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THE THREAT OF ROOT-KNOT NEMATODES (M ELOIDOGYNE SPP.)

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ABSTRACT

Meloidogyne species represent a significant threat to sustainable crop production considering the substantial yield lossescaused by these parasitic nematodes in various agricultural crops. The plant-parasitic nematodes establish a nutritional relationship with the host plant through specialized feeding sites (galls) induced by them in the root region. The direct and indirect stress caused by various *Meloidogyne* species results in impaired plant growth exhibiting delayed maturity, extensive toppling, poor quality,and reduced yields of crop, ultimately leading to high costs of production. Further, the emergence of resistance-breaking *Meloidogyne* species has intensified the complications bypartially renderingthe pre-existing standard pest management strategiesineffectual, therefore increasing the global burden of agronomic production and putting food security at risk. Moreover, considering the current scenario of on-going withdrawal of nematicides due to their undesirable consequences, greater losses may be experienced in the near future. This review discusses the mode of parasitism and the factors contributing to the overall threat posed by M. incognita. The paper will further discuss the agronomic practices and management strategies

Keywords: Economic impact, identifications, pest management, Meloidogyne incognita, life cycle

Introduction

Meloidogyne incognita, commonly known as the "southern root-nematode" or "cotton root-knot nematode" is a plant-parasitic roundworm belonging to the family Heteroderidae, and is grouped among the four predominant species existing worldwide. These nematodes are named on the account of characteristic galls or knots they form on the roots of infected plants. They are reported to invade a wide range of hosts enforcing complex plant-pathogen interactions.They exhibit a sedentary endoparasiticlife-stylesince they depend on the induction of permanent feeding site/saround the host root vasculatureto sustain throughout their life cycle. RKN are recognized as the most widespread and destructive plant-parasitic nematode pests, accounting for global loss in reference to a wide-range of agricultural crops (1). They are scientifically classified in the genus *Meloidogyne* (Tylenchida: Meloidogynidae) with over 100 species characterized at molecular level to date (2). This diverse group of pathogens affectsboth the quantity and quality of commercial yields resulting in extensive economic losses annually.

In the recent past, various chemical based nematode controlling strategies have led to a significant mitigation of *Meloidogyne* spp. populations acrosscultivation sites. However, the raising concerns of their toxic and detrimental effects on the environment as well as the public health have led to withdrawal of a number of regularly practiced nematicides from commercial supply. The existing scenario has now, therefore constrained *Meloidogyne* spp. to the forefront as inextricable pathogens ruining various important agricultural crops. In fact, *Meloidogyne* spp. had been voted concordantly as one of the top ten plant parasitic nematodes

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in the survey conducted in 2013 for the journal *Molecular Plant Pathology* (3). This article details the parasitic mechanism and the associated factors contributing to survival of *Meloidogyne* spp. It also discusses thecurrently available management techniques along with the futuristic approaches to combat *Meloidogyne* spp. derived plant infections.

Figure 1: Meloidogyne incognita

Parasitic effects of M. incognita

Roots serve as the primary pathway of plants for acquisition of adequate water and nutrients to accomplish proper growth and development. Recently documented below-ground interactions studies in the subterranean environment have revealed that herbivore-induced plant volatiles (HIPVs) can play defensive role for plants by recruitingnatural assailants of herbivorous insects.

Plant-parasitic nematodes (PPNs) listed under genus *Meloidogyne* are sedentary endo-parasites, typically polyphagous in nature and cause massive damage to a diverse range of economically important crops across the globe (4). Several factors such as thepopulation density of pathogen,susceptibility of plantand primary environmental components (e.g. soil moisture and fertility, occurrenceof other co-inhabitant pathogens) govern the degree of nematode inducedplant damage.*Meloidogyne*derived infections, particularly in popular high-value vegetablesdeteriorate quality and hence marketability resulting in gross yield losses of up to 100% (5,6).

