

REVIEW ARTICLE: *MELOIDOGYNE INCOGNITA* (ROOT-KNOT NEMATODE) A RISK TO AGRICULTURE

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Abstract. Phylum Nematoda is one of the most abundant group of metazoans. Root-knot nematodes (*Meloidogyne* spp.) pose a risk to agricultural crops in the world. The *Meloidogyne* genus comprises about 100 species and their host range includes more than 3000 plant species. *Meloidogyne incognita* is one of the most predominant species of this genus damaging a variety of field crops and vegetables. It is very difficult for farmers to diagnose its symptoms due to similarities with nutritional deficiencies. However to overcome this issue, the literature review of researches on the identification, classification, life cycle, symptoms, economic impact and management strategies of *M. incognita* was planned. The literature review provides an overview and useful information regarding decisions about management of this nematode species in the future.

Keywords: *Nematoda, Metazoan, economic impact, management, deficiencies*

Introduction

Phylum “Nematoda” is an abundant collection of metazoan on earth (Ahmed et al., 2016; Kergunteuil et al., 2016). Nematodes are common, extensively distributed and well adaptable group of organism that directly impact economy due to massive losses to crops. Nematodes covered about 90% of all multicellular organisms (Çetintaş et al., 2017). Nematodes are usually rounded in cross-section, both ends tapering and elongated in shape. They are heterosexual and possess all systems of higher organisms excluding the circulatory or respiratory systems. They are parasites of animals, insects, humans, and plants. Some of them feed upon decaying matters, bacteria and on other micro-organisms.

Plant parasitic nematodes caused lesions in plants and produced secondary infection in them by facilitating other organisms such as fungus, bacteria and viruses (Smant et al., 2018). However, damage caused by nematodes is frequently not easy to differentiate from other reasons because of their microscopic size. They are usually live in soil, roots and in leaves and cause enormous threat to agriculture, about upto US \$ 157 billion

annual losses (Youssef et al., 2013). Some of them are migratory in nature whereas others are sedentary (Kihika et al., 2017; Palomares-Rius et al., 2017).

The most destructive nematodes genera are *Heterodera*; *Meloidogyne*; *Rotylenchulus*; *Helicotylenchus*; *Tylenchorhynchus*; *Pratylenchus*; *Ditylenchus*; *Xiphinema*; *Longidorus*. Most of plant parasitic nematodes belong to order Tylenchida while *Xiphinema* and *Longidorus* belong to order Dorylaimida. They caused extensive losses to the crops because a number of them are vectors of some viruses (Lizanne and Pai, 2014).

Meloidogyne genus is one of the most destructive pathogen (Kamran et al., 2014; Xiang et al., 2017). They are economically important parasites and one of the most damaging pests of vegetables and others crops (Anwar and McKenry, 2010; Kamran et al., 2012; Castagnone-Sereno et al., 2013). They are cosmopolitan and recorded from Africa, Asia, Caribbean, Central, North and South America, Europe and Oceania. They are obligate parasites of woody plants, monocotyledonous and dicotyledonous herbaceous plants. This genus has approximately 100 species while four major species are *M. arenaria*; *M. heplia*; *M. incognita* and *M. javanica* (Hunt and Handoo, 2009; Lunt et al., 2014).

The major four species of Root-knot nematodes (RKN) are present in People's Republic of China but *M. incognita* is one of the most predominant (Dong et al., 2014). It has wide host range and cause dramatic yield loss in China (Naranjo and Ellsworth, 2001; Shun-xiang et al., 2001). It directly and indirectly damages the crop like toppling, loss of yield, poor quality, delay in maturity and also causes losses of economic importance etc. (Yan et al., 2011; Onkendi et al., 2014).

They have been controlled by synthetic chemicals but pose risks to soil environment, costly, highly toxic. Some of them are a carcinogenic agent, that's why most nematicide chemicals have been withdrawn from market for example methyl bromide, ethylene dibromide (EDB) and dibromochloropropane (Onkendi et al., 2014; Nicol et al., 2011). Nowadays scientists are mainly focused on crop rotation, plant resistance, bio-control and cultural practices to overcome this problematic issue (Chitwood, 2002). Bio-control is safe and eco-friendly in application compared to chemicals because it has no residual effects on food (Cetintas et al., 2018).

Identification of *Meloidogyne incognita*

For identification of *M. incognita* mostly morphological, molecular and isoenzymatic characters are used. Morphological study of perineal patterns of female has been most commonly used character for the identification. Whereas, sometimes morphological characters of different species overlap with each other that is why molecular identification is used for accurate diagnosis. Different methods have been employed for molecular identification like DNA Marker; ribosomal Large Subunits (LSU) D2/D3 expansion segments (Rius et al., 2007), Small Subunits (SSL) (Powers, 2004), Mitochondrial DNA (Xu et al., 2004; Jeyaprakash et al., 2006), intergenic spacer (IGS) (Wishart et al., 2002), Random amplified polymorphic DNA (RAPD) (Adam et al., 2007), internal transcribe spacers (ITS) (Skantar et al., 2008) and Sequence-Characterized-Amplified Regions (SCAR) (Randig et al., 2002). Isoenzyme phenotyping is based upon relative mobility of enzymes extracted from mature females of *M. incognita* on gel electrophoresis (Cunha et al., 2018). Morphological, molecular and biochemical data should be combined to improve the determination and reliability of diagnosis.

