

Plant induced resistance in *Solanacearum lycopersicum* species against root knot nematodes

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ABSTRACT

The impact of root-knot nematodes of the tomato, *Solanacearum lycopersicum*, has resulted in severe damage and reduction in crop yields of both temperate and tropical agriculture systems. Keeping in mind the economic significance of the plant, the parasitic nematodes have not only been a burden for plant production but also cause for global agricultural economy depletion. At present, various countries have banned the nematicides after analyzing their consequence on environment and humans thereby making it an imperative to find an alternative method for the inhibition of nematodes against *S. lycopersicum*. With the plant root comprising of several bioactive secondary metabolites, a self-defense mechanism can be initiated against the infecting parasites. Not with standing, limited research has been carried out to understand the efficacy of induced resistance between or within the same species. Hence, the current review, we summarize on how hypersensitivity-like reactions can enhance plant resistance inducers in solanaceous species and their effects of various root metabolisms, chemical compounds which can act as repellents, hatching stimulants, attractant, or as inhibitors. The review focuses on the objective of understanding the mechanistic intricacies of how RNA interference acts on a root-knot nematode.

1. INTRODUCTION

Tomato, Solanacearum lycopersicum, is the second most consumed plant organ worldwide. This berry, commonly mistaken to be a vegetable originated from the regions of South America, is the basic indigent for various raw, cooked, or processed foods. Thereby making it the most adopted occupational crop worldwide, either for local use or export [1]. China has been the primary producer of tomato accounting for about 31% of the total global production, followed by India and the United States of America [2]. Tomato belongs to the Solanaceae family, of the plant kingdom, which also comprises various other economically important crops such as the Solanum tuberosum (Potato), Capsicum annuum (Capsicum/Bell peppers), and Solanum melongena (Brinjal/Eggplant) [3]. Tomato constitutes numerous phytocompounds such as the Vitamins A and C, and lycopene, a pigment as well as an antioxidant capable of reducing the risk factors associated with cancer and neurodegenerative diseases [4]. The importance of tomato plant has also been linked to numerous evolutionary researches carried out to understand the metabolic and fruit development processes [5].

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The depletion in quality and quantity of tomato crops has been occurring due to unviable cropping with monoculture coupled with expansion of crops to newer regions, leading to the occurrence of a wide range of infections [6]. Most common among such infections in the one caused by root-knot nematode, which is capable of causing severe damages to the plant leading to reduced yield. Globally, an approximation of about >\$80 billion losses are incurred annually due to such infection [7]. The root-knot nematodes, which are primarily parasites, may also act specifically as vectors binding to other pathogenic organisms, either way resulting in disease aggregation. Nematodes comprise over 100 species, of which those belonging to the genus Meloidogyne, are associated with tomato crop pathology. Meloidogyne hapla, Meloidogyne naasi, Meloidogyne chitwoodi, and Meloidogyne fallax are commonly found in cold environment. However, Meloidogyne arenaria, Meloidogyne javanica, and Meloidogyne incognita are the most important root-knot nematodes known to cause severe damage in tomato crop in humid condition [8]. The root-knot nematodes adopt the endoparasitic behavior, allowing them to feed and reproduce within the plants and survive in the soil as egg mass and plant debris. During this event, the infective second-stage juveniles move to the root tip to form large spindle-shaped gall like structures. The size of these gallslike masses may vary and reach up to 15 mm in diameter [9].

Since the parasites such as root-knot nematodes cause a major loss in the agricultural system, an integrated use of pest, crop rotation, and

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biological practices is deemed to be a successful controlling strategy. The consequences of such exercises have been unsatisfactory since about 95% of spray pesticides fail to reach the target parasites and thereby causing a severe effect on the environment and humankind [10]. In addition, the tomato crops have been found to have different degrees of sensitivity toward each Meloidogyne species with the previous studies suggesting that each nematode species exhibited a different degree of parasitism on specific tomato cultivation [11]. While the *M. hapla* was reported to form small, distinct galls, the M. incognita and M. javanica produced large galls and huge root-swellings which made the infected plants to appear yellow, stunted, and wilt easily [12]. Furthermore, severe infection leads to a reduction of yield and ultimately killing the plants. Furthermore, the root-injuries caused by the nematodes may also act as the point of entry for infectious bacteria and fungi. Particularly in the wilt-resistant varieties, intake of necessary nutrients and water by the host plant is significantly reduced resulting in weak plants with low yields as their physiological processes are affected [13]. Various studies suggest the use of plant resistance inducers to mitigate these adversities and to increase the plant metabolic activity and development of defense mechanism against various parasites. Such an effort would also add value to our understanding of the interactions occurring naturally between plant and root-knot nematodes [14]. The current review provides with an overview of the root-knot nematodes, their mechanism of action against S. lycopersicum, and the possibilities of plant resistance that can act against these nematodes.

