INTERNATIONAL JOURNAL OF AGRICULTURE & BIOLOGY
ISSN Print: 1560–8530; ISSN Online: 1814–9596
15–093/2015/17–6–1071–1082
DOI: 10.17957/IJAB/15.0037
http://www.fspublishers.org

***Review Article***

# Plant-nematode Interactions: From Genomics to Metabolomics

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## Abstract

Plant parasitic nematodes are obligate parasites causing serious reduction in crop yields. Several economically important species parasitize various plant species, but the root knot and cyst nematodes belonging to the Heteroderidae family are especially dangerous. Plant parasitic nematodes result in crop losses of over $150 billion worldwide. This review gives an account of morpho-physiological and molecular events during parasitism of root-knot and cyst nematodes. It describes the transcriptomes and parasitomes of various nematodes indicating that the effector proteins are crucial for the compatible plant nematode interactions. Various sequencing techniques used in plant-nematode genomics and transcriptomics are discussed. Moreover, the dynamics of host transcriptomes in response to infection with different nematode species have been reported. The host transcriptomes have unrevealed many candidate genes, which are involved in both compatible and incompatible plant nematode interactions. The strategy of manipulation of expression of the genes induced and suppressed by the nematodes in the feeding sites has also been suggested for enhancement of resistance against nematodes. This review will provide the researchers with the information regarding transcriptional changes in the nematodes as well as host plants, which would be important for the induction of resistance against nematodes in different crop plants. 

**Keywords:** Plant parasitic nematodes; Transcriptomes; Genomes; Plant resistance

## Introduction

The nematodes are omnipresent in nature and found ubiquitously from the high mountains to sediment of the oceans, inhabiting a diversity of climates ranging from tropical to Polar Regions. Most of them are free-living worms, living as bacterial or fungal feeders or as algivore-omnivore-predators in diverse environments (Blaxter *et al.*, 1998; Williamson and Gleason, 2003; Irshad *et al.*, 2013). Moreover, some are parasites of animals, both invertebrates and vertebrates, including humans, causing serious health problems. Examples are the intestinal worm *Ascaris lumbricoides* and the guinea worm *Dranunculus medinensis* (Decraemer and Hunt, 2006). There are also many nematode species which are parasitic to plants. Decraemer and Hunt (2006) characterized 4,100 species of nematodes as plant parasites, which can infect a range of crop plants like wheat, soybean, potato, tomato, and sugar beet etc. Nematode infection can result in different above-ground symptoms in plants such as leaf chlorosis, patchy and stunted growth, wilting and susceptibility to other pathogens (Webster, 1995). The symptoms on Arabidopsis and Okra roots and soybean plants with plant parasitic nematodes are shown in Fig. 1.

Most of the nematodes that are parasitic to different plant species are characterized as obligate biotrophic parasites and exert harmful effects on agricultural production by direct damage to crops or serving as vectors for plant invading viruses. Therefore, these parasites result in crucial economic and social impacts worldwide. Due to their wide host range, the plant-parasitic nematodes cause a serious reduction in crop yields resulting in annual crop losses worth over $150 billion worldwide (Bird and Kaloshian, 2003; Abad *et al.*, 2008).

Several economically important species parasitize various crop plants, but the root-knot and cyst forming nematodes belonging to the family *Heteroderidae* are especially dangerous. The members of this family are obligate sedentary endoparasites. They penetrate the plant roots as $J_2$ larva (second stage juveniles) and launch specific feeding sites (Wyss and Zunke, 1986; Hussey and Grundler, 1998). The member of genus Meloidogyne are known as root-knot nematodes, which induce feeding structures called "galls", each of which comprises of several giant cells

**To cite this paper:** Ali, M.A., A. Abbas, F. Azeem, N. Javed and H. Bohlmann, 2015. Plant-nematode interactions: From genomics to metabolomics. *Int. J. Agric. Biol.*, 17: 1071–1082

(Jones and Payne, 1978). Two genera, Heterodera and Globodera are especially dangerous in case of cyst nematodes and induce specialized feeding cells called syncytia (Jones, 1981; Hussey and Grundler, 1998). Another economically important category of nematodes is the migratory endoparasitic nematodes. These nematodes spend most of their time in migrating through root tissues following the destructive feeding on plant cells (Moens and Perry, 2009). This results in massive plant tissue necrosis. The most important examples of migratory nematodes are the genera of lesion nematode (*Pratylenchus*), burrowing nematodes (*Radopholus*) and rice root nematode (*Hirschmanniella*). However, the events in life cycles of only cyst forming and root-knot nematodes are discussed here in detail.

**Life Cycle of Root-knot Nematodes**

Root-knot nematodes moves towards plant roots and enter the root as second-stage juveniles ($J_2$). They repetitively strike their head to the root cells near elongation zone to enter into the root and follow a non-destructive intercellular migration (Williamson and Gleason, 2003). When the $J_2$ reach the differentiating vascular cylinder near the elongation zone, they induce a feeding structure that consists of a number of giant cells. They are called root-knot nematodes, because the resulting giant cells become multinucleate (up to >100 nuclei) and are surrounded by cortical and pericycle cells that divide and proliferate resulting in the development of 'galls' or 'root knots' (Gheysen and Mitchum, 2011). The developing giant cells contain thick cytoplasm packed with organelles and undergo a series of synchronous nuclear division without cytokinesis. As a result, each nucleus becomes highly polyploid (Bird and Kaloshian, 2003). During development, nematodes feed alternatively from the different giant cells. After three moultings they grow entirely into female adults, which reproduce parthenogenetically (not all species) and deposit their eggs in gelatinous egg sacs (Hussey and Grundler, 1998; Williamson and Gleason, 2003).

