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Mechanistic insights toward identification and interaction of plant parasitic nematodes: A review

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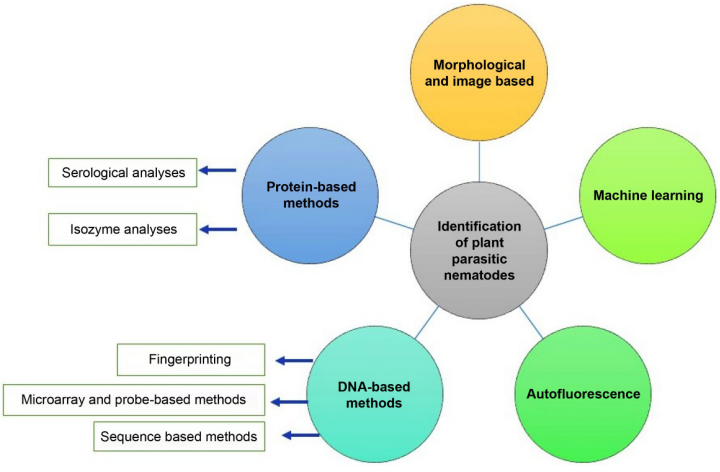
ABSTRACT

- Nematode identification serves as an important parameter to study their behaviour, importance and pathogenicity.
- Application of classical morphometric based identification methods prove to be lacking due to insufficient knowledge on morphological variations among closely related taxa. Molecular approaches such as DNA and protein-based information, microarray, probing, sequence-based methods and others have been used to supplement morphology-based methods for nematode identification.
- Ascarosides and certain protein-based nematode-associated molecular patterns (NAMPs), can be perceived by the host plants, and can initiate a signalling cascade.
- This review primarily emphasizes on an updated account of different classical and modern tools used for the identification of nematodes. Besides we also summarize the mechanism of some important signalling pathways which are involved in the different plant nematode interactions.



Nematodes constitute most diverse and least studied group of soil inhabiting invertebrates. They are ecologically and physiologically important, however, wide range of nematodes show harmful impact on the individuals that live within their vicinity. Plant parasitic nematodes (PPNs) are transparent, pseudocoelomate, free living or parasitic microorganisms. PPNs lack morphometric identification methods due to insufficient knowledge on morphological variations among closely related taxa. As such, molecular approaches such as DNA and protein-based information, microarray, probing, sequence-based methods and others have been used to supplement morphology-based methods for their identification. To invade the defense response of different plant species, parasitic nematodes have evolved different molecular strategies. Ascarosides and certain protein-based nematode-associated molecular patterns (NAMPs), can be perceived by the host plants, and can initiate a signaling cascade. To overcome the host confrontation and develop certain nematode feeding sites, some members can inject effectors into the cells of susceptible hosts to reprogram the basal resistance signaling. This review primarily emphasizes on an updated account of different classical and modern tools used for the identification of PPNs. Besides we also summarize the mechanism of some important signaling pathways which are involved in the different plant nematode interactions.

Keywords nematode identification, plant nematode interaction, DNA fingerprinting, nematode-associated molecular patterns, signaling pathways

1 Introduction

Nematodes constitute the most diverse, dynamic, ecologically and physiologically important group of lower invertebrates (Murfin et al., 2012). They are multicellular, pseudocoelomate animals with tapering body ends that are translucent, bilaterally symmetric and unsegmented (Murfin et al., 2012). Due to the simple body structure and wider morphological plasticity, nematodes have adapted to every biological niche and environment (Yeates, 1993). Nematodes are

abundant in all soil types and sediments of rivers, lakes, and oceans, as well as parasites on plants and animals (Zeppilli et al., 2018). They differ widely in their feeding habitats and are classified as phytophagous, bacterivores, fungivores, predatory, and omnivores (Yeates, 1993). These feeding method aids in the decomposition and recycling of minerals and other nutrients from their hosts (fungi, bacteria, and other substrates), which are then returned to the soil and made available to plants (Gebremikael et al., 2016). Correct identification of plant parasitic nematodes is of paramount significance for understanding their diversity and to design effective protocols for different management strategies. Traditional morphology-based identification parameters and other physical characters prove inadequate due to lack of clear variation among closely related taxa (Blaxter et al., 2011). Protein- and DNA-based methods have been employed to circumvent the limitations associated with morphology-based classification of nematodes (Blaxter et al., 2011). Nematodes facilitate their interactions with plant species by bringing certain morphological and genetic changes within themselves.

In order to provide better insights into the diversity, identification and plant nematode interactions, present review is designed to gather the available information on:

(i) the diversity of nematodes on the basis of their feeding habits;

(ii) traditional and molecular based approaches for identification of plant parasitic nematodes;

(iii) strategies adopted by PPNs to facilitate their interactions with plant species;

(iv) signaling pathways of plant nematode interactions.

The selection of relevant literature was made through electronic search using keywords such as nematodes, plant parasitic nematodes, strategies for nematode identification and interaction in different scientific databases such as google scholar, science direct, research gate, jstor, pubmed and others.

2 Plant parasitic nematodes and their dissemination

Despite being highly diverse, nematodes are among the least studied organisms with less than 0.01% of their species described (Abad et al., 2008). Among the 26 000 species of nematodes that have been identified so far, over 4100 are plant-parasitic in nature (Jones et al., 2013). Plant parasitic nematodes are transparent, microscopic organisms that share both terrestrial and aquatic habitats and can be either epiphytic or endophytic in nature. They infest the plant body, especially the roots, by distinctive feeding apparatus that consists of needles-like stylets. These penetrate host plant cells and then suck the contents (Poveda et al., 2020). Plant parasitic nematodes (PPNs), such as the root-knot nematode (RKN) and the cyst nematode, are projected to cost the agriculture industry more than US$157 billion each year (Abad et al., 2008). Globally, PPNs are reported to cause the annual agricultural damage estimated to the cost of 173 billion dollars with over 13 billion loss in the United States (Elling, 2013). These parasitic nematodes not only inflict direct damage to plant roots, but they can also make other phytopathogens, such as fungus, bacteria, and viruses, easier to infect (Poveda et al., 2020). Data pertaining to some of the important crops damaged by PPNs across the globe is provided in Table 1.

The feeding method of plant parasitic nematodes harm the root system of the plant and diminishes its ability to absorb water and nutrients. Root mass loss, root structure distortion, and/or root expansion are all typical nematode damage symptoms (Lambert and Bekal, 2002; Basyoni and Rizk, 2016). Nematode damage to the plant's root system also allows other plant infections to infiltrate the root. Shoot-feeding nematodes cause direct damage to plant tissues, and results in a diminished vigor, deformation of plant parts, and death of infected tissues (Lambert and Bekal, 2002; Basyoni and Rizk, 2016). Nematodes are removed from soil by floating

Table 1 Important crop species affected by plant parasitic nematodes across the globe.