1.1. Morphology of Root-knot Nematodes

The root-knot nematodes belong to the genus *Meloidogyne*. These nematodes are typically elongated, triploblastic, unsegment, and bilaterally symmetrical with pseudocoelomate morphology. They exhibit sexual dimorphism, where the female nematode is up to 3mm long with a soft and pearl white colored body. The neck of a female protrudes anteriorly, while the excretory pore is situated anterior to



Figure 1: Morphology of male and female root-knot nematodes. (Source: Handoo *et al.*, 2004)

the median bulb near the stylet base, with the stylet being shorter, and vulva as well as anus is located terminally surrounded by cuticular striae. Paired gonads represent the ovaries. In addition, six large unicellular rectal glands, responsible for gelatinous matrix production, are present in the posterior. Meanwhile, the male nematodes exhibit a vermiform morphology unlike the pear-shaped distended bodies of female nematodes. Male nematodes are shorter, being only 1.2–1.5 mm long. The body of the worm is thin and cylindrical shape [15] and male nematodes consist of a large labial disk that binds to medial lips to form a dorsoventral elongate lip region. Males have a delicate stylet and the developmental factor may influence the pattern shape [Figure 1] [16].

1.2. Life Cycle of Root-knot Nematodes

The lifecycle of all *Meloidogyne* spp. constitutes six stages [Figure 2] occurring within a duration of about 3-6 weeks. First stage is known as the egg stage, where the nematodes deposit over 1000 eggs in the form of a sticky mass which manages to survive on the soil surface as well as plant residues. In these masses, eggs are clustered to prevent loss of viability due to dehydration. After deposition, the eggs start to multiply to form a first juvenile stage. In the first juvenile stage (J1), coil-like structures appear inside the egg membrane and are characterized by the presence of a stylet. Hence, obtained first juvenile stage gives rise to an infective second-stage juvenile (J2) which hatches within 48 h. Among various nematodes, the *Meloidogyne* spp. juveniles are only such nematodes that inject esophagus gland secreted substances to apical meristem cells in an attempt to create feeding sites known as giant cells, which act as a channel to pass nutrients from the plant to nematode. Soon after, the second-stage juvenile (J2) becomes adult. In the adult stage, the male nematodes disappear from the roots, while the females swell on maturity producing several numbers of eggs, with or without the involvement of males. Interestingly, the male: female ratio in the nematode population, during this event of reproduction, is balanced generally. This can be attributed to the unique character of immature females to undergo metamorphosis into males, in an instance where the population density does not equate [17].

1.3. Symptoms of Infected Plants

In an event of *Meloidogyne* spp. infection, the S. lycopersicum plants show stunted growth, wilting, yellowish of leaves, and death in severe cases, due to lack of nourishment. The infection of root-knot nematodes causes cell expansion, resulting in swallow or gall like structures as shown in Figure 3. Compared to the other Meloidogyne species, the M. hapla has been reported to form process smaller galls. The root-knot nematodes deprive the plants of their required nutrition thereby increasing their susceptibility other bacterial and fungal invasions. In addition, these plant parasitic nematodes which develop below the soil level are difficult to control by chemical means due to their vast quantities. Several experimental studies, carried out under plot, micro plot, and filed experiments, have suggested that the factors such as: (i) Inoculums type (s) and inoculation technique; (ii) extraction technique and efficiency in laboratory condition; (iii) inoculum density or nematode species and its population level; and (iv) variation in environment and soil type; affect the nematode growth population which is responsible to cause intense damage on tomato cultivation [18,19].

