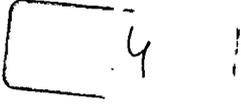


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## 10

# Nematode Diseases of Citrus

Eli Cohn

*The Volcani Institute of Agricultural Research  
Bet Dagan, Israel*

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### I. The Citrus Industry

Citrus is a multifarious evergreen fruit tree crop comprising several thousands of kinds—species, varieties and hybrids. The commonly cultivated citrus fruits belong to three genera, *Citrus*, *Fortunella* and *Poncirus* of the family Rutaceae (Swingle and Reece, 1967). In general, the citrus fruits of principal commercial importance fall into four reasonably well-defined horticultural groups: the oranges, the mandarins, the pummelos (grape-fruits) and the common acid group (citrus, lemons and limes).

The citrus-producing regions have tropical and subtropical climates occupying a belt extending around the world at both sides of the equator to a latitude of 35°N and 35°S. Conditions limiting its distribution in these areas are soil type, sufficient moisture to sustain tree growth, and lack of severe frost. In regions such as the Mediterranean basin and California, citrus orchards are irrigated during the summer and local frosts are common in the winter; there is a distinct harvest season, fruit yields are high and of good quality. In tropical regions,

there is a tendency to produce more than one crop a year, fruit quality is poorer and most of the production is directed to local consumption. In regions with intermediate climatic conditions, such as Florida and Brazil, effective cultural practices result in high yields and excellent quality fruits.

An estimate of the world citrus planted area for 1968, based on several sources (Burke, 1967; Burke, 1969; Gonzalez-Sicilia, 1969; Mendel, 1969; Oberholzer, 1969; Singh, 1969; Spurling, 1969) is presented in Table I. About 61% of the total citrus area in the world is concentrated in the Mediterranean and North and Central America; the Far East accounts for about 21% of the world total, South America about 12%, and other countries, principally South Africa and Australia, about 6%. Approximately 60% of the total world plantings are commercial orchards, and almost 80% of these are concentrated in the Mediterranean region and in North and Central America.

Citrus production is one of the world's largest agricultural industries, world trade in citrus being second only to bananas and more than double the volume of apples. In the U.S.A. alone, more oranges are produced than any other fruit crop, comprising one-third of the total fruit tonnage in that country (Hedlund, 1969). Total world citrus production in 1967, based on FAO data (Anon., 1969a) was approximately 29 million metric tons (Table I). About 81% of this volume were oranges and mandarins, about 8% grapefruits, and about 11% lemons and other citrus fruits. Of the total citrus production, about 32% was produced in North and Central America and 30% in the Mediterranean. The increase in citrus production in recent years has been spectacular. In the early 1950s world citrus production totalled 16 million metric tons; by 1965 it had reached 26.5 million metric tons, attaining 29 million metric tons in 1967. Increased production has, in turn, led to increased trade, and the export of fresh citrus from the producing countries has risen from an average of 2.5 million metric tons between 1950-1954 to 4.5 million metric tons in the 1965-1966 season; this represents a rise in exports of 80% as against a rise in production of 65% for the same period (Levin, 1969). FAO studies indicate that the demand for citrus fruit—both for consumption as fresh fruit and for processing—is expected to reach 33-36 million metric tons by 1975 (Anon., 1968).

## II. Nematode Diseases of Citrus

Although many pests and diseases of citrus are of economic importance to the industry and millions of dollars have been spent in combating Tristeza disease and fruit flies, recognition of nematodes as a cause of

TABLE I. World citrus area and citrus production (1968)

Region and major producing countries	Total citrus area (1000 hectares)	Total citrus production (1000 metric tons)
<b>NORTH &amp; CENTRAL AMERICA</b>		
U.S.A.	405	7555
Mexico	101	1062
Others	28	613
Total	534	9230
<b>MEDITERRANEAN REGION</b>		
Spain	155	2197
Italy	127	2160
Israel	41	1082
U.A.R. (Egypt)	45	705
Morocco	55	629
Turkey	39	545
Algeria	45	400
Greece	25	305
Lebanon	13	238
Others	35	582
Total	580	8843
<b>SOUTH AMERICA</b>		
Brazil	101	2747
Argentina	57	912
Peru	10	270
Paraguay	8	243
Ecuador	8	230
Others	34	466
Total	218	4868
<b>FAR EAST</b>		
Japan	109	1945
India	105	1370
China (Mainland)	101	650
Pakistan	24	399
Thailand	31	228
Others	11	276
Total	381	4868
<b>OTHER COUNTRIES</b>		
South Africa	32	673
Australia	30	223
Others	43	424
Total	105	1320
World Total	1818	29,129

losses in citrus production has been slow to emerge. Nematodes are root pathogens of citrus so that the resultant above-ground symptoms on host plants are usually non-specific, and diagnosis and proof of pathogenicity are difficult to establish. Although some nematodes were discovered on citrus roots at the turn of the century, it was not until the mid 1950s that they were recognized as causing economic damage to the citrus industry, and research was intensified on developing means for their control.

The first record of an association between a nematode and citrus appears to be that of Neal (1889), who found *Heterodera radicicola* (= *Meloidogyne* sp.) parasitizing citrus roots in Florida. The number of species of plant-parasitic nematodes known to be associated with citrus by 1949 was 8, by 1959, 28, and by 1968, 189 belonging to 39 genera (DuCharme, 1968). However, most of these nematodes are not known pathogens of citrus and their true relationship with their host plant still remains to be established. This section will be devoted to the comparatively few cases of nematode-citrus relationships that have been adequately described. These include two citrus diseases of recognized economic significance—slow decline caused by *Tylenchulus semipenetrans*, and spreading decline caused by *Radopholus similis*.

#### A. Slow Decline

“Slow decline” of citrus is a diseased condition of trees with symptoms similar to those caused by drought and malnutrition. Affected trees exhibit reduced vigour, chlorosis and falling of leaves, twig dieback and, consequently, reduced fruit production. This decline of the tree is gradual and persists until the crop is so small that tree maintenance may become uneconomical.

*T. semipenetrans* was discovered in 1912 in California on the roots of citrus trees that exhibited a “mottled” appearance (Thomas, 1913). It was described by Cobb (1913) a year later and by 1914, it had already been reported parasitizing citrus roots in Florida, Malta, Spain, Israel, Australia and South America (Cobb, 1914). Since that time its occurrence on citrus roots has been reported from all the major citrus-growing regions in the world and its ubiquitous association with the crop has earned it the common name of the “citrus nematode”.