Life cycle of *Meloidogyne incognita*

The life cycle of *M. incognita* consists of five different stages; egg, J2, J3, J4 and adults (*Figure 1*). The female present in plant roots laid eggs, that developed into J2 juveniles. Hatching of eggs are temperature driven usually without requiring any stimulus from plants (Karssen et al., 2013). J2 infecting host roots and complete further developmental stages on feeding sites however J3 and J4 juveniles have sedentary nature and J4 molt into female or male adult. After fertilization females remained in plant roots and produced egg masses. Usually females reproduce through mitotic parthenogenesis (Hussey and Janssen, 2002).

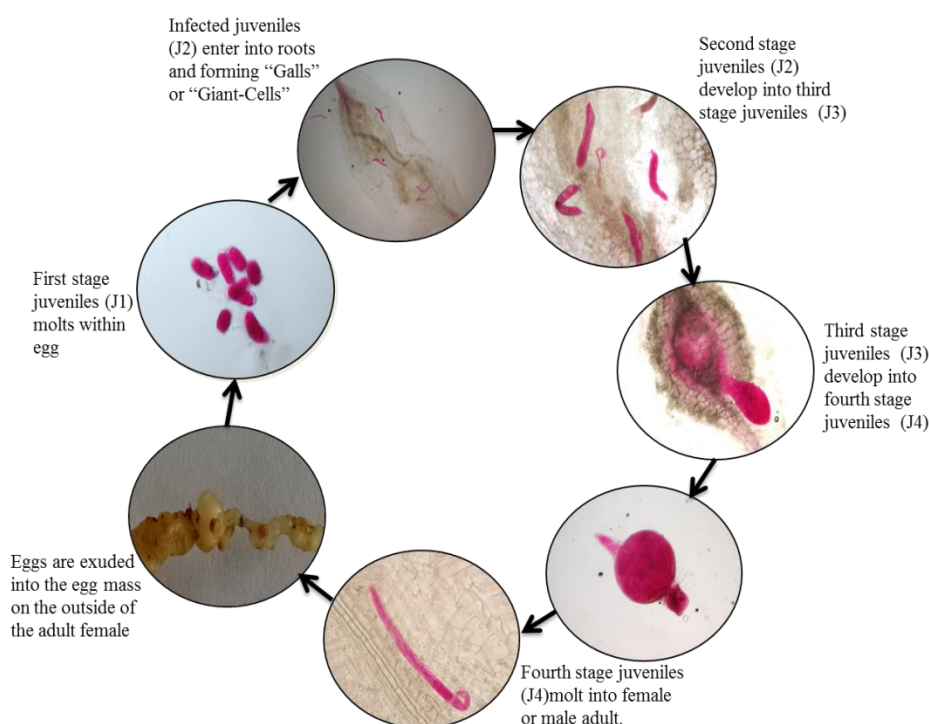


Figure 1. Life cycle of *Meloidogyne incognita*

Symptoms produced by *Meloidogyne incognita*

Plants infected by *M. incognita* showed nutritional deficiency i.e. yellowing of leaves, stunted growth, wilting and plant death (Priya et al., 2011). The farmers did not diagnose its damage due to similarities with nutritional deficiencies like chlorosis (Zeng et al., 2018; Ye et al., 2015). It developed the gall or swelling and cell expansion in roots of infected plant. Infected roots showed bushier and shorter length compared with healthy roots (Miyashita et al., 2014; Ma et al., 2013). The host range of root knot nematodes included more than 3000 plant species (Abdellatif et al., 2016). That's why it is difficult to find any common crop which was not parasitized by it (Castagnone-Sereno et al., 2013). They directly feed upon plants and cause the lesion in it which helps secondary pathogens such as pathogenic bacteria, fungus and viruses that cause secondary infections (Smant et al., 2018; Palomares-Rius et al., 2017).

Management strategies

The main objective of controlling *M. incognita* in soil is to secure crops from its attack to obtain maximum yield (Norshie et al., 2011). Different approaches have been implemented to control *M. incognita* such as chemical control, biological control, cultural control and use of resistant cultivars.

Chemical control

Nematicides are the most effective method to control the *Meloidogyne* spp. but they contain active components of Aldi-carb (Temik), methyl bromide and some other compounds which are prohibited. Chemical nematicides contain usually harmful agents which severely damage the ecosystem (Onkendi et al., 2014). Nematicides can reduced the high populations of root knot nematodes but unable to eliminate completely and accumulate in plant tissues (Sirias, 2011). Chemical nematicides are grouped into non-fumigant and fumigant and non-fumigant depend upon their volatility in soil. The first commercial non-fumigant active ingredient was O-2,4-dichlorophenyl O,O-diethyl phosphorothioate (Taylor, 2003). A few non-fumigant nematicidal active ingredients are ethoprop, fluazaindoline, fluensulfone, fluopyram, oxamyl, spirotetramate and terbufos (Wram and Zasada, 2019; Hajihassani et al., 2019; Giannakou and Panopoulou, 2019). Chemical fumigant type nematicides are highly effective in controlling root-knot nematodes. Some common nematicidal active ingredients of fumigants are allyl isothiocyanate, chloropicrin, dimethyl disulfide, metam potassium, metam sodium and 1,3 dichloropropene (1,3-D) (Desaeger et al., 2017; Sikora and Roberts, 2018). They are very toxic for animals and human beings because its residues may be present in food chain (Walters and Heil, 2007).

