International Journal of Research and Review
Vol.7; Issue: 3; March 2020
Website: www.ijrrjournal.com
E-ISSN: 2349-9788; P-ISSN: 2454-2237

Review Article

Plant-Parasitic Nematodes: Nature's Most Successful Plant Parasite

Yogendra Kumar[1], Bindhya Chal Yadav[2]

[1]Assistant Professor, Department of Botany, Govt Degree College Nanauta, Saharanpur
[2]Assistant Professor, Department of Botany, Govt PG College Fatehabad, Agra

Corresponding Author: Yogendra Kumar

ABSTRACT

Nematodes are thread-like roundworms that live in a wide range of environments including soil and fresh and salt water. There are species of nematodes that feed on fungi, bacteria, protozoans, other nematodes, and plants. They can also parasitize insects, humans, and animals. Nematodes that feed on plant parts are called plant parasitic nematodes (PPN) and are ubiquitous in agricultural soils. The life cycle of a nematode includes eggs, juveniles and adults, and they can overwinter at any of these stages. Crop damage is the result of a complex interaction of the environment, initial nematode populations at planting, the pathogenicity of the nematode species and the ability of the plant to tolerate nematode feeding. Most PPNs feed by piercing and killing root cells with needle-like structures called stylets. Nematodes that utilize this type of feeding include lesion, lance, needle, sting, stunt, and sting nematodes. Some of the most economically damaging nematodes like the root knot nematode (RKN) enter roots and establish a permanent feeding site where they complete their life cycles without killing the cells around them. Symptoms associated with nematode infection are similar to those caused by impaired root growth and function; therefore they may resemble abiotic stress like drought and nutritional deficiencies as well as biotic factors like stem and root rots. General symptoms from nematodes include yellowing, stunting, and wilting, accompanied by a yield decline. In the case of SCN, signs of infection are white-to-pale-yellow female bodies present in roots that can be seen with the naked eye. Nonetheless, above ground symptoms are not always obvious and infections can go undetected until populations are well-beyond economic thresholds. The RKN causes root galling, however, the degree of galling may depend on the interaction between the plant and the RKN species.

Keywords: Nematode, root-knot, *Meloidogyne* PPN

INTRODUCTION

Plant parasitic nematodes are the nature's most successful of all parasites. These nematodes have been reported from all terrains from all continents. Some of the members are adapted to survive on coldest of the temperature. Ability to survive of any plants makes them most difficult to control. The biology of these enigmatic worms are slowly beginning to unfold. Most of the information about these tiny worm is obtained from one of the most extensively studies nematode *Caenorhabditis elegans*, a free living nematode. Still the parasitic arsenal of these plant parasitic nematodes remains largely unknown. ESTs studies and also the complete genomic sequences allowed scientist to peep in to the secret world of these nematodes. Members of the phylum Nematoda (round worms) have been in existence for an estimated one billion years, making them one of the most ancient and diverse types of animals on earth (Wang et al. 1999). They are thought to have evolved from simple animals some 400 million years before the "Cambrian explosion" of invertebrates able to be fossilized (Poinar 1983). The two nematode classes, the Chromadorea and Enoplea, have diverged so long ago, over 550 million years that it is difficult to accurately know the age of the two lineages of the phylum