##### 1. Life History and Habits of *T. semipenetrans*

The larvae hatch as the second stage and the male larva undergoes three additional moults within 7–10 days without the need to feed. The non-feeding adult male has an insignificant stylet, a degenerate, non-functional oesophagus and apparently plays no role in the disease

syndrome. The female larva is capable of persisting in the second stage for several years, and cannot develop without feeding. In the presence of a host plant, it penetrates the outermost root cell layers, where it undergoes the three additional moults. The nematode usually enters the 4–5 week old “feeder” roots (Cohn, 1964), and becomes permanently established with its anterior end embedded within the plant tissue and its posterior end protruding from the root. The mature female lays eggs into a gelatinous matrix which covers almost the entire protruding part of the female’s body. Reproduction is parthenogenetic, and unfertilized females lay eggs that hatch into larvae of both sexes.

The life-cycle of *T. semipenetrans* from egg to egg is completed at temperatures of 24–26°C within 6–8 weeks (Van Gundy, 1958; Cohn, 1964).

## 2. Effect on Host

Feeding of *T. semipenetrans* is limited to the cortex of host roots where a permanent feeding site consisting of three to four parenchyma cell layers around the nematode head is formed. The head itself is located in a cavity formed from one cell, and is free to move in different directions (Van Gundy and Kirkpatrick, 1964). The “nurse cells” around the nematode head are not unlike the normal adjacent parenchyma cells in shape or size, but differ in their reaction to stains. Starch has been shown to be depleted in these cells as a result of nematode feeding. As the parasite continues to feed, the cells in the feeding site break down, and appear as a mass of disorganized tissue. Subsequently, secondary micro-organisms invade the tissue along the path of nematode penetration and develop in the feeding site causing dark necrotic lesions within the cortex (Cohn, 1965a).

Heavily infested feeder roots of citrus may harbour over a hundred nematodes per centimetre of root. Such roots bear numerous lesions, which give them a darkened appearance. Furthermore, soil particles usually cling tightly, even after washing, to the gelatinous egg masses which cover the protruding part of the nematode body. In extremely heavily infested roots, the entire cortex may separate from the vascular stele (Figs 1 and 2).

The role of secondary organisms in the disease syndrome caused by *T. semipenetrans* is significant and histological studies show that the major part of tissue destruction in roots can be attributed to such organisms invading the nematode feeding site (Cohn, 1965a). Various bacteria and weak pathogenic fungi have been isolated from the feeding sites. Van Gundy and Tsao (1963) demonstrated a greater reduction in citrus seedling growth due to *T. semipenetrans* and *Fusarium solani* combined, than to either alone. However, the exact

nature of the relationship between root-rot fungi and the nematode is still unclear.

There is no evidence of a systemic factor being induced by the nematode in the roots and transported through the plant. As the nematode feeds and reproduces, a large proportion of the feeder roots of citrus trees, particularly in the upper soil layers, is inactivated or destroyed, the uptake of water and minerals from the soil is reduced, and the symptoms appear in the above-ground tree parts.

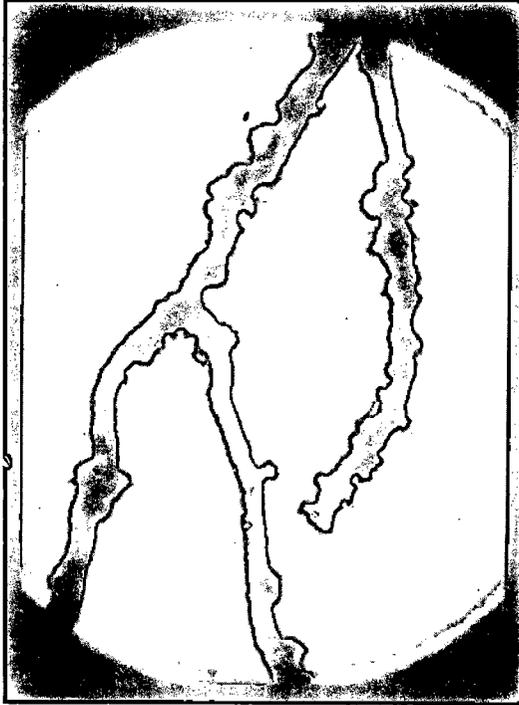


FIG. 1. *Tylenchulus semipenetrans* infection in citrus. Nematode-infected feeder roots covered with females, egg masses and adhering soil particles ( $\times 12$ ).

### 3. Host Range

*T. semipenetrans* is one of the more host-specific plant parasitic nematodes. An attempt to compile a complete list of hosts was made by Vilardebo and Luc (1961) and they recorded 29 species of *Citrus*, 21 citrus hybrids, and 11 other rutaceous species, as hosts. The number of non-rutaceous hosts was six, while seven rutaceous species, all of them other than *Citrus*, were considered proven non-hosts. One additional *Citrus* species, three other rutaceous species, and two

non-rutaceous species, have since been reported as hosts. No species of *Citrus* is known to be immune to the nematode. Hence, the evidence is presumptive that all species and hybrids of *Citrus* may act as hosts to *T. semipenetrans*, while the host range among non-*Citrus* forms is limited.



FIG. 2. *Tylenchulus semipenetrans* infection in citrus. Adult females attached to the roots ( $\times 125$ ).

Hosts of *T. semipenetrans*, including species of *Citrus*, vary considerably in their host status, with some affording a more rapid nematode build-up on their roots than others (Cohn, 1965b). Different populations of *T. semipenetrans* have been shown to exhibit different host preferences, suggesting the existence of biotypes (Baines *et al.*, 1969). Furthermore, different hosts may react differently to parasitism by *T. semipenetrans*. Van Gundy and Kirkpatrick (1964), identified three host reactions in citrus varieties resistant to the nematode—a hypersensitive cell reaction to the feeding of the nematode, a formation of wound periderm in the root cortex and a toxic factor in the root juice.

#### 4. Ecology

The pathogenicity of *T. semipenetrans*, and therefore the manifestation of decline symptoms, is closely related to nematode density. Tree

performance deteriorates when the nematode infestation attains a critical level; in Israel this level is approximately 40,000 larvae per 10 g of feeder roots (Cohn *et al.*, 1965). Over the years, populations build up to maximum "ceiling" levels. Although ceiling population levels may vary from one climatic region to another, they are usually attained in orchards in Israel 12–17 years after infested seedlings are planted in virgin soil (Cohn *et al.*, 1965). This is a relatively long time in comparison with other endoparasitic nematodes. However, the duration of the life-cycle of *T. semipenetrans*, even under optimal temperature conditions, is almost twice as long as that of most other endoparasites. Also, the invasion process of *T. semipenetrans* is relatively slow (Cohn, 1964). Hence, citrus trees in their first 2 years in the orchard still usually harbour few nematodes in their roots even if the population of the free-living stages in the soil is high.

