



A Review on Plant-parasitic Nematode Mimics Acting as a Smart Tool for Establishing Parasitism in Host

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Molecular mimics are an excellent example of nature's survival tool adopted by different pathogens. Plant-parasitic nematodes especially the sedentary endoparasites like Cyst nematodes and Root-knot nematodes are one such dangerous pathogens which were mastered in mimicking their host proteins crucial for cell growth and development. At the time of infection, a nematode fight against the host immune response with simultaneously establishing its feeding site. Thus, this parallel reprogramming of plants cell growth and development at the feeding site is what make these pathogens the most dangerous and at the same time intrigued pathogen to study. Plethora of studies have demonstrated that different effector proteins like CLE peptide, AUX1, PHAN, WRKY, RALFs, LBD16, SPRYSEC etc. secreted by nematode mimicking genes playing role in lateral root

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development; growth hormone regulators; shoot meristem; procambium development; and in immune responses. This review is a brief focusing on genes that are mimics in nematode and can be utilized for biotechnological strategies of plant disease control.

Keywords: *Plant-parasitic nematodes; cyst nematode; root-knot nematode; effector proteins; mimic molecules; plant growth.*

1. INTRODUCTION

Parasites adopt various strategies to survive inside their host. Molecular mimics are the molecules which share structural, functional or immunological similarities between host and pathogens [1]. These molecules mimic host factors, ligands of several receptors, plant growth hormones etc. [2]. Host mimics released by pathogens most likely developed through convergent evolution or horizontal gene transfer [3]. Molecular mimicry is a shrewd strategy to intimidate structural, functional or immunological similarities of molecules that are shared between infectious pathogens and their hosts. Researchers have discovered molecular mimicry orchestrated by bacteria, nematodes and fungal pathogens infecting both the plants and animals [4]. Here, in this review we focus on the recent development and examples of molecular mimics in plant-parasitic nematodes (PPNs) infecting plants. PPNs poses a serious threat to agricultural crops [5]. Among them the most devastating are the sedentary endoparasites such as (i) cyst nematodes, CN (*Heterodera* and *Globodera* spp.) and (ii) root-knot nematodes, RKN (*Meloidogyne* spp.), [6]. Thus, these two groups drew attention of the plant protection scientists globally.

Sedentary endoparasites are known to manipulate the host pathways involved in root development to establish specialized feeding sites such as syncytia and giant cells by cyst and RKNs respectively. Giant cells followed by galls and syncytium could be considered as a *de novo* originated pseudo-organ in roots with similarities with the formation of post-embryogenic organs, e.g., lateral roots (LRs), adventitious roots (ARs) or nodules induced by rhizobia [7]. It has been observed that plants produce certain peptides in the feeding site that mimics the vital plant transcription factors and other molecular components which are required by plants for lateral root development [8–10]. A parallelism between plant lateral root and root-knot formation has been well documented based on the similar expression patterns of genes encoding transcription factors and other regulators [11]. In

nematodes this crucial role of mimicking is performed by effector proteins produced by esophageal glands. The effector proteins hijack the plant root development process to establish feeding site for their own survival [12]. Nevertheless, there are different types of molecular components secreted by nematodes imitating the function of various plant proteins and components for specific functions. This review discusses about these molecular mimics of PPNs in brief.

1.1 Effector Proteins and their Significant Roles

Plant parasitic nematode secretes protein molecules during root invasion through needle like stylet, these molecules are effectors. Majority of the effectors are secreted by esophagus glands (2 Sub-ventral and one dorsal gland) [13,14]. These effectors target cell wall, apoplast, cell membrane and host defense system. Effector proteins of nematodes have earlier been studied only for their role in host parasitism [15,16], Recently the attention has been shifted towards investigating the other important functional role of nematode secretions like control of plant hormone pathways, controlling plant homeostasis and other key signaling pathways; during the course of parasitism [17,18], including effectors of phytonematodes [16,19,20]. Combinatorial approach of transcriptomics with bioinformatics of nematode esophageal gland cell aided in discovering role of numerous parasitism genes in sedentary endoparasites like RKN and cyst nematodes. . Many effector proteins have been identified as mimics, these are INFLORESCENCE DEFICIENT IN ABSCISSION signaling peptide, LATERAL ORGAN BOUNDARIES-DOMAIN 16 (LBD16), CLAVATA like proteins (CLE-peptides), Procambium associated genes (ATHB8, REVOLUTA (REV), PHABULOSA (PHB), PHAVOLUTA (PHV) and CORONA (CAN, PHAN, KNOX, WRKY23, Regulators of plant hormones (AUXIN) and TRACHEARY ELEMENT DIFFERENTIATION INHIBITORY FACTOR TDIF-TDR (TDIF receptor)-WOX4, and receptor

kinase FERONIA and its peptide ligands, rapid alkalization factors (RALFs).