**Establishment of Syncytia by Cyst Nematodes in Plant Roots**

During the course of parasitism, the cyst nematodes start hatching from eggs packed in strong case called cyst as $J_2$ larvae which move towards the host plant root (Fig. 2A). This hatching is induced by some stimuli from the soil or from the root exudates of the plants (Hallem *et al.*, 2011; Rasmann *et al.*, 2012). After penetrating into roots, the $J_2$ larvae migrate intercellularly through cortical cells to search out the vascular cylinder.

The secretions, from nematode dorsal and sub-ventral glands, facilitate the migration of the nematode through induced expression levels of plant genes encoding for the cell wall degrading and modifying enzymes such as cellulases, expansins, glucanases and pectate lyases (Wyss and Grundler 1992; Golinowski *et al.*, 1996; Smant *et al.*, 1998; Goellner *et al.*, 2001; Wieczorek *et al.*, 2006; Abad *et al.*, 2008).

After arriving at the root vascular bundle, nematodes induce an initial syncytial cell (ISC) to initiate specialized feeding structures, which are called syncytia (singular; syncytium). The syncytium develops from an ISC through incorporation of quite a few hundred neighboring cells by localized degradation of cell wall (Golinowski *et al.*, 1996; Grundler *et al.*, 1997). Within 24 h after selection of an ISC, the cell cytoplasm becomes proliferated which is associated with a decrease in the size of vacuoles (Magnusson and Golinowski, 1991). The secretions from nematode could be secreted outside the cell membrane or nematodes could use their stylet orifice to inject them directly into the cytoplasm of the target cell. In both cases, specific molecules from nematode secretions, which are protein in nature, may bind to plant cell receptors and enter directly into the plant cell nucleus. A signal transduction cascade is stimulated that modify gene expression in the infected root cell (Davis and Mitchum, 2005; Davis *et al.*, 2008; Mitchum *et al.*, 2008; Hewezi and Baum, 2012).

In the absence of any strong and adverse response from the root cell, like localized cell death or callose deposition, a syncytium is initiated from ISC. The syncytium turns out to be the sole nutrient source for the developing nematodes throughout the subsequent sedentary life stages (Grundler *et al.*, 1997). However, the unfavorable conditions lead to the failure in syncytial development resulting in the inhibition in the establishment of female nematodes on plant roots (Sobczak *et al.*, 1997).

A syncytium typically comprises of around 200 cells with many nuclei and enormous hypertrophy of the syncytial elements, which leads to an enlargement of the feeding site, usually the region nearest to the head of the nematode (Fig. 2B). de Almeida Engler *et al.* (1999) reported that the enlarged nuclei and nucleoli in these expanding syncytia might be due to endocycles taking place within the feeding cells. The shape of esophageal glands also differs in the sedentary stages as compared to the motile 2$^{nd}$ stage juvenile stage (Curtis, 2007) (Fig. 3A and B).

However, the adult $J_4$ male cyst nematodes are contained in a thin cuticle casing which is associated to small syncytia (Fig. 2C). At adult stage, they are motile and come out of the cuticular covering to fertilize the eggs contained in the body of adult females. The females remain associated with their syncytia throughout their lives. After mating, the male nematode dies, whereas the female nematode continues fetching nutrients from the syncytia. The female nematode dies soon after the advent of egg development. At this stage the dead female develops hard covering around hundreds of the eggs to form a cyst that protects the eggs from environmental hazards (Fig. 2B). The eggs hatch under favourable conditions to release infectious

$J_2$ to start another parasitic cycle (Hussey and Grundler, 1998).


**Fig. 1:** Plant symptoms in response to nematode infections Arabidopsis roots infected with beet cyst nematodes (*H. schachtii*) containing cysts (A). The roots of Okra plants uninfected (B) and infected with M. incognita (C) and Soybean plants infected with soybean cyst nematodes (*H. glycines*) (reproduced from http://www.extension.umn.edu/agriculture/crop-diseases/soybean/soybeancystnematode.html (D).

