

## PLANT-NEMATODE INTERACTIONS: ENVIRONMENTAL SIGNALS DETECTED BY THE NEMATODE'S CHEMOSENSORY ORGANS CONTROL CHANGES IN THE SURFACE CUTICLE AND BEHAVIOUR

CURTIS R.H.C.\*

### Summary:

Plant parasitic nematodes have developed the capacity to sense and respond to chemical signals of host origin and the ability to orientate towards plant roots enhances the nematode's chance of survival. Root exudates contain a range of compounds which mediate belowground interactions with pathogenic and beneficial soil organisms. Chemical components of root exudates may deter one organism while attracting another and these compounds alter nematode behaviour and can either attract nematodes to the roots or result in repellence, motility inhibition or even death. *In vitro*, plant signals present in root exudates, trigger a rapid alteration of the surface cuticle of *Meloidogyne incognita* and the same changes were also induced by indole-acetic acid (IAA). IAA binds to the chemosensory organs of *M. incognita* and it is possible that IAA acts as a signal that orientates the nematode on the root surface in the rhizosphere and/or inside the root tissue and thereby promotes nematode infection.

**KEY WORDS :** *Meloidogyne* spp., indole-acetic acid, plant signals, cuticle, amphids.

### PLANT-NEMATODE INTERACTIONS IN THE RHIZOSPHERE

Plant parasitic nematodes are of considerable economic importance world-wide, *Meloidogyne* spp. (root-knot nematodes) and *Globodera* spp. (potato cyst nematodes) being particularly destructive, contributing greatly to an estimated annual yield loss of \$ 100 billion.

During co-evolution with the host plant, parasitic nematodes have developed the capacity to recognise and respond to chemical signals of host origin. Understanding the complexity of the molecular signal exchange and response during the early stages of the host-parasite interactions is important to identify vulnerable points in the parasite life cycle that can be targeted to disrupt nematode-host recognition. Nematode invasion of roots and the migration to the nematode feeding sites result in changed root architecture and significant reductions in nutrient and water uptake and consequent crop yields.

\* Nematode Interactions Unit, Rothamsted Research, Harpenden, AL5 2JQ, UK.  
Tel.: +44 (0)1 582 763 3133 – Fax: +44 (0)1 582 760 981.  
E-mail: [rosane.curtis@bbsrc.ac.uk](mailto:rosane.curtis@bbsrc.ac.uk)

The plant-nematode relationship is governed by a complex network of interactions resulting in the formation of feeding sites. The infective second-stage juveniles (J2) of *Globodera* spp. penetrate roots and migrate intracellularly towards the vascular cylinder and establish an intimate nutritional relationship with their host through the development of syncytial feeding sites. In contrast, J2 of *Meloidogyne* spp. after penetrating the root epidermis migrate intercellularly between cortical cells until they find a suitable root cell to form their feeding site. Root cells around the nematode's head are stimulated to go through repeated rounds of mitosis uncoupled from cytokinesis, leading to multinucleated giant cells (Gheysen & Fenoll, 2002). Ultimately, the formation of the feeding site is the result of nematode-induced alterations in plant gene expression (reviewed in Gheysen & Fenoll, 2002). Feeding cell formation is presumably initiated in response to signal molecules released by the J2, but the nature of the primary stimulus is unknown. The most widely held hypothesis is that the necessary metabolic reprogramming of root cells is triggered by specific nematode secretions, which presumably interact with membrane or cytoplasmic receptors in the plant to switch on cascades of gene expression that alter cell development (Williamson & Hussey, 1996). Syncytia and giant cells require repeated stimulation from the nematode to maintain their function and cyst and root-knot nematodes depend entirely on functional feeding cells to complete their life cycles.