1.4. Host Identification through Chemosensory Perception

The root-knot nematodes recognize surrounding habitat through chemosensory impression or through root exudate signals. The tomato plants are capable of producing various chemical gradients across the root



Figure 2: Complete lifecycle of root-knot nematodes Julie (Source: Nicol *et al.*, 2002)



Figure 3: The effect of root-knot nematodes causes (a) wilt, (b) yellowish of leaves and (c) gall formation in *Solanacearum lycopersicum* species (Source: Atamian *et al.*, 2012)

nodules, attracting the parasite invasion [20]. A range of phytochemicals have been identified as chemotactic elicitors in *Meloidogyne incognita* two second-stage juvenile (J2) larvae. The J2 were found to adapt their behavioral responses post-exposure to phytochemicals such as ethephon (Eth), potato root diffusate, and salicylic acid, supporting the existence of long-term habituation traits mediated by the serotonergic-dependent neurotransmission. Understanding of such host-parasite interactions will help develop a pragmatic approach to protect the tomato crops from nematode invasions [21].

1.5. Attractants and Repellants

The J2 root-knot nematode larvae target mostly the root tip of a host. In an attempt to ward off any such infection, the host plants develop unique chemical and physical signals including change (s) in temperature, pH, iron, and carbon dioxide concentrations in the root tips. Such phenomena may either attract or repel the parasite. In addition, carbohydrates, phenolic compounds, chelating compounds, amino acids, and redox potentials of the plant may also regulate the root-knot nematode behavior [22]. The mechanistic intricacies underlying the chemical signaling responsible for such behaviors are poorly understood. Yet, a few studies suggest that when any of the above signaling molecules of chemical nature come in contact with the amphidal duct root-knot nematode, which provides a satisfactory information about root-knot nematode sensory perception, because this is where the phytohormones trigger receptors for induction and secretion of signals by a diffusion process [23]. In Arabidopsis thaliana it was observed that the suppression of ethylene synthesis attracted more M. hapla nematodes toward root tip, whereas an overexpression showed the least attractive capability in the same rootknot nematode species. Indicating that the ethylene and by products of ethylene related pathways repelled the parasites [24]. Based on proven evidences, various studies have been carried out to identify root metabolites detected in root exudates of tomato plants [Table 1]. Of which, methyl salicylate, zeatin, quercetin, specific to tomato root, were found to attract M. incognita J2 larvae, while the metabolites of the ethylene pathway attracted M. hapla, M. incognita, and M. javanica. Meanwhile, palmitic acid and linoleic acid, 1-octanol, trans-cinnamic acid, and p-Coumaric acid showed excellent repellent activity in M. incognita, as other root tip exudates were repellent to J2s, by inducing a quiescence response due to which >80% of the *M. incognita* nematodes lost motility [32].

Table 1: Compound of root metabolites involved in attraction and repletion of root-knot nematodes

Sl. No	species/synthetic chemicals	Root metabolites	Nematodes affected	Effect	Reference
1.	Tomato S. lycopersicum	Methyl salicylate	M. incognita	Attractant	[25]
2.	Tomato S. lycopersicum	Zeatin	M. incognita	Attractant	[26]
3.	Tomato S. lycopersicum	Quercetin	M. incognita	Low concentration act as an attractant and higher concentration as a repellent	[26]
4.	Tomato <i>S. lycopersicum</i> and Rice Oryza sativa	Small lipophilic molecules	<i>M. incognita</i> and Heterodera glycine	Repellent	[27]
5.	Tomato <i>S. lycopersicum</i> and barrel clover Medicago truncatula	Metabolites of ethylene pathway	<i>M. hapla, M. javanica,</i> and <i>M. incognita</i>	Ethylene signaling attract more toward hosts compared to wild type	[28]
6.	Synthetic chemicals	Isoamyl alcohol,1- butanol and 2-butanone	M. incognita	Attractant	[29]
7.	Synthetic chemicals	Salicylic acid	M. incognita	Attractant	[30]
8.	Synthetic chemicals	Dopamine	Radophus Similis	Attractant	[30]
9.	Ricinus communis	Palmitic acid and linoleic acid	M. incognita	Repellent	[31]
10.	Synthetic chemicals	1-octanol	M. incognita	Repellent	[29]
11.	Marigold Tagetespatula, Pepper <i>Capsicum annuum</i> , and Soybean Glycine max	Root exudate compounds	M. incognita and Heteroderaglycines	Repellent to root knot nematode	[32]
12.	Pea Pisum sativum, Snap bean Phaseolus vulgaris, and Alfalfa Medicago sativa	Root tip exudate	M. incognita	Repellent to J2s; induced quiescence response, > 80% of the nematodes lost motility	[32]
13.	Synthetic chemicals	Protocatechuic acid, umbelliferone, caffeic acid, ferulic acid, luteolin, daidzein, genistein, Kaempferol, quercetin, myricetin	Radopholus similis	Repellent and nematicidal	[30]
14.	Synthetic chemicals	Trans-cinnamic acid; p-Coumaric acid	M. incognita	Repellent	[33]
15.	Synthetic chemicals	Salicylic acid, ethephon, vanillic acid, gibberellic acid, indole-3-acetic acid,6- dimethylallylamino purine, mannitol, arginine and lysine	M. incognita	Attractants	[33]
16.	Synthetic chemicals	Salicylic acid, methyl jasmonate, ethephon, indole-3-acetic acid, mannitol	Globodera pallida	Attractants	[33]