Biological control

Biological control is usually safer than chemical. Fungi belong to genera *Acremonium*, *Chaetomium*, *Paecilomyces* and *Trichoderma* have been known as antagonistic to plant parasitic nematodes (Govinden-Soulange and Levantard, 2008; Sharon et al., 2009). Colonization of these genera of fungus showed that seedling on cucumber was very low because they suppressed plant parasitic nematodes before penetration into host (Kiewnick and Sikora, 2006). Saprophytic fungi demonstrated to reduce rate of penetration of root knot nematodes in tomato roots (Dababat and Sikora, 2007). Obligate symbiotic arbuscular mycorrhizal fungi can alter the finding host behavior in *Meloidogyne* spp. (Reimann et al., 2008). Roots colonization by *Fusarium oxysporum* led to accumulation of root that showed repelling effect on *M. incognita* in tomato (Selim, 2010). Nonpathogenic *Fusarium* strains were capable in reducing *M. incognita* on tomato (Terra et al., 2018). Certain endophytes can be used as controlling nematodes (Zabalgogezcoa, 2008). *Penicillium chrysogenum* is one of the most important fungi to control *M. incognita* (Yao et al., 2014). However level of inoculums can be reduced by seed treatment (Athman, 2006). (Dababat and Sikora, 2007) reported that systemic resistance against *M. incognita* was induced by changing chemical composition through nonpathogenic *Fusarium* Fo162. Arbuscular mycorrhizal (AM) fungi reduced severity of diseases in plants due to plant parasitic nematodes (Akköprü and Demir, 2005). Different mutualistic endophytes were used as antagonists against plant parasitic nematodes. Microorganisms such as fungi and rhizobacteria show

efficiency to control *Meloidogyne* spp. (Vos et al., 2013). The endophytic bacteria reduce root-knot nematodes penetration in plants (Padgham and Sikora, 2007).

Cultural control

The use and development of resistant crop cultivars and the use of cleaning of farm implements, intercropping, clean planting materials and crop rotation showed influence on cultural practices (Briar et al., 2016). Heat solarization and treatment of the soil before cultivation of seed played role for controlling *Meloidogyne incognita* (Ioannou, 2000). Egg infectivity of *M. incognita* can be reduced through solarization of soil for 3 weeks (Nicol et al., 2011).

Resistant cultivars

Several studies are going on throughout the world to extend the crops with resistance against root knot nematodes (Norshie et al., 2011). Resistance gene Rmc-1 located on chromosome 11 of wild potato was found resistant against *Meloidogyne* spp. (Brown et al., 2006). In isogenic tomato cultivars resistance gene Mi-1.2 confers best for huge nematode pressure (200,000 eggs/plant) (Corbett et al., 2011). The Me and N genes from pepper and the Mi2 through Mi8 genes from *Lycopersicon* identified against root knot nematodes (Mitkowski and Abawi, 2003). Some crops have been rendered susceptible with entering resistance breaking *Meloidogyne* spp. (Brown et al., 2009; Kiewnick et al., 2009).

Mode of reduction of *Meloidogyne incognita*

Four possible mode of action can reduce the *M. incognita* (i) inhibition (ii) development of antagonistic microbiota (iii) altered or enhanced plant growth, nutrition and morphology (iv) induced resistance (Whipps, 2004). Resistance is a safer and economically more important method than other disease controlling strategies (cultural or chemical control) due to its environmental friendly nature and disease controlling potential (Ibrahim et al., 2016).

Induced resistance

Induced resistance can be defined as a development of defensive capacity of plant against broad-spectrum of pests and pathogens that are attained after appropriate stimulation. The resulting evaluated resistance due to inducer upon infection or disease by a pathogen or pest is called systemic acquired resistance (SAR) or induced systemic resistance (ISR) (Ramamoorthy et al., 2001). The resistance in Nematology can be defined as the ability of a plant to inhibit the reproduction of nematode species relative to reproduction on plant lacking such resistance. There is a great potential in managing *M. incognita* because it is economically highly effective (Starr and Roberts, 2004). At least two forms of induced resistance, induced systemic resistance (ISR) and Systemic acquired resistance (SAR) have similar phenomenon responses but involve different pathways (Vallad and Goodman, 2004). The downstream components are similar but upstream components are usually different, mainly involving the ethylene (Et) or jasmonic acid (JA) pathways for induced systemic resistance and Salicylic acid (SA) for systemic acquired resistance (Pieterse and Van Loon, 2007). Systemic acquired resistance is usually triggered by local infections and disease, provides long-lasting

systemic resistance to successive pathogen or pest attack, and it is associated with PR genes activation and requires involvement of signaling molecules such as salicylic acid (Shoresh et al., 2010).

Induced resistance may be local or systemic. Local induced resistance response is local whereas systemic induced resistance is induced in a part of the plant that is separated spatially from the point of induction. When protection from disease is specific to a plant region which is treated with inducing agents is called local induced resistance. Whereas systemic induced resistance occurs when the plant is protected systemically due to the application of inducers to a single part of the plant. Induced systemic resistance is not necessarily confined to roots only (Vos et al., 2012), its extension towards aerial parts of plant seems possible (Fritz et al., 2006). Plant immune system proposes two pathogen induced defense responses such as effector-triggered immunity (ETI) and pattern-triggered immunity (PTI) (Shukla et al., 2018).

Inducers

Plant resistance against nematodes could be successfully induced by the application of different biotic and abiotic inducers resulting in broad-spectrum responses (Nikoo et al., 2014). These agents involve jasmonic acid (JA) and salicylic acid (SA) as key signaling molecules (Pieterse et al., 2012). Induced disease resistance is the process of an active resistance which depends upon host's barriers, activated by abiotic or biotic agents called elicitors (Fatma et al., 2014).