NEMATODE BIOLOGY

The study of nematode biology has led to a dramatic increase in understanding of how all animals function. In fact, the bacterial-feeding nematode, *Caenorhabditis elegans*, is one of the best-understood animals on earth. The fate of every cell in *C. elegans* development has been carefully mapped. It was the first animal to have its DNA sequence completely deciphered, and it is amenable to detailed genetic analysis. The study of *C. elegans* has led to new insights into the details of animal development, neurobiology, behavior, and has been of great value in biomedical research as well as in the understanding of nematode biology (Riddle *et al.* 1997). The reason nematodes are so useful for biological research is due to their simple anatomy and transparent bodies. Nematodes are simple animals, often only containing 1000 cells or less. Nematodes in all or part of their life cycle are worm-shaped (vermiform), although some species become swollen and rounded in later life stages. The basic body plan of a nematode is a tube within a tube. They have an outer skin or cuticle that is secreted from an inner hypodermis. The muscles are attached longitudinally to the nematode's hypodermis, allowing them to move only in the dorsal ventral direction (snake-like movement). Inside the nematode there is an inner tube, the alimentary canal, which runs inside the nematode from head to tail. Between the alimentary canal and the body wall is fluid that provides pressure against the wall to maintain body shape and allow movement. At the head of a plant-parasitic nematode is a hollow mouth spear (like a hypodermic needle) called a stylet. The nematode uses this stylet to puncture plant cells, to withdraw food and also to secrete protein and metabolites that aid the nematode in parasitizing the plant. The stylet is connected to the pharynx that, in turn, is connected to the intestine. The intestine ends at the rectum in the female nematode and the cloaca in the male. Attached to the pharynx are three - five salivary glands which produce secretions that may be emitted from the stylet and that assist the nematode in plant invasion and parasitism. The nematode pharynx is muscular and specialized areas can contract and expand the esophageal lining. The expansion and contraction of the pharynx muscles allow the nematode to pump food into its intestine through its stylet or eject secretions from its salivary glands into and around plant cells. In rhabditidan nematodes, the esophageal muscles are localized in a muscular organ called the metacorpus. In enoplean nematodes, the esophageal muscles are more spread out and do not form a compact pumping organ. In the middle to posterior of the nematode are the reproductive organs. Nematode species often have both males and females, but it is not uncommon for plant nematodes to reproduce asexually by parthenogenesis. In females the reproductive organs are used as traits for identification because the number of ovaries and the position of the vulva in the female nematode's body are easily seen under the light microscope. Male nematodes have one or two testes and they are easily identified by the presence of spicules. Spicules are copulatory structures that are used during mating to guide the sperm into the vagina of the female nematode.

The common plant-parasitic nematode genera are fairly easy to identify to that level using a standard compound microscope. Identification of nematodes to the species level often requires detailed morphological analysis, growth of the nematode on different host plants, or DNA or isozyme analysis. Common morphological features used in nematode identification include the mouth cavity (presence or absence and shape of a stylet), the shape and overlap of the pharyngeal glands with the intestine, size and shape of the nematode body at the adult stage, size of the head, tail, and number and position of ovaries in the female. More subtle characters may include number of lines on the nematode's cuticle or the presence or absence of pore-like sensory organs. An excellent guide to nematode identification is "Plant-Parasitic Nematodes: a Pictorial Key to Genera" by William F. Mai et al., 1996.

Plant-parasitic nematodes occur in all sizes and shapes. The typical nematode shape is a long and slender worm-like animal, but often the adult animals are swollen and no longer even resemble worms. Plant-parasitic nematodes range from 250 um to 12 mm in length, averaging 1 mm, to about 15-35 um in width. While nematodes may look dramatically different, they all share some common features. Nematodes often look segmented because of the numerous annulations (accordion-like transverse grooves) on the cuticle that allow the nematode to bend without kinking, but in fact nematodes are unsegmented and have no replication of body parts throughout the worm. Like most higher animals nematodes possess bilateral symmetry, but with a superimposed trilateral and hexalateral symmetry. Developmentally, nematodes are triploblastic, containing three body layers (ectoderm, mesoderm and endoderm) in the embryo. Most higher organisms are tripoblastic and have a coelom, a body cavity surrounded by mesoderm. Nematodes have a body cavity that is not totally surrounded by mesoderm, so they are pseudocoelomic.