Endoparasitic plant nematodes do not feed during their migrations in soil and in roots and their survival depends on finding a food source or sexual partner without unnecessary energy expenditure. They rely on stored lipid reserves to provide the energy for their movement. As with heminths, these infective stages recognise their hosts via complex sequences of behavioural patterns in response to various environmental cues (Haas *et al.*, 1997; Haas, 2003). Plant signals are essential for nematodes to locate hosts and feeding sites, nematodes with > 60 % of their lipid reserves depleted are no longer capable of directed movement (Robinson *et al.*, 1987). However, the identity of the plant signals involved in key stages of the plant-nematode interactions are not yet clearly defined.

Many parasitic nematodes enter their hosts by active invasion and their transmission success is often based on a mass production of infective stages which show a highly specific host-finding behaviour. These infective stages recognise their hosts via complex sequences of behavioural patterns with which they successfully respond to various environmental and host cues (Haas *et al.*, 1997; Haas, 2003). After invasion animal parasites navigate through their host's tissues to their very specific microhabitats and some of these migrating parasitic stages can follow chemical gradients of skin and blood compounds (Haas *et al.*, 2002). It is suggested that the high complexity, specificity and diversity of host-recognition strategies devised by parasites are important determinants in the evolution of their life cycles.

## BELOWGROUND CHEMICAL COMMUNICATION: ROOT EXUDATES AND HOST RECOGNITION

The rhizosphere encompasses the soil within millimetres of a plant root where complex biological and ecological processes occur. Plant roots exude a range of compounds into the rhizosphere which mediate belowground interactions with pathogenic and beneficial soil organisms. Root exudates include secretion of ions, free oxygen and water, enzymes, mucilage and a diverse array of primary and secondary metabolites (Bertin *et al.*, 2003). Although, the functions of most root exudates have not been determined, several compounds play important roles in biological processes (reviewed in Bais *et al.*, 2006). Root compounds are secreted into the surrounding rhizosphere or released from root border cells which separate from the roots as they grow.

Chemical components of root exudates may deter one organism while attracting another and these compounds alter nematode behaviour (Fig. 1) and can either attract nematode to the roots or result in repellence, motility inhibition or even death (Robinson, 2002; Wuyts *et al.*, 2006; Zhao *et al.*, 2000). It seems that a combination of signals in a given set of exudates determines the nematode behaviour in a given plant-nematode interaction. Following fractionation of cucumber root exudates, fractions with both repellent and attractant activity to *Meloidogyne incognita* were isolated (Castro *et al.*, 1988). Root border cells play an important role in protecting the root tip from infection by acting as a natural trap for pathogenic organisms (Wuyts *et al.*, 2006; Zhao *et al.*, 2000). Indeed, root cap exudates, whose secretions include enzymes, antibiotics, other soluble molecules and high molecular weight mucilage that encases border cells. They repelled both plant nematodes and the free-living nematode *Caenorhabditis elegans* and producing a reversible state of immobility

### Belowground chemical communication Root exudates and host recognition

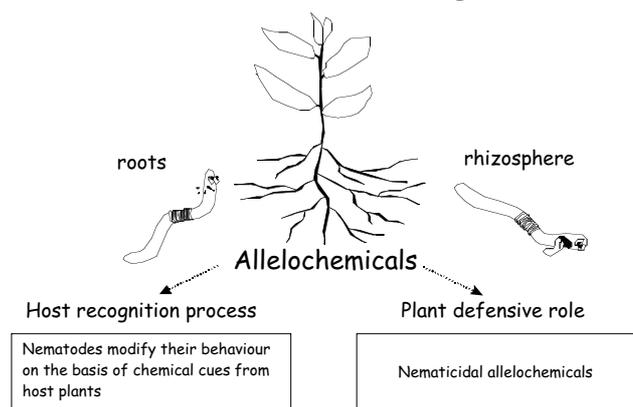


Fig. 1. – Allelochemicals can be found in parts of the plant and can also be secreted as root exudates or released as volatile compounds. They mediate chemical interactions between two plants as well as plant-pathogen chemical communication. Attraction, penetration and feeding behaviour of plant parasitic nematodes involve molecular communication between the nematode and respective plants. Root exudates can induce attraction, repellence, inhibition and hatching stimulation.

