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NEMATODES AS PLANT PARASITES

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Contents

8.1 Introduction

Nematodes are the most abundant group of multicellular animals on earth in terms of numbers of individuals. There are at least as many nematode species as insect species. In a square metre of moderately fertile soil to 30 cm depth, there are about 50 million nematodes. Nathan Cobb, father of nematology in Australia, provided a good mental picture of the importance and diversity of nematodes when he stated that 'if all matter in the universe except nematodes were swept away, our world would still be dimly recognisable—we would find its mountains, hills, valleys, rivers, lakes and oceans represented by a film of nematodes'. About half of all nematode species are marine nematodes, 25% are free-living, soil-inhabiting nematodes, 15% are animal and human parasites and 10% are plant parasites. Today, even with modern technology, 5–10% of crop production is lost to nematodes in developed countries.

8.2 General structure of nematodes

Nematodes are generally worm-shaped, being cylindrical but tapering at both ends. However, adult females of some species swell to become kidney-shaped, lemon-shaped or spherical. Some plant parasites may be up to 3 cm long but most nematodes found in soil are 0.5 to 1 mm long.

Regardless of their feeding habits, all nematodes have the same basic structure. Just behind the mouth is a **stoma** (a chamber lined with cuticle) through which the nematode ingests food. Nematodes have evolved a wide variety of feeding structures, each adapted to a particular method of feeding. Species that feed on bacteria have a large cylindrical or funnel-shaped stoma through which the nematode sucks its food. Some have lip extensions to tear dead plant tissues apart. Carnivorous species have teeth for holding or piercing their victims which may include other nematodes. Most plant-parasitic nematodes have a hollow spear, called a **stylet**, with which the nematode pierces cell walls to suck cytoplasmic contents from plant cells. Stylet shapes and sizes are useful taxonomic characters as they vary markedly in different species.

Behind the stoma is the **oesophagus** (sometimes spelt esophagus) (Fig. 8.1). This is a muscular, glandular tube with a lumen which is usually triradiate in cross section. The lumen is also lined with cuticle. Radial muscles attached to the lumen contract, pulling the walls apart, creating a suction. The oesophagus of many nematodes is subdivided into four main regions (Fig. 8.2). The **procorpus** connects the stoma to the **metacorpus** or **median bulb**. In plant parasites, the median bulb contains a valvular apparatus which creates suction and allows the nematode to feed via the style. The **isthmus** joins the metacorpus to the basal bulb. The basal bulb is glandular and is sometimes expanded into a flap which overlaps the intestines.

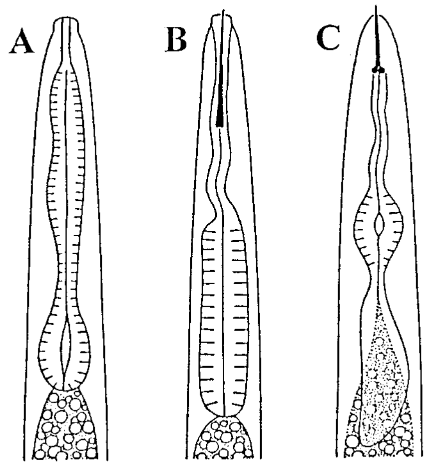

Figure 8.1 Structure of nematode oesophagus. (A) *Rhabditida* (bacterial feeder). (B) plant parasitic form of Dorylaimida. (C) *Tylenchida* (plant parasite).

Nutrients from the oesophagus are metabolised and absorbed by the intestine into compounds required by the nematode. The intestine also stores reserve food and excretes wastes combining the functions of both the intestine and liver of mammals. Intestinal cells of adequately fed nematodes contain large numbers of proteinaceous and lipid globules as well as glycogen and other storage products. Without access to a suitable host, plant-parasitic nematodes starve, utilising intestinal reserves so that the intestine becomes clear.

In most nematode species, the sexes are separate with females being generally larger than males. Adults of the two sexes are easily distinguished morphologically (Fig. 8.2A and D). The female gonad has one or two elongated tubes which may be longer than the nematode's body and therefore they are coiled or reflexed. At the distal end of the gonad is the **ovary** where cells divide forming **oocytes**. The oocytes enlarge and move to the uterus via the **oviduct**. In some species, there is a specialised pouch between the oviduct and uterus. This is the **spermatheca** which stores sperm. The eggshell is formed around the fertilised oocyte in the uterus. The egg is laid from the uterus via the vagina. This leads to the vulva which is an opening on the ventral wall of the nematode.

