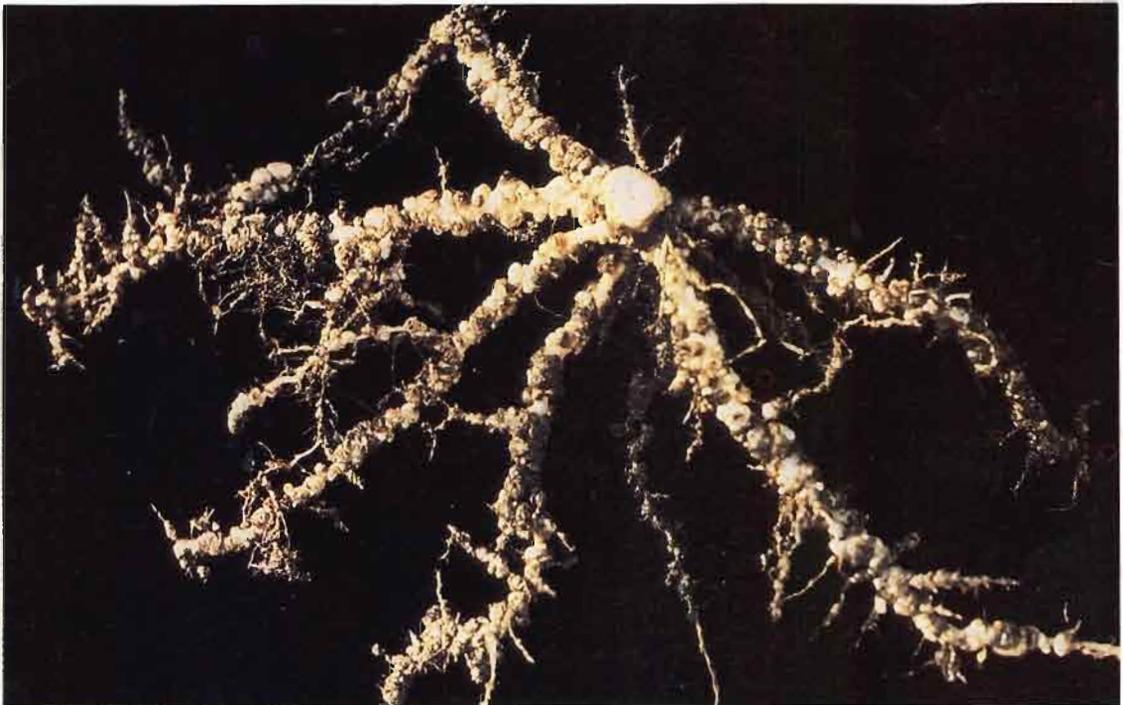


INTRODUCTION TO PLANT PARASITIC  
NEMATODES

# NEMATODE PARASITES OF VEGETABLE CROPS



by

J.C. PROT – Laboratoire de Nématologie, ORSTOM,  
B.P. 1386, Dakar, Sénégal

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Consortium For International Crop Protection, U.S.A.

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## FOREWARD

This booklet was originally written for plant protection personnel in Senegal and the neighbouring countries of Sahelian West Africa. It is designed to provide basic information regarding the biology of plant parasitic nematodes particularly with respect to managing the damage they cause to vegetable production in that region.

Although the specific examples cited in this booklet (resistant and susceptible host plants, for instance) will necessarily change from one region to another, several underlying principles regarding nematode parasites of vegetable culture remain constant. Among these are the facts that **Meloidogyne** sp. are the primary nematode threat to tropical vegetable production and that a variety of cultural and physical methods exist to manage **Meloidogyne** population levels.

Thus, although the program of nematode management suggested herein is highly specific and designed for conditions in Senegal, programs for other regions based on the principles outlined are perfectly feasible. The basic biological and agronomic information for specific locations is all that is necessary to design a safe, economic program of nematode management.



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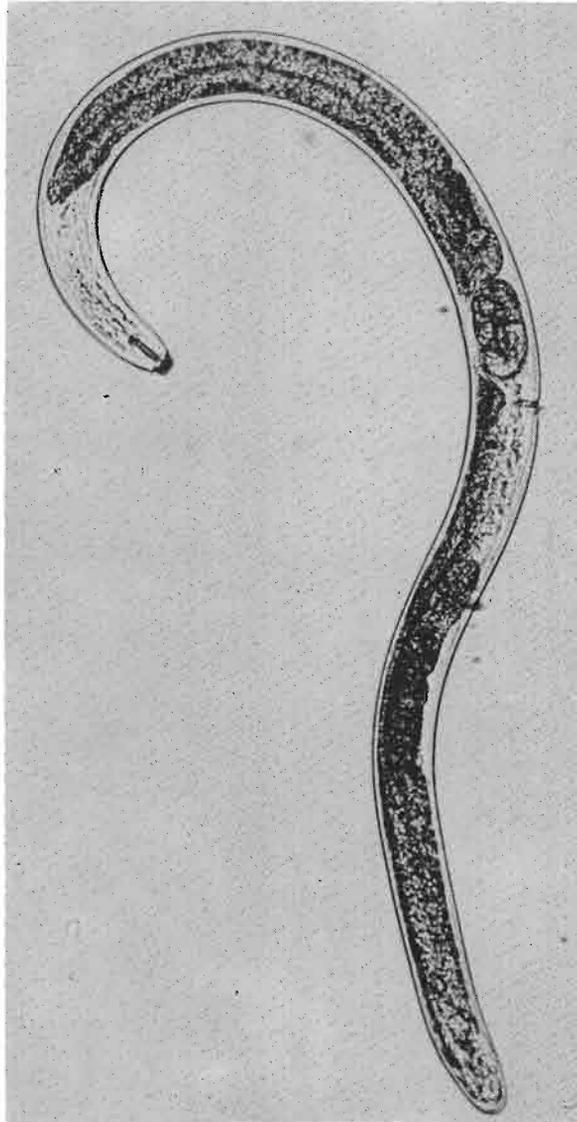


Figure 1:  
*Female of Scutellonema cavenessi, a parasite of peanuts in Senegal*

# INTRODUCTION TO PLANT PARASITIC NEMATODES

## 1. INTRODUCTION

Plant parasitic nematodes are needlelike roundworms (Figure 1) with the exception of females of some species which become rounded or pyriform. They live in the arable layer of the soil and are microscopic in size, measuring between 0.3 and 5 mm in length and only 0.03 to 0.05 mm in diameter. They cannot be seen without the aid of magnification.

They are very numerous. Cultivated soils can contain several million per m<sup>2</sup>. There are hundreds of species, some tropical and others more common in temperate zones.

Almost all plants, cultivated and wild, are parasitized by one or several nematode species. Some cause serious damage to crops, especially in the tropics where temperatures are always favorable for reproduction.

## 2. MORPHOLOGY

Nematodes are vermiform in appearance (Figure 2). Their body is cylindrical more or less tapered at the ends and covered with a cuticle. The mouth is at the anterior end. It has a stylet, a hardened cuticular structure analogous to an hypodermic syringe. The stylet is extendable, and a nematode feeds by perforating the cell walls sucking the cell contents. Suction is produced by the contractions of the median bulb, a muscular bulb which acts like a pump.

The digestive tube includes the oesophagus, the intestine and the rectum, which opens to the exterior through an anus situated at the base of the tail.

The male reproductive apparatus consists of one or two testes and two spicules which are the copulatory organs and which are extruded through the anus, guided by the gubernaculum. The caudal bursa, when present, is a membrane that holds the female during mating.

