**Plant defense mechanisms against plant parasitic nematodes**

**Abstract**

Plant-parasitic nematodes (PPNs) feed on plant tissues and cause yield losses in agricultural crops. PPNs enter the host plant by penetrating host cells and suppress plant defense response. The defense mechanisms in plant may involve a physical barrier, synthesis of anti-nematode compounds, and transcriptional regulation of defense-related genes. Through strengthening their cell walls plants make physical barriers to PPNs attack. PPN attack produces reactive oxygen species (ROS), anti-nematode compounds or secondary metabolites which are lethal to PPNs. Moreover, some metabolites impede hatching; reduce movement or host searching ability; restrict completion of life-cycle. This review highlights the recent findings of plant defense mechanism against PPNs which will be helpful in developing innovative nematode management strategies and improve food production.

*Key words:* Plant-parasitic nematodes, Plant defense system, Reactive oxygen species, Plant defense-related genes, Plant anti-nematode compounds, Plant physical barrier, PRRs, PAMPs.

1. **INTRODUCTION**

Plant-parasitic nematodes (PPNs) invasion and feeding causes plant damage leading to a considerable yield loss in agricultural crop throughout the world. There are about 4100 nematode species that parasitize hundreds of crop plants and cause significant damage. They are widely distributed and highly adaptable parasite (Jones *et al*.,2013); causing estimated global economic losses of USD 173 billion annually (Elling, 2013). According to their mode of parasitism, PPNs can be classified as endoparasitic, semi-endoparasitic and ectoparasitic (Palomares-Rius *et al*., 2017). *Trichodorus* spp., *Longidorus*spp., and  *Xiphinema*spp. are ectoparasitic nematodes, they penetrate their stylet for feeding and remain outside the plant, whereas endoparasitic nematodes , both migratory (*Pratylenchus* spp., and *Anguina* spp.) and sedentary enter the host plant and feed on the plant tissue. Sedentary endoparasites nematodes like root-knot nematodes (RKN), *Meloidogyne* spp., and the cyst nematodes (CN) *Globodera*spp., and *Heterodera*spp., create their feeding sites near to vascular region and feed on the cell cytoplasm. Successful host-parasite interaction needs entering nematodes inside the host plant by invading physical barriers. To aid penetration, nematode juveniles thrusting their stylet and breakdown of the cell wall by various enzymes. A balance is maintained between plants and PPNs, including various signal exchanges (Siddique *et al*., 2022). As the plants are stationary, they utilize a variety of host defenses concerning both structural components as well as chemical compounds. Both constitutive or pre-formed and inducible defense responses occur after invasion of nematodes. Signaling of these actions is essential for showing defense responses against nematode attack and their spread. This review summarizes the recent findings on how plants recognize PPNs and defend themselves in reaction for penetration and feeding by PPNs. Knowledge about the plant defense mechanism against PPN attack is of crucial importance in developing successful control strategies (Giebel, 2003; Abd-Elgawad, 2022).

1. **PLANTS DEFEND THEMSELVES FROM NEMATODE INFECTION BY SEVERAL WAYS**

Plants adapt their defense strategies to defend nematode attack, while nematodes frequently try to avoid plant defenses. Chemical signals are generated and transmitted in different parts of plant to defend against nematodes (Kaplan & Keen,1980; Gillet *et al*.,2017; Zou *et al*.,2024).