Some fairly specific environmental factors are important in determining the rate and extent of nematode build-up. Optimal nematode reproduction occurs at soil temperatures of 28–31°C (Kirkpatrick *et al.*, 1965) and the nematode tolerates wide extremes of soil types. In California, nematode reproduction occurred in soils with a clay content of 5–50%, although optimum reproduction occurred with 10–15% clay (Van Gundy *et al.*, 1964). In fine-textured soils, reproduction was favoured by dry conditions, probably because of an oxygen deficiency when soil moisture was high. No significant differences in population levels were observed in soils of varying texture in Morocco (Vilardebo, 1963). A pH range of 5.6–7.6 has been found favourable for nematode reproduction (Van Gundy and Martin, 1961), and irrigation with water-containing salts has even been reported to favour population build-up (Machmer, 1958). There is some evidence that build-up of *T. semipenetrans* is suppressed in calcareous soils and in orchards irrigated with sewage water (Cohn *et al.*, 1965).

Environmental and cultural conditions, however, may influence the expression of nematode pathogenicity directly, and not only by determining the rate of nematode reproduction. In general, the effect of the nematode on tree performance has been found to be more marked under conditions marginal to citrus cultivation. Martin and Van Gundy (1963) showed that plant growth was inhibited to a greater degree by *T. semipenetrans* when the soil phosphorus level was below the optimum for healthy plant development. Oxygen deficiency in the soil has a more adverse effect on the nematode-infested roots than on nematode reproduction (Stolzy *et al.*, 1962). Also, damage to citrus has been observed to be more severe in wet soils, although the nematode reproduction was better in drier soils (Van Gundy *et al.*, 1964). Finally, the temperature level appears to have a direct influence on disease

expression, and workers in California reported that there was greater decrease in weight of *T. semipenetrans*-infested plants at 30°C than at 25°C (Stolzy *et al.*, 1962).

#### 5. Spread and Survival

Spread of *T. semipenetrans* is effected primarily by movement of infested plant material and soil. Of these two carriers, there is no doubt that the former is the more effective. The widespread distribution of *T. semipenetrans* throughout the citrus-growing regions of the world was undoubtedly achieved mainly by the transfer of infested citrus planting material. Movement of soil accounts for more local and short distance spread of the free-living stages of the nematode, and its efficiency is dependent on the capacity of the nematodes to survive adverse environmental conditions in the soil. Agricultural implements, animals and man, winds and water are common agents in spreading the nematode in soil. The re-use of sub-soil drainage water in irrigation supplies has led to a widespread contamination of orchards with *T. semipenetrans* in Australia (Meagher, 1969).

Some 70% of a population of free-living stages of the nematode survived storage in water at 10°C for 24 months, 85% of these being second stage female larvae (Cohn, 1966). In soil, the nematode may remain viable in the absence of a host for as long as 9 years (Baines *et al.*, 1962), and can withstand temperatures as high as 45°C for several hours (Feldmesser and Rebois, 1963).

#### B. Spreading Decline

This disease differs symptomatically from "slow decline" primarily in the increased rate and severity of tree deterioration, in the quick local spread, and in its limited international distribution. An area of spreading decline in a citrus grove has been described as "a group of trees that show the same degree of decline and the area increases in size each year" (Poucher *et al.*, 1967). Affected trees have fewer, smaller leaves, and dead twigs and branches are abundant. The tree appears to be under-nourished although no specific nutritional deficiency symptoms are evident, and it wilts readily during periods of mild moisture stress. Seasonal flushes of growth are weak and although bloom is often profuse, fruit set is sparse and yields are low. The trees do not generally die and they often show temporary recovery after rainy periods. However, normal productivity is never regained (Fig. 3).

Spreading decline was first observed in Polk County, Florida about 1928, increasing in severity in the state during the next decades. By 1957, 2800 ha and by 1966, 6000 ha of citrus were estimated to be

affected (Suit and DuCharme, 1957; DuCharme, 1968). In 1953, the nematode *Radopholus similis* was implicated as the causal agent of spreading decline (Suit and DuCharme, 1957).

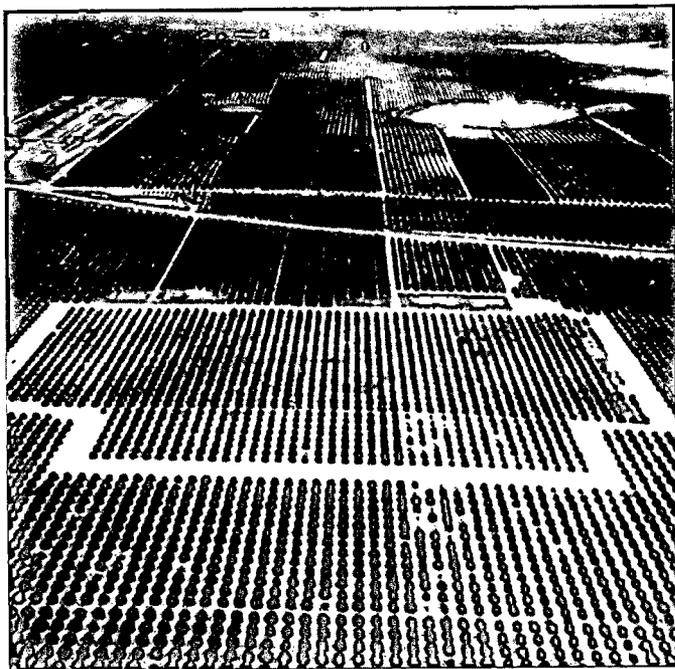


FIG. 3. *Radopholus similis* infection in citrus.  
Aerial view of citrus orchards showing "spreading decline". (By courtesy of the Florida Department of Agriculture, Bureau of Plant Industry.)

*R. similis* was first discovered parasitizing banana roots in Fiji in 1893 and was described by Cobb in the same year. It is widely distributed throughout virtually all the tropical and some subtropical regions of the world, but is not known as a pathogen of citrus outside Florida. On account of the cavities and tunnels it produces in the root tissues of its host, *R. similis* is often referred to by its common name—"the burrowing nematode".

#### 1. Life History and Habits of *R. similis*

All larval stages and adults of *R. similis* are vermiform and possess powers of locomotion. It is an endoparasite and may spend its entire life within the host root. Larvae and females penetrate the young and succulent citrus root tips and once inside the root, the nematodes reproduce rapidly. Eggs are laid singly inside the root and larvae hatch

within 3–7 days. Males are not capable of penetrating roots and probably do not feed. Females are capable of producing viable eggs in the absence of males, from which colonies of males and females develop. The life-cycle, from egg to egg, requires 18–20 days at 24–26°C (DuCharme and Price, 1966).



FIG. 4. *Radopholus similis* infection in citrus.

Citrus feeder roots with lesions caused by *R. similis*. (By courtesy of E. P. DuCharme.)

Migration from roots into the soil occurs as a result of population density, food shortage, putrefaction by secondary root invaders, fouling of the habitat from accumulation of nematode waste products, and deposition of wound gum by the plant (DuCharme, 1968).

