Diseases caused by Nematodes (Parasitic)

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General Introduction

There is limited information available on crop losses in spinach due to plant-parasitic nematodes, but have been estimated to be 5% in California and 0-1% in Virginia. Dramatic symptoms may be seen on spinach. Nematodes are microscopic aquatic roundworms that move in the film of water that lines soil pores. All nematodes have similar life cycles, consisting of adult, egg, and four juvenile stages with a molt between stages (Fig 1). Nematodes exhibit three life cycle patterns: ectoparasitic, in which adults, eggs, and juveniles remain in the soil, feeding externally on the roots; migratory endoparasitic in which adults, eggs and juveniles can be in soil, in roots, or in plant tissue; and sedentary endoparasitic in which sedentary adults are found in roots, but eggs are laid either in the soil or in plant tissues, and migratory infective juveniles penetrate the root, establish a feeding site, and become sedentary.

Spinach is reported to be susceptible (high level of reproduction) or moderately susceptible (nematode reproduction is somewhat reduced) to nematode species in 12 genera: *Heterodera, Meloidogyne, Pratylenchus, Nacobbus, Longidorus, Paralongidorus, Xiphinema, Trichodorus, Paratrichodorus, Ditylenchus, Scutylenchus,* and *Paratylenchus*. Most of the information available on the biology of these genera has been developed on hosts other than spinach. Spinach is reported to be moderately resistant (nematode reproduction considerably reduced), resistant (nematode reproduction severely suppressed), or immune (no evidence of nematode feeding or reproduction) to some species in these genera.

Symptoms of nematode damage can vary, but often include chlorosis, premature leaf drop, and stunting. However, other plant pathogens, particularly damping-off pathogens, pests, herbicides, and nutritional deficiencies can cause similar symptoms. As a result, soil and plant tissue samples can be taken and analyzed by a diagnostic laboratory to confirm a suspected nematode diagnosis. Frequently reported aboveground symptoms of nematode damage include chlorosis, premature leaf drop, and stunting.

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(Prepared by B. B. Westerdahl)

Cyst Nematodes

Introduction

Three species of cyst nematode have been reported to parasitize spinach: *Heterodera schachtii* (sugar beet cyst nematode), *H. trifolii* (clover cyst nematode), and *H. betae* (yellow beet cyst nematode). In 1859, *H. schachtii* was discovered parasitizing sugar beets in Germany and is now widespread in the United States, Canada, and Europe. *H. trifolii* (clover cyst nematode) was discovered on sugar beet in the Netherlands in 1975. It has also been found in Sweden, Switzerland, Germany, and the United States.

Spinach is reported to be immune to the following species of cyst nematodes: *H. cajani*, *H. ciceri*, *H. medicaginis* (alfalfa cyst nematode), *H. zeae* (corn cyst nematode), and *Cactodera betulae* (birch cyst nematode).

Symptoms

Above ground symptoms of damage caused by cyst nematodes can vary, but often circular or oval-shaped areas of small, chlorotic, stunted seedlings can be evidence of infestation. Even with adequate soil moisture, leaves of infested plants may wilt during the hottest times of the day, only to recover overnight. Root decay may occur following infestation of damaged roots by secondary organisms. Slower growth of infested plants results in uneven plant maturity within a field. This can lead to higher growing costs due to the need for multiple harvests. Over time, infested areas become larger because nematodes are spread by tillage and movement in irrigation water.

Causal Organism

Cyst nematodes are sedentary endoparasitic nematodes in the order Tylcnchida, family Heteroderidae. Tylenchida nematodes possess a stomatostylet and a three-part esophagus. Early stage adult females of *H. schachtii* are white, saccate or lemon-shaped cysts. They are 0.5-0.8 mm long and can be seen on roots without magnification. A few eggs (1 to 200) may be released in a mucoid mass as each cyst forms, but most (10 to 600) are laid within the body of the adult female. When mature, the females die, turn reddish brown, and are more difficult to see on roots. The hardened cuticle of the cyst protects the eggs from desiccation for several years. Initially, cysts are found within the depth of the root zone of plants, but tillage can distribute the cysts to greater depths. Infective second stage juveniles and mature males (1.0-1.5 mm long) remain vermiform. Unlike *H. schachtii, H. trifolii* is yellow, rather than white prior to cyst formation. The cyst, like that of *H. schachtii* is reddish brown.