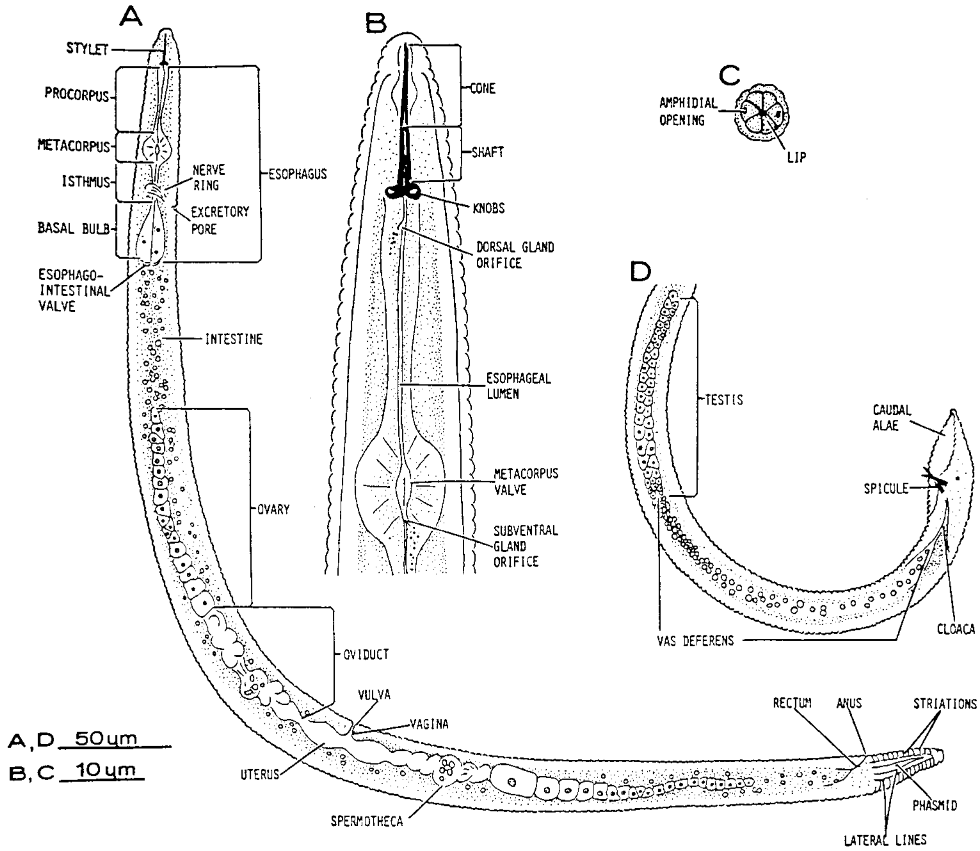

Figure 8.2 Morphology of the stunt nematode (*Tylenchorhynchus* spp.). (A) female; (B) anterior region of female (lateral view). (C) face view of female. (D) posterior region of male (lateral view). (From O'Brien and Stirling, 1991.)

The testis of the male reproductive system (Fig. 8.2D) is similar to the ovary, having a zone of cell division, which produces sperm, and a growth zone, where the sperm cells enlarge. Sperm accumulates in the enlarged **seminal vesicle** and is conducted to the exterior via the **vas deferens** which is a glandular and muscular tube. The exterior opening of the reproductive system, the **cloaca**, is shared with that of the alimentary canal. The male gonad also possesses two hook-like structures, the **spicules**, which originate inside the cloaca. They form a passageway for sperm during mating when they are inserted into the vagina of the female. In some species, the male has lateral cuticular flaps, the **caudal alae** or **bursa**, in the tail region which they use to grasp the female during copulation.

Many types of reproduction have evolved. In most species the sexes are separate but some species reproduce without males. These may be hermaphroditic with a gonad that can produce sperm or eggs at different times. Where only females are known, they lay eggs that develop parthenogenetically. **Parthenogenesis** (development of an individual from an egg without fertilisation by a sperm) is the most common form of reproduction in *Meloidogyne* (root-knot nematode). Depending on the species, the mechanism may be either mitotic or meiotic. In meiotic parthenogenesis, the second nuclear division does not occur so that the normal somatic chromosome number is restored and embryogenesis can proceed. In mitotic parthenogenesis, the mature oocyte undergoes a single mitotic division, forming a diploid egg. The somatic chromosome number is conserved and embryogenesis can proceed.

The most obvious component of the nervous system of nematodes is the **nerve ring** which encircles the oesophagus just behind the median bulb. This connects several hundred cells and some sense organs. Longitudinal nerve trunks run from the nerve ring to the head and to the rest of the body. The nematode's nervous system is quite sophisticated for an animal of its size. It allows the nematode to move in any direction, to detect touch and changes in temperature, to use chemical gradients to find members of the opposite sex and sources of food, to feed by probing with the stylet or by activating the stoma, to move components of the oesophagus to swallow and digest food and to defecate, to mate, lay eggs and to produce and secrete various compounds from their glands.

The nematode's sense organs are found near the head and around the vulva and cloaca. A ring of papillae encircles the opening of the stoma. Two pouches in the head, the **amphids**, are connected to slits or pores on the lips through which secretions are released. The amphids combine nerve endings and gland cells. In hookworms, these are used to secrete anticoagulants into the host's blood. Amphids of both plant- and animal-parasitic nematodes contain the enzyme, acetylcholinesterase, which is important in nerve physiology. This enzyme is the target of several nematicides and is similar to that in humans and other animals.

8.3 Life cycle

Typically, there are six stages within a nematode's life cycle: an egg, four juvenile stages and the adult stage (Fig. 8.3). Each juvenile stage and the adult are separated by a moulting phase. The first stage occurs in the egg. For most plant-parasitic nematodes, the first moult also occurs in the egg so that it is the second-stage juvenile which hatches.

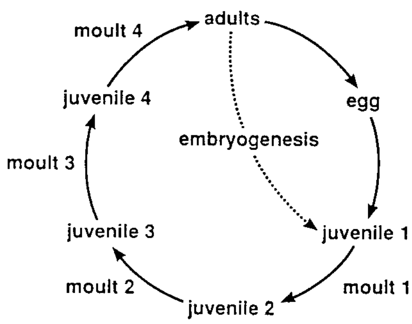

Figure 8.3 Generalised life cycle of nematodes. (From O'Brien and Stirling, 1991.)

