PLANT-NEMATODE INTERACTIONS

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 (Figure 1). 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 1 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.

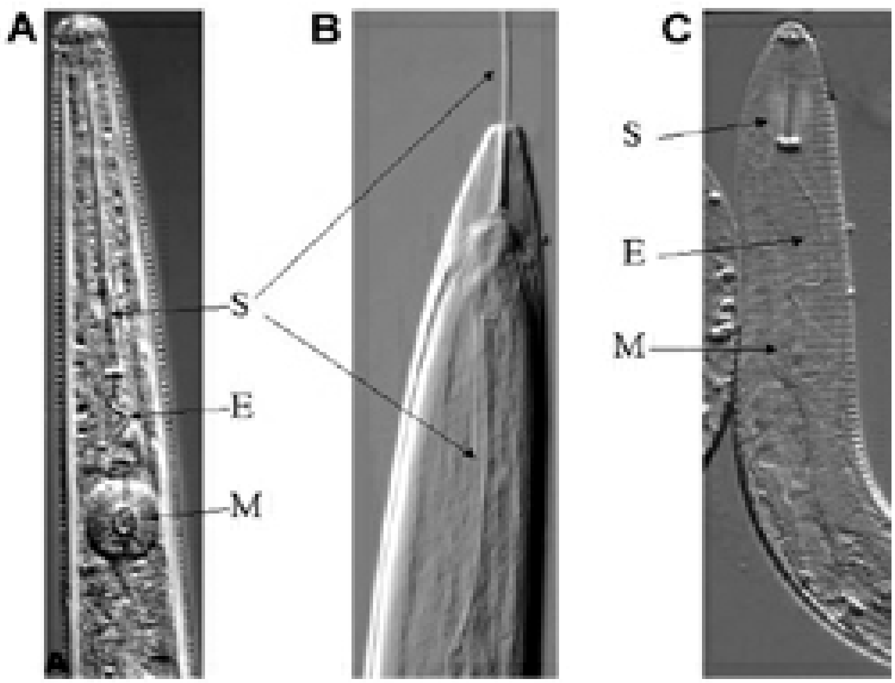

Figure 1.

Figure 4. M=metacarpus; E= esophagus; S= 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.

Ectoparasites: 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.

Semi-endoparasites: 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.

Migratory endoparasites: 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.

Sedentary endoparasites: 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.

Stem and bulb nematodes: Stem and bulb nematodes (*Ditylenchus* sp.) are, as their name suggests, nematodes that attack the upper and lower parts of plants. They use water films to migrate up the stem of the plant and therefore are more damaging under wet conditions. The infectious stage of the stem and bulb nematodes is the fourth stage juvenile. This stage often enters emerging plant tissues below ground, but can crawl up stems in a film of water and enter shoots via buds, petioles, or stomata. Once in the host plant, they destructively feed as migratory endoparasites, molt into adults and reproduce.

Seed gall nematodes: Seed gall nematodes (*Anguina* sp.) were the first plant-parasitic nematodes to be described in the scientific literature in 1743. These nematodes migrate as J2s in water films to the leaves of plants where they feed as ectoparasites at the tips, causing distortion of the leaves. Once the plant starts to flower the J2 penetrates the floral primordia and starts to feed on the developing seed. Once in the seed, the nematode undergoes its molts, continues to feed, and eventually kills the seed to form a blackened "cockle" (seed gall). The adults sexually reproduce, the eggs hatch as J1 and then quickly molt into a J2 survival stage. The environmentally resistant J2 desiccates with the seed gall and overwinters. The nematodes in the seed gall can survive for 30 years if kept in a dry location. When proper moisture and temperature conditions arise, the cryptobiotic J2 becomes active and starts the life cycle over again.

Foliar nematodes: Foliar nematodes are in the genus *Aphelenchoides*. The adult nematodes migrate in water films on the stems to the leaves of their host plant and penetrate the leaves through natural openings (stomata). Once in the leaves the nematodes migrate, destructively feed, molt and lay eggs. The feeding activity of the nematodes causes characteristic interveinal chlorosis and necrosis of the leaf, ultimately killing it. The nematodes are able to move from leaf to leaf if the proper (moist) environmental conditions exist and can severely damage a plant. In the winter the adult nematodes persist in the dead leaves until favorable conditions arise in the spring. If the dead, nematode-infested leaves are moved or blown around this will help disperse the nematode near new host plants (Hesling and Wallace 1961).

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). There are seven major types of nematode feeding strategies used by plant parasitic nematodes (Table 1).

Table 1. Summary of Plant Parasitic Nematode Feeding Strategies

Feeding Strategy	Example Genera	Infective Stage
Ectoparasite	*Belonolaimus*	J2-Adult
	Trichodorus	J2-Adult
Semi-Endoparasites	*Rotylenchulus*	J4
	Tylenchulus	J2
Migratory Endoparasites	*Pratylenchus*	J2-Adult
Sedentary Endoparasites	*Meloidogyne*	J2
	Naccobus	J2
Stem and Bulb Nematodes	*Bursaphelenchus*	J4
Seed Gall Nematodes	*Anguina*	J2
Foliar Nematodes	*Aphelenchoides*	J2-Adult

Plant Nematode Control:

There are several methods commonly used to control plant-parasitic nematodes. These methods can be divided in to three main types: biological control, cultural control and chemical control. The most practical form of biological control is the use of nematode-resistant plants. In this control method, plant breeders cross natural nematode resistance genes into cultivated plant species to improve their resistance to nematodes. The benefit of this method is that it is a very inexpensive way for growers to control their nematode problems. The main disadvantage is that it takes years to screen for resistant plant varieties and more time to breed resistance traits into commercial varieties. Further complications are that natural sources of nematode resistance do not exist for all cultivated species and some species of nematodes are able to grow on resistant plants. However, when "good" resistant plants are available, they are an effective method of nematode control. Other biological control methods use natural predators or pathogens of nematodes. While biological control agents kill nematodes in controlled laboratory settings, implementation of biological control methods in the field is not done due to the expense and difficulty of growing large amounts of nematode pathogens.

Crop rotation with a non-host plant is a very effective method to limit nematode growth. Typically, a cropping system is devised that selects plants that nematodes can and cannot grow on. These plants are grown in alternate years and the problematic nematode population decreases dramatically, below damage threshold levels, in the years that the non-host is grown. This can be an effective method if a producer has the choice of several different crops that can be grown and if the problematic nematode does not have a broad host range or survive in the soil in a cryptobiotic state for long periods of time.

For the past 50 years nematodes have been effectively controlled using chemical nematicides. These are inexpensive chemicals that effectively kill nematodes in soil. There are two types of nematicides, soil fumigants (gas) and non-fumigants (liquid or solid). Soil fumigants became popular because they did not rely on alternative host crops for rotation; they drastically reduced nematode populations in the soil, and were cost effective for most crops. Such fumigants are 1,3 dichloropropene (Telone II), chloropicrin (tear gas), and dazomet (Basamid). . Non-fumigant nematicides such as fenamiphos (Nemacur) and aldicarb (Temik) are based upon the same kinds of active ingredients as many insecticides (i.e. nerve poisons) and can be applied in liquid or granular formulations. While non-fumigant nematicides reduce nematode populations, their effectiveness is not as consistent as that of fumigant nematicides. .

Plant nematodes are not typically controlled using just one method mentioned above, but instead they are managed using a combination of methods in an integrated pest management system.