**2.1. Ability of the host plants to identify the invading pathogen:** Host plants are able to sense, recognize and responses accordingly to the invading pathogen (Desmedt *et al*., 2020). In order to identify the invading pathogens there are two types of recognition system at the molecular level in host plants. These include pattern recognition receptors (PRR) or specified protein receptors and microbial or pathogen-associated molecular patterns (MAMPs or PAMPs) (Chen *et* *al*., 2024). PAMPs are often present at low concentrations and induce specific defense responses (Manosalva *et al.,* 2015). PPN infection may cause damage to the plant tissues which can activate wounding-related plant defense responses through release of damage associated molecular patterns (DAMPs) (Siddique *et al*.,2022). Mendy *et al*., (2017) demonstrated that J2 of *H. schachtii* also induce general PAMP recognition reactions. Release of PAMPs or DAMPs, after that activation of complex signaling pathways commences pattern-triggered immunity (PTI) against an invading pathogen (Przybylska and Obrępalska-Stęplowska, 2020). Sato *et al*., (2019) described that Ascarosides (evolutionary conserved group of pheromones derivatives of dideoxysugar ascarylose) and oligogalacturonides released by different PPNs are nematode-associated molecular patterns (NAMPs) are detected by the host plant. De Lorenzo and Cervone, (2022) reported Ascaroside (Asc#18) as a NAMP of *Heterodera glycines* .The MAMP/ NAMPs activate a series of immune responses (PTI) such as the production of reactive oxygen species (ROS) and secondary metabolites, cell death around the PPN-migratory tract, reinforcement of cell walls and activation of the salicylic acid (SA) and jasmonic acid (JA) signaling pathways (Manosalva *et al*., 2015; Desmedt *et al*., 2020; Yuan *et al*., 2021). Nematodes can manipulate plant anatomy and physiology through the secretion of effector molecules that impede plant defenses and promote nematode feeding site establishment. Thus, plants activate their immune response by recognizing the nematode invasion leading to effector triggered immunity (ETI) (Diaz-Granados *et al*., 2016; Khan and Khan, 2021). Both the ETI and PTI are activated by the extracellular receptor-like kinases/proteins comprising nucleotide-binding domain leucine-rich repeat proteins (NB-LRRs) and/or cytoplasmic kinase (Teixeira *et al*., 2016; Meresa *et al*.,2024 ; Zhiqi *et al*.,2025). For example, host plants recognize effectors from RKNs and CNs through NB-LRR receptors (Jones and Dangl, 2006; Diaz-Granados *et al*., 2016). Gr-Vap1 and GrEXPB2 are effector allergen-like protein from *Globodera rostochiensis* and 10A06 from *Heterodera glycines* (Lee *et al*.,2018; Lozano-Torres *et al*.,2014; De Lorenzo and Cervone, 2022) that can activate ETI in plants.

**2.2.Cell wall as physical barriers in plant:**

A plant cell wall is consisting of various polysaccharides, proteins, and polyphenols that may be change during growth and development in different tissues. The cell wall acts as a physical barrier and can detect any instability caused by biotic and abiotic stresses through specific immune signaling pathways (Swaminathan *et al*., 2022). Structure and composition of cell wall, waxes or hairs are physical barriers in plant (Malinovsky *et al*.,2014; Molina *et al*.,2024). Through the process of callose deposition and lignification, plants strengthen their cell walls to make it difficult for nematode to penetrate and feeding. Biosynthesis and deposition of lignin in plant tissues increases its resistance to degradation by enzymes ([Menden *et al*., 2007](https://www.scielo.org.mx/scielo.php?pid=S0185-33092016000100043&script=sci_arttext&tlng=en#B36)), reduces the transmission of toxins secreted by the pathogen and of nutrients from the host to the pathogen, and also a cause for the production of toxic precursors and free radicals. In peripheral tissues lignin are syntheses through either mechanical wounding, or infection by pests and pathogens .Similarly, plants may deposit phenolic substances that are toxic substances formed in cell walls or epidermal tissues ([Nicholson and Hammerschmit, 1992](https://www.scielo.org.mx/scielo.php?pid=S0185-33092016000100043&script=sci_arttext&tlng=en#B38)). Certain plants have glandular trichomes that secrete compounds, act as repellents or even trap nematodes. Suberin and lignin-based Casparian strips have been observed in roots during RKN infection. Thus, different types of cell wall compositions form a part of inducible defense mechanism in infested plant (Holbein *et al*., 2019).