in these nematodes (Hubbard, *et al.*, 2005; Wuyts *et al.*, 2006; Zhao *et al.*, 2000). Therefore, localised sites on the root surface and rhizosphere drive population dynamics. This ability of the root tip to deliver products that temporally immobilises nematodes could play a role in plant defence for abiotic and biotic factors. Indeed, the root cap provides physical protection for the apical meristem especially against the soil pathogens (Zhao *et al.*, 2000). This phenomenon might account in part, for the fact that the normal site of infection by nematodes is behind the root tip, just past the region where border cells are released (Zhao *et al.*, 2000).

The role of plant signals in synchronising host and parasite life-cycle is best illustrated with the two species of potato cyst nematodes (*Globodera* spp.), as these nematodes almost completely depend on root exudates for hatching. Various hatching factors have been identified in crop plants and these compounds are potential candidates for agrochemical use (Devine & Jones, 2001). Hatching is an important step in the nematode life-cycle leading to parasitism and this dependence of the *Globodera* spp. on hatching factors have been exploited to reduce the number of nematodes in infested fields (Timmermans *et al.*, 2007). *Solanum sisymbriifolium* is used successfully as a trap crop for potato cyst nematodes in Europe, as this plant stimulates hatch of second stage juveniles but does not support their development and is completely resistant to *G. pallida* and *G. rostochiensis* (Timmermans *et al.*, 2007).

The ability to orientate towards plant roots enhances the nematode survival. Long distance attractants' can enable nematodes to locate roots; whilst attractants that cause

the nematode to move to individual host roots may be termed as “short distance attractants” and the orientation to the preferred site of invasion in the root tip might be mediated by “local attractants” (reviewed in Perry, 2001). So far, only CO<sub>2</sub> has been identified as a prime long distance attractant for plant parasitic nematodes, including *M. incognita* (Robinson, 2002). Additional attractants are aminoacids, sugars and metabolites (Bird, 1959; Robinson, 2002; Perry, 2001; Prot, 1980). It has been suggested that nematodes orientate to an electrical potential gradient at the elongation zone of the root tip (Bird, 1959).

The chemotactic response of *Bursaphelenchus xylophilus*, the pine wood nematode, to a variety of chemicals varied according to the nematodes lipid content. Nematodes with the lowest lipid content were attracted to the pine wood volatile  $\alpha$ -myrcene, while nematodes with the highest lipid content were attracted to a toluene hydrocarbon in the cuticle of the beetle vector for the nematode (Stamps & Linit, 2001). Therefore, nematode lipid contents seem to be an important factor in the nematode's response to host signals. Plant roots also trigger *C. elegans* behavioural response by emitting volatile signals attracting nematodes to the root proximity (Horiuchi *et al.*, 2005).

Plant roots also produce allelochemicals to defend the plant against potential soil-borne pathogens and a number of plant secondary metabolites have been shown to function as nematode antagonists (reviewed in Guereña, 2006) For example, the triterpenoid compound, cucurbitacin A, from cucumber plants repels nematodes and a  $\beta$ -terthienyl compound from *Tagetes erecta* is repellent and nematotoxic (Castro *et al.*, 1988). Allelochemicals present in the root exudates of maize such as cyclic hydroxamic acid, have been shown to affect the behaviour of *Pratylenchus zea*, *M. incognita* and *Xiphinema americanum*. The methoxylated hydroxamic acid (DIMBOA, dihydroxy-7-methoxy-1,4-benzoxazin-3(4H) increased attraction and its degradation product (MBOA, 6-methoxy-2-benzoxazolinone) induced repellence to roots (Friebe *et al.*, 1997; Zasada *et al.*, 2005).

