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Strategies used by plant parasitic nematodes to conquer the host

Review paper

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1 SUMMARY

Plant parasitic nematode (PPN) employs a combination of behavioral and physiological survival strategies to conquer its host. For instance, the PPN uses its style to inject a number of secretions, commonly called effectors into the host tissues or suck food from the host into its intestines. The effectors assist the nematode to gain entry, circumvent host defense and mimic some plant cellular processes to sustain colonization. In this review, the main strategies used by PPN during its parasitism have been reviewed and demonstrated in order to obtain more understanding on how the PPN parasites its host.

2 INTRODUCTION

Plant parasitic nematodes (PPN) are vermiform microscopic animals that infect plants, causing yield loss in crops and cost of about US$ 125 billion annually in world agriculture (BES,2009). These organisms employ a combination of behavioral and physiological survival strategies to conquer its environment (Lambert and Beker, 2009). The PPN must circumvent predators, tolerate changes in soil moisture and temperature, and escape other dangers such as dying when host plant perishes. To contend with these obstacles, some PPN are ectoparasites and they spend most of their time in the soil to avoid perishing with the plant host and others are endoparasites and spend most of their time within plant tissue to escape predators (Lambert and Beker, 2009). The PPN also can be i) sedentary ectoparasites which, feed and remain outside the root or other feeding area throughout the life e.g. sheath nematodes, ii) sedentary endoparasites which, invades the tissues soon after hatching and lose the ability to move to new sites, therefore they maintain an active feeding site. e.g. cyst nematodes (*Heterodera* and *Globodera*) and the root-knot nematodes (*Meloidogyne*), iii) migratory ectoparasites which, feed on the epidermis of roots and retain the ability to move to new feeding sites e.g. pin, ring and stubby-root nematodes in mint or iv) migratory endoparasites which, feed on external surfaces of roots and later on burrow to the cortex of the plant e.g. *Pratylenchus* (Root-lesion nematodes) in mint, and *Hirschmanniella* (rice root nematode) in rice (Ingham and Merrifield, 1996; Baldwin *et al.*, 2004; Lambert and Beker, 2009). The PPN must also be able to allocate its host and break a complex barrier or plant cell wall made of cellulose, hemicelluloses, and pectin for successful parasitism (Stewart *et al.*, 1993; Cosgrove, 2005). In addition, for PPN to conquer its host, it must overcome a variety of

other defense strategies used by the host to halt colonization (Kyndt *et al*., 2012). Some of such strategies include production of anti-pathogenic toxins including phytoalexins, terpenoid and isoflavoids (Wuyts *et al*., 2006) and production of reactive oxygen species (ROS) which can activate some plant pathways responsible for strengthening plant cell wall (Smat and Jones, 2011). The aim of this review is to summarize the most important strategies used by PPN to conquer its host.

3 HOW DOES NEMATODE ALLOCATE AND INFECTS ITS HOST?

3.1 Host allocation : In order to locate host roots, PPNs respond to different attractants, which may be long-distance attractant (CO_2), short distance attractant (root diffusates), and local attractants (specific chemicals in root diffusates) through the input from their sense organs (Perry, 2005). These attractants help the PPN to move to individual host root and to preferred site of invasion where its surface is explored for a site suitable for penetration. The PPN possess two anterior sensila, (sense organ) called the amphids which, have glandular sheath cells used for chemoreception and host allocation (Stewart *et al*., 1993; Jones *et al*, 2000). The amphids through its sheath cells secrete a protein called MELOIDOGYNE AVIRULENCE PROTEIN-1 (MAP-1) which, play a role in PPN parasitism and other amphidial functions (Semblat *et al*., 2001). Another protein called CELL DIVISION CONTROL 48 (CDC48)-like protein is produced from the sensillae caudal end of nematode (phasmids), which also produce some secretions (Perry, 1996). Once it reaches the root surface, the PPN explore the root surface and start thrusting its stylet, which, is accompanied by release of secretions as a preparation for root penetration.

3.2 Functional parts and mechanisms involved during nematode infection on it host plant : The PPN use mechanically specialized needle-like structure called stylet to punch host tissues to draw food (Lambert and Bekal, 2009) and inject effectors (EPs) including proteins, peptides and other molecules into host tissue to facilitate plant parasitism (Hogenhout *et al*., 2009; Haegeman *et al*, 2011). The nematode's stylet is connected to the pharynx which has specialized areas that can expand and contract to pump EPs into the host tissues or suck food and push it into the intestine (Fig 1).