Species No.	Crop	Countries	References
1	*Arabidopsis thaliana*	Belgium, France, Germany, Japan,	Mesa-Valle et al., 2020
2	*Daucus carota*	Canada, France, South Africa	Ghareeb et al., 2020
3	*Fragaria ananasa*	Egypt, Germany, Spain, Turkey	Sani and Haruna, 2020
4	*Glycine max*	Brazil, South Africa, United States	Mesa-Valle et al., 2020
5	*Ipomea batatas*	East Africa, India, United States, West Africa	Mburu et al., 2020
6	*Oryza sativa*	South Africa, United States, Vietnam	Nzogela, 2020
7	*Solanum melongena*	Egypt	Abd-Elgawad, 2021
8	*Solanum tuberosum*	Canada, Netherlands, UK	Mesa-Valle et al., 2020
9	*Triticum aestivum*	Australia, China, India, Pakistan	Akram et al., 2020
10	*Solanum lycopersicum*	China, Egypt, India, Italy, South Africa, Spain	Mesa-Valle et al., 2020

them in water to remove heavy soil particles, then trapping them on fine-pore sieves (Lambert and Bekal, 2002; Basyoni and Rizk, 2016). Motile nematode-infected plant tissues can be incubated in a Baermann funnel or moist chambers to harvest worms that will depart the tissues. The only approach to diagnose nematode disease accurately is to collect soil and plant material from suspected sites and extract nematodes for testing (Lambert and Bekal, 2002; Basyoni and Rizk, 2016).

While plant parasitic nematodes are mobile, the majority of them only traverse several meters through the soil in their lifetime. They are dispersed across vast distances by the movement of water during floods and irrigation (Lambert and Bekal, 2002; Basyoni and Rizk, 2016). The ability of nematodes to produce environmentally resistant stages further facilitates their spread, as dried nematodes can be carried by the wind or plant detritus across long distances (Basyoni and Rizk, 2016).

3 Classification of plant parasitic nematodes

Depending upon their feeding habits, plant parasitic nematodes are divided into following categories.

3.1 Ectoparasites

These nematodes feed from the cells with their stylet while remaining outside the plant in the first feeding phase known as ectoparasitic. Ectoparasite nematodes can have exceptionally lengthy stylets, which help them feed on nutrient-rich plant cells (Lambert and Bekal, 2002; Basyoni and Rizk, 2016). Some of these nematodes cause the plant to develop larger cells from which the nematodes feed for a longer durations. Nematodes that adopt this feeding method can cause severe root system stunting by forming terminal galls in the roots (Lambert and Bekal, 2002; Basyoni and Rizk, 2016). Nematodes that are semi-endoparasitic might poetically enter the plant and feed at various points during their life cycle (Basyoni and Rizk, 2016). The nematode's head usually enters the root, allowing the nematode to establish a permanent feeding cell. Once they enter the endoparasitic phase of their life cycle, these nematodes enlarge and stop moving (Lambert and Bekal, 2002; Basyoni and Rizk, 2016).

3.2 Migratory endoparasites

Endoparasitic nematodes that enter into root tissues spend much of their time-consuming plant cells (Lee, 2002). Because of their movement and feeding, these nematodes induce extensive plant tissue necrosis. When feeding from the plant they simply suck out the cytoplasm of the plant cell using their stylet, killing the plant cell and moving ahead of the lesion, they do not create any long-term feeding cells (Lee, 2002). The nematode hatches from the egg as a second-stage juvenile and begins feeding on the plant in a typical life cycle (Lee, 2002). The nematodes typically eat, molt, and reproduce within plant tissue. All motile stages are capable of feeding on the plant and moving into the soil in search of fresh roots to infect (Zunnke, 1991).

3.3 Sedentary endoparasites

The most dangerous nematodes on the globe are sedentary endoparasitic worms. The two main worms in this group (*Meloidogyne*) are the cyst nematodes (*Heterodera* and *Globodera*) and the root-knot nematodes (Maggenti, 1981). During their early stages of growth, these nematodes are entirely lodged in the root, but later on, the cyst nematodes protrude from the root (Maggenti, 1981). These nematodes inject secretions into plant cells to encourage the development of enormous feeder cells, which they use to consume the nutrition without causing harm to the plant over their whole life cycle (Lee, 2002). In the absence of cell division, root-knot nematode feeding cells (gaint cells) are formed by repetitive nuclear division. While as, cyst nematode feeding cells are formed by the fusion of adjoining cell walls. Once the feeding cells are developed, the juveniles feed, grow, and molt three times before reaching adulthood (Lee, 2002). These nematodes block the plant's vascular tissue with enormous feeding cells, making it vulnerable to water stress.

3.4 Stem and bulb nematodes

Stem and bulb nematodes (*Ditylenchus* spp.) are nematodes that attack the shoot and root system of plants, respectively (Lee, 2002). They travel up the plant's stem using water films, making them more harmful under wet environments. The stem bulb nematode's infectious stage is the fourth stage juvenile. This stage usually enters emerging plant tissues below ground, although it can also climb up stems in a film of water and enter shoots through buds, petioles, or stomata (Lee, 2002).

3.5 Foliar nematodes

Adult nematodes move to the leaves of their host plant by water films on the stems and penetrate the leaves through natural openings (stomata) (Maggenti, 1981). The nematode migrates to the leaves, where it feeds destructively, molts, and lay eggs. The nematode's feeding activity causes interveinal chlorosis and necrosis of the leaf, which eventually kills it (Maggenti, 1981).

3.6 Seed gall nematodes

The earliest plant-parasitic nematodes to be described were seed gall nematodes (*Anguina* spp.) (Lee, 2002). These nematodes enter plant leaves at juvenile stage 2 (J2) and feed as ectoparasites at the tips, causing deformation of the leaves. J2 penetrates the floral primordium and starts to feed on the developing seed. Once within the seed, the worm moults, feeds, and eventually kills the seed, resulting in the blackened cockle (seed gall) (Maggenti, 1981).

4 Identification of plant parasitic nematodes

Nematodes, are the most varied and numerous metazoans to be found in soil and aquatic ecosystems (Abad et al., 2008). Traditionally, identification of nematodes is based on traits like physical size, the shape of the sexual organs, the shape of the lips, and additional physical characteristics, such as tail pieces. This classification, based on morphology may not be sufficient. Due to the absence of distinct differences between closely related taxa and the requirement for highly qualified taxonomists (De-Oliveira, 2011). Morphology-based identification can be challenging, particularly when there are many samples involved. Protein- and DNA-based techniques have been used to complement or get around the restrictions with nematode taxonomy based on morphology. It is crucial to comprehend the importance of accurate nematode identification and, more specifically, how we identify a nematode species (Adams, 2001) (Fig. 1). Here, we explore existing techniques and their ancestors in nematode taxonomy methods and recommend future developments.