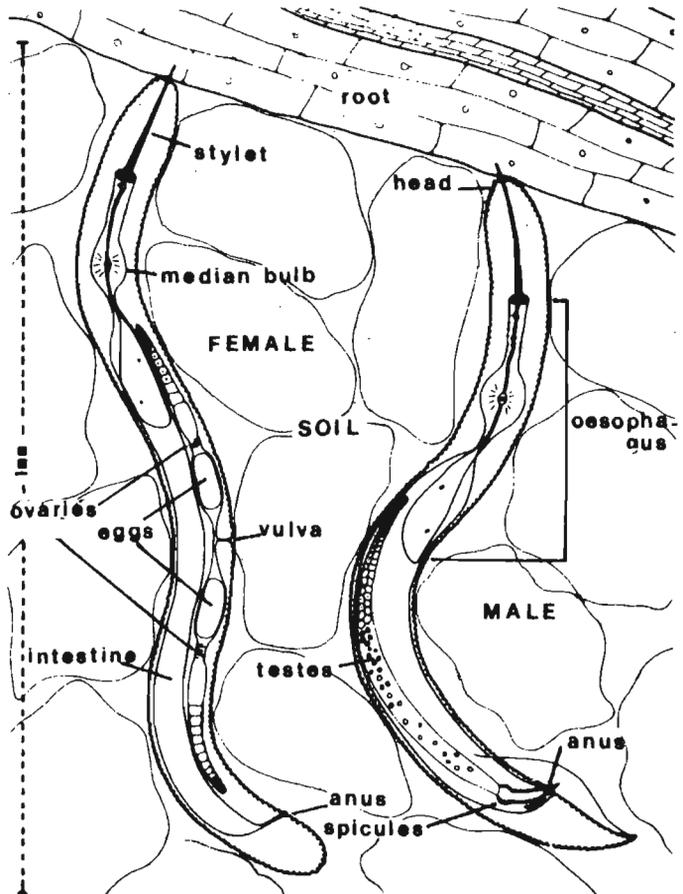


Figure 2: Structure of male and female plant parasitic nematodes.

The female reproductive structures include one or two ovaries, a spermatheca, a uterus and a vagina. The position of the vulva varies with species, but it is generally situated at the middle of the body when there are two ovaries.

Nematodes also have :

- An excretory system
- A muscular system consisting of four muscle fields
- A nervous system composed of a nerve ring, nerve cords, tactile sense organs and chemoreceptors.



Figure 3: Traces left by a juvenile **Meloidogyne** as it moves in agar.

### 3. BIOLOGY

#### 3.1. Ecology

Nematodes respire, and their bodies are 75 % water. They are actually aquatic animals, living in the film of water that coats soil particles. With few exceptions, they move between particles with undulatory movements (Figure 3).

The soil texture, temperature, pH, etc. influence the distribution and abundance of the different species. Some can't survive prolonged submersion, others are found only in flooded rice paddies. Some proliferate in sandy soils and others prefer clay soils. The Sahelian climate imposes a strong selective pressure; in the absence of irrigation, the only nematodes that can survive are those that are very resistant to desiccation. **Scutellonema cavenessi** (a peanut pest) and **Alphelenchus avenae** (a non-plant parasite) survive nine months of drought in a dried form (Figure 4) and become active again with the first rains.

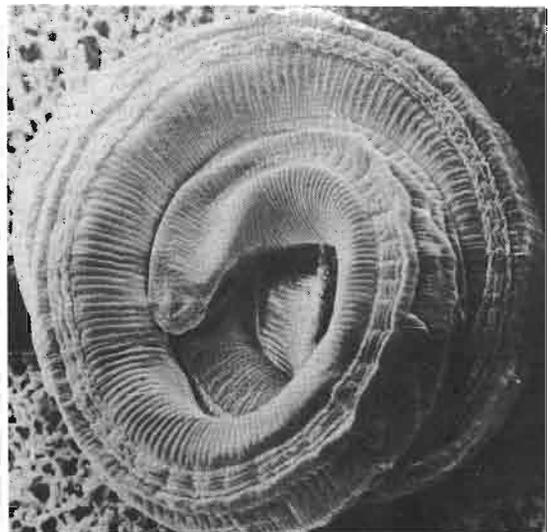


Figure 4: Desiccated female of **Aphelenchus avenae**.

### 3.2. Reproduction and Development

There are two principal types of reproduction in plant parasitic nematodes :

- a. Sexual reproduction. The female is impregnated by the male (Figures 5 and 6) ;
- b. Parthenogenesis. The eggs develop without fertilization. Eggs are laid in roots (Figure 7), in soil, in a gelatinous envelope called an egg mass (Figure 8), or protected inside the encysted body of the female (Figure 9).

The egg undergoes a series of cell divisions (Figure 10 A-E), resulting in the first juvenile stage. It molts to the second juvenile stage while still inside the egg (Figure 10 F). It then breaks the shell and emerges (Figure 10 G). This second juvenile stage is often called the infective stage, because nematodes usually do not develop further until they have found a living plant root and begun to feed. There are three further molts before the adult stage is reached. Males always remain vermiform. In some genera such as **Heterodera** and **Meloidogyne**, the female becomes pyriform.

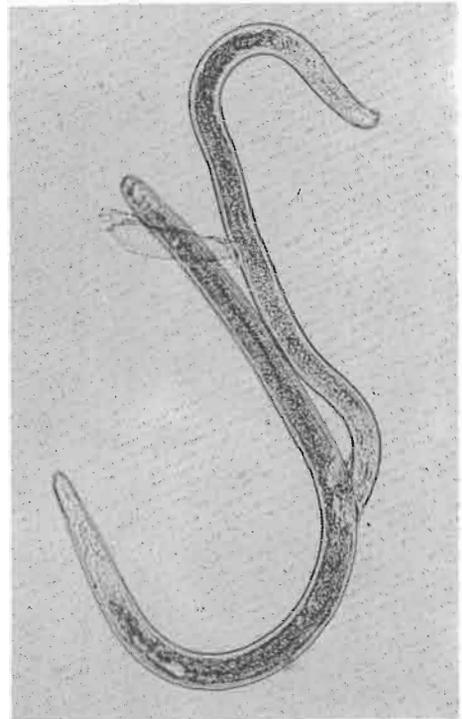
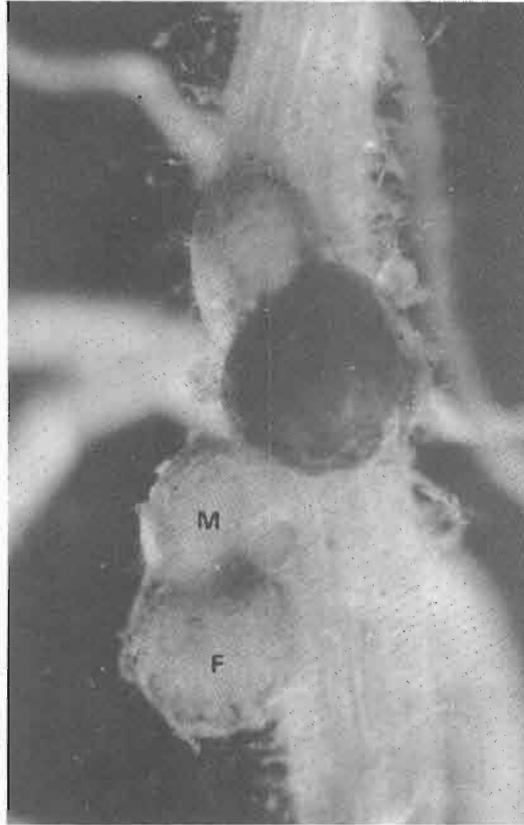


Figure 5: Copulation of *Scutellonema cavnessi*.



Figure 6: Copulation of *Scutellonema cavnessi*.