M. incognita: Meloidogyne incognita, Solanacearum lycopersicum: S. lycopersicum

1.6. Hatching Stimulation

Most of the nematode hatching mechanisms are focused during their parasitic venture, particularly occurring between the host and root-knot nematodes lifecycle. In general, few nematodes depend on the particular host system for their hatching mechanism. The injected juveniles process less energy leads to starvation and finally to death (*M. javanica* and *M. incognita* spp.) whereas, few other nematodes enclose dormant eggs that are capable of surviving for decades to reactivate the host-specific active stimulants. There by suggesting the use of hatching stimulants, in the absence of host, to obtain a promising reduction of nematode population. For example, the use of 4-Hydroxyl benzene ethanol to induce hatching in *M. incognita*; root-exudates derived stimulants as hatching inhibitors of *M. hispanica*, *M. hapla*, and *M. arenaria* has resulted in providing protection to the tomato crops by inhibiting the J2 from penetrating the plant [Table 2] [34].

1.7. Mode of Action of Root Metabolites in Root Knot Nematodes

Plants employ a defense mechanism to elude from pathogenic nematodes. Such plants generally consist of different proteinase inhibitors, which provide a suitable defense mechanism against those pathogens. These proteinase inhibitors act on nematode proteases, causing starvation due to nutrition depletion. The nematode surfaces consist of various small signaling molecules, such as the Molecular Patterns/Nematode-Associated Microbe-Associated Molecular Patterns (NAMP), which have a root surface pattern recognition receptor (PRR) [41]. On binding to the PRR, triggering of the pattern or NAMP triggered immunity (PTI) occurs [Figure 4] and thereby initiates the Mitogen-activated protein kinase cascade to eventually activate the plant genes responsible for defense. Countering this, the nematodes secrete an effectors molecule, as caroside, along with the effector molecules to hijack the plant cellular system [42]. About time, sensor proteins such as the nucleotide binding leucine-rich repeat proteins are also put into action, while the pathogen detection would have stimulated the R-gene activation to produce the resistance protein. Soon after activation, the resistance protein causes an ion-flux, involving potassium and hydrogen ions to initiate a hypersensitive response (HR) [43]. This HR causes oxidative burst by producing reactive oxygen species mediated cell death to trigger the deposition of lignin and cellulose around the surrounding cells in an attempt to contain the pathogen infection. Such an event is considered to be a short-term response to infection by the plant. The HR also triggers other types of effectors-triggered immunity inducing systemic acquired



Figure 4: Mechanism of action root metabolites against root-knot nematodes (Source: Hyong et al., 2016)

Table 2: Suppression of root-knot nematode hatching against root metabolites

Sl. No.	Plant species/synthetic chemicals	Root metabolites	Nematodes affected	Effect	Reference
1.	Welsh onion Allium fistulosum	4-Hydroxyl benzene ethanol	Meloidogyne incognita	Hatching inhibitor	[35]
2.	Sticky nightshade Solanum sisymbriifolium	Root exudate compounds	Root-knot nematodes	Hatching inhibitor of <i>Meloidogyne hispanica</i> , <i>Meloidogyne hapla and Meloidogyne arenaria;</i> J2s not able to penetrate the plant and highly resistant	[36]
3.	Sticky nightshade Solanum sisymbriifolium	Root exudate compounds	Root-knot nematodes	Hatching inhibitor of <i>Meloidogyne javanica</i> , <i>Meloidogyne arenaria</i> and <i>Meloidogyne hapla</i> ; J2s not able to penetrate the plant and highly resistant	[37]
4.	Sticky nightshade Solanum sisymbriifolium	Root exudate compounds	Globodera pallida	Hatching stimulants, reduced number of J2s per cyst and decreased population	[38]
5.	Sticky nightshade Solanum sisymbriifolium and Nightshade Solanum nigrum	Root exudate compounds	Globodera rostochiensis and Globodera pallida	Hatching stimulants, reduced number of J2s per cyst and decreased population	[39]
6.	Nightshade Solanum nigrum	Root exudate compounds	Globodera tabacum	Hatching stimulants	[40]

