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REVIEW ARTICLE

MOLECULAR AND GENETIC INSIGHTS OF ROOT-KNOT NEMATODES PATHOGENICITY: A REVIEW

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ABSTRACT

Plant parasitic nematode must develop molecular strategies to get around the plants defense mechanism in order to successfully enter and infect their host plants. Root cells in galls show altered gene expression, indicating morphological and physiological changes. Protein analysis and molecular databases help identify down-regulated and up-regulated genes. Microarray technology can provide large-scale gene expression data on plant-nematode interaction, aiding in understanding nematode selection and feeding site alteration, thereby identifying genes controlling cell differentiation and division. The first level of resistance is known as pre-infectional resistance, and it occurs before the nematode has entered the plant. Plants have evolved a second level of basic resistance, known as non-host immunity, against pathogens that can overcome the first level of resistance. The non-host immune system resembles the innate immune system of animals in many ways. For the enhancement of plant resistance against root knot nematode there is development of the latest plant nematode interactions and manifold approach outline in the review. We will emphasize on molecular mechanism, the way of pathogenicity the different proteins hormones needed, the resistance of host plant and the future perspective. Much research is being done on molecular mechanisms underlying interactions between plants and nematodes as well how plants react to various invasive diseases.

KEYWORDS

Root-knot nematode, Signaling pathway, Effector protein, JA-SA signaling

1. Root Knot Nematode Overview

The two apomictic species that are most significant commercially are *Meloidogyne incognita* and *M. arenaria, M. incognita* is a crop disease that is potentially the most destructive in the world and may be found in all temperate and tropical countries (as reviewed in Trudgill and Blok, 2001). M hapla and M incognita are the two whole- genome sequences phytonematodes accessible for now (Abad et al., 2008; Opperman et al., 2008). Conventional techniques used diagnosing nematodes based on morphometric traits are challenging since they require a lot of time training and experience (Eisenback et al., 1985). Previously, morphometric features were the only means of diagnosing Phyto nematodes (Aslan and Elekcioğlu, 2022). Meloidogyne species are recognized by a lot of available techniques. Among these approaches, Polymerase Chain Reaction (PCR) identify as the most exposed, rapid and precise one (Niu et al., 2012). It is a molecular detection tool that uses a variety of molecular techniques to know seven commercially pertinent Root Knot Nematodes very often found in lab for diagnosis. With the advent in DNA-based sequencing, multiple recurring sections of the18S,ITS1,5.8S regions of the mitochondrial DNA and ribosomal DNA array have also demonstrated to be useful tools for expressing Root Knot Nematodes (Landa et al., 2008)

2. Molecular Mechanism of Pathogenicity

Pathogenicity components produced by nematodes have been believed to play important roles in parasitism. Similar released molecules may be responsible for root tissue irruption or root cell separation into technical feeding cells (Hussey, 1989). After injecting secretory composites into the manufacturing cell or at a distance from the secreted feeding point, similar signals can be generated. Under an electron microscope, it was observed that the nematode uses its stylet to pierce the cell wall in order to eat. Multiple feeding tubes are formed when the stylet breaks through the tube membrane of the cell. These tubes are probably the result of proteins released by nematodes coming together. The feeding tubes, closely linked to the endoplasmic reticulum, can facilitate the extraction of nutrients from the far end of the feeding cell or act as molecular filters to aid in stylet inhibition (Hussey and Mims, 1991).

Various structures found in nematodes can serve as storage sites for molecules that are released during the interaction between plants and nematodes. The amphids, cephalic sensilla, and phasmids function as chemoreceptors secretory, much like the esophageal glands, excretory system, and rectum. When combined, these structures form a protective matrix that safeguards the eggs against predators and dehydration (Eisenback,1989). Furthermore, the nematode's cuticle plays a crucial role in controlling the passage of fluids across its body wall and could potentially release certain substances that the plant identifies as signaling molecules. The nematode possesses bilateral amphids, which are two highly sensitive organs situated on its cephalic region. Amphids consist of various cells, such as nerve cells and secretory cells. These amphids closely interact with the plant cells, which undergo division to form feeding cells.

It has been established that the amphids release several glycoproteins, a few of which play a role in perceiving environmental stimuli (Stewart et al., 1993). The oesophageal glands contain particular cells that are made to secrete fluids through the stylet. It has been proven that the functions of the oesophageal glands undergo alterations in the presence of a parasite (Hussey and Mims,1990). During the migratory stage of parasitism, the subventral glands display significant enlargement and are densely filled with vesicles, whereas the dorsal gland initiates active secretion production only subsequent to the process of sedentarization. Upon

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initiation of feeding by the nematode, a decrease in activity is observed in the sub frontal glands. Consequently, it can be observed that the subventral and rearward glands are situated in separate locations during the parasitic phase.