4.1 Morphological and image-based analysis

The traditional method of nematode identification is one of the more affordable identification techniques that rely on microscopic image analysis of morphological and anatomical variations (De Oliveira et al., 2011). Nematodes that share small morphological and morphometric characteristics, such as body length, the existence and shape of a stylet, tail, etc., are challenging to differentiate morphologically. Adult female perineal patterns i.e., the posterior region, which includes the perineum, vulva-anus area, tail terminal, phasmids, lateral lines, and nearby cuticular striae were previously used to identify root-knot nematodes (RKN; *Meloidogyne* spp.) (Karssen and Van-Aelst, 2001; Eisenback and Hunt, 2009). These group of characteristics were first suggested to discriminate between *Meloidogyne incognita, M. javanica, M. arenaria,* and *M. hapla* (Chitwood, 1949). RKN species are currently identified by combining morphological and molecular properties (Da Cunha et al., 2018). *Heterodera* species and *Globodera* species are two cyst nematodes that are among the major globally distributed plant parasitic pathogenic nematodes (Turner and Subbotin, 2006). *Globodera* and *Heterodera* can be separated from one another based on the appearance of their cysts: the former is shaped like a lemon. The latter is rounded (Cook and Noel, 2002). *Heterodera* species are distinguished by a

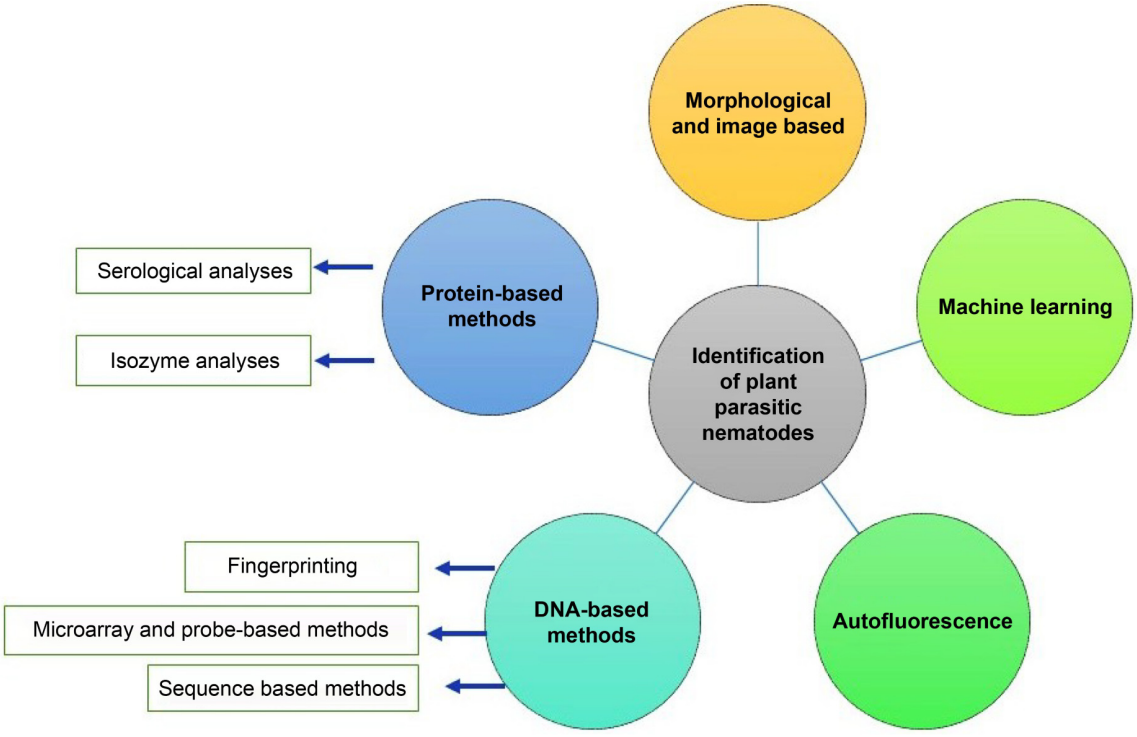


Fig. 1 Different approaches for identification of plant parasitic nematodes

limited number of morphological characteristics including the vaginal (Green 1975), lip (Stone, 1977), cone top (Mathews, 1970), and vulval cone (Mulvey, 1972), components. The form of cysts and second stage juveniles is the primary basis for taxonomic differentiation within the genus *Globodera* (Stone, 1983).

4.2 Machine learning

Artificial intelligence (AI), also known as deep learning or machine learning, has made it possible to identify and quantify nematodes using picture analysis. The method is particularly well suited for processing vast quantities of samples as well as finding rare things and tiny items with intricate backgrounds, like nematode eggs. Multiple phases of machine learning are involved in the automated detection of phenotypes. A significant number of images (of nematodes, their eggs, or cysts) are first taken and independently annotated (recognized) by a team of experts in order to reduce subjectivity. These are then used to create an algorithm, while rejecting (masking) the background noise, layer-wise extracts (captures) and essential details from the image structure are recorded. The popularity trend of the input, a network model with supervised learning is then used to rebuild an image. This approach was used by Akintayo et al. (2018), to account for differences in background noise across data from diverse sources, a unique end-to-end Convolutional Selective Autoencoder (CSAE) was developed to recognize soybean cyst nematode (SCN) eggs in various backgrounds. The authors trained the CSAE to recognize SCN eggs using multiple annotated picture patches (segments) that were smaller than the entire image. The existence of an egg in a given patch was then determined by combining data from several overlapping local patches to recreate an entire image.

While deep learning approaches are ideal for identifying discriminative nematode traits and managing big specimens, they have emerged as an option for expediting the identification process of nematodes. Several deep learning categorization methods (Keras and TensorFlow) are widely accessible and simple to use. By giving enough data, the deep learning approaches have also demonstrated their ability to accurately identify nematode induced illnesses, such as those that affect leaves (Li et al., 2021). Transfer learning was used to create Convolutional Neural Networks (CNN) for the categorization of images of many crop leaf diseases. This proposed study classified grape and tomato leaf diseases with 98.40% and 95.71% accuracy, respectively (Paymode and Malode, 2022).