Nematodes are evolutionarily related to insects, and one feature they have in common is the requirement to molt between juvenile stages. All nematodes undergo four molts from the juvenile to the adult phase of their life cycle. They have four juvenile stages and an adult stage. In many nematodes the first molt usually occurs in the egg and it is the second-stage juvenile that hatches. While all nematodes undergo four molts, molting is not required for growth of the nematode as it is in insects because of the elasticity of the nematode cuticle. Nematodes do not have a skeleton, but they do have a hypodermis which functions as a flexible support for their muscles. Nematode muscles are arranged along the longitudinal axis of the worm, thus allowing the body of the nematode to move only in a sinusoidal (snake-like) motion. Nematodes have no defined respiratory or circulatory systems; they depend on diffusion of water, gasses and metabolites in and out of their semi-permeable body walls and internal transport by mixing of the pseudocoelomic fluid as the nematode moves. This lack of respiratory/ circulatory systems prevents nematodes from becoming larger in cross sectional area, but does not limit their length. The largest nematode found thus far was more than 7 meter long and 1 cm in diameter. Sorry, no giant nematodes; they are only in the movies. Nematodes have a sophisticated nervous system and sensory organs to help them find their host plant, to locate specific plant cell types, and to mate and reproduce.

HOW THE NEMATODE SURVIVE IN NATURE

One might think of soil as a safe environment, but to a microscopic nematode it is a hostile world filled with danger. A nematode must contend with voracious predators, changes in soil temperature and moisture, and the death of its host plant. For a nematode population to survive, it must be able to circumvent these obstacles. Nematodes evade these biotic and abiotic obstacles by employing a combination of behavioral and physiological survival strategies. While all nematodes feed on other organisms, the soil is filled with bacteria, fungi and other nematodes that would gladly consume a nutrient-rich plant-parasitic nematode. In fact, the study of nematode predators and pathogens is an important area of study in nematology because nematode predators can be used (in theory) to control populations of plant-parasitic nematodes. While nematodes do possess a thick cuticle that may provide some protection from predation, this type of defense is easily breached by specialized nematode pathogens. The most common method plant nematodes use to evade predation is by living inside plant tissue or by limiting their mobility in the soil environment. By spending less time moving in the soil, a nematode can reduce its chance of "running into" a predator or pathogen. Some plant nematodes spend most of their time in the soil (ectoparasites) and others are mostly contained within the plant tissue (endoparasites). Nematodes that live inside plants have some degree of protection from predation, but they risk death if their host plant succumbs to disease. In contrast, nematodes that move from host to host reduce the risk of perishing with their host, but have a greater chance of encountering a predator or pathogen.

Nematode survival is not impacted only by biotic factors, but also by abiotic ones such as temperature and water availability. The onset of winter or the drying of the soil can be disastrous for a nematode. Interestingly, many nematodes are well adapted to abiotic stress and are capable of cryptobiosis (hidden life): the ability to enter a state of suspended metabolic activity during unfavorable environmental conditions (drying, heat, cold). While not all nematode are capable of cryptobiosis, the ones that are can often survive for years in a cryptobiotic state awaiting favorable conditions that will trigger their revival. The ability of nematodes to undergo cryptobiosis is one reason some nematode species are very difficult to eradicate from a field.

Although cryptobiosis is a useful survival strategy, not all nematodes can enter such a survival stage. Instead, some nematodes have adapted to feed upon many different plant species, thus avoiding the disaster of losing a host plant. Nematodes with a broad host range can feed upon weeds and wild plants making their eradication virtually impossible. By using a complex network of behavioral and biochemical protections nematodes are able to survive and prosper in what would seem to us to be hostile environments.

DISTRIBUTION OF NEMATODES IN FIELDS

While nematodes are motile animals, most are able to move no more than a meter through the soil within their lifetime. However, this lack of long distance crawling does not mean nematodes cannot rapidly spread from field to field. Farm equipment and even muddy shoes contaminated with nematode-infested soil can rapidly disperse nematodes. The movement of water during floods and irrigation can disperse nematodes over long distances. Likewise the movement of nematode infected plants, seeds, and bulbs can give nematodes international tickets to travel the world if plant quarantine officials are not careful. The ability of nematodes to form environmentally resistant stages makes their dissemination even easier, since dried nematodes can be blown with the wind or plant debris over large geographical regions. Even migrating birds are suspected to be able to carry nematodes along their flight paths, assisting the nematodes in their quest for new homes. Essentially any process that moves soil or plant tissue has the ability to disperse plant nematodes, making them difficult plant pathogens to quarantine.

