# STUDIES ON THE FALSE ROOT-KNOT NEMATODE *NACOBBUS ABERRANS*.

BY

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Dedicated to my daughter Fernanda.

## ABSTRACT

Aspects of the biology, morphology and host-parasite relationships of Ecuadorian and British isolates of the "false root-knot" nematode Nacobbus aberrans were studied. Interactions between N. aberrans and Meloidogyne incognita were also investigated.

Morphometric studies revealed that both isolates belong to the same species, Nacobbus aberrans Thorne 1935 (Sher, 1970).

Life cycles were studied on tomato under ambient and constant temperatures. From $J_2$ to egg under ambient temperature (July to November) usually took 60 days for the Ecuadorian isolate, and 45 days for the British isolate. Immature females and males of both isolates were observed after 119 days under constant temperature at 14°C but no eggs were produced. At 19°C the life cycle for Ecuadorian and British isolates was completed in 80 and 70 days respectively, while at 25°C the Ecuadorian isolate took 35 days and the British isolate, 28 days. During the winter season, the low temperature adversely affected the development of the British isolate, and galling was not recorded. The Ecuadorian isolate could induce galling throughout the year, although during winter there was no egg production.

Two infective stages were revealed, the first was the $J_2$ and the second was the immature female that induced gall formation. The $J_4$ was found to be a survival stage of the nematode.

Histopathological observations on the two parasitic stages in tomato roots showed that the feeding of $J_2$ stages in the cortex produced necrosis and cavities surrounded by cells with thickened cell walls, while the female fed within the vascular system, producing

a syncytium and root galling.

The pathogenicity of N. aberrans was related to temperature and population levels in the soil. Fruiting of tomato was delayed and the yield reduced significantly.

When Nacobbus and Meloidogyne were inoculated together, the root system was further reduced and gall size was bigger than those produced by single inoculations of either nematodes.

N. aberrans grew in all the root-knot susceptible and resistant tomato varieties screened. Egg-plant, tomato, tree-tomato and naranjilla were also susceptible.

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# SECTION 1

## GENERAL INTRODUCTION

The "false root-knot nematode" Nacobbus aberrans is one of the lesser studied plant parasitic nematodes. This is probably for many reasons, such as, little is known of its economic importance, the nematode can be confused with other gall-forming nematodes belonging to the genus Meloidogyne, and it has a limited geographical distribution.

The common name of "false root-knot nematode" or forming-rosario, as it is known in Bolivia, is due to the similarity in forming galls like Meloidogyne spp., the root-knot nematodes. Nacobbus was first reported in 1918 when N.A. Cobb published illustrations that he supposed were a male and a small, blunt-tailed larva of the sugar beet nematode Heterodera schachtii, according to Thorne and Allen (1944). Thorne in 1935 discovered some specimens of a species of the false root-knot nematode attacking shadscale (Atriplex confertifolia) in the U.S.A., and made it the type species of a new genus, Nacobbus, named in honour of the late N.A. Cobb.

Since Thorne's original description, further species have been reported. Thorne and Allen (1944) discovered N. dorsalis producing galls on the roots of alfileria (Erodium cicutarium) sampled in California. In 1956, Thorne and Schuster reported N. batatiformis attacking the roots of sugar beet (Beta vulgaris) in Nebraska. Franklin (1959) reported Nacobbus on the roots of glasshouse tomatoes (Lycopersicon esculentum) in Berkshire, England, and described it as N. serendipiticus. The first report of Nacobbus in South America, was

by Lordello, Zamith and Boock (1961), who described a new sub species of N. serendipiticus Franklin, N. serendipiticus bolivianus on the roots of potatoes (Solanum andigenum) from Bolivia. In 1962, this same nematode was detected in some potato-growing areas of Huaylas-Huaraz in Peru (Gómez Tovar, 1973). Nacobbus has also been recorded in cultivated fields of green pepper (Capsicum annuum) in some of the central states of Mexico (Sosa Moss and González, 1973).

Nacobbus was found in soil samples from a cold glasshouse at Wageningen,Netherland, and this constituted the first report of Nacobbus on the continent of Europe (Bruijn and Stemerding, 1968).

Nacobbus has also been found associated with oregano (Origanum vulgare) in Chile (Jiménez, 1972), and on some natural weeds in Ecuador (Gowen, 1977 pers. comm.). The latter author considered that Nacobbus was also probably attacking some important crops, such as tomatoes and potatoes in Ecuador. The latest report came from Argentina, where Costilla, Ojeda and Gómez (1977) found Nacobbus on potato, beet root and some weeds (including Amaranthus sp. and Brassica sp.)

With four species and one sub species having been described, Sher (1970) reviewed the genus Nacobbus and proposed that N. batatiformis Thorne and Schuster, 1956; N. serendipiticus Franklin, 1959 and N. serendipiticus bolivianus, Lordello et al, 1961, were synonyms of N. aberrans (Thorne, 1935), Thorne and Allen, 1944. He considered that there are only two species, N. aberrans and N. dorsalis.

Studies on the biology of Nacobbus are scarce. Thorne and Schuster (1956) were the first to demonstrate the life cycle of N. aberrans (formerly N. batatiformis) on sugar beet. Two periods of parasitism were reported. They also pointed out that, as Nacobbus

has a wide range of taxonomically diverse plant hosts, there may be some variations in its life history depending on the host.