## 2. Effect on Host

The penetration and histopathology of *R. similis* on citrus was studied in detail by DuCharme (1959). Females and larvae enter

growing feeder roots near their tips in the region of cell elongation and root hair production. Upon penetration, the nematode feeds on the cortical parenchyma cells and gradually burrows towards the stele, creating tunnels and cavities in the tissue. Large numbers of nematodes accumulate in the phloem cambium ring region. This part of the root is often completely destroyed, leaving a cavity filled with nematodes. Cell reaction involves hypertrophy and, when the nematode penetrates the pericycle, hyperplasia and tumour formation occur, and wound gum accumulates in the parasitized tissues.

Infested roots bear numerous lesions (Fig. 4) from which nematodes have been extracted from citrus feeder roots in extremely large numbers, e.g. 1-739 in individual lesions (Poucher *et al.*, 1967). Under controlled conditions, a single female created a colony of 47,000 nematodes in 85 days. Such high populations are not attained in the field because of the activity of secondary organisms which invade the roots after nematode penetration. Hence, populations are usually higher in roots of trees marginal to the diseased area, than on trees in a state of advanced decline.

Spreading decline in a tree is due to the combined activity of the nematode and other organisms that are always found in the parasitized roots. Although it is recognized that the nematode is the primary cause of disease, pathogenic fungi such as *Fusarium*, *Sclerotium* and *Thielaviopsis* are commonly found in lesions soon after nematode invasion. Subsequently, bacteria and cellulose-destroying fungi such as *Penicillium* and *Aspergillus* invade the root, causing additional destruction. Finally, oligochaete worms, mites and other soil-inhabiting organisms enter the decaying roots and feed on the fungi and the decomposing root tissues. As the nature of the root tissue changes, the nematodes leave their habitat and migrate to new healthy roots (DuCharme, 1968).

The decline symptoms in the above ground parts of the tree are a result of the destruction of feeder roots. Symptoms of decline appear about one year after initial infection of roots. Thus, under orchard conditions, *R. similis*-infected trees that appear healthy occur one to three rows in advance of trees with visible decline symptoms.

### 3. Host Range

*R. similis* has a large host range. In 1967, 244 species, both herbaceous and woody plants, were recorded as hosts. In Florida, lists of non-hosts are also periodically compiled to aid growers in selecting cover crops in *R. similis*-infected areas; the non-host list in 1967 included only forty plant species (Poucher *et al.*, 1967). 1275 different kinds of citrus were found to act as hosts of *R. similis* to varying degrees in Florida (Ford *et al.*, 1960).

Two physiological races of *R. similis* have been identified: the "citrus race" which parasitizes both citrus and banana, and has been recorded only in Florida, and the "banana race" which parasitizes banana but not citrus (DuCharme and Birchfield, 1956).

#### 4. Ecology

Populations of *R. similis* are high in the autumn and low in late spring in spreading decline-affected orchards. These fluctuations appear to be primarily a temperature effect. The optimum temperature for nematode reproduction and root invasion is 24°C, the minimum 12°C and the maximum 29.5–32.5°C (DuCharme, 1969).

Population levels of *R. similis* at individual sites vary considerably. More nematodes are found on roots of trees newly infected than on trees infected for 2 or more years (DuCharme and Price, 1966). Unlike *T. semipenetrans*, which is concentrated in the upper soil layers of the grove, *R. similis* is rarely found in the top 15 cm of soil. Highest populations are found between 30 and 180 cm and nematodes have been found feeding on roots at a depth of 4 m (Suit *et al.*, 1953). In trees affected by spreading decline, 25–30% of the feeder roots at depths of 25–75 cm, and 90% of the feeder roots below 75 cm, are destroyed (Ford, 1953). Spreading decline occurs predominantly in areas with sandy soils, where spread of disease and nematode movement are rapid. One nematode was shown to travel through sand to a distance of 100 mm in 96 h (Tarjan and Hannon, 1957), and new areas have been found to become infested with nematodes at a rate of 15.24–21.59 cm per month (Feldmesser *et al.*, 1960).

#### 5. Spread and Survival

The spread of *R. similis* to new regions is effected, as in the case of *T. semipenetrans*, by the movement of soil and infected plants. The limited international distribution of spreading decline, as compared with slow decline, appears to be partly due to a lesser ability of *R. similis* as compared with *T. semipenetrans* to withstand adverse conditions. Populations of *R. similis* do not survive more than about 6 months in soil free of citrus and other hosts, and even in such cases the nematode probably survives in pieces of living root scattered in the soil (Hannon, 1963).

Unassisted spread of *R. similis* is somewhat dramatic in comparison with that of other plant-parasitic nematodes, and the name of the disease it causes is indicative of this characteristic. The nematode has been reported to infect new groves from existing centres of infestation by crossing under clay and asphalt roads up to over 30 m wide, and even under a railway line (DuCharme, 1968). Spread occurs in all

directions. The average yearly rate of spread in Florida groves has been calculated as 1.6 trees, or 15.2 m, per year. Sub-soil drainage and topography influence the rate of spread (DuCharme, 1955), and in one instance the nematode was found to spread downhill at a rate of 66 m in one year, while the uphill rate was less than 8 m. The rapid unassisted spread of the nematode has led to efforts to create barriers in an attempt to halt its movement.

### C. Other Nematode Pathogens

Soil samples from around citrus trees throughout the world have revealed the presence of numerous species of nematode but only a few of these have been confirmed as being pathogens. Information on other nematodes found attacking citrus is summarized in Table II. Most of the genera listed are fairly widespread, and several species are known as pathogens of other crops of economic importance. It is characteristic, however, that most of the data contained in Table II represent knowledge obtained during the last decade; and the damage these organisms do to citrus still needs to be evaluated.

## III. Control

There is no single method of controlling all nematode pests of citrus. Nematodes differ in their biology and parasitism and so require different methods of control. Furthermore, the diversity of climatic, edaphic and cultural conditions under which such a broad spectrum of citrus varieties and rootstocks are cultivated throughout the world necessitates different and sometimes highly specific solutions to nematode control problems.

It should be emphasized from the outset that prevention is generally cheaper and more effective than cure. Once the nematode becomes established, its complete extermination is virtually impossible. Most of the ways and means of controlling nematodes known to us today are directed towards reducing populations to a minimum, and thereby creating optimum conditions in which the citrus trees can thrive. These means are sub-divided in this section under two fairly broad titles—chemical and cultural control measures.