Abiotic inducer

Chemical defense activators can efficiently protect the crops against pests and pathogens such as *M. incognita* but they are rarely used in practice due to various reasons such as chemical induced resistance slowing down the progression of disease rather than completely eliminating it (Walters and Heil, 2007). Whereas when these chemicals applied in higher concentration negative effects are imposed on seed, plant growth and vigor (van Hulten et al., 2006). Chemicals can adversely affect the plant growth promoting microorganisms (de Roman et al., 2011).

Biotic inducer

Microorganisms such as fungi and rhizobacteria are efficient to control *Meloidogyne* spp. (Vos et al., 2013). These microorganisms are able to induce resistance through activation of jasmonic acid, salicylic acid and ethylene pathways which promote the production of PR proteins, reactive oxygen species and phenolic compounds (Hao et al., 2012). Fungi have the potential to induce resistance against *M. incognita* (Mascarin and Junior, 2012). *Trichoderma harzianum* have the ability to increase enzymatic activities against root-knot nematodes (Naserinasab et al., 2011). It has been reported that *T. harzianum* induces resistance against *M. incognita* in tomato (Harman et al., 2004) adopts priming of JA and SA related defense responses according to the stages of nematode (de Medeirosa et al., 2015; Martínez-Medina et al., 2017). Non-pathogenic *Fusarium oxysporum* changed the chemical composition of root exudates so it reduced invasion and attraction of *M. incognita* and thus induced systemic resistance in plants (Dababat and Sikora, 2007). Induced systemic resistance by plant growth promoting rhizobacteria (PGPR) has been successfully achieved in large number of agricultural crops including cucumber, potato, Arabidopsis, tomato, chili, sugarcane, rice, mango

and carnation against broad-spectrum of pathogens including bacteria, viruses, fungi and nematodes etc. (Reddy, 2012; Alizadeh et al., 2013).

Seed coating

Seed coating with resistance biotic inducing agents efficiently protected the plants against pathogens and pests (Paudel et al., 2014; Worrall et al., 2012). It is a common technique to improve seed germination and conservation while protecting the emerging seedling against pathogens (Govinden-Soulange and Levantard, 2008). Fermentation liquid of *Penicillium chrysogenum* induced resistance to *M. incognita* in *Solanum lycopersicum* and *Cucumis sativus* (Yao et al., 2014; Sikandar et al., 2019).

Conclusion

It is concluded that *M. incognita* is a great risk to agriculture because its above ground symptoms are usually similar with nutrition deficiencies. Although, chemical control is effective they contain harmful agents that rigorously damage any ecosystem. However, biological control and induced resistance in crop plants are safer strategies because of their eco-friendly nature. Thus, it is recommended to adopt biological control strategies rather than utilizing synthetic chemical agents.

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REFERENCES

- [1] Abdellatif, K. F., Abdelfattah, R. H., El-Ansary, M. S. M. (2016): Green Nanoparticles Engineering on Root-knot Nematode Infecting Eggplants and Their Effect on Plant DNA Modification. – Iranian Journal of Biotechnology 14: 250.
- [2] Adam, M. A. M., Phillips, M. S., Blok, V. C. (2007): Molecular diagnostic key for identification of single juveniles of seven common and economically important species of root-knot nematode (*Meloidogyne* spp.). – Plant Pathology 56: 190-197.
- [3] Ahmed, M., Sapp, M., Prior, T., Karssen, G., Back, M. A. (2016): Technological advancements and their importance for nematode identification. – Soil 2: 257-270.
- [4] Akköprü, A., Demir, S. (2005): Biological control of *Fusarium* wilt in tomato caused by *Fusarium oxysporum* f. sp. *lycopersici* by AMF *Glomus intraradices* and some rhizobacteria. – Journal of Phytopathology 153: 544-550.
- [5] Alizadeh, O., Azarpanah, A., Ariana, L. (2013): Induction and modulation of resistance in crop plants against disease by bioagent fungi (*Arbuscular mycorrhiza*) and hormonal elicitors and Plant Growth Promoting Bacteria. – International Journal of Farming and Allied Sciences 2: 982-998.
- [6] Anwar, S. A., McKenry, M. V. (2010): Incidence and reproduction of *Meloidogyne incognita* on vegetable crop genotypes. – Pakistan Journal of Zoology 42: 135-141.
- [7] Athman, S. Y. 2006. Host-endophyte-pest interactions of endophytic *Fusarium oxysporum* antagonistic to *Radopholus similis* in banana (*Musa* spp.). PhD, University of Pretoria
- [8] Briar, S. S., Wichman, D., Reddy, G. V. P. (2016): Plant-Parasitic Nematode Problems in Organic Agriculture.- In: Nandwani, D. (ed.) (eds.) Organic Farming for Sustainable