PLANT AND PARASITIC INTERACTION

Nematodes feed on all parts of the plant, including roots, stems, leaves, flowers and seeds. Nematodes feed from plants in a variety of ways, but all use a specialized spear called a stylet. Note the differences in stylet length and shape. The size and shape of the stylet is used to classify nematodes and also can be used to infer their mode of feeding. All three nematodes in Figure 4 are ectoparasites,

but *Belonolaimus* and *Longidorus* feed deep within the roots using their long stylets, while *Helicotylenchus* feeds on the exterior of the root or partially burrows into the root to feed using its short stout stylet.

Often nematodes withdraw the contents of plant cells, killing them. When this type of feeding occurs, large lesions are formed in the plant tissue. Some nematodes do not kill the plant cells they feed upon but "trick" the plant cells to enlarge and grow, thus producing one or more nutrient-rich feeding cells for the nematode. These feeding cells enable long term feeding associations, and form by repeated nuclear division in the absence of cell division (giant cells) or by the incorporation of adjacent cells into a syncytium formed by the breakdown of neighboring cell walls. Collectively, nematodes can feed on almost any plant cell type, and form a variety of feeding cell types. The number of feeding cells can vary from one to a half dozen depending on the nematode species. Many plant-parasitic nematodes feed on the roots of plants. The feeding process damages the plant's root system and reduces the plant's ability to absorb water and nutrients. Typical nematode damage symptoms are a reduction of root mass, a distortion of root structure and/or enlargement of the roots. Nematode damage of the plant's root system also provides an opportunity for other plant pathogens to invade the root and thus further weakens the plant. Direct damage to plant tissues by shoot-feeding nematodes includes reduced vigor, distortion of plant parts, and death of infected tissues depending upon the nematode species. The aboveground symptoms of nematode damage to roots are relatively nondescript, including nutrient deficiency, incipient wilt, stunting, poor yield and sometimes plant death. Few diagnostic signs and symptoms of plant damage by nematodes exist except root galls, cysts, "nematode wool," and seed galls. Thus, damage to crops by root-infesting nematodes often goes unnoticed by growers. Field patterns of nematode damage to roots begin in a small area and spreads radially from the initial infection site, often assisted by farm equipment. The only way to accurately diagnose nematode disease is to sample soil and plant material from suspected sites and extract nematodes for analysis. Nematodes are extracted from the soil by floating them in water to remove heavy soil particles and then catching the floating nematodes on sieves with fine pore sizes. Plant tissues infected with motile nematodes can be incubated in a Baermann funnel or moist chambers to collect nematodes that will exit the tissues. Most plant parasitic nematodes are soilborne root pathogens, but a few species feed primarily upon shoot tissues. The majority of plant parasitic nematode species are in the class Chromodorea, order Rhabditida (formerly placed in the order Tylenchida).

ECTOPARASITIC NEMATODE

The first feeding type is the ectoparasitic mode, in which the nematode remains outside of the plant and uses its stylet to feed from the cells of the plant roots. Nematodes that use this strategy can graze on numerous plants, making it easier for them to switch hosts, but their added mobility makes them very susceptible to environmental fluctuations and predators. Ectoparasitic nematodes can have extremely long stylets, which assist them in feeding deep within the plant root on nutrient rich plant cells. Some of these nematodes induce the plant to form an enlarged cell(s) that the nematode feeds from for an extended period of time. Note, in all life cycle diagrams in this article the abbreviation J=juvenile and the number refers to the stage of the nematode and M=molt and refers to how many molts the nematode has completed.