4.3 Autofluorescence

The natural autofluorescence of microorganisms can be utilized to complement conventional light microscopy. The emission and excitation spectra of the bacterial genera *Lactobacillus* and *Saccharomyces* have been found to differ (Bhatta et al., 2006). Qazi et al. (2020), elaborated on this and showed that when light at various wavelengths ranging from white light to infrared, the eggs of various helminths developed distinctive florescence. Additionally, they demonstrated that variations in florescence lifetime values (florescence intensity decay) were indicative of the two species under consideration, *Ascaris lumbricoides* and *A. suum.* The spectroscopic properties and lifespan value evaluations of nematode autofluorescence, are promising techniques for categorizing these creatures (Qazi et al., 2020).

4.4 DNA-based methods

4.4.1 Fingerprint based method

There are many DNA-based methods for nematode identification (Semblat et al., 1998; Randig et al., 2001; Abd Elazim et al., 2019). These can be roughly divided into approaches based on fingerprints and nucleotides. Analysis of Amplified Fingerprints (AFA), the outcome of the PCR amplification dictates whether or not to perform the species-specific primers, random amplification of polymorphic DNA (RAPD), amplification fragment length polymorphism (AFLP), and restriction fragment length polymorphism (RFLP). All fingerprint-based approaches require PCR, with the exception of RFLP, where it may not be necessary, using an electrophoresis. The final DNA fingerprint, or the resolution pattern of the DNA pieces, is employed for nematode taxonomic identification and/or phylogenetic analysis. Nucleotide-based techniques, on the other hand, entail PCR amplification, particular probe hybridizations, and DNA sequencing of an area (or regions) that is then employed in phylogenetic analysis. Although nematode sequences have significantly improved, it is noteworthy that impacted our comprehension of the links between taxa in terms of evolution (Blaxter et al., 1998). RFLP analysis can make use of the fingerprints created by genomic DNA (gDNA) that has been digested with one or more endonucleases. As an alternative, PCR-RFLPs can be used to produce fingerprints (Smith et al., 2015; Handoo et al., 2020). gDNA-RFLPs are frequently complicated, however they may reveal due to the size of the gDNA template, more polymorphisms, unlike PCR-RFLPs, gDNA-RFLPs do not require prior knowledge of the sequence data. However, it is important to let restricted digestions complete because partially digested substances can cause problems. By selectively amplifying fewer restriction products and creating less complicated fingerprints, the AFLP approach outperforms gDNA-RFLP (Correa et al., 2013; Smith et al., 2015; Abd Elazim et al., 2019; Handoo et al., 2020).

Two restriction enzymes are used to degrade gDNA, resulting in sticky ends to which adaptors are attached. Among these the adaptor ligation primer sets that identify the adaptor sequences are then used to selectively amplify the fragment, the restriction sites, one to three nucleotides are inside, with the sticky ends. The same as gDNA-RFLPs, AFLPs do completion of restriction digestions is essential, and prior knowledge of sequence information is not necessary for fingerprints that are repeatable. In RAPD, gDNA fragments are amplified by PCR using short (often 10 bp) primers of arbitrary sequences (Abd Elazim 2019; Naz et al., 2013). The primers attach to various DNA locations, and amplification happens when two primers bind to the DNA's opposing strands with their 3′ ends facing one another at a distance that the polymerase is able to cover. As a result, fragments of different sizes will generate, the size of the larger fragments will depend on how well the polymerase is working. That is why it is crucial to use a big, undamaged gDNA template. Due to RAPDs being performed at lower temperatures that make primer annealing less stringent and more reproducible, especially between laboratories also has a drawback.

4.4.2 Microarray and probe-based methods

A DNA microarray is a collection of precisely positioned DNA fragments that are placed in a pattern on a flat surface, such as a glass slide. SCARs, or sequence-characterized amplified regions, can be used to create these DNA fragments, which can be used as nematode identification probes, test samples are designed to hybridize with fluorescently labeled PCR products or gDNA diagnostics with a high output. An array scanner is used to collect information from hybridization slides at the wavelengths at which the fluorescent dyes utilized emitted light. François et al. (2006), investigated whether *M. chitwoodi* specific oligonucleotides could be used as probes in DNA microarray techniques for nematode identification. The probes were created using the intrinsic nucleotide sequences of the SCAR and satellite DNA fragments were amplified by primer sets in *M. chitwoodi* but not in *M. arenaria*, *M. hapla, M. fallax*, and *M. javanica*. According to the specificity of the primer sets used in conventional PCRs, regardless of the geographic location, *M. chitwoodi* was found by both SCAR and satellite DNA-based probes, where the nematode came from. However, cross-hybridization with *M. chitwoodi* targets was seen when satellite DNA-based probes developed from the pMfFd satellite DNA family of *M. fallax*, a closely related species, were utilized. This demonstrates the significance of appropriate probe selection

4.4.3 Sequence-based methods

Analysis of nucleotide sequence data from specific mitochondrial DNA (mtDNA), nuclear DNA (nDNA), or genome segments can be done using sequence-based approaches (Van Megen et al., 2009). The mitochondrial, rDNA and cytochrome c oxidase subunit I (COX1) genes having variable areas surrounded by conserved ones are commonly used in diagnosis (Van Megen et al., 2009; Derycke et al., 2010; Hadziavdic et al., 2014). The greater degree of the variable region's sequence variety makes COX1 more advantageous for resolution at lower taxonomic levels. Groups of levels like species and subspecies, whereas the higher level of sequence conservation in the flanking regions, enables development of "universal" primers (Hadziavdic et al., 2014). The rDNA has tandem repeats of both variable non-coding (ITS and ETS, the external-transcribed region) and conserved coding (28S, 18S, and 5.8S subunits) parts, with intergenic spacers separating the repeating units (Long and Dawid, 1980). The 5.8S coding region in the rDNA cistron divides the internal transcribed spacer (ITS) into ITS1 and ITS2 (Long and Dawid, 1980). These regions include distinctive nucleotide sequences that can be utilized to identify each species, scientists have proposed using a number of rDNA sections as DNA barcodes in a variety of organisms. With ITS for fungi (Schoch et al., 2012), 16S for bacteria (Hugenholtz et al., 1998), and 18S for worms (Floyd et al., 2002; Blaxter et al., 2011), COX1 area of the barcode is used for animals (Hebert et al., 2003). Because of this, the ITS is valuable in the molecular systematics for finding relatedness among closely related nematodes (Powers et al., 1997; Bu et al., 2013).