- Agriculture. Sustainable Development and Biodiversity, Springer International Publishing, Cham, Springer
- [9] Brown, C. R., Mojtahedi, H., James, S., Novy, R. G., Love, S. (2006): Development and evaluation of potato breeding lines with introgressed resistance to Columbia root-knot nematode (*Meloidogyne chitwoodi*). – American Journal of Potato Research 83: 1-8.
 - [10] Brown, C. R., Mojtahedi, H., Zhang, L. H., Riga, E. (2009): Independent resistant reactions expressed in root and tuber of potato breeding lines with introgressed resistance to *Meloidogyne chitwoodi*. – Phytopathology 99: 1085-1089.
 - [11] Castagnone-Sereno, P., Danchin, E. G. J., Perfus-Barbeoch, L., Abad, P. (2013): Diversity and evolution of root-knot nematodes, genus *Meloidogyne*: new insights from the genomic era. – Annual Review of Phytopathology 51: 203-220.
 - [12] Çetintaş, R., Kareem, K. H., Nassar, H. A. (2017): Diagnosis of Nematode Populations Found in Chard, Barley and Onion Grown in North of Iraq and South of Turkey. – Doga Bilimleri Dergisi 20: 28.
 - [13] Cetintas, R., Kusek, M., Fateh, S. A. (2018): Effect of some plant growth-promoting rhizobacteria strains on root-knot nematode, *Meloidogyne incognita*, on tomatoes. – Egyptian Journal of Biological Pest Control 28: 7.
 - [14] Chitwood, D. J. (2002): Phytochemical based strategies for nematode control. – Annual Review of Phytopathology 40: 221-249.
 - [15] Corbett, B. P., Jia, L., Sayler, R. J., Arevalo-Soliz, L. M., Goggin, F. (2011): The effects of root-knot nematode infection and mi-mediated nematode resistance in tomato on plant fitness. – Journal of Nematology 43: 82-89.
 - [16] Cunha, T. G. d., Visôto, L. E., Lopes, E. A., Oliveira, C. M. G., God, P. I. V. G. (2018): Diagnostic methods for identification of root-knot nematodes species from Brazil. – Ciência Rural 48:
 - [17] Dababat, A. E.-F. A., Sikora, R. A. (2007): Influence of the mutualistic endophyte *Fusarium oxysporum* 162 on *Meloidogyne incognita* attraction and invasion. – Nematology 9: 771-776.
 - [18] de Medeirosa, H. A., Resendea, R. S., Ferreira, F. C., Freitas, L. G., Rodriguesa, F. Á. 2015. Induction of resistance in tomato against *Meloidogyne javanica* by *Pochonia chlamydosporia*. Nematoda. ed.: Brazilian Nematological Society.
 - [19] de Roman, M., Fernandez, I., Wyatt, T., Sahrawy, M., Heil, M., Pozo, M. J. (2011): Elicitation of foliar resistance mechanisms transiently impairs root association with arbuscular mycorrhizal fungi. – Journal of Ecology 99: 36-45.
 - [20] Desaegeer, J., Dickson, D. W., Locascio, S. (2017): Methyl bromide alternatives for control of root-knot nematode (*Meloidogyne* spp.) in tomato production in Florida. – Journal of Nematology 49: 140-149.
 - [21] Dong, S., Qiao, K., Zhu, Y., Wang, H., Xia, X., Wang, K. (2014): Managing *Meloidogyne incognita* and *Bemisia tabaci* with thiacloprid in cucumber crops in China. – Crop Protection 58: 1-5.
 - [22] Fatma, M. A. M., Khalil, A. E., El Deen, N. A. H., Dina, S. (2014): Induction of Systemic Resistance in Sugar-Beet against Root-Knot Nematode with Commercial Products. – Journal of Plant Pathology and Microbiology 5: 1.
 - [23] Fritz, M., Jakobsen, I., Lyngkjær, M. F., Thordal-Christensen, H., Pons-Kühnemann, J. (2006): Arbuscular mycorrhiza reduces susceptibility of tomato to *Alternaria solani*. – Mycorrhiza 16: 413.
 - [24] Giannakou, I. O., Panopoulou, S. (2019): The use of fluensulfone for the control of root-knot nematodes in greenhouse cultivated crops: Efficacy and phytotoxicity effects. – Cogent Food & Agriculture 5: 1643819.
 - [25] Govinden-Soulange, J., Levantard, M. (2008): Comparative studies of seed priming and pelleting on percentage and meantime to germination of seeds of tomato (*Lycopersicon esculentum* Mill.). – African Journal of Agricultural Research 3: 725-731.