**2.3. Reactive oxygen species:** Reactive oxygen species (ROS) are important regulating factor in metabolic activity pathways in plants for the growth and development as well as disease resistance (Zheng *et al.,* 2025). The aerobic respiration of many organisms including higher plants is strongly inhibited by negative ions such as cyanide, azide or sometimes CO. The inhibitory effect of these ions affects the electron transport system. The pathway allows the organism to continue cellular respiration in the presence of cyanide where electrons flow through an alternative oxidase. This type of respiration is said to be cyanide resistant respiration (Feng *et al*.,2013). During the early stages of nematode invasion, the plant cells generates an unfavourable oxidative environment by formation of hydrogen peroxide with superoxides as intermediate and activate local and systemic defense responses (Torres, 2010; Melillo *et al.,* 2011; Lin *et al*.,2016). The rapid release of superoxide and hydrogen peroxide, is a key mechanism to damage nematode tissues and inhibit their development (Goverse and Smant, 2014). The early detection response to nematode attack aims to detain nematode to their entry sites through on-site programmed cell death, known as hypersensitivity (HR) (Balint-Kurti, 2019). Marinho *et al*., (2014) observed that HR is mostly toxic for microbial invaders, as H2O2 reaches an estimated concentration of 5–10 mM. HR cells shows the symptoms of an accumulation of cytoplasm around the invading pathogen, decrease in flaccid membrane potential, loss of electrolytes from cells, or loss of plasmolysing ability of cells (Morel & Dangl, 1997). Some of the tomato, cowpea, potato and pea cultivars shows hypersensitively to *M.incognita*, *G.rostochiensis* and *H.goettingiana* infection by showing the symptoms of extremely vacuolated cytoplasmic contents of syncytial component with a thin layer around cell walls (Leone *et al*., 2001; Oliveira *et al*., 2012; Price *et al*.,2021). However, Siddique *et al.,* (2014) observed a promoting role by ROS (H2O2) in cyst nematodes infection. In order to neutralize the excess ROS, plants start initiating antioxidant defense mechanisms in the later stages of infection (Goverse and Smant, 2014; Holbein *et al*., 2016). The toxic effect of superoxides is diluted by the action of superoxide dismutase (SOD) making disproportionate to H2O2 and O2 . H2O2 is further diluted by catalase or by peroxidase within the cell (Sies, 2014). Antioxidant defense mechanism enables the expression of some other genes encoding ROS-scavenging enzymes (thioredoxins, glutathione peroxidase, xanthineoxidases, oxalate oxidases, amine oxidases) (Delaunois *et al*., 2014; Iberkleid *et al*., 2015; Alhoraibi *et al*., 2019). The 10A06-homologue effector secreted by *H. schachtii* interacts with *Arabidopsis* spermidine synthase 2(SPDS2), which increases the activity of polyamine oxidase (PAO) and consequently enhances the antioxidant pathway in host plants (Hewezi *et al*., 2010).Strong oxidative bursts have been identified through up-regulation of several peroxidases in early responses of resistant wheat cultivars against *Heterodera avenae*, (Kong *et al*., 2015). Non-expressor of pathogenesis-related 1(NPR1), a key regulator is associated with a decrease in the number of galls and egg masses in response to *M. incognita* infection (Priya *et al*., 2011; Siddique *et al*., 2014). In *Arabidopsis*, ten homologs of respiratory burst oxidase homologs (RBOHs) are prominent during nematode invasion (Mittler *et al*., 2011). Vicente *et al*., (2015) observed a correlation between nematode virulence and resistance to oxidative stress in pinewood nematode, *Bursaphelenchus xylophilus*. However, Das *et al*., (2010) observed that RKN infection is not sufficient to trigger ROS in resistant cowpea and leads to a delayed defense response. Nitric oxide (NO), also another ROS affecting nematode motility, feeding, and development plays a role in plant defense (Khan *et al.,* 2023). NO can control cell death in plants by S-nitrosylating nicotinamide adenine dinucleotide phosphate (NADPH) oxidase (Yun *et al*., 2011). Moreover, ROS involved in reinforcing plant cell walls and inducing callus deposition to limit pathogen entry. In resistant tomato roots infected with *M.incognita,* found to increase the callus deposition in cells surrounding the necrotic areas (Camejo *et al.,* 2016).