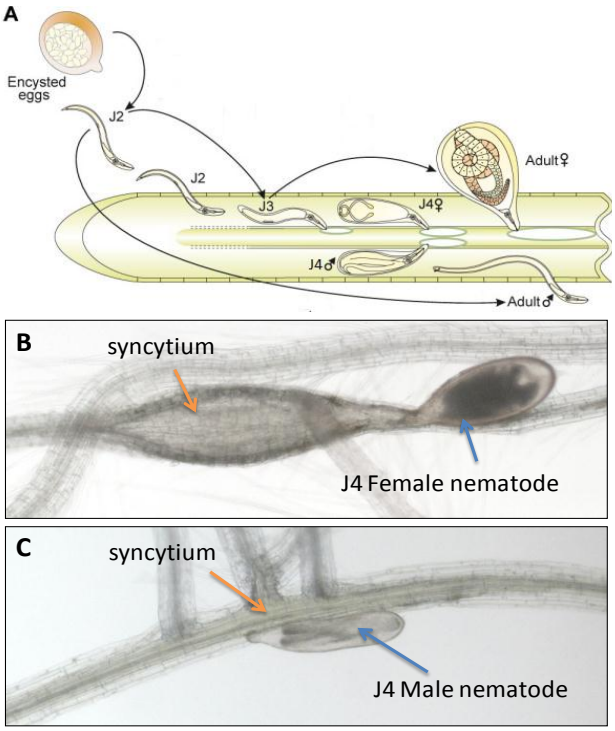


**Fig. 2:** Cartoon diagram of life cycle of cyst nematodes. A: $J_2$, $J_3$, $J_4$ juveniles infecting the plant roots in the second, third and fourth developmental stages respectively (reproduced from Cotton *et al.*, 2014), B: Real time picture of $J_4$ *H. schachtii* female and syncytium associated with the female nematode in Arabidopsis roots, C: Real time picture of $J_4$ male nematode and associated syncytia

**Nutrient Transport into the Feeding Cells**

It is a subject of debate that how nutrients enter into the syncytia or giant cells from the root vascular bundle. There are two possibilities of nutrient transport into the syncytia and giant cells i.e., symplasmic movement through plasmodesmata and/or apoplasmic pathway of phloem unloading. Only a few plasmodesmata were microscopically observed between syncytia and phloem but these were considered to be non-functional (Böckenhoff and Grundler, 1994; Grundler *et al.*, 1997). The function of these plasmodesmata was studied afterwards, which showed that during the establishment of the syncytium, plasmodesmata are important connections to the phloem for the symplastic movement of nutrients (Hofmann and Grundler, 2007). Another report confirmed the symplasmic isolation of syncytia in early events of nematode development on the plant roots (Hofmann *et al.*, 2007). Moreover, Hoth *et al.* (2008) demonstrated that despite their origin from the same nematode family, cyst and root-knot nematodes employ primarily different strategies for nutrient import from the host plants. In the case of giant cells induced by root-knot nematodes, apoplastic loading of assimilates occurs through transport proteins, while syncytia are mostly loaded symplastically via plasmodesmata. These differences could be a possible reason why root-knot nematodes have a vast host range as compared to cyst nematodes. However, it has been reported that more than one transport process is important for nematode feeding site establishment and maintenance (Hammes *et al.*, 2006).

**Parasitomes/secretomes and parasitism genes of the nematodes**

For plant parasitism, the nematodes have evolved considerably sophisticated ways. One of different strategies adopted by nematodes is the expression of parasitism genes in their esophageal gland cells, which are secreted (also called secretome or parasitome) via their stylet into host tissue (Davis *et al.*, 2000; Hussey *et al.*, 2002; Hewezi *et al.*, 2012). The esophageal glands consist of two types of glands, dorsal and subventral (Fig. 3A and B), which are involved in the synthesis of these secretions. Stylet secretions are directly involved in the infection and parasitism of plants; however, the secreted proteins are considerably different during specific nematode parasitic stages (Hussey, 1989; Davis *et al.*, 2000). Moreover, for compatible interactions, the nematodes have developed various changes in morphology of their stylet and esophagus (Fig. 3A and B) (Hussey, 1989).

The nematode effector proteins originate in the secretory gland cells and their synthesis as well as secretion is developmentally regulated throughout the parasitic cycle of the nematode (Wyss and Zunke, 1986; Hussey, 1989; Davis *et al.*, 2008). It is hypothesized that these secretions modify the plant cells into complex feeding structures (Burgess and Kelly, 1987; Davis *et al.*, 2000; Gheysen and Fenoll, 2002; Hewezi and Baum, 2012).

A variety of parasitism genes from different nematode species has been identified. For instance, Gao *et al.* (2003) studied the transcriptome of nematode secretions and

reported 51 gland-expressed candidate parasitism genes from *H. glycines*. Furthermore, the secretome of *M. incognita* has directly been identified by using mass spectrometry resulting in the identification of 486 proteins secreted by *M. incognita* (Bellafiore *et al.*, 2008). Most of them were homologous to plant proteins, which they may induce or suppress. Some nematode proteins might have functions of regulating the plant cell cycle or growth while others could reprogram the genetic events taking place in the host cells to facilitate compatible interactions (Bellafiore *et al.*, 2008).

Secretome contains products of diverse parasitism genes. The genes encode for plant cell wall degrading/modifying enzymes including cellulases or β-1,4-endoglucanases (Smant *et al.*, 1998; Goellner *et al.*, 2000; Gao *et al.*, 2002; Gao *et al.*, 2004), chitinases (Gao *et al.*, 2002), xylanases (Opperman *et al.*, 2008), pectate lyases and pectinases (Abad *et al.*, 2008; Opperman *et al.*, 2008), and expansins (Qin *et al.*, 2004; Kudla *et al.*, 2005). These cell wall degrading enzymes help the infective $J_2$ nematodes to migrate through the plant roots by softening the cell wall. The effector proteins include CLAVATA3 (CLV3) /ESR (CLE) -like (Wang *et al.*, 2005; Patel *et al.*, 2008; Lu *et al.*, 2009; Wang *et al.*, 2010a; Wang *et al.*, 2010b), SPRY domain-containing (SPRYSEC) effector proteins (Huang *et al.*, 2006; Rehman *et al.*, 2009; Sacco *et al.*, 2009; Postma *et al.*, 2012), *Mi-EFF1* (Jaouannet *et al.*, 2012), calreticulin *Mi-CRT* (Jaubert *et al.*, 2002; Jaubert *et al.*, 2005; Jaouannet *et al.*, 2013), and *Hs19C07* (Lee *et al.*, 2011). These proteins are involved in plant-nematode compatible interactions by suppressing the defense mechanisms of host plants in some cases. Interestingly, a recent study showed that a *M. incognita* effector protein 7H08 is imported into the nucleus of plant cells and it has the ability of to activate transcription of plant genes (Zhang *et al.*, 2015). This is the first report on nematode effector protein with transcriptional activation activity.