4.5 Protein-based methods

4.5.1 Isozyme analyses

One of the earliest non-morphology-based techniques for nematode identification is finding enzyme phenotypes. This method entails extracting soluble proteins from entire nematodes in buffer solutions, resolving the extracts using starch or polyacrylamide gel electrophoresis, and then labeling for certain enzymes. The migratory patterns of isozymes are essential to this electrophoretic method, also known as Multi-locus Enzyme Electrophoresis (MEE), because of variances in electrical charge, molecular weight, and conformation brought on by slight variations in amino acid compositions. Although glutamate-oxaloacetate transaminase, superoxide dismutase, and malate dehydrogenase have also been used to varying degrees (Esbenshade and Triantaphyllou, 1990). Most frequently utilized enzymes were esterases (Esbenshade and Triantaphyllou, 1990). This approach provided insight into the evolutionary relationships, particularly those between the main species of the genus *Meloidogyne*.

4.5.2 Two-dimensional gel analyses

The taxonomy of nematodes has been studied using two-dimensional gel electrophoresis (2-DGE). Using isoelectric focusing, the method enables the charge-based resolution of complicated protein mixtures in one dimension, followed by the mass-based resolution in the dimension opposite the first. The similarities and differences between isolates are then determined by comparing their resolution patterns; the presence or absence of these similarities and differences can subsequently be determined for phenetic and/or cladistic analyses of the resulting data matrix. For 18 root-knot nematodes from four different species' proteome discrepancies were shown by Navas et al. (2002). They observed that some of these differences were species-specific while others highlighted links between various species across different genus. As it relates to nematode taxonomy, the approach has a number of benefits and drawbacks. The ability to draw conclusions about the species under consideration's evolutionary history is one advantage of 2-DGE. Mass spectrometry can also be used to isolate and study species-specific polypeptides, allowing conclusions to be drawn about the encoding genes. The procedure employed and the amount of samples examined affects the number of polypeptides resolved and the polymorphism seen.

4.5.3 Serological analyses

Numerous researchers have looked at the use of poly- and mono-clonal antibodies (mAbs) since Bird (1964), first proposed manufacturing antisera against worms, with variable degrees of success (Schots et al., 1989). For instance, Lee (2002) reported that the Ouchterlony double diffusion assay did not reveal any cross-reactivity when antiserum raised against *M. incognita* was combined with antigens from *M. hapla,* a different species within the same genera. It was pointed out, nonetheless, that the apparent selectivity might be caused by the assay's use of a relatively limited number of nematodes. Later, Misaghi et al. (1974), also supported the lack of specificity in the reactivity of antisera from *Meloidogyne* spp., *Heterodera*, and *Globodera* species of cyst nematodes showed similar mixed findings (Schots et al., 1989). It is common for polyclonal antibodies made against fully macerated nematodes, as well as the metabolites and accompanying microbiota, to show cross-reactivity.

5 Plant-nematode interactions

Plant-nematode interactions usually begin in the soil, where PPNs use a variety of detecting techniques to identify various host signals, including chemo sensing, mechanosensing, thermosensing, redox potential sensing, humidity sensing, osmotic sensing, and electrosensing (Perry, 1996). PPNs are assumed to have similar neuroanatomy and neurobiology to *Caenorhabditis elegans*, despite the fact that these processes are poorly understood in PPNs (Perry, 1996). Chemosensation in PPNs is highly correlated with the host range of the organisms; PPNs with limited host ranges, such as the potato cyst nematodes (*Globodera pallida* and *G. rostochiensis*) and the soybean cyst nematode (*Heterodera glycines*) are thought to have sensitive chemosensation because they react strongly to particular chemicals in the root exudates by hatching and moving toward the chemical (Rasmann et al., 2012). PPNs with a broad host range, such as the *Meloidogyne* spp. root-knot nematodes, rely on non-specific abiotic cues, such as low pH and CO_2 gradients (Wang and Fiers, 2010). The chemoreceptors in the anterior receptors, the amphids, and the posterior receptors, the phasmids, assess these signals simultaneously to identify the orientation of the PPN (Rasmann et al., 2012). In the event of a positive response, the PPN positions itself toward the cue and starts to migrate toward the source. The PPN will slow down its metabolism through diapause (delaying egg hatching) or quiescence (e.g., the pre-parasitic juvenile worm stops moving unless prompted) if it is unable to find a compatible cue during its pre-parasitic life cycle (i.e., the egg and juvenile phases) (Sommerville and Davey, 2002; Evans and Perry, 2009). Aerial nematodes continue their upward journey to the stem whereas root nematodes either enter the root tissue or remain outside the root at the root interface. The PPNs then begin to eat and develop before beginning to multiply either inside or outside the host (Fig. 2).

Root nematodes dwell primarily on the root, while aerial nematodes feed on the bulb, stem, and leaves (Tytgat, et al.,

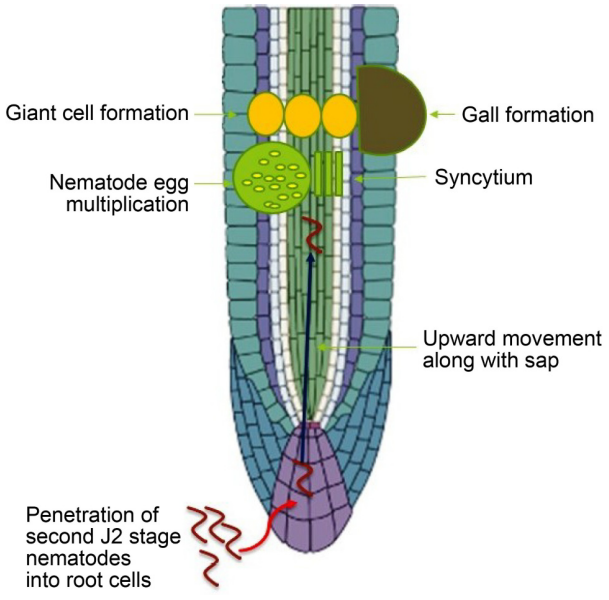


Fig. 2 Invasion, penetration, hatching and multiplication of plant parasitic nematode inside the plant roots.

2000; Lambert and Bekal, 2002). In addition to migratory or stationary feeding, endoparasitic or ectoparasitic feeding and reproduction are two of the parasitic strategies used by root PPNs (Wyss and Grundler, 1992; Tytgat et al., 2000). The most dangerous PPNs are the root knot nematodes (*Meloidogyne* species), cyst nematodes (*Globodera* and *Heterodera* species), migratory endoparasites (*Pratylenchus* species), and burrowing nematodes (*Radopholus* species) (Jones et al., 2013). The success of root sedentary endoparasites can be attributed to their intricate exploitation of numerous plant response pathways to alter plant defense responses and induce long-term feeding sites, as well as the challenge of diagnosing infections because of symptoms that are only visible below ground (Lambert and Bekal, 2002). Overexpression of certain genes, such as proteinase inhibitors, or expression of RNAi constructs targeting nematode-specific genes in transgenic plants have been used to deliver nematode resistance (Fuller et al., 2008). In addition, multiple parasitic nematode resistance genes have been cloned, many of which are similar to genes that give resistance to other infections. The *Mi*, *Hiro A*, *Gpa2*, and *Gro1-4* genes, for example, belong to the NBS-LRR gene family and provide resistance to a variety of endoparasitic nematodes (Williamson and Kumar, 2006). Other resistance genes, such as soybean's *Rhg1* and *Rhg4*, encode proteins with extracellular LRR domains, while others, such as Hsp1-pro1, are unrelated to any other known genes (Williamson and Kumar, 2006). It has proved challenging so far to transfer these resistance genes to heterologous species.