resistance enhancing the immunity in plants [44]. In an event of failure of HR, activation of hormonal signaling pathway begins, which is a parasite species specific response. While the necrotrophic parasites induce the jasmonic acid pathway [45], the biotrophic parasites will initially induce the salicylic pathway, which further prompts different hormonal pathways and to activate pathogen-related defense gene(s) of the plant [46]. Following this, PR protein expression is upregulated to act against the nematode infection, in combination with various other protein factors.

1.8. Role of RNA Interference (RNAi) in Inhibiting Root-knot Nematode Effectors

RNAi has been an important tool for gene controlling, with an aim to analyze the function of different genes by inhibiting their activity. Such techniques have been demonstrated in various organisms including the root-knot nematodes [47]. The nematodes intake expressible doublestranded RNA molecules, showing a systemic RNAi response in root-knot nematodes as mechanistically explained in Figure 5. Here, the interaction of the particular nematode effector gene(s) with the dsRNA will remains crucial form the infection to be initiated [48]. Studies reveal the importance of controlling root-knot nematodes through host induced gene silencing for a better understanding of possible knockdown on the nematodes. This is also known to control the damage or yield loss in *S. lycopersicum* species. The functional analysis of these root-knot nematode genes depends on development of a reverse genetic tool acquired by these obligate parasites [49]. Many studies suggest that the RNAi genes are involved in silencing of dicer and pasha genes of *M. incognita* juveniles using siRNAs [50]. Urwin *et al.*, 2002, studied the plant-parasitic cyst nematode and concluded that octopamine induces the FITC uptake through the



Figure 5: Mechanism of RNA interference (RNAi), double-stranded RNA (dsRNA) is processed by plant dicer enzyme (1) into (2) once this dsRNA was uptake by these nematodes during feeding (3) once they uptake dsRNA, the nematodes execute dsRNA to shorter interference RNA (4) and also unwind the sense and antisense strands. The RISC complex is filled with antisense strand interacts with the corresponding mRNA in nematodes (5), this makes mRNA to cleave by RISC (6) and leads to degradation of mRNA (7) (Source: Agrawal *et al.*, 2003)^[53]

secretory system [51]. Iqbal *et al.*, 2016, have explained the behavioral and infectivity variations in the J2 of *M. incognita* and reported the RNAi influence on such plant-parasitic nematodes [52].

1.9. Biological Control

Various bacteria and fungi are also involved in the inhibition of rootknot nematodes. The nematophagous fungi involve in toxin production, behave as endoparasites and/or also capable of trapping the nematodes. *Aspergillus* spp. and *Trichoderma* spp. inhibit the tomato plant affecting *M. incognita* effectively [54]. *P. lilacinum* fungi (strain 251) were reported to mitigate *M. javanica* and *M. incognita* infections apart from reducing gall formation in tomato crop [55]. The bacteria also inhibit root-knot nematodes efficiently [56]. Dababat and Sikora, 2007, concluded that the *Fusarium oxysporum Fo162* was capable to induce resistance in tomato plant against *M. incognita* [57]. Thereby implying that biological control is another important technique to be considered for the control of parasitic infections of *S. lycopersicum*.

2. CONCLUSION

The economic consequence faced globally due to crop loss through nematode infections is relatively high. These nematodes are unique due to the characteristic feature wherein they are difficult to manage or suppress on introduction to cropland. Various researches are being carried out to understand such nematodes, morphologically, as well as behaviorally, in an attempt to eradicate them. To overcome this, it is essential to understand the mechanistic pathways supporting the nematodes to affect a particular crop, apart from realizing the speciesspecific damages caused in the host. The imperative use of molecular approaches, such as RNAi, as an alternative to the chemical means can be considered for further evaluation due to their cumulative impact on sustainable as well as profitable agricultural practices.