Root exudates not only contain compounds that induce nematode hatching, attraction and repellence to roots but also compounds that induce characteristic nematode exploratory behaviour, including stylet thrusting; release of secretions in preparation for root penetration; aggregation and increase in nematode mobility (Clarke & Hennessy, 1984; Curtis, 2007; Grundler *et al.*, 1991; Robinson, 2002).

## SURFACE CUTICLE CHANGES IN RESPONSE TO ENVIRONMENTAL SIGNALS

The epicuticle forms the outer cuticular layer of nematodes, which is covered in many species by a fuzzy coating material termed the “surface

coat” (SC). The SC is composed mainly of proteins, carbohydrates and lipids (Spiegel & McClure, 1995). The nematode surface coat, being the outermost layer of the cuticle, is considered one of the major targets for developing new control strategies against plant-parasitic nematodes. Nematode secretions and surface coat antigens are likely to be the first signals perceived by the plant and they probably have important roles in the host-parasite relationship (Jones & Robertson, 1997). They may help with the initial penetration, migration of the second stage juveniles in the plant tissues and digestion of host cell contents (Williamson & Hussey, 1996) and are also probably involved in the protection of the nematode from plant defense responses (Prior *et al.*, 2001; Robertson *et al.*, 2000). Interfering with nematode movement affect nematode invasion of plants (Sharon *et al.*, 2002; Fioretti *et al.*, 2002) and can render nematodes vulnerable to anti-nematode control strategies in the rhizosphere and/or root tissue.

Nematodes can rapidly change their surface composition in response to environmental signals, which may enable animal parasitic nematodes to escape host immune responses and free-living nematodes to escape pathogenic infections (Olsen *et al.*, 2007; Proudfoot *et al.*, 1993). Surface composition can also change within a single stage during entry of parasitic nematodes into a new host or host tissue (Modha *et al.*, 1995; Proudfoot *et al.*, 1993). One of the most interesting features of the nematode SC is its dynamic nature; there is a continuous turn-over of the surface associated antigens, which are shed and replaced (Blaxter & Robertson, 1998). In plant-parasitic nematodes this was demonstrated for the pre-parasitic juveniles of *Meloidogyne* spp. (Lin & McClure, 1996; Spiegel *et al.*, 1995), the importance of these changes in the surface coat for host-parasite interactions is less well understood.

Considerable similarities were found in the surface cuticle of certain plant and animal parasitic nematodes (Lopez de Mendoza *et al.*, 1999). Monoclonal antibodies (mAb) raised to excreted/secreted (ES) products of the plant parasitic nematode *Heterodera avenae* was also shown to bind to secretions from the cuticle surface and amphids of *Meloidogyne incognita* (Curtis, 1996) and to the surface coats of the animal parasites *Trichinella spiralis* and *Haemonchus contortus* (Curtis, 1996; Lopez de Mendonza *et al.*, 1999).

## ROOT EXUDATES AND PHYTOHORMONES INDUCE CHANGES IN THE SURFACE CUTICLE OF NEMATODES

Plant signals present in root exudates, trigger a rapid alteration of the surface cuticle of *Meloidogyne incognita* and *Globodera rostochiensis*

and the same changes were also induced by phytohormones, in particular indole-acetic acid (IAA) to *M. incognita* but not *G. rostochiensis* (Akhkha *et al.*, 2002, 2004; Curtis, 2007; Lopez de Mendoza *et al.*, 2000). As the former nematode can infect a large range of host plants it was not surprising that responded to such a general plant compound. This surface change induced by plant signals might allow *M. incognita* to adapt and survive plant defence processes. However, more specific host cues from root exudates of solanaceous plants were responsible for increasing the lipophilicity of the surface cuticle of infective juveniles of *Globodera* species (Akhkha *et al.*, 2002). *In vitro*, IAA has also been shown to induce the production of nematode secretions (Duncan *et al.*, 1995) and an increase in nematode mobility (Curtis, 2007). *Globodera pallida* (Duncan *et al.*, 1995) but not *Meloidogyne* spp. (R. Curtis unpublished data) was shown to have an immunological cross-reactivity to the maize auxin binding protein, indicating that these sedentary plant parasitic nematodes with their very different host specificities may respond differently to IAA.