Nematodes can track their hosts over long distances and that host roots generate some helpful substances that work as stimulants for worms (Steiner,1925). Besides, amphids served as active sensory organs for nematodes, allowing them to respond to stimuli created by plant roots (Steiner, 1925). Viglierchio (1961) found that there is no conclusive relationship between host efficacy and capacity to get orientated toward PPNs after completing tests on *Heterodera schachtii*, which shown low attractions toward tomato plants and oat plants (var. Kanota). Nonetheless, *Meloidogyne hapla* was discovered to be attracted to oat roots by stimulatory chemicals released by the roots, which aid in nematode proliferation near host plants (Viglierchio, 1961). Klingler (1965) expanded on these findings, claiming that chemical factors like metabolites and carbon dioxide are primarily responsible for nematode attraction to host roots. As a result, nematodes migrate in accordance with the orientation gradient, and chemoreception via chemoreceptors (Steiner, 1925; Klingler, 1965).

5.1 Role of miRNA in plant-nematode interactions

It is generally recognized that miRNA plays a crucial role in plant-nematode interactions (Hewezi and Baum, 2015). They attach to certain mRNA sections, modulating the levels of gene expression resulting in mRNA degradation, translational repression, and transcriptional stuttering (Borges and Martienssen, 2015). Dicer proteins synthesize non-coding RNA, and miRNAs which are nearly 22 nucleotides long (Reinhart et al., 2002). Promoters and RNA polymerase II transcribe the MIR genes, producing precursor miRNA inside of the nucleus (Lee et al., 2004). In the cytoplasm, the precursors take the shape of looping hairpin-like structures that are then broken down by DCL proteins to release miRNA duplexes (Bartel, 2004). The duplex is subsequently incorporated into the RNA-induced silencing complex (RISC), where it suppresses translation or argonaute- mediated mRNA production (AG01). In the regulation of nematode parasitism gene expression, miRNA is crucial (Cabrera et al., 2015). For example, in *Heteroderaschachtii*-infested *Arabidopsis*, differentially regulated gene miRNA families were investigated, revealing their critical function in plant-nematode relationship (Hewezi et al., 2008). Furthermore, downregulation of miRNA was discovered during the early stages of the *M. javanica-Arabidopsis* association (Cabrera et al., 2015). The transcripts that are downregulated during nematode infection are known as miRNA targets. As a result of interactions between plants and nematodes, miR396 regulates growth regulation factors, miR171 regulates scarecrow-like transcripts, miR156 regulates promoter binding protein transcripts, miR159 regulates myeloblastoma transcripts, miR166 regulates homeobox, miR319 regulates Teosinte Cycloidea proliferating (TCP) factors, and miR390/TAS3 regulate (Cabrera et al., 2015). Furthermore, it has been demonstrated that miR396 regulates growth regulation and syncytium formation during nematode parasitism, which also regulates various defense systems in plants (Hewezi et al., 2012).

Auxin modulation during nematode infection has been reported to be regulated by miR319-TCP and miR390-TAS3 in *Arabidopsis* (Zhao et al., 2015; Cabrera et al., 2015). Nonetheless, mutant plants with inhibited miRNA have been found to be less susceptible to nematodes, indicating that they play a function in the establishment of feeding sites (Medina et al., 2017). The fundamental processes by which miRNA contributes to transcriptome programming for syncytium and giant cell development (Siddique and Grundler, 2018). By expressing its transcript MYB83, miR858, for example, plays a critical role in the formation of syncytia. When miR858 is expressed constitutively, susceptibility is decreased, and when miR858 is decreased, susceptibility is raised. Overexpression of MYB83, which miR858 is unable to cleave, increases susceptibility. It is important to note that miR858-MYB83 regulation has a more significant role in nematode parasitism (Piya et al., 2017). As a result of all of these factors, the host miRNA pathway appears to be a promising target for nematodes in terms of

influencing syncytium gene expression on a larger scale. However, the precise mechanism by which they influence the host miRNA biosynthesis pathway is unknown. Different effector proteins obstruct a miRNA pathway, which in turn regulates the expression of miRNA genes. Plants have a defense mechanism called host-mediated gene silencing, which employs short RNAs to parasitize genes by suppressing their expression levels (Weiberg and Jin, 2015). miRNA may play a role in host gene expression alterations during plant-nematode interactions.

5.2 Role of TLRs in plant-nematode interaction

Because nematodes are obligatory parasites on roots, they can infiltrate plant host cells and cause tissue damage, triggering the host's basal defense mechanisms. Until now, plant-nematode relationships have primarily focused on effector-triggered immunity, with a few basal defense responses (Holbein et al., 2016). Toll-like receptors, or TLRs, are crucial elements of innate immunity. These membrane proteins identify illnesses, parasites, and other living things. TLRs, on the other hand, are thought to have a little role in infection detection and resistance. TLRs are well-studied in humans and insects, but little is known about their involvement in nematode immunity. TLR pathway has been examined in *C. elegans*, a soil nematode, with TLR, TOL-1 playing a key role. In *C. elegans*, three putative TLR signaling pathway components, PIK-1, IKB-1, and TRF-1, have been identified (Pujol et al., 2001). It alters the behavior of *C. elegans* and modulates neural responses, as well as growth resistance to various pathogens. It sends out a CO_2 signal, which is used to understand their defensive responses (Brandt and Ringstad, 2015). TLR recognition is important for mounting immune/defense responses, and Rel-like transcripts govern this. Heat shock proteins and the defense molecule ABF-2 are both expressed by TOL-1, and both are necessary for immunity (Singh and Aballay, 2006). Due to their conserved architectures, TLRs are also known as pathogen-associated molecular patterns (PAMPs) or microbe-associated molecular patterns (MAMPs) (Janeway and Medzhitov, 2002). TLR recognition triggers cell signaling and immune response activation (Ricci-Azevedo et al., 2017).