The secreted proteins collected were analyzed using 2D-electrophoresis, with the identification of the most prevalent proteins accomplished through micro sequencing techniques (Jaubert et al., 2002). A 14-3-3 protein and a calreticulin, known for their diverse functions in regulating signaling and metabolic pathways, as well as controlling cell cycle, cell proliferation, and apoptosis, were identified as some of the most plentiful proteins. In situ hybridization has revealed that the corresponding genes are specifically active in the esophageal glands of second stage juveniles. Animal parasitic flatworms synthesize 14-3-3 proteins, whereas animal parasitic roundworms and flukes generate calreticulin. Despite the uncertain nature of their function in animal parasites, their participation in various host parasite interactions suggests that this protein may play a role in the association between plants and nematode. The identification of secreted proteins in plants parasitized by bacteria, fungi, and nematodes can be achieved through the implementation of a candidate gene strategy.

This approach serves as an alternative method for the discovery of these proteins (Robertson et al., 2000; Smant et al.,1998). Key genes involved in the invasion of plant parasites consist of pectinolytic and cellulolytic enzymes, as well as detoxification enzymes. The insulation of these genes can be achieved through PCR modification or the use of expressed sequence tags (ESTs). Various studies have been conducted to analyze the gene expression differences in parasitic life stages, uncovering a set of enzymes responsible for breaking down cell walls that may play a role in root penetration. The presence of different isoforms of β-1, 4-endoglucanases and a cellulose binding protein indicates that nematode cellulases may work together in a synergistic manner or be part of multi-enzymatic complexes. It is difficult to comprehend the role of these proteins in the interaction because they serve various functions in other eukaryotes.

3. Genetic Factors Influencing Pathogenesis: RKN

The nematode's secreted pathogenicity factors are thought to be important during parasitism. According to these secreted products may play a role in the invasion of the root tissues or the differentiation of the root cells into specialized feeding cells (Grundler and Wyss, 1995; Hussey, 1989). These signals can be produced by injecting secretor compounds into the plant cell or at a distance from the differentiating feeding site.

One of the main obstacles to comprehending how nematodes drastically change root development to create and maintain giant cells is the identification of nematode-responsive plant genes. The genetic requirements of plants for the development and upkeep of these specialized cells are poorly understood. Since Meloidogyne can develop giant cells in several thousand host plants, the mechanisms by which nematodes influence plant cell metabolism should share regulatory features in different plant species. Identification of targets for the creation of novel strategies to engineer plant resistance would be made possible by a greater understanding of the plant response during the compatible interaction.

Affected root cells shows altered gene expression, indicating the complex morphological and physiological changes that occur during the establishment of giant cells (Gheysen and Fenoll, 2002; Williamson and Hussey, 1996). Methods utilizing protein analysis and the distinction between the expression of genes from healthy and infected roots have made it possible to identify both down- and up-regulated genes in galls. Molecular databases can be searched by computers to find potential uses for the products they encode. It has been demonstrated that there is an up-regulation of cDNAs homologous to a Myb-type transcription factor, which is a late embryogenesis-abundant protein, and a 20S proteasome α-subunit (Bird and Wilson, 1994; Van der Eycken et al., 1996; Vercauteren et al., 2001). For their true function to be revealed, this method needs to be combined with accurate cellular expression pattern analysis, knockout mutant characterization, and biochemical investigations. An examination of the function of nematode responsive genes in feeding cell development should be aided by the recent advancement of gene silencing technology in a variety of plants.

One sensitive technique for monitoring changes in gene expression in giant cells is the use of promoter- GUS fusion constructs, which allow for temporal and spatial expression analysis. Numerous plant genes that are likely to be involved in the creation or upkeep of feeding sites have been investigated. During the formation of giant cells, the expression of genes encoding proteins involved in the regulation of the cell cycle, reorganization of the cell wall, metabolic pathways, osmoregulation, and hormone responses was investigated. Thus, it has been demonstrated that M. incognita-induced tobacco giant cell reactivates the root-specific gene TobRB7, which encodes a putative water channel expressed in root meristematic and immature vascular cylinder regions (Opperman et al., 1994). Similar to this, early feeding cell formation is marked by the transcriptional activation of cell cycle markers like the mitotic cyclin CYC1At and the cyclin-dependent kinase CDC2a (Niebel et al., 1996). Furthermore, nematode feeding sites have down-regulated versions of other genes. For instance, a few days after nematode infection, the promoter of the plant phenylalanine ammonia-lyase I gene, which is extremely active in non-infected roots, becomes silent (Goddijn et al., 1993).