*Figure 8: Females (F) and egg masses (M) of **Heterodera oryzae** on a banana root.*

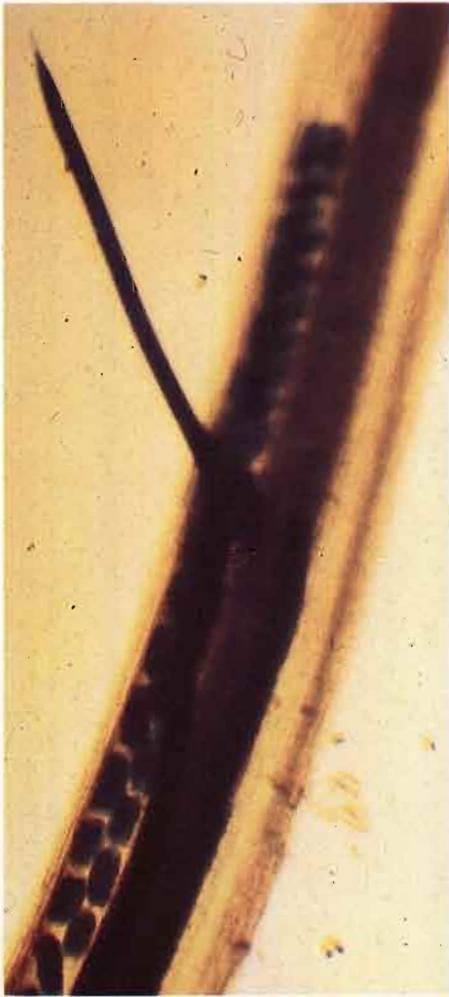


Figure 7: Female **Hirschmanniella spinicaudata** leaving a rice root after depositing its eggs.

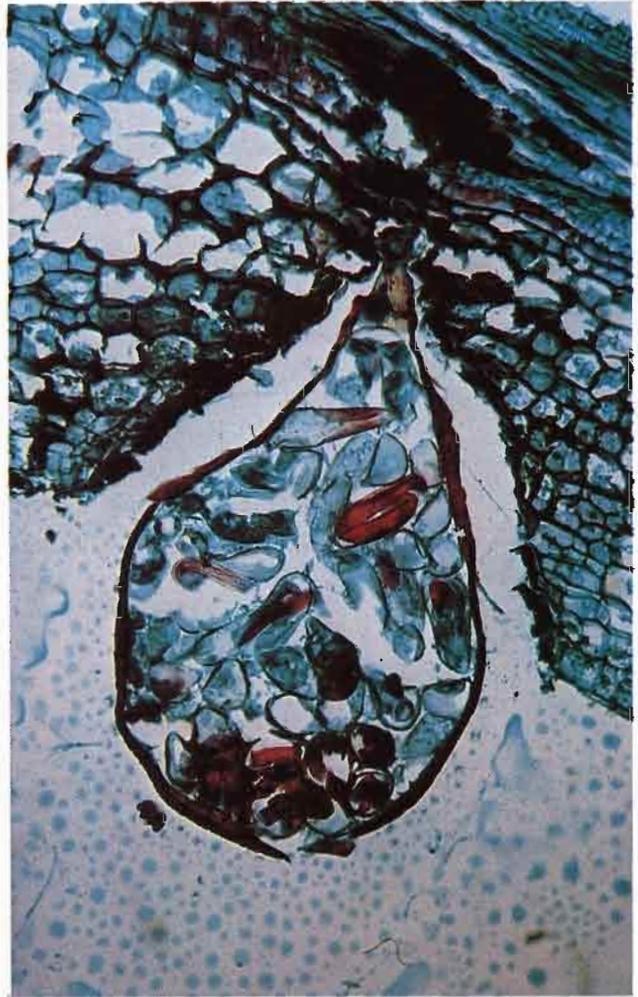


Figure 9: Section of an encysted female **Heterodera oryzae**. Note the eggs in her body.

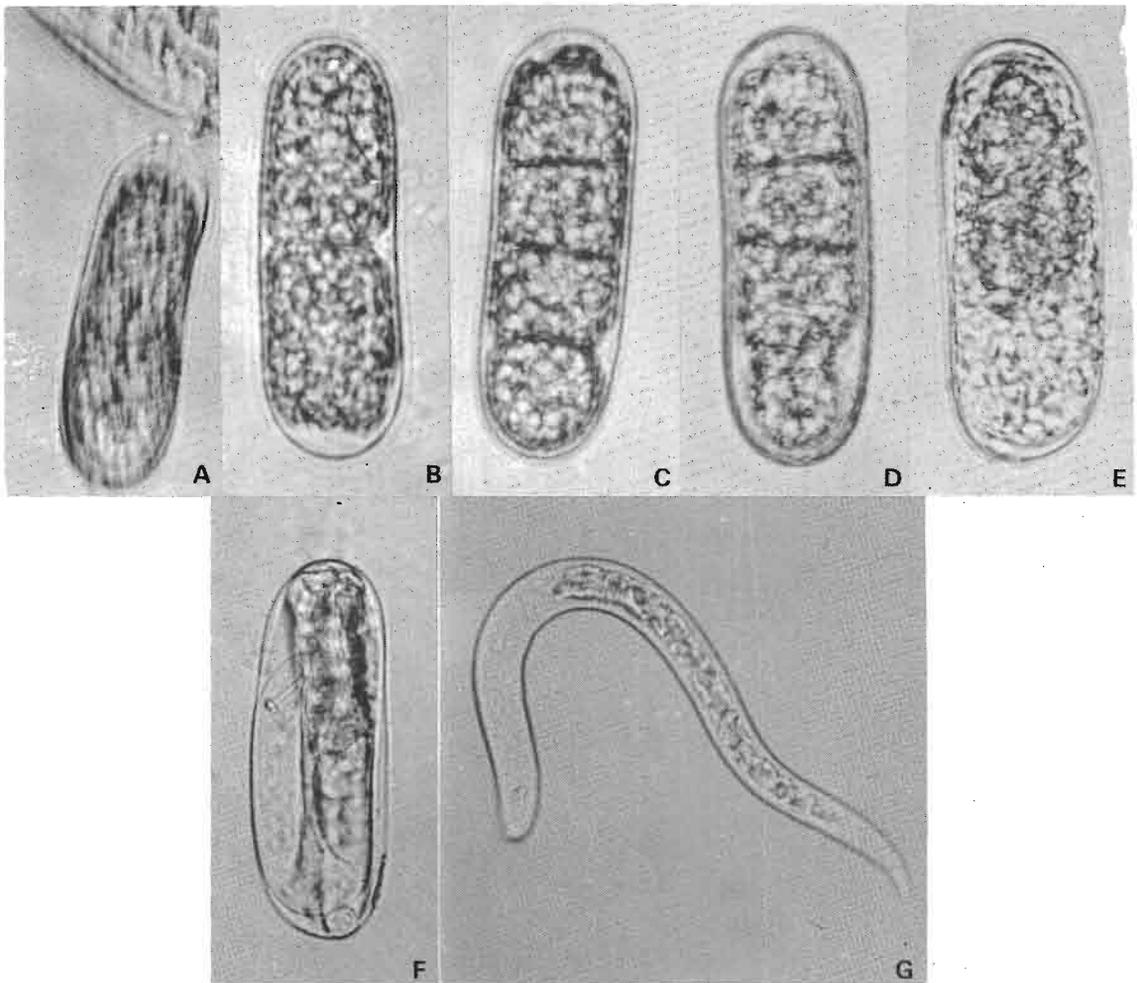


Figure 10: Embryonic development of **Scutellonema cavenessi** :

- A : egg at oviposition
- B : stage 2 cells
- C : stage 4 cells
- D : stage 5 cells
- E : gastrula
- F : second stage juvenile in the egg
- G : second stage juvenile after eclosion

### 3.3. Host Relationships and Damage to Plants

Plant parasitic nematodes are obligate parasites. This means that they must nourish themselves on the roots or aerial parts of a living plant in order to survive, develop and reproduce. Some have a very restricted host range while others are polyphagous. **Meloidogyne incognita** has over 2000 known host plants.

