# Chapter 7

# Nematode Parasites of Vegetables

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Vegetables are an extremely important component of our daily diet as well as a high value cash crop for small and large growers alike. Vegetables, especially the leaf vegetables, are rich in protein, vitamins, minerals and fibre. Leaf vegetables, for example, are a major source of protein in the humid tropics (Rhem & Espig, 1976). Mass transportation and modern processing has made many of these often highly perishable foods – which were previously only available on a seasonable basis in local markets or in restricted growing regions – more readily available both nationally and internationally. Many vegetables that were once only of local or regional importance are now standard produce on markets throughout the world. The major vegetables common to the subtropics and tropics are given in Table 1.

In most areas of the world vegetable consumption and production is expanding rapidly. This is especially evident in countries with rapidly expanding populations, where large amounts of land near urban centres have been devoted to vegetable production. Large scale vegetable production has been further stimulated by advances made in the processing industry.

The rapid development of vegetable production in the tropics is illustrated by an 18% increase in production between 1981 and 1985. Conversely, in the more developed countries, vegetable production only expanded 7.7% in the same time span (FAO, 1985). Production figures for some typical subtropical and tropical vegetable crops are given by region in Table 2. The major producers of vegetables in the tropics in order of importance are: Asia, Africa, South America and Central America.

The types of vegetables grown are numerous and full coverage is beyond the scope of this chapter. Many of the important crops that can be used as vegetables, for example the leaves of cassava, and taro, have been discussed under root and tuber crops (Chapter 5). Similarly, many of the crops covered under food legumes (Chapter 6), such as peas and haricot beans, which are considered vegetables, will not be dealt with here.

## Cultivation techniques

Depending on demographic structure and economic development of a region, vegetable growing in the subtropics and tropics varies from gathering of fruits, leaves and tubers found amongst the natural vegetation and various forms of multiple cropping to large scale commercial production (Kassam, 1976).

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TABLE 1. Common name, botanical name, use, economic importance and origin of the most common subtropical and tropical vegetables (Zeven & de Wet, 1982).

| Common name | Botanical name | Use | Economical importance | Origin |
|---|---|---|---|---|
| Beetroot | *Beta vulgaris* L. | Roots | S | S. Europe, India |
| Black mustard | *Brassica nigra* L. | Leaves | S | Europe |
| Broccoli | *Brassica oleracea* L. v. *botrytis* | Flower | S | Europe |
| Carrot | *Daucus carota* L. | Roots | S | Europe, N. Africa |
| Calabash | *Lagenaria vulgaris* Ser. | Fruits | S | Africa, Asia, Trop. Aus. |
| Cabbage | *Brassica oleracea* L. v. *capitata* | Leaves | I | Europe |
| Cauliflower | *Brassica oleracea* v. *botrytis* L. | Flower | M | Europe |
| Celery | *Apium graveolens* L. | Leaves | S | S. Europe |
| Chayotte | *Sechium edulis* Schwartz | Fruits | S | C. America |
| Chilli | *Capsicum annuum* L. | Fruits | I | S. America |
| Chinese cabbage | *Brassica chinensis* L. | Leaves | M | East China |
| Cucumber | *Cucumis sativus* L. | Fruits | M | N. India |
| Eggplant | *Solanum melongen* L. | Fruits | I | India |
| Garlic | *Allium sativum* L. | Bulbs | M | C. Asia |
| Kale | *Brassica oleracea* L. v. *acephale* | Leaves | S | Europe |
| Leek | *Allium porrum* L. | Leaves | M | Middle East |
| Lettuce | *Lactuca sativa* L. | Leaves | M | N. Africa |
| Sponge gourd | *Luffa cylindrica* | Fruits | S | India |
| Melon | *Cucumis melo* L. | Fruits | M | Africa |
| Okra | *Abelmoschus esculentus* (L.) Moench | Fruits | I | India |
| Onion | *Allium cepa* L. | Bulbs | I | C. Asia |
| Parsley | *Petroselinum crispum* Nym. ex A. W. Hill | Leaves | S | S. Europe |
| Pumpkin | *Cucurbita pepo* L. | Fruits | S | S. America |
| Radish | *Brassica sativus* L. | Roots | S | Japan |
| "Spinach" | *Amaranthus hybridus* L. | Leaves | M | N. Africa |
| | *Amaranthus viridis* L. | Leaves | M | S. America |
| | *Basella alba* L. | Leaves | S | S. E. Asia |
| | *Ipomoea reptans* Poir | Leaves | S | Tropics |
| | *Solanum nigrum* L. | Leaves | S | W. Africa |
| Sweet pepper | *Capsicum annuum* L. v. *grossum* | Fruits | M | S. America |
| Tomato | *Lycopersicon esculentum* Mill. | Fruits | I | S. America |
| Watermelon | *Citrullus vulgaris* Schrad. | Fruits | M | Africa |

S = Small, locally produced in home and small market gardens. M = More important production often near big centres. I = Important, generally produced throughout the tropics, major vegetables.

In humid tropical forests, shifting cultivation, where forests are cleared and burned, cropped, then abandoned again for up to 30 years, was the prevalent system. In most tropical areas today, however, a multiple cropping system is now practised with up to twenty different plant species grown simultaneously on a small plot of land. Shifting cultivation has been gradually replaced in many areas by different forms of multiple crop farming systems (Norman *et al.*, 1981). In many of these situations, survival of the subsistence farm family is governed by the quantity and quality of the crops produced.

Large scale vegetable production is more input orientated than traditional methods and is dependent on higher levels of mechanization, a secure water supply, effective and safe pesticides, and high quality seed or planting material.

TABLE 2. Area, yield and total production of different vegetables in tropical regions in 1985 (FAO, 1985).*

| | *Africa* | | | *C. America* | | | *S. America* | | | *Asia* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Area | Yield | Prod. | Area | Yield | Prod. | Area | Yield | Prod. | Area | Yield | Prod. |
| Cabbage | 30 | 25.7 | 767 | 27 | 15.7 | 424 | 21 | 21.6 | 460 | 796 | 20.3 | 161 |
| Cantaloupes and other melons | 48 | 15.9 | 756 | 34 | 12.5 | 425 | 26 | 13.6 | 351 | 317 | 12.9 | 4083 |
| Cauliflower | 7 | 22.2 | 185 | 1 | 13.0 | 13 | 5 | 15.8 | 72 | 195 | 10.8 | 2105 |
| Chillies, pepper, green | 170 | 7.2 | 1221 | 69 | 8.2 | 566 | 20 | 8.5 | 172 | 608 | 5.7 | 3468 |
| Cucumber and gherkin | 23 | 16.2 | 368 | 36 | 7.3 | 262 | 3 | 16.6 | 47 | 420 | 15.5 | 6512 |
| Eggplant | 378 | 14.0 | 5293 | – | – | – | 1 | 13.1 | 9 | 328 | 13.0 | 4257 |
| Garlic | 8 | 24.2 | 195 | 7 | 7.4 | 52 | 26 | 4.7 | 124 | 382 | 5.0 | 1928 |
| Onions | 157 | 13.1 | 1974 | 12 | 7.2 | 86 | 111 | 14.7 | 1635 | 950 | 12.1 | 11524 |
| Pumpkins, squashes and gourds | 69 | 14.9 | 984 | 41 | 7.0 | 288 | 75 | 9.8 | 741 | 202 | 12.4 | 2498 |
| Tomato | 445 | 13.6 | 6042 | 154 | 19.3 | 2974 | 133 | 25.7 | 3426 | 798 | 19.0 | 15183 |
| Watermelon | 120 | 18.4 | 2200 | 34 | 13.2 | 449 | 120 | 9.3 | 1118 | 970 | 16.6 | 16125 |

*Area in 1000 ha, Yield in MT/ha, Production (Total) in 1000 MT

## Nematodes of Vegetables

The role plant parasitic nematodes play in limiting vegetable production depends to a large extent on the farming system employed. In general, nematodes will be less important under more extensive and varied growing systems typical of shifting cultivation and multiple-crop farming in subsistence agriculture or in widely spaced rotations of commercial farming systems than in more intensive production where monocropping and narrow rotations are practiced. This was observed in Senegal where crops grown under local cropping conditions were not parasitized by root-knot while neighbouring irrigated vegetable fields were heavily infested (Netscher, 1978).

The crops grown in shifting cultivation and in the other multiple-crop systems common to subtropical and tropical areas still have much in common with the natural flora from an ecological standpoint. The distribution of important plant parasitic nematodes associated with the natural vegetation is clustered, and so the distribution of the species which survive the drastic shift to multiple cropping will also be heterogeneous even if polyphagous species are present. Extensive damage by nematodes, therefore, is extremely rare in the crops produced directly after clearing. Exceptions to the rule occur in those instances where nematode infested planting material in the forms of seedlings or tubers are used for planting (Bridge, 1987).

Multiple cropping systems, although initially reflecting the natural flora, will promote nematode population build-up with time. The extent of the increase will depend on the nematodes initially present and on the percentage of susceptible plants per unit area. Damage intensity usually increases slowly with time in the multiple cropping system, as compared to the rapid increase in damage encountered in large scale vegetable production where near monoculture is practiced.

Great differences exist between the plant parasitic nematode communities of tropical and temperate regions. Most vegetable crops have been recorded as a host for at least one of the most frequently occurring species of root-knot nematodes, *M. incognita, M. javanica* and *M. arenaria*. Important temperate parasites like *Ditylenchus dipsaci* and species of *Heterodera* are only of local importance in the warm tropics. Conversely root-knot nematodes that predominate in tropical regions are uncommon in temperate regions (Taylor, 1976).

Root-knot nematodes, which increase to damaging levels within a few seasons under susceptible crops, are so common in subtropical and tropical vegetable production that frequently they are taken to represent "nematodes" in general. Other economically important nematode species are often overlooked, because of a lack of distinct symptoms and are often neglected by plant protection agencies. This has been particularly true for cyst nematodes.

Research has shown that a number of other parasites frequently encountered in vegetable production such as *Rotylenchulus reniformis* and *Paratrichodorus minor* are of economic importance in vegetable production. Other nematodes like *Heterodera schachtii, Nacobbus aberrans, Belonolaimus longicaudatus* and *Tylenchorhynchus brassicae* have also been shown to be serious pests of local importance.

## *Meloidogyne*

Initially, all root-knot nematodes were considered to belong to one extremely polyphagous species, *Heterodera marioni* (Cornu 1887) Goodey, 1932, until Chitwood (1949) re-established the genus *Meloidogyne* Goeldi, 1987. Although 51 species of *Meloidogyne* have been described to date (Jepson, 1987), four species are of particular economic importance to vegetable production, *M incognita, M. javanica, M. arenaria*, and *M. hapla*. Out of 1000 root-knot populations collected in 75 countries, 53% were identified as *M. incognita*, 30% as *M. javanica*, 8% as *M. arenaria*, 8% as *M. hapla* and 2% *M. exigua* or other species (Johnson & Fassuliotis, 1984).

*M. incognita, M. javanica, M. arenaria* and *M. hapla* have the widest host ranges. *M. incognita* and *M. javanica* are commonly found in the tropics, whereas *M. arenaria* which is also found sporadically in the tropics, is more common in the subtropics. *M. hapla*, a species common in the temperate regions, can occasionally be found in the cooler upland tropics. *M. incognita* var. *acrita* Chitwood, 1949, later promoted to specific rank (Esser *et al.*, 1976; Jepson, 1987), is synonymized in this chapter with *M. incognita* (Triantaphyllou & Sasser, 1960).

In Table 3 the main species of *Meloidogyne* found parasitizing vegetables are listed by crops and their relative level of importance noted.

### Symptoms of damage

The presence of galls on the root system is the primary symptom associated with *Meloidogyne* infection. In galls formed by one female a swelling of the central cylinder, highly deformed vascular elements and the spherical part of the female surrounded by the cortical parenchyma can be easily observed at low magnification in stained roots (Plate 5H).

The size and form of the gall depends on the species involved, number of nematodes in the tissue, host and plant age. In cucurbits, the roots react to the presence of *Meloidogyne* by the formation of large, fleshy galls (Fig. 1), whereas in most other vegetables, galls are large and firm (Plate 5D). Occasionally very small galls develop (Plate 5E) and in some cases galls are not visible. Symptoms of root-knot on monocotyledonous crops like onion and leek are very discrete, the main symptom being the presence of the protruding egg masses. Galls on sweet and chilli pepper, for example, are also frequently small. The symptoms caused by *M. hapla* differ from those produced by most other species in that only small, more or less spherical galls are produced with profuse root branching originating from the gall tissue causing a "bearded root" system (Plate 5F).