Molecules present in root exudates, including IAA may act as environmental signals to induce these behavioural changes and therefore play a vital role in the host-recognition processes for sedentary plant parasitic nematodes. Exogenous application of IAA shifted the response of resistant tomato plants towards susceptibility (Dropkin *et al.*, 1969; Sawhney & Webster, 1975) and these results support the importance of phytohormones for plant-nematode interactions.

The nematode life-cycle may be synchronised by the IAA concentration in the root tissues. The preferred site for root invasion is at the elongation zone of growing tips (Fig. 2a & b), where higher levels of IAA fluxes have been recorded (Mancuso *et al.*, 2005). Transport of IAA in plants occurs from the shoot to the root tip and then laterally to the epidermis. The J2 of *Meloidogyne* spp. migrate inside the roots from the elongation zone to the tip and thence to the stele in the opposite direction to

the IAA transport gradient (reviewed in von Mende, 1997). High concentrations of IAA have also been detected around the root cells surrounding the nematode head (Karczmark *et al.*, 2004). It is possible that IAA acts as a signal that orientates the nematode on the root surface in the rhizosphere and inside the root tissue and thereby promotes nematode infection.

However, whether nematodes perceive IAA as host cues in the rhizosphere, at the root surface and/or in the root tissue is not known. Nematodes may encounter an IAA gradient inside roots and free IAA has been detected up to concentrations of 1  $\mu$ M in phloem exudates (Friml, 2003). But, yet it is not known if nematodes are affected by IAA from plant origin in the rhizosphere and so far, only auxin conjugates such as IAA methyl-glutamate have been shown to be present in root exudates of *Arabidopsis thaliana* (Narasimham *et al.*, 2003).

## NEMATODES DETECT ENVIRONMENTAL SIGNALS PRESENT IN THE RHIZOSPHERE USING THEIR CHEMOSENSORY ORGANS

The nematode nervous system is the conduit between stimulus, reception and behavioural output and multicellular animals use their chemical senses to trigger complex behaviours and developmental processes. The main nematode chemosensory organs involved in host-recognition processes are two bilaterally symmetrical amphids (Fig. 3) in the nematode head and two paired pore-like phasmids located in the lateral field of the nematode tail. Nematodes have the ability to chemo-orientate using a combination of head to tail chemosensory sensors to simultaneously compare the intensities of the stimulus across their body length (Hilliard *et al.*, 2002).

The amphids contain a number of dendritic processes which are surrounded by secretions produced by the

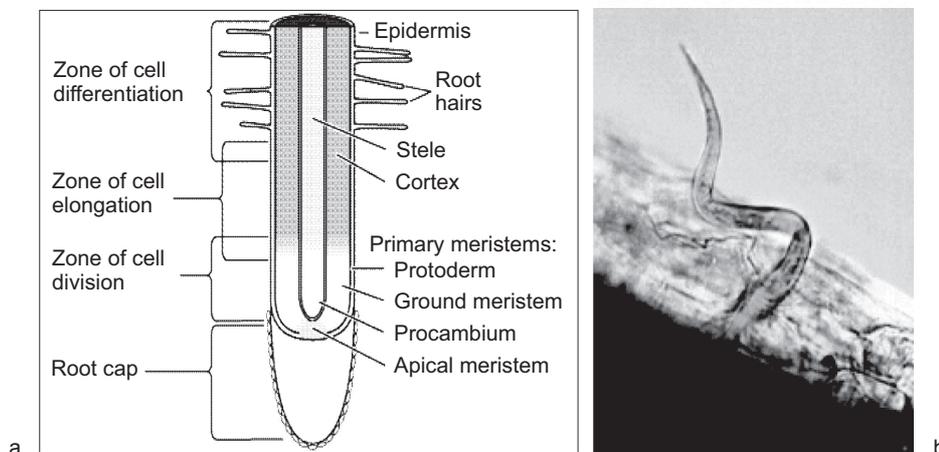


Fig. 2 a & b. – a. Root anatomy: the zone of elongation is preferred site of penetration for sedentary plant parasitic nematodes and chemical gradients can be used as orientation markers for short distances on the root surface and within the root tissue. b. Photograph showing *M. incognita* second stage juveniles invading a tomato root at the zone of elongation.