However, some nematode effector proteins are also involved in incompatible interactions. For example, *M. incognita* secreted *map-1.2* protein shows specifically increased expression in *Mi-1* resistant tomato lines. It suggests that the *map-1.2* might be a putative avirulent (Avr gene) response to *Mi* gene (Castagnone-Sereno *et al.*, 2009). A similar effect has been shown for *H. glycines* chorismate mutase (*Hg-cm-1*) in soybean cultivars. But still the plant targets for both these *Avr* candidate genes and their particular function are unknown (Bekal *et al.*, 2003; Lambert *et al.*, 2005; Castagnone-Sereno *et al.*, 2009). However, another *M. incognita* gene, *Cg-1*, was confirmed as an *Avr* gene corresponding to the *Mi-1* resistance gene in tomato (Gleason *et al.*, 2008). Moreover, *SPRYSEC-19* (Rehman *et al.*, 2009; Postma *et al.*, 2012), *Gp-Rbp-1* (Blanchard *et al.*, 2005; Sacco *et al.*, 2009) and *Gr-VAP1* (Lozano-Torres *et al.*, 2012) are some other examples of nematode effector proteins involved in incompatible plant-nematode interactions.

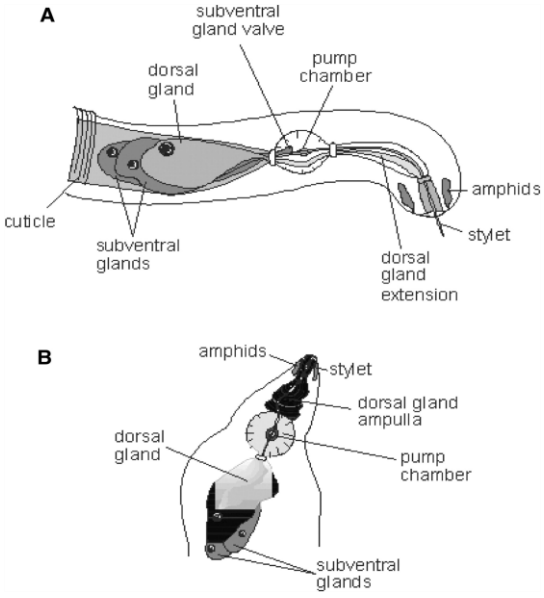


**Fig. 3:** Diagram of the esophageal glands in the body of a motile second stage juvenile (A) and an adult female (B) of a typical sedentary plant parasitic nematode (reproduced from Curtis, 2007). The morphology of esophageal glands changes in the subsequent sedentary stages of the plant parasitic nematodes

## Genomes and Transcriptomes of Plant-parasitic Nematodes

Due to the advancements in sequencing techniques and data analysis, the genome sequencing is providing a lot of information about nematodes. The genomes of different nematodes have been published i.e., *Meloidogyne incognita* (Abad *et al.*, 2008), *Meloidogyne hapla* (Opperman *et al.*, 2008), bacteriovore nematodes *Caenorhabditis elegans* (Consortium, 1998) and *Caenorhabditis briggsae* (Stein *et al.*, 2003) and animal parasites *Brugia malayi* (Ghedin *et al.*, 2007), *Trichinella spiralis* (Mitreva *et al.*, 2011), *Ascaris suum* (Jex *et al.*, 2011) and *Pristionchus pacificus*, a species associated with beetles (Dieterich *et al.*, 2008). Dieterich and Sommer (2009) have compared the different published genomes of nematodes and discussed in detail the evolution of parasitism with special reference to *Pristionchus pacificus*. However, a major breakthrough was the genome sequencing of the most devastating plant parasite *Meloidogyne incognita* (Abad *et al.*, 2008). In this genome, having just over 25% protein coding sequence, they recognized a total of 81 cell wall degrading enzymes. There were 21 cellulases, 6 xylanases belonging to GH5 family and two arabinanases and pectinases each from GH43 and GH28 families, respectively (Table 1). Similarly, 20 candidate genes encoding expansins were identified (Abad *et al.*, 2008). In the genome of *Meloidogyne halpa*, 30–40%

of the total annotated genes were involved in molecular functions like protein binding and catalytic activities, respectively (Opperman *et al.*, 2008). *M. halpa* genome contains 39 genes having the putative function of cell wall degradation with the biggest family of 22 expansins (Opperman *et al.*, 2008) (Table 1). The comparison of different published genomes on the basis of various putative cell wall degrading enzymes is given in the Table 1.