When plants are severely infected by *Meloidogyne* the normal root system is reduced to a limited number of severely galled roots with a completely disorganized vascular system. Rootlets are almost completely absent (Plate 5D). The roots are seriously hampered in their main functions of uptake and transport of water and nutrients. Plants wilt rapidly, especially under dry growing conditions, and are often stunted. Growth is retarded and leaves may be chlorotic (Plate 5A,B). In Thailand, wilting often occurs in non-chlorotic plants and has given rise to the term "Green wilt disease" (S. Sontirat, pers. comm.). In cases where seedling infection has taken place, numerous plants die in the seedbed and seedlings do not survive transplanting. In those plants that do survive, flowering and fruit production is strongly reduced. The losses caused by *Meloidogyne* on root and tuber crops like carrot, are both quantitative and qualitative, because nematode galling affects marketability

TABLE 3. Root-knot nematodes, *Meloidogyne* spp., associated with major vegetable crops in the subtropics and tropics and their relative economic or potential importance.

| Botanical Name | Common Name | *Meloidogyne arenaria* | *Meloidogyne acronea* | *Meloidogyne cruciani* | *Meloidogyne ethiopica* | *Meloidogyne exigua* | *Meloidogyne hapla* | *Meloidogyne incognita* | *Meloidogyne javanica* | *Meloidogyne thamesi* |
|---|---|---|---|---|---|---|---|---|---|---|
| *Abelmoschus esculentus* | Okra | V | | | | | | | V | V |
| *Allium asacolonium* | Shallot | | | | | | | U | U | |
| *A. cepa* | Onion | L | | | | U | | | L | U |
| *A. porrum* | Leek | | | | | | | U | L | |
| *A. sativum* | Garlic | | | | | | | U | | |
| *A. schocnoprasum* | Chives | | | | | | | | U | |
| *Amaranthus hybridus* | Spinach (bajem) | | | | | | | M | M | |
| *A. viridis* | African spinach | | | | | | | | M | |
| *Apium graveolens* | Celery | | | | | | | V | V | V |
| *Basella alba* | Spinach | | | | | | | M | M | |
| *Beta vulgaris* | Beetroot | L | | | | | L | | | |
| *Brassica chinensis* | Chinese cabbage | | | | | | | M | | |
| *B. nigra* | Black mustard | U | | | | | | | | |
| *B. oleracea* v *acephale* | Kale | U | | | | | | | U | |
| *B. oleracea* v. *botrytis* | Cauliflower | L | | | | | | | L | |
| *B. oleracea* v. *capitata* | Cabbage | L | | | | | L | L | L | |
| *Capsicum annuum* | Sweet pepper, chilli | L | | | | L | | M | | |
| *C. frutescens* | Cayenne pepper | L | | | | | | M | L | |
| *Celosia argentea* | African spinach | L | | | | | L | M | M | |
| *Citrullis vulgaris* | Watermelon | V | | | | | | V | V | |
| *Cucumis melo* | Melon | L | | | | | | V | V | |
| *C. sativus* | Cucumber | V | | | | | | V | V | |
| *Cucurbita maxima* | Squash | V | | | | | | V | V | |
| *C. pepo* | Pumpkin | V | | | | | | V | V | |
| *Daucus carota* | Carrot | L | | | | | L | V | V | |
| *Ipomea reptans* | "Spinach" (kangkung) | | | | | | U | | | |
| *Lactuca sativus* | Lettuce | L | | | | | U | V | V | L |
| *Lagenaria siceraria* | Bottle gourd | M | | | | | | | V | |
| *L. vulgaris* | Calabash | M | | | | | | V | V | |
| *Luffa cylindrica* | Sponge gourd | | | | | | | V | V | |
| *Lycopersicon esculentum* | Tomato | V | U | U | U | | | V | V | L |
| *Momordica charantia* | Balsam pear | | | | | | | U | | |
| *Petroselinum crispum* | Parsley | L | | | | | L | V | | U |
| *Sechium edule* | Chayotte | | | | | | | | V | |
| *Solanum melongena* | Eggplant | V | | | | | | V | V | |
| *S. nigrum* | Black nightshade | U | | | | | | U | U | |

V = Very important. M = Moderately important. L = Limited or of local importance and U = Unknown importance.

Fig. 1. Massive galls produced by *Meloidogyne javanica* on cucurbit roots in India.

(Fig. 2; Plate 5F). As the season advances the galls are often invaded by fungi and bacteria that induce rotting (Fig. 3; Plate 5D). In severe cases the firm stele of the primary root is the only remnant of the original intact root system.

## Biology and life cycle

There are optimum temperatures for different phases of the life cycle of *M. javanica* (Ferris & Van Gundy, 1979). Optimum temperature range for an Australian population was 25–30°C and those for a California population between 32–34°C. Dao (1970) demonstrated that populations adapt to local climatic conditions. Optimum temperatures, for nematode development correspond to those found in tropical vegetable growing regions, a factor insuring serious root-knot infestations. Survival of eggs and juveniles of *M. javanica* decreased strongly when submitted to a temperature of 45°C for three hours (Demeure, 1978). Temperature optimums for *M. hapla* are at least 5°C lower than for the other major species in the tropics. *M. hapla* is therefore limited to the upland tropics and temperate growing regions. *M. incognita, M. javanica* and *M. arenaria* occur in areas with an average temperature of 36°C or lower in the warmest month. *M. hapla* conversely, occurs in areas having a

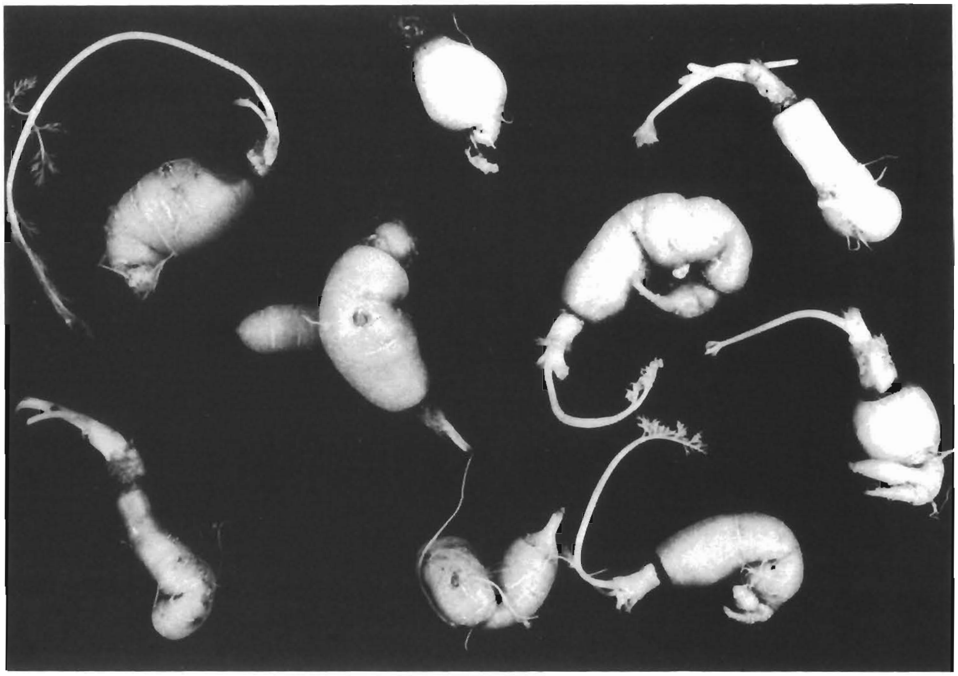

Fig. 2. Deformed carrots caused by *Meloidogyne* sp. in Tonga.

temperature as low as −15°C during the coldest month, but is limited to regions with an average high of less than 27°C during the warmest month (Taylor *et al.*, 1982).

Soil texture and structure are directly related to water holding capacity and aeration and influence nematode survival, emergence, and disease severity. Sikora (1989), studying paddy rice – vegetable cropping systems, detected severe root-knot damage on vegetables grown in sandy soils after paddy but a total absence in clay soils. Soil type and soil pH has also been shown to influence nematode distribution (Taylor *et al.*, 1982). Soil type may also influence the types of crops grown, thereby affecting nematode distribution, population buildup and damage intensity. Juveniles in sandy soils are able to move horizontally and vertically over distances of up to 75 cm in 9 days (Prot, 1977). Prot and Van Gundy (1981) found that migration decreased with increasing clay content of the soil with no migration in soils with more than 30% of clay. The effect of soil pH on root-knot varies greatly. *Meloidogyne* species survive and reproduce at pH levels ranging from 4.0–8.0 (Ferris & Van Gundy, 1979). Emergence of *M. javanica* was greatest between 6.4 and 7.0 and inhibited below pH 5.2 (Wallace, 1966). Many tropical soils are very acid (pH of 4.5 is rather common), a fact that does not seem to prevent *Meloidogyne* buildup to extremely high densities.

## Races

Sasser (1954) proposed a method for the identification of the four major species, *M. incognita, M. javanica, M. arenaria* and *M. hapla*, based on the reaction of four hosts. The host differentials were expanded to include a tobacco cultivar with resistance to many *M. incognita* populations following the discovery of physiological races within *Meloidogyne* species (Taylor & Sasser, 1978).

It soon became evident that within species great physiological variability existed. Riggs and Winstead (1959) demonstrated that when populations of *M. incognita* and *M. arenaria* were inoculated to resistant cultivars of tomato, enough selection pressure was exerted by the cultivar that within a short time resistant breaking populations called "B races" were created. Sasser (1966) found that when different populations of the same species were inoculated to certain hosts, they often reacted differently. Thus certain populations of *M. incognita* parasitized cotton while others did not. In the same way, two categories of *M. arenaria* populations could be distinguished using peanut as a differential host. When a resistant cultivar of tobacco, NC 95, was included in the host range, the situation became still more complicated, according to the reactions on the two differential hosts, cotton and tobacco, *M. incognita* populations could be split into four races. From these and other observations (Southards & Priest, 1973) it became evident that in contrast to other genera of parasitic nematodes, like *Heterodera*, the identification of root-knot did not automatically give exact indications of the host range of that population.

The use of host differentials allows determination of the four main species and races of *Meloidogyne* (Table 4). Based on the results obtained with several hundred *Meloidogyne* populations, Sasser (1979*a*) concluded that there is considerable uniformity in host response and that resistance breaking races are not common. However, Southards and Priest (1973) demonstrated that host differentials can react differently to populations of the same species.

Fig. 3. Root degradation in tomato caused by the concomitant infestation of *Meloidogyne incognita* and root-rotting fungi in the Philippines.

TABLE 4. Differential host test identification of the most common *Meloidogyne* species and races (Hartman & Sasser, 1985).

| | Tobacco | Cotton | Pepper | Watermelon | Peanut | Tomato |
|---|---|---|---|---|---|---|
| *M. incognita* | | | | | | |
| Race 1 | – | – | + | + | – | + |
| Race 2 | + | – | + | + | – | + |
| Race 3 | – | + | + | + | – | + |
| Race 4 | + | + | + | + | – | + |
| *M.arenaria* | | | | | | |
| Race 1 | + | – | + | + | + | + |
| Race 2 | + | – | – | + | – | + |
| *M.javanica* | + | – | – | + | – | + |
| *M.hapla* | + | – | + | – | + | + |

Cotton: cv Deltapine; tobacco: cv N.C.95; pepper: cv Early California Wonder; watermelon: cv Charleston Gray; peanut: cv Florunner; tomato: cv Rutgers. (–) indicates a resistant host, (+), a susceptible host.

Further complicating identification is the fact that many populations are composed of more than one species (Netscher, 1978; Fargette, 1987). From one point of view, identification of *Meloidogyne* to species has little practical importance to vegetable growers, since most vegetables are susceptible to the major species encountered in the tropics. Amaranthus, celosia, beetroot, swiss chard, lettuce, most cabbages, cauliflower, most cucurbits, beans, peas, tomato, potato, eggplant, okra, carrot and many other vegetables have all been reported to be hosts of *M. arenaria, M. incognita* and *M. javanica* (see also Chapter 4 Food Legumes for other hosts). Correct species identification of *Meloidogyne* is important, however, in the correct selection of non-host crops for rotation purposes or a resistant cultivar.

## Survival and means of dissemination

Root-knot nematodes are obligate parasites, therefore, the absence of suitable host plants for prolonged periods ultimately leads to their disappearance. In the absence of susceptible crops, however, they often survive on weed hosts. In general, conditions favourable for plant growth will also be favourable for *Meloidogyne* reproduction. De Guiran and Demeure (1978) found that the optimum moisture levels for emergence of *M. incognita* juveniles was slightly above field capacity. If, under conditions optimum for emergence, host plants are absent, juveniles will deplete their energy reserves in the soil and eventually die. Although nematode populations rapidly decline, a proportion of the eggs in the eggmass are in diapause and assure perpetuation of the species (de Guiran, 1979; de Guiran & Villemin, 1980).

Under adverse environmental conditions, emergence and juvenile activity is reduced, thus, increasing the chances of survival. Survival is mainly influenced by moisture content of the soil and to a lesser extent by temperature. High temperatures are often associated with low soil moisture content, whereas in the cases of waterlogged or inundated soils, high temperatures rarely occur. Juveniles and eggs survive periods of moisture stress in a state of anhydrobiosis. Egg masses collected from dry soils will contain empty eggs and anhydrobiotic eggs with second stage juveniles in diapause.

In field soil, the number of juveniles decreased from an initial infestation of approximately 10 000 nematodes/$dm^3$ of soil to zero after 12 weeks, when the soil was gradually dried (de Guiran, 1979). Similar effects were found in the dry season in Senegal (Demeure, 1977). Nematodes could not be detected in the top twenty cm of the soil at the end of the dry season. The number of nematodes in the 20 – 40 cm horizon, where available soil moisture was slightly higher, reached 0.9% of the initial population.