Nematode-associated molecular patterns have been linked to signaling and nematode resistance in several studies. They produce PAMP/ETI-triggered immunity to fight nematode infections by turning on MAPKs, ROS, jasmonic acid, and SA signaling (Sidonskaya et al., 2016). Ascarosides, which act as pheromones in nematode signaling, are primarily responsible for this (Choe et al., 2012). These are most likely NAMPs detectable components that cause the defense pathway to activate. Phytoalexins and other metabolites engaged in defensive mechanisms during plant-nematode interactions are also found (Ali et al., 2014). Additionally, a series of signaling events that make up the immune system include the gene WRKY33, which is necessary for camalexin- based PAMP-triggered immunity (PTI) in plants (Mao et al., 2011). Through the actions of MAPKs, phosphorylation, and dephosphorylation, transmembrane receptors receive signals (Rushton et al., 2010). The PAD3 encoding camalexin synthesis is further activated by a signaling cascade that upregulates WRKY33 (Mao et al., 2011). In comparison to non-infected *Arabidopsis* roots, WRKY33 was found to be downregulated in the syncytium of *H. schachtii* (Ali et al., 2014). MKK4 was also discovered to be a signaling kinase that activates WRKY33 and PTI based on camalexin. Resistance to *H. schachtii* was induced by overexpression of WRKY33 and MKK4, respectively (Ali et al., 2014).

5.3 Cellular signal transduction in plants

Plants and pathogens have been co-evolving for millennia in the struggle for supremacy between hosts and pathogens. Invading pathogens are met with a multi-layered defense response from the host plant cells. Pathogens such as PPNs, fungi, bacteria, and viruses contact the plant cell wall as their first physical barrier. Once the virus has overcome the physical barrier, the host cytoplasm becomes a battleground where host and pathogen molecules battle it out. Proteins, lipids, carbohydrates, and cell wall derivatives are examples of pathogen- and microbe-associated molecular patterns (PAMPs/MAMPs) that are recognized by membrane-localized pattern recognition receptors (PRRs) that are present close to the cell wall. PAMP/MAMP identification by PRRs results in the initiation of a conserved downstream cellular signaling cascade known as PAMP-triggered immunity (PTI) inside the cytoplasm of the host cell (Stael et al., 2015). Reactive oxygen species (ROS), the activation of mitogen-activated protein kinases (MAPKs), and the stimulation of signaling pathways by salicylic acid (SA) and jasmonic acid (JA) are a few of the reactions (Tsuda and Katagiri, 2012). All PRRs in plants are transmembrane proteins with an extracellular ligand binding domain. The two forms of PRRs are receptor-like kinases (RLKs), which feature an intracellular kinase domain for cytoplasmic signaling, and receptor-like proteins (RLPs), which do not appear to have any cytoplasmic signaling domain (Macho and Zipfel, 2014). For ligand-specific intracellular signal transduction, RLPs are thought to always work in tandem with one or more RLKs (Zipfel, 2014). Plants are usually protected against non-adapted bacteria by PTI-triggered immunity (Cui et al., 2015).

5.4 Signaling pathway of nematode interaction

Nematode-associated molecular patterns (NAMPs), which

PPNs can activate, allow for appropriate plant interactions (Holbein et al., 2016). Similar to this, nematode secretions can set off a number of signaling cascades that activate plant genes that support the growth of PPNs in plants. The basal immune system, which defends the plants from nematode invasion, is activated concurrently with the host plants' detection of these NAMPs (Choi and Klessing 2016). To circumvent the host's fundamental parasitism defense, it has also been proposed that nematodes may produce effector proteins that alter the plant's cell cycle, cytoskeleton, and small RNA synthesis (Hewezi et al., 2008; Hewezi et al., 2012). Gene silencing, JA-SA routes, gibberellin (GA) pathways, cytokinin pathways, and post-transcriptional modifications are only a few of the signaling pathways that PPNs might affect in their hosts (Branch et al., 2004; Bhattarai et al.,2008; Absmanner et al., 2013; Ali et al., 2017).

5.4.1 NAMP signaling for nematode resistance

Activation of mitogen-activated protein kinases (MAPKs), apoplastic reactive oxygen species (ROS) bursts, and jasmonic acid (JA) and salicylic acid (SA) signaling are only a few of the PAMP-triggered immunity (PTI) and Effector triggered immunity (ETI) responses that plants exhibit in response to nematode infection (Hamamouch et al., 2011; Manosalva et al., 2015; Sidonskaya et al., 2016; Kandoth et al., 2018). Ascarosides generated by nematodes are recognized by plant cells, causing gene expressions associated with MAMP-triggered immunity as well as the activation of MAPKs, JA, and SA signaling, according to the first thorough research of NAMPs (Manosalva et al., 2015). Small molecules called ascarosides serve as pheromones in the social behavior of nematodes. Nematode ascaroside synthesis and signaling are mostly conserved (Choe et al., 2012). Despite having a diverse origin and ecosystem. In *C. elegans*, a free-living nematode, and many other species, ascarosides have a role in social signaling, dauer formation, determining mating partners, and coordinating worm behaviors (Choe et al., 2012). Nematodes secrete ascarosides into their surroundings, the structural differences between them and ascarylose, a 3,6-dideoxy-L-sugar modified with side chains produced from fatty acids, are determined by the amount of carbons in the side chains (Kaplan et al., 2011; Choe et al., 2012; Panda et al., 2017). Ascarosides, a root knot and cyst-forming nematode belonging to the three genera of plant parasitic nematodes, has the highest abundance. It has an 11-carbon side chain. Systemic resistance in the plant's leaves and broad resistance to bacteria, fungus, and nematodes were both produced by priming *Arabidopsis* roots with ascarosides (Manosalva et al., 2015; Zhao et al., 2016). All of this information suggests that nematode-secreted ascarosides are potential NAMPs for inducing basal defense systems in plants. However, there is still no indication that plants' cell surface-based receptors are capable of detecting ascarosides.

5.4.2 NAMP-Triggered Immunity (NTI) via, Phytoalexin Pathway

NAMP-Triggered Immunity (NTI) and Phytoalexin Pathway signal reception by transmembrane receptors is followed by the initiation of signaling cascades involving several phosphorylation and dephosphorylation processes through numerous MAPKs such as MPKs, MKKs, MKKKs, and others. These signaling pathways cause the WRKY33 protein to be upregulated, which then activates the PAD3 gene, causing camalexin synthesis (Mao et al., 2011). When compared to uninfected *Arabidopsis* roots, WRKY33 was the WRKY transcription factor that was most downregulated in the *H. schachtii* induced syncytia (Ali et al., 2014). The primary signaling kinase that activated WRKY33 and camalexin-mediated PTI was discovered to be MKK4. While overexpression of WRKY33 and MKK4 increased resistance to *H. schachtii* in *Arabidopsis*, a T-DNA insertion mutant of PAD3 increased susceptibility (Ali et al., 2014). Nevertheless, more research is still needed to fully understand how this signaling cascade's phosphorylation and dephosphorylation processes work.

