

Nematodes are second only to insects in the number of species in the animal kingdom. However, only about 3 % of all nematode species have been studied and identified. One cubic foot of soil may contain millions of individual nematodes belonging to several different taxonomic groups. Plant-parasitic nematodes are nearly microscopic, worm-shaped animals virtually invisible to the naked eye when in the soil. Phytonematodes can cause significant plant damage ranging from negligible injury to total destruction of plant material. The severity of plant injury resulting from nematode activity depends on several factors such as the combination of plant and nematode species and prevailing environmental factors including rainfall, soil types, land contour, and culture practices.

Although a few nematode species feed on aboveground plant parts, such as leaves, stems, flowers, and seeds, the majority of these parasites feed on underground parts of plants, including roots, bulbs, and tubers. Because of this belowground, “hidden” feeding activity, nematode damage to plants cannot always be diagnosed readily. Nematodes are microscopic roundworms that live in many habitats. At least 2,500 species of plant-parasitic nematodes have been described, characterized by the presence of a stylet, which is used for penetration of host plant tissue. Most attack roots and underground parts of plants, but some are able to feed on leaves and flowers.

Phytonematodes are of great economic importance. However, because most of them live in the soil, they represent one of the most difficult pest

problems to identify, demonstrate, and manage. Often, plant damage caused by nematodes is overlooked because the resulting nonspecific symptoms, such as slow growth, stunting, and yellowing, can also be attributed to nutritional and water-associated disorders (Stirling et al. 1998). Their effects are commonly underestimated by growers, horticulturists, and nematode management consultants, but it has been estimated that around 10 % of world crop production is lost as a result of plant nematode damage (Whitehead 1998). Most nematodes feed on bacteria, fungi, or other microscopic creatures. As such, they are a major component of soil and sediment ecosystems.

Of late, nematodes are being considered as a very successful class of animals. Four out of five multicellular animals on earth are nematodes. They are present almost everywhere: in cultivated fields, in sand dunes, in the sediments beneath the ocean floor, in groundwater, in plants, in animals, and even in humans. Some of the best-known nematodes are animal parasites such as heartworms, pinworms, and hookworms. Another important group of nematodes parasitize plants, which results in an estimated \$8 billion a year loss to US agriculture/horticulture and nearly \$78 billion loss worldwide.

The importance of nematodes especially in horticultural productivity was realized during the Second World War. The famous quote by Thorne, a renowned nematologist, “each year phytonematodes exact an ever increasing toll from almost every cultivated acre in the world—a bag of potatoes

in England, a box of apples in New York or a crate of oranges in California...” clearly depicts the significance of plant-parasitic nematodes in horticulture. In developing countries like India, the 1960s was considered as the most active phase of nematology. In spite of significant contributions being made to manage phytonematodes during the past few decades, new and serious nematode problems warrant considerably increased effort and support than they are currently receiving. The problems are real and the challenge is great.

There are numerous estimates of the economic importance of nematodes in crop production on a worldwide and individual country basis, but precise values cannot be determined. For many countries, few or no studies have been made to determine the prevalence and extent of damage caused by parasitic nematode. Extensive research in developed countries and in more than 70 developing countries leaves little doubt concerning the destructive nature of plant-parasitic nematodes and the importance of their management for successful crop production. However, the overall average annual yield loss in important horticultural crops worldwide accounts to 13.54 % (Reddy 2008). Sasser and Freckman (1987) summarized the estimated annual losses in the yields of life-sustaining and economically important horticultural crops (Table 2.1).

In general, root symptoms vary widely but can include galling, lesions, cysts, stunting, and decay. Roots infected by parasitic nematodes are often darker than healthy roots. In addition, infected roots are often more susceptible to secondary infection by opportunistic bacteria and fungi. Often, new growth is stunted and infected plants are smaller than their healthy counterparts.

Nematodes continue to threaten horticultural crops throughout the world, particularly in tropical and subtropical regions. For centuries, crop plants have been plagued by these microscopic organisms. The degree of damage to a particular crop is influenced by the crop and cultivar nematode species, level of soil infestation, and environment. Severe damage may result if high infestation levels occur in soil where susceptible crops are planted. These deleterious effects on

Table 2.1 Estimated annual yield losses in horticultural crops due to phytonematodes

| Life-sustaining crops | Loss (%) | Economically important crops | Loss (%) |
|---------------------------------|----------------|------------------------------|----------------|
| Banana | 19.7 | Brinjal | 16.9 |
| Cassava | 8.4 | Cacao | 10.5 |
| Coconut | 17.1 | Citrus | 14.2 |
| Field bean | 10.9 | Coffee | 15.0 |
| Potato | 12.2 | Cowpea | 15.1 |
| Sugar beet | 10.9 | Grape | 12.5 |
| Sweet potato | 10.2 | Guava | 10.8 |
| | | Melons | 13.8 |
| | | Okra | 20.4 |
| | | Ornamentals | 11.1 |
| | | Papaya | 15.1 |
| | | Pepper | 12.2 |
| | | Pineapple | 14.9 |
| | | Tea | 8.2 |
| | | Tomato | 20.6 |
| | | Yam | 17.7 |
| Average | 12.77 % | Average | 14.31 % |
| Overall average: 13.54 % | | | |

plant growth result in low yields and poor quality. Worldwide, major horticultural crops such as vegetables, fruit crops, flower crops and ornamentals, plantation crops, spices and condiments, medicinal and aromatic crops, crops grown under protected conditions/polyhouse, and tuber crops are severely affected by phytonematodes. Nematodes often cause decline or death of several of these highly prized crops including turf.