Disease Cycle and Epidemiology

Egg hatch and the first molt both occur within the cyst (Fig 2). The second-stage juvenile that emerges from the cyst is the infective stage. Some juveniles will emerge from cysts in a field each year, and emergence is stimulated by host root exudates. The second-stage juvenile enters the cortical tissue of roots of host plants, migrates through the root, and feeds with the stylet.

Sexual differentiation does not occur until the third-stage juvenile. The nematodes are amphimictic (reproduce sexually with males and females). At maturity, the head of the adult female remains within the root with the swollen posterior end protruding. The mature male emerges from the root, becomes free-living, and stops feeding on roots.

The life cycle varies from 4 to 6 weeks, depending on soil temperature. Reproduction occurs between 10 and 32°C but is most rapid between 21 and 27°C. The optimum temperature for hatching is 25°C. The annual rate of decline of cyst nematode populations in soil in the absence of a host crop varies from 20 to 80%, and is affected by soil temperature, soil moisture, and feeding by predators and parasites.

The life cycle of *H. trifolii* is similar to that of *H. schachtii*, except that females reproduce parthenogeneticallv (asexually). Males have not been reported.

Management

In addition to sugar beet and spinach, many plants in the Brassicaceae (Cruciferae), including broccoli, Brussels sprouts, cabbage, canola, cauliflower, mustard, radish, and turnip are known to be hosts to cyst nematodes. A number of weeds are hosts for *H. schachtii* including black nightshade (*Solanum nigrum*), buckwheat (*Polygonum* spp.), charlock (*Sinapis arvensis*), common chickweed (*Stellaria media*), lambsquarters (*Chenopodium album*), mustards (*Brassica* spp.), purslane (*Portulaca oleracea*), redroot pigweed *(Amaranthus retroflexus*), and shepherd's-purse (*Capsella bursa-pastoris*). In addition to sugar beet and spinach, carnation (*Dianthus caryophyllus),* Golden Wax bush bean (*Phaseolus vulgaris*), and *Sesbania macrocarpa* have been reported as hosts to *H. trifolii*.

Once infested, eradication of nematodes from a field is not practical, so steps should be taken to minimize spread to non-infested fields. Infested soil can be moved on equipment, wind and water, in crop residue, and on the hooves of animals.

Planting when the soil temperature is below 10°C may allow some hosts become established before juveniles of *H. schachtii* become active. Crop rotation to non-host crops or less susceptible crops, such as cereals, corn, alfalfa, clover, potato, and tomato, is an effective means of control. However, since eggs are protected within cysts, rotations of four to five years typically are required. Weeds listed as hosts of *H. schachtii* must be controlled for rotations to be effective.

Applications of fumigant nematicides, such as 1,3-dichloropropene and isothiocyanate, can provide effective pre-plant control of cyst nematodes. An economic threshold has not been established in spinach, and no resistant cultivars have been reported. The cultivars Sharp Seed, Savory Leaved, Round Seed, and Bloomsdale have been reported to be susceptible to *H. schachtii.*

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(Prepared by B. B. Westerdahl)

Root-knot Nematodes

Introduction

Root-know nematodes are economically important worldwide, and as a result, are among the most widely studied genus of nematodes. Spinach is reported to be susceptible or moderately susceptible to seven species of root-knot nematode: *Meloidogyne arenaria, M. artiellia, M. ethiopica, M. graminicola, M. hapla, M. incognita*, and *M. javanica*. Of these, *M. arenaria, M. hapla, M. incognita,* and *M. javanica* are of the most important for spinach production worldwide.