After the publication of *M. incognita* genome, Danchin and Perfus-Barbeoch (2009) discussed the mechanisms of parasitic adaptation of *M. incognita* and suggested that the genes coding for the enzymes involved in cell wall degradation would be possibly adapted through horizontal gene transfer from pathogenic bacteria. Another interesting aspect of *M. incognita* genome was the presence of similar but distinct copies of the genome. It might be the explanation for the parasitic success of *M. incognita* in terms of its global distribution and broad host range (Danchin and Perfus-Barbeoch, 2009).

Kikuchi *et al.* (2011) has published the genome sequence of pine wood migratory nematode *Bursaphelenchus xylophilus*. They also compared the *B. xylophilus* genome to the genomes of plant parasitic nematodes (*M. incognita* and *M. hapla*), nonparasitic nematode belonging to different species of genus Caenorhabditis and two other nematodes *Pristionchus pacificus* and *Brugia malayi*. In this comparison, *B. xylophilus* showed maximum similarity with the genomes of plant parasitic nematodes *M. incognita* and *M. hapla* with 202 uniquely shared protein families by *M. incognita* and *B. xylophilus*. The genomes of both parasitic nematodes were considerably different from other nonparasitic nematode and other two nematode species (*Pristionchus pacificus* and *Brugia malayi*). It suggested that plant parasitic nematodes need special proteins for infecting the plants, for fighting with the plant innate immune system and to sustain their life on the plants. *B. xylophilus* in total showed 34 genes coding for enzymes with predicted plant cell wall degrading actions including 11 genes for cellulases, 15 for pectate lyases and 8 for expasins (Kikuchi *et al.*, 2011) (Table 1). Kikuchi *et al.* (2011) also listed 20 effector genes from *B. xylophilus* genome, which showed similarity with the effector genes of different plant parasitic nematodes, specifically the members of genera Heterodera and Globodera. In addition to the conventional cell wall degrading enzymes, B. *xylophilus* genome includes carbohydrate active enzymes (CAZymes), which could be recruited for cell wall degradation or modification (Kikuchi *et al.*, 2011). Similarly, a recent study of cellulases belonging to glycoside hydrolase family 45 (GH45) has supported a close relationship between the sequences of GH45 from nematodes and fungi. This strongly sustains the hypothesis that nematode GH45 cellulases were acquired via horizontal gene transfer from fungi (Palomares-Rius *et al*., 2014).

Moreover, the genomes and life-stage specific transcriptomes of *Globodera pallida* infecting potato roots have elucidated key features of plant parasitism (Cotton *et al.*, 2014). In spite of the close phylogenetic relationship between cyst and root-knot nematodes, diverse gene families have been observed between these two groups of nematodes. These differences include a huge expansion of the SPRY domain protein family effectors in *G. pallida*. Cotton *et al.* (2014) have suggested immense importance of this data for exploitation of post-genomic approaches to develop novel strategies aimed at nematode resistance.

**Various Sequencing Technologies used for Nematode Genomes/Transcriptomes**

Over the last couple of decades, sequencing technology has switched from the hierarchical sequencing and assembly of cloned fragments of DNA (i.e., Sanger sequencing as used for sequencing genomes of *C. elegans*, *M. incognita*, *M. halpa*), to the shotgun or Roche/454 sequencing, producing 500 bp reads (i.e., Sequencing of *P. pacificus* by Dieterich *et al.*, 2008; Pham *et al.*, 2014) and the even cheaper and the latest, Illumina sequencing produces 150 bp reads with more turnover (Mardis, 2008). The Illumina sequencing has been used by Kikuchi *et al.* (2011) for sequencing of pine wood migratory nematode *B. xylophilus*. Due to the rapid progress and increased turnover in sequencing technologies, these technologies have been emerged as 'next-generation' (next-gen) technologies (Mardis, 2008). These technologies have made it affordable to sequence the whole genomes of nematodes, which are almost less than 1/15 of the size of the 3.2 Gb human genome (Dillman *et al.*, 2012). Besides genome sequencing, these next-gen technology like Roche/454 technology are also being used to study the transcriptomes of different organisms (Cheung *et al.*, 2006; Weber *et al.*, 2007) and plant parasitic nematodes (Haegeman *et al.*, 2011; Nicol *et al.*, 2012).

Although each individual cell of any organism contains its complete set of genes in distinctive chromosomes, the transcriptional activity of each gene is a quite dynamic and multifactorial process. This determines that the 'genome' of an individual or cell is evidently distinguishable from its complete set of transcripts the 'transcriptome' under defined conditions. The first whole transcriptome of *M. incognita* was studied by McCarter *et al.* (2003), who investigated 5,700 expressed sequence tags (ESTs) from $J_2$ larvae, which were classified by function into 1,625 ESTs using the Gene Ontology (GO) hierarchy. They showed that $J_2$ larva express a variety of ligand-binding proteins and numerous cytoskeletal proteins (McCarter *et al.*, 2003). In this transcriptome the enzymes involved in glyoxylate pathway were found transcriptionally active. It proposed that larvae of this nematode can metabolize its own lipid stores while searching for a host. The gene ontology mappings showed that out of 133 genes involved in metabolism, 30% are involved in protein degradation and