**2.4.** **Transcriptional regulation of defense-related genes**: In plants the defense related genes are activated by transcription factors (regulatory proteins) in response to stress (Ling *et al*., 2017). The regulatory proteins from different families such as WRKY, MYB, AP2 and Bzip are induced in response to various biotic and abiotic stresses (Jiang *et al*., 2017). These regulatory proteins bind to the promoters of plant genes for establishment of nematode feeding sites PPNs or bind to the suppressors of host genes involved in resistance responses. In case of ETI, pathogen effectors are recognized by plant resistance proteins known as R proteins (Andersen *et al*., 2018). Generally R proteins induce a rapid and powerful immune response leading to a hypersensitive response. After J2 invasion, the expression of various genes with many different functions is induced, which is associated with defense responses (Gheysen and Fenoll, 2002). In an incompatible host-parasite interaction the single dominant resistance genes from plants interact exclusively with analogous virulence protein (Avr proteins) in the nematode (Ali *et al.,*2017). Kaloshian and Teixeira (2019) identified nucleotide-binding LRR (NB-LRR) proteins that induce resistance to nematodes. Postnikova *et al*., (2015) found that the genes encoding LRR and TIR-NBS class proteins were up-regulated in a resistant variety of alfalfa against *M. incognita*. Similarly, cyst nematode (*Globodera pallida*) secreted effector like SP1a and RYanodine receptor (SPRY) domain (SPRYSEC) proteins Gp RBP-1, that triggers with Ran GTPase-activating protein 2 (RanGAP2) and GPA2 leading to cell death in potato (Sacco *et al*., 2009). R-genes Ma, CaMi, Mi-1.2, Mi-9 and Mex-1 gene offer resistance against RKN (Claverie *et al*., 2011) whereas Hero-A, Grol-4, and Gpa2 gene gives resistance against CN (Sato *et al*., 2019). Although a single gene in the cluster may offer resistance, multi-gene families are also found in plant R-genes (Friedman & Baker, 2007). Although ten genes are recognized for resistance against *Meloidogyne* spp. in tomatoes, only seven genes (Mi-2, Mi-3, Mi-4, Mi-5, Mi-6, Mi-9, and MI-HT) can activated at high temperatures, e.g., above 32oC (El-Sappah *et al*.,2019; Devran *et al*.,2023). Likewise, H1 locus harbors a cluster of intracellular nucleotide-binding (NB)-LRR proteins (NLR) candidate genes which is a single dominant R-gene recognized for resistance against cyst nematode (*Globodera rostochiensis*) (Abd-Elgawad, 2022). In resistant varieties of peanut, the number of induced proteins like putative PR proteins, patatin-like proteins and other stress-related proteins is also found as defense responses (Huang *et al*., 2023). Resistant tomato genes encoding the defense in protein and subtilisin-like protease, through the production of phytoalexins and stress-induced proteolysis (Figueiredo *et al*., 2018). Thus the plant defense system depends on activating many known and unknown R-genes or Quantitative Trait Loci (QTLs). Resistance genes could be cloned and transferred from some plant cultivars to others. Recognition and cloning of such genes with desirable traits in a plant species can allow the transfer of resistance into other susceptible cultivar(s) of the same species, or even into cultivars of different species. for examples, the Mi-1.2 from tomato against RKN (*Meloidogyne incognita*), Gpa-2 from potato against potato CN (*Globodera pallida*) and Hero A from tomato against potato CNs (*G. pallida* and *G. rostochiensis*) and Cre loci from *Aegilops* spp. against cereal CN (*H. avenae*) in wheat (Kong *et al*.,2015). Therefore, plant genes responsible for PPN resistance are very useful in lowering PPN population levels and enhancing crop yields. **2.5.Phytohormone biosynthesis and signaling:** Hormones synthesized by plants like jasmonate (JA), salicylic acid (SA), ethylene (ET), and auxin involve in defense strategies against PPNs (Hewezi,2015; Gheysen & Mitchum ,2019; Sikder *et al*.,2021). Salicylic acid (SA) and jasmonic acid (JA) can play an important role in the expression of innate and R-gene-associated defense responses (Zhang *et al*.,2025). SA regulates many genes encoding pathogenesis-related (PR) proteins, mainly PR1 and PR proteins, while the JA regulates the expression of genes encoding defense in thionin, PR3 and PR8 proteins ([Kumar](https://onlinelibrary.wiley.com/authored-by/Kumar/Paramdeep) *et al*., 2025). Molinari and Loffredo (2006) speculated that *G. rostochiensis* may trigger early but temporary rise of SA to cause early and profuse necrosis. Nguyen *et al*., (2016) did not find increased susceptibility to *H. schachtii* in *Arabidopsis* SA signaling mutants. Wang *et al*.,(2018) demonstrated that temporary expression of chorismate mutase by *M. incognita* in *Nicotiana benthamiana* cause a lower SA levels. Over expression of chorismate mutase or an isochorismatase by *Hirschmanniella oryzae* in rice also enhances susceptibility to this nematode (Bauters *et al*., 2020). Kempster *et al*., (2001) demonstrated resistance in tomato against *M. incognita* (Molinari, 2015), *M. javanica* (Moslemi *et al*.,2016) and *M. chitwoodi* (Vieira dos Santos *et al*., 2013), and also in white clover against *Heterodera trifolii* (Kempster *et al*.,2001) through application of SA.