Symptoms
Symptoms of *Meloidogyne* infestation include wilting, stunting, reduced yield, and galls on roots (Fig 3). Infested plants are more susceptible to vascular wilts and to foliar diseases. Very low levels of infestation can stimulate an increase in growth and yield. Below-ground, symptoms include stunting and galling of roots. Damaged roots are susceptible to secondary invasion by soilborne bacteria and by fungi such as *Fusarium, Pythium,* and *Rhizoctonia*, resulting in rotting of galled tissue.

Causal Organism
Meloidogyne spp. are sedentary endoparasites in the order Tylenchida, family Heleroderidae. Tylenchida nematodes possess a stomatostylet and a three-part esophagus. Mature males (1.1-2.0 mm long) are vermiform. Mature females (0.4-1.0 mm long) are globose with a short, projecting neck. Eggs are deposited in a matrix secreted by the female. Distinguishing among the species of *Meloidogyne* has, historically, been difficult. Striations on the cuticle in the perineal region form patterns that are used to separate species. Variations in these patterns complicate identification. Effective application of cultural management techniques, such as crop rotation and trap cropping, rely on knowing the species present in a field. The ability to analyze DNA sequences of root-knot nematodes has progressively led to more advanced and accurate methods of species identification, including the ability to distinguish mixed populations of single juveniles and juveniles extracted directly from soil. Races exist for some root-knot nematode species that can only be distinguished by a differential host range test . For example, there are four races of *M. incognita*. Races 3 and 4 reproduce on cotton, while races 1 and 2 do not. Race 2 has been reported to parasitize spinach.

Disease Cycle and Epidemiology
All species of root-knot nematodes have a similar life history (Fig. 2). Second-stage juveniles of this sedentary endoparasitic nematode that hatch from eggs are the infective stage. They use a stylet to penetrate root tips at the zone of elongation and migrate to the vascular cylinder where they establish a feeding site. During feeding, secretions from the esophageal gland are released through the stylet and cause changes in the surrounding plant cells, resulting in the formation of "giant cells" and development of a gall. The juveniles become sedentary and, after molting three times, become adults that are spherical or pear-shaped. Each female adult lays 150 to 250 eggs in a gelatinous matrix on the surface of the root, or just below the root surface. Under optimum environmental conditions, development of the nematode is completed in 20-25 days, but this is influenced by soil temperature and host plant. Depending on soil temperature, four or more generations can develop in a single growing season. Different species of *Meloidogyne* have different optimum temperature ranges for development. For example, at 26 to 28°C, the life cycle of *M. incognita* takes 4 to 6 weeks for completion. Juveniles are active at temperatures of 18°C or above. Reproduction is parthenogenetic for many species and there are, typically, few males present. Greater numbers of males can be found late in the growing season when high nematode populations result in greater plant stress.

Management
Root-knot nematode species typically have wide host ranges, making crop rotation difficult. Resistant cultivars are available for some *Meloidogyne*-susceptible crops, including cotton, cowpea, lima bean, tomato, and sweet potato. Weed hosts of *Meloidogyne* spp., such as

solanaceous nightshade (*Solanum* spp.), need to be controlled if rotation crops are to be used successfully. Mixed populations of two or more species of *Meloidogyne* are possible in a field, as is the presence of other nematode genera, which complicates the effective use of crop rotation and resistant cultivars. Tomato cultivars are available with the *Mi* gene located on chromosome 6 that imparts resistance to *M. incognita, M. javanica*, and *M. arenaria,* but not to *M. hapla. Mi*-mediated resistance is characterized by a localized necrosis of host cells near the invading nematode feeding site, that begins about 12 h after infestation. Resistance mediated by *Mi* is lost above 30°C. The selection of resistance-breaking populations of root-knot nematodes in fields cropped to resistant cultivars for multiple years began to be seen in 1995.