SEMI ENDO-PARASITIC NEMATODE

Nematodes that feed as semi-endoparasites are able to partially penetrate the plant and feed at some point in their life cycle. Usually the head of the nematode penetrates into the root and allows the nematode to form a permanent feeding cell. These nematodes swell and do not move once they have entered into the endoparasitic phase of their life cycle. By giving up their mobility, the nematodes risk death if their host plant dies, but they also benefit from forming a permanent feed site, which increases their nutrient uptake and reproductive potential. A typical nematode with this life cycle is *Rotylenchulus reniformis*, the reniform (kidney-shaped) nematode. This nematode hatches from the egg as a J2, then quickly molts in the soil to the adult stage without feeding. The anterior end of an adult female enters the plant root and forms a feeding cell. After mating, the female lays its eggs outside of the root in a gelatinous egg mass Maggenti (1981). Another nematode with a similar feeding strategy is *Tylenchulus semipenetrans*, the citrus nematode, although the juvenile stages of this nematode do feed as ectoparasites. As is common in biological systems, it is often difficult to precisely classify animals due to variation in their behavior. True to this rule, several species of ectoparasitic nematodes (e.g. *Helicotylenchus*) are also capable of partially penetrating the root and feeding. However, we do not classify these nematodes as semi-endoparasites because they do not exhibit a consistent endoparasitic feeding behavior.

MIGRATORY EDNO-PARASITIC NEMATODE

Migratory endoparasitic nematodes spend much of their time migrating through root tissues destructively feeding on plant cells. These nematodes cause massive plant tissue necrosis because of their migration and feeding. When they feed from the plant, they simply suck out the plant cell cytoplasm using their stylet, killing the plant cell and moving ahead of the lesion. They make no permanent feeding cells. In a typical life cycle, the nematode hatches from the egg as a second-stage juvenile and starts feeding on the plant. The nematodes feed, molt and reproduce primarily within the plant tissue. All motile stages are capable of feeding from the plant and they are able to move into the soil in search of new roots to invade. Because these nematodes create extensive wounds in the plant root, secondary infection by bacteria and fungi can often occur, further damaging the root system (Zunke 1991).

SEDENTARY ENDO-PARASITIC NEMATODE

The most damaging nematodes in the world have a sedentary endoparasitic life style. The two main nematodes in this group are the cyst nematodes (*Heterodera* and *Globodera*) and the root-knot nematodes (*Meloidogyne*). In these nematodes, the J2 invades the plant near the tip of a root and migrates through the tissue to the developing vascular cells. These nematodes are completely embedded in the root during their initial stages of development, but later the cyst nematodes protrude from the root. The J2 nematodes inject secretions into and around the plant cells to stimulate the formation of large feeder cell(s), which they non-destructively feed on throughout their life cycle. Feeding cells of root-knot nematodes (giant cells) form by repeated nuclear division in the absence of cell division. Feeding cells of cyst nematodes form by the incorporation of neighboring cells into a syncytium formed by the breakdown of neighboring cell walls. Once the feeding cells are formed, the juvenile nematode rapidly becomes sedentary because their somatic muscles atrophy. The juveniles feed, enlarge and molt three times to the adult stage. The large feeding cells formed by these nematodes plug the vascular tissue of the plant making it susceptible to water stress. Female sedentary endoparasites enlarge considerably into a saclike shape and are capable of laying large numbers of eggs. Eggs are typically laid outside the nematode in a gelatinous egg mass, but in cyst nematodes most eggs are retained inside the female body. Both types of nematode have the same basic feeding strategy, but many cyst nematodes have an obligate sexual cycle, whereas the most common species of root-knot nematodes reproduce largely by parthenogenesis.

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How to cite this article: Kumar Y, Yadav BC. Plant-parasitic nematodes: nature's most successful plant parasite. International Journal of Research and Review. 2020; 7(3): 379-386.

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