The pharynx is connected to the intestine which is responsible for nutrient absorption, excretion of waste, lipid storage and rapid movement. The intestine is connected to the rectum (in female) or cloaca (in males) which, is used for excretion (Fig 1). Most EPs, produced by PPN are secreted at the salivary/ pharyngeal gland (Lambert and Beker, 2009; Haegeman *et al*, 2011). Other parts of PPN known to secrete EPs are sensilla ends (Perry 1996; Semblat *et al*., 2001) and cuticle which secrete a bunch of antioxidants for neutralization of host toxins. Example, PPN cuticle produce glutathione peroxidase to coat themselves and break hydroperoxides and peroxiredoxine to metabolize the reactive oxygen species (ROS) produced by the host (Li *et al*., 2011). PPN can also slough off its cuticle to avoid recognition by the host (Spiegel and Mcclure, 1995, Jones *et al*., 2000).

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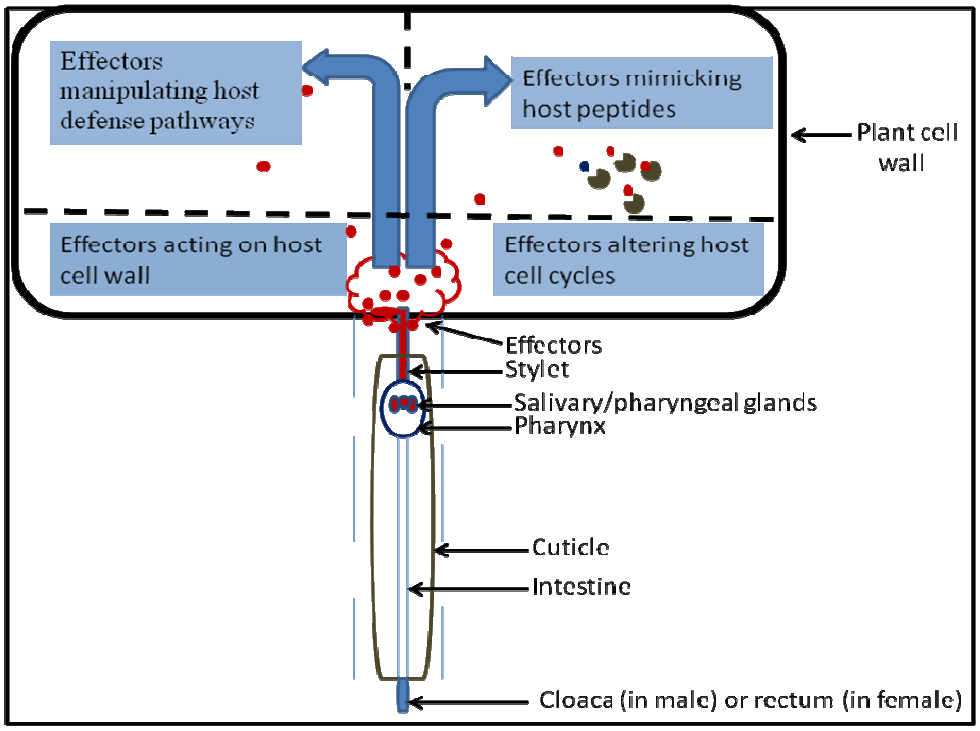

Figure 1: A model illustrates functional parts involved during infection by sedentary plant parasitic nematode on it host plant. In this scheme, the nematode uses its stylet to punch plant cell, to draw food and also inject effector proteins (red circles), that aid in parasitizing the plant. The effectors can mimic host (blue circles) peptides, cause cell wall expansion and/or dissolution, alter cell cycles and manipulate host defense pathways. The stylet is connected to the pharynx which, pumps effectors into the host cells or food into its intestine. The waste is expelled through the rectum/cloaca.