8.4 Feeding types

Plant-parasitic nematodes feed either ecto- or endoparasitically (Fig. 8.4). **Ectoparasites** feed from the outside of the root, inserting the stylet only or the head and neck. Examples of **ectoparasites** are *Xiphinema* (dagger nematodes), *Longidorus* (needle nematodes), *Trichodorus* (stubby-root nematodes), *Helicotylenchus* (spiral nematodes), *Criconemoides* (ring nematodes), *Paratylenchus* (pin nematodes) and *Tylenchorhynchus* (stunt nematodes). In contrast, **endoparasites** enter root or shoot tissue and feed within the plant. They can be **sedentary**, establishing specialised feeding sites and remaining there until they die. Examples of sedentary endoparasites include *Heterodera* and *Globodera* (cyst nematodes), *Meloidogyne* (root-knot nematode), *Rotylenchulus reniformis* (reniform nematodes) and *Tylenchulus semipenetrans* (citrus nematodes). Alternatively, they may be **migratory**, moving through plant tissue and feeding along the way. Examples of migratory endoparasites of roots are *Pratylenchus* (lesion nematodes) and *Radopholus* (burrowing nematodes). Other migratory endoparasites can feed above ground in stems, leaves, flowers, etc. Examples of these are *Ditylenchus dipsaci* (stem and bulb nematodes), *Aphelenchoides* (leaf nematodes) and *Anguina* (seed gall nematodes). By combining the means of parasitism with the plant organ attacked and the type of symptoms produced, a useful practical scheme for classifying nematodes can be obtained (Table 8.1).

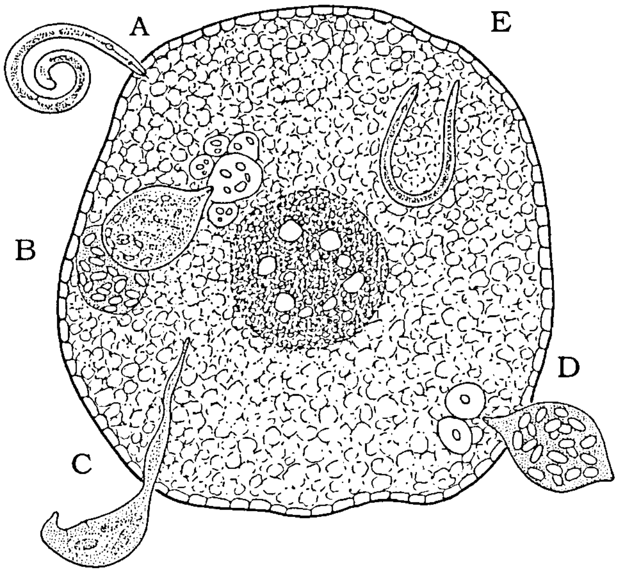

Figure 8.4 Common feeding types of nematodes. (A) Ectoparasite (*Helicotylenchus*); (B) Sedentary endoparasite (*Meloidogyne*); (C) Semi-endoparasite (*Tylenchulus*); (D) Cyst-forming sedentary endoparasite (*Heterodera*); (E) Migratory endoparasite (*Pratylenchus*).

8.5 Symptoms of nematode damage

Nematode infestation can affect all root functions. For example, affected root systems are often stunted, so that they are less able to take up water and nutrients. This is common in plants affected by *Meloidogyne* or *Pratylenchus*. Many nematode genera, such as *Pratylenchus* and *Helicotylenchus* cause extensive lesions on roots. These lesions may be invaded by secondary fungi so that necrotic areas become more extensive. Necrotic roots are less able to anchor plants. This is a particular problem with bananas infested by *Radopholus similis*, as whole plants can fall over. *Meloidogyne* and *Heterodera* can cause galling and distortion of roots. Production of gall tissue is not necessary for nematode reproduction but is a reaction of the plant to the presence of the nematode. Photosynthates and assimilates which would otherwise contribute to yield are redistributed to maintain gall tissue. Nitrogen fixation by *Rhizobium* and infection by mycorrhizas may be reduced by nematode attack.

Nematodes which attack above-ground parts of plants often produce diagnostic symptoms. For example, *Aphelenchoides* causes typical angular lesions between leaf veins of several plant species including chrysanthemum and strawberry. Some grasses infested by *Anguina* produce nematode galls in place of seed. *Ditylenchus dipsaci* causes stunting and distortion of leaves and flowers and, in some cases, stems may become cracked and rotten. Some nematodes, including *Aphelenchoides composticola* and *Ditylenchus myceliophagus* are mycophagous and important pathogens in the mushroom industry. They cause poor growth and breakdown of mycelium.

Table 8.1. Classification of plant parasitic nematodes on the basis of plant organ attacked and mode of parasitism.

1. Sedentary endoparasites of roots
Root-knot nematodes (*Meloidogyne*)
Cyst nematodes (*Heterodera*, *Globodera*, *Punctodera*)
Cystoid nematodes (*Cryphodera*, *Meloidodera*)

2. Sedentary semi-endoparasites of roots
Citrus nematode (*Tylenchulus semipenetrans*)
Reniform nematodes (*Rotylenchulus*)

3. Migratory endoparasites of roots
Burrowing nematodes (*Radopholus*)
Root-lesion nematodes (*Pratylenchus*)

4. Migratory ectoparasites of roots
Sheath nematodes (*Hemicycliophora*, *Colbranium*)
Dagger and needle nematodes (*Xiphinema*, *Longidorus*, *Paralongidorus*)
Stubby root nematodes (*Trichodorus*, *Paratrichodorus*)
Stunt nematodes (*Tylenchorhynchus*, *Merlinius*)
Sting nematodes (*Belonolaimus*)
Ring nematodes (*Criconema*, *Criconemella*, *Macroposthonia*, *Nothocriconema*)
Pin nematodes (*Paratylenchus*)
Spiral nematodes (*Rotylenchus*, *Helicotylenchus*, *Scutellonema*, *Hoplolaimus*)

5. Stem and bulb nematode (*Ditylenchus dipsaci*)

6. Bud and leaf nematodes (*Aphelenchoides*)

7. Gall nematodes (*Anguina*)

8. Nematodes that attack fungi (*Ditylenchus myceliophagus*, *Aphelenchoides* spp., *Aphelenchus avenae*, *Paraphelenchus* spp.)