### A. *Tylenchulus semipenetrans*

#### 1. Preventive Measures

The most common measures taken to prevent contamination of citrus trees by *T. semipenetrans* are directed at precluding the spread

TABLE II. Nematodes known to attack citrus

Nematode	Feeding habit	Root symptoms	Occurrence	Reference
<i>Aphelenchoides citri</i>	endoparasite	blinded tips, terminal lesions	Hungary (greenhouse) Florida, U.S.A.	Andrassy (1957) Standifer and Perry (1960)
<i>Belonolaimus longicaudatus</i> *	ectoparasite		Queensland, Australia Maryland, U.S.A.	Colbran (1963) Steiner (1949)
<i>Criconema australis</i>	ectoparasite		(greenhouse) Florida, U.S.A.	Steiner (1949)
<i>C. civellae</i>	ectoparasite		Canary Islands California, U.S.A.	Guiran (1962) Van Gundy and McElroy (1969)
<i>Criconemoides citri</i>	ectoparasite	swellings or galls on tips	Queensland, Australia Taiwan; India	Colbran (1963) Chitwood and Young (1960)
<i>Helicotylenchus multicainctus</i>	endoparasite	terminal galls	Surinam	Ouden (1965)
<i>Hemicyclophora arenaria</i> *	ectoparasite	galls and browning	Queensland, Australia India	Colbran (1958) Whitehead (1968)
<i>H. nudata</i>	ectoparasite	galls	Israel	Minz (1956)
<i>Meloidogyne</i> sp.*	endoparasite	galls	Florida, U.S.A.	Brooks and Perry (1967)
<i>M. exigua</i>	endoparasite	galls	Florida, U.S.A.	Feldmesser and Hannon (1969)
<i>M. incognita</i>	endoparasite	galls	Ghana	Peacock (1956)
<i>M. indica</i>	endoparasite	galls	Indonesia	Goodey (1958)
<i>M. javanica</i>	endoparasite	galls	Florida, U.S.A.	Standifer and Perry (1960)
<i>Pratylenchus brachyurus</i> *	endoparasite	lesions	Florida, U.S.A.	Cohn and Orion (1970) Tarjan (1964)
<i>P. coffeae</i> *	endoparasite	lesions	Florida, U.S.A.	Cohn and Orion (1970) Tarjan (1964)
<i>Rotylenchus reniformis</i>	semi-endoparasite	stubby-root	Florida, U.S.A.	
<i>Sphaeronema munitissimum</i>	semi-endoparasite		Israel	
<i>Trichodorus christiei</i> *	ectoparasite	browning and lesions	Florida, U.S.A.	
<i>Xiphinema brevicolle</i> *	ectoparasite	browning and lesions	Israel	
<i>X. coxi</i>	ectoparasite	browning and lesions	Florida, U.S.A.	
<i>X. index</i> *	ectoparasite		Israel	
<i>X. vulgare</i>	ectoparasite		Florida, U.S.A.	

\* Proven pathogens.

of the nematode—on a local or international level—through infested nursery stock. In most countries quarantine precautions are taken to ensure that imported, rooted citrus seedlings are free of the nematode. In several countries, regulations exist prohibiting the sale of nematode-infested plants, although enforcement of such laws has proved difficult. Nematode-free seedlings are produced in nurseries in virgin and/or fumigated soil remote from existing citrus orchards. Prior to their transfer to orchards, roots of seedlings can be dipped in hot water at 45°C for 25 min; this treatment kills the nematode without injuring the roots (Baines, 1950). Aqueous emulsions of various systemic organophosphates are effective control agents (O'Bannon and Taylor, 1967).

Other preventive measures are directed against the spread of nematodes in soil. Farm implements and machinery used in infested areas should be cleaned preferably with disinfectants, before being transferred to other regions. Re-use of drainage water from infested regions for irrigation of citrus orchards should be avoided (Meagher, 1969).

## 2. Chemical Control

Essentially, chemical control of *T. semipenetrans* is being practised by two different approaches, pre-plant and post-plant fumigation which, accordingly, have two different aims.

(a) *Pre-plant Fumigation.* The aim of pre-plant treatments is to kill the free-living stages of the nematode (larvae and males) and, if possible, the eggs present in the soil. These treatments, done in the absence of the host, can be drastic. They are applied primarily on land where young trees are to be introduced in place of old infested trees which have been removed. The chemicals selected for such procedures are often products not only highly nematicidal, but also generally biocidal; methyl bromide and chloropicrin are the most common chemicals of this type, but they are relatively expensive and, being highly volatile and toxic, usually require application under gas-tight covers for good results. Recently some applicators have been devised for applying them without need for covers (Amstutz, 1968). Less costly nematicides such as DD (dichloropropane-dichloropropene), ethylene dibromide or DBCP (1,2-dibromo-chloropropane) applied by soil injection or drench techniques can be used for pre-plant fumigation, but their effects in improving tree growth are not as impressive or as persistent as those of the overall biocides. It is sometimes convenient and economical to confine treatments of replants to small areas around the planting sites, rather than fumigating the entire area, unless the replanted area is large.

A temporary inhibition of growth of citrus has been observed on seedlings following either soil fumigation (Cohn *et al.*, 1968) or heat

treatment of soil (Martin *et al.*, 1963). Consequently, it is advisable to extend the interval between fumigation and planting beyond that normally maintained for other crops. Under subtropical climatic conditions, the most suitable procedure is to fumigate in the late summer or in autumn, prior to the introduction of replants in the following spring or early summer.

Pre-plant soil fumigation usually results in a marked increase in growth and development of replants. It must be emphasized, however, that the effect of such treatment is to reduce the nematode population temporarily and thereby give the young citrus trees a good start in the orchard. Nematode populations in re-set orchards build up relatively rapidly and critical population levels are usually attained within 4-7 years after planting (Cohn *et al.*, 1965).

(b) *Post-plant Fumigation.* The aim of post-plant fumigation is to kill both the free-living stages of *T. semipenetrans* in the soil and, especially, the numerous females attached to the feeder roots of the citrus tree, without adversely affecting plant growth. Only DBCP, the least phytotoxic of the fumigants at present on the market, has been used successfully for this purpose. Excellent nematode control, following DBCP treatments in established orchards, usually results in yield increases. Rates of DBCP applied (ranging between 11 and 67 litres active ingredient per hectare) and modes of application differ in accordance with varying local conditions. In general, three principal modes of application, modified and improvised to suit local needs, have been used: application as a soil drench in irrigation basins or flood systems, application by chisel injection, and application through sprinkler irrigation systems. Drench treatments have usually resulted in the best nematode control (Baines *et al.*, 1960; Cohn and Minz, 1965), but not the most favourable increase in yields, probably because of a phytotoxic effect. This application method is, of necessity, limited to flood-irrigated groves, or groves where preparation of basins is feasible from the standpoint of existing cultivation methods, topography and low labour costs. Application methods based on chisel injection are popular in the U.S.A. and have resulted in satisfactory nematode kill and increased fruit yields (Baines *et al.*, 1963; O'Bannon and Tarjan, 1969), but these methods are liable to cause some root damage where citrus trees have shallow root systems. Sprinkler application methods have so far been the least effective in controlling *T. semipenetrans* (Baines *et al.*, 1960; Baines and Small, 1969), apparently because of poor penetration of the chemical to the site of action and its adsorption on to soil particles. Improved nematode control by sprinkler application has been achieved by using a special drill-perforated irrigation pipe which produces water trajectories closer to the ground, thereby

enabling larger quantities of water to reach under the tree canopy (O'Bannon and Tarjan, 1969).