The infective stage (the second stage juvenile) is, at least in certain species, attracted by the roots of the plants that it parasitizes. Upon having found a root, the juvenile begins to feed. Plant parasitic nematodes can be divided into four broad groups according to their mode of parasitism :

- a. Ectoparasites. These never enter the roots, but rather feed on the peripheral cells or the apex. They can move from one root to another. **Trichodorus**, **Longidorus** and **Xiphinema** belong to this group.
- b. Migratory endoparasites. These enter and move within a root, and can leave it and enter another one. **Pratylenchus** and **Scutellonema cavenessi** (Figure 11) are examples.
- c. Semi-endoparasites. These are fixed at one place on the root. Only the head penetrates the root ; the rest of the body stays outside. This is the case with **Rotylenchulus reniformis** (see Figure 13), which becomes sessile. The body of the female swells.
- d. Endoparasites. These enter the root completely and establish themselves there. **Meloidogyne**, **Heterodera** and **Hylonema** (Figure 12) are endoparasites. In these three genera, the body of the female becomes pyriform and sometimes protrudes on the outside of the root.

Damage to plants and the resulting yield losses are the consequence of nematode feeding :

1. They divert a part of metabolism for their consumption ;
2. They damage the plant's root system by destruction and elimination of roots and radicles ; this reduces intake of water and mineral salts ;

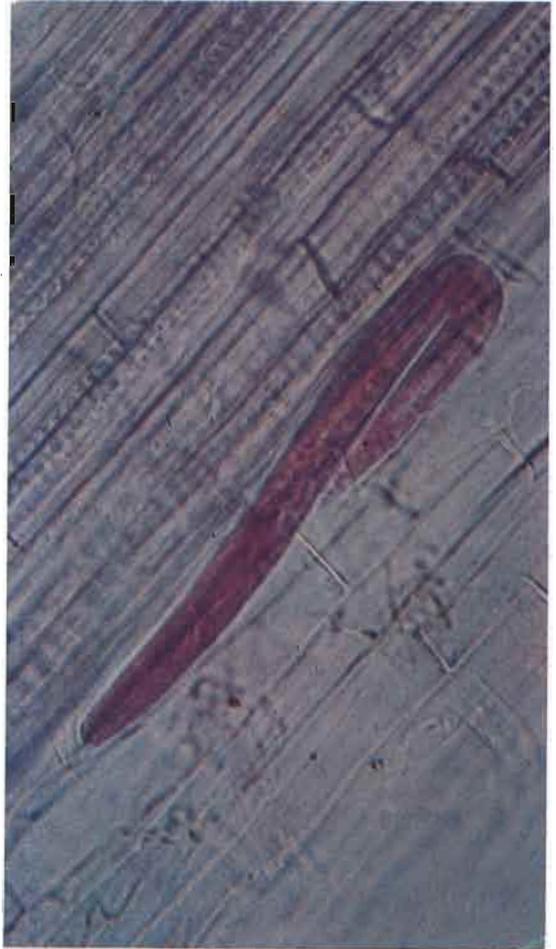


Figure 11 : Second stage juvenile **Scutellonema cavenessi** in a millet root.

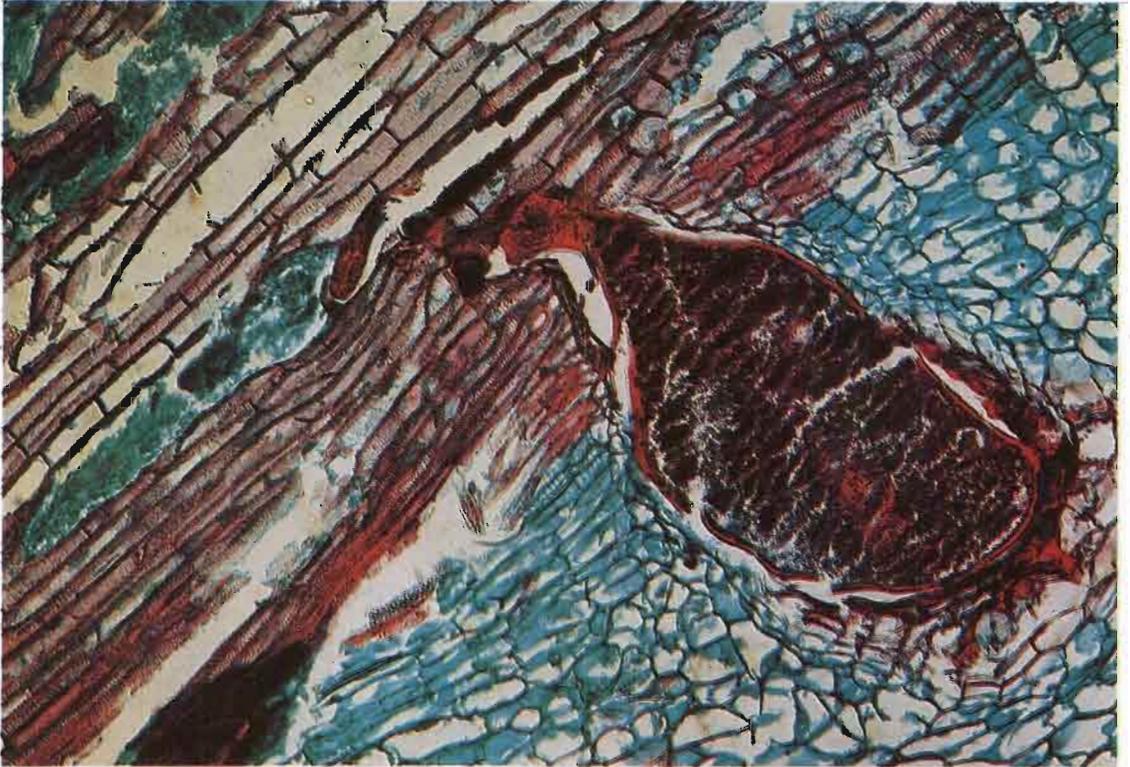


Figure 12 : Female **Hylonema ivorensis** in a (avodiree) root.

3. They inject glandular secretions into the cells which liquify the cell contents preparatory to absorption. These secretions are generally toxic to the cells, and kill them. In this way, **Trichodorus** totally destroy the zones of multiplication and elongation at the root apices (see Figure 14) ;
4. Endoparasitic nematodes generally secrete substances that modify the cells of the central cylinder and cortex of the plant, causing giant cells to form. This creates galls above the attacked area. Sap circulation is greatly disturbed by deformation of the cells of the central cylinder ;
5. Certain nematodes, such as **Scutellonema cavenessi**, hinder the establishment of **Rhizobium** on legume roots, thus substantially depriving the plants of nitrogen ;
6. Nematodes in the genera **Trichodorus**, **Longidorus** and **Xiphinema** can vector viruses, which they inject into the plant with their saliva ;
7. By perforating and entering cells, nematodes create lesions which permit the entrance of other pathogens such as fungi and bacteria.



Figure 13: Female **Rotylenchulus reniformis** on a tomato root.