Dissemination takes place when juveniles or eggs are transported from infested to uninfested areas. Wind-borne dissemination of root-knot nematodes has been reported (Orr & Newton, 1971) and may occur in regions where wind storms occur. Spread with irrigation water has been demonstrated in the U.S.A. (Faulkner & Bolander, 1970) and in Spain (Tobar & Palacios, 1974). Dispersal in runoff water produced during rain storms is another source of spread. Soil adhering to animals, foot wear and agricultural implements also spread infestations. Dispersal over great distances and over international borders occurs by movement of infested plants. Farms are often infested and damage maintained and intensified by growers using infested planting material.

### Disease complexes

Many examples of disease complexes are known (Pitcher, 1963; Powell, 1971*a*, *b*; Taylor, 1979; Webster, 1985). Tomato plants wilt more quickly and can be killed when *Fusarium oxysporum* is simultaneously present (Plate 5C). Resistance in tomato cultivars to fungal wilt caused by *Fusarium oxysporum* f. sp. *lycopersici* was reduced in the presence of *Meloidogyne* (Jenkins & Coursen, 1957; Sidhu & Webster, 1977). Conversely, Abawi and Barker (1984) did not detect any synergistic effect of *M. incognita* or *Fusarium* wilt on either resistant or susceptible tomato. Field studies on the importance of complex disease interrelationships to crop production are scarce and many of the experimental techniques used in the past are considered inadequate (Wallace, 1983; Sikora & Carter, 1987).

Damage to the root system caused by root-knot nematode attack has been considered responsible for increases in the intensity of bacterial wilt caused by *Pseudomonas solanacearum* (Valdez, 1978) and bacterial canker caused by *Corynebacterium michiganense* (Moura *et al*., 1975). The interrelationship between pathogenic bacteria and root-knot have not been studied in detail and are probably highly complex (Taylor, 1979). Many plants are susceptible to weak fungal pathogens only in the seedling stage. However, when simultaneously present with *Meloidogyne*, these fungi may increase damage to mature plants.

The weight of the roots and shoots of tomato plants was more strongly reduced when secondary microbial invasion existed following inoculation with *M. incognita* than when aseptic juveniles were added (Mayol & Bergeson, 1970). Van Gundy *et al.* (1977) demonstrated that leachings of nematode infected plants, applied to tomato inoculated with *Rhizoctonia* resulted in the appearance of severe rot, when compared to the controls. Suppression of this disease complex, which is very common in the tropics, by the control of *Meloidogyne*, could increase yields significantly.

### Economic importance

Estimations of vegetable crop losses in the tropics (Sasser, 1979*b*) ranged from 17–20% on eggplant; 18–33% on melon and 24–38% on tomato. The role *Meloidogyne* plays in total crop loss is difficult to ascertain in cases where crops are suffering from simultaneous attack by fungi, viruses, insects and other nematodes, a situation, very common in tropical countries. Nematicide trials have been used to demonstrate losses associated with *M. incognita* infestations on a number of crops (Lamberti, 1979*b*). Crop loss due to this nematode ranged from 30–60% on eggplant and 50% on cantaloupe and watermelon. In the United States, yield on plots infested with *M. incognita* and treated with DD-MENCS and planted with beans, summer squash, okra or cucumber, increased 128, 180, 507 and 1175%, respectively (Johnson, 1985). These figures must be used with caution because nematicides affect other soil organisms and indirectly stimulate plant growth. Proper crop loss assessment trials, especially under multiple cropping systems, are lacking and are needed to demonstrate the true impact of nematodes on vegetable production in small scale subsistence farming systems.

### Economic threshold level

In Table 5, *M. arenaria* and *M. incognita* tolerance limits (T), or the population density at which damage is first observed, are given for a number of vegetables (Seinhorst, 1965; Barker & Olthof, 1976; Barker *et al.*, 1985; Di Vito *et al.*, 1986; Ferris *et al.*, 1986). The wide variation in tolerance limits reflects the great difference in plant response to nematode infection as well as the influence of soil type and environmental conditions on disease development and severity (Ferris *et al.*, 1986).

TABLE 5. Tolerance limit of some vegetables to *Meloidogyne* species.

| | *Meloidogyne* species* | |
|---|---|---|
| Crops | *M. arenaria* | *M. incognita* |
| Bell pepper | – | 65 |
| Cabbage | – | 150–1000 |
| Cantaloupe | – | 20 |
| Chilli pepper | – | 39 |
| Eggplant | – | 5.4 |
| Lettuce | – | 60 |
| Tomato | 2–100 | 2–100 |
| Watermelon | 2–50 | 2–50 |

*Number of juveniles/100 $cm^3$ of soil

In the San Joaquin Valley of California, U.S.A., the number of juveniles in samples taken from sandy loam soils has been used for estimating potential yield loss in processing tomato production areas (Table 6). These figures are given here to be used as guidelines for estimating possible loss in other growing regions. Environmental factors, soil types and cropping sequences will affect damage threshold levels, therefore, caution should be used when using these figures.

TABLE 6. Effect of root-knot nematode populations on processing tomato yield in San Joaquin Valley sandy loam soil (Anon., 1985).

| Number of Root-knot Juveniles Per Kilogram in Soil Samples | | Percent of Normal Yield |
|---|---|---|
| Autumn Samples | Spring Samples | |
| 0 to 160 | 0 to 25 | 100 |
| 310 | 50 | 98 |
| 620 | 100 | 95 |
| 940 | 150 | 91 |
| 1250 | 200 | 88 |
| 1560 | 250 | 85 |
| 1870 | 300 | 82 |
| 2190 | 350 | 79 |
| 2500 | 400 | 77 |
| 2810 | 450 | 74 |
| 3120 | 500 | 72 |
| 3440 | 550 | 69 |
| 3750 | 600 | 67 |
| 4060 | 650 | 65 |
| 4370 | 700 | 63 |
| 4690 | 750 | 61 |
| 5000 | 800 | 60 |
| 5310 | 850 | 58 |
| 5620 | 900 | 56 |
| 5920 | 950 | 55 |
| 6250 | 1000 | 53 |

## Control

The variation in vegetable growing techniques that range from shifting cultivation to large scale commercial production systems prevents the development of one control strategy applicable to all situations. For example, the subsistence farmer frequently utilizes a mixture of local cultivars of a crop to assure himself a minimum yield and will usually not follow recommendations to grow an unfamiliar nematode resistant cultivar. On the other hand, a commercial plantation manager will not hesitate to utilize resistant cultivars or expensive nematicides to protect a crop (Radewald *et al.*, 1987). In the first case, crop improvement is more difficult.

Control strategies should be preventative rather than curative in nature and aimed from the onset at preventing the buildup of high population densities. It should be noted that many of the techniques used for control of *Meloidogyne* on vegetables simultaneously control other plant parasitic nematodes affecting the crop. This is especially important where multiple species of economically important nematodes affect crop growth (IFAS, 1989).

Once high populations of *Meloidogyne* have developed in a field, it is virtually impossible to suppress and maintain populations at sufficiently low levels without repeated treatment, regardless of the control method practiced. For example, although *M. javanica* densities were reduced to low levels (following either two non-hosts, or a resistant cultivar, or a poor host) and eggplant yield increased significantly, nematode population density rose to high levels at season end (Netscher, 1981*a*).

### Cultural practices

*Root-knot free nurseries*

Only seedlings with roots free of galls should be selected for transplanting. Nurseries must be free of root-knot nematodes in order to reduce dissemination into root-knot free production areas on contaminated transplants. All the techniques described below can aid in maintaining nematode free nursery areas and in some cases to eradicate the nematode from the soil. Seedbeds should be selected on sites which previously were not planted to host plants. To reduce contamination, seedbeds should be planted for dry season crops on land normally flooded during the wet season e.g. in previous paddy fields (Bridge, 1987; Sikora, 1988).

Chemical disinfestation is a common and effective practice in large production operations, whereas, other methods must be considered for subsistence farming. Fumigant nematicides could be used in nurseries even in the case of traditional farming systems, because of the small amount needed and low impact on the environment.

Soil can be heated in drums or on old sheets of metal before being added to trays or plastic bags for seedling production. Solarization of small quantities of soil may also prove feasible. The burning of straw, paddy husks or sawdust on land to be used for seedbeds has been suggested (Choudhury, 1981). Although this method reduces populations, quantities of 20 kg paddy husk per $m^2$ must be burned to obtain control (Krishnamurthy & Elias, 1969).

*Rotation*

Page (1979) and Sikora *et al.*, (1988) suggested rotations designed to reduce the impact of root-knot nematodes in tropical vegetable cropping systems in Bangladesh and Niger, respectively. A number of rotations exist in the tropics, especially in Asia, which are predominantly composed of cruciferous crops moderately resistant or tolerant to root-knot nematodes, together with a small number of highly susceptible crops (Fig. 4). Rotations of this design can be effectively used to reduce root-knot nematode densities.

Vegetables can be classified according to their susceptibility to root-knot nematodes e.g.: *very susceptible:* tomato, eggplant, lettuce, melon etc.; *moderately susceptible:* cabbage, cauliflower; *slightly susceptible:* onion; *resistant:* mint, (Netscher & Luc, 1974). These reactions seem to be

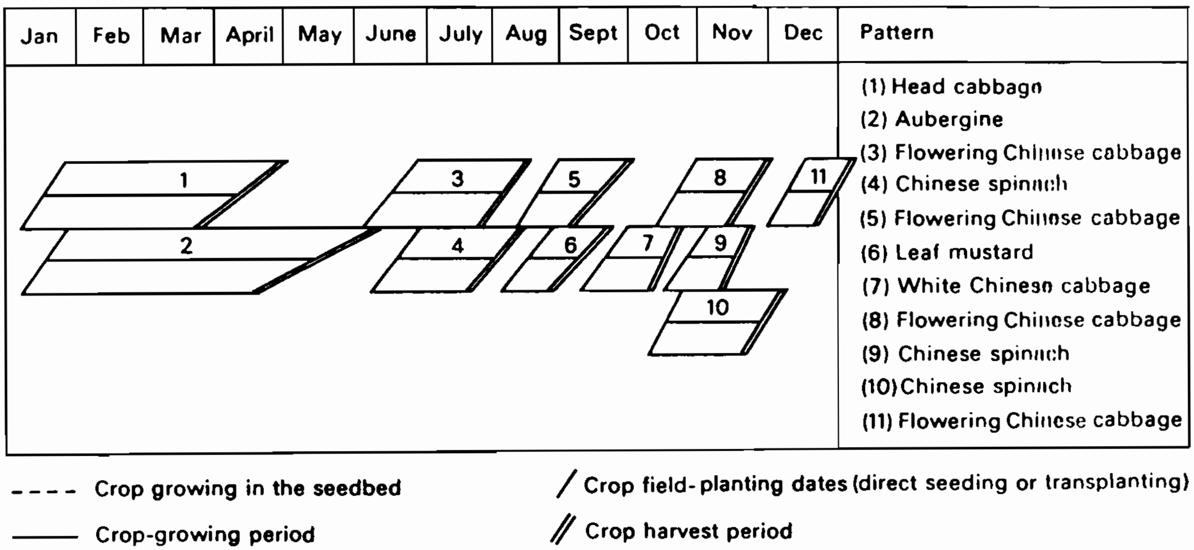


Fig. 4. Rotation with relay-planting and intercropping in Taiwan and China (Ruthenberg, 1983).

independent of the *Meloidogyne* species concerned but vary from one population to another (Netscher, 1970).

Similar classifications have been made for vegetable crops in Mauritania, Malawi, Bangladesh and Niger and have been used to formulate new crop rotations for control of root-knot nematodes. Vegetables considered moderately susceptible or tolerant to root-knot were: cabbage, cauliflower and onion in Mauritania (Netscher & Luc, 1974) all cruciferous crops, onion and leek in Malawi (Bridge & Page, 1977) and broccoli, cauliflower, cabbage and onion in Bangladesh. Amaranthus and chilli were considered resistant in Bangladesh (Page, 1979) onion and amaranthus were resistant in Niger (Sikora *et al.*, 1988).

Caution must be taken with regards to variation in nematode populations and to the composition of root-knot species present in a field. Often the *Meloidogyne* populations are composed of several species. Detection of species that make up less than five percent of the population is difficult. The fact that the minimum temperature required for *M. incognita* development in the root is significantly lower than the minimum "activity threshold" of 18°C for *M. incognita* second stage juveniles (Roberts *et al.*, 1981) has been used to alter date of planting for control of root-knot. Changing the normal date of planting to coincide with low soil temperature was considered an important control tactic on carrots (Roberts, 1987) and could be used to limit nematode damage on vegetables in cool upland tropical regions.

In areas where the climate is characterized by a prolonged and severe hot dry season, fallow during the dry season followed by non-hosts during the wet season for a period of two to three years, may result in the reduction of *Meloidogyne* populations (Duc, 1980).

The effect of crop rotations may be seriously compromised, however, if susceptible weeds are present. Proper weed control can be a vital factor in nematode control, reducing multiplication of *Meloidogyne* on weed hosts.

*Root destruction*

Galled roots remaining in the field after harvest, should be eliminated by uprooting and destruction. The spread of the nematode will be retarded and the initial population density reduced because the nematode can survive and reproduce on the roots in the soil after harvest. It has been estimated that, when soil temperatures are high, each month that the root system survives causes a 10-fold increase in root-knot nematode densities (IFAS, 1989).