*M. incognita*completes maximum period of their life span within the roots of host plant (Figure 10). The life cycle of *M. Incognita*encompasses four juvenile stages and four moults besides the adult and egg. The second juvenile stage (J2) serves as the infective phase, wherein, after hatchingout from the eggs,juveniles move through soil searching for the suitable host and infestvascular tissues of susceptible host plant roots. The juveniles typically penetrate near the root tip and modify the respective regions to metabolically active ‘giant cells’, hence establishing their permanently secured feeding sites associated with the surrounding root tissue to siphon plant’s nutrition and other photosynthates (7).Duggal et al., 2017 studied the life cycle and pathogenicity of M. incognita in cultivated capsicum plants. Under screen house conditions, J2 penetration was observed to initiate at root tips on 2nd day with a maximal penetration recorded on 6th day of infection. On 11th day, J2 population started to develop swelling and matured to third juvenile stage (J3) by the end of2 week. The fourth juvenile stage (J4) observed on 23rd day gradually enlarged swollen region eventually giving rise to an adult female after 6 days. M. incognita required 40-45 days to develop and produce J2 juveniles in capsicum plants.

Under polyhouse conditions, J2 penetration started at root tips on 2nd day and maximum penetration was observed on 4th day, J2 started swelling on 8th day (J2 with spike tail) which became J3 on 11th day. There

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was no further development of J3 up to 17th day. On 20th day, J4 stage was detected which started further swelling. After 6 days i.e. on 26th day, female was observed while gravid female was observed on 29th day. Gravid female with eggmasses and J2 in soil were observed on35th day. Same observations were recorded up to 45th days.

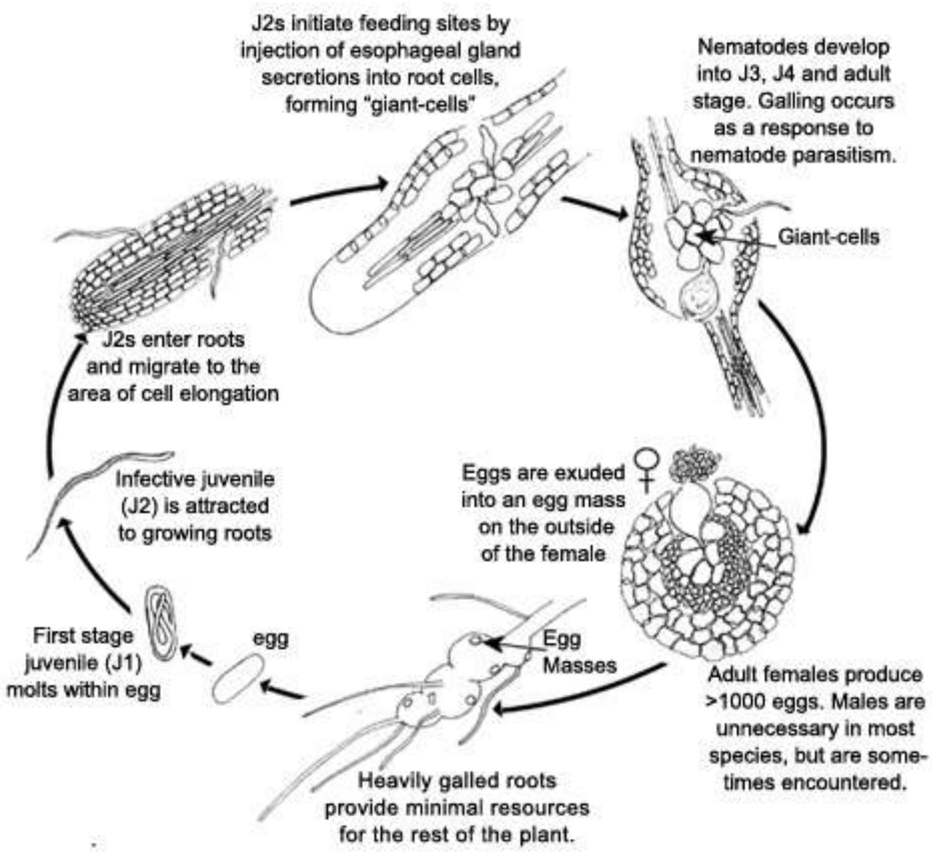

Figure 2: life cycle of M. incognita

Economic Impact

Commented that *Meloidogyne* spp. account for an estimated loss of 157 billion USD annuallyon global scale (8). However, the impact of *Meloidogyne* spp. is believed to be grossly understated since an accurate evaluation is not easy pertaining to insignificant consideration and characterization of emerging species. Particularly in African continent, it is a big challenge to generate reliable estimates of economic losses incurredby root knot nematodes. Therefore, nematode induced overall annual crop losses are likely to be much greater than generally contemplated.