For *M. incognita*, delaying planting of a host crop until soil temperature cools to below 18°C can be used to minimize damage because the plants will not become infected and, therefore, nematode development and reproduction will not occur. Planting at temperatures above this threshold can result in nematode development and reproduction. Plowing fallow fields every two to four weeks can expose eggs and juveniles to desiccation and decrease root-knot nematode populations.

Biofumigation is a management technique that has been investigated for management of , fungi, and nematodes. Brassica species such as broccoli produce glucosinolates, which are degraded in soil and release isothiocyanates that are similar to the active ingredient in metam sodium, one of the more widely used nematicides. Marigolds have also been found to reduce damage by *Meloidogyne.*

Trap cropping can be utilized for sedentary endoparasitic nematodes such as root knot nematodes. When a susceptible host crop is planted, larvae of the sedentary parasitic nematode are induced to enter and establish feeding sites within the roots. Once this has occurred and the female nematodes begin to mature, the nematodes are unable to leave the roots. The plants are then destroyed before the life cycle of the nematode can be completed, trapping nematodes within the roots.

Fumigant nematicides such as 1,3-dichloropropene and isothiocyanate can provide effective pre-plant control of root-knot nematode.

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(Prepared by B. B. Westerdahl)

Lesion Nematodes

Introduction
Spinach has been reported to be susceptible or moderately susceptible to four species of lesion nematode: *Pratylenchus neglectus*, *P. penetrans* (Cobb's lesion nematode), *P. pratensis* (meadow nematode), and *P. thornei* (Thorne's lesion nematode). The common name of lesion or root-lesion nematode arose because of necrotic spots sometimes visible on roots at the nematode feeding sites. Because of its importance worldwide, *P. penetrans* has been studied the most widely.

Symptoms
Stunting, chlorosis, and wilting of plants during warm weather are common symptoms but are not diagnostic (Fig 4-5). Below-ground, dark lesions resulting from nematodes moving through roots, feeding on plant cells, and causing mechanical and enzymatic damage may contain eggs, juveniles, and adults. Lesions may become infected by soilborne bacteria and fungi.

Causal Organism
Pratylenchus spp. are migratory endoparasitic nematodes in the order Tylenchida, family Pratylenchidae, that feed within root cortical tissue and are also found in the surrounding soil. They are vermiform and 0.3 to 0.9 mm long. Characteristic diagnostic features using a dissecting microscope are an esophagus ventrally overlapping the intestine, and a posteriorly located vulva. Microscopic dentification to species is difficult and is greatly aided by recently developed molecular diagnostic techniques.

Disease Cycle and Epidemiology
Reproduction in *P. penetrans* is sexual but males are not often found in other species. Depending on soil temperature, the life cycle takes 30 to 90 days. Eggs are deposited singly

in roots or in soil. The first molt occurs in the egg. The second-stage juvenile hatches from the egg and molts three more times to become an adult. All motile stages are capable of root penetration and feeding on cortical cells within the root.

Management

P. penetrans has more than 350 hosts. *P. thornei* has a wide host range, including field crops, vegetable crops, fruit and nut trees, and ornamental plants. In warm areas, this species causes damage on small grains. *P. neglectus* has a very wide host range and is found on annual crops, including barley, oat, and potato, and on perennial crops, including alfalfa. Because most species have very wide host ranges, crop rotation is difficult to utilize effectively for control of lesion nematodes. Applications of fumigant nematicides, such as 1,3-dichloropropene and isothiocyanates, can provide effective pre-plant control of lesion nematodes.

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(Prepared by B. B. Westerdahl)

False Root-knot Nematode

Introduction

Spinach is susceptible to the false root-knot nematode *Nacobbus aberrans*. The common name is derived from root gall symptoms similar to those caused by the root-knot nematode, *Meloidogyne* spp., in the family Heteroderidae. However, morphologically, *Nacobbus* spp. are more similar to lesion nematodes and so are in the family Pratylenchidae.

Symptoms

Stunting and chlorosis are typical aboveground plant symptoms of damage from the false root-knot nematode. Below-ground, false root-knot nematodes cause galling similar to that caused by root-knot nematodes. Multiple galls may occur in chains on root tissue.