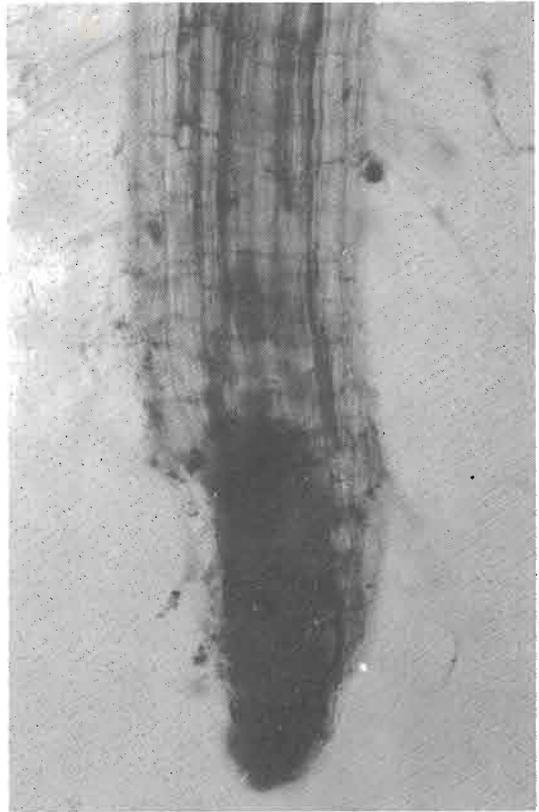


Figure 14: Necroses of the apex of a cabbage root caused by **Paratichodorus minor**.

# NEMATODE PARASITES OF VEGETABLE CROPS IN SENEGAL

## 1. INTRODUCTION

Many genera of plant parasitic nematodes attack vegetable crops in Senegal. The table below shows the frequency with which different genera were encountered in 120 random samples taken from various plants cultivated in the Niayes area north of Dakar.

Three of these thirteen genera are recognized as serious crop pests. In increasing order of importance, these are :

- a. **Rotylenchulus** is represented in Niayes by **Rotylenchulus reniformis**, which is a bi-sexually reproducing sedentary semi-endoparasite (Figure 13). In Senegal, it is associated with a large number of crops, including egg-plant, cabbage, lettuce, peppers, potatoes, and tomato.
- b. **Trichodorus** is represented by **Paratrichodorus minor**, present on a great number of vegetables. It is a strict ectoparasite. **Trichodorus** can be a virus vector, but it doubtless causes much more damage by destroying the root apices, halting root growth and killing the roots (Figure 14).
- c. **Meloidogyne** is the most common genus in Niayes, found in 92 % of samples analyzed. It is recognized worldwide as a major pest of vegetable and is without doubt one of the principal factors limiting the development and profitability of vegetable farming in Senegal. Thus, it merits particular attention.

## 2. MELOIDOGYNE PARASITES OF VEGETABLE CROPS IN SENEGAL

These are parthenogenetic endoparasites. Even though the systematic of this genus is unresolved we can assert that the three principal tropical species are present in Senegal : **M. javanica**, **M. incognita** and **M. arenaria**. Very polyphagous, they parasitize virtually all cultivated vegetables.

Genera	% of fields infested
Meloidogyne .....	92
Helicotylenchus .....	44
Pratylenchus .....	29
Rotylenchulus .....	24
Trichodorus .....	21
Scutellonema .....	14
Xiphinema.....	12
Tylenchorhynchus .....	12
Telotylenchus .....	10
Criconemella .....	4
Tylenchulus .....	2
Peltamigratus .....	1
Belonolaimus.....	1

## 2.1. Symptoms

**Meloidogyne** weaken the plant and cause wilting and yellowing of the leaves even on well-irrigated and fertilized soil. When they are numerous, they kill the plants (Figure 15).

It is easy to identify a **Meloidogyne** infestation because they cause characteristic galls on roots and tubers (Figures 16, 17, 18, 19, 20). These are easy to distinguish from root nodules formed on legumes by **Rhizobium**. Galls are integral to the root and situated on its axis, whereas nodules are easily detached, away from the root.

## 2.2. Life Cycle

After eclosion, second-stage juveniles (Figure 21) are attracted by the host's roots. They penetrate the sub-apical zone of growing roots (Figure 22). The juveniles move intra- and intercellularly in the root and come to rest in the central cylinder. Their salivary secretions cause the formation of polynucleate giant cells in the vascular tissue from which they nourish themselves. The toxins also induce hypertrophy of the cortical cells. These deformations cause the characteristic galls.

The juveniles then undergo three successive molts and become adult males (Figure 23) or females (Figures 24 and 25). Males stay mobile and vermiform. They are very rare in Senegal **Meloidogyne** populations, which all belong to parthenogenetic species. Females rapidly grow stouter and become pyriform or spherical. Oviposition begins about three weeks after penetration. Five hundred to 1000 eggs are deposited in a gelatinous mass secreted by the female and attached to her posterior end (Figure 26). The eggs and the mucilaginous mass are called the « egg mass ». Most of the eggs can develop immediately into new infective stages. There is a new generation about every four weeks.

---

*Figure 15: Green beans attacked by **Meloidogyne** (Niayes région).*

*Figure 16: Surviving plants from the group shown in Fig. 15. Note the root galls.*

*Figure 17: Root system of okra attacked by **Meloidogyne**.*

*Figure 18: Potato roots attacked by **Meloidogyne**.*

*Figure 19: **Meloidogyne** galls on potato tubers.*

*Figure 20: **Meloidogyne** galls on tomato roots.*

*Figure 21: Second stage juveniles (infective stage) of **Meloidogyne**.*

*Figure 22: Second stage juveniles **Meloidogyne** in a tomato root.*

*Figure 23: Male **Meloidogyne** in a tomato root.*

*Figure 24: Young female **Meloidogyne** in a tomato root. Note the beginning of gall formation and the deformation of the central cylinder.*