2. DIFFERENT TYPES OF PHYTO NEMATODE EFFECTORS AS MOLECULAR MIMICS IN NEMATODES

2.1 Inflorescence Deficient in Abscission Signaling Peptide (IDA)

IDA gene is one of the conserved gene family in dicots regulating vital functions like cell separation, floral organ abscission and lateral root emergence. There have been many reports indicating presence of IDL like mimics in different pathogens [21,22]. An elevated expression of IDL6 in Arabidopsis during infection by *Pseudomonas syringae* increased susceptibility to the pathogen. Its mimic peptide has been identified in *Meloidogyne incognita* [22] known as MiIDL-1 like protein. RNAi mediated silencing of MiIDL-1 revealed reduced infection of *M. incognita* in transgenic Arabidopsis. IDA-like genes such as MiIDL1 and MiIDL2 have also been found in other *Meloidogyne* spp. [23].

2.2 Lateral Organ Boundaries-Domain 16 (LBD16)

Establishment of syncytia or gall development have certain similarities with plant lateral root development on the basis of the type of genes/transcription factors or regulators that play role. One of the most important class of gene family, LATERAL ORGAN BOUNDARIES-DOMAIN 16 (LBD16) in plants has its homologous sequence found in PPNs. The studies have shown that the expression of LBD-16, mimics the pathways that occurs during lateral root development at the site of gall formation [10, 24]. ALF4, a crucial gene involved in LR initiation, callus formation, and reconnection of vascular arteries after grafting, is also required for proper gall development [25]. Although a direct relationship between the pathways involving development of lateral root and gall formation is yet to be established. But the existing findings does suggest the mimicry role of nematode effector peptides.

2.3 CLAVATA Like Proteins (CLE-peptides)

Among the most studied and characterized effector of root-knot nematode is 16D10 proteins. It has been found to be a very good target for developing management strategies based on

RNAi technology for nematodes [12]. The Mi16D10 gene has a striking similarity with the plant CLAVATA like proteins (CLE-peptides). The CLE proteins functions during shoot stem meristem differentiation and vascular development. The nematode CLE-peptide interacts with CLE plants CLE receptors to elicit CLE like differentiation at the site of gall formation [26]. A study has reported the role of that CLE receptor CLV1, the CLV2/ CRN receptor complex and RPK2, which transmit the CLV3 signal in the SAM, are involved in nematode CLE peptide perception and proper feeding cell formation in Arabidopsis and soybean [27]. By interacting with AtSNAP2 and AtPR1 via their respective t-SNARE domains and uncharacterized N-terminal fragments, as well as by significantly suppressing both AtSHMT4 and AtPR1, HsSNARE1 encourages cyst nematode disease [28].

2.4 Procambium Associated Genes

The plant vascular system is the heart of transportation of all the required nutrients, minerals, water and signals. This vascular system consists of procambial cells which differentiates to form different cells that together forms the vascular system [29]. As we know that for parasitic nematode to survive in its host cell requires a constant flow of nutrients. It secretes peptides of similar functions that of procambium cells. In a study comparative transcriptome of gall and normal root revealed a similarity in their transcriptional profile. Further more the experimental validation confirmed the presence of procambium marker genes like ATHB8, REVOLUTA (REV), PHABULOSA (PHB), PHAVOLUTA (PHV) and CORONA (CAN). The promoters of numerous procambial marker genes, including ATHB8, TDR, and WOX4, were active in *Heterodera schachtii*- and *M. javanica*-induced galls as well as *M. incognita*-induced syncytia which alter the host's control over the vascular stem cells' developmental regulation during gall formation [30].

2.5 PHAN, KNOX, WRKY23, Tracheary element Differentiation Inhibitory Factor TDIF-TDR (TDIF receptor)-WOX4

Genes that play role in development of roots is the prerequisite need for the nematode to establish these feeding sites (giant cell or syncytia). Genes like PHAN and KNOX have

been reported in the tomato giant cells [8]. Similar class of genes have been found during the interaction of Rhizobia with its host in host roots [10]. Thus, processes like proliferation and differentiation of cells is what nematode relies upon for its establishment. In 2017, plants infected with *Heterodera schachtii*, a cyst nematode, were studied and a connection between the WOX-4 pathway promoting procambial meristem cell proliferation and nematode CLE-signaling pathway was clearly demonstrated [26]. However, it is still unclear how different pathogens have their unique molecular and cellular mechanism for host invasion and parasitism. In lieu of that, an attempt to study this aspect concerning feeding site development related molecular and cellular processes was carried out in Arabidopsis infected with RKNs. Lateral Organ Boundaries Domain (LBD)/Asymmetric Leaves2-like (ASL) transcription factors were common in hormone induced calli, lateral and adventitious roots [31]. A member of this TF family, LBD16, was reported as a switch between those developmental, environmental, and biotic (RKNs) signals triggering cell proliferation and/or formation of a new organ [10,24]. Thus, this again indicates the utility of this aspect of lateral root development for advanced technological based management strategies.