Table 2.2 presents the avoidable losses in the yield of some horticultural crops due to phytone-matodes (Reddy 2008).

Although over 4,100 species of plant-parasitic nematodes have been identified (Decraemer and Hunt 2006), new species are continually being described while others, earlier considered as minor or non-damaging, are becoming pests as cropping patterns change (Nicol 2002). However, the phytonematodes of economic importance can be grouped into relatively restricted specialized groups that either cause direct damage to their host or act as virus vectors (Table 2.2). Most nematodes affect crops through feeding on or in plant roots, while a minority are aerial feeders. It is a known fact that in addition to direct feeding and migration damage, nematode feeding facilitates

Table 2.2 Major horticultural crops and the avoidable yield losses caused by phytonematodes

| Crop | Phytonematode | Yield loss (%) |
|--------------------------|----------------------------------|----------------|
| Banana | <i>Radopholus similis</i> | 32–41 |
| Betel vine | <i>Meloidogyne incognita</i> | 21.1–38 |
| Bitter gourd | <i>M. incognita</i> | 36.72 |
| Black pepper | <i>R. similis</i> | 59 |
| | <i>M. incognita</i> | 46 |
| Brinjal | <i>M. incognita</i> | 27.30–48.55 |
| Cardamom | <i>M. incognita</i> | 32–47 |
| Carnation | <i>M. incognita</i> | 27 |
| Carrot | <i>M. javanica</i> | 56.64 |
| Chilli | <i>M. javanica</i> | 24.54–28 |
| Coconut | <i>R. similis</i> | 30 |
| <i>Coleus forskohlii</i> | <i>M. incognita</i> | 70.2 |
| Colocasia | <i>M. incognita</i> | 24 |
| Coriander | <i>M. incognita</i> | 51 |
| Cowpea | <i>M. incognita</i> | 28.60 |
| | <i>Rotylenchulus reniformis</i> | 13.2–32.0 |
| Crossandra | <i>M. incognita</i> | 21.64 |
| Cumin | <i>M. incognita</i> | 34 |
| <i>Cymbopogon</i> | <i>M. incognita</i> | 20 |
| Davana | <i>M. incognita</i> | 50 |
| Fennel | <i>M. incognita</i> | 39 |
| French bean | <i>M. incognita</i> | 19.38–43.48 |
| Gerbera | <i>M. incognita</i> | 31 |
| Ginger | <i>M. incognita</i> | 29.60–74.10 |
| Grapevine | <i>M. javanica</i> | 53–55 |
| Lemon | <i>Tylenchulus semipenetrans</i> | 29.0 |
| Menthol mint | <i>M. incognita</i> | 30 |
| Mushroom | <i>Aphelenchoides sacchari</i> | 40.6–100 |
| | <i>A. composticola</i> | 35–60 |
| | <i>A. avenae</i> | 25.8–53.5 |
| Okra | <i>M. incognita</i> | 28.08–90.90 |
| Papaya | <i>R. reniformis</i> | 28 |
| Patchouli | <i>M. incognita</i> | 47 |
| Peach | <i>Macroposthonia xenoplax</i> | 33 |
| Peas | <i>M. incognita</i> | 20–50.61 |
| Plum | <i>M. xenoplax</i> | 10 |
| Pointed gourd | <i>M. incognita</i> | 30–40 |
| Pomegranate | <i>M. incognita</i> | 27.0 |
| Potato | <i>M. incognita</i> | 42.50 |
| | <i>Globodera rostochiensis</i> | 99.50 |
| Sweet lime | <i>T. semipenetrans</i> | 19.0 |
| Sweet orange | <i>T. semipenetrans</i> | 69.0 |

(continued)

Table 2.2 (continued)

| Crop | Phytonematode | Yield loss (%) |
|------------|----------------------|----------------|
| Tomato | <i>M. incognita</i> | 30.57–46.92 |
| | <i>M. javanica</i> | 77.50 |
| | <i>R. reniformis</i> | 42.25–49.02 |
| Tuberose | <i>M. incognita</i> | 13.78 |
| Turmeric | <i>M. incognita</i> | 18.6–25.0 |
| | <i>R. similis</i> | 46.76 |
| Watermelon | <i>M. incognita</i> | 18–33 |

subsequent infestation by secondary pathogens, including soil fungi and bacteria (Powell 1971), that complicates the condition of the host.