5.4.3 CLE signaling and parasitic success of nematodes

PPNs contain members of the CLAVATA/ESR (CLE) peptide family, which has been linked to both cell differentiation promotion and inhibition in plant meristematic tissues. KRLVPSGPNPLHH and LxLxxxLILxLLLxS are two highly conserved motifs found in CLE peptides. Numerous PPNs have CLE motifs that are very comparable to those in the matching host plants (Ali et al., 2017). The PPN CLE peptides may operate as stimulators of cell differentiation and/or proliferation in host plants. Because of this, syncytia development and the differentiation of vascular tissues like xylem are quite. In CLE signaling involvement in plant development and interactions with nematodes is covered in great detail. The development of syncytia produced by *H. schachtii* and compatible plant-nematode interactions require CLE signaling in *Arabidopsis*, which has been demonstrated to require the CORYNE (CRN) and CLAVATA2 (CLV2) receptor kinases (Replogle et al., 2013). The maintenance of the shoot apical meristem in *Arabidopsis* depends on receptor kinases such as CLV1 and RECEPTOR-LIKE PROTEIN KINASE 2/TOADSTOOL2 (RPK2). These two receptors can also transmit CLV2/CRN signaling that is independent of CLV3 for the parasitic success of PPNs in plants (Replogle et al., 2013). Similar to this, the potato CLV2-like receptor (StCLV2) was specifically bound

to the CLE peptide from *G. rostochiensis*, GrCLE1, after it was glycosylated into a 12-amino acid arabinosylated glycopeptide (Chen et al.; 2015). This demonstrates the importance of glycosylation in the CLE signaling mechanism for plant-nematode interactions that are compatible. GrCLE1 can also directly bind to the plant CLE receptors CLV2, BAM1, and BAM2 and alter their activities after being processed by host plant proteases (Guo et al., 2011).

To establish NFSs in roots, CLE peptides interact with plant genes (Kiyohara and sawa; 2012). The TDIF (tracheary element differentiation inhibitory factor)-TDR (TDIF receptor)-WOX4 pathway, which encourages the production of NFSs, was found to include B-type CLE peptides from *Arabidopsis* (Guo et al., 2017). The main function of this route is to promote procambial meristematic cell proliferation. However, it has been demonstrated that the TDIF pathway is activated in syncytia inflicted by *H. schachtii* in *Arabidopsis* roots (Guo et al., 2017). Loss-of-function mutations of many genes associated with this system decreased the number of nematodes and the formation of syncytia (cle41, tdr-1, wox4-1, and double mutant tdr-1 wox4-1). These studies revealed that CLE peptides have a role in meristem formation and are also engaged in CLE signaling that promotes nematode parasitism in plants.

6 Chemical nematicides: potent nematode suppressors

Chemical nematicides have been used to effectively manage nematodes for the past 50 years. These are low-cost insecticides that successfully destroy soil nematodes. Soil fumigants were popular because they didn't require alternative host crops for rotation, significantly reduced nematode populations in the soil, and were relatively inexpensive for most crops. With the exception of 1, 3 dichloropropene (Telonell), chloropicrin (tear gas), and dazomet, most fumigant nematicides have been outlawed as environmental poisons by the Environmental Protection Agency (EPA), (Basmid). Methyl bromide, a multipurpose soil fumigant, is similarly effective at reducing soil nematode populations, but it was largely phased out in 2005. Non-fumigant nematicides like fenamiphos (Nemacur) and aldicarb (Temik) use the same active components as many insecticides (i.e., nerve toxin) and can be used in liquid or granular forms (Lambert and Bekal, 2002; Basyoni and Rizk, 2016). Non-fumigant nematodes lower nematode populations, although their efficacy is inconsistent compared to fumigant nematodes. Non-fumigant nematicides are likewise being restricted by the Environmental Protection Agency (EPA). Due to the high cost of developing nematicides, new ones are rarely introduced on the market nowadays. While nematodes can be controlled using nematicides, they are only practical for high-value crops (Lambert and Bekal, 2002; Basyoni and Rizk, 2016).

7 Summary and future directions

The present study about nematode diversity, their interaction with plants and procedures employed in their identification broadened the horizon at a multiscale level across the globe. Plant parasitic nematodes (PPNs) invading aerial, sub-areal and belowground parts account for a significant loss via, the destruction of the crop plants. Feeding on the vascular sap, their invasion is followed by migration to different plant species with severe consequences on the growth and development of plants that together put forth the need to have effective measures as part of their management strategies. Being tiny creatures, their study at the microscopic level based on the morphological features does not provide a definite taxonomic resolution in their identification and as such highlights the importance of modern tools in resolving the bottleneck regarding proper identification of PPNs. The application of modern techniques (based on DNA, RNA and Protein) has left a great impact on the taxonomical resolution of PPNs and as such their use in attributing proper annotation for their classification into definite and well-known classes of nematodes. The relative ease of molecular methods has led to the recognition of many new taxa; which otherwise have been impossible to describe on the basis of morphological features. Additionally, DNA fingerprinting, microarray and probe-based methods, isozyme and serological analysis have created an unmatched impact in the identification of nematodes. Artificial intelligence (AI) supplemented with modern high-end equipment's offered many advantages to taxonomists in decision-making by enabling them to have an accurate and fast identification of the creatures under study.

The plant-nematode interactions in the soil begin with the appropriate detection of the host signals including chemo-, mechano-, and thermo-sensing along with detection of the redox potential, humidity, and osmotic pressure. In the procedure, they avoid the response of the host plant species via, the development of nematode-associated molecular patterns (NAMPs) that are well-perceived by the host plants and helps in initiating the signaling cascade. Additionally, some members avoid confrontation with the host by injecting stable effectors that help in reprogramming the basic resistance approaches. With a main focus on agricultural productivity, the interaction of the PPNs with different agricultural crops needs strategic development for their proper identification and classification using different molecular markers for the known genes and improved methods for less known nematode species as part of the futuristic approach. The approach will not only help in tracing their transmission

through asymptotic plants but will help in developing the diagnostic techniques to contain their spread and as such prevent loss in agricultural productivity. Keeping in view the UN sustainable goals of zero hunger, high-yielding, profitable cultivars of the crops are needed to be developed as part of the strategic management options for the control of nematodes.

Author contributions

All the authors have contributed equally in drafting the different sections of the manuscript.

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