2.6 Regulators of Plant Hormones (AUXIN)

The involvement of plant growth hormones as regulatory mechanism for growth and development of organs and various process is not unknown. One such vital and most studied hormone is Auxin, which is essential for root development [32]. The auxin influx and efflux-based transportation is dependent on transmembrane proteins like AUXIN Resistant 1 (AUX1) and Like AUX1 (LAX) and PIN domain containing proteins, respectively [33]. Apparently crucial role of auxin inducing development of syncytia by cyst nematode was documented [34]. The study also reported downregulation in the transcript level of PIN1 protein, required for auxin efflux during auxin transport. Another study also reported elevated expression level of AUX1, protein responsible for auxin influx in the primary syncytial cells [35]. An interaction between Hs19C07 effector secreted by *H. schachtii* was and auxin influx protein LAX3 produced in Arabidopsis roots was reported [36]. Likewise, role of auxin during gall formation by RKN has also been an area of interest for biologists. An

induced synthetic auxin to the peach plant *Prunus persica* resulted in enhanced *M. javanica* infection. The *Prunus persica* is otherwise a resistant host for nematode infection [37]. The susceptibility of soybean plants to SCN was similarly increased by overexpression of SCN-27D09 (Family-Hg10A07) in the hairy root of soybeans [38]. Downregulation of root knot nematodes *MigPSY* (*Peptides containing Sulfated Tyrosine*) transcript with highly sequence similar to to both bacterial RaxX and plant PSYs reduces root galling and egg production [39]. There are other similar reports of imparting induced auxin to plants and increase in RKN susceptibility [40]. Although plethora of studies indicating the role of auxin in giant cell formation reported, importance of factors regulating the transport this auxin is an area understudied.

2.7 Plant Immune System Regulating Genes (RALFs)

Recently, it has been observed that RKNs not only can produce molecules that can mimic the host growth and differentiation related proteins but also secretes proteins that can mimic plant immune regulators, receptor ligands and cell expansions [41,42]. The plant receptor kinase FERONIA and its peptide ligands, rapid alkalization factors (RALFs), are essential for regulating plant immune responses and cell expansion. Thus once, hijacked nematode is successful in its parasitism. Receptor like-Kinases (RLKs) are a class of transmembrane receptors that can sense signals at the plasma membrane (Shiu and Bleecker, 2001). One such most commonly studied RLK is FERONIA (FER), is an example of plant immune regulons [43]. These immune receptors are mimicked by other pathogens than nematodes as well. For instance, studies reporting enhanced blast resistance in FER-like mutant of rice [44]. Another member of plant immunity, ligands for FER, such as Rapid alkalization factor 23 (RALF23) inhibits the receptor scaffolding function of FER thereby negatively regulating FER regulation for antibacterial resistance [45]. The FER receptors and their RALF like ligands (Control plant immune signalling) have been exploited by many other pathogens in facilitating parasitism [43]. There are eight putative RALF-likes were identified in nematode genomes: three putative RALF-likes in *Meloidogyne arenaria*, one putative RALF-like in *Meloidogyne enterolobii*, six putative RALF-likes in *Meloidogyne floridensis*, three putative RALF-likes in *Meloidogyne hapla*, four

putative RALF-likes in *M. incognita*, and one putative RALF-like in *Meloidogyne javanica* [42]. In the recent study a *MiRALF1/3 RNAi* line via host-induced gene silencing (HIGS) was developed and reduction in RKNs parasitism was observed. However, the overexpressed lines expressing *MiRALF3* resulted in facilitation of nematode parasitism [46]. The pathogenicity of root knot nematode was significantly decreased in Arabidopsis plants through gene silencing of effector *Minc03329* which contains signal peptide for secretion and a C-type lectin domain [47]. *StCLV2* and *StRPK2* are involved in parallel CLE signalling pathways that are crucial for PCN parasitism, and manipulating nematode CLE signalling may be a practical strategy to engineer nematode resistance in crop plants, including potatoes [48].

Table 1. List of Mimic Genes/Proteins

Mimic Gene/Protein	Reference
HsSNARE1	[28]
SCN-27D09	[38]
MigPSY	[39]
StCLV2, StRPK2	[48]
Minc03329	[47]
MiRALF1	[42]
MiRALF3	[42]
MiIDL1	[22]
CEP like peptide	[49]
CKs	[50]
HgCLE2	[51]
Mi16D10	[52]
GrCLE1	[53]
Hs19C07	[36]
Hs10A07	[13]
Chorismate mutase	[54]
Annexin like protein	[55]
SPRYSEC	[56]
CLV3	[57]

3. CONCLUSIONS

In order to establish itself in the host root, parasitic nematodes have evolved in terms of secreting not only effector proteins that aid in its growth and development and protecting from plant attack. But also, are masters in secreting proteins that could exactly mimics the host molecular and cellular pathways genes essential for the cell differentiation and organ development. Thus, by hijacking its host molecular machinery both cyst and RKN nematodes survive in its host. The accumulating evidences, suggests numerous such class of genes that are mimicked by parasitic nematodes

and the number is still going. These are enough evidence to start exploring and exploiting this aspect of parasitic pathogens for developing new biotechnological tools-based strategies. In summary, future studies focusing on highly conserved molecules across plant kingdom, that are mimicked by various pathogens (nematodes, bacteria and fungi) will facilitate the programs for developing pathogen resistant varieties.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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