There are several factorsconsidered to be the reason for the limited availability of statistical information on the economic impact of *Meloidogyne* spp. The lack of general awareness of the *Meloidogyne* spp. induced effectson crop production is the first and foremost reason behind the data scarcity and pathogen inadvertence by farmers or agricultural practitioners. Apart from this, the long-term practice of nematicides has led to unrefined evaluation and thereof an underestimated impact of *Meloidogyne* spp. However, alternative strategies employing bio-control agentshave minimized the usage of nematicides, leading to steady resurgence of *Meloidogyne* spp. associated problems. Considering the current scenario, lack of

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information can be accredited to the acute paucity of financial as well as human resources needed to undertake large-scale projects to comprehensively assessthe worldwide situation of *Meloidogyne* spp. (9).

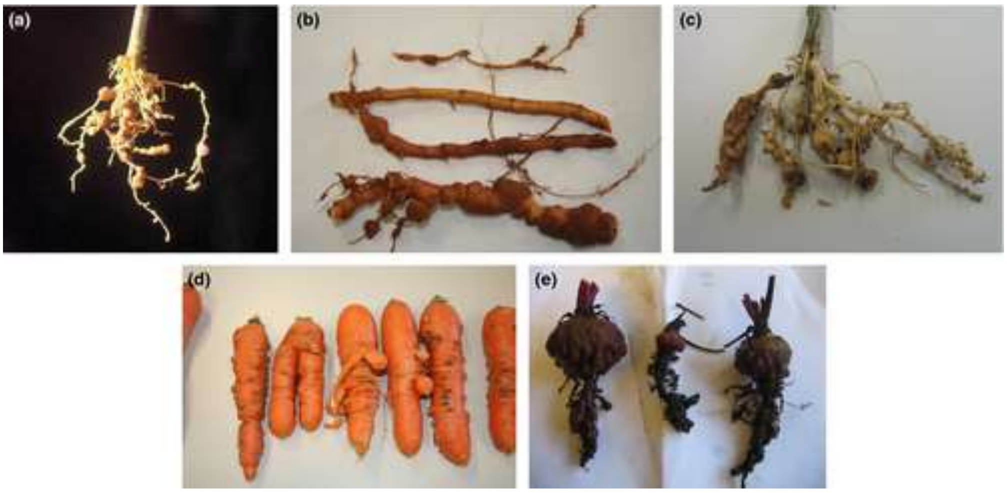

Figure 3: Meloidyne incognita affecting roots of various plants causing galls and other varied symptoms. Figure (a) shows Galls on tomato root infected by M. enterolobii. Figure (b) shows Galls on grenadella roots caused by M. incognita, Figure (c) Galls on cucumber roots caused by M. javanica. Figure (d) Galls and damage symptoms on carrot caused by M. Arenaria and M. incognita. Figure (e) Galls on beetroot caused by M. Javanica and M. incognita. Figure d and e shows the harm caused during coinfection

Although limited data informationregarding the impact of *Meloidogyne* spp. in crop production, a number of evidences have become available which indicate that the severe threat of *Meloidogyne* spp.in agricultural crop production has become the utmost concern across the globe.

The process of nematode infestation leads to impeded uptake of nutrients and water by the host plant resulting in stunted growth and poor crop yield (10). Furthermore, such damage augments the severity of other infections by favouring the opportunistic pathogensinhabiting the soil (11). Considering their broad host range along with a high reproduction rate, the southern RKN, *M incognita* (Kofoid and White) Chitwood, are one of the most damaging nematode species. *M. incognita* possess high propensity towards solanaceous crops, mainly infesting tomato, potato, pepper and African Leafy Vegetables (ALV) (12).

Numerousintegrated strategies have been employed to combat*M. incognita* and other RKNs, including cultural practices such as crop rotation and intercropping, resistant crop cultivars, biocontrol agents and nematicides, (13). In consideration of prejudicial effects of conventional chemical methods on the environmental and human health, usage of many nematicides has been abandoned. Methyl bromide (MeBr), considered as one of most promising chemical agent has been discontinued owing toits ozone-depleting properties(10). The above discussed circumstances necessitate the development of alternative eco-friendly strategies to control these pathogens.