Despite the many convincing results of increased yield and size of citrus fruit following nematode control, there have also been reports on a lack of tree response to DBCP treatments, although nematode population levels were adequately reduced (Cohn *et al.*, 1968; Mendel *et al.*, 1969). Although our knowledge of these factors limiting the success of DBCP fumigation is still fragmentary, some factors have been isolated. Citrus appears to be more susceptible to the phytotoxicity of DBCP than many other plant species (Cohn *et al.*, 1968), although different rootstocks may differ in their degree of susceptibility (Mendel *et al.*, 1969). Consequently, it is always necessary to experiment with different doses and application techniques of DBCP under various local conditions, before embarking on a particular control programme. Also, in fine textured soils, DBCP fumigation should be avoided, as it results in marked phytotoxicity as well as poor nematode kill. Finally, old trees, especially if they are in an advanced state of decline, often do not respond to DBCP treatments, since DBCP is specifically nematicidal and has little effect on the micro-organisms involved in the disease complex caused by *T. semipenetrans*. It is feasible that the fumigant will be less effective in curing old trees in long-standing orchards, where high populations of these organisms have become established.

As a result of these limitations of DBCP fumigation, chemicals less phytotoxic than DBCP have been tested for use in established orchards, and the systemic compounds Furadan, Mocap and Temik have given promising results in nematode control (Baines and Small, 1969).

### 3. Cultural Measures

Work was recently begun in California on the breeding of citrus rootstocks resistant to *T. semipenetrans*. These are intergeneric hybrids of *Poncirus trifoliata* and several species of *Citrus*. Preliminary results are promising, with most of the selected hybrids showing initial resistance in greenhouse pot tests and about half of them showing high resistance in the field (Cameron *et al.*, 1969). Different selections of *P. trifoliata* vary in their tolerance to *T. semipenetrans* (Feder, 1968) and a further problem in the practical use of nematode-resistant rootstocks is the possibility of resistant breaking biotypes among field populations of *T. semipenetrans* (Baines *et al.*, 1969).

Tichinova (1957) reported that two applications of manure ( $\frac{2}{3}$  cow manure +  $\frac{1}{3}$  water, diluted by 1:10 before application) in 2 months controlled *T. semipenetrans* and improved tree growth in Uzbekistan. This finding is corroborated by the report of Cohn *et al.* (1965) who observed that in an orchard in Israel irrigated with sewage water,

nematode populations were very low, while in neighbouring fresh water-irrigated orchards, nematode infestation was heavy. The nature of this effect is not clear, but organic amendments have been shown to reduce soil populations of *T. semipenetrans* apparently by increasing the microbial activity which is unfavourable for survival of the nematode (Mankau and Minter, 1962).

### B. *Radopholus similis*

The control of *R. similis* has proved infinitely more difficult than that of *T. semipenetrans*. This is undoubtedly due to the true endoparasitic habit of the nematode, its concentration in the lower soil layers, the complex and more acute nature of spreading decline disease, and its rapid rate of natural spread through the soil. On the other hand, the limited occurrence of the disease to Florida in comparison with the world-wide distribution of slow decline, has made it possible to devise more uniform control measures applicable to the specific local conditions. A state-wide control programme is based on (a) preventing the nematode from becoming established in new areas, (b) eliminating the nematode in commercial orchards, and (c) slowing down the rate of natural spread through the soil to areas adjacent to infested orchards. This control programme (Poucher *et al.*, 1967), administered by the Florida Department of Agriculture, is included in the following review.

#### 1. Preventive Measures

All citrus-growing countries have special regulations, especially for plant material entering from Florida, to preclude the entry of *R. similis*, and particularly the "citrus race" of the nematode. Stringent intra-state regulatory measures exist also in Florida itself to prevent spread of the nematode. Citrus nursery sites and the movement of material from clay, soil or sand pits to citrus producing areas in the state are subject to approval by the authorities. *R. similis*-infested seedlings are treated before planting in approved sites within an infested region by immersing bare roots of seedlings in hot water at 50°C for 10 min and then immediately cooling them in cold water for 10 min. Nursery trees thus treated require more care and more frequent watering than non-treated trees. More recently, O'Bannon and Taylor (1967) have shown that bare-root dips of citrus seedlings in 250–600 ppm of B-68138 (ethyl 4-(Methylthio)-*m*-tolylisopropylphosphoramidate) and 1000 ppm of Cynem, Dasanit and Mocap, gave 100% control of the nematode, without phytotoxic effects.

Movement of infested soil is minimized by cleaning cultivation equipment after use in infected groves. Disinfectants, such as 1% caprylic acid and 2.6% sodium hypochlorite, can be used in the wash water (Tarjan, 1957).

The migration of the nematode from an infested site to adjacent groves is slowed by treating strips of land (buffer zones or barriers) around an infested area. These buffers are at least 4.8 m wide and are placed six rows in advance of the visible decline symptoms in a grove. They are fumigated with ethylene dibromide at 560 litres/ha during initial application and 280 litres/ha every 6 months thereafter, while the surface is maintained clean of weeds and cover crops by cultivation and herbicide treatment.

### 2. Chemical Control

Nematicidal control of spreading decline has not been very successful. The only effective treatment found to date is the procedure known as "Push and Treat". This involves pushing out all infested trees and the two uninfested outside rows of trees, stacking and burning them, raking the infested field to remove as many roots as possible, levelling the land and treating it with DD at the rate of 1120 litres/ha with injections spaced no farther than 45 cm apart to a depth of 25–30 cm, maintaining the land free of all vegetation for a minimum of 6 months, and releasing the land for replanting of citrus not earlier than 2 years after the original soil treatment. The entire "Push and Treat" programme in Florida is under direct state supervision.

Post-plant treatment to *R. similis* under field conditions has failed, apparently because of poor soil penetration and diffusion of the fumigant throughout the subsoil. Experiments are still under way to achieve successful field control by improving methods of DBCP application (Suit, 1969).

### 3. Cultural Measures

A large variety of methods and materials including soil conditioners and amendments, exposure of trees to electricity and radiation, "buck horning" or cutting back of trees, deep ploughing and frequent cultivation have been tested throughout the years as a possible cure for spreading decline. Generally, those treatments with some fertilizer value tend to promote a slight temporary improvement in growth, but no treatment successfully controls the disease or even reduces nematode numbers.

Attempts at biological control—either by the use of nematode-trapping fungi (Tarjan, 1961) or by growing *Tagetes* as a cover crop (Tarjan, 1960)—have proved ineffective.