On a global scale, the distribution of nematode species varies greatly. Some are cosmopolitan, such as certain *Meloidogyne* spp., while others are particularly restricted geographically as *Nacobbus* spp. or are highly host specific, such as *Heterodera carotae* which attacks only carrots. Some crops may have very few nematode pests, while others have a particularly wide range of genera and species associated with them leading to difficulties for nematode management strategies. Distribution maps and host range data are available and updated regularly as a useful source for determining nematode damage potential. One difficulty with assessing nematode impact is that damage resulting from nematode infection is often less obvious than that caused by many other pests or diseases. Losses that result from nematode attack may not necessarily be as a consequence of direct cell death, necrosis, or “diseased” tissue, but may derive from other more insidious aspects, such as interference with the root system, reducing their efficiency in terms of access and uptake of nutrients and water; to the unaware, nematode-affected plants present typical drought and nutrient stress symptoms, which are easily and often misdiagnosed.

In the USA, a survey of 35 states on various crops indicated nematode-derived losses of up to 25 % (Koenning et al. 1999). Handoo (1998) estimated global crop losses due to nematode attack in the region of \$80 billion, which, given the more subtle effects of low infestation levels, is probably a vast underestimate. Globally, a wide range of crops are produced, with some grown in specific areas,

Table 2.3 Phytonematodes of economic importance

| Genus | Common name | Type of parasitism | Plant tissue affected |
|-------------------------------------|---------------|------------------------------|-----------------------|
| <i>Anguina</i> | Seed gall | Migratory endoparasite | Seeds, stems, leaves |
| <i>Bursaphelenchus</i> | Red ring/wilt | Migratory ectoparasite | Seeds, stems, leaves |
| <i>Criconemella</i> | Ring | Sedentary ectoparasite | Roots |
| <i>Ditylenchus</i> | Stem and bulb | Migratory ectoparasite | Stems, leaves |
| <i>Globodera</i> | Golden cyst | Sedentary endoparasite | Roots |
| <i>Helicotylenchus</i> | Spiral | Migratory ecto-/endoparasite | Roots |
| <i>Heterodera</i> | Cyst | Sedentary endoparasite | Roots |
| <i>Hirschmanniella</i> | Rice root | Migratory endoparasite | Roots, tubers |
| <i>Hoplolaimus</i> | Lance | Migratory ectoparasite | Roots |
| <i>Meloidogyne</i> | Root knot | Sedentary endoparasite | Roots |
| <i>Pratylenchus</i> | Lesion | Migratory ecto-/endoparasite | Roots |
| <i>Radopholus</i> | Burrowing | Migratory endoparasite | Roots, tubers |
| <i>Rotylenchulus</i> | Reniform | Sedentary semi-endoparasite | Roots |
| <i>Scutellonema</i> | Yam | Migratory ecto-/endoparasite | Roots, tubers |
| <i>Tylenchulus</i> | Citrus | Sedentary semi-endoparasite | Roots |
| Virus vectors | | | |
| <i>Xiphinema</i> | Dagger | Migratory ectoparasites | Roots |
| <i>Longidorus, Paralongidorus</i> | Needle | Migratory ectoparasites | Roots |
| <i>Trichodorus, Paratrachodorus</i> | Stubby root | Migratory ectoparasites | Roots |

Table 2.4 Estimated global annual monetary losses due to nematodes for major horticultural crops

| Crop | No. of estimates/crop | FAO production estimates ('000MT) | Estimated price/MT (US\$) | Estimated yield loss due to nematodes (%) | Estimated monetary loss due to nematodes (US\$) |
|--------------|-----------------------|-----------------------------------|---------------------------|---|---|
| Banana | 78 | 2,097 | 431 | 19.7 | 178,049,979 |
| Cassava | 25 | 129,020 | 90 | 8.4 | 975,391,200 |
| Citrus | 102 | 56,100 | 505 | 14.2 | 4,022,931,000 |
| Cocoa | 13 | 1,660 | 2,584 | 10.5 | 450,391,200 |
| Coffee | 36 | 5,210 | 3,175 | 15.0 | 2,481,262,500 |
| Field bean | 70 | 19,508 | 544 | 10.9 | 1,156,746,300 |
| Potato | 141 | 312,209 | 152 | 12.2 | 5,789,403,696 |
| Sugar beet | 51 | 293,478 | 37 | 10.9 | 1,183,596,774 |
| Sweet potato | 67 | 117,337 | 219 | 10.2 | 2,621,073,906 |
| Tea | 16 | 2,218 | 2,807 | 8.2 | 510,562,300 |
| | | | | Total | 19,369,408,865 |

which are infested by one or the other phytonematodes. Some phytonematodes, apart from inciting diseases, also carry viral pathogens (Table 2.3).

Nematode attack can also predispose plants to attack by other pathogens through mechanical damage but also on a genetic basis. Monetary annual losses due to phytonematodes on major crops including “life-sustaining crops” have been

estimated at \$77 billion (Sasser and Freckman 1987) (Table 2.4). The loss in the USA alone accounts to \$5.8 billion. However, when all crops are taken into consideration, the loss may exceed up to \$100 billion. Due to the higher percentage of crop losses, the dollar value losses are higher in developing countries as compared to developed ones.