Above-ground symptoms following nematode damage to roots are usually not diagnostic. In infested areas, plants are stunted, yellow and often wilt, especially in hot weather. Because affected crop plants grow poorly, weeds are better able to compete and weedy patches are common. Symptoms may occur in patches because nematodes are not evenly distributed in the soil.

In addition to their direct effects, nematodes may interact with other pathogens to increase the damage caused by that pathogen. Nematodes may predispose plants to infection by acting as a vector for the pathogen, by creating a wound in healthy tissue for pathogen entry or by modifying host tissue which may otherwise have been resistant to the secondary pathogen. Examples are given later in this chapter.

8.6 Population dynamics and threshold levels

Plant-parasitic nematodes are obligate parasites but they do not necessarily cause disease or yield loss. The amount of damage caused by nematodes is the result of a complex interaction between the nematode, the host, the environment and other organisms. Therefore, many factors need to be considered in the interpretation of the real effects of nematodes on plants.

One important factor is the population dynamics of the nematode species involved, particularly the relationship between nematode numbers (population) of a particular species and plant yield (Fig. 8.5). Three concepts are useful in interpreting this relationship. Firstly, the minimum density of nematodes which causes symptoms or yield loss is known as the **tolerance limit** or **level**. The nematode density at planting which will eventually reach the tolerance limit and cause yield loss is the **threshold level**. Finally, the nematode density which will cause yield loss equal to the cost of control is the **economic** (or **treatment**) **threshold level** (Fig. 8.5). This determines the need for nematode control such as nematicide application, which usually occurs before or at planting, or the use of resistant cultivars. The economic threshold refers to the nematode density at the time of making decisions about nematode control options. In many crops, this occurs before planting. For other crops, particularly for perennial crops, decisions must also be made long after planting.

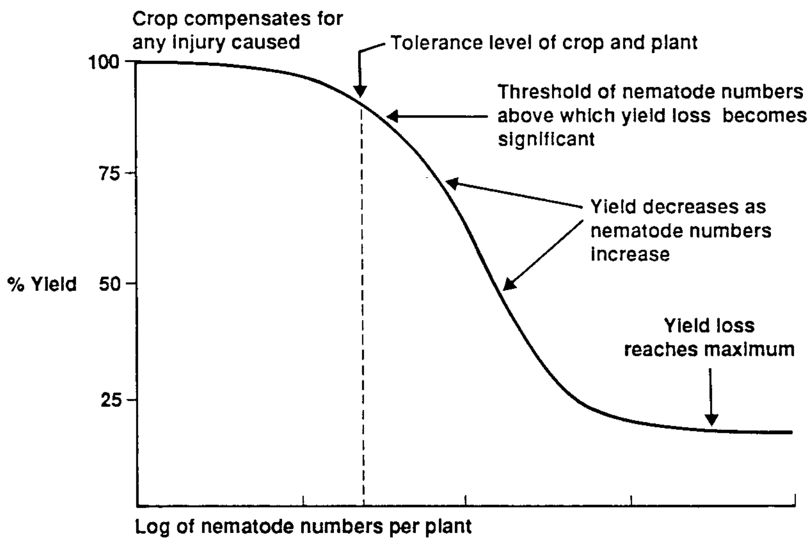

Figure 8.5 Relationship between nematode numbers and yield. (From O'Brien and Stirling, 1991.)

The economic threshold level depends upon many factors including the form of parasitism, life cycle, rate of reproduction and survival of the nematode, tolerance of the crop, length of the growing period and the marketable product of the host plant. Environmental conditions are particularly important because under good growing conditions, with adequate soil moisture and nutrition, plants can tolerate more nematodes than under conditions of stress. Economic thresholds are often difficult to determine because environment and market values cannot be predicted with certainty.

Populations of plant-parasitic nematodes in agricultural soils are constantly changing. Because plant-parasitic nematodes are obligate parasites, they decrease in number when a host is not present or when conditions are not favourable for reproduction. Therefore, the correlation between nematode populations and plant yield can change during the season. During the early period of growth, when there is relatively little nematode damage, higher plant yield is usually found where there are fewer nematodes. However, this relationship can be reversed later in the season because nematode reproduction may be reduced on severely damaged plants while nematode numbers increase more rapidly on actively growing roots.

The rate of reproduction usually increases as the initial density of nematodes decreases. High initial densities can cause root damage so that population increase tends to be curtailed, whereas low numbers increase rapidly on healthy root systems. This explains why the use of nematicides may not always reduce nematode numbers at crop harvest.

8.7 Nematode survival

Nematodes owe much of their success in the soil environment to their ability to survive in the absence of host plants and, especially in Australia, this usually requires some mechanisms to overcome the effects of desiccation. Eggs of root-knot (*Meloidogyne*) and cyst nematodes (*Globodera* and *Heterodera*) survive in gelatinous egg masses and cysts, respectively. These structures ensure slower desiccation particularly in those eggs in the centre of the egg mass or cyst.

Some cyst nematode species also have hatching mechanisms which ensure hatching only when a host plant is present. The cereal cyst nematode (*H. avenae*) requires a period of low temperature followed by a period of higher temperature before exposure to adequate soil moisture will allow hatching. This is explained further in Chapter 31. Eggs of the potato cyst nematode (*Globodera rostochiensis* and *G. pallida*) will hatch only in the presence of root exudates from host crops such as potato. This ensures that eggs do not hatch in a 'no-win' situation when no hosts are available on which to feed.