A promoter-less GUS gene construct was randomly inserted into the Arabidopsis genome using Agrobacterium transformation in order to discover new genes and gain a better understanding of the molecular mechanisms underlying giant cell induction and maintenance. This method was created as a component of the promoter trapping plan (Barthels et al., 1997; Favery et al., 1998). Screening for GUS expression following M. incognita infection reveals that the genes up-regulated giant cells are also expressed in healthy plants in various cell types or at different developmental times (Favery et al., 1998). These findings from the Arabidopsis plant validate the intricate morphological and physiological alterations that take place in cells during their transformation into nematode feeding sites and lend credence to the theory that 'normal' biochemical processes have been recruited to play crucial roles in permitting pathogen growth. The validation of this promoter trap approach came from the molecular characterization of RPE, a plant gene that is strongly upregulated and involved in the initial stages of giant cell formation (Favery et al., 1998).

It is likely that this gene plays a direct role in the biochemical composition of giant cells. A crucial enzyme in the pentose phosphate pathway, D-ribulose 5-phosphate 3-epimerase, is encoded by RPE. By generating the NADPH needed in various biosynthetic reactions (such as the synthesis of fatty acids and isoprenoid compounds like sterols) and by generating the carbohydrate intermediates needed for the synthesis of nucleotides and cell wall polymers, this metabolic pathway is essential to the growth of actively growing cells. The early stages of giant cell formation require RPE, as demonstrated by the analysis of homozygous rpe mutants. Ultimately, the expression of RPE at the root tips in proliferating cells and in a small subset of cells involved in the initiation of lateral roots suggests that there are common steps in the genetic regulation of nematode feeding sites and root formation.

Large-scale data on patterns of gene expression during plant–nematode interaction, and in particular about the genes that are down-regulated during giant cell establishment can be available by the application of microarray technology. Finally, comprehending how a nematode selects particular root cells and modifies them to serve as a feeding site can contribute to our understanding of typical cell development and aid in the identification of genes that regulate different aspect of cell differentiation and division.

4. Signaling Pathway

In order to ease the creation of feeding sites, plant parasitic nematodes (PPN) generate a number of structure, biochemical processes and molecular modifications in plant root cells (Ali, Azeem, Abbas, et al., 2017) . Nematode releases via their stylets have a major impact on these processes by initiating a chain of signals in the recipient cells. The sign of second-stage juvenile (J2) towards plant root via. Chemotaxis, which is mediated by host plants root exudates is the initial chain of signals in plant-nematode interactions (Kumar et al., 2017). PPNs reach cells of the roots and locate the vascular tissues in the absence of resistance reactions from the plant featuring the formation of Reactive Oxygen Species (ROS) alongside the accumulation of callose to signal feeding sites (Golinowski et al., 1996; Wyss and Grundler, 1992). The one and only food sources for the sedentary development of the nematode is the nematode feeding site through following inactive life cycle (Endo and Wyss, 1992; Grundler et al., 1997). SA as well as JA are important participants for the defence mechanism of plants by activating various signaling pathways (Bhattarai et al., 2008; Branch et al., 2004; Hamamouch et al., 2011). But rather than the usual JA signaling, SA signaling is principally linked to tomato resistance over *M. incognita* (Bhattarai et al., 2008; Branch et al., 2004).

5. Nematode Effector Protein

A growing number of pathogen nematode the effectors have been found to get involved in biological processes which promote conversion of the cells

being attacked onto biologically active sources.it significantly alters the host roots However, various other potential places of entry were additionally considered nematodes effector amino acids are synthesized in the esophageal glands and released throughout the hosts cells and tissues by means of stylet (Perry, 1996). In a subsequent study, it has been discovered that five *M. incognita* effector proteins were secreted after giant-cell growth and between cells movement across an apoplast of Arabidopsis roots (Vieira et al., 2011). There is scientific proof which suggests that the effectors of nematode that cause knotting in roots are also found inside the cells of their hosts. According to the M. incognita 7H08 effector candidate was anticipated to be directed towards the nucleus and possessed a conventional NLS (Huang et al., 2003). Furthermore, it has been demonstrated that the M.incognita 16D10 protein interacts with transcription components found in plants (Huang et al., 2006b). Lastly, it came to light that the secreted *M.incognita* EFF1 protein appeared localized in the nucleus of large cells (Jaouannet et al., 2012).