JA may play a major role in plant-nematode interaction in the roots of both monocotyledons and dicotyledonous plants (Mendy *et al*., 2017). JA acts as a signal molecule, triggering the production of plant defenses like proteinase inhibitors, terpenoids, and oxylipins. These plant metabolites contribute to the overall defense against nematodes (Gheysen & Mitchum, 2019). Przybylska & Spychalski, (2021) suggested the role of JA- and SA-mediated pathways in maize infected by *M. arenaria* that showed changes in the expression levels of genes encoding the PR3, PR4 and PR5 proteins.Several workers have demonstrated that JA signaling is implicated in plant defense against *M. incognita* , *M. chitwoodi* ,*M. graminicola* ,*H. glycines* and *H. schachtii* (Cooper *et al*.,2005; Kammerhofer *et al*., 2015; Zhou *et al*., 2015; Lin *et al*., 2017). Zhao *et al*., (2015) observed that highly susceptible tomato plants to *M. incognita* over expressing miR319and to *M.javanica* over expressing MjFAR showed lower JA levels. This observation is associated with lower expression of the JA-responsive proteinase inhibitor 2; however, some genes in the JA pathway are expressed at higher levels in these roots (Iberkleid *et al*., 2015).

Ethylene (ET) is a gaseous hormone interacting synergistically with auxin to control root cell development and root hair growth (Strader *et al*., 2010; Kyndt *et al*., 2016)). Arabidopsis roots exposed to an ethylene (ET)-synthesis inhibitor attracted more *M.hapla* J2 than in control roots and that ET-overproducing mutants were less attractive to the zone of elongation of roots ( Fudali *et al*., 2013). Nahar *et al*., (2011) observed that ET and JA synergistically induced a systemic defense response against *M. graminicola* in rice.

Strigolactones (SL) are carotenoid-derived hormones that regulate various plant developmental and adaptation processes as well as many biotic and abiotic stress responses (Kun-Peng *et* *al*.,2018). In tomato, silencing of SL biosynthesis genes resulted in higher infection rates of *M.incognita* (Xu *et al*., 2019).