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4. AUTHOR'S CONTRIBUTION

NB, CD, LKC, and VCV developed the concept. BS, CS, SKP, CD, and NB wrote the review.

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6. CONFLICTS OF INTEREST

The authors report no conflicts of interest in this work.

REFERENCES

- Sun S, Luo C, Wei Q, Zhang J. International research status analysis of tomato molecular breeding based on literature survey. Am J Biosci 2016;4:53-7.
- Kumar P, Chauhan RS, Grover RK. Economics analysis of tomato cultivation under poly house and open field conditions in Haryana, India. J Appl Natl Sci 2016;8:846-8.
- Knapp S, Bohs L, Nee M, Spooner DM. Solanaceae-a model for linking genomics with biodiversity. Comp Funct Genomics 2014;5:285-91.
- Sundaramoorthy S, Balabaskar P. Biocontrol efficacy of *Trichoderma* spp. Against wilt of tomato caused by *Fusarium oxysporum* f. sp. lycopersici. J Appl Biol Biotechnol 2013;1:36-40.
- Quinet M, Angosto T, Yuste-Lisbona FJ, Blanchard-Gros R, Bigot S, Martinez JP, *et al.* Tomato fruit development and metabolism. Front Plant Sci 2019;10:1554.

- Nicol J, Turner D, Coyne L, Den Nijs L, Hockland S, Maafi Z. Current Nematode Threats to World Agriculture. Berlin, Germany: Springer Science Business Media; 2011. p. 21-43.
- Seid A, Fininsa C, Mekete T, Decraemer W, Wesemael WM. Tomato (*Solanum lycopersicum*) and root-knot nematodes (*Meloidogyne* spp.) a century-old battle. Nematology 2015;17:995.
- Back MA, Haydock PP, Jenkinson P. Disease complexes involving plant parasitic nematodes and soil borne pathogens. Plant Pathol 2002;51:683-97.
- Gharabadiyan F, Jamali S, Komeili HR. Determining of root-knot nematode (*Meloidogyne javanica*) damage function for tomato cultivars. J Agric Sci 2013;58:64-265.
- Aktar MD, Sengupta D, Chowdhury A. Impact of pesticides use in agriculture: Their benefits and hazards. Interdiscipl Toxicol 2019;1:1-12.
- El-Sappah AH, Islam MM, El-Awady HH, Yan S, Qi S, Liu J, et al. Tomato natural resistance genes in controlling the root-knot nematode. Genes (Basel) 2019;10:925.
- Ladner DC, Tchounwou PB, Lawrence GW. Evaluation of the effect of ecologic on root knot nematode, meloidogyne incognita, and tomato plant, *Lycopersicon* esculenum. Int J Environ Res Public Health 2008;5:104-10.
- Bartlem DG, Jones MG, Hammes UZ. Vascularization and nutrient delivery at root-knot nematode feeding sites in host roots. J Exp Bot 2014;65:1789-98.
- Dutta KT, Papolu KP, Banakar P, Choudhary D, Sirohi A, Rao U. Tomato transgenic plants expressing hairpin construct of a nematode protease gene conferred enhanced resistance to root-knot nematodes. Front Microbiol 2015;6:260.
- Garcia LE, Sanchez-Puerta MV. Characterization of a root-knot nematode population of *Meloidogyne arenaria* from Tupungato (Mendoza, Argentina). J Nematol 2012;44:291-301.
- Sirca S, Urek G, Karssen G. First report of the root-knot Nematode Meloidogyne ethiopica on Tomato in Slovenia. Am Phys Soc 2007;6:191-2917.
- Chukwurah PN, Poku SA, Yokoyama A, Takeda A, Shishido M, Nakamura I. Mitigating root knot nematode propagation on transgenic tobacco via in planta hairpin RNA expression of *Meloidogyne incognita*-specific PolA1 sequence. Am J Plant Sci 2019;10:866-84.
- Berliner J, Ganguly AK, Kamra A, Sirohi A, Pathak H. Effect of elevated carbon dioxide on life cycle of root-knot nematode, *Meloidogyne incognita* in tomato. Indian J Nematol 2012;42:111-7.
- Morgan JB, Connolly EL. Plant-soil interactions: Nutrient uptake. Nat Educ Knowl 2013;4:2.
- Perry RN, Nematol JR. An evaluation of types of attractants enabling plant-parasitic nematodes to locate plant roots. Russ J Nematol 2005;13:83-8.
- Fleming TR, Maule AG, Fleming CC. Chemosensory responses of plant parasitic nematodes to selected phytochemicals reveal longterm habituation traits. J Nematol 2017;49:462-71.
- Kihika R, Murungi LK, Coyne D, Nganga M, Hassanali A, Teal PE, et al. Parasitic nematode *Meloidogyne incognita* interactions with different *Capsicum annuum* cultivars reveal the chemical constituents modulating root herbivory. Sci Rep 2017;7:2903.
- Kirwa HK, Murungi LK, Beck JJ, Torto B. Elicitation of differential responses in the root-knot nematode *Meloidogyne incognita* to tomato root exudate cytokinin, flavonoids, and alkaloids. J Agric Food Chem 2018;66:11291-300.
- 24. Diez JA, Dusenbery DB. Repellent of root-knot nematodes from exudate of host roots. J Chem Ecol 1989;15:2445-55.
- Murungi LK, Kirwa H, Coyne D, Teal PE, Beck JJ, Torto B. Identification of key root volatiles signaling preference of tomato over Spinach by the root knot nematode *Meloidogyne incognita*. J Agric Food Chem 2019;66:7328-36.