**Table 1:** Comparison of predicted cell wall degrading enzymes from the sequenced genomes of different nematode species

| Nematode species | Size (Mb) | CDs (#genes) | Cellulases | Xylanases | Arabinanases | Pectinases | Expesins | Total | Reference |
|---|---|---|---|---|---|---|---|---|---|
| *Bursaphelenchus xylophilus* | 75 | 18,074 | 11 | 0 | 0 | 15 | 8 | 34 | Kikuchi *et al.*, 2011 |
| *Meloidogyne incognita* | 86 | 19,212 | 21 | 6 | 2 | 32 | 20 | 81 | Abad *et al.*, 2008 |
| *Meloidogyne hapla* | 53 | 13,072 | 6 | 1 | 2 | 24 | 6 | 39 | Opperman *et al.*, 2008 |
| *C. elegans* | 100 | 20,431 | 0 | 0 | 0 | 0 | 0 | 0 | Consortium 1998 |
| *Pristionchus pacificus* | 173 | 24,216 | 6 | 0 | 0 | 0 | 0 | 6 | Dieterich *et al.*, 2008 |
| *Bursaphelenchus mucronatus* | 96 | 21,252 | 0 | 0 | 0 | 0 | 0 | 0 | Pereira *et al.* 2013 |

modifications (McCarter *et al.*, 2003).

Similarly, Haegeman *et al.* (2011) used Roche/454 technology to sequence the transcriptome of *Pratylenchus coffeae.* In this transcriptome, successful annotation of over 10,000 sequences was done followed by the identification of several cell wall modifying enzymes including cyst nematodes specific arabinogalactan galactosidase. Some new enzymes belonging to GHF5 and GHF16 with the putative function of cell wall modifications were traced out. They also found the transcript of a homologue of chorismate mutase suggesting the wider occurrence of this parasitism gene in plant parasitic nematodes.

Recently, the *de novo* transcriptome analysis of the root lesion nematode, *Pratylenchus thornei* was carried out by Nicol *et al.* (2012) using 454 GS FLX sequencing. They assembled 34,312 contigs from 787,275 reads. 6,989 contigs were annotated and it resulted in functional assignments for 3,048 contigs. They particularly studied the transcripts related to cell wall degradation, neuropeptides and putative plant parasitism genes. The 14 contigs matched with effector genes, which are proposed to suppress the host defense responses (Nicol *et al.*, 2012). The large proportion of total annotated contigs was common between Heteroderidae and Meloidogynidae families. Hence, providing considerable new information on those genes shared between migratory and sedentary endoparasitic nematodes. Palomares-Rius *et al.* (2012) carried out the comparative analysis of transcriptomes of different life stages (7, 14 and 30 days after infection) of the nematode *G. pallida* followed by the interaction with different potato genotypes. They demonstrated that different stages of *G. pallida* revealed differential expression of various genes including formerly characterized genes coding for effectors like SPRYSEC proteins. Moreover, several genes showed differential expression in $J_2$ infecting the susceptible and resistant potato lines (Palomares-Rius *et al.*, 2012). Rockey *et al.* (2013) studied 1,515 secreted proteins from pine wood nematode *Bursaphelenchus xylophilus* using Nano LC-MS/MS analysis. The comparative study of the secreted protein profiles among various plant parasitic nematodes demonstrated an obvious expansion of peptidases and peptidase inhibitors in *B. xylophilus* through horizontal gene transfer from plant pathogenic fungi and bacteria (Rockey *et al.*, 2013).

**Host Transcriptomes in Response to Nematode Infection**

In addition to drastic structural changes in the cell morphology of nematode infested roots, the gene expression is significantly affected at the whole plant level. These transcriptional changes have been studied using a variety of techniques. For instance, differential display and promoter tagging have been used for quite a number of the genes which are specifically induced in syncytia or in giant cells (Gheysen and Fenoll, 2002). However, in the last decade or more, micro-array and Affymetrix GeneChips have been very popular for studying the whole transcriptome of the host plant in response to nematode infections.

The beet cyst nematode, *Heterodera schachtii* can complete its life cycle on Arabidopsis roots *in vitro* within 6 weeks and this model system has been widely exploited (Sijmons *et al.*, 1991). The first generation Affymetrix GeneChips cover around 30% of the Arabidopsis genome, however, on the other hand, the 2nd generation ATH1 GeneChip covers more than 75% of the Arabidopsis genome. Hammes *et al.* (2005) first time used the second generation ATH1 GeneChip to study the transcriptome of galls in Arabidopsis roots induced by *M. incognita.* They reported the expression of 1400 genes coding for transport proteins. Similarly, CATMA microarrays containing probes for 22,089 genes were used to study the transcriptome of *M. incognita* induced galls (Jammes *et al.*, 2005). Working on Arabidopsis- beet cyst nematode interaction, Szakasits *et al.* (2009) performed the comparative transcriptmics of 5 and 15 old syncytia as compared to unifected roots in Arabidopsis by using Affymetrix GeneChip. This transcriptome revealed differential regulation of 34.2% out of a total of 21,138 genes compared to uninfected roots. This proportion was divided into 18.4% (3893) up-regulated and 15.8% (3338) down-regulated genes in syncytia. Barcala *et al.* (2010) have also studied the early transcriptomic events in micro-dissected Arabidopsis 3dpi giant cells induced by *M. javanica*. Both these studies showed that the transcriptomes of syncytia and giant cells were distinctive on a molecular level as compared to the transcriptomes from other plant

parts. Most of the transcriptome studies verified higher metabolic activity in nematode feeding sites and suppression of defense mechanisms of the plants in most of the cases (Puthoff *et al.*, 2003; Bar-Or *et al.*, 2005; Hammes *et al.*, 2005; Jammes *et al.*, 2005; Szakasits *et al.*, 2009; Barcala *et al.*, 2010; Beneventi *et al.*, 2013; Ji *et al.*, 2013).