*Organic amendments*
The incorporation of organic material into the soil reduces root-knot densities (Muller & Gooch, 1982). Oil cakes, sawdust, urea and bagasse have been used with some success (Singh & Sitaramaiah, 1966, 1967; Sikora *et al.*, 1973*a*). Chitin in combination with waste products from the paper industry has been used to reduce root-knot nematodes (Culbreath *et al.*, 1985). Although the use of organic amendments for effective nematode control is often limited by the large quantities needed, they will reduce nematode population densities to different degrees. In addition to their suppressive effects on nematode density, organic amendments improve soil structure and waterholding capacity.

**Physical**

*Flooding*
*Meloidogyne* densities drop significantly when soils are flooded for prolonged periods of time and are, therefore, often not considered severe problems in the dry season in tropical regions where paddy rice is a normal component of the rotation system. Thames and Stoner (1953) demonstrated that flooding of rice fields for three months gives acceptable control of root-knot nematode for two succeeding vegetable crops. Root-knot nematode densities were lower on susceptible dry season crops in paddy rice rotations than in upland areas in the Philippines (Castillo *et al.*, 1976*b*).

Sikora (1989) showed that the degree of root-knot damage in Philippine vegetable production was less severe in cropping systems based on paddy rice – vegetable rotations than in rotations without paddy rice when flooding was maintained for at least 4 months. The level of galling decreased significantly with increasing clay content of the soil, indicating that soil type plays an active role in population reduction under flooded conditions. Similar effects of paddy rice cropping patterns were noted in northern Java, Indonesia (C. Netscher, unpub.). In Florida, flooding alternated with drying during the summer is recommended for vegetables grown on muck soils to reduce root-knot nematode densities (IFAS, 1989). Crops grown in fields not flooded were frequently severely damaged. Working the soil during the dry cycle is also recommended to prevent weed growth that could harbour other hosts.

*Solarization*
Soil solarization with clear plastic tarps has been attempted as a means of raising temperatures to lethal levels to control soil-borne diseases (Katan, 1980). The technique, however, is only adaptable to regions where sufficient solar energy is available for long periods of time. In many climatic regions and in subsistence agriculture the costs of using transparent plastic can be a factor limiting application. Solarization has been shown to have a potential in the subtropical climate of Florida where it reduced root-knot, *Verticillium* wilt, and weeds in the autumn crops, even though climatic conditions are not considered ideal for soil solarization (Overman & Jones, 1986). The techniques may, however, have application as a means of eliminating nematodes from seedbeds. Black plastic (Abu-Gharbieh *et al.*, 1987) with the simultaneous use of solar heated water applied by drip irrigation, increases hot water penetration into deeper soil horizons, and may be promising for high value crops (Saleh *et al.*, 1988).

**Resistance and tolerance**

*Non-host crops*
Root-knot nematodes are extremely polyphagous, therefore, relatively few non-host plants are available for control through crop rotation. Unfortunately, there are many reports of *Meloidogyne* populations parasitizing plants which have been reported non-hosts, an important factor in developing rotation based control systems (Netscher & Taylor, 1979). Peanut, for example, is often considered

a non-host of *M. incognita*, and *M. javanica* (Netscher, 1975). However, it is attacked by *M. javanica* in Zimbabwe (Martin, 1956), Egypt (Ibrahim & El Saedy, 1976) and USA (Minton *et al.*, 1969) and is tolerant to *M. javanica* in Bangladesh (Page, 1979).

Fodder and green manure crops considered to be non-hosts to species of *Meloidogyne*, which could be used in developing rotations, are listed in Table 7. Differences, however, in susceptibility between cultivars of the fodder grass *Panicum maximum*, considered a non-host of the more common tropical root-knot nematodes, has been detected in South African populations of *M. incognita* (van der Linde, 1956). Therefore these crops should be used for control only after testing with local populations.

TABLE 7. Fodder crops and green manures considered non-hosts of *Meloidogyne* species.

| Plant | *M. arenaria* | *M. javanica* | *M. incognita* |
|---|---|---|---|
| *Aeschynome* | – | – | + |
| *Arachis hypogaea* | +* | + | + |
| *Crotalaria fulva* | – | + | + |
| *Crotalaria grahamiana* | – | + | + |
| *Crotalaria retusa* | – | + | + |
| *Crotalaria usaramoensis* | – | – | + |
| *Eragrostis curvula* | – | + | + |
| *Glycine javanica* | – | – | + |
| *Indigofera hirsuta* | – | – | + |
| *Panicum maximum* | – | + | + |
| *Stylosanthes gracilis* | – | + | + |

+ = Resistant, – = not tested, * = Susceptible to many populations.

Plants considered good host plants of a *Meloidogyne* species in one part of the world are not necessarily hosts to all populations of that species (Southards & Priest, 1973). Two races of *M. arenaria* were identified using peanut, previously considered a non-host, as a differential host (Sasser, 1966). Netscher (1970) showed that different populations within a species can be characterized by differences in virulence to a host. Lamberti (1979*a*) obtained similar results on tomato with 12 populations of *M. incognita* in southern Italy (Table 8). Because of this large variation in host status within species of root-knot, all crops being considered for rotation must be tested for host status to local populations before rotation schemes are recommended for the field.

TABLE 8. Differences in virulence of *Meloidogyne incognita* populations to tomato expressed as severity of galling (Lamberti, 1979).

| Origin of population | Degree of galling (scale 0–5) |
|---|---|
| Control | 0.0 |
| Altomonte, Cosenza (Tomato) | 1.1 |
| Monopoli Bari (Lettuce) | 1.3 |
| Vicio Equense, Napoli (Squash) | 2.6 |
| Lecce (Tobacco) | 2.8 |
| Torino (Celery) | 2.9 |
| Margherita di S, Foggia (Tomato) | 2.9 |
| Bari (Tomato) | 3.0 |
| Fondi, Latina (Eggplant) | 3.3 |
| Ragusa (Tomato) | 3.4 |
| Casterlamare di S, Napoli (Tomato) | 4.1 |
| Scafati, Salerno (Anemone) | 4.5 |

Local shade trees as well as plants being selected for wind-breaks, e.g. the baobab tree, *Adansonia digitata* (Taylor *et al.*, 1978) or *Prosopis juliflora* (Netscher & Luc, 1974), can be good hosts. Conversely, neem (*Azadirachta indica*), cashew nut (*Anacardium occidentale*) and *Eucalyptus camaldulensis* may be resistant to *Meloidogyne* (Netscher, 1981*b*). Fruit trees like papaya are also good hosts (Chapter 10).

Furthermore, roots of some non-host crops can react to root-knot penetration with local necrosis. In the case of very high nematode densities, roots are badly damaged and the crop does not become well established. This situation can be easily avoided by delaying sowing for a few weeks after soil preparation, to reduce juvenile density through starvation.

*Resistance*

The use of resistant cultivars is an elegant, economical and environmentally safe method for controlling root-knot nematodes (Netscher & Mauboussin, 1973). Fassuliotis (1979) gives a comprehensive review of most aspects of resistance to *Meloidogyne*.

There are few sources of resistance amongst crops susceptible to *Meloidogyne*. Resistance has been found in pepper and bean cultivars and was incorporated into tomato via an embryo culture of a hybrid between a resistant line of *Lycopersicum peruvianum* and tomato (Smith, 1944). In most cases, the genetic basis for resistance is determined by one major gene (Gilbert & McGuire, 1956; Hare, 1957). However, Hendy *et al.*, (1985) reported the presence of five dominant genes which when present in one genotype protect against *M. incognita, M. javanica* and *M. arenaria*.

Resistance has been found in melons and eggplants. It was originally detected in *Solanum sisymbrifolium*, closely related to the eggplant. Several wild *Cucumis* species with resistance to root-knot also have been reported (Fassuliotis, 1979). However, genetic barriers make it extremely difficult to introduce the resistance of the "wild" species in the cultivated ones. Modern techniques like protoplast culture and somatic hybridization may make it possible to create viable hybrids and attempts are being made to develop interspecific hybrids.

*Solanum torvum* which has shown a high level of resistance to *M. incognita* and *M. arenaria*, but is a poor host for *M. javanica*, has been successfully used as a rootstock for eggplant (Dunay & Dalmasso, 1985). In some cases such "Wild" species can be used as resistant rootstock of susceptible grafts. In the Congo, the use of a local eggplant (N'drowa) seems to protect grafts of eggplant against root-knot and *Pseudomonas solanacearum* (Declert, pers. comm.).

Lists of plants reported resistant to species of nematodes in general (Armstrong & Jensen, 1978) and crop cultivars with resistance to species of *Meloidogyne* specifically (Sasser & Kirby, 1979) have been compiled. A list of vegetable cultivars resistant to root-knot nematodes is given in Table 9. The list should be used with caution, because it is often based on a limited number of field observations and does not guarantee that a cultivar is resistant to all populations of *Meloidogyne*. Resistant cultivars of crops susceptible to *Meloidogyne* do not necessarily protect the crop against all species of the genus. In addition, races may exist which are able to break resistance. The Mi gene does not confer immunity to *M. incognita* and *M. javanica* (Roberts & Thomson, 1986). Resistance breaking races have been selected out of field populations of *M.incognita, M. javanica* and *M. arenaria* (Riggs & Winstead, 1959; Sauer & Giles, 1959). Root-knot populations which were capable of attacking resistant cultivars have been detected even though they had previously never been exposed to the cultivars (Sikora *et al.*, 1973*b*; Netscher, 1977; Prot, 1984; Fargette, 1987; Berthou *et al.*, 1989). Resistance breaking races were also selected from single egg mass populations of *M. incognita* and *M. javanica* in laboratory experiments (Triantaphyllou & Sasser, 1960; Netscher, 1977). Resistant cultivars therefore should be used judiciously and with caution or should be tested using small microplots with the cultivar or cultivars in question (Roberts *et al.*, 1986). Approximately 30% of all processing tomato now produced in California has the Mi gene for resistance or enough to cover over 70% of the area infested with root-knot (P. A. Roberts, pers. comm.). This must be considered an important development in any growing region where the growers have been totally dependent on fumigants for crop production.

TABLE 9. Vegetable cultivars reported as resistant to *M. arenaria, M. incognita* and *M. javanica*.

| | *Meloidogyne* species | | |
|---|---|---|---|
| Crop | *M. incognita* | *M. javanica* | *M. arenaria* |
| **Bean** | | | |
| Contender | S | MR | |
| Kibuu | R | R | |
| Manoa Wonder | R | R | |
| Red Haricot | R | R | |
| Rono | R | R | |
| Saginaw | R | R | |
| 2.2.3.V | R | R | |
| **Lima bean** | | | |
| Nemagreen | R | | |
| Ventura N | MR | | |
| Westan | HR | | |
| **Pea** | | | |
| Wando | HR | MR | |
| **Edible soybean** | | | |
| Kahala | R | | |
| Kailua | R | | |
| **Muskmelon** | | | |
| Edisto | | RH | |
| Honey Rock | | R | |
| Perlita | | R | |
| **Watermelon** | | | |
| Dixie Queen | | R | |
| **Okra** | | | |
| Clemson spineless | | | MR |
| **Eggplant** | | | |
| Black Beauty | MR or S, HR or S | | |
| Vijaya | MR | | |
| Banaras Giant | MR | | |
| Pusa Purple V | T | | |
| **Pepper** | | | |
| All big | MR | | |
| Black indica | R | | |
| California Wonder | | R | |
| Early Cal. Wonder | S | MR | S |
| Naharia | R | R | R |
| Pant Cl | R | | |
| **Tomato** | | | |
| Allround | R | | |
| Anahu | R | R | |
| Anahu R | R | R | |
| **Atkinson** | **R** | **R** | **R** |

TABLE 9. *Continued*

| Crop | *Meloidogyne* species | | |
|---|---|---|---|
| | *M. incognita* | *M. javanica* | *M. arenaria* |
| Auburn 76 | R | | |
| Beefeater | R | | |
| Beefmaster | R | | |
| Better Boy | R | | |
| Bicol | R | | |
| Big Seven | R | | |
| Big seven | R | | |
| Calmart | R | R | |
| Carmen | R | | |
| Catala | R | | |
| Cavalier | R | | |
| Chicogrande | R | | |
| Duchess | R | | |
| Eurocross | R | | |
| Extase | R | | |
| Florida | R | R | |
| Florida-Hawaii Cross | R | | |
| Gawaher (Giza-1) | R | R | |
| Gilestar | R | | |
| Hawaii-55 | R | | |
| Hawaii-7746 | R | | |
| Hawaii-7747 | R | | |
| Hawaiian Cross | R | R | |
| Healani | R | R | |
| H.-7741 | R | | |
| Hope 1 | R | | |
| Hope 2 | R | | |
| Ife-1 | R | | |
| Illinois T-19 | R | | |
| Jackpot | R | | |
| Kalohi | R | R | |
| Kewalo | R | | |
| Kewalo-C | R | R | |
| KNVC | R | | |
| Kolea | R | | |
| Komea-C | R | R | |
| Kyoryoku Goko | R | | |
| Leader | | R | |
| Linda | R | | |
| Manalucie K | R | R | R |
| Marmar | | R | |
| Marsol | R | R | R |
| Martarum | R | R | |
| Meltino | R | | |
| Monita | R | | |
| Montfavet | T | | |
| Motabo | R | R | R |
| Nemacross | R | | |
| Nemared | R | R | |
| Nematex | R | R | R |
| NVFC | R | | |
| NFVR | R | | |