- Dyer S, Weir R, Cox D, Cheseto X, Torto B, Dalzell JJ. Ethylene Response Factor (ERF) genes modulate plant root exudate composition and the attraction of plant parasitic nematodes. Int J Parasitol. 2019; 49:13-4.
- Dutta TK, Khan MR, Phani V. Plant-parasitic nematode management via bio fumigation using brassica and non-brassica plants: Current status and future prospects. Curr Opin Plant Biol 2019;17:17-32.
- Cepulyte R, Danquah WB, Bruening G, Williamson VM. Potent attractant for root-knot nematodes in exudates from seedling root tips of two host species. Sci Rep 2018;8:10847.
- 29. Shivakumara TN, Dutta TK, Rao U. A novel in vitro chemo taxis bioassay to assess the response of *Meloidogyne incognita* towards various test compounds. Curr Opin Plant Biol 2018;50:487-94.
- 30. Wuyts N, Swennen R, De Waele D. Effects of plant phenyl propionic pathway products and selected terpenoids and alkaloids on the behavior of the plant-parasitic nematodes *Radopholus similis, Pratylenchus penetrans* and *Meloidogyne incognita*. Brill J 2006;8:89-101.
- Dong L, Xiaolin L, Huang C, Lu Q, Yao Y, Liu T. Reduced *Meloidogyne incognita* infection of tomato in the presence of castor and the involvement of fatty acids. Sci Horticu 2018;237:169-75.
- Zhao X, Schmitt M, Hawes MC. Species-dependent effects of border cell and root tip exudates on nematode behavior. Phytopathology 2000;90:1239-45.
- 33. Farnier K, Bengtsson M, Becher PG, Witzell J, Witzgall P, ManduricS. Novel bioassay demonstrates attraction of the white potato cyst nematode *Globodera pallida* (Stone) to non-volatile and volatile host plant cues. J Chem Ecol 2012;38:795-801.
- Clarke AJ, Shepherd AM. Picrolonic acid as a hatching agent for the potato cyst nematode, *Heterodera rostochiensis*. Nature 1966;211:546.
- Li T, Wang H, Xia X, Cao S, Yao J, Zhang L. Inhibitory effects of components from root exudates of Welsh onion against root knot nematodes. PLoS One 2018;13:e0201471.
- Meyer SL, Nyczepir AP, Rupprecht SM, Mitchell AD, Martin PA, Brush CW. Tall fescue Jesup (max-Q): *Meloidogyne incognita* development in roots and nematotoxicity. Agron J 2013;105:755-63.
- Dias MC, Conceiçao IL, Abrantes I, Cunha MJ. Solanum sisymbriifolium-a new approach for the management of plantparasitic nematodes. Eur J Plant Pathol 2012;133:171-9.
- Timmermans BG, Vos J, Stomph TJ, Van Nieuwburg J, Van Der Putten PE. Growth duration and root length density of *Solanum* sisymbriifolium (Lam.) as determinants of hatching of *Globodera* pallida (Stone). Ann Appl Biol 2006;148:213-22.
- Schenk H, Driessen RA, Gelder RD. Elucidation of the structure of solanoeclepin A, a natural hatching factor of potato and tomato cyst nematodes, by single-crystal X-ray diffraction. Croat Chem Acta 1999;72:593-606.
- La Mondia JA. Hatch and reproduction of *Globodera tabacum* tabacum in esponse to tobacco, tomato, or black nightshade. J Nematol 1995;27:382-6.
- 41. Choi HW, Klessig FD. DAMPs, MAMPs, and NAMPs in plant innate immunity. BMC Plant Biol 2016;16:232.
- Teixeira MA, Wei L, Kaloshian I. Root-knot nematodes induce pattern-triggered immunity in *Arabidopsis thaliana* roots. New Phytol 2016;211:276-87.
- Dhandaydham M, Charles L, Zhu H, Starr LJ, Huguet T, Cook DR, et al. Characterization of root-knot nematode resistance in *Medicago* truncatula. J Nematol 2008;40:46-54.
- Niu J, Liu P, Liu Q, Chen C, Guo Q, Yin J, *et al.* Msp40 effector of root-knot nematode manipulates plant immunity to facilitate parasitism. Sci Rep 2016;6:19443.
- 45. Nahar K, Kyndt T, De Vleesschauwer D, Hofte M, Gheysen G. The jasmonate pathway is a key player in systemically induced defense