*Figure 25: Section of a female **Meloidogyne** in tomato root tissue.*

*Figure 26: A mature female **Meloidogyne** and its egg mass.*



Figure 15



Figure 16

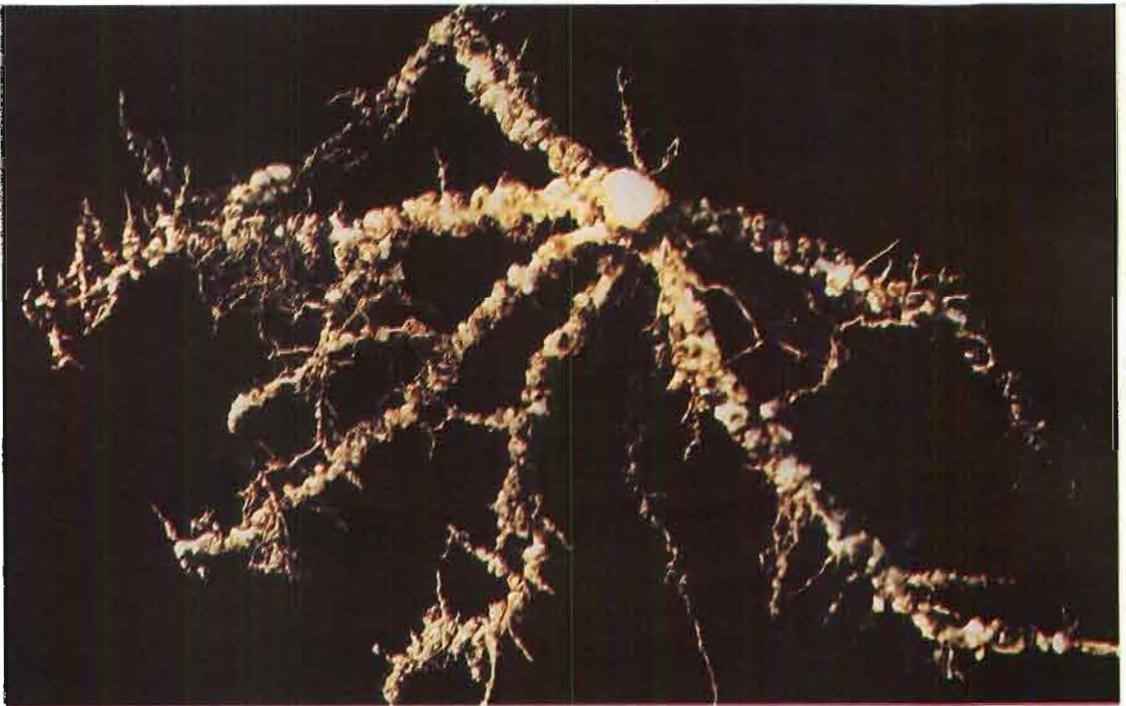


Figure 17



Figure 18

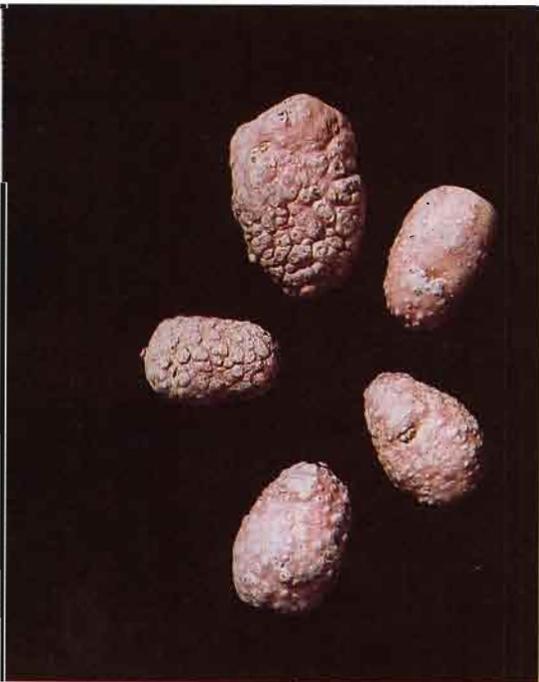


Figure 19

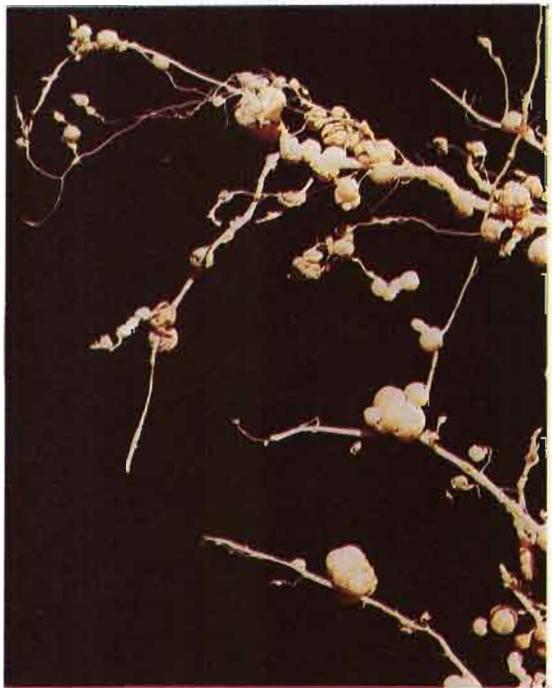


Figure 20

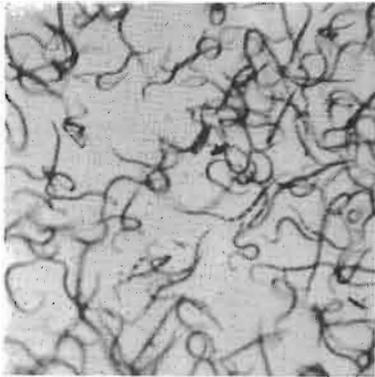


Figure 21



Figure 22



Figure 23

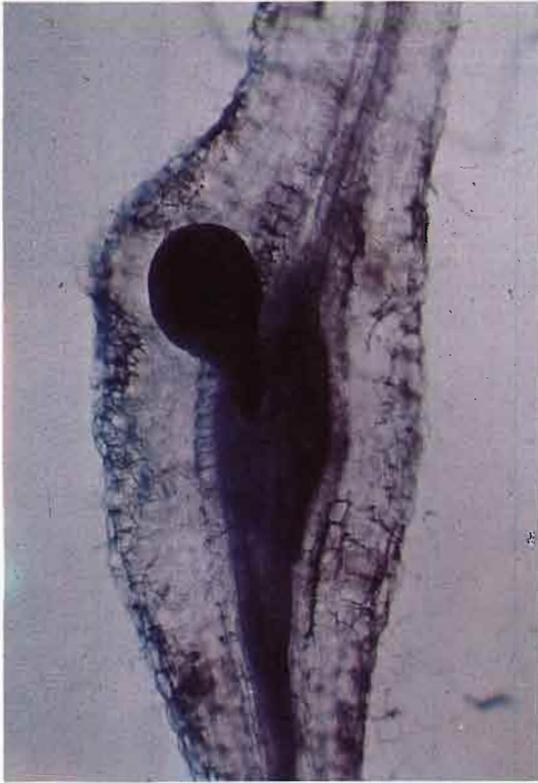


Figure 24



Figure 26

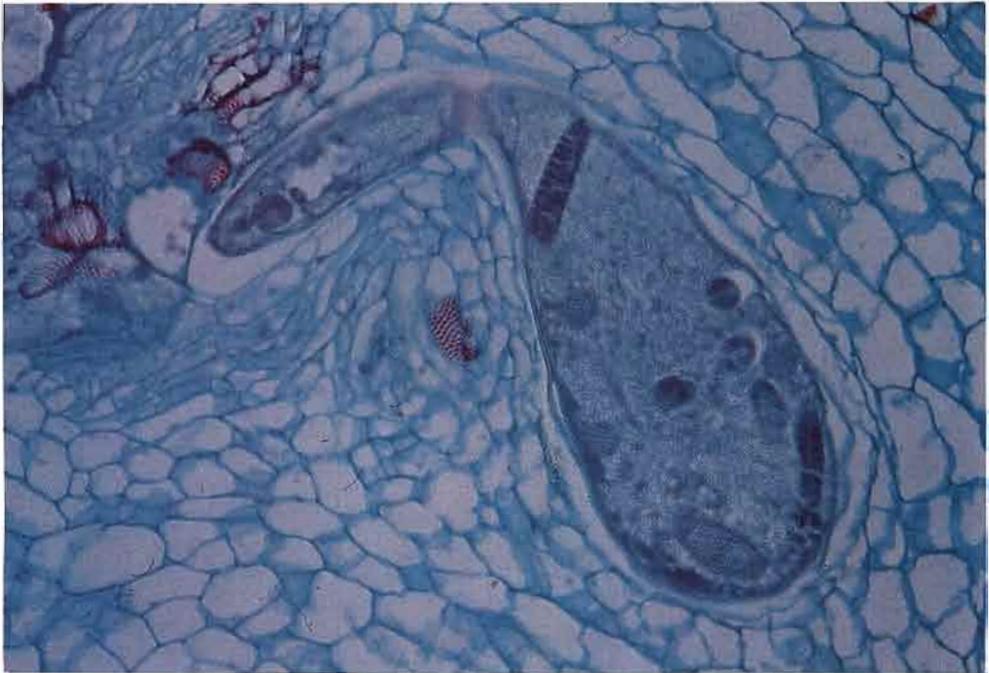


Figure 25



### 2.3. Causes of Pathogenicity

When a large number of juveniles penetrate the apex of a young root, they destroy the apical meristem. When the infestation is heavy, all roots are killed and the young plant dies.

If the plant resists the infection, the central cylinder deformations reduce sap circulation, diminishing the flow of water and mineral salts to the aerial parts of the plant and causing wilting. In extreme cases, the plant withers and dies.