One of such novel approaches would be to unravel and exploit the chemical signalling interplay involved in key stages of host plant-RKN interaction. Precise knowledge of chemical communication mechanisms governing plant-parasite interactions can help in establishing an alternative strategy to control plant-parasitic nematodes.

Development of'push-pull' technology involving a repellent intercrop and an attractive trap plant to control stem borer and striga weed is a dramatic example (14-15). In an effort to control RKNs, one of the

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possible strategies would be to target the potential stage involving chemical mediated host location by second stage juveniles (J2s).

Volatile compounds (VOCs) secreted by the roots of the host plants or the associated Rhizospheric microbes facilitate long-distance attraction of J2s to the vicinity of the plant roots (10), which is assisted by head and tail chemosensory organs of nematodes (10). Although olfactory system is considered to play a fundamental role in locating host plant, there are limited reports on specific olfactory cues involved in the process.Carbon dioxide (CO_2) has been reported to be the prime long distance attractant for many nematodes16), however a recent study suggests its role as response enhancer evidenced by the synergistic action of CO_2 and specific root volatiles towards plant nematodes (17).

The occurrence of a suite of *Meloidogyne* spp. in agricultural regions imposes a dire risk to global crop production contemplating the lack of authentic information available to the farmers regarding species heterogeneity of *Meloidogyne* spp. in the agricultural farms. The challenges associated with the inappropriate knowledge about the actual invasive species and monitoring tactis hampers the discernment of relevant approaches, thereby causing risk of alarming yield losses. In here, coupled with the phase-out of some of the cogent chemical agents (such as methyl bromide) effective against a wide range of *Meloidogyne* spp. and the paucity of potential alternative strategies, the circumstances may dramatically contribute to incidents of food crisis worldwide. Of the invasive *Meloidogynespp.*distributed worldwide,*Meloidogyne fallax* and *Meloidogyne chitwoodi* are designated as quarantine organismsin Europe by EC Directive of 2000/29/EC and EPPO region (18,19,20).*Meloidogyne enterolobii* has also been listedas the quarantine organismacross Europe (EPPO, **2011**) and moreover, this particular specieshas been considered to possessmore the characteristics of an EU-quarantine organism than *Meloidogyne chitwoodi*and*Meloidogyne falla.* Aregional nematode survey conducted by revealed that *Meloidogyne* species escalates the constraints suffered by farmers in tropical countries duringagricultural exports, particularly to the European markets, as *Meloidogyne spp*mediated contamination of the farm productsleads torejection at international markets(20). It is very well recognized that forest cover cushions several countries from adverse ecological as well as climatic conditions such as floods and drought.In this context, resistance-breaking species including *M. enterolobii* are being considered as a significant threat to global forest wealth, eventually affecting water catchment areasandavailability of water in the long term. This event may happen viaexclusive singular modeor in alliance with other highly invasive forest pathogens.

Management Strategies

The ultimate goal of combating a range of *Meloidogyne* spp. existing in the soil is to ensure crop protectionagainst*Meloidogyne*mediatedinfestation as well vulnerability tosecondary infections, thereby recovering maximum crop yield in cost-effective manner (12). However, controlling *Meloidogyne* spp. is quite intricateowing to their endo-parasitic nature, diverse population, broad host range, short life-span, and high reproductive frequency. Measures for economic control of pestsadopted globallycan be categorized broadly as chemical, biological or cultural. These methodsare either employed singly or in combination to attain desired outcomes.Integrated pest management (IPM)approach helps maximising benefits andreducingrisks by restricting pesticide application.

Chemical control methods

The chemical methods available for root-knot nematode management involvethe application of various inorganic formulations, which abolish pathogen by direct killing or by impeding the reproduction of *Meloidogyne* spp. in infested soils. Nematicides are usually regarded as the most effective mode of curbing high levels of *Meloidogyne* spp. in agricultural farms.

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However, certain nematicidal chemicals containing methyl bromide and Aldicarb (Temik) as their active ingredient have been discontinued in various countriesover theconcern of their hazardous environmental as well as health consequences. Other mainstream nematicides for controlling various *Meloidogyne* spp. include fenamiphos, oxamyl, 1, 3 dichloropropene (1, 3-D), dazomet and metam-sodium. Nematicides tend to curtail high populations of various *Meloidogyne* spp. in the soil, however they become in-effective to completely eliminate the very same*Meloidogyne* species, once the symptoms are developedin plant tissue (17).