The transcriptome of giant cells in rice induced by *Meloidogyne graminicola* has recently been studied by using laser-capture microdissection for the isolation of cells (Ji *et al.*, 2013). The expression profiles demonstrated a general activation of the genes involved in primary metabolism in the giant cells. However, majority of the genes involved in defense pathways and secondary metabolism were significantly down-regulated in the giant cells. Moreover, 7 days after infection, a significant stimulation of expression of epigenetic processes was also detected in the giant cells (Ji *et al.*, 2013).

In addition to their parasitism/effector genes, the nematodes are able to induce or suppress particular plant genes for compatible interactions. The plant's transcriptomes in response to infection of various nematodes have resulted in the induction of various genes involved in the establishment of nematode feeding sites in the plant roots. For example, endo-1,4-β-glucanases, expansins, cellulases, pectate lyases, tubulins are reported to be involved in modification and degradation of plant cell walls to support the nematode invasion and the ultimate establishment of nematode feeding sites (Goellner *et al.*, 2001; Wieczorek *et al.*, 2006; Wieczorek *et al.*, 2008; Szakasits *et al.*, 2009; Barcala *et al.*, 2010; Banora *et al.*, 2011). Similarly, an Arabidopsis AAA+ATPase gene has been found to be highly upregulated in syncytia induced by *H. schachtii* (Ali *et al.*, 2013b). The knockdown and knockout mutants of this gene supported less number of nematodes revealing the significance of AAA+ATPase gene nematode establishment and development on the Arabidopsis roots. The plant defensins in Arabidopsis are also induced in response to nematode infection, but the function of these defensins is not worked out yet (Siddique *et al.*, 2011; Ali *et al.*, 2012). Moreover, WRKY23 transcription factor has been reported to be upregulated in syncytia induced by beet cyst nematode (*H. schachtii*). WRKY23 was found to be important for development of syncytia in Arabidopsis roots (Grunewald *et al.*, 2008). Recently, amino acid transporters have been demonstrated to be involved in the establishment of syncytia in Arabidopsis roots (Elashry *et al.*, 2013).

On the other hand, the downregulated genes in most of the plant transcriptomes, in response to nematode infection, were related to the plant defense pathways. It seems that the nematodes are able to suppress the genes controlling natural immune responses of the plants (Szakasits *et al.*, 2009; Barcala *et al.*, 2010; Kyndt *et al.*, 2012). Several peroxidases genes were found to be strongly downregulated as out of top 100 suppressed genes in syncytia, 14 were peroxidases (Szakasits *et al.*, 2009).

A strongly downregulated transcription factor in syncytia, AtRAP2.6 was overexpressed in Arabidopsis under the constitutive promoter CaMV.35S. It resulted in enhanced nematode resistance in overexpression lines (Ali *et al.*, 2013a). The resistance in AtRAP2.6 overexpression lines was mediated by enhanced callose deposition and increased expression of JA inducible genes. Similarly, most of the investigated defense-related genes were shown to be induced in rice shoots, 3 days post infection in response to root-knot nematode, including the genes involved in pathways like phenylpropanoid, ethylene and PR proteins, however, many of these activated genes were found to be downregulated at 7 dpi (Kyndt *et al.*, 2012). Similar reduction in the expression of genes related to methyl jasmonate biosynthesis was noticed in the older giant cells (Kyndt *et al.*, 2012). This could be the interesting for the scientists working on plant nematode interactions to investigate that which tools are used by the nematodes to suppress systemic plant defense mechanisms.

Various WRKY transcription factors like WRKY6, WRKY11, WRKY17, WRKY25 and WRKY33, which have been reported to be involved in plant defense responses, were also downregulated in response to beet cyst nematode infection in Arabidopsis. The overexpression and knockout mutants of these WRKY genes resulted in increased resistance and susceptibility against the nematodes, respectively (Ali *et al.*, 2014). This is obvious from various transcriptome studies of the host plants infected with nematodes that most of the downregulated genes belong to defense pathways of the plants. However, the most suppressed gene was AtRBoHB that entails the production of reactive oxygen species (ROS) (Szakasits *et al.*, 2009). However, interestingly, in a very recent study, it has been shown that nematodes are able to manipulate the genes involved in the production of ROS like RBohF and RBohD in their own favour for compatible interactions (Siddique *et al.*, 2014). In this study, they have confirmed that the nematodes stimulate host genes like RBohF and RBohD to generate ROS that results in the limitation of plant cell death coupled with the promotion of infection in the plant roots. Nonetheless, many stress-related genes were up-regulated in the soybean resistant line containing Rhg1 gene. These genes include those coding for the enzymes involved in the biosynthesis of ROS (Kandoth *et al.*, 2011). Kandoth *et al.* (2011) also indicated that the feeding sites induced by *Heterodera glycines* in the resistant line experienced severe oxidative stress coupled with imbalanced endoplasmic reticulum homeostasis, and both of these processes contribute toward the plant resistance. So this is still debatable that whether the genes involved in the synthesis of ROS are important for compatible interactions or resistance response.