The only effective cultural measure available for checking spreading decline is the use of tolerant or resistant rootstocks. Since 1951 more than 1400 different kinds of citrus have been screened, and in 1964 three rootstocks were formally released to the industry in Florida for planting on land in spreading decline areas which had been pushed and treated (Ford, 1964). "Estes", a rough lemon, is a rootstock which

supports a relatively high level of *R. similis* but is classified as "tolerant" because its growth is not reduced to an appreciable degree. "Ridge pineapple", a sweet orange variety, is resistant to *R. similis* and, where planted, existing nematode populations gradually diminish. "Milam" lemon, a citrus hybrid of unknown parentage, also is resistant to *R. similis* and gradually eliminates nematode populations from the soil by preventing egg development within the root cortex. It is, however, susceptible to nematode penetration and feeding. All three rootstocks are tolerant to several virus diseases, but contain no resistance to *T. semipenetrans*. Recently Carrizo citrange (navel orange × *Poncirus trifoliata*) rootstock has been shown to eliminate *R. similis* populations within 2 years, although suffering some growth reduction during this period, but is also tolerant to *T. semipenetrans* and produces good fruit quality on scion varieties (Ford and Feder, 1969). It is recommended to fumigate the old grove soil before replanting with any of the nematode-tolerant or resistant rootstocks.

The use of *R. similis*-resistant rootstocks as biological buffers or barriers has been advocated. This involves the planting of four rows of "Milam" or "Ridge Pineapple" as a biological barrier zone and maintaining a narrow chemical root-killing strip between these trees and the nematode-infested grove. Trials have shown that over a 5-year period so far tested, such barriers have effectively contained *R. similis* migration (Ford and Feder, 1969).

### C. Other Nematodes

Although little or no direct work has so far been carried out on the control of other nematodes on citrus, many of the methods discussed above are probably effective also against other nematode species. Several reports indicate sharp reductions of various species of ectoparasitic nematodes following soil fumigation for *T. semipenetrans* or *R. similis* control in citrus orchards.

*Hemicycliophora arenaria*, an ectoparasite native to the desert valleys of California, was eradicated, with no damage to citrus seedlings, in hot water (46°C for 10 min) and VC-13 dip treatments. Soil fumigation with DD, DBCP and methyl bromide at standard application rates gave complete kill of the nematode to a depth of 1.5 m. Of twelve common citrus rootstocks tested as hosts, six were resistant, namely: sweet orange, sour orange, Marsh grapefruit, Trifoliate orange, Troyer citrange and Carrizo citrange (Van Gundy and McElroy, 1969).

Post-plant treatments of DBCP and the organo-phosphate chemicals Mocap, Dasanit and B-68138 reduced the populations of *Pratylenchus brachyurus* and *P. coffeae* to varying degrees, and increased the growth

of rough lemon seedlings in comparison with untreated controls (Tarjan and O'Bannon, 1969).

The only other nematode on citrus for which specific control measures have been considered is *Meloidogyne* sp. ("the Asiatic Pyroid citrus nema") in Taiwan. Chitwood and Toung (1960) suggested as an interim measure the use of several non-hosts as cover and trap crops in citrus orchards, until long-term economic control measures are developed.

#### IV. Economics

An accurate appraisal of the economic effects of nematodes is dependent on the results of surveys and experiments. Since the severity of nematode damage to plants varies in relation to environmental factors, this information must be based on studies done under a wide range of ecological conditions. Since prices and production costs are prone to regional and seasonal fluctuations, estimates of average annual losses must be made over a range of conditions and seasons. It is not surprising, therefore, that present data, both on measurements of nematode damage and on their conversion to estimates of regional losses, are extremely meagre. Only the economics of slow decline and spreading decline will be considered here. Owing to the scarcity of data, some generalizations in place of more valid estimates are inevitable.

The economic effects of nematodes fall into three broad categories which will be discussed separately:

- A. Reduction in quantity and quality of fruit
- B. Increase in production costs
- C. Indirect losses to the community

##### A. Reduction in Quantity and Quality of Fruit

LeClerc (1964) recognizes two phases in the study of losses in crops due to disease: determination of disease intensity and the establishment of the relationship between intensity and loss of production.

##### 1. Disease Intensity

The prevalence of the causal organism usually serves as an indicator of disease intensity. Surveys of the occurrence of *T. semipenetrans* indicates that the nematode is present in all citrus-growing countries in the world. Furthermore, distribution within those countries is widespread, and estimates range between a low of 53% of all groves in Florida (Tarjan, 1967) to a high of over 90% in Spain (Scaramuzzi and Perrotta, 1969). On the strength of published surveys, a figure of

70–80% of all citrus trees throughout the world could be realistically considered to be infested to some degree with *T. semipenetrans*.

On the other hand, spreading decline is much more limited in its occurrence. Surveys in Florida have established that in 1967, the disease occurred in about 1.9% of the total citrus acreage of the state (6000 out of 325,000 hectares). Since Florida plantings constitute about 18% of the world citrus acreage, this represents only 0.35% of the total world citrus plantings infected with spreading decline disease.

## 2. Relationship between Intensity and Loss

The effect of the disease on the crop is dependent not only on the infestation level, but also on the susceptibility and age of the host and the influence of environmental conditions. Consequently, losses are variable according to different conditions and must be evaluated on a local basis. Estimates of loss can be attained by measuring yield increases as a result of disease elimination through successful nematode control, and by comparing the performance of infested with that of uninfested trees. Data are available on yield increases following *T. semipenetrans* control with DBCP under diverse conditions: 5–40% in Mediterranean countries (Scaramuzzi and Perotta, 1969), 6–34% in Florida (O'Bannon and Tarjan, 1969) and 10–30% in Australia (Meagher, 1969). In most cases the increased yields persist for approximately 3 years after a single treatment. In Arizona, U.S.A., where more than 970 hectares, representing about 5% of the total citrus acreage of the state, have been treated, yield increases of 12–38% have been reported (Reynolds, 1969). In California, where research on *T. semipenetrans* control has been more intensive than anywhere else, citrus yields following DBCP treatments have increased by 10–50%, with an average of 27% (Baines and Small, 1969). On the basis of these studies, a world average range of 20–30% increase in citrus yield resulting from the control of *T. semipenetrans* appears likely. To this estimate must be added the effects of secondary organisms which are not controlled by nematicide treatments and allowance must also be made for the mild phytotoxicity of DBCP which prevents treatments from attaining their full potential effect. Accordingly, a final estimate of 25–35% as an average world yield reduction due to *T. semipenetrans* on citrus would be more accurate.

Comparison of yields of infested with those of uninfested trees has proved far more difficult and less practical. However, it has been established that a critical infestation rate of *T. semipenetrans* exists below which tree performance is hardly affected. Surveys in Israel have revealed that 35% of all citrus trees in that country are infested with critical and higher levels of *T. semipenetrans*; this figure is an

average of five regions, differing markedly in prevailing climatic and edaphic conditions (Cohn, 1969). Similar information from other countries is not available. On the assumption that this figure is close to the world average, the actual reduction in world citrus yields due to *T. semipenetrans* could be estimated at 8.7–12.2% (25–35% of the world total).