TABLE 9. *Continued*

| Crop | *Meloidogyne* species | | |
| --- | --- | --- | --- |
| | *M. incognita* | *M. javanica* | *M. arenaria* |
| Patriot | HR | HR | |
| Pearson VFN | R | R | |
| Pelican | R | R | |
| Peto 662 VFN | R | | |
| Piernita | R | | |
| Piersol | R | R | R |
| Pinta | R | | |
| Ponderoda | MR | | |
| President | R | | |
| Puunui | R | | |
| Red glow | R | | |
| Red Supreme | R | | |
| Rich Reward | R | | |
| Rossol | R | R | R |
| Royal Flush | R | | |
| Super Fantastic | R | | |
| Valerie | R | | |
| VFN 8 | R | R | R |
| 70T 82 | | R | |
| **Sweet potato** | | | |
| Arcadian | | | R |
| Carver | MR | | |
| Centennial | | | R |
| Drivi Drivi | S | MR | S |
| Dliula | MR | HR | S |
| Gold Rush | | | R |
| Jasper | R | | |
| Jewel | R | | |
| Navuso Local | MR | MR | S |
| N.C. Porto Rico | S | R | R |
| Porto Rico | S | R | R |
| Samoa Pink | MR | HR | S |
| Whitestar | R | | |

HR = highly resistant; MR = moderately resistant; R = resistant; T = tolerant; S = susceptible.
Sasser & Kirby, 1979; Sumeghy, 1979; Nandawa *et al.*, 1980; Bridge, 1983; Ogbuji & Okafor, 1984; Peter *et al.*, 1984; Roberts & Thomason, 1986

Dropkin (1969) showed that at 28°C the resistant cultivar Nematex was highly resistant to *M. incognita*, whereas at 32°C it was susceptible. In Senegal as well as in India a breakdown in resistance due to high soil temperatures has been observed (Sikora *et al.*, 1973*b*; Berthou *et al.*, 1989). In areas with extreme temperatures, cultural practices such as appropriate watering and mulching, may reduce soil temperature to counteract and prevent loss of resistance. However, plastic mulches used for fumigation and solarization may elevate soil temperature above 28°C if planting is made directly through the plastic tarp (R. Dunn, pers. comm.). The root-knot – *F. oxysporum* wilt complex can be controlled by growing cultivars resistant to either the fungus or the nematode or both. The root-knot – *Rhizoctonia solani* root-rot complex, which is common in the tropics and responsible for severe losses, can only be suppressed by controlling *Meloidogyne*, because of the lack of resistance to the fungus.

**Chemical**

Nematicides used in control of root-knot nematodes are either fumigants which are usually liquids and enter the soil water solution from a gas phase, or non-fumigants, granular or liquid compounds which are water soluble. In most cases the fumigants are broad spectrum contact nematicides effective against juveniles and eggs as well as fungal pathogens and weeds. Non-fumigant nematicides have either contact and/or systemic activity. In most cases the mechanism of action is associated with suppression of nematode mobility during the period when adequate concentrations are in the soil solution. The non-fumigant nematicides are not effective against the eggs of nematodes and in most cases do not kill the juveniles at the concentrations now being recommended for use. They give the plant a "head start" by delaying nematode penetration during the highly sensitive seedling or post-transplant stage of plant development.

Fumigant nematicides are generally more effective in controlling root-knot nematodes and in increasing crop yield than are non-fumigant nematicides, because fumigant nematicides have a broader spectrum of activity, controlling soil insects, fungal diseases and weeds in addition to other plant parasitic nematodes. This broad spectrum of activity also decreases the need for additional pesticide inputs and field work, reducing overhead costs associated with crop production. Most of the fumigant nematicides listed in Appendix A have been shown to be highly effective in control programmes designed to reduce losses due to *Meloidogyne* in vegetables (Lamberti, 1979*b*; Johnson, 1985). They are extensively used for nematode control in large scale production systems. Many vegetables grown on a large scale basis in infested areas, can only be produced economically together with fumigant application (Radewald *et al.*, 1987). In some growing areas fumigants are applied under plastic mulch and the vegetables are planted through the mulch. In these areas, soil temperatures may be too high for effective use of resistant cultivars.

The majority of small farmers, especially those living at the subsistence level, cannot use fumigants because of a lack of capital for equipment and nematicides. Although a number of fumigant nematicides have been removed from the market because of detection in groundwater and/or other negative side effects on the environment, some fumigants are still in widespread use and are effective control tools. When used as directed they will give excellent nematode control and increase yield significantly. Because registration requirements and efficacy vary with country and crop, no attempt will be made here to list those still being used for the control of root-knot nematodes in vegetables.

The granular or liquid formulations of contact and/or systemic nematicides are more suitable for use on small farms, provided the growers are made aware of proper handling and application techniques as well as time of application. They are often not as effective as fumigants in increasing yields because they usually do not have broad spectrum activity. It must be realized that climatic conditions in many tropical countries do not favour high yields. A yield of 40 t/ha of canning tomatoes in northern Senegal is considered exceptionally good. Under subtropical conditions, for example in Italy and California, yields of 65 t/ha can be attained. When good growing conditions exist, however, yields in excess of 100 t/ha are possible. High yield, increased costs for nematicides, and competition with tomato concentrate from other countries leaves a rather small margin for the use of nematicides in many tropical countries.

Nematicides can be applied effectively by surface and drip irrigation (Overman 1974; Johnson, 1985; IFAS, 1989). The fumigant, metam-sodium, was effective in controlling root-knot and soil fungi when applied through drip irrigation (Roberts, 1988). Local experimentation is, however, needed to determine optimum dosage and time of application. Alternative approaches such as dip treatment or treatment of transplants in nurseries (Ahuja, 1978; Mateille & Netscher, 1985) and seed coating (Schiffers *et al.*, 1985) have been suggested.

**Biological**

Progress has been made regarding the incorporation of nematode parasites or antagonists into the soil for control of root-knot nematodes on vegetables (Kerry, 1987). Too little is known, however, about the factors affecting survival and infection once they are introduced into the soil. A strain of

*Arthrobotrys irregularis* grown on rye grain reduced root-knot galling and increased tomato yields when it was introduced in the soil at 140 g/m$^2$ (Cayrol & Frankowski, 1979; Cayrol, 1983). The large amounts of inoculum (1.4 t/ha) and the need for alkaline soils favourable to fungal growth probably limit this approach to glasshouse production systems.

*Pasteuria penetrans* is an obligate parasite of some plant parasitic nematodes including *Meloidogyne* (Birchfield & Antonpoulos, 1976) but cannot be produced, at the present time, in large numbers *in vitro*. *P. penetrans* is a very common parasite of *Meloidogyne* and is often observed attached to juveniles. The spore form can resist both drought and exposure to non-fumigant nematicides (Mankau & Prasad, 1972). Stirling and Wachtel (1980) were able to produce large numbers of spores by inoculating tomato with infected *Meloidogyne* juveniles. Dried tomato roots were then milled into a powder containing *Pasteuria* spores. This method might be adapted to produce inoculum of the parasite for local use on small farms. There is also a possibility of increasing the parasite in root-knot nematode infested fields by growing tolerant or moderately resistant crops.

The colonization of plants with endomycorrhizal fungi apart from providing plants with nutrients has been reported to have a depressive effect on root-knot nematodes. According to Sikora (1978) penetration and development of *M. incognita* in tomato was significantly reduced by *Glomus mosseae* in glasshouse studies. Attempts to find highly active symbiont-crop combinations that are effective in suppressing the nematode in the field are needed.

Conflicting reports exist on the efficacy of the fungal egg parasites for control of root-knot nematodes. The high amounts of organic matter needed for fungal establishment and spread in the soil environment, at the present time, limit practical application in most large scale production systems. The alternative use of cereal grain for fungal inoculum production prevents any application in subsistence agriculture.

A promising group of microorganisms that may be effective in reducing nematode damage are the plant health promoting rhizobacteria (Sikora, 1988; Oostendorp & Sikora, 1989) which could be applied as seed dressings or as a drench treatment for transplants. Application through drip-irrigation systems may prove to be an effective method of post-planting application (Zavaleta-Meija & Van Gundy, 1982).

## Summary of control measures

The principles and main components of effective control programmes and integrated pest control in vegetables as well as other crops have been discussed in this chapter and elsewhere in detail (Taylor & Sasser, 1978; Johnson & Fassuliotis, 1984; IFAS, 1989). The main aspects we consider important are listed below.

1) Prevention of infestations by controlling nematode spread must be top priority.

2) Only root-knot nematode free transplants should be used as planting material.

3) In view of the high multiplication rate of root-knot nematodes and difficulty in determining occurrence of low population densities, previously infested land should always be considered infested, even if the presence of *Meloidogyne* can not be demonstrated by soil analysis.

4) Efforts should be made when planning vegetable crop rotations to select and develop pest management approaches that prevent the build-up of high nematode densities.

5) Integrated pest management should combine rotations with non-host crops, resistant, tolerant and susceptible cultivars as well as judicious use of nematicides, based on proper soil sampling estimations of damage threshold levels.

6) An integrated approach will control economically important nematodes, reduce pesticide costs and prevent unnecessary environmental contamination.

7) Proper selection of a combination of resistant, moderately resistant and tolerant vegetable crops can increase the number of vegetables in a short rotation cropping system.

8) Resistant cultivars should be used in rotation with susceptible cultivars and with other control techniques to prevent the development of resistant breaking pathotypes.

9) All non-host crops and resistant cultivars should be challenged by local populations to determine true host status.

10) In regions where irrigated rice (or flooding) constitute one of the components of the farming system, inundation can give good control.

11) Destruction of roots after harvest, soil drying and cultivation as well as "clean" fallow will significantly reduce population densities.

12) Time of planting may be effective in the cooler upland tropics and in the winter season in the subtropics.

13) Organic amendments or the use of non-host cover crops and green manures can reduce nematode densities.

### Methods of diagnosis

The scattered or clustered distribution of most nematodes in the field makes reliable estimation of occurrence and/or population density extremely difficult. Due to the presence of egg masses, the spatial distribution of root-knot is very heterogeneous. Techniques have been developed for extraction that are based on the fact that the egg masses remain intact in the soil either free or attached to host roots or root fragments (Dickson & Strubel, 1965; Byrd *et al.*, 1972; Gooris & d'Herde, 1972). After separating the organic matter from the soil using sieving or elutriation techniques, eggs are liberated from egg masses either chemically (Byrd *et al.*, 1972) or mechanically (Gooris & d'Herde, 1972). Demeure and Netscher (1973) observed egg masses present in the coarse sandy soil fraction and suggested incubation of this fraction also.

Even if the methods of extraction are sufficiently reliable, it is still virtually impossible to determine whether or not land is free from root-knot, even when the results of soil analyses are negative. The majority of the methods used will not always detect egg masses in fields with low to moderate root-knot infestation levels. Accuracy can be increased by increasing the volume of the soil sample taken from the field as well as the number of cores taken per unit area and by extracting greater quantities of soil than the usual 100–250 $cm^3$ recommended. The accuracy of the extraction method used in determining population densities is extremely important in estimating threshold levels. Barker (1985*a*, *b*) discusses sampling and extraction techniques and lists their relative efficiency.

Another problem, related to determination of population densities in sandy soils, is the migration of juveniles over substantial distances to the plant (Prot & Netscher, 1978).

Bioassay techniques, in which susceptible plants growing in the field are uprooted and examined for the presence of galls after a period of three to six weeks, constitute a means to evaluate the infestation levels of soils with greater accuracy than soil analysis (McSorley & Parrado, 1983).

An accurate evaluation of root-knot infestations in a field can be obtained at the end of the vegetative cycle of a susceptible crop. Plants are systematically uprooted and scored for severity of root galling, thereby giving an accurate estimation of the severity and the distribution of *Meloidogyne* in a field. This is the only method available for workers lacking basic nematological extraction equipment. A number of different root-knot indices have been proposed (Barker, 1985*b*). The root-gall index proposed by Zeck (1971) is typical of those often used in the field (Fig. 5). Yield losses and root-gall indices have a linear relationship which vary in degree as to crop and environmental conditions (Barker *et al.*, 1981). A nomograph of root-knot galling indices is shown in Fig. 6.