The target of the *M. incognita* 16D10 effector was found to represent scarecrow-like crop transcription variables, despite it being that the sole Meloidogyne effector has been effectively subjected to Y2H studies to yet (Huang et al., 2006). Mi-EFF1,an effector protein of *M.incognita,* has just been found in the nuclei of multinucleate NFSs and was suggested to be important in the control of host cells gene regulation (Jaouannet et al., 2012). However, the exact purpose of this effector remains unclear. a novel *M.javanica effector,* Mj-NULG1a, was found to have a similar internal location. It was intended to create appropriate connections with a host by targeting the nucleus of giant cells (Lin et al., 2013). Related to this, M.incognita calreticulin known as Mi-CRT had been identified in cell apoplasm and played a significant role in inhibiting the basic defence of affected Arabidopsis plants (Jaouannet et al., 2013; Jaubert et al., 2005; Jaubert, Laffaire, et al., 2002). Genes implicated in JA-SA signaling and callose production were downregulated in the Mi-CRT overexpression lines, indicating this suppression of basal defense after applying a PAMP, elf18 (Jaouannet et al., 2013)

It was proposed that during plant nematode interactions, the nematode effector protein Mj-FAR-1 from M javanica may be involved in regulating lipid-based molecular signaling and inhibiting JA mediated signaling (Iberkleid et al., 2013). Comparable research has also shown that many effector proteins that are involved in host plants baseline defensive reaction as well as repression (Mantelin et al., 2015). In general, most effectors that have been identified work primarily changing the host nuclear activities in order to produce NFSs (Ali et al., 2017). Some of today's newest genetic technologies, deep sequencing may be helpful for rapid research to give a comprehensive picture of the signaling processes governing plant-nematode interactions (Zhang et al., 2017). RNA sequencing of cells from glands may be used to comprehend how different effectors connected to the signaling pathway function (Maier et al., 2013). Similarly, genome editing methods like CRISPR-Cas9 can be applied for exploring functions of various gene in nematodes and plants which are connected with each other's favorable and unfavorable interactions. these genome editing technologies (GETs) may be useful in comprehending how R proteins from plan interact with nematode effector proteins (Andolfo et al., 2016).

6. Resistant Plant Responses

Plants are attack by various pest and infectious agent such as virus, fungus, nematode, bacteria, oomycetes on a regular basis. Fortunately, the bulk of interactions between plants and pathogens are incompatible because of the infection to find a possible host plant or to enlist the right batteries altering the enzymes required for parasitism. Furthermore, the interaction between the evolution of infectious agents and plants led to the development of a defense system that, in contrast to animals possessing both a natural and an immune system that is adaptable, is entirely organic (Zipfel and Felix, 2005). Major crop infectious agents such as cereals, soybeans, potatoes, tomatoes, and sugar beets are cyst and root-knot nematodes. Due to the scarcity of plenty of defensive genes in plant and absence of biological agents, crops are prone to these microorganisms which causes massive destruction of crop plants.

The annual global approximate losses resulting from nematodes that attack plants to be around US $ 125 billion (Chitwood, 2003). One control strategy is using varieties immune to nematodes. There are different functional and morphological levels of resistance to nematodes. Pre-infectional resistance is the initial stage of resistance, which develops prior to the nematode entering the plant. In order to ward off infections that are able to get previous their initial line of defense, plants have developed a second degree of fundamental resistance known as non-host immunity (Tomczak et al., 2008). The defense mechanism of the non-host has numerous parallels between the innate immune system of animals.

7. PRE-INFECTION RESISTANCE

Prior to causing damage to a plant species, a pre-parasitic juvenile of cyst and root-knot nematodes needs to hatch from the egg, attract the plant roots, and enter the plant tissue. The plant looks to be resistant to this nematode if the infectious juvenile is stopped at any of these stages. We're going to refer to this resistance as pre-infectional resistance because it develops prior to the pre-parasitic nematode having an opportunity to enter the plant. A tough cell wall surrounds plant cells to keep out outside invaders. However, a number of studies on the infection of resistant and disease-prone varieties by nematodes, as well as host and non-host plants demonstrate that nematodes easily enter both host and non-host plant roots, and that plant-parasitic nematodes rarely seem to be resistant to mechanical barriers (Kaplan, 1980). Nematicides, or naturally occurring repellents, are released by some plants, which act as a chemical barrier to keep nematodes out. When compared to isogenic cucumbers lacking this locus (Da Costa and Jones, 1971), cucumbers with the dominant Bi (bitter) locus draw significantly fewer M. incognita. Additionally, the decorative grass species Eragrostis curvula has high levels of pyrocatechol in its roots, which prevents Meloidogyne species from entering (Scheffer et al., 1962).