3.3 Nematode weaponry: Several techniques such as copy DNA-amplified fragment length polymorphism (Tytgat *et al*., 2004), microarrays (Elling *et al*., 2009), expressed sequenced tags (Karim *et al*, 2009; Haegeman *et al*., 2011), proteomics (Mbeunkui *et al*., 2010) and specific life stages and organs (Jones *et al*., 2009; Wubben *et al*., 2010; Hussey *et al*., 2011) have been used to identify nematode weaponries (NW) responsible during its interaction with its host. Most of those NW also referred to as genes are believed to be derived from bacteria and fungi through multiple genes transfer (Jones *et al*., 2005, Danchin *et al*., 2010). The nematode genes encode a number of EPs with specific target roles on their hosts to aid parasitism. In the following section, some highlights of EPs target have been described**.**

3.3.1 EPs that target the host cell wall: The PPN can release specialized EPs into its host to facilitate ease entry. During penetration and migration, PPNs employ a bundle of EPs to penetrate their host cell wall. Some examples of EPs already reported are beta-1,4-endoglucanase which, degrade cellulose of plant cell wall (Smant *et al*., 1998); pectate lyase which, cleaves the alpha-1,4-linkages of pectate and polygalacturonase which, hydrolyse 1,4-alpha-D-galactosiduronic linkages (Abd *et al*., 2008; Haegeman *et al*., 2011); xylanase which, hydrolyse 1,4-beta linkages in xylan, arabinogalactan endo-1,4-beta-galactosidase and arbinase of cell wall pectin (Haegeman *et*

al., 2011). In compatible interaction, the ejected EPs or microbial/pathogen/herbivore-associated molecular patterns (MAMPS, PAMPS, or HAMPS) can alter host cell structure and function to promote infection by PPN (Hogenhout *et al.*, 2009). The PPN also secrete other compounds which, can promote the activities of the EPs such as cellulose binding protein which, binds plant pectin methylesterase (Heweze *et al.*, 2008) and expansins which, disrupts non-covalent bonds between polysaccharide chains making it easy for cell wall degrading enzymes to act (Abda *et al.*, 2008; Karim *et al.*, 2009; Danchin *et al.*, 2010). PPN also can secrete EPs which can degrade host proteins. Some examples of such proteins are cystein protease and aminopeptidases (bellafiore *et al.*, 2008), aspartyl proteases from Meloidogyne incognita (Vieira *et al.*, 2011). These proteins secreted by PPN must overcome host R-genes such as Hs1pro-1, Gro1-4, Gpa2 and Mi (Jones and Dangl, 2006; Sacco *et al.*, 2009) and other plant defense pathways (Doyle and Lambert, 2003; Jammes *et al.*, 2005).

3.3.2 EPs that respond to host defense: The PPN can produce compound such as glutathione-S-transferases (GST) to detoxify host nematocidal compound (Dubreuil *et al.*, 2007). PPN such as *G. rostochiensis* is capable of producing antioxidant compounds such as glutathione peroxidase and superoxide distimutase that can break host ROS (Jones *et al.*, 2004, Bellafiore *et al.*, 2008, Nagano *et al.*, 2009). PPNs are capable of suppressing host defense by disrupting some plant metabolic pathways (Kyndt *et al.*, 2012). Example, chorismate mutase (CM) produced by root-knot nematodes, cyst forming nematodes and migratory endoparasites (Jones *et al.*, 2003; Lambert *et al.*, 1999). The CM is thought to reduce a pool of chorismate required in salicylic acid (SA) plant pathway, which is important in the activation of host defense (Wildermuth *et al.*, 2001).

3.3.3 EPs that ensure sustainability of PPN: Up on successful entry, PPN establish a single feeding site (Wyss, 1997; Grunewald *et al.*, 2009). The PPN can release EPs to manipulate plant auxin levels and distribution (Lee eta l., 2011); block, hijack or modulate cellular process (Ni and Clark, 2006)) and vascular development (Kondo *et al.*, 2011); regulate cellular division and differentiation (Mitchum *et al.*, 2008); mimic host peptides to promote formation of giant cells, syncytia and facilitate parasitism by nematode (De Meutter *et al.*, 2003, Hueng *et al.*, 2003).

4 CONCLUSIONS

Plant Parasitic Nematodes employ different strategies to circumvent the host. For successful allocation, establishment and colonization on its host, PPN uses specialized morphological features and produce a number of EPs, peptides and other molecules with targets on host. Until the time of writing this review, it has not been unveiled whether the EPs work dependently or independently of each other during PPN parasitism. Future research could therefore, be targeted on this quest in order to obtain more understanding on these strategies used by PPN to parasite its host.

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