficial than individual approach for effective management of RKN. Still, none of the present approaches can completely eradicate the RKN infection from infected areas. Therefore, modern techniques like biotechnological and omics approaches are required to be implemented for identification of novel biocontrol agents and development of cost-effective, more precise and targeted nematicides for sustainable management of RKN. However, genome sequencing, data storage, data integration, bioinformatics analysis and cost of omics and biotechnological discoveries are required to be standardised for commercial application of omics technologies and their field-level applications.

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Authors' contributions

AKP and BK contributed to the conceptualisation of the study and preparation of the original draft manuscript. SK contributed to manuscript review and editing. BK was responsible for supervision. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None.

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