They can be practiced either as pre-plant nematicides, fumigants or as contact acting nematicides (13). The cultivation practices such as removal of large soil lumps and crop remnants of the previous season along withexcellent soil humidity effectuate the maximum activity of these nematicides . The disadvantages associated with the chemical methods tocounter these *Meloidogyne* spp. include their toxicity towards humans and animals through pesticide residues, adverse impact on environment through the ozone-depletion (such as methyl bromide), and unaffordablepricingforsmall-scale farmers. The researchers have earlier warnedregarding the advent of resistance in plant parasitic nematode species arising due to continued usage of nematicides for the agricultural purpose. As stated by Blouin et al., 1995,the development of resistance can be mainly attributedto the genetic mutations, considering the high evolution rates of phylum Nematoda (18).

Biological control methods

Biological control agents considered as an excellent alternative to chemical methods imply the usage of living organisms either in the form of pure cultures or as mixtures to deter *Meloidogyne* spp. Some biological products,in particular those developed by Pasteuria Inc. and Koppert Biological Systems against certain *Meloidogyne* spp. have manifestedsubstantial effects in the control of these plant parasitic nematodes. These bio-control agents are usually developed from microorganisms such as *Pasteuriapenetrans*, *Pasteuriahartismeri*, *Pochoniachlamydosporia*, *Bacillusfirmus* , *Paecillomyceslilacinus* an *Trichoderma* spp. The mode of action conferring antagonistic effect ofthese microorganisms against nematodes involves their attachment to the nematode cuticle or to the parasitized female eggs, subsequently killing the pathogen (16,17).

In addition, another biological strategy has been reported by Walters, 2009, exemplifyingtomato plants, wherein endophytes such as *Fusarium oxysporum* (FO162) could induce systemic resistance against *Meloidogyne* species(9). The study demonstrated that the colonization of tomato roots by *F. oxysporum* (FO162) promoteaccumulation of root exudates, which possess repelling effect towards *M. incognita* .

Certain nematode-antagonistic practices have also been explored as prospected biological control methods .Soil amendment procedures such as application of organic composts, manures or the extracts from marigold (*Tagetes* spp.) can stimulate nativemicroflora ofthe soil andexertrepressive effect on plant-parasitic nematode populations. *Pseudomonas aeruginosa* prevailingin the decomposing organic matterinhibit nematode population either by competing for an ecological niche and/or a substrate or by releasing metabolic toxins capable of altering nature of root exudates. It is desirable to apply organic matter or bio-fertilizers at frequent rates to have a significant effect on nematode populations in an effort toobtain better results from soil amendment strategies (32). In general, theregular use of organic material not only offers certain economical benefitsbut also amelioratesthe efficiency of antagonistic microorganismsby providing them withnutrients vitalfor their growth and survival.

Cultural control methods

Cultural practices are the primary preventive measures which include sanitization, intercropping, crop rotation and the use of resistant crop cultivars . Many of these practices are routinely performed in various

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parts of the world to reduce the progressive burden of *Meloidogyne* spp. and other phytoparasitic nematode populations. However, the cost and availability of clean soil, clean planting material and sanitization of agricultural equipmentscan sometimes be cumbersome to many small-scale farmers. The limited amount of arable landavailable for agricultural production is a furtherchallenge that escalates the problem of small-scale growersby restricting the practice of crop rotation as a control measure. For instance, crop rotationis not feasible from economic perspective under the situation of financial losses incurred during fallow periods or during establishment of large-scale production of new crops over successive years.

Moreover, the growth challenges associated with the human populace also constrain crop rotation making it virtually impractical in certain regions across the globe. Prior to the use of any culture method, it is important to assessand evaluate the species identityand host range of *Meloidogyne* spp, along the cropping history of the field. A proper understanding of nematode biology, population dynamics and the milieu of the field soilis critical for adopting sustainable resolutionin order toprevent indiscriminate application of nematicides and to minimize management costs. Physical methods such as soil solarisation and heat treatmentcan be coupled with conventional cultural methods for effective control of various *Meloidogyne* spp. . demonstrated the contribution ofphysical methods in nematode management as the of solarisation of nursery soil for 3 weeks was found to effectively reduce egg infectivity .