against root knot nematodes in rice. Plant Physiol 2011;157:305-16.

- 46. Matthews FB, Beard H, Brewer E, Kabir S, MacDonald HM, Youssef MR. Arabidopsis genes, AtNPR1, AtTGA2 and AtPR-5, confer partial resistance to soybean cyst nematode (*Heterodera glycines*) when over expressed in transgenic soybean roots. BMC Plant Biology 2014;14:96.
- Lilley CJ, Davies LJ, Urwin PE. RNA interference in plant parasitic nematodes: A summary of the current status. Parasitology 2012;139:630-40.
- Njezic B, De Sutter N, Moens M. Interaction of *Tagetes patula* single gold with the life cycle of the plant-parasitic nematodes *Meloidogyne chitwoodi* and *Pratylenchus penetrans*. Russ J Nematol 2014;22:101-8.
- Youssef RM, Kim KH, Haroon SA, Matthews BF. Posttranscriptional gene silencing of the gene encoding aldolase from soybean cyst nematode by transformed soybean roots. Exp Parasitol 2013;134:266-74.
- Dalzell JJ, McVeigh P, Warnock ND, Mitreva M, Bird DM, Abad P, et al. RNAi Effector diversity in nematodes. PLoS Neglect Trop Dis 2011;5:e1176.
- Urwin PE, Lilley CJ, Atkinson HJ. Ingestion of double-stranded RNA by preparasitic juvenile cyst nematodes leads to RNA interference. Mol Plant Microbe Interact 2002;15:747-52.
- 52. Iqbal S, Fosu-Nyarko J, Jones MG. Attempt to silence genes of the

RNAi pathways of the root-knot nematode, *Meloidogyne incognita* results in diverse responses including increase and no change in expression of some genes. Front Plant Sci 2020;11:328.

- Agrawal N, Dasaradhi PV, Mohmmed A, Malhotra P, Bhatnagar RK, Mukherjee SK. RNA interference: Biology, mechanism, and applications. Microbiol Mol Biol 2003;67:657-85.
- Goswami BK, Mittal A. Management of root-knot nematode infecting tomato by *Trichoderma viride* and *Paecilomyces lilacinus*. Indian Phytopathol 2004;57:235-6.
- Kiewnick S, Sikora RA. Biological control of the root-knot nematode Meloidogyne incognita by Paecilomyces lilacinus strain 251. Biol Control 2006;38:179-187.
- Manakau R. Biological control of nematode pests by natural enemies. Ann Rev Phytopathol 1980;81:415-40.
- Dababat AA, Sikora RA. Induced resistance by the mutualistic endophyte, *Fusarium oxysporum* 162, toward *Meloidogyne incognita* on tomato. Biocontrol Sci Technol 2007;17:969-75.

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