Some nematodes, such as *Anguina funesta* and *Ditylenchus dipsaci*, can survive for many years without water by a process known as anhydrobiosis. In this state, they are metabolically inactive with a loss of up to 99% of their body water. When water becomes available, the nematodes rehydrate and are fully functional.

8.8 Ecology

Physical and chemical aspects of the environment, such as temperature, light, moisture, soil type, and nutrition have a marked effect on the nematode and its host plant. Because the environment can affect pathogenicity through its effects on the host plant, prevention or avoidance of conditions which place the host under stress can offset nematode damage to crops. Practices, such as irrigation, conservation of moisture by mulching and using the correct fertiliser application are effective in limiting yield loss by raising the plant's tolerance level. Such practices, however, only provide temporary relief as nematode numbers will increase under these favourable conditions. Nematodes increase to enormous numbers without causing significant plant damage when placed in near optimal environments such as in a glasshouse.

All plant-parasitic nematodes complete part of their life cycle in the soil and are influenced by the soil environment. Since soil is a complex system with properties that can vary in localities of close proximity, it is not surprising that field distributions of nematodes are normally erratic and patchy. Nematode populations may also show wide fluctuations throughout a year and from one year to another. Distribution of nematodes in soil can be affected by many factors. Spatial distribution varies both horizontally and vertically and is affected by plant spacing, soil fertility and root depth. Nematodes are usually clustered, particularly among roots and tend to migrate downwards as soil dries. Generally reproduction is seasonal, with populations increasing when temperatures are optimal.

There are several important relationships involving soil, physical and environmental factors and nematodes. Soil moisture, texture, structure and temperature are particularly significant.

Water provides an important medium for active migration of nematodes in soil. Nematodes are also dispersed passively by rivers, streams, irrigation canals, floodwaters and percolating water. Nematodes normally live in moisture films surrounding soil particles and exploit the surface tension of this film for their movement. If the film is too thick, nematodes may slip and if the film is too thin there is too much friction for movement. Thus, there is probably an optimum soil texture and film thickness for each nematode species. Plant nematodes generally infect and develop best when the soil moisture is just below field capacity. This provides a favourable moisture film for movement and also allows efficient oxygen exchange.

Soil texture and structure affect nematode movement directly through their effects on pore size. Small pores in clay soils prevent nematode passage so that nematodes must move in the spaces between aggregates. The larger pores in coarse sands may be too big to allow nematodes to gain leverage between particles. Nematodes therefore tend to reproduce best in fine sands, sandy loams and well-aggregated loams and clay loams.

Soil temperature, which changes constantly, is a major factor influencing nematode development. Diurnal fluctuations in temperature vary in extent and depend upon soil type, texture, moisture, atmospheric conditions, latitude, elevation, season and soil cover. Fluctuations are greatest at the soil surface and decrease with increasing depth. In tropical regions, nematodes multiply throughout the year but in subtropical and temperate climates, most of the important plant parasites are most active during the warm summer months, when soil temperatures of 20–30°C are common. Cool climate species often develop slowly in winter and become more active when temperatures rise in spring.

8.9 Control of nematode diseases

Resistance / tolerance

Resistance to nematodes is defined as the ability of the host to reduce reproduction by the nematode. Nematodes, therefore, fail to multiply or multiply poorly on resistant plants. The opposite of resistance is susceptibility. This is genetically distinct from **tolerance** which relates to the ability of the host to withstand attack by the nematode (Table 8.2).

Table 8.2 Definition of resistance and tolerance to nematode infection.

		Nematode reproduction	
		Low	High
Plant yield	High	resistant/tolerant	susceptible/tolerant
	Low	resistant/intolerant	susceptible/intolerant

Resistance is found most commonly against nematodes which establish complex host-parasite interactions (e.g. *Meloidogyne*, *Heterodera*, *Globodera*) and results from a change in the balance of reactions between nematode and host. The most common mechanisms of resistance are associated with a hypersensitive reaction to the nematode, particularly to sedentary endoparasites, and a failure of the nematode to induce compatible responses in the plant to allow feeding. Less common mechanisms include a failure of plants to attract nematodes, inhibition of egg hatching, resistance to penetration by nematodes and production of toxins by plants (e.g. *Tagetes*).

One advantage of resistance as a form of control is that it entails no extra cost once the planting material is purchased. It does not depend on suitable soil and climatic conditions. Resistance inhibits growth and development of the nematode so that the post-cropping population is decreased. For some crops, resistance may be the only economic method of control. However, a resistant host may still be damaged if it is intolerant of the nematode. It takes 10–15 years to develop a resistant cultivar, whether by conventional breeding or genetic engineering, and to date very few have been developed.

The mechanisms involved in tolerance of nematodes and other plant parasites are not well understood. However, some mechanisms that have been suggested include plant growth in excess of that required to produce an economic yield, growth compensation for damage caused by nematodes and lack of response to the presence of the nematode. For example a tolerant plant may produce less gall tissue than an intolerant one, thereby enabling it to conserve photosynthates for normal growth. An advantage of tolerance as a control strategy is that it does not exert selection pressure on the nematode as resistance may. However, if the host is also susceptible, the nematode population may reproduce and eventually exceed the tolerance limit and so cause yield loss.

Crop rotation

Rotation is a long recognised method of controlling nematodes. It aims to keep a balance between the population of the nematode and cropping frequency by allowing sufficient time after each host crop for the nematode population to decline below the economic threshold of the next susceptible host crop. To plan a suitable rotation, the identity of the nematode must be known as well as its host range, degree of susceptibility of various hosts, population dynamics, and the relationship between nematode density and yield loss (crop tolerance).