- [26] Hajihassani, A., Davis, R. F., Timper, P. (2019): Evaluation of selected nonfumigant nematicides on increasing inoculation densities of *Meloidogyne incognita* on cucumber. – Plant Disease 103: 3161-3165.
- [27] Hao, Z., Fayolle, L., van Tuinen, D., Chatagnier, O., Li, X., Gianinazzi, S., Gianinazzi-Pearson, V. (2012): Local and systemic mycorrhiza-induced protection against the ectoparasitic nematode *Xiphinema index* involves priming of defence gene responses in grapevine. – Journal of Experimental Botany 63: 3657-3672.
- [28] Harman, G. E., Howell, C. R., Viterbo, A., Chet, I., Lorito, M. (2004): *Trichoderma* species—opportunistic, avirulent plant symbionts. – Nature Reviews Microbiology 2: 43.
- [29] Hunt, D. J., Handoo, Z. A. (2009): Taxonomy, identification and principal species.- In: Perry, R. N., Moens, M., J.L., S. (eds.) Root-knot nematodes, CABI, Wallingford, UK
- [30] Hussey, R. S., Janssen, G. J. W. (2002): Root-knot nematodes: *Meloidogyne* species.- In: Starr, J. L., Cook, R., Bridge, J. (eds.) Plant resistance to parasitic nematodes, CABI Wallingford, UK
- [31] Ibrahim, A., Shahid, A. A., Noreen, S., Ahmad, A. (2016): Physiological changes against *Meloidogyne incognita* in rhizobacterial treated eggplant under organic condition. – JAPS, Journal of Animal and Plant Sciences 26: 805-813.
- [32] Ioannou, N. (2000): Soil solarization as a substitute for methyl bromide fumigation in greenhouse tomato production in Cyprus. – Phytoparasitica 28: 248-256.
- [33] Jeyaprakash, A., Tigano, M. S., Brito, J., Carneiro, R., Dickson, D. W. (2006): Differentiation of *Meloidogyne floridensis* from *M. arenaria* using high-fidelity PCR amplified mitochondrial AT-rich sequences. – Nematropica 36: 1-12.
- [34] Kamran, M., Anwar, S. A., Javed, N., Khan, S. A., ul Haq, I., Ullah, I. (2012): Field evaluation of tomato genotypes for resistance to *Meloidogyne incognita*. – Pakistan Journal of Zoology 44: 1355-1359.
- [35] Kamran, M., Javed, N., Khan, S. A., Jaskani, M. J., Ullah, I. (2014): Efficacy of *Pasteuria* penetrans on *Meloidogyne incognita* reproduction and growth of tomato. – Pakistan Journal of Zoology 46: 1651-1655.
- [36] Karssen, G., Wesemael, W. M. L., Moens, M. (2013): Root-knot nematodes.- In: Perry, R. N., Moens, M. (eds.) Plant nematology, CABI, Wallingford, UK
- [37] Kergunteuil, A., Campos-Herrera, R., Sánchez-Moreno, S., Vittoz, P., Rasmann, S. (2016): The abundance, diversity, and metabolic footprint of soil nematodes is highest in high elevation alpine grasslands. – Frontiers in Ecology and Evolution 4: 84.
- [38] Kiewnick, S., Dessimoz, M., Franck, L. (2009): Effects of the Mi-1 and the N root-knot nematode-resistance gene on infection and reproduction of *Meloidogyne enterolobii* on tomato and pepper cultivars. – Journal of Nematology 41: 134-9.
- [39] Kiewnick, S., Sikora, R. A. (2006): Biological control of the root-knot nematode *Meloidogyne incognita* by *Paecilomyces lilacinus* strain 251. – Biological Control 38: 179-187.
- [40] Kihika, R., Murungi, L. K., Coyne, D., Hassanali, A., Teal, P. E. A., Torto, B. (2017): Parasitic nematode *Meloidogyne incognita* interactions with different *Capsicum annum* cultivars reveal the chemical constituents modulating root herbivory. – Scientific Reports 7: 2903.
- [41] Lizanne, A. C. M., Pai, I. K. (2014): A preliminary survey on soil and plant parasitic nematodes of southern Goa, India. – Journal of Threatened Taxa 6: 5400-5412.
- [42] Lunt, D. H., Kumar, S., Koutsovoulos, G., Blaxter, M. L. (2014): The complex hybrid origins of the root knot nematodes revealed through comparative genomics. – PeerJ 2: e356.
- [43] Ma, J., Kirkpatrick, T. L., Rothrock, C. S., Brye, K. (2013): Effects of soil compaction and *Meloidogyne incognita* on cotton root architecture and plant growth. – Journal of Nematology 45: 112-121.
- [44] Martínez-Medina, A., Fernandez, I., Lok, G. B., Pozo, M. J., Pieterse, C. M. J., Van Wees, S. (2017): Shifting from priming of salicylic acid-to jasmonic acid-regulated

- defences by *Trichoderma* protects tomato against the root knot nematode *Meloidogyne incognita*. – *New Phytologist* 213: 1363-1377.
- [45] Mascarin, G. M., Junior, M. F. B. (2012): *Trichoderma harzianum* reduces population of *Meloidogyne incognita* in cucumber plants under greenhouse conditions. – *Journal of Entomology and Nematology* 4: 54-57.
 - [46] Mitkowski, N., Abawi, G. (2003): Root-knot nematodes. The Plant Health Instructor. – <http://www.apsnet.org/edcenter/intropp/lessons/nematodes/pages/rootknotnematode.aspx>:
 - [47] Miyashita, N., Yabu, T., Kurihara, T., Koga, H. (2014): The feeding behavior of adult root-knot nematodes (*Meloidogyne incognita*) in rose balsam and tomato. – *Journal of Nematology* 46: 296-301.
 - [48] Naranjo, S. E., Ellsworth, P. C. 2001. Special issue: Challenges and opportunities for pest management of *Bemisia tabaci* in the new century. Elsevier.
 - [49] Naserinasab, F., Sahebani, N., Etebarian, H. R. (2011): Biological control of *Meloidogyne javanica* by *Trichoderma harzianum* BI and salicylic acid on tomato. – *African Journal of Food Science* 5: 276-280.
 - [50] Nicol, J. M., Turner, S. J., Coyne, D. L., Nijs, L. D., Hockland, S., Maafi, Z. T. (2011): Current Nematode Threats to World Agriculture.- In: Jones, J., Gheysen, G., Fenoll, C. (eds.) *Genomics and molecular genetics of plant-nematode interactions*, Springer, London,
 - [51] Nikoo, F. S., Sahebani, N., Aminian, H., Mokhtarnejad, L., Ghaderi, R. (2014): Induction of systemic resistance and defense-related enzymes in tomato plants using *Pseudomonas fluorescens* CHAO and salicylic acid against root-knot nematode *Meloidogyne javanica*. – *Journal of Plant Protection Research* 54: 383-389.
 - [52] Norshie, P. M., Been, T. H., Schomaker, C. H. (2011): Estimation of partial resistance in potato genotypes against *Meloidogyne chitwoodi*. – *Nematology* 13: 477-489.
 - [53] Onkendi, E. M., Kariuki, G. M., Marais, M., Moleleki, L. N. (2014): The threat of root-knot nematodes (*Meloidogyne* spp.) in Africa: a review. – *Plant Pathology* 63: 727-737.
 - [54] Padgham, J. L., Sikora, R. A. (2007): Biological control potential and modes of action of *Bacillus megaterium* against *Meloidogyne graminicola* on rice. – *Crop Protection* 26: 971-977.
 - [55] Palomares-Rius, J. E., Escobar, C., Cabrera, J., Vovlas, A., Castillo, P. (2017): Anatomical alterations in plant tissues induced by plant-parasitic nematodes. – *Frontiers in plant science* 8: 1987.
 - [56] Paudel, S., Rajotte, E. G., Felton, G. W. (2014): Benefits and costs of tomato seed treatment with plant defense elicitors for insect resistance. – *Arthropod-Plant Interactions* 8: 539-545.
 - [57] Pieterse, C. M., Van Loon, L. 2007. Signalling cascades involved in induced resistance. In: Walters, D., Newton, A. C., Lyon, G. (eds.) *Induced resistance for plant defense: A sustainable approach to crop protection*. ed. Oxford, UK.: Blackwell.
 - [58] Pieterse, C. M. J., Van der Does, D., Zamioudis, C., Leon-Reyes, A., Van Wees, S. C. M. (2012): Hormonal modulation of plant immunity. – *Annual Review of Cell and Developmental Biology* 28:
 - [59] Powers, T. (2004): Nematode molecular diagnostics: from bands to barcodes. – *Annual Review of Phytopathology* 42: 367-383.
 - [60] Priya, D. B., Somasekhar, N., Prasad, J. S., Kirti, P. B. (2011): Transgenic tobacco plants constitutively expressing Arabidopsis NPR1 show enhanced resistance to root-knot nematode, *Meloidogyne incognita*. – *BMC Research Notes* 4: 231.
 - [61] Ramamoorthy, V., Viswanathan, R., Raguchander, T., Prakasam, V., Samiyappan, R. (2001): Induction of systemic resistance by plant growth promoting rhizobacteria in crop plants against pests and diseases. – *Crop protection* 20: 1-11.
 - [62] Randig, O., Bongiovanni, M., Carneiro, R. M. D. G., Castagnone-Sereno, P. (2002): Genetic diversity of root-knot nematodes from Brazil and development of SCAR markers specific for the coffee-damaging species. – *Genome* 45: 862-870.