Resistant cultivars

One of the best and safest approaches to tackle nematodes is to use resistant or tolerant crop varieties.Norshie *et al* ., 2011commented that the rationale of employing resistant cultivars tocombat *Meloidogyne* spp. relies on accurate knowledge ofspecies to target. Several research investigations are underway to develop crops harbouring resistance (R) genes against diversified *Meloidogyne* spp. The commercially cultivable crop varieties expressing resistant genes exemplify tomatoes carrying Mi genes. There are also certain reports identifying resistant genes in wild potato (*Solanum bulbocastunum*). The best characterized RKN-resistant gene*RMc1*in wild potato (*Solanum sect. Petota, solanaceae*), has been reported to confer resistance against some races of *M. Chitwoodi*such as *M. fallax* and *M. hapla* (Gebhardt &Valkonen, 2001; Brown *et al* ., 2006) .Unfortunately, the emergence of resistance-breaking *Meloidogyne* spp. has rendered some of these cropspathogen-susceptible (Janssen *et al* ., **1998**; Brown *et al* ., **2009**; Kiewnick*et al* ., **2009**) . In recent report,Norshie *et al* ., 2011 revealed that certain potatobreeds arepartially resistant towards *M . chitwoodi* mediated infection(19).

Furthermore, the modern biotechnological techniques including expressed sequence tags (ESTs), genome, transcriptome and proteomic sequencesenabled generation of enormous amount of information, and offered opportunity to introduce/manipulate genes encoding protein inhibitors such as chitinases,cytotoxins, collagenases, lectins, and other genes imparting resistance against plant parasitic nematodesinto various plants. Considering the current scenario of technological advancement, it is anticipated that a number of transgenic and/or genome edited crops having resistance to *Meloidogyne* spp.will be developed in the nearfuture (Fuller *et al* ., 2008). Resistant cultivars developed against nematode infectionwill not only curtail the cost of production but also ensure the environmental protectionagainst undesirable residual chemicals associated with nematicides. In order to attainpromising results using of resistant cultivars, it is necessary to carry outauthentic speciesidentification and constant surveillance. Also, it is important to educate agricultural growersregarding thesignificanceof resistance-breaking *Meloidogyne* spp. (e.g. *M. Enterolobii*), particularly in therespective areas of resistance outbreak.Ultimately, the cost and availability of resistant lines will be a substantial factorin determining the accessibilityof benefits to small-scale growers across the world.

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Concluding Remarks

The recent identification of 'emerging' resistance-breaking populationsof *Meloidogyne* spp. globally poses a ponderous challenge to available standard formulation effective against root knot nematode species. Besides the polyphagous nature of these pathogens,lack of significant and up-to-date data regarding *Meloidogyne* spp. occurring in different parts of the continent present ahuge risk food security in the upcoming years.

To efficiently address the emerging as well as prevailing *Meloidogyne* spp., it is imperative to harness the available resources adequately,in order tointensify the research intended toassess and comprehend the species identity, genetic heterogeneity, population structure, mode of parasitic action and the relevance of these elements to the overall threat posed by these phytoparasitic pathogens .These considerations necessitate theadoption of modernrevolutionary technology in conjunction with conventionalmethods. It is of paramount importanceto use biological, cultural and chemical methodsof nematode management in accordance with regulatory guidelines of integrated pest management (IPM) practices considering the human health and environment safety. Therefore,this should be preceded by a comprehensiveinspection of farms following an accurate diagnosis of *Meloidogyne* spp. and the co-habiting microflora. Molecular-based species identification methods should be used alongwith classical methods for reliableand rapid identification (Oliveira *et al*, 2011).Thecoordinated functioning of these strategies will lead to gradual management of *Meloidogyne* spp., and other root nematodes, thereby diminishing the levels of associated damage,eventually benefiting growers by reducedthe production costs. In view of the phasing out of various effective nematicidal products, the environment friendly potential alternative should be explored. In the meantime,more robust diagnostic methodsshould be endorsed for accurate identification to avoid further spread of the highly invasive resistance-breaking *Meloidogyne* spp. together with sustainable application of management strategies.

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