Causal Organism

Nacobbus *aberrans* is in the order Tylenchida, family Pratylenchidae. They are sedentary endoparasites. Mature females (0.7 to 1.9 mm long) are sedentary and oval-shaped, (semisaccate) with a very long neck and a swollen body. Unlike root-knot nematodes, there are no striations in the perineal region. Eggs are deposited in a gelatinous matrix outside the body of the female. Males (0.8 to 1.2 mm long) and juveniles are vermiform.

Disease Cycle and Epidemiology

Juveniles, young females, and males are migratory endoparasites that damage roots as they move intercellularly through the cortex. Young females are long and slender and migrate from the cortex to a position near the vascular cylinder. Females become sedentary and, as they mature to adults, galls develop around the females. Females produce an egg sac that extends to the outside of the root surface. The optimum temperature for egg hatch is 25°C at which temperature the life cycle takes about 45 days.

Management

In addition to spinach, other plant hosts include broccoli, cabbage, carrot, cucumber, lettuce, pea, pumpkin, radish, rutabaga, sugar beet, tomato, and turnip. Non-host rotation crops include alfalfa, potato, and grain. Weed hosts that must be controlled during rotations include *Kochia* spp., common lamb's-quarters (*Chenopodium album*), Russian thistle (*Salsola autralis*), puncturevine (*Tribulus terrestris*), common purslane (*Portulaca oleracea*), and cacti *(Cory-phantha vivipara, Opuntia fragilis,* and *O. tortispina).* Pre-plant application of nematicides can control false root-knot nematodes.

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(Prepared by B. B. Westerdahl)

Needle and Dagger Nematodes

Introduction

Spinach is susceptible to the needle nematode, *Paralongidorus maximus*, moderately susceptible to the needle nematodes, *Longidorus africanus* and *L. elongatus,* and susceptible to the dagger nematode, *Xiphinema* spp. Stunting of lettuce seedlings in the Imperial Valley of southern California led to recognition of the importance of *L. africanus* and to research on the biology and host range of this needle nematode.

Symptoms

Root tips attacked by needle nematodes become swollen and may develop necrotic spots. Root systems of older infected plants are greatly reduced in size. Seedlings are severely stunted and infected plants may never reach harvest-maturity. Even low populations in soil (less than 5 nematodes per 250 g soil) can cause significant seedling losses.

Causal Organism

Needle and dagger nematodes are in the order Dorylaimida, family Longidoridae. They are migratory ectoparasites, and all stages are vermiform. They have a two-part esophagus with a

slender anterior part and a swollen glandular and muscular posterior bulb. They are also characterized by the presence of a very long odontostyle. The stylet and extension are approximately 150 µm or more in length. They are relatively large nematodes. *Longidorus* spp. are 2 to 8 mm in length. *Xiphinema* spp. are 2 to 5 mm in length.

Disease Cycle and Epidemiology
A characteristic of the order Dorylaimida is that the first stage juvenile hatches from the egg, followed by four molts to reach the adult stage. Nematodes in this order can transmit some plant viruses. Needle and dagger nematodes have relatively long lifecycles. Reproduction is greatest at soil temperatures around 28°C. The life cycle of *L. africanus* can be completed in 7 weeks. For *L. elongatus*, the life cycle requires 19 weeks. All motile stages are capable of feeding on plant roots. Depending on species, reproduction can be either sexual or parthenogenetic.

Management
L. africanus has a wide host range, including barley, Bermuda grass, cantaloupe, corn, cotton, cucumber, eggplant, lima bean, okra, snap bean, sorghum, sugar beet, and wheat. *L. elongatus* also has a wide host range. Because of the wide host range of these nematodes, crop rotation may not be an effective control measure. Damage can be reduced by planting at soil temperatures less than 17°C. Needle and dagger nematodes can be controlled effectively with nematicides.