8. Immunity in Non-Host Plant Against Nematodes

Plants have developed a non-host immune system that is similar to animal innate immunity to fight off infections that can get past constitutive barriers (Zipfel and Felix 2005). The foundation of this resistance type is the identification of nonspecific factors, such as structures related to wounds and injuries that are came subsequently from pathogens during infection or directly obtained pathogen-associated molecular patterns (PAMPs) (Matzinger, 2002; Janeway Jr and Medzhitov, 2002). PAMPs are shared by all members so they functionally very important component (Chisholm et al., 2006). Two PAMPs that have been identified thus far are xylanase and chitin from fungi and flagellin from bacteria (Nürnberger and Lipka, 2005). Increased production of defense compounds like waxy substances, cutin, suberin, lignin, and callose, or increased production of oxidative reaction elements like reactive oxygen species (ROS), free radicals, and peroxidases, are examples of how non-host immunity in plants indicates up locally as changes and implementation of the plant's basal defense system (Kawalleck et al., 1995). It has been demonstrated that when plants become infected with nematodes, they strengthen their cell walls by accumulating callose at the stylet penetration site (Grundler et al., 1997).

9. Future Perspective and Research Direction

The recent rapid progress in genetic innovation has impacted the field of subatomic plant pathology and enabled the identification of novel effector properties at the molecular level in a wide range of plant microorganisms. Since most of these effectors are without arrangement homology to proteins with known capabilities, the persistent test will be to determine the commitment of these effectors to parasitism.

According to study, parasitic nematodes probably affect important developmental pathways and regulatory signaling that is greatly controlled by microRNAs (miRNAs) (Hewezi et al., 2008). It is a complicated subject to understand how nematode effectors regulate the expression and activity of miRNA genes for effective parasitism. Since miRNAs are conserved across a wide range of plant species, answering this query may reveal developmental pathways and common signaling networks in host plants that are targeted by distinct parasitic nematodes. It will soon be feasible to compare the parasitomes of various strains and virulence groups thanks to developments in the identification and isolation of esophageal organ cells from plant-parasitic nematodes. This makes it possible to correlate effector gene polymorphisms with certain detrimental or avirulent traits. Certain nematode effectors in this context are members of gene families and exhibit high rates of of changes in amino acid composition, especially outside the indication amino region. The study of comparable and unidentified mutation rates across all members of a specific nematode gene will be made possible by the availability of comprehensive parasitome data. This technique can be used to evaluate the role of positive selection on nematode virulence as well as identify the selective pressures causing sequence variation.

Determining these effectors' commitment to parasitism will be a persistent test, given the majority of them lack arrangement homology to proteins with established capabilities. Two plant-parasitic nematodes, M. incognita and M. hapla, have their whole DNA makeup readily available, and more nematode genomes, such as those of *H. glycine, G. pallida, G. rostochiensis, M. arenaria, M. javanica,* and *M. chitwoodi*, will probably

become available in the near future. Examining their genomes offers an excellent chance to pinpoint every genetic component accountable for parasitism. Understanding the infection mechanism and the host range evolution of these plant-parasitic nematodes is facilitated by comparing genomic data across different species of nematodes. Additionally, the contributions of horizontal gene transfer (HGT) to parasitism can be discovered using comparative genomic investigations. Certain effector genes seem to be acquired through several HGT events, particularly those associated with cell wall functions.

These genes are typically found in particular genomic regions, which are distinguished from one another by variations in the GC content relative to the core genome, the existence of mobile elements, and the lack of genes that are identical in genomes that are closely related. Studying these areas in worm genomes can reveal information about effector gene variety and evolutionary history. The identification of regulatory factors that guarantee coordinated expression of nematode effector genes in different esophageal organ cells will also be aided by genome sequencing. Effectors generated in various organ cells most likely have unique regulatory sequences to guarantee coordinated expression at various stages of parasitism, and genomic research will make it possible to locate precise regulatory patterns.

10. Conclusion

Conventional control methods are insufficient to counter the threat posed by nematode infections, which cause devastating crop losses due to their widespread spread throughout the world. Therefore, it will be easier to develop new methods to create plant lines that are more resistant to nematode infection if we understand the molecular underpinnings of plant-nematode interactions and identify important genes and proteins involved in the infection process and the plant resistance response. In this review we explored the different methods and techniques. The identification of potential genes that effect at the genomic level in a variety of plant diseases has changed molecular plant pathology as a result of recent advances in sequencing technology. Recognizing the significance of these effectors in generating parasitism remains a problem, since most of them do not resemble recognized protein activities.

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