



Parasitic nematodes manipulate plant development to establish feeding sites

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Cyst and root-knot nematodes, the two economically most important groups of plant parasitic nematodes, induce neoplastic feeding sites in the roots of their host plants. The formation of feeding sites is accompanied by large-scale transcriptomic, metabolomic, and structural changes in host plants. However, the mechanisms that lead to such remarkable changes have remained poorly understood until recently. Now, genomic and genetic analyses have greatly enhanced our understanding of all aspects of plant–nematode interaction. Here, we review some of the recent advances in understanding cyst and root-knot nematode parasitism. In particular, we highlight new findings on the role of plant hormones and small RNAs in nematode feeding site formation and function. Finally, we touch on our emerging understanding of the function of nematode-associated secretions.

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Introduction

Plant-parasitic nematodes (PPNs) affect almost all major crops. The presently more than 4100 described PPN species are estimated to cause over 80 billion USD in agricultural loss per year [1]. The full extent of worldwide nematode damage is likely underestimated, particularly in developing countries, since growers are often unaware of the presence of these small, soil-borne pathogens. Additionally, the symptoms caused by PPNs are often non-specific, making it difficult to attribute crop losses to nematode damage. The small size, biotrophic life style, non-synchronized infection, and lack of a reliable transformation method make PPNs difficult experimental organisms. Studies on the molecular aspects of plant–

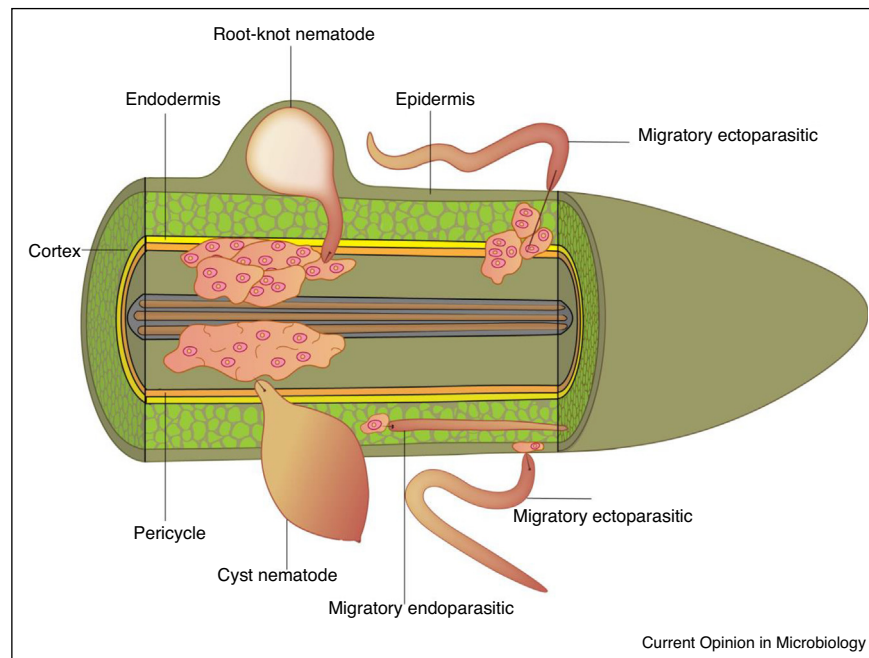
nematode interactions have therefore lagged behind those in other pathosystems.

PPNs use a hollow protrusible stylet to break into the plant cells, withdraw nutrients, and release both proteinaceous (effectors) and non-proteinaceous molecules. The hollow stylet is connected to three enlarged, specialized esophageal gland cells, which produce the effector molecules that are secreted into the host tissues to facilitate parasitism. Each of the three esophageal glands consists of a single cell that contains an unusually long cytoplasmic extension ending in an ampulla. The effector proteins are synthesized in the gland cell and transported to the ampulla in membrane-bound granules. The ampulla in turn is connected to the lumen of the oesophagus by a valve. Some of the genes encoding oesophageal secretions are likely to have been acquired from prokaryotic microbes via horizontal gene transfer [2]. The development of stylet and esophageal gland cells producing effector molecules are among the most striking adaptations that enable PPNs to maintain a unique long-term parasitic relationship with their hosts.