- [63] Reddy, P. P. (2012): Plant Growth-Promoting Rhizobacteria (PGPR).- In: Reddy, P. P. (ed.) (eds.) Recent advances in crop protection, Springer India, New Delhi, India
- [64] Reimann, S., Hauschild, R., Hildebrandt, U., Sikora, R. A. (2008): Interrelationships between *Rhizobium etli* G12 and *Glomus intraradices* and multitrophic effects in the biological control of the root-knot nematode *Meloidogyne incognita* on tomato. – Journal of Plant Diseases and Protection 115: 108-113.
- [65] Rius, J. E. P., Vovlas, N., Troccoli, A., Liébanas, G., Landa, B. B., Castillo, P. (2007): A new root-knot nematode parasitizing sea rocket from Spanish Mediterranean coastal dunes: *Meloidogyne dunensis* n. sp. (Nematoda: Meloidogynidae). – Journal of Nematology 39: 190.
- [66] Selim, M. E. M. 2010. Biological, chemical and molecular studies on the systemic induced resistance in tomato against *Meloidogyne incognita* caused by the endophytic *Fusarium oxysporum*, Fo162. PH.D., University of Bonn.
- [67] Sharon, E., Chet, I., Spiegel, Y. (2009): Improved attachment and parasitism of Trichoderma on *Meloidogyne javanica* in vitro. – European Journal of Plant Pathology 123: 291-299.
- [68] Shores, M., Harman, G. E., Mastouri, F. (2010): Induced systemic resistance and plant responses to fungal biocontrol agents. – Annual Review of Phytopathology 48: 21-43.
- [69] Shukla, N., Yadav, R., Kaur, P., Rasmussen, S., Goel, S., Agarwal, M., Jagannath, A., Gupta, R., Kumar, A. (2018): Transcriptome analysis of root-knot nematode (*Meloidogyne incognita*)-infected tomato (*Solanum lycopersicum*) roots reveals complex gene expression profiles and metabolic networks of both host and nematode during susceptible and resistance responses. – Molecular plant pathology 19: 615-633.
- [70] Shun-xiang, R., Zhen-zhong, W., Bao-li, Q., Yuan, X. (2001): The pest status of *Bemisia tabaci* in China and non-chemical control strategies. – Insect Science 8: 279-288.
- [71] Sikandar, A., Zhang, M. Y., Zhu, X. F., Wang, Y. Y., Ahmed, M., Iqbal, M. F., Javeed, A., Xuan, Y. H., Fan, H. Y., Liu, X. Y., Chen, L. J., Duan, Y. X. (2019): Effects of *Penicillium chrysogenum* strain Snf1216 against root-knot nematodes (*Meloidogyne incognita*) in cucumber (*Cucumis sativus* L.) under greenhouse conditions. – Applied Ecology and Environmental Research 17: 12451-12464.
- [72] Sikora, R. A., Roberts, P. A. (2018): Management Practices: An overview of integrated nematode management technologies.- In: Sikora, R. A., Coyne, D., Hallmann, J., Timper, P. (eds.) Plant parasitic nematodes in subtropical and tropical agriculture, Cabi, Wallingford, UK
- [73] Sirias, H. C. I. 2011. Root-knot nematodes and coffee in Nicaragua: management systems, species identification and genetic diversity. PH.D., Swedish University of Agricultural Sciences.
- [74] Skantar, A. M., Carta, L. K., Handoo, Z. A. (2008): Molecular and Morphological Characterization of an Unusual *Meloidogyne arenaria* Population from Traveler's Tree, *Ravenala madagascariensis*. – Journal of Nematology 40: 179.
- [75] Smant, G., Helder, J., Govers, A. (2018): Parallel adaptations and common host cell responses enabling feeding of obligate and facultative plant parasitic nematodes. – The Plant Journal 93: 686-702.
- [76] Starr, J. L., Roberts, P. A. (2004): Resistance to plants parasitic nematodes.- In: Chen, Z. X., Chen, S. Y., Dickson, D. W. (eds.) Nematology: advances and perspectives, CABI, Wallingford, UK
- [77] Taylor, A. (2003): Nematocides and nematicides-a history. – Nematropica 33: 225-232.
- [78] Terra, W. C., Campos, V. P., Martins, S. J., Costa, L. S. A. S., da Silva, J. C. P., Barros, A. F., Lopez, L. E., Santos, T. C. N., Smant, G., Oliveira, D. F. (2018): Volatile organic molecules from *Fusarium oxysporum* strain 21 with nematicidal activity against *Meloidogyne incognita*. – Crop Protection 106: 125-131.
- [79] Vallad, G. E., Goodman, R. M. (2004): Systemic acquired resistance and induced systemic resistance in conventional agriculture. – Crop science 44: 1920-1934.