2.1 Ten Economically Important Genera of Phytonematodes Associated with Horticultural Crops

The list of economically important ten genera of phytonematodes associated with various horticultural crops around the globe comprises of *Meloidogyne* (root-knot nematode), *Heterodera* (cyst nematode), *Ditylenchus* (stem and bulb nematode), *Globodera* (golden cyst nematode), *Tylenchulus* (citrus nematode), *Xiphinema* (dagger nematode), *Radopholus* (burrowing nematode), *Rotylenchulus* (reniform nematode), and *Helicotylenchus* (spiral nematode). However, this order of genera may vary depending upon a specific location, with some more added genera. For example, in Europe, the top ten most destructive phytonematodes include *Heterodera*, *Globodera*, *Meloidogyne*, *Ditylenchus*, *Pratylenchus*, *Aphelenchoides*, *Xiphinema*, *Trichodorus*, *Longidorus*, and *Tylenchulus* (Sasser and Freckman 1987).

The importance of nematodes in world horticulture can be judged by whether or not their damage is catastrophic to major crops. Several phytonematodes are responsible for this kind of damage. Some of the important ones affecting major horticultural crops include the following.

1. Root-Knot Nematode (*Meloidogyne* spp.):

It is the most common sedentary endoparasite on horticultural crops and can damage and cause severe economic loss. It has worldwide distribution though more common in temperate, subtropical, and tropical areas. Female embedded in root tissue, melon shaped, induces characteristic knots/galls on the roots of affected plants. This genus includes more than 60 species, with some species having several races. However, four species, *M. incognita*, *M. javanica*, *M. arenaria*, and *M. hapla*, are major pests worldwide. They modify normal cells into giant cells before feeding. Female produces a large number of eggs embedded in a gelatinous egg mass attached to the knot on the root, which is produced by six rectal glands and secreted before and during egg laying.

Normally, 500–1,000 eggs are laid per female. Gall formation is a visible sign of root-knot nematode infection resulting from the hypertrophy and hyperplasia indicative of feeding site formation within the roots. The matrix initially forms a canal through the outer layers of root tissue and later surrounds the eggs, providing a barrier to water loss by maintaining a high moisture level around the eggs. As the gelatinous matrix ages, it becomes tanned, turning from a sticky, colorless jelly to an orange-brown substance which appears layered. This egg mass serves as a dormant structure for this group of nematodes. Males are vermiform and free living in soil. Juveniles are slender and vermiform, about 450 µm long. These nematodes are more destructive when they associate with other soilborne fungal and bacterial pathogens to form complex diseases. The major hosts of root-knot nematodes include most horticultural crops, viz., vegetables, fruits, ornamentals, polyhouse-grown crops, plantation crops, and medicinal, aromatic, and spice crops.

2. **Burrowing Nematode (*Radopholus* spp.):** It constitutes an important group of endoparasitic nematodes of plant roots and tubers, which is migratory. The major species is *R. similis* with two host races that differ in parasitism of citrus. It completes its entire life cycle within the root tissue. Infected plants experience malnutrition. It induces lesions and burrows in the roots, which later turn into tunnels and cavities causing destructive damage. Infection by burrowing nematode causes toppling-over disease in banana, yellows disease in pepper and spreading decline in citrus. Because of the damage it causes worldwide, burrowing nematode is considered as one of the most regulated nematode pests. Burrowing nematode, although native to Australasia, is found worldwide in tropical and subtropical regions of Africa, Asia, Australia, North and South America, and many island regions. The widespread range of this nematode is due to its dissemination with propagative plant material, especially infected banana