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(Prepared by B. B. Westerdahl)

Stubby Root Nematodes

Spinach is susceptible to the stubby root nematodes *Trichodorus* spp. and *Paratrichodorus minor.*

Symptoms
The name stubby root is derived from the symptoms this group of nematodes produces on host plants. Symptoms of injury consist of general stunting of the entire plant and shortened, branched root systems. Yellowing of leaves may result from a mineral deficiency associated with reduced function of injured roots. Nematodes may kill the tips of growing taproots early in the seedling stage or cause the formation of stubby-ended lateral roots, that may eventually turn brown and die.

Causal Organism
Stubby-root nematodes are in the order Triplonchida, family Trichodoridae. They are migratory ectoparasites and all stages are vermiform. These nematodes have a two-part esophagus with the posterior part broadening posteriorly. Members of Triplonchida feed with a movable tooth (onchiostyle) that may vary from curved and grooved to convoluted and complex. The adults vary in length from 0.4 to 1.8 mm. Nematodes in this order are capable of transmitting certain plant viruses such as tobacco rattle virus. This virus is not common in spinach, but if a new virus disease is found, nematodes should be considered as a possible vector.

Disease Cycle and Epidemiology
These nematodes have wide host ranges. Reproduction in some species is parthenogenetic and sexual in others. The eggs are laid in the soil. The life cycle is generally completed in 6 to 7 weeks at optimal temperatures between 20 and 25°C. Feeding occurs in the epidermal root cells and outermost cortical cells. Cells are punctured by a rasping motion. Damage to roots is caused by decreased cell multiplication in root tips rather than by mechanical destruction of cells.

Management
Because of the wide host range, crop rotation is not an effective control measure. Applications of synthetic nematicides can provide satisfactory control of these nematodes.

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(Prepared by B. B. Westerdahl)

Stem and Bulb Nematode

Introduction
The stem and bulb nematode, *Ditylenchus dipsaci*, parasitizes more than 500 host plants. The species is a complex of races that can be differentiated only by host range. Some races are host-specific while others have a wide host range. More than 20 biological races have been identified and named after their preferred hosts or those plants on which they were first detected. Spinach is susceptible to the sugar beet race, moderately resistant to the chicory and onion races, and immune to the garlic race of *D. dipsaci*.

Symptoms
As the name suggests, the stem and bulb nematode feeds on aerial parts of various host plants, within parenchymatous tissue of stems, bulbs, leaves, inflorescences, and buds, and within bulbs,

tubers, rhizomes, stolons, and roots. As a result of nematode feeding, general symptoms develop that include swelling, distortion, discoloration, and stunting of aerial plant parts, and necrosis and rotting of below-ground tissues. Root rot, which results from the invasion of secondary soilborne pathogens, may develop during the growing season.

Causal Organism

Ditylenchus spp. are in the order Tylenchida, family Anguinidae. They are migratory endoparasites that feed on parenchymatous tissue in both the stems and bulbs of numerous hosts. Adults and juveniles are vermiform with a small, delicate stylet with distinct basal knobs. Adults are 1.0 to 1.3 mm long. The glandular region of the esophagus abuts the intestine.

Disease Cycle and Epidemiology

The life cycle of the stem and bulb nematode is completed in 3 to 4 weeks. Like other members of the Tylenchida, there are four juvenile stages with a molt between stages, and the first molt occurs within the egg. Mating is necessary for reproduction. A single female can lay 200 to 500 eggs within plant tissue. Several generations can occur in one crop season. All post-embryonic stages of *D. dipsaci* can infect plants, but the fourth stage juveniles have the ability to withstand desiccation by undergoing anhydrobiosis and surviving for long periods. Under dry conditions, they may survive for several years. Plants are invaded through stomata or tissue is penetrated directly at the base of stems and leaf axils. The nematodes may invade seedlings below the soil surface.

Management

Rotation to non-host crops is feasible, depending on the host preference of the race present. Weeds must be controlled. Sanitation, such as the destruction or removal of infected plant debris, can reduce subsequent infestations. Applications of synthetic nematicides can provide satisfactory control of these nematodes.