- [80] van Hulten, M., Pelsler, M., Van Loon, L. C., Pieterse, C. M. J., Ton, J. (2006): Costs and benefits of priming for defense in *Arabidopsis*. – *Proceedings of the National Academy of Sciences* 103: 5602-5607.
- [81] Vos, C., Schouteden, N., Van Tuinen, D., Chatagnier, O., Elsen, A., De Waele, D., Panis, B., Gianinazzi-Pearson, V. (2013): Mycorrhiza-induced resistance against the root-knot nematode *Meloidogyne incognita* involves priming of defense gene responses in tomato. – *Soil Biology and Biochemistry* 60: 45-54.
- [82] Vos, C. M., Tesfahun, A. N., Panis, B., De Waele, D., Elsen, A. (2012): Arbuscular mycorrhizal fungi induce systemic resistance in tomato against the sedentary nematode *Meloidogyne incognita* and the migratory nematode *Pratylenchus penetrans*. – *Applied Soil Ecology* 61: 1-6.
- [83] Walters, D., Heil, M. (2007): Costs and trade-offs associated with induced resistance. – *Physiological and Molecular Plant Pathology* 71: 3-17.
- [84] Whipps, J. M. (2004): Prospects and limitations for mycorrhizas in biocontrol of root pathogens. – *Canadian journal of botany* 82: 1198-1227.
- [85] Wishart, J., Phillips, M. S., Blok, V. C. (2002): Ribosomal intergenic spacer: a polymerase chain reaction diagnostic for *Meloidogyne chitwoodi*, *M. fallax* and *M. hapla*. – *Phytopathology* 92: 884-892.
- [86] Worrall, D., Holroyd, G. H., Moore, J. P., Glowacz, M., Croft, P., Taylor, J. E., Paul, N. D., Roberts, M. R. (2012): Treating seeds with activators of plant defence generates long-lasting priming of resistance to pests and pathogens. – *New Phytologist* 193: 770-778.
- [87] Wram, C., Zasada, I. A. (2019): Short-term effects of sub-lethal doses of nematicides on *Meloidogyne incognita*. – *Phytopathology* 109: 1605-1613.
- [88] Xiang, N., Lawrence, K. S., Kloepper, J. W., Donald, P. A., McInroy, J. A., Lawrence, G. W. (2017): Biological control of *Meloidogyne incognita* by spore-forming plant growth-promoting rhizobacteria on cotton. – *Plant Disease* 101: 774-784.
- [89] Xu, J., Liu, P., Meng, Q., Long, H. (2004): Characterisation of *Meloidogyne* species from China using isozyme phenotypes and amplified mitochondrial DNA restriction fragment length polymorphism. – *European Journal of Plant Pathology* 110: 309-315.
- [90] Yan, X.-n., Sikora, R. A., Zheng, J.-w. (2011): Potential use of cucumber (*Cucumis sativus* L.) endophytic fungi as seed treatment agents against root-knot nematode *Meloidogyne incognita*. – *Journal of Zhejiang University Science B* 12: 219-225.
- [91] Yao, Q., Lu, X., Zhu, X., Wang, Y., Chen, L., Duan, Y. (2014): Resistance against *Meloidogyne incognita* in tomato induced by fermentation liquid of *Penicillium chrysogenum* strain 1216. – *Acta Phytopathologica Sinica* 44: 693-699
- [92] Ye, W., Zeng, Y., Kerns, J. (2015): Molecular characterisation and diagnosis of root-knot nematodes (*Meloidogyne* spp.) from turfgrasses in North Carolina, USA. – *PloS one* 10: e0143556.
- [93] Youssef, R. M., Kim, K.-H., Haroon, S. A., Matthews, B. F. (2013): Post-transcriptional gene silencing of the gene encoding aldolase from soybean cyst nematode by transformed soybean roots. – *Experimental Parasitology* 134: 266-274.
- [94] Zabalgogezcoa, I. (2008): Fungal endophytes and their interaction with plant pathogens: a review. – *Spanish Journal of Agricultural Research* 6: 138-146.
- [95] Zeng, J., Zhang, Z., Li, M., Wu, X., Zeng, Y., Li, Y. (2018): Distribution and Molecular Identification of *Meloidogyne* spp. Parasitising Flue-cured Tobacco in Yunnan, China. – *Plant Protection Science* 1-7.