- corms/rhizomes/suckers. This devastating nematode has been observed infecting more than 300 plant species including banana, coconut, areca nut, tea, ginger, pepper, betel vine, turmeric, avocado, coffee, ornamentals, sugarcane, and citrus; *R. similis* infects both banana and citrus, while *R. citrophilus* infects only citrus. However, these two species are categorized as the “banana race” and “citrus race,” respectively, within *Radopholus similis*.
3. **Cyst Nematode** (*Heterodera* species): This sedentary endoparasite is a potential pathogen on several crop plants. Different species of this genus attack several crops, often causing great economic damage. The genus is unique among nematode genera because of the ability of the female to transform into a tough, brown cyst. Cysts are either partially enclosed in the root tissue or in the soil. It is called a cyst nematode because the greatly swollen, egg-filled adult female is referred to as the “cyst stage.” Female appears swollen or obese and lemon shaped with a distinct neck. Females produce several hundred eggs, and after death, the female cuticle forms a protective cyst. Eggs are retained within the cyst. Males are vermiform which are present in soil. The genus has worldwide distribution with a wide host range including horticultural crops. Major species include *H. avenae*, *H. glycines*, *H. cajani*, *H. schachtii*, *H. trifolii*, *H. gottingiana*, *H. carotae*, *H. cruciferae*, *H. ciceri*, *H. oryzae*, *H. oryzicola*, *H. sacchari*, and *H. polygoni*.
 4. **Potato Cyst Nematodes** (*Globodera rostochiensis* and *G. pallida*): *Globodera* is similar to *Heterodera* but the cyst is globose in shape. Golden cyst nematode, *Globodera rostochiensis*, and pale cyst nematode, *G. pallida*, are major pests on potato. Altogether 90 species of the genus *Solanum* are known to be hosts for this group of nematodes. Both species are confined to the cooler places. Apart from potato, they are also pests on tomato, eggplant, members of the Solanaceae plant family (such as nightshade), and other root crops. Both species feed on and produce cysts on potato roots, thus causing substantial damage to potato crops. The cysts are typically yellow-brown/golden yellow in color. Both the golden and pale cyst nematodes are regulated federally. Major species include *G. rostochiensis*, *G. pallida*, and *G. tabacum*.
 5. **Lesion Nematode** (*Pratylenchus* spp.): It is an important group of migratory endoparasites on roots of several crops. It causes serious damage to many economic plants worldwide including coffee. Root lesion nematodes infect a great variety of hosts. *Pratylenchus penetrans* alone has over 350 host plants. Major hosts include coffee, potato, ornamentals, mint, plantation crops, corn, banana, turf, peanut, and wheat. They induce lesions on root surface. The major species are *P. penetrans*, *P. brachyurus*, *P. coffeae*, *P. pratensis*, *P. zaeae*, *P. teres*, *P. goodeyi*, *P. thornei*, and *P. vulnus*.
 6. **Reniform Nematode** (*Rotylenchulus reniformis*): This is a common pest associated with the rhizosphere of several horticultural crops. *R. reniformis*, a semi-endoparasite, exists practically everywhere in tropical and subtropical soils. The term “reniform” refers to the kidney-shaped body of the mature female. The female penetrates the root and remains in one position at a permanent feeding site with its posterior end projecting from the root. The immature female is the infective agent, attacking the root and growing to maturity at its feeding site. Males are vermiform. Eggs are laid in gelatinous matrix. At least 314 plant species are hosts to reniform nematode including cotton, castor, cowpea, pigeon pea, various fruit trees, tea, tobacco, soybean, banana, pineapple, cucumber, radish, and eggplant. The major species is *R. reniformis*, which is found in both tropical and warm temperate soils.
 7. **Stem and Bulb Nematode** (*Ditylenchus dipsaci*): It is a slender, vermiform, migratory endoparasite of plant stems and leaves. *D. dipsaci* is one of the most devastating phytonematodes in the world. Its races are very diverse and found in most temperate areas of the world. In this nematode, in the

fourth stage, juveniles are infective but not in the second stage, as in most other phytonematodes. It produces a dormant structure known as “nematode wool,” which is a bundle of juveniles to survive under adverse climatic conditions. This pathogen infects 400–500 plant species worldwide including onion, narcissus, potato, garlic and other bulb crops, alfalfa, strawberry, carrot, tobacco, tulips, and faba beans. Potato rot nematode (*D. destructor*) is another destructive pest on potato.

8. **Citrus Nematode** (*Tylenchulus semipenetrans*): It is a major pest on all members of *Citrus* group fruits. Their feeding strategy is semi-endoparasitic and has a very narrow host range among commonly grown crops. Apart from *Citrus* group, they can also attack olive, grape, persimmon, and lilac. It is the causal agent of slow decline in citrus. Mature females are non-vermiform; the anterior part is embedded in root tissues, while the slender posterior part protrudes from roots and is swollen. Males and juveniles are vermiform and slender.
9. **Spiral Nematode** (*Helicotylenchus* spp.): This nematode attains usually spiral shape and is distributed worldwide, and endoparasitic nematodes on roots of several crops, viz., banana, maize, ornamentals, plantation crops, fruit trees, turf, etc. They are also ectoparasites of several plant roots, which insert their stylets into root epidermis to feed. Some species live half-buried in the root tissue, while others penetrate the root and live inside. Out of 200, the most damaging species is *H. multicinctus*, apart from *H. mucronatus*, *H. dihystra*, *H. pseudorobustus*, and *H. vulgaris*.
10. **Dagger Nematode** (*Xiphinema* spp.), **Needle Nematode** (*Longidorus* spp. and *Paralongidorus* spp.), and **Stubby-Root Nematode** (*Trichodorus* spp. and *Paratrachodorus* spp.): All these are slender pests on crop plants and also are involved in transmitting plant viruses. They are ectoparasites on roots of perennial and woody plants with a worldwide distribution.

Dagger nematode is of economic importance on grape, strawberry, hops, and a wide range of crops, viz., nectarine, oak, rose, grapevine, raspberry, carrot, cherry, peach, woody plants, fruit trees, soybean, corn, and some cereals. *Xiphinema* has around 163 species, the major ones being *X. americanum*, *X. diversicaudatum*, *X. index*, *X. italiae*, and *X. pachtaicum*. They have a very long life cycle, several months to 2 years. Nematodes induce “giant cells and galls” and necrosis; giant cells are caused by karyokinesis without cytokinesis yielding multinucleated cells. They are easily recognizable, due to a long body length and a long stylet capable of reaching vascular tissue. Major species include *X. americanum*, *X. elongatum*, *L. africanus*, and *P. minor*.