Weedy fallows, commonly used between crops, usually contain host plants which can maintain or increase nematode populations. Since a bare fallow is often impractical because of the risk of soil erosion, the use of a nematode-resistant crop during this period is preferable. Crops, such as marigold (*Tagetes*) and castor bean (*Ricinus*), which produce compounds that actively kill nematodes are often promoted as having potential for use as rotation crops. Other crops which are non-hosts of certain nematode species are also useful because nematodes die of starvation in the same way as they do in bare fallow.

Another factor which may be considered when planning a rotation is the choice of planting date. The amount of nematode damage to crops may be reduced if seedlings are establishing after a peak in nematode numbers in the soil or if plant growth occurs when nematode reproduction is slowest. Often, damage to vegetable crops by *Meloidogyne* is much reduced if the crop is grown during winter when nematode reproduction is slow.

Chemical control

Chemicals which have been used for nematode control in Australia can be divided into two main groups—the fumigants and the non-volatile nematicides.

Because of their cost, nematicide use is usually restricted to intensive agriculture with high-value crops rather than broadacre crops, such as temperate cereals.

Before about 1980, several **soil fumigants**, including methyl bromide, chloropicrin, dichloropropene, ethylene dibromide (EDB), dibromochloropropane (DBCP), dazomet and metham-sodium were widely used for nematode control in Australia. All of these chemicals are general biocides and affect all soil organisms including fungi, bacteria, weeds, nematodes and other invertebrates.

The fumigants used for nematode control move in the gaseous phase through the pore spaces in soil and by diffusion through the water films surrounding soil particles. Their movement and therefore their efficacy is influenced by factors such as soil temperature, soil moisture, soil texture and the amount of undecomposed organic matter in soil. These materials kill nematodes rapidly and then dissipate quickly from soil. They are excellent nematicides and generally provide a high level of nematode control. All the fumigants are normally phytotoxic and must be used as preplant treatments. They are generally used on high-value crops (e.g. horticultural and nursery crops) where a broad spectrum of activity is required.

There are two types of **non-volatile nematicides**, the organophosphates and the carbamates. The most commonly used organophosphates are ethoprophos, terbufos, fenamiphos and cadusaphos. Carbamates used for nematode control include aldicarb, oxamyl and carbofuran. All of these chemicals are highly toxic to mammals, birds and fish and can affect humans.

The organophosphate and carbamate nematicides are normally incorporated into the top few centimetres of soil using cultivation equipment and are dispersed to depth by the movement of water. Although they are all highly toxic to mammals, they are rarely phytotoxic at the concentrations used for field control. Organophosphates and carbamates tend to be nemastatic in action rather than nematoxic, temporarily inactivating nematodes by preventing egg hatch, reducing motility, inhibiting feeding and retarding development. Since they are effective in soil for only a limited period (usually 2–6 weeks), nematodes tend to resume normal activities when the chemical dissipates.

Non-volatile nematicides can be used successfully on annual crops because nematodes need to be controlled only for relatively short periods. However, several applications per year are needed to obtain control on perennial crops. The development of strategies in which these materials are applied through trickle irrigation systems has increased their use in such situations.

The future of nematicides

Chemical control of nematodes is expensive ($500–$3,000/ha/year) and the availability of some chemicals is now threatened by health, environmental and efficacy issues. Perhaps the main concern is that the most widely-used nematicides have been found to contaminate ground-water supplies. In the mid-1970s, the registration of DBCP was withdrawn and this was followed by ethylene dibromide (EDB). Methyl bromide, which is used extensively in the floriculture, strawberry and vegetable industries for control of nematodes and soil-borne fungal pathogens, has been implicated in the degradation of the ozone layer and is also likely to be withdrawn from the soil fumigation market. The long-term effectiveness of non-volatile nematicides such as fenamiphos is in doubt because their repeated use can result in an increase in degradative soil micro-organisms which reduce their efficacy. Since these chemicals also rank amongst the most toxic of the agricultural chemicals used today, it is unlikely they will remain registered for use.

Biological control

A wide range of fungi, bacteria and invertebrates is known to parasitise or prey on nematodes, and soils that are biologically suppressive to nematodes have been identified. The bacterium, *Pasteuria penetrans* (Fig. 8.6B) is an efficient parasite of *Meloidogyne* spp. The endospores of the bacteria attach to the cuticle of the second-stage juvenile and germinate after the nematode becomes parasitic in roots. The bacterium then grows in the body of the developing nematode and eventually occupies the body of the mature female, preventing it from producing eggs. Excellent nematode control has been achieved in small-scale field trials but the commercial potential of *P. penetrans* is currently limited by the inability to culture this obligate parasite.

Many fungi are known to attack nematodes or their eggs. The nematode-trapping fungi possess specialised structures which can trap vermiform (worm-like) stages of nematodes. Some examples are *Arthrobotrys dactyloides* (Fig. 8.6A), which produces constricting rings of three cells which lasso nematodes, *Dactylella candida*, which produces sticky knobs and non-constricting rings and *Monacrosporium cianopagum* which entangles nematodes in a three-dimensional network of traps.

Among the fungi that parasitise saccate female nematodes or their eggs, those that show promise as biological control agents include *Nematophthora gynophila* which parasitises *Heterodera avenae* and *Verticillium chlamydosporium* (Fig. 8.6C) and *Paecilomyces lilacinus* which can attack eggs of *Meloidogyne* spp.