Local crop losses due to spreading decline are appreciably higher than those caused by slow decline, and have been estimated at 50–80% for grapefruits and 40–70% for oranges (DuCharme, 1968). However, in terms of the world citrus industry, these losses have only a relatively minor impact. Since Florida produces about 18% of the world's citrus, and spreading decline affects only 1.9% of the state's orchards, the total reduction in world citrus yields due to spreading decline would be 0.14–0.27%.

Reduction in fruit quality is also a consequence of nematode pathogenicity. Thus, for instance, DBCP-treated grapefruit trees produced 510% and 242% more fruit size 40s and 48s or larger, respectively, than untreated trees during a 7-year period in Arizona (Reynolds, 1969). However, since the industries for citrus-juice and other citrus by-products provide markets for fruit of reduced quality, such losses, although sometimes fairly substantial, particularly in citrus-exporting countries, do not significantly affect the estimates given above in terms of total world production.

The total annual reduction in the world citrus crop due to both slow decline and spreading decline is therefore estimated at 8.8–12.5%.

## B. Increase in Production Costs

Nematodes cause losses also by increasing the costs of production primarily through increased maintenance costs of infested orchards, and extra expense incurred by nematode control measures.

### 1. Maintenance Costs

Nematode-infested groves demand additional care and investment which increases with time. In inoculation trials with *T. semipenetrans*, 10–50% weight reductions in citrus seedlings were obtained (Baines and Clarke, 1952). Additional amounts of fertilizers and water must be supplied to nematode-infested trees in order to maintain a profitable production level. Ironically, the increase in maintenance costs is probably a more important factor in orchards with slow decline than in spreading decline areas, not only because of its wider occurrence, but because disease expression is not so dramatic and diseased orchards are maintained for longer periods, whereas spreading decline is

recognized comparatively early and drastic control measures are taken sooner.

Reliable figures from citrus-producing countries on the losses resulting from increased maintenance costs are lacking and an estimate on a world-wide basis would be impractical because of the extreme variability of both production costs and citrus production values in different parts of the world. Some national data on maintenance expenses in citrus orchards, however, are available, and might be useful in attempting to evaluate the part played by nematodes in increasing costs. Data in Israel, for instance, indicate that all cultivation costs (predominantly labour) constituted an average of about 25% of the annual national citrus production value over a 5 year period. Materials (mainly water and fertilizers) constituted only 6.8% of the production value (Anon., 1969b). The extent of losses due to *T. semipenetrans* is not known, but growers have often claimed that 20–50% additional amounts of these materials (the equivalent of 1.4–3.4% of the production value) are needed to maintain the thriftiness of infested orchards. Since 35% of the citrus trees are infested with critical and higher population levels, as indicated earlier, the net loss due to *T. semipenetrans* in Israel could be roughly estimated at 0.5–1.2% of the annual production value. Similar estimates could also be made for other countries where profitability surveys on citrus have been done.

Similarly an estimate of the increasing maintenance costs in Florida due to *R. similis* could be calculated. However, because its occurrence is restricted to Florida, such losses in terms of the world citrus industry would assume much smaller proportions than those caused by *T. semipenetrans*.

## 2. Nematode Control Costs

Pre-plant fumigation of *T. semipenetrans*-infested orchard soil is usually a once-only operation and so is relatively unimportant. On the other hand, DBCP treatment for control of *T. semipenetrans* on existing trees is a recurrent expense item, the cost of which depends primarily on the rate of the chemical used and the application method employed. These costs can be estimated on a yearly basis by considering a single treatment effective for an average of 3 years, before retreatment is necessary. Reynolds (1969) has calculated that the average cost of chisel application of DBCP in Arizona is about U.S. \$0.10–0.12 per tree per year, which is equivalent to approximately U.S. \$50–62 per hectare. In nematode control trials in California, costs ranged between U.S. \$47–124 per hectare per year, depending on application doses (Baines *et al.*, 1960). The average cost per year of DBCP treatment by chisel application in Israel is estimated at U.S. \$35–47 per hectare.

Basin application usually requires more labour expenses, and has been reported to cost an average of U.S. \$0.80 per tree in Italy (Scaramuzzi and Perrotta, 1969), or approximately U.S. \$131 per hectare per year. The average yearly cost of basin treatment in Israel is estimated at U.S. \$57-74 per hectare.

The profitability of nematicide treatments on a regional basis can best be appraised by considering the costs in relation to the production value. In Israel, for example, the cost per hectare per year of chisel treatment represents about 1.2-1.7% of the average citrus production value per hectare for the 1967/68 season (Anon., 1969a), when taking into consideration that only about 35% of all trees in the country require treatment. The actual loss to the world citrus industry as a result of *T. semipenetrans* control costs can be estimated only if the total citrus acreage treated annually is known. Such data are not readily available, but reports indicate that treatments on a commercial scale are still very limited. Thus, in California, only about 1% of the total citrus acreage of the state was treated with DBCP during 1970 (Anon., 1971).

Control of *R. similis*, in terms of cost per unit area, has proved infinitely more expensive than control of *T. semipenetrans*. Indeed, the programme in Florida for eradicating spreading decline stands out as a stern warning of the potential danger of nematodes to world agriculture. Between 1954 and 1955, \$70,000 was released by the Florida state authorities for the purpose of identifying diseased areas. In 1955, \$1,756,300 was appropriated for controlling or containing the disease (Suit and DuCharme, 1957). Between 1955 and 1966 nearly 3240 hectares were pushed and treated, 360 of them having been double-treated with DD; more than one million citrus nursery trees were treated in the central state-owned hot-water treating tank alone; and 356 km of buffers were installed, within which there were 3250 hectares of infested groves (Poucher *et al.*, 1967). Owing to the preventive nature of these drastic measures, the losses accountable to nematode control within the affected areas of Florida represent more than a total loss of production, but it has been estimated that more than 21,500 hectares would have become infested by 1967 if these measures had not been taken (Poucher *et al.*, 1967).

### C. Indirect Losses to the Community

The economic effects of nematodes extend also to fields of activity beyond the citrus industry. This is particularly manifest with *R. similis*. Nematodes reduce soil use, and, therefore, more land is required for citrus production, usually at the expense of other crops. The wide

host range of *R. similis* and the resultant need to control the growth of such potential hosts in Florida, has affected other aspects of agriculture. The stringent quarantine regulations existing in most countries of the world, particularly those aimed at preventing importation of *R. similis*, have curtailed international trade of different agricultural products. Thus, the losses caused by nematodes on citrus are by no means confined to the producer, consumer and trader of citrus produce. In fact, although not always immediately identifiable, and largely still immeasurable, these losses are also suffered by the community at large, which, in turn, is a partner in bearing the burden of financing the investigation and the control of the microscopic organisms which cause them.

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