## *Rotylenchulus*

After *Meloidogyne*, the reniform nematode, *Rotylenchulus reniformis*, is the most important nematode affecting vegetables. The nematode attacks over 100 plant species including many vegetable crops and is a limiting factor in vegetable production, but is often neglected or overlooked where it occurs concomitantly with *Meloidogyne*. The nematode has been detected in more than 36 countries

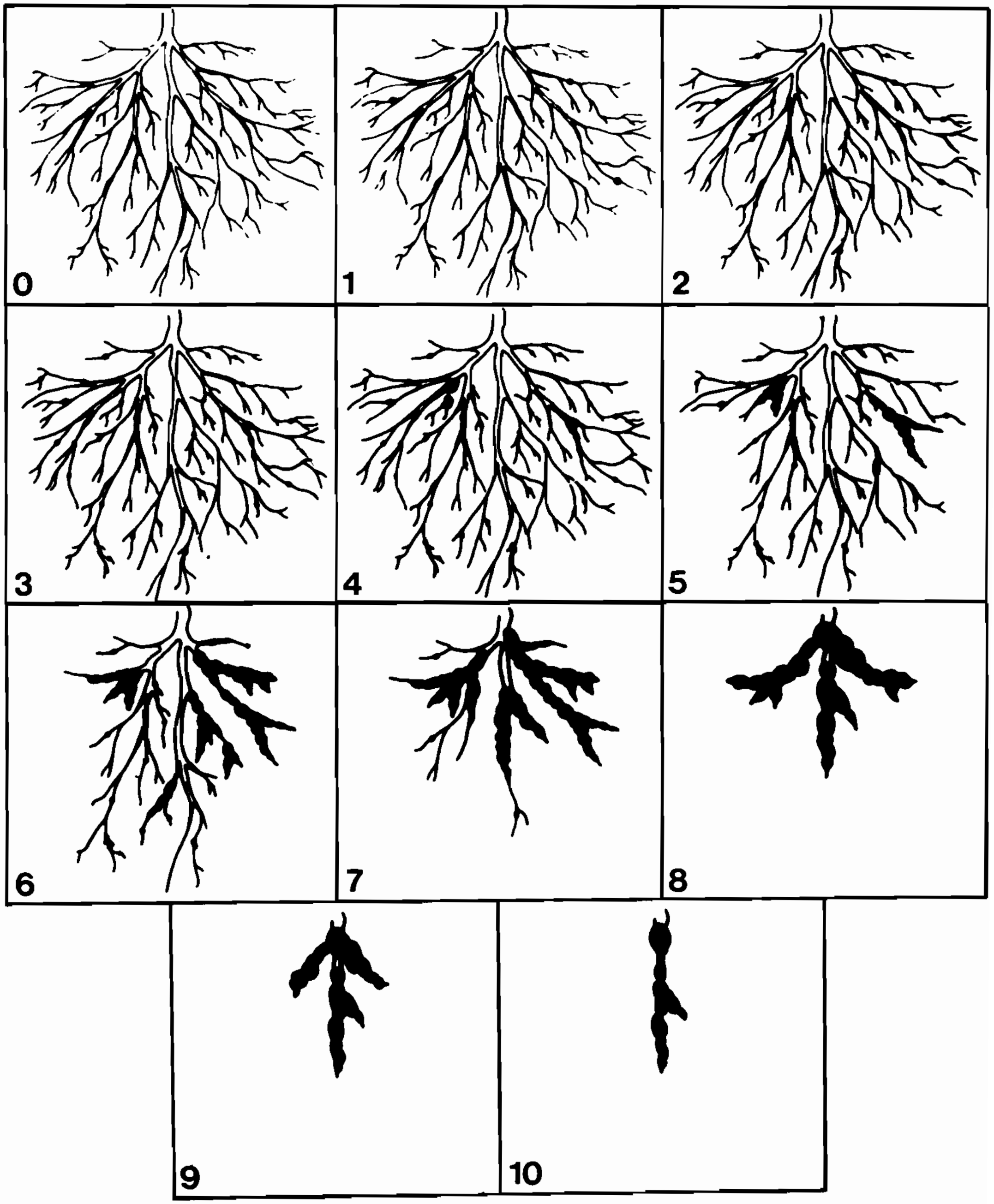


Fig. 5. Rating scheme for evaluation of root-knot infestation (Zeck, 1971).

Explanation of ratings (modified)

0 = Complete and healthy root system, no infestation
1 = Very few small galls can only be detected upon close examination
2 = Small galls as in "1" but more numerous and easy to detect
3 = Numerous small galls, some grown together, function of roots not seriously affected
4 = Numerous small galls, some big galls, majority of roots still functioning
5 = 25% of root system severely galled and not functioning
6 = 50% of root system severely galled and not functioning
7 = 75% of root system severely galled and lost for production
8 = No healthy roots, nourishment of plant interrupted, plant still green
9 = The completely galled root system is rotting, plant is dying
10 = Plant and roots are dead

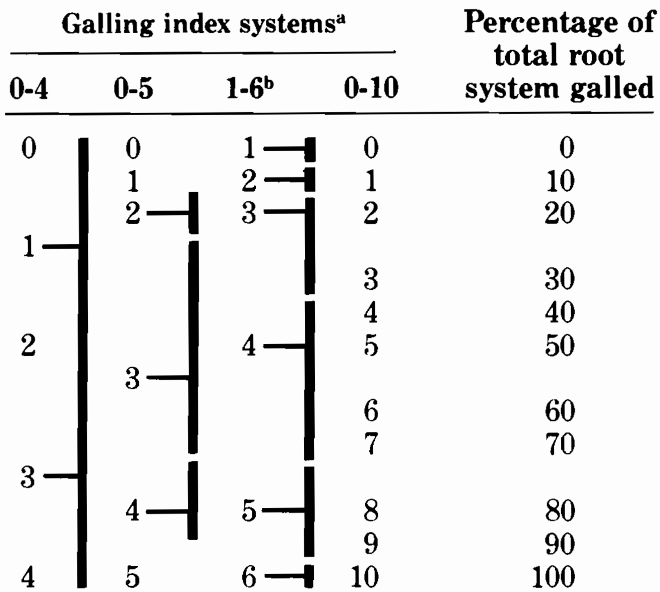


Fig. 6. Nomograph of root-knot galling indices for *Meloidogyne* spp. (Barker, 1978).

(Heald & Thames, 1982). It has been recorded in Hawaii where it was first described (Linford & Oliviera, 1940) and in the southern U.S.A., Mexico, the Caribbean, South America, the Middle East, most of Africa, India, South East Asia and the Pacific.

## Symptoms of damage

Above-ground symptoms include stunting and leaf curling (Singh & Khera, 1979). Root necrosis and cortical necrosis has been observed following infection. Cantaloupe growing in heavily infested soil was badly stunted and yields were greatly reduced (Heald, 1975). Leaf chlorosis can be produced (Bridge 1983). Females and their adhering egg masses can be easily observed under the dissecting microscope (Fig. 7). Soil adhering to the gelatinous egg masses often give them a dark appearance aiding in detection.

## Biology

Immature females penetrate the root and become sedentary. Galls are not produced. The life cycle is completed on okra in 24 to 29 days (Sivakumar & Seshadri, 1971). The existence of amphimictic and parthenogenetic races of *R. reniformis* has been demonstrated by Hirschmann and Triantaphyllou (1964).

The reniform nematode can survive in soil in the absence of hosts for seven months in moist soil and for six months in dry soil. After four months, 84% of the nematodes were still alive (Sivakumar & Seshadri, 1979). Stoyanov (1971) reported that *R. reniformis* was able to survive 29 months in the absence of host plants.

Intensity of Brinjal Mosaic Virus and Okra Yellow Vein Mosaic were promoted on plants parasitized by *R. reniformis* (Naqvi & Alam, 1975; Sivakumar & Merrzainudeen, 1973). Charcoal rot caused by *Macrophomena phaseolina* on cantaloupe was significantly higher when the roots were infested with the reniform nematode (Carter, 1980).

Fig. 7. Females of *Rotylenchulus reniformis* on roots of tomato.

## Economic importance

Tomato yield was reduced following inoculation with 100 juveniles/plant (Singh & Khera, 1979). Snake gourd (*Trichosanthus dioica*) plants inoculated with 1000 nematodes were stunted and had smaller leaves than controls and the roots were brown and showed cortical necrosis (Nath *et al.*, 1979). The nematode has been shown to damage a number of vegetable and melon crops. Yield increases on okra, tomato, lettuce and squash of 19, 15, 57 and 69% were obtained with granular nematicides, respectively (Heald, 1978).

## Control

### Cultural

A two year rotation of cotton with sorghum was as effective as fumigation in reducing the nematode (Thames & Heald, 1974). Rotations which include soybeans resistant to the nematode also reduce densities (Gilman *et al.*, 1978). Nematode densities have also been reduced in rotations with maize, sugarcane and Pangolagrass (Heald & Thames, 1982). A number of other crops are also known to be resistant to the nematode including finger millet, peanut, chillies, sugarcane, and other grasses (Armstrong & Jensen, 1978; Bridge, 1983).

Soil amendments such as animal manure and cotton seed cakes have been used with success to control the reniform nematode (Badra *et al.*, 1979). In glasshouse experiments, peanut was a poor host of two populations of *R. reniformis* (Germani, 1978). Short periods of flooding of tomato in pot experiments reduced populations of the reniform nematode (Castillo *et al.*, 1976*a*). The nematode was also eradicated from infested soil following treatment with 50°C hot water for 5 minutes (Heald & Wayland, 1975).

#### Resistance

There are only a few reports concerning resistance in vegetables to *R. reniformis*. In Egypt, the tomato cv VFN 8 was shown to be moderately resistant to the reniform nematode (Oteifa & Osman, 1974). Balsubramanian and Ramakrishnan (1983) found that the tomato cvs Kalyanpur Sel 1 and Sel 2 were immune to the reniform nematode while lines EC 118272 and EC 118276 were resistant. Sitaramaiah and Sikora (1982) were able to demonstrate that the penetration and reproduction of *R. reniformis* on tomato and cucumber was significantly reduced in the presence of the endomycorrhizal fungus *Glomus fasciculatum*.

#### Chemical

A wide range of fumigant and non-fumigant nematicides are effective in controlling *R. reniformis* (Birchfield & Martin, 1976; Heald & Thames, 1982). Rich and Bird (1973) were able to reduce nematode penetration by a single foliar application of oxamyl. However, McSorley (1980) could not demonstrate effective nematode control following six weekly sprays with oxamyl on snapbean.

## *Nacobbus*

Little is known about the distribution and importance of the false root-knot nematode, *Nacobbus*, in tropical and subtropical agriculture. The two species *N. aberrans* and *N. dorsalis* have been detected in North, Central and South America. The nematode has also been detected in glasshouses in Europe. *N. aberrans* has been reported from cabbage, turnip, sweet pepper, chilli pepper, squash gourd, lettuce, tomato, *Cucumis sativus*, and *Daucus carota*.

### Symptoms of damage

The nematode produces galls similar in size to *Meloidogyne hapla*. The galls are characteristically produced in strands or a bead-like fashion along the root (Plate 5G). The penetration of juveniles and immature females into the root can cause root necrosis (Bridge, 1983). Stunting, poor growth and chlorosis are typical above-ground symptoms associated with the endoparasitic nematode. Yield reduction can be significant (Schuster *et al.*, 1965). *N. aberrans* may be an important pathogen in Mexico (Marbán, pers. comm. cited in Johnson & Fassuliotis, 1984) and, according to Román (1978), causes yield loss on pepper and tomato.

The galls of *Nacobbus* spp. are often overlooked or mistaken for those produced by root-knot nematodes, *Meloidogyne* species, because of the similarity in gall form. Galls only occur in the presence of the adult females which retain their eggs, in contrast to root-knot nematode females.

### Biology

The females vary greatly in shape and will produce an egg sac that extends to the outside of the root (Clark, 1967; Johnson & Fassuliotis, 1984). According to Prasad and Webster (1967) the nematode completes a life cycle in 36 days at 25°C and in 43 days at 20°C or 30°C. There are indications that races may exist.

### Control

*Nacobbus* can be controlled with both fumigant and non-fumigant nematicides. However, crop rotation with non-host crops is effective and more economical. Gomes Tovar (1973) reported that *Erodium cicutariuim* and *Brassica campestris* were not susceptible and hybrids of *Solanum andigenum* were resistant to the nematode. Bridge (1983) listed melon, squash, watermelon, peanut, soybean, lucerne, oats, barley, rye, sorghum, wheat, maize, onion, okra, cotton, sunflower, *Phaseolus* spp., sesame, winged bean, and rice as non-host crops that could be used in rotation. Because of the possible existence of races, re-testing each crop with local populations was suggested as a necessary precaution.

### Methods of diagnosis

The nematode can be easily detected by examining the root system during the growing season. Attention should be given to the size of the galls and their orientation along the root system. If they are small and form bead-like strands along the root, they should be examined for *Nacobbus* females either by teasing out the females or by staining (Chapter 2).

## *Globodera*

*G. rostochiensis*

The potato cyst nematode, *G. rostochiensis* will infect and damage tomato and eggplant. The potato cyst nematode has been found infesting tomato in North, Central and South America (Bridge, 1983). The nematode is also present in Pakistan, India, Mediterranean basin, South Africa, and the Philippines. Symptoms include chlorosis, stunting and general poor growth. Detailed studies on yield losses and control, however, have not been reported for either crop.

## *Heterodera*

*Heterodera schachtii*

This nematode has been found in Mexico (Sosa-Moss, 1986), U.S.A. and Canada (Miller, 1986), Iraq (Stephan, 1986), Libya (Edongali, 1986), Senegal (Luc & Netscher, 1974) and Gambia (Bridge & Manser, 1980). The nematode causes significant losses on cruciferous crops. Yield reductions of 50 percent or more have been measured on Brussels sprouts, cabbage, broccoli and cauliflower when population densities are high (Miller, 1986). The nematode also attacks kale, Chinese cabbage, red beet, rutabagas, spinach and turnip (Anon, 1987).