Needle nematodes are very large, ranging in length from 2 to 8 mm. Odontostyle in these nematodes is long. They have a worldwide distribution, usually moist environments. At least seven species of *Longidorus* are reported from grape vineyards throughout the world, viz., *L. attenuatus*, *L. diadecturus*, *L. iranicus*, *L. macrosoma*, *L. protae*, *L. sylphus*, *Paralongidorus maximus*, *P. bullatus*, *P. iberis*, *P. lutensis*, etc. Lettuce, corn, mint, bean, pea, radish, tomato, spinach, rose, avocado, broccoli, watermelon, carrot, and fig are some other hosts.

Stubby-root nematodes are short, with a cigar-shaped body. Feeding activity stops root growth resulting in stubby roots. Common species are *T. christiei*, *T. nanus*, *T. obscures*, *T. pachydermis*, *T. porosus*, *T. primitives*, *Paratrachodorus minor*, *P. divergence*, *P. teres*, etc. *Trichodorus* species are worldwide in distribution on a wide range of crops including apple, onion, turf, forest trees, vegetables, ornamentals, rose, tomato, sugarcane, mulberry, grape, avocado, fig, banana, pear, walnut, citrus, beet, date palm, and spinach.

2.2 Less Widely Distributed Phytonematodes

In addition to the above worldwide distributed phytonematodes, some pose problems on horticultural crop plants in several regions (Ravichandra 2008). They are as follows.

1. **Lance nematode** (*Hoplolaimus* spp.): This is a major migratory ectoparasite, which feeds mostly on roots of various crops, viz., pepper, tomato, citrus, pines, banana, pine, oak, and grasses. Major species include *H. columbus*, *H. seinhorsti*, and *H. indicus*.
2. **Ring nematode** (*Criconemella*, *Criconemoides*): It is a migratory ectoparasite associated with rhizosphere of several horticultural crops, viz., all *Prunus* species, including peach, almond, apricot, cherry and plum, apart from lettuce, carnation, pine, turf, walnut, and grapes. Major species include *C. xenoplax*, *C. axestis*, and *C. spharocephalum*.
3. **Bud and leaf nematode** (*Aphelenchoides* spp.): It is a foliar nematode and has a world-wide distribution. *A. fragariae*, *A. ritzemabosi*, and *A. besseyi* are major pests on strawberry, chrysanthemum, and rice, respectively. The strawberry crimp nematode/fern nematode *A. fragariae* also infects carnation, fern, African violet, Easter lily, etc. The chrysanthemum foliar nematode *A. ritzemabosi* causes necrosis on leaves of chrysanthemums and other ornamentals.
4. **Pine wood nematode** (*Bursaphelenchus xylophilus*): It has been implicated in a serious disease of pine trees, "pine wilt disease," which has devastated pine forests in Japan and occurs in North America. In 1997, white pine trees in Maryland were devastated due to the heavy infestation of this nematode. This foliar nematode is a serious quarantine pest, and all pine wood chips or wood products for import and export purposes need to be checked for this nematode. When the beetle feeds on a susceptible host pine, the pine wilt nematode enters the tree and feeds on the epithelial cells which line the resin ducts, which results in pine wilt disease. Water transport in the tissues of the infested tree is disrupted and the disease can manifest within a few weeks. Major signs include browning of the needles or yellowing of the leaves, and the tree may die within 2–3 months. Susceptible pine species include Scotch, slash, Japanese red, and Japanese black pines.
5. **Red ring nematode of coconut** (*Bursaphelenchus/Rhadinaphelenchus cocophilus*): Red ring nematode causes red ring disease of palms. It parasitizes the palm weevil *Rhynchophorus palmarum* L., which is attracted to fresh trunk wounds and acts as a vector for *B. cocophilus* to uninfected trees. The major internal symptom of red ring infection is the "red ring" for which the disease is named. A crosscut through the trunk of an infected palm 1–7 ft above the soil line usually exhibits a circular, colored band around 3–5 cm wide. External symptoms include shortening and deformation of already established leaves that might turn yellow-bronze and later deep reddish-brown. The discoloration usually begins at the tip of each leaf and starts in the older leaves before moving to the younger ones. As the leaves change color and dry up, they wilt and die. It has not been reported to be present in some regions including continental USA, Hawaii, Puerto Rico or the Virgin Islands, and India.

2.3 General Characteristics of Phytonematodes

The nematodes are a very successful group of animals that can destroy up to 10 % of all arable crops, a figure that is comparable with the destructive effects of insects. Despite the tremendous economic importance of nematodes, the great majority of them are free living and they occur in every conceivable environment. It has been claimed that "if all matter was destroyed except nematodes, one would still be able to see the world outlined by nematodes." Nematodes are "hidden and unseen enemies" of crop plants as they are microscopic and present in soil, particularly in rhizosphere. They are microscopic animals, which are vermiform, bilaterally symmetrical, unsegmented, pseudocoelomatic, and triploblastic. Their body is not segmented as in earthworms. There are no respiratory or circulatory organs present in nematodes. All phytonematodes possess a structure called "stylet" or spear,

which is a unique feature. The stylet is the major feeding organ present in the mouth of phytonematodes that penetrates into the host tissue. Non-plant parasitic and other forms do not possess the stylet.