Different species of PPNs feed on a range of plant tissues, including flowers, stems, leaves, and roots; however, most species feed on roots. Based on their feeding habits, PPNs can be broadly categorized as either ectoparasitic or endoparasitic (Figure 1). In this review, we focus on a complex and economically devastating group of sedentary endoparasitic PPNs including cyst nematodes (CNs; *Heterodera* spp. and *Globodera* spp.) and root-knot nematodes (RKNs; *Meloidogyne* spp.).

Infective-stage CN and RKN juveniles (J2) invade the plant root near the tip and move through different tissue layers to reach the vascular cylinder, where CNs induce the formation of a syncytium (a multinucleate fusion of cells resulting from partial cell wall dissolution) and RKNs induce the formation of 5–7 giant cells (Figure 2). In the case of RKN, proliferation of the tissue surrounding the nematode and the giant cells leads to the formation of a typical gall, which is observed as a primary symptom of infection. The establishment of feeding sites (syncytia and giant cells) enables CNs and RKNs for taking large amounts of nutrients from the plant, facilitates nematode growth, and induces a pathologically disturbed allocation of photosynthetic products that reduces plant growth and yield.

Figure 1



Overview of feeding habits of plant-parasitic nematodes. Plant-parasitic nematodes display a variety of feeding habits and can be broadly categorized as either ectoparasites or endoparasites. Migratory ectoparasitic nematodes stay vermiform throughout their life cycle and all stages are capable of feeding on roots of a broad range of host plants. Examples of migratory ectoparasitic nematodes include awl nematodes (*Dolichodorus* spp.), sting nematodes (*Belonolaimus* spp.), needle nematodes (*Longidorus* spp.), and dagger nematodes (*Xiphinema* spp.). Members of the latter two genera extend periods of feeding at their feeding sites and are able to induce the formation of nurse cell in the root tip. They also act as vectors of specific plant viruses. Migratory endoparasitic nematodes can cause high yield losses in a variety of field crops. In addition to the direct damage they inflict on the host, these nematodes promote secondary bacterial and fungal infections. Examples of migratory endoparasitic nematodes include lesion nematodes (*Pratylenchus* spp.), burrowing nematodes (*Radopholus* spp.), and rice root nematodes (*Hirschmanniella* spp.). Sedentary endoparasitic plant-parasitic nematodes include cyst nematodes (*Heterodera* spp. and *Globodera* spp.) and root-knot nematodes (*Meloidogyne* spp.). Both cyst and root-knot nematodes induce hypermetabolic feeding sites in roots, which are the only source of nutrients for nematodes throughout their life cycle. While the host range of most *Meloidogyne* species tends to be broad, it remains rather narrow for most cyst nematode species.

As obligate biotrophs, CN and RKN are entirely-dependent on plant-derived nutrients and solutes to fulfil their energy requirements throughout their weeks-long life cycles. Thus, both the syncytium and giant cells have evolved into a sink tissue that caters to the needs of the rapidly developing nematode. The cytoplasm of these feeding sites is dense and contains numerous organelles, including mitochondria, plastids, ribosomes, the Golgi apparatus, and the smooth endoplasmic reticulum. Furthermore, the central vacuole in these cells is replaced by several small vacuoles, and numerous ingrowths are formed at the cell wall interface with xylem cells, which are thought to increase the surface area for translocation of nutrients.

A series of transcriptomic, metabolomic, and proteomic analyses performed over the last decade showed that the genes and pathways involved in primary metabolism are specifically upregulated in both syncytia and giant cells [3–5]. As previous excellent reviews describe the metabolism and functioning of feeding sites [6–8] and discuss

the modulation of plant immunity in response to nematode infection [9,10], we will focus on recent progress in understanding the formation and functioning of both types of feeding sites. The first section of our review explores homeostasis of two crucial plant hormones (cytokinin and gibberellin) that facilitate the formation and functioning of nematode feeding sites. The second section reviews current progress in understanding the role of small RNAs in syncytium and giant cell formation. The last section highlights our nascent understanding of nematode-associated secretions that are released into hosts to facilitate various aspects of parasitism.

Changes in hormone homeostasis during the formation of feeding sites

The involvement of various plant hormones in plant–nematode interaction is well-documented, and we refer readers to previous excellent reviews on the roles of auxin, salicylic acid, jasmonic acid, and ethylene [6,11]. Research during the last few years has established cytokinins and gibberellins as important players in nematode

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