The sugar beet cyst nematode is often found together with the cabbage cyst nematode, *H. cruciferae*. Proper identification therefore, is necessary in selecting control measures. Approximately 2–4 eggs/g of soil is used as a rough guideline for damage threshold levels in the Imperial Valley in California, U.S.A. (Anon., 1987). The nematode is controlled by long rotations or with fumigant nematicides (Lear *et al.*, 1966; Anon., 1987). Winter season crops and crops grown at higher altitudes are not damaged as severely.

*Heterodera cruciferae*

The cabbage cyst nematode, *H. cruciferae*, has been detected in California (Siddiqui *et al.*, 1973) and Libya (Edongali & Dabaj, 1982). The nematode causes significant damage to cruciferous crops in California, where it often occurs together in the same fields with *H. schachtii* (Anon., 1987). Although the nematode has many common hosts with the sugar beet cyst nematode, its host range is somewhat smaller (Johnson & Fassuliotis, 1984). Seedlings infested with the nematode are stunted and exhibit interveinal chlorosis or leaf reddening (McCann, 1981). Cauliflower curd quality is reduced at 75 eggs/g soil (Sykes & Winfield, 1966) and cabbage are severely stunted at 20 cysts/100 g of soil (McCann, 1981). Control is usually accomplished by crop rotation with non-host plants or by pre-plant fumigation (Anon., 1987).

## *Cactodera*

*Cactodera amaranthi*

This cyst nematode has been found attacking spinach in central Mexico (Sosa-Moss, 1986) on *Amaranthus viridis* in Cuba (Stoyanov, 1972) and was detected in Florida (G. Rau, unpub. cited in Luc, 1986). The host range of the nematode is limited to *A. viridis, A. Spinosus*, and *A. retroflexus* (Luc, 1986). Golden and Raski (1977) discussed the biology of the nematode.

### Methods of diagnosis

All these endosedentary nematodes produce cysts on the surface of the root system at specific times in their life cycle. The presence of cyst nematodes can be determined by carefully removing growing plants at different intervals during the growing season and examination of the roots with a hand lens. The detection of cysts imbedded in the root tissue is a clear sign of pathogenicity. Cysts can also be extracted from the soil using the techniques described in Chapter 2. The time of cyst appearance on the root surface is determined mainly by temperature. The cysts will also vary in colour from white through beige to dark brown. Cyst production and detection will also vary depending on the number of life cycles produced e.g. the potato cyst nematode only has one generation per year, whereas the cabbage and sugar beet cyst nematodes have many generations in a cropping season.

## *Ditylenchus*

The normal race of the stem nematode, *D. dipsaci*, can cause severe damage to species of *Allium*, especially onion and garlic, in the winter season and in the cooler upland tropical and subtropical regions. The nematode is a problem on lucerne in the subtropical regions of the U.S.A., but does not seem to affect other crops in the region. *D. dipsaci* is known to attack *Beta vulgaris* (M. Ammati, pers. comm.) and *Vicia faba* during the cool rainy winter growing season in the subtropical regions of North Africa (Saxena *et al.*, 1987). There are also reports from Europe that the nematode can attack carrot, celery, tomato and cucumber (Decker, 1969). Vegetables growing in the warm tropics or during the summer season in the subtropics are not attacked. The nematode has been reported attacking species of *Allium* in a number of subtropical and tropical countries: Mexico, Venezuela, Ecuador, Peru, Colombia, Dominican Republic, and various countries in the Mediterranean, Asia and the Pacific (Bridge & Hunt, 1986).

### Symptoms of damage

Penetration of onion leaves by this endoparasite causes leaf deformation and leaf swellings or blister-like areas on the surface (Fig. 8). The leaves grow in a disorderly fashion and often hang as if wilted. As the season progresses they become chlorotic (Decker, 1969). Young plants can be killed when high infestations exist. Infected onions become swollen (bloat) and the bulbs may rot during storage (Bridge & Hunt, 1986). The inner scales of the bulb are usually more severely attacked than the outer scales. As the season advances the bulbs become soft and when cut open show browning of the scales in concentric circles. Conversely, *D. dipsaci* on garlic does not induce deformation or swellings, but causes leaf yellowing and death (Decker, 1969).

### Biology

The fourth stage juveniles penetrate the stem and leaf tissue through the stomata. Egg laying begins at temperatures of 1–5°C with the optimum at 13–18°C. *D. dipsaci* completes one generation in 19–23 days at 15°C. Nematode activity stops at 36°C. The nematode prefers the cool moist climatic conditions existing in the upland tropics and wet winter seasons in the subtropics. *D. dipsaci* can parasitize plants on both heavy and light soils, although a higher incidence of infestation seems to occur on heavy soils.

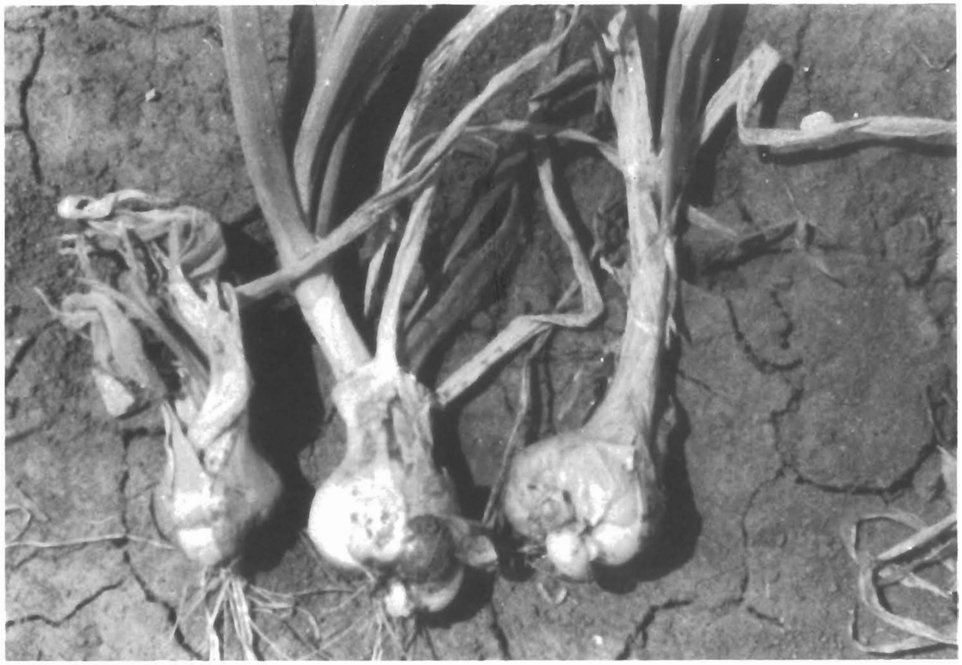

Fig. 8. Deformed onions in a field infested with *Ditylenchus dipsaci* (Photo: D. Taylor & D. Edwards).

## Races

Although many races of *D. dipsaci* have been described (Sturhan, 1969) nothing is known about the race spectrum in those countries in the tropics where the nematode has been detected. It should be noted that onion is attacked by a number of known races, which could make determination of threshold levels difficult. The host range of many races has not been adequately determined.

## Survival and means of dissemination

The nematode can survive in the soil without a host plant for more than one year and the fourth juvenile stage can survive in anabiosis for many years. The nematode can be disseminated by transportation in infested bulbs, plant residue and adhering soil. Seed-borne infections also are responsible for long distance dissemination in onion, broad bean, beet and lucerne. Other hosts and weeds are responsible for maintaining infestations between onion and garlic. Bulbs harbouring light infestations will survive storage, and increase the level of infestation and losses in the following season when used as planting material.

## Economic threshold level

According to Seinhorst (1956) the economic threshold level for onion is reached when 10 or more nematodes are detected in 400 $cm^3$ of soil.

## Control

Rotations with non-host crops for 3 years can be an effective means of control once the host range for a specific population or race is determined. Resistant cultivars of onion and garlic have not been developed for the commercial market (Bergquist & Riedel, 1972).

The nematode can be controlled in onion bulbs by dipping in hot water at 44–45°C for 3 h (Bridge & Hunt, 1986). Temperature and time ratios are important for control and may vary with crop and cultivar. Formaldehyde was used until recently for control in onion bulbs but has been removed from use for environmental and toxicological reasons.

Fumigant nematicides are effective in reducing nematode infestation levels in the field.The stem nematode also can be controlled in infested onion and garlic seed by treatment with methyl bromide (Hague, 1968; Infante & Sosa-Moss, 1971).

The nematode also attacks many weeds (Augustin & Sikora, 1989) present in field crops and these must be examined for host status, since the high nematode densities can be maintained on these hosts.

### Methods of diagnosis

The presence of *D. dipsaci* can be easily determined by submerging small amounts of seed, stem, leaf or bulb tissue in water overnight to allow the active stages to escape (See Chapter 2). Detection in soil is more difficult because of the low population levels normally present.

## *Pratylenchus* and *Radopholus*

Ten species of the lesion nematode, *Pratylenchus* have been found in the rhizosphere or roots of vegetable crops: *P. brachyurus, P. barkati, P. dasi, P. coffeae, P. delattrei, P. loosi, P. singhi, P. thornei* and *P. zeae*. All species of *Pratylenchus* should be considered of potential importance when encountered in root tissue. Lesion nematodes are important parasites of many crops and are known to form disease complexes with many different soil-borne root rotting fungi, thereby increasing root damage. *Pratylenchus brachyurus* and *P. zeae* have been detected in great numbers in the roots of vegetables. Little is known, however, about their impact on vegetable production. The overriding importance of *Meloidogyne* in vegetable production, and the resulting lack of research on other plant parasitic nematode species, has limited our knowledge as to the exact importance of lesion nematodes in vegetable production.

The closely related burrowing nematode, *Radopholus*, has been detected in a number of vegetable crops, including: kale, radish, tomato, eggplant, okra, carrot, onion, African spinach, watermelon, melon, calabash, pumpkin, and squash. Crop loss studies have not been conducted.

### Control

Lesion nematodes can be controlled with fumigant and non-fumigant nematicides, although this is probably not practical on an economic basis. Many species of *Pratylenchus* have wide host ranges making the development of rotations difficult. Plants having been reported to be resistant to the various species of *Pratylenchus* have been compiled by Armstrong and Jensen (1978).

### Methods of diagnosis

Lesion nematodes produce small dark necrotic lesions on the root surface on many crops, which is the result of interrelationships with soil-borne fungal pathogens. The presence of lesions is a good indication that lesion nematodes are causing damage. The presence of the nematode should then be determined by extraction from the root tissue (see Chapter 2).

## *Belonolaimus*

The sting nematodes, *B. gracilis, B. longicaudatus, B. euthychilus, B. maritimus* and *B. nortoni*, are common plant parasitic nematodes in the subtropical regions of the lower Coastal Plain of the southeastern U.S.A. from Virginia to Florida and along the Gulf Coast into Texas. Note that the genus *Ibipora* found in Brazil is considered to be identical to *Belonolaimus*. Physiological races of *B. longicaudatus* have been detected (Abu-Gharbieh & Perry, 1970).

## Symptoms

Damaged plants are stunted, chlorotic and wilt prematurely with severe damage leading to plant death (Fig. 9). Nematode feeding induces stubby roots and necrotic lesions which can expand to girdle the root (Fig. 10). Perry and Rhoades (1982*a*) stated that "infested areas consist of spots that vary in size and shape, but the boundary between diseased and healthy plants usually is fairly well defined" (Fig. 11). Although disease complex associations have been detected on other hosts, they have not been observed on vegetable crops.

## Biology

The nematodes are obligate parasites that cause damage to vegetables by feeding ectoparasitically on or near the root tip. The ectoparasite completes one generation within 28 days at an optimum temperature of 28–30°C.

## Survival and means of dissemination

There is no definite survival stage in the life cycle of the nematode with all stages of development present in the rhizosphere. The nematode may have been spread to many warmer regions of the world on golf course bermudagrass sod (Perry & Rhoades, 1982*a*), but because of its dependency on extreme sandy soil (Thames, 1959; Brodie & Quattlebaum, 1970) establishment has probably only occurred in a limited number of instances. The nematode seems to be most damaging on irrigated light soils, because of the nematodes requirement of uniform soil moisture, sandy soil and temperatures of 25–30°C for survival and multiplication.

## Other hosts

The nematode causes severe damage to most agricultural crops including many wild plants and most vegetable crops (Graham & Holdeman, 1953; Good & Thornton 1956; Robbins & Barker, 1973; Williams, 1974). Forage grasses and turf are also damaged by the nematode, whereas, tobacco and watermelon are considered non-hosts. Because of the presence of races, variation in host range between populations should be expected.

Fig. 9. Celery growth in a *Belonolaimus longicaudatus* infested field in Florida (left) furadan 2 pd/acre (right) check (Photo: H. Rhoades).