The common facets of resistance have been explored during both susceptibility and resistance of soybean in response to soybean root-knot nematode using 454 sequencing technology (Beneventi *et al.*, 2013). In this transcriptome, the key role of glycosyltransferases and the main players involved in signal transduction, biosynthesis and deactivation of gibberellic acid has been demonstrated in the resistance reaction. It is also found that these genes participate in the signaling of methyl jasmonate and ROS production in response to nematode infection (Beneventi *et al.*, 2013).

The expression profiles of syncytia from the roots of soybean near-isogenic lines differing at Rhg1 (resistant against *H. glycines*) locus were compared, which revealed 1,447 differentially regulated genes between these two lines. Out of these differentially expressed genes, 241 (16.8%) were related to stress and defense responses (Kandoth *et al.*, 2011). They demonstrated the up-regulation of defense genes related to hypersensitive response, apoptotic cell death, and salicylic acid signaling in the syncytia of resistant line. The expression of genes related to defense pathways was triggered by pine wood nematode infection in the transcriptomes of two Pinus species (i.e., *P. pinaster* and *P. pinea*) (Santos *et al.*, 2012). The transcriptional profiles of *P. pinaster* species displayed an activation of regulatory genes and those involved in terpenoid secondary metabolism and pathogen establishment on the plant. However, on the other hand, in the transcriptome of *P. pinea*, numerous general stress responsive genes were highly expressed with main emphasis on genes related to oxidative stress.

Analysis of MicroRNAs (miRNAs) in soybean during the infection with soybean cyst nematode demonstrated 20 miRNAs with diverse expression pattern between resistant and susceptible cultivars (Li *et al.*, 2012). It suggests that miRNAs play vital job in soybean response to soybean cyst nematode and would have future prospects to understand plant-nematode interactions at molecular level.

**Metabolomics of Plant Nematode Interactions**

The nematodes are able to mediate the expression of genes controlling the synthesis of various metabolites. The genes, like sucrose transporters, starch synthases, myo-inositol oxygenases, myo-inositol phosphate oxygenase, sucrose UDP-glucose dehydrogenase (UGD) and ascorbic acid metabolism related to high metabolic activity, were preferentially upregulated (Hofmann and Grundler 2007; Hofmann *et al.*, 2007; Hofmann *et al.*, 2008; Afzal *et al.*, 2009; Hofmann *et al.*, 2009a; Hofmann *et al.*, 2009b; Siddique *et al.*, 2009; Szakasits *et al.*, 2009; Barcala *et al.*, 2010; Hofmann *et al.*, 2010; Siddique *et al.*, 2012).

Recently, Hofmann *et al.* (2010) studied the metabolome to evaluate the systemic local effects of *H. schachtii* infection in Arabidopsis roots. Elevated levels of many phosphorylated metabolites and specifically sugars were observed in syncytia. For instance, the infected roots showed accumulation of 1-kestose, which normally do not accumulate in uninfected Arabidopsis roots. Similarly, the metabolites like 1-kestose, raffinose and α,α-trehalose and some un-identified metabolic compounds revealed obvious accumulation at systemic level in the infected plant roots. This suggested that diagnostic and comprehensive metabolic profiling of nematode infected plants would infer some important information regarding plant nematode interactions. This further pointed out the smartness of nematodes that they are somehow able to trigger the remodeling of plant metabolic processes in their own favour.

**Conclusions and Future Prospects**

Plant parasitic nematodes use their secreted effectors for triggering the development of specialized feeding structures and successful parasitism in plants. Targeted silencing of known nematode effector proteins through *in planta* RNAi technology holds a great potential for inducing plant resistance against various species of nematode (Gheysen and Vanholme, 2007). So the knowledge of effector proteins from nematodes could point out many candidate genes for nematode resistance in crop plants. A recently developed virus-induced gene silencing (VIGS) method provides a new tool to identify putative genes involved in soybean-nematode interactions (Kandoth *et al.*, 2013). This method could be adapted to study genes associated with any root pathogenic or symbiotic associations. Similarly, very recently a micro device called StyletChip is invented. This is a microfluidic that chip could be launched to study stylet activity and for recording the host invasion as well as migration behavior and feeding of plant parasitic nematodes.

The transcriptomes of several plant species have shown many upregulated genes found to be involved in the development of nematode feeding sites. These genes could be potential candidates for site specific silencing in syncytia/giant cells to induce resistance in plants (Klink and Matthews, 2009). During compatible plant-nematode interaction, nematodes are somehow able to suppress the defense related genes. The overexpression of these genes has led to enhanced nematode resistance (Ali, 2012; Ali *et al.*, 2013a). It could be an interesting starting point for further studies to explicate how nematodes are able to suppress systemic plant defense mechanisms. Recently, a simple and versatile spreadsheet NEMATIC was developed for the *in silico* analysis of plant-nematode interactions based on transcriptome of various plant and nematode species (Cabrera *et al.*, 2013). This data-mining spreadsheet would be important for the understanding of the molecular bases related to feeding site formation and for the selection of genes as potential tools for biotechnological control of nematodes.

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**(Received 24 January 2015; Accepted 13 March 2015)**