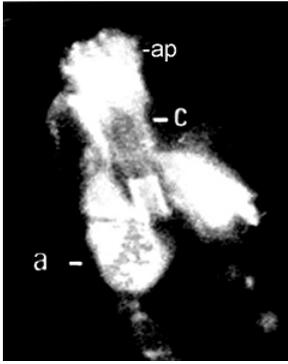


Fig. 3. – Immunofluorescence photograph of a cryostat section of the anterior head of the second stage juvenile of *Globodera pallida*, the section was probed with a monoclonal antibody reactive with the nematode amphids. a = amphidial glands; c = amphidial canal; ap = amphidial pores.

glandular sheath cell. Disruption of chemoresponses render nematodes disorientated in the soil and unable to find a host (Fioretti *et al.*, 2002; Perry 2005; Zuckerman, 1983). The nematicide aldicarb disturbed nematode orientation and caused changes in the ultrastructure of the amphidial sheath cell of affected nematodes (Trett & Perry, 1985). Also, interference with nematode chemoreception, by blocking amphidial secretion using monoclonal and polyclonal antibodies, stopped nematode movement and significantly reduced infection of plants (Fioretti *et al.*, 2002; Sharon *et al.*, 2002; Stewart *et al.*, 1993).

Chemo-orientation in a concentration gradient is vital for nematode survival and is essential for detection of host plant exudates, food stimulants, food deterrents and sex pheromones (<http://www.wormbook.org>). The free living nematode *C. elegans* changes its surface in response to environmental chemical signals detected by the nematodes's chemosensory organs (Olsen *et al.*, 2007). Plant nematodes also rely on chemoreception, *e.g.* to find a host in the soil, and when a root is encountered, its surface is explored for a suitable penetration site. IAA binds to the chemosensory organs of *M. incognita* (Curtis, 2007). IAA has been implicated in the recognition process of host plants by fungi. During this interaction *Saccharomyces cerevisiae* differentiates into an invasive form, which enables infection. In this case IAA induces morphogenetic changes, such as adhesion and filamentation, which are mediated by fungal transcription factors and a family of transporters, which are up-regulated in the fungus. These transporters are members of the amino acid/auxin:proton symport permeases (AAP) superfamily, which includes *Arabidopsis* AUX1, a putative IAA transporter from plants, and families related to neurotransmitter transporters such as the  $\delta$ -aminobutyric acid (GABA) transporters in *C. elegans* (McIntire *et al.*, 1997; Prusty *et al.*, 2004). Indeed, GABAergic neurons act to control the body and enteric muscles necessary for different behaviours in *C. elegans* (McIntire *et al.*, 1997). Amino acid and neurotransmitter transporters are highly conserved in animals and plants and they function in vesicle-based cell-to-cell transport (Baluska *et al.*, 2003; Chen *et al.*, 2001).

Plant, animals and pathogens share elements such as fatty acids, proteins, neurotransmitters and in some of the signalling machinery underlying responsiveness to the environment (Schultz, 2002). Therefore, it is not surprising that plants produce signalling molecules for which there are nematode receptors/binding proteins. Nematode signalling components present in the chemosensory organs are in contact with the external environment and therefore are exposed to antagonistic molecules that could block their interaction with host cues. Understanding the signalling and perception processes occurring in plant-nematode interactions will reveal targets for chemical or genetic intervention.

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