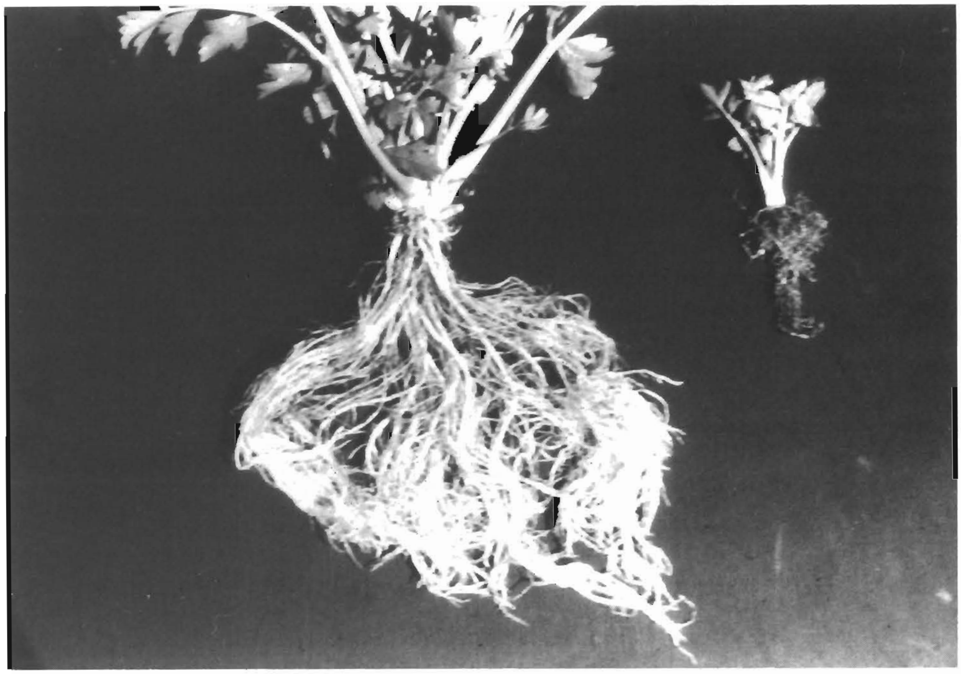

Fig. 10. Root damage and poor growth caused by *Belonolaimus longicaudatus* on celery (right) in Florida (Photo: H. Rhoades).

Fig. 11. Stunted celery plants in a field infested with *Belonolaimus longicaudatus* in Florida (Photo: H. Rhoades).

### Economic importance

*B. longicaudatus* is the only species that has been shown to cause serious crop loss to vegetables. The species has been considered responsible for greater yield loss to vegetables in Florida than any other single plant pest of any type (Perry & Rhoades, 1982*a*). The nematode is highly pathogenic and even a single specimen in a soil sample can indicate that severe damage to a vegetable crop can occur. The sting nematode has been shown to damage a wide range of crops including okra, onion, celery, beetroot, cabbage, pepper, cucumber, pumpkin and carrot.

### Control

#### Cultural

The addition of organic amendments that alter soil conditions has been shown to suppress the nematode, because of its extreme sensitivity to changes in soil environmental conditions (Heald & Burton, 1968). Rotations designed to reduce population densities are difficult to select because of the wide host range, lack of resistant cultivars and possible presence of races in the species. A number of non-hosts are listed by Armstrong and Jensen (1978). Perry and Norden (1964) developed successful rotations using peanut, bahiagrass and maize, although only the latter is a non-host throughout the nematode's range. The nematode did not reproduce on *Crotalaria spectabilis* in glasshouse tests (Rhoades, 1964) and, in the field, a summer cover crop of hairy indigo prevented population increase (Rhoades, 1976*a*; Rhoades & Forbes, 1986). Fallowing and summer cover crops also reduced populations and increased yield (Rhoades, 1983). In field experiments, high populations developed on *Tagetes patula*, whereas, low build-up was detected on joint vetch, *Aeschynomene americana* (Rhoades, 1980).

#### Physical

In Florida some growers control the nematode by flooding the land for periods of about three months (IFAS, 1989). Soil drying can also be used to reduce nematode densities.

#### Chemical

Nematicides are effective and widely used to control this nematode (Williams, 1974; Perry & Rhoades, 1982*a*). Good control has been obtained with pre-plant fumigant and non-fumigant nematicide treatment of cabbage and onion (Rhoades, 1969, 1971) and with both granular and transplant water application of non-fumigant nematicides on cabbage (Rhoades, 1976*b*). Johnson and Dickson (1973) obtained improved results when the nematicides were applied at planting as compared to pre-plant or post-plant treatments.

### Methods of diagnosis

The nematode is an ectoparasite and can be easily extracted from the sandy soils with modified Baermann dishes or sieving and elutriation techniques (See Chapter 2).

## *Trichodorus* and *Paratrichodorus*

Species of stubby-root nematodes, *Trichodorus* and *Paratrichodorus*, have been found throughout the world associated with vegetable crops. *Paratrichodorus minor* is considered an important limiting factor on vegetables grown in light soils in the subtropical regions of the U.S.A. (Perry & Rhoades, 1982*b*). *P. minor* attacks a wide range of vegetable crops and most other cultivated crop plants (Rohde & Jenkins, 1957; Perry & Rhoades, 1982*b*). (*Paratrichodorus mirzai* and *T. viruliferus* are considered important on carrot and pepper, respectively. The stubby-root nematodes prefer sandy or sandy-loam soils, but can occur in high numbers in organic soils (Perry & Rhoades, 1982*b*). This is probably true for all species in the two genera.

The nematodes are ectoparasites feeding mainly on the root tip where damage suppresses elongation of the root and is responsible for the stubby-root symptoms associated with these nematodes. The amount of damage to the root system varies with vegetable crop attacked, but is characterized by reduced size and fewer shorter rootlets (Johnson & Fassuliotis, 1984). The roots become discoloured and necrotic as the season advances. Netscher (1970) reported that *P. minor* caused a 50% reduction in root weight of tomato.

Plant growth is retarded and the foliage on stunted plants may become chlorotic (Christie & Perry, 1951). Some vegetables wilt when exposed to moisture stress. The nematodes cause severe crop losses to a variety of vegetable crops including: onion, tomato, pepper, eggplant, beet, broccoli, Brussels sprouts, cabbage, cauliflower, Chinese cabbage, radishes, rutabagas, turnips, endive, lettuce and spinach (IFAS, 1989). This group of nematodes are also known virus vectors and in potato can be important both for direct damage and as a virus vector.

Control by crop rotation is difficult because of the wide host range of this nematode. *Crotalaria spectabilis* has been shown to be a non-host of the nematode and when used as a cover crop will reduce nematode densities (Rhoades, 1964). *Asparagus officinalis* var. *altilis* L. has also been shown to be resistant to attack which is induced by the production of a highly toxic glycoside (Rohde & Jenkins, 1958). Fumigant and non-fumigant nematicides are effective in reducing initial damage and in giving the vegetable crop a head-start on the nematode. However, it has been shown that nematode populations build-up quickly (Perry, 1953). Some of the carbamate and phosphate non-fumigant nematicides exhibit longer durations of control than the fumigants (Rhoades, 1967, 1968). Flooding for two weeks reduced populations significantly and the effect was improved by flooding followed by two weeks of drying (Overman, 1964).

## *Longidorus*, *Paralongidorus* and *Xiphinema*

These nematodes have been shown to be potential problems in local areas. They can cause severe damage especially on sandy soils and are probably often overlooked wherever root-knot nematode predominate.

*Longidorus africanus* caused damage to lettuce in the subtropical regions of southern California. Patchy growth and wilted seedlings were observed together with leaf margin chlorosis (Radewald *et al.*, 1969). Nematode feeding caused a reduction in elongation of the tap root and root tip swelling, typical of damage by a number of species of *Longidorus* and *Xiphinema* on other crops. *L. vineacola* was reported to cause damage to celery in Israel (Cohn & Auscher, 1971). Although viruliferous *Xiphinema americanum* have been found associated with watermelon, virus transmission does not seem to be a major problem in melon or vegetables (McGuire, 1982).

## Other Nematodes of Vegetables

Stunt nematodes, are often found associated with vegetables. Twenty-two species of *Tylenchorhynchus* (three formerly named *Telotylenchus* and two *Quinisulcius*) and four species of *Merlinius* have been found in the rhizosphere of vegetable crops. With the exception of *Tylenchorhynchus brassicae*, none of the other species have been shown to be of significant economic importance on vegetable crops. *T. mashoodi* has been considered to be of potential importance on tomato.

*Tylenchorhynchus brassicae* has been detected in India, the Sultanate of Oman (Waller & Bridge, 1978) and Egypt (Oteifa & Elsharkawi, 1965). The nematode is a serious problem on most cruciferous crops and, when high populations of this nematode occur, growth is negatively affected (Khan, 1969). The nematodes penetrate through the cortical region and are mainly confined in the outer layers of the cortex with their body lying parallel to the longitudinal axis of the roots and the anterior part of the body curved towards the conducting tissue. Occasionally the nematodes are situated in the stellar region with their entire body embedded in the stele. Of 22 vegetables inoculated with 1000 nematodes, cabbage and cauliflower were the most suitable hosts. Great differences in the response of cultivars to the stunt nematode exist. The most favourable temperature for reproduction

Fig. 12. Stubby-root injury to celery caused by *Dolichodorus heterocephalus* (Photo: H. Rhoades).

was 30°C and the most favourable soil moisture was 25–30%. In the absence of hosts, the nematode could survive up to 240 days in moist soil. When the nematode was associated with *Rhizoctonia solani*, the emergence of vegetable seedlings was strongly reduced (Khan & Saxena, 1969).

The awl nematode, *Dolichodorus heterocephalus*, can cause damage to vegetables, especially on wet, sandy soils. In Florida, the nematode causes severe damage to tomato and celery with losses on heavily infested soil often exceeding 50% (Tarjan *et al.*, 1952; Perry, 1953; Johnson & Fassuliotis, 1984). The nematode causes stubby root symptoms and severe root necrosis (Fig. 12), indicating a close association with root-rotting fungi. The nematode also can attack the base of the hypocotyl where necrotic tissues can be observed (Johnson & Fassuliotis, 1984).

Spiral nematodes, *Helicotylenchus* spp. and *Scutellonema* spp. are commonly found in vegetable crops. Although more than 14 species of *Helicotylenchus* and 3 of *Scutellonema* have been detected in the rhizosphere of the various vegetable crops, none has been shown to be of economic importance in the field.

Species of *Hoplolaimus*, *Aorolaimus* (*syn. Peltamigratus*) and *Zygotylenchus* have been found in soil samples from vegetable crops. Their importance to vegetable production has still not been determined.

Six species of ring nematodes, *Criconemella* (under the names *Criconemoides* or *Macroposthonia*) have been detected in the rhizosphere of a wide range of vegetables. These nematodes are known to increase to high numbers in many subtropical soils and have been implicated as important limiting factors on a number of perennial crops and could be important on vegetables.

## Future prospects

Agricultural production is increasing in most subtropical and tropical countries, in contrast to forced reduction in production being experienced in western Europe and north America. Similarly, the increase in vegetable production in the subtropics and tropics will require increased inputs in the form of fertilizer and pesticides; components being reduced in western Europe and North America, because of a lack of government subsidies and public awareness of the impact of agricultural inputs on the environment.

If environmentally safe nematicides are available in the future, an increase in use can be expected in many subtropical and tropical vegetable growing regions. A new generation of nematicides is needed that are both effective and safe. There still will be an imbalance in the availability of pesticides between commercial growers and poor or subsistence farmers, with the latter in most cases excluded for cost reasons.

Determination of threshold levels will be required to aid in selection of specific control measures for pest management programmes. Vegetables are often attacked simultaneously by a multitude of different plant parasitic nematodes. This requires an expanded view of threshold levels, involving the effects of all the species involved. Therefore, when determining damage intensity in the field, composite threshold levels, which include the interrelationship between all economically important nematode species, must be developed.

More emphasis must, therefore, be placed on determining the importance of plant parasitic nematodes, other than root-knot nematodes, to vegetable production. The losses caused by *Belonolaimus, Trichodorus, Ditylenchus, Heterodera, Pratylenchus, Nacobbus* and those species that may be of potential importance, indicate a need for more intensive study of these groups.

The development of resistant cultivars is playing an important role today and will increase in importance in the future. More stress must be placed on breeding for resistance to nematodes and diseases as well as for plant growth and quality characteristics important in tropical zones. This programme should be a priority in planning national and international research strategies. The use of embryo, tissue and protoplast cultures, as well as somatic hybridization will undoubtedly enable research to incorporate resistant genes present in botanical, but incompatible relatives, into useable cultivars.

Biological control is an alternative that is being studied in detail in many areas of the world. Fungal egg or female parasites, mycorrhizal fungi and plant health promoting rhizobacteria may prove to be effective control alternatives in future control programmes. Advances in biotechnology should make some of these biological control systems available to the farmer in the future. In most cases, however, they will not be as effective as present day nematicides and will require integration in extended rotation programmes.

With a reduction in the use of nematicides, the amount of nematode damage to vegetables will increase in those areas where alternative control components do not exist. Stress must be placed on developing integrated control programmes involving non-host crops and vegetable crops with resistance or tolerance not only to root-knot nematodes but other important species. Integrated pest management, however, must be developed to prevent monoculture of these cultivars and the consequent selection of resistant breaking pathotypes.

The "all or nothing approach" to nematode control is most probably a thing of the past, while "living with the nematodes" at or below threshold levels a thing of the near future.

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