The lesions caused by the penetration of the juveniles and gall formation are paths of infection for other pathogenic agents. The physiological changes induced in the plant by the nematodes favor the establishment and development of fungal or bacterial pathogens.

### 2.4. Susceptibility and Resistance of Plants

The susceptibility of a plant to **Meloidogyne** is defined by the degree to which the parasite can reproduce on it, rather than by the seriousness of the damage caused. Several degrees of plant host susceptibility can be distinguished. Considering their average performance in the field, vegetables cultivated in Senegal are classified as follows :

- a. Susceptible plants. Plants that permit normal reproduction of the parasite : eggplant, squash, bitter tomato, okra, green beans, lettuce, melon, peppers, potato, tomato ;
- b. Slightly susceptible plants. Plants that generally permit only low levels of reproduction by the parasite : cabbage, onion, navet, leek, radish ;
- c. Resistant plants. Plants selected for this purpose that rarely permit reproduction : mint, strawberries, some tomato varieties, beans, sweet potatoes, etc.

This classification is not absolute. Cabbage, for example, is generally not very susceptible, but is strongly attacked in certain fields. This sizable difference between fields is the result of the existence of at least three tropical species of **Meloidogyne** and also of the variability between populations of the same species.

Susceptible plants can be tolerant. This means that they permit normal nematode reproduction, but their growth is not much affected. This is often the case for eggplant in Senegal, which can bear fruit in spite of heavy infestation.

Just as susceptible plants can be tolerant, resistant plants can be heavily damaged. Resistance to **Meloidogyne** is often due to a hypersensitive reaction. The plant reacts violently to infection, the root tissues die (Figure 27) and the infective juveniles are trapped in dead tissue and can't feed or complete their development. In soil lightly infested by **Meloidogyne**, necroses are few and the plants don't suffer. However, if the soil is severely infested the root apices are destroyed, the plants are weakened and in extreme cases, they die.

Peanuts merit special attention among resistant plants in Senegal even though they are not « vegetables ». They are trap crop for **Meloidogyne** : infective juveniles are attracted by the

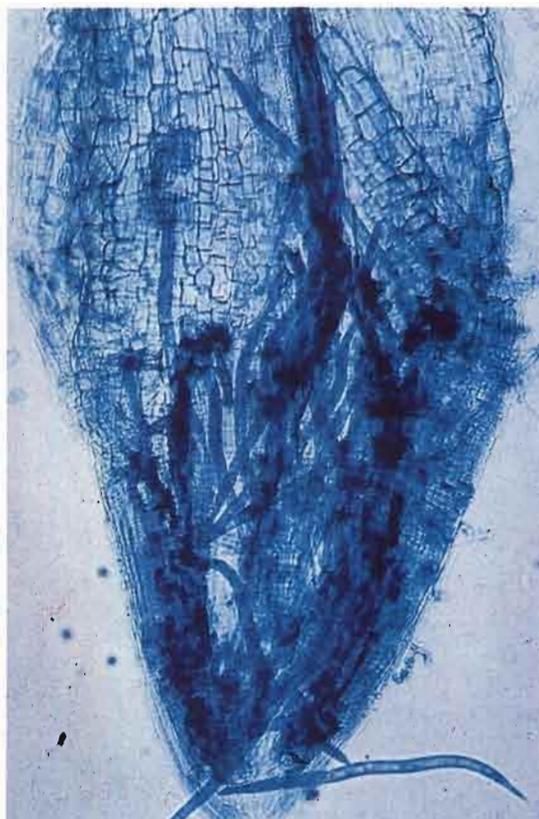


Figure 27 : Hypersensitive reaction (necroses) in a resistant tomato root (Rossol) after penetration by **Meloidogyne** juveniles.

roots and penetrate them, but can't develop there because they provoke necrosis of the tissue (hypersensitive reaction). Peanuts can thus actively reduce soil infestations.

## 2.5. Control Methods

### 2.5.1. Elimination of Factors Favoring Infestation

Reservoir plants must be eliminated. These are hosts which permit the survival of **Meloidogyne** in their roots despite control actions. Papaya is very susceptible and should be planted away from vegetables. Baobabs should also be avoided. Windbreaks should be chosen carefully. **Euphorbia tirucalli** and **Prosopis juliflora** are often used in Senegal, but are very susceptible and should be rejected in favor of resistant plants such as neem (**Azadirachta indica**), **Anacardium**, **Eucalyptus**, citrus or filao.

Soil in seedling nurseries must be treated (see the chapter on chemical control), and plants or roots from infested nurseries must be avoided in order to prevent the spread of the parasites.

In infected fields, parasitized roots should be collected and burnt to the degree possible.

Avoid planting a succession of very susceptible crops.

### 2.5.2. Chemical Control

Nematicides are one of the most effective and widely used control methods available (Figure 28). Two products can be recommended for vegetables: metham sodium for nurseries and DD (a mixture of dichloropropane and dichloropropene) for nurseries and fields. These are fumigants that require good soil preparation and heavy wa-

tering before and after application. They should be used at least three weeks before sowing or transplanting. They are very effective and destroy not only nematodes, but also insects, fungi and weeds.

Metham sodium (Vapam or Mapasol) has the advantage of being water-soluble, so that it can be applied with watering apparatus at about 800 to 1500 l/ha. Its two drawbacks are that it is not very effective against cyst nematodes (genus **Heterodera**) and that its price prohibits treatment of large areas (it costs almost \$ 1000/ha). It is recommended for treating nurseries.

DD can be injected into soil every 30 cm at a rate of 300 l/ha. Small areas can be treated with a hand-held injector (Figure 29). Large areas require tractor drawn (Figure 30). Not counting equipment and labor, a DD treatment cost about \$ 500/ha (1982 prices).

To be effective, DD must be applied to properly prepared soil. It must be evenly distributed, and it is necessary to frequently check the flow through the system. For good diffusion in the soil, the injection holes should be covered over and the treatment should be made during the coolest hours. It is very corrosive, and equipment must be taken apart and cleaned with petrol after every application. For all these reasons, applications should be made only by or under the direction of qualified personnel.

The expense of nematicide treatments, the conditions under which they must be applied and the fact that they protect just one susceptible crop necessitate other control methods for nematodes.



*Figure 28: Results of a nematocidal treatment of okra*

*Middle ground : treated plot  
Foreground : untreated plot*



*Figure 29: Treatment by hand-held injector.*



*Figure 30: Tractor drawn fumigation apparatus for the treatment of large areas.*

### 2.5.3. Physical Control

Fallow: **Meloidogyne** are obligate parasites and are also very vulnerable to desiccation. A good way to reduce infestation is to leave soil fallow for two to four months during the dry season.

Submersion: **Meloidogyne** can not survive several months' submersion. Flooding can be natural or artificially induced in the Senegal River irrigated areas where rice is rotated with vegetables. Infection can then be avoided simply by disinfecting the nurseries, which are generally outside the flooded zone.

### 2.5.4. Crop Rotation

The goal of crop rotation is to avoid or limit **Meloidogyne** development so that the infestation remains below a level that endangers crop profitability and requires nematicide treatment. Two types of plant can be used in rotations to prohibit or greatly reduce nematode reproduction: resistant plants and trap crops.

Resistant cultivars generally do well on moderately infested soil. Their development and production remain satisfactory where the development of susceptible plants would be greatly reduced and their production practically nil (Figure 31). However, for several reasons these cultivars must be used with caution.

High temperatures lessen and may even eliminate resistance. The physiological variability of **Meloidogyne** is such that certain strains can reproduce on « resistant » cultivars. It is rare that the majority of nematodes in a population are capable of this, and it has only been observed

twice in Senegal (Figure 32). Usually only a very small proportion of infective juveniles can overcome resistance. Since **Meloidogyne** are parthenogenetic, all or part of the offspring of these individuals are capable of reproducing in turn. Thus a new race can emerge that is capable of breaking plant resistance.