Gibberellic acid (GA) is well known hormone that stimulate plant growth by the degradation of DELLAs, a class of growth-repressing nuclear proteins. Studies in *Arabidopsis* revealed that GA decreases JA action and increases SA signaling and perception (Navarro *et al*., 2008; De Vleesschauwer *et al*., 2016).

Abscisic acid (ABA) may intervene both positive and negative defense responses by cross-talking with JA, SA and ET signaling pathways (Yang *et al*.,2019). Nahar *et al*., (2012) speculated that the rice plant response against root lesion nematodes depends on the balance between ABA,SA,JA and ET.

**2.6. Production of anti-nematode phytochemicals:** Both constitutive and inducible secondary metabolites are synthesized in plants against nematodes which is known as ANPs. Plants obtain constitutive forms of metabolites that do not require any pest or pathogen invasion. Some of the secondary metabolites, like terpenoids, saponins, benzoxazinoids, organosulfur compounds, alkaloids, chlorogenic acid, and glucosinolates have been shown to inhibit nematode activity (Desmedt *et al*.,2020). In *Brassica* , glucosinolates offer resistance to plant-parasitic nematodes (Potter *et al*., 2000). In Marigold roots, α-terthienyl compounds exhibits high nematicidal activity against several plant parasitic nematodes (Hamaguchi *et al*., 2019). Glyceollin and terpenoid aldehyde inhibits oxygen uptake and function as nematistatic to the J2 of *M.incognita* (Veech & McClure, 1977). Resistant cultivar ‘Centinniel’ of soybean showed an increase level of glyceollin1 nearby the head of the nematode, *H.glycines* race 1 (Huang & Barker, 1991). These secondary metabolites can affect the biology of PPNs in the root system (Lee *et al*., 2017). Another secondary metabolite phytoalexins are synthesized and accumulated in plants. These are low molecular weight compounds accumulated with the formation of root border cells when the root tips are exposed to PPNs elicitor (esophageal gland secretion, excretory products and various surface compounds of nematodes) (Desmedt *et al*.,2020). The elicitor may lead to *de novo* synthesis of enzymes like Phenylalanine ammonia lyase (PAL) and chalcone synthatase ([Veech](https://pubmed.ncbi.nlm.nih.gov/?term=%22Veech%20JA%22%5BAuthor%5D) 1982). Ho¨lscher *et al*.,(2014) revealed synthesize and accumulation of phenalenone-type phytoalexins after root infection in banana by *Radopholus similis*. Over expression of the *Arabidopsis* phytoalexin-deficient 4 gene (AtPAD4), a lipase-like protein activated by salicylic acid (SA) and phytoalexins, enhances resistance in soybean roots in response to *Meloidogyne incognita* and *H.glycines* (Youssef *et al*., 2013).

Phytoecdysteroids may also provide an important plant defense against nematodes (Schmelz *et* *al*., 2000). Plant defense have been observed through 20-hydroxyecdysone (20E), a molting hormone-ecdysteroid inducible in spinach on *Pratylenchus, Heterodera* and *Meloidogyne* spp. Since spinach also contains a minor phytoecdysteroid, polypodine B, was applied exogenously Abnormal molting, immobility, reduced invasion, impaired development, and death in nematodes, *H. avenae* was observed after exposure to 20E either directly at concentration above 4.2 × 10-7 M or in plants (Soriano *et al*.,2004).

**3. CONCLUSION AND FUTURE PERSPECTIVES**

With the advancement of high throughput molecular technologies especially the use of untargeted metabolomics techniques based on nuclear magnetic resonance (NMR) and mass spectrometry (MS), plant defense mechanisms against PPN attacks can be better understandable. Moreover, understanding of the host-parasite interaction and activities like PPN recognition, species-specific responses and immune signaling networks in plant system will benefit the development of nematode disease control strategies. Strategies should be taken into consideration to identify anti-nematode metabolites and their use in agriculture and crop protection.

**DISCLAIMER (ARTIFICIAL INTELLIGENCE)**

Author hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

**COMPETING INTERESTS**

Author has declared that no competing interests exist.

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