Although a number of parasitic fungi and bacteria appear to have considerable biological control potential, there is still no commercially available biological agent against nematodes. The main problems in developing biocontrol agents include unpredictable survival in soil, inability to mass produce the organisms and difficulties in developing commercial formulations with adequate activity and shelf-life.

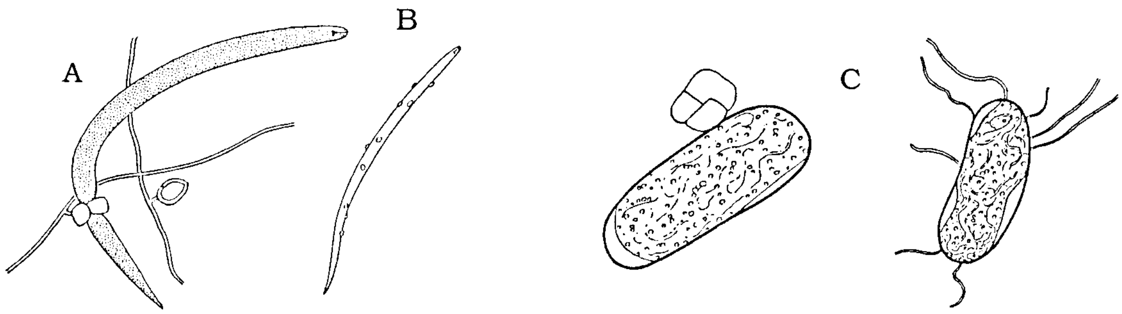

Figure 8.6 Some antagonists of nematodes. (A) Constricting rings of *Arthrobotrys dactyloides* (nematode-trapping fungus). (B) Endospores of *Pasteuria penetrans* attached to the cuticle of a juvenile nematode (juvenile-parasitic bacterium). (C) *Verticillium chlamydosporium* attacking an egg of a nematode (egg-parasitic fungus). (Diagrams not to scale.)

Organic amendments

Numerous reports from many countries have shown that crop losses from plant parasitic nematodes can be reduced by adding organic matter to soil. Chitin protein-based amendments are already being marketed commercially for nematode control. The mechanisms by which organic matter acts against nematodes are complex and poorly understood but probably involve improvements in soil structure, fertility and water-holding capacity, so that plants are better able to tolerate the effects of nematodes. Organic matter also increases the activity of parasites and predators of nematodes and results in the production of decomposition products, such as ammonia, which are toxic to nematodes.

Practical systems using organic materials for nematode control are still to be developed but these are likely to involve the use of specific amendments, such as those containing chitin, growing suitable cover crops for incorporation, and mulching with locally available organic wastes. For example, some control of root-knot nematode has been obtained in Australia by the addition of large amounts of sawdust, poultry manure or molasses to soil.

Physical control

Physical control strategies aim to prevent or reduce nematode spread and generally involve sterilisation of the growing medium or use of uninfested planting material. These techniques are usually only cost effective in high-value systems such as hydroponics. For example, mushroom compost and nursery soil may be steam sterilised. Irrigation water may be disinfested with chlorine, ultraviolet radiation or microfiltration.

Selection of healthy propagating material for use in uninfested soil is a useful strategy. For example, banana planting material is certified suitable for planting in Queensland only if it has been tested and found to be free from *Radopholus similis*, *Pratylenchus coffeae* and *Helicotylenchus multicinctus*. Approved strawberry runners must be free of *Meloidogyne hapla*, *Pratylenchus vulnus*, *P. brachyurus* and *Aphelenchoides fragaria*. Mechanical screening removes *Anguina tritici* galls from wheat.

Hot water treatment of bulbs, strawberry plants, chrysanthemums and banana rhizomes is effective in killing nematodes but the temperature must be monitored carefully to ensure efficacy without phytotoxicity.

Nematodes do not move far of their own accord so most spread is passive. They are spread with soil (in runoff, floodwater, water courses, irrigation), plant material and in wind-borne soil. General sanitation such as washing pots and implements being reused, preventing runoff from infested areas and choosing clean sites for nurseries may reduce nematode problems. Restricting movement of soil and machinery may be a useful method of quarantine. However, it is usually not practical as it is very difficult to prevent spread of soil on farm machinery.

Interactions with other organisms

Under field conditions, plant disease is rarely the result of a single organism. If more than one pathogen is causing disease, there may be no interaction, with each organism contributing an effect cumulatively. However, organisms may interact in a number of ways and all of the following possibilities have been observed with nematodes.

Many plant-parasitic nematodes predispose plants to infection by other organisms and interact producing a **synergistic interaction**. For example, *Globodera rostochiensis* may increase the severity of disease in potato cultivars which are susceptible and intolerant to *Verticillium dahliae*. Alternatively, *Meloidogyne incognita* can negate the genetic resistance and/or tolerance of tomato to *Fusarium oxysporum* f.sp. *lycopersici*. In each situation, the total damage or severity of disease is more than the sum of the effects of each pathogen alone.

Antagonism between organisms may reduce the severity of disease in a susceptible and/or intolerant host. This has been observed for *Heterodera* *schachtii* and *Fusarium oxysporum* on sugar beet. On the other hand, root-knot nematodes on various hosts have been shown to reduce infection by vesicular-arbuscular mycorrhizal fungi which in turn can lead to a reduction in the plant's ability to absorb nutrients and water from soil leading to an increase in the severity of disease.

Of the many species of plant-parasitic nematodes, only species in the order Dorylaimidae, such as *Xiphinema, Longidorus* and *Paratrichodorus*, have been established as **virus vectors**. Some viruses are transmitted by several nematode vectors while others have only one vector. The virus may be harboured in the lumen of the stylet and/or oesophagus. In Australia, only one important virus disease involves a nematode vector. Grapevine fanleaf virus, which is vectored by *Xiphenema index*, is present in vineyards near Rutherglen, Victoria.