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Other Nematodes

Spinach is susceptible to the pin nematode, *Paratylenchus projectus*, and moderately susceptible to *Scutylenchus rugosus*. Spinach is immune to the reniform nematode, *Rotylenchulus reniformis*.

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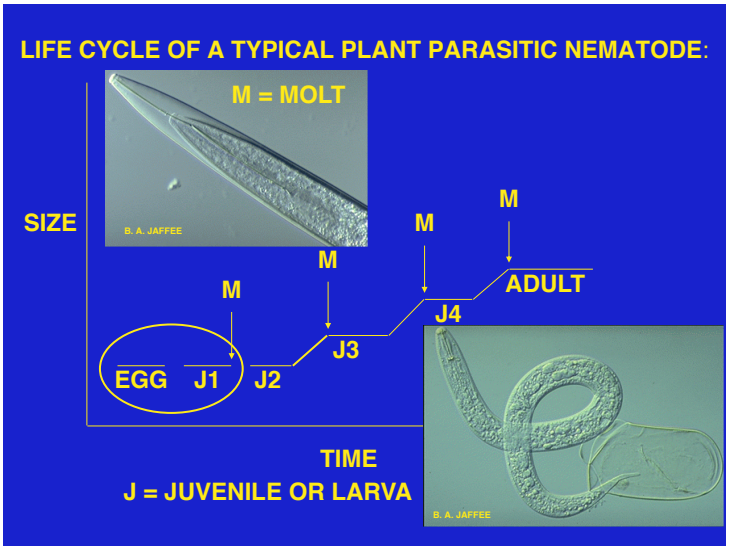

Figure 1. Life cycle of a typical plant parasitic nematode. (Modified from Lee, 1964, Fig 28)

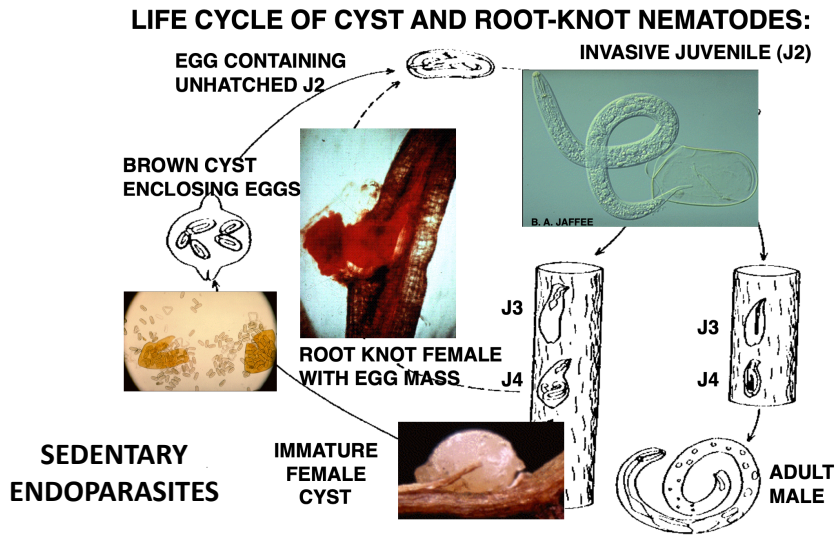

Figure 2. Life cycle of cyst and root-knot nematodes. (Modified from Roberts and Thomason, 1981, Fig 1)

Figure 3. Galls on the roots of spinach plants caused by root-knot nematodes (Spin RKN 040). (Photo courtesy Mark Black/Larry Stein)

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Figure 4. Severe stunting in a bed of baby leaf spinach from damage by root lesion nematode and *Pythium* spp. Damage from root lesion nematodes often is more severe in the presence of root pathogens, such as *Pythium* spp. and *Rhizoctonia* spp. (Photo courtesy Lindsey du Toit)

Figure 5. A spinach plant wilting as a result of *Pythium* and root lesion nematodes. (Photo courtesy Lindsey du Toit)