In practice, certain **Meloidogyne** populations appear to have gradually developed the capacity to parasitize resistant plants. Cases have been confirmed in which the same resistant crop was planted five or six times in a row and the entire nematode population then became capable of parasitizing and reproducing on other plants which have the same type of resistance. To avoid the risk of creating a race that can overcome resistance, resistant crop cultivars should be used only on lightly infested soils and should not be planted in sequence. Susceptible or mildly susceptible plants should be used in the succession of crops.

Peanuts are considered to be a trap crop for **Meloidogyne** in Senegal. Out of thousands of peanut plants inspected in the field or tested in the laboratory, none has yet supported reproduction of **Meloidogyne**. Thus, peanuts are a good crop to rotate with vegetables. They lower soil infestation and substantially raise the yield of a following susceptible crop (Figure 33). They can be grown during the rainy season when vegetable crops are usually not planted, and may be used either for green manure or for a harvest. However, the same precautions must be taken with peanuts as with other resistant cultivars. The risk of creating a nematode race capable of attacking them cannot be ignored.



*Figure 31: Performance of susceptible variety Roma (left) and resistant variety Rossol (right) in moderately infested soil.*



*Figure 32: Meloidogyne arenaria attacking resistant tomato (Rossol).*



*Figure 33 : An example of rotation. On the left, susceptible tomato (Roma) after peanuts ; on the right, susceptible tomato (Roma) after another susceptible crop.*

### 2.5.5. Biological Control

Plant parasitic nematodes are attacked by many predators and parasites: predatory nematodes, amoebas, tardigrades, mites, enchytreids, bacteria fungi and insects. Two among these organisms have been most particularly studied: **Bacillus semipenetrans** (Figure 34), present in many Senegalese fields, attacks infective juveniles and prevents their development and reproduction; fungi of the genus **arthrobotrys** digest nematodes after having trapped them in their hyphae (Figure 35). **Arthrobotrys** has begun to be used for nematode control in European greenhouses, but biological control of nematodes in the field is still in the experimental stage.

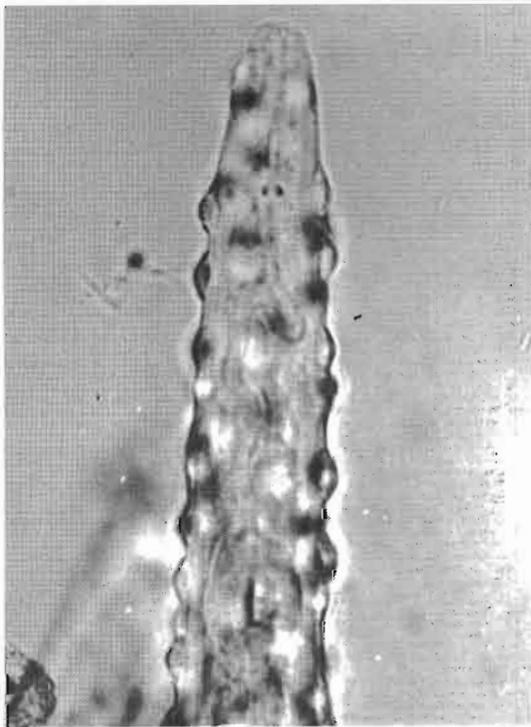


Figure 34 : Second stage juveniles **Meloidogyne** parasitized by **Bacillus semipenetrans**.

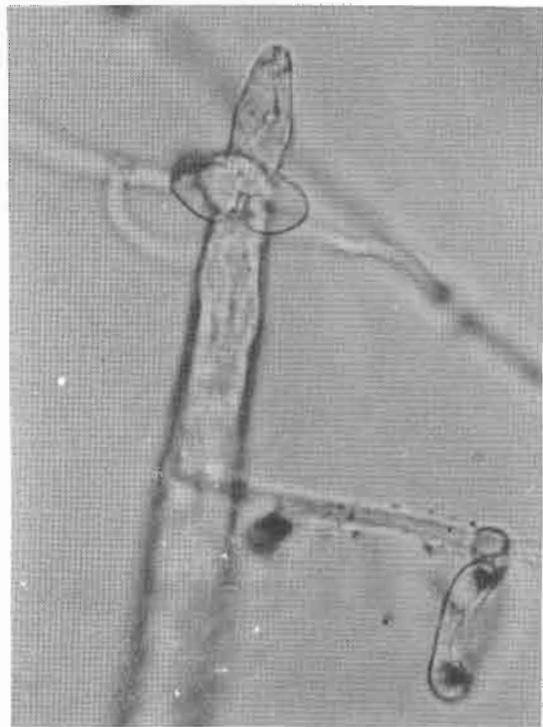


Figure 35 : Second stage juveniles **Meloidogyne** trapped in a ring formed by a fungus in the genus **Arthrobotrys**.

### 3. CONCLUSION

Nematodes in the genus **Meloidogyne** are among the principal factors limiting vegetable farming in Senegal. All efforts should be made to avoid their multiplication in lightly infested soil and to diminish their numbers where they endanger crops.

Nematicide treatments are expensive and require trained personnel, and can only be considered a panacea. They remain indispensable for reclaiming heavily infested soil, but the number used should be as limited as possible. To this end, they should be part of an integrated control system that includes preventive measures, physical control and crop rotation.

Preventive measures includes :

- a. Treatment of nurseries ;
- b. Elimination of reservoirs : baobab, papaya, **Prosopis** ;
- c. Resistant windbreaks : **Anacardia**, neem, **Eucalyptus**, filao or citrus.

Physical control would include :

- a. Flooding. Where paddy rice can be rotated with vegetables, **Meloidogyne** should not be a problem if nurseries are treated with nematicide. **Meloidogyne** cannot survive prolonged inundation.
- b. Dry season fallow. **Meloidogyne** need a host plant in order to reproduce and are vulnerable to dessication ;
- c. Crop rotations should hinder **Meloidogyne** multiplication and avoid creating races capa-

ble of infecting resistant cultivars. Peanuts should be planted during the rainy season. An example of a crop succession that would permit intensive use of the soil :

1st rainy season	peanuts or another suitable trap-crop
1st dry season	long-cycle resistant crop and short-cycle susceptible crop
2nd rainy season	peanuts or another suitable trap-crop
2nd dry season	long-cycle susceptible crop and fallow during the hot-test period
3rd rainy season	peanuts or another suitable trap-crop
3rd dry season	long-cycle resistant crop and short-cycle, slightly susceptible crop
4th rainy season	peanuts or another suitable trap-crop
4th dry season	long-cycle susceptible crop and fallow during the hot-test period
5th rainy season	peanuts

This sort of crop succession should avoid parasite build up by making sure that susceptible crops are not planted continuously.

It should also work against the development of nematode races that can successfully attack resistant cultivars. An initial nematicide treatment may be necessary if the soil is heavily infected, and should be applied as soon as appreciable damage is noticed.

Figures 1, 5, 6 and 10 from Demeure, Y., Netscher, C. & Quénéhervé, P. (1980). Biology of the plant-parasitic nematode **Schutellonema cavenessi** Scher, 1964 : reproduction, development and life cycle. **Revue Nématol.** 3 : 213-225 by permission.

Figures 4 from Demeure, Y., Freckman D.W. & Van Gundy, S.D. (1979). In vitro response of four species of nematodes to dessication and discussion of this and related phenomena. **Revue Nématol.** 2 : 203-210 by permission.

The others come from the « laboratoire de Nématologie ORSTOM de Dakar ».