Annual ryegrass toxicity is caused when the bacterium, *Rathayibacter toxicus* becomes attached to the cuticle of *Anguina funesta* and is carried into the inflorescences of *Lolium rigidum*. After flowering, many seeds are replaced either by nematode galls or by toxic bacterial galls which kill thousands of sheep each year in South Australia and Western Australia.

8.10 Classification of plant parasitic nematodes

Nematodes are divided into two subclasses, Secernentea and Adenophorea. Most plant-parasitic nematodes are found in the order Tylenchidae and some in Aphelenchidae within the subclass Secernentea. A few plant-parasitic genera are found in Dorylaimidae (Longidoridae and Trichodoridae) within Adenophorea. The most commonly found nematodes may be classified on their morphology using Table 8.3.

Table 8.3 Key to genera of common nematodes. (Adapted from Mai and Lyon 1975.)

1.	Stylet absent	2
	Stylet present	3
2.	Stoma cylindrical, never armed with teeth; oesophagus with terminal vulvate bulb	RHABDITIDA
	Stoma cup-shaped, often armed with teeth; oesophagus cylindrical, without terminal bulb	MONONCHIDA
3.	Two-part oesophagus, no valvate bulbs, anterior part slender, posterior part glandular and muscular; stylet without basal knobs	DORYLAIMIDA (4)
	Three-part oesophagus usually with a valvate median bulb followed by a slender isthmus and glandular basal bulb; stylet usually with basal knobs	6
4.	Stylet short, curved; body short and thick (0.45 to 1.5 mm long)	*Trichodorus*, *Paratrichodorus*
	Stylet long, straight, tapering to a long slender point with long posterior extensions; body long and slender	5
5.	Stylet extensions sclerotised and swollen; thin sclerotised ring around stylet (guiding ring) near base of stylet just anterior to junction of stylet and stylet extensions	*Xiphinema*
	Stylet extensions not swollen; guiding ring near apex of stylet	*Longidorus*, *Paralongidorus*

Table 8.3 (Continued)

6. Metacorpus very large, often appears nearly as wide as the body .... APHELENCHOIDEA (7)
   Metacorpus less than 3/4 body width .... TYLENCHOIDEA (8)

7. Tail of female blunt; male with bursae .... *Aphelenchus*
   Tail of female usually conoid, often with 1 or more sharp points at the terminus (mucron); male without bursae .... *Aphelenchoides*

8. Mature female greatly enlarged (lemon-shaped, kidney-shaped or saccate); found in roots of plants, either embedded or attached by neck; some occur as cysts in the soil 9
   Mature females vermiform, may be slender to slightly swollen 13

9. Mature female bodies soft, sausage- or kidney-shaped with tail 10
   Mature females becoming cysts or remaining soft bodied; saccate, spherical or lemon-shaped, usually without a tail 11

10. Mature female has 2 ovaries .... *Rotylenchulus*
    Mature female has 1 ovary .... *Tylenchulus*

11. Females with irregular body annules around anus and vulva; second-stage juvenile stylet less than 20 μm long; weakly developed lip region; usually marked galling of the host roots .... *Meloidogyne*
    Females with no irregular body annules around anus and vulva; second-stage juvenile stylet usually more than 20 μm; well-developed lip region; usually no galling of the host roots 12

12. Mature female lemon-shaped .... *Heterodera*
    Mature female spherical except for head .... *Globodera*

13. Tail equal to or longer than 6 times the anal body diameter (tail filiform, with pointed or club-shaped terminus) .... *Tylenchus*
    Tail generally less than 6 times the anal body diameter 14

14. One ovary (vulva usually located in posterior third of body) 15
    Two ovaries (vulva located near centre of body) 21

15. Procorpus and metacorpus not swollen and combined into a large valvular bulb 16
    Procorpus and metacorpus swollen and combined into a large valvular bulb 18

16. Stylet strong (generally more than 15 μm in length); tail tapering or bluntly rounded; oesophageal glands overlapping intestine ventrally .... *Pratylenchus*
    Stylet delicate (15 μm or less in length); tail acute or subacute 17

17. Mature female slender; found in bulbs, stems, leaves and tubers .... *Ditylenchus*
    Mature female obese; found in galls in leaves or flower parts .... *Anguina*

18. Mature female with extra cuticle .... *Hemicycliophora*
    Mature female without extra cuticle 19

19. Cuticle without prominent annules directed backwards .... *Paratylenchus*

Table 8.3 (Continued)

Cuticle with prominent annules directed backwards	20
20. Annules of female ornamented with spines, scales, etc	*Criconema*
Annules of female smooth or notched	*Criconemoides*
21. s (stylet length/body diameter at base of stylet) = 2.5 or more; body length 1.75 or more	*Belonolaimus*
s = less than 2.5	22
22. Tail 1.5 or more times as long as anal body diameter	23
Tail less than 1.5 times anal body diameter	24
23. Oesophageal glands overlapping intestine dorsally; tail tapering to a rounded or almost pointed terminus	*Radopholus*
Oesophageal glands contained in a basal bulb; female tail conoid with terminus usually bluntly rounded	*Tylenchorhynchus*
24. Oesophageal glands overlapping intestine dorsally; dorsal oesophageal gland opening usually less than 1/4 of the stylet length behind stylet knobs	*Rotylenchus*
Oesophageal glands overlapping intestine ventrally; dorsal oesophageal gland opening usually 1/4 or more of the stylet length behind stylet knobs	*Helicotylenchus*

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8.11 Further reading

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