2.3.1 Body Size

There is a great variability in the size of nematodes. Free-living nematodes in soil and freshwater vary in length from about 150 μm to 10 mm. Marine species vary from 83 μm to about 50 mm in length. The animal parasites range from about 1 mm to 7 m in length, the largest being nematodes parasitic in whales. However, most plant parasites are microscopic and range from 0.25 mm to approximately 12 mm in length with a body width from 0.01 to 0.5 mm. The longest phytonematode is *Paralongidorus* and the smallest is *Paratylenchus*.

2.3.2 Body Shape

Nematodes generally are elongate, cylindrical, unsegmented worms. They are bilaterally symmetrical. Though most of them are vermiform, in some genera the body of the adult female may be greatly modified (*Meloidogyne*, *Heterodera*, *Rotylenchulus*, *Tylenchulus*, etc.). In these genera, the body may be melon shaped, spindle shaped (fusiform), pear shaped, kidney shaped, lemon shaped, or variations of saccate. The entire nematode body may be divided into three regions: the outer body tube or body wall, the inner body tube, and the body cavity of pseudocoelom.

The outer body tube constitutes cuticle (exoskeleton), hypodermis, and muscle layer. The body wall is composed of a thick cuticle, which may be considered to be an exoskeleton, a syncytial hypodermis, and the mucus layer composed of a single layer of longitudinal muscle only. Pseudocoelom is the false body cavity (the area between the body wall and the digestive tract), which is not lined with epithelial tissue. It is filled with pseudocoelomic fluid, which bathes the

muscles, the digestive system, the reproductive system, and some or all of the excretory system. The fluid in the pseudocoelom serves as a transport system for oxygen, food materials, and products of metabolism. The gut of nematodes consists of a terminal mouth, buccal cavity with six lips, pharynx, intestine, rectum, and subterminal anus. In the male, there is cloaca, with the rectum and vas deferens opening into the same cavity. The inner body tube consists of the digestive system, esophagus, intestine, rectum, and cloaca. The nervous system and reproductive system are well developed, while the excretory system is not very well developed in phytonematodes. The nervous system is well equipped with a range of sophisticated sense organs. Reproduction in nematodes is well developed and of diverse types, which plays a major role in the pathogenicity of a phytonematode.

2.3.3 Reproduction in Nematodes

The reproductive systems are major organs of the nematodes and can occupy a large portion of the body cavity in males and females. There are many morphological and physiological differences between the species and so they are separated here.

2.3.4 Males

Males are either monorchic (most Secernentea) or diorchic (most Adenophora), with regard to the number of testes present. The testes are tubular structures lined with epithelium and glandular tissue; sperms are produced at the end and mature as they migrate toward the shared opening of the cloaca. Many males have paired chitinous protrusion from the cloaca known as spicules, which are main copulatory organs and are used for attaching to a female during copulation. The spicules are easily seen under a microscope due to their chitinous structure and their position, and shape may be used as an identifying feature. Sperms are ejaculated from the cloaca around

the spicule, rather than through it. The sperm produced by nematodes is amoeboid and is very motile, employing the same locomotion mechanism as seen in amoeboid species.

One of the most distinctive features of some male nematodes is the presence of a copulatory bursa, seen in nematodes of the order Strongylida. Nematodes with a copulatory bursa are known as bursae, while those without are non-bursae. This bursa is at the posterior end of the nematode and is formed from alae with lateral rays that are used for grasping onto the body of the female during copulation.

2.3.5 Females

Female nematodes usually have a single genital pore through which sperm may enter the uterus and oviduct; this pore is also referred to as a vulva and may be covered by a vulval flap. The uterus may take many forms from being short and straight, long with a single bend, or a coiled form. Eggs produced in the ovaries populate the oviducts and uterus and may be released as embryonated or nonembryonated eggs once fertilization has occurred. Nematodes may have either one (monodelphic) or two ovaries (didelphic) with various types of orientation in case of two ovaries. A small muscular organ exists at the vulval opening of some species known as the “ovijector,” which aids in the expulsion of eggs from the vulva. Unlike in males, the end of the female is usually blunt ended with the anus being positioned proximally on the body wall.

Male and female nematodes are usually similar in appearance except for the reproductive systems. It mainly includes one or two tubular gonads which may vary in length and may be straight, reflexed, or coiled back and forth. In males and females, the genital tubes are lined with a single layer of epithelium which covers the germ cells and forms the ducts. In majority of nematodes, the germ cells are proliferated only in the distal end of the gonad, i.e., telogonic. In a few nematodes, the germ cells are formed along the entire length of the gonad, i.e., hologonic. Most phytonematodes are characterized by an

increase in the size of the entire reproductive system. The uteri and the growth zone of the ovary are lengthened that leads to more egg production. However, pronounced dimorphism occurs in some species. Females become swollen and males remain slender and cylindrical.

2.3.6 Major Types of Reproduction

1. *Bisexual (amphimixis)*: Male and female reproductive structures are present on two different individuals (e.g., burrowing nematodes, root-knot nematodes).
2. *Parthenogenesis*: Fertilization of eggs occurs without the help of males in this type. Mating and genetic recombination do not occur (e.g., root-knot nematodes, citrus nematodes, cyst nematodes).
3. *Hermaphroditism*: Both male and female reproductive structures are present on the same individual (e.g., root-knot nematodes, stem and bulb nematodes).

Intersexes are also common in some nematodes like root-knot nematodes. It is a variation in sex characteristics including chromosomes, gonads, and/or genitals that do not allow an individual to be distinctly identified as male or female. These intersexes have normal male head and tail structures and exhibit some mating behavior, but possess hermaphrodite-like gonads which produce no sperm and usually contain a few oocytes.

All nematodes pass through an embryonic stage, four larval/juvenile stages, and an adult stage. Juveniles hatch from eggs as vermiform, second-stage juveniles, the first molt having occurred within the egg. Newly hatched juveniles may reinvade the host plants of their parent or migrate through the soil to find a new host root. In most nematode genera, second-stage juveniles and adult females only are plant parasitic. The duration of life cycle depends on important factors like nematode species, soil temperature, soil moisture, soil structure, soil texture, and type of host.

Most phytonematodes attack roots/underground parts (bulbs, suckers, rhizomes, corms,

etc.) of host plants, while some attack aerial plant parts too. General aboveground symptoms of nematode infestation on horticultural crops include stunted growth, wilting, and yellowing in patches. However, characteristic symptoms are expressed in belowground, which may comprise the presence of knots/galls, cysts, lesions, and cavities/tunnels on the roots. Excessive branching of roots, deformed/abnormal roots/rootlets, rotting and discoloration of roots, and decreased/complete destruction of feeder roots are some of the symptoms of nematode damage, which contribute to overall reduction in the growth and development of plants. This affects the quality and quantity of the produce that ultimately affects the grower. Each phytonematode possesses a common and a scientific name as listed below.

2.4 Common Names of Major Phytonematodes of Horticultural Crops

Anguina spp.: Seed and leaf gall nematode

A. agrostis: Bent grass nematode

Aphelenchoides spp.: Bud and leaf nematode, foliar nematode

A. besseyi: Rice white-tip nematode, strawberry bud nematode, summer crimp, summer dwarf nematode

A. fragariae: Spring crimp nematode, spring dwarf nematode, strawberry bud nematode

A. ritzemabosi: Chrysanthemum foliar nematode

Bursaphelenchus cocophilus: Coconut palm nematode, red ring nematode

Bursaphelenchus xylophilus: Pinewood nematode

Cacopaurus pestis: Walnut nematode

C. cacti: Cactus cyst nematode

Criconeal/Criconemoides: Ring nematode

D. destructor: Potato rot nematode

D. dipsaci: Stem and bulb nematode, alfalfa stem nematode

Dolichodorus spp.: Awl nematode

G. pallida: Pale/white potato cyst nematode

G. rostochiensis: Golden nematode, golden potato cyst nematode

H. multicinctus: Banana spiral nematode, spiral nematode

Hemicriconemoides spp.: False sheath nematode

Hemicycliophora spp.: Sheath nematode

Heterodera carotae: Carrot cyst nematode

H. cruciferae: Cabbage cyst nematode

H. cyperi: Nutgrass cyst nematode

H. fici: Fig cyst nematode

H. goettingiana: Pea cyst nematode

H. schachtii: Sugar beet cyst nematode

Hoplolaimus spp.: Lance nematode

Longidorus spp.: Needle nematode

Meloidodera spp.: Cystoid nematode

Meloidogyne spp.: Root-knot nematode

M. carolinensis: Blueberry root-knot nematode

M. exigua: Coffee root-knot nematode

M. graminis: Grass root-knot nematode

M. hapla: Northern root-knot nematode

M. incognita: Southern root-knot nematode

M. javanica: Javanese root-knot nematode

M. konaensis: Kona coffee root-knot nematode

M. lusitanica: Olive root-knot nematode

M. megatyla: Pine root-knot nematode

M. nataliei: Michigan grape root-knot nematode

M. pini: Sand pine root-knot nematode

Nacobbus spp.: False root-knot nematode

Paratrichodorus spp.: Stubby-root nematode

Paralongidorus spp.: Needle nematode

Pratylenchus spp.: Pin nematode

Pratylenchoides spp.: False-burrowing nematode

Pratylenchus spp.: Lesion nematode

P. coffeae: Coffee lesion nematode

P. penetrans: Meadow nematode

P. vulnus: Boxwood lesion nematode, walnut lesion nematode

Punctodera punctata: Grass cyst nematode

R. similis: Banana burrowing nematode, burrowing nematode

Rotylenchulus reniformis: Reniform nematode

Rotylenchus spp.: Spiral nematode

Scutellonema bradys: Yam nematode

Subanguina radicola: Grass root-gall nematode

Trichodorus spp.: Stubby-root nematode

Tylenchorhynchus spp.: Stunt nematodes

Tylenchulus semipenetrans: Citrus nematode

Xiphinema spp.: Dagger nematode

X. americanum: American dagger nematode

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