Clark (1967) studied the life-history of N. aberrans from egg to maturity and demonstrated that four moults occurred, the first in the egg. Prasad and Webster (1967) determined how temperature affects the rate of development of Nacobbus using excised tomato roots in nutrient agar. Temperature seems to be an important factor in the development of Nacobbus as demonstrated by Schuster et al (1966) in a study on the effect of different soil temperatures on the infection and development of N. aberrans in sugar beet. Few or no root-galls were formed at 10°C and 15°C. Increased galling occurred with increased temperature.

Alarcón and Jatala (1977) tested three different populations of Nacobbus against one susceptible and one resistant potato variety in Peru, under two different regimes of temperature (18° - 30°C in Lima and 10° - 22°C in Huancayo). They found that temperature must be considered as an important factor in the expression of resistance.

Histological observations of Nacobbus on sugar beet were done by Schuster and Thorne (1956). They described the syncytium as a "spindle" shaped structure, with cells that retained their identity. Schuster et al (1965) again studied the histopathology induced by N. aberrans in sugar beet and found that the syncytium is located entirely within the cortex and bounded by the endodermis, or, on occasions, by the xylem elements. The syncytium of Nacobbus is different from that of Meloidogyne and Heterodera, in that transfer cells are not present (Jones and Payne, 1977b).

Schuster et al (1965) examined the life history and host parasite relationship of Nacobbus. They found that the immediate

reaction of root tissues to the invasion of the nematodes was necrosis and hypertrophy, followed by galling due primarily to hypertrophy of the cortical cells.

Economic importance

Nacobbus has been reported to cause economically important losses of sugar beet and potatoes. Between 1956 and 1966 some research was done on Nacobbus attacking sugar beet in North America. (Thorne and Schuster, 1956; Schuster and Thorne, 1956; Schuster et al 1966), reflecting its increasing potential of economic importance.

Schuster and Thorne (1956), studied the distribution, relationship to weeds, and histopathology of Nacobbus. Caveness (1959) clarified the incidence of some parasitic nematodes present in sugar beet growing areas in the U.S.A. by studying the distribution of cyst and gall-forming nematodes. The economic importance of H. schachtii, some Meloidogyne spp. and the presence of N. aberrans was demonstrated.

The importance of N. aberrans as a pest of potatoes has been demonstrated since its first report by Lordello et al in 1961. It has caused and continues to cause, economic losses of potatoes in Bolivia and Peru, the main potato-growing areas of South America.

Gómez Tovar (1973) in Peru showed that the spread of Nacobbus was from an initial focus in Huaylaz to the principal potato-growing areas and it has reduced potato yield to between 60 and 90%. In this same country, after Globodera spp., Nacobbus is the second most important pest of potatoes in Southern, Central and Northern sierras (in order of importance) (Herrera, 1977).

Thus, the recognition of Nacobbus as an important pest has

increased in Bolivia and Peru. Alarcón (1977) evaluated 741 native clones of potatoes from the potato germoplasm collection of the Toralapa Experimental Station, Bolivia, including diploids, triploids and tetraploids; 23 of the clones showed some resistance to the nematode.

Cornejo (1977a) evaluated ten varieties of potatoes as hosts for Heterodera and Nacobbus, and found that the varieties sacomponya, Cochabamba, Mantaro and Tomasa Tito Condemayta had lower levels of galling and cysts. Varieties Compis, Sipeña, and Mi Perú were more susceptible under field experiments in Peru. A chemical study has also been done in an attempt to control Nacobbus and Globodera (Cornejo, 1977b). Ten nematicides were tested in a field infested with both nematodes in Peru, but there were no significant differences in yields between treated and untreated plants.

Cornejo (1977c) tested Tarwi (Lupinus mutabilis) as an antagonistic crop to Nacobbus and Heterodera. He found that there was a reduction in the number of galls and new white cysts on roots of potatoes, when either potato plants were surrounded by four Tarwi plants or potato plants were watered with Tarwi root leachate.

Potato is not the only host of Nacobbus and Cobb's nematode is able to develop in many other crops, as has been observed by Thorne and Schuster (1956), Clark (1967) and Cornejo (1977d), who demonstrated that Nacobbus has a wide host range on different crops.

To demonstrate the damage caused by this nematode, investigations on its pathogenicity have been done on tomato and chilli pepper. Sosa Moss and Muñoz (1973) testing different inoculum levels of Nacobbus on two tomato varieties, determined that this nematode

reduced plant height and yield significantly. Also Nacobbus negatively affected growth and yield of three varieties of chilli pepper (Sosa Moss and González, 1973).

Nacobbus is of special interest to me because the genus is found in my home country, Ecuador, and its pest status has yet to be demonstrated there. Considering it a potential enemy, and because little information is available, in these studies I have attempted to answer some of the basic questions on the biology, pathogenicity and identification of Nacobbus, and its important interaction and relationship with Meloidogyne.

# SECTION 2

## GENERAL MATERIALS AND METHODS

### Populations

Two isolates of Nacobbus were used. The Ecuadorian isolate was collected by Dr. S. Gowen in 1978 from Guayllabamba, Ecuador, 2.300m. above sea level in the Andes with a mean temperature of 17°C per year. The British isolate was from a culture maintained at Silwood Park, Ascot on tomato, which originally came from Dr. M.T. Franklin's culture (formerly N. serendipiticus) at Rothamsted where it has been maintained since 1959.

### Cultures and seedlings for experiments.

Tomato seedlings (var. Moneymaker) were grown in 9 in. diameter pots containing sterilized soil. Egg-masses of N. aberrans were picked off and were then used to inoculate the tomato seedlings. Tomato seedlings (var. Moneymaker), 15 days old, were used in all the experiments., except experiments : 4.2., 6.3 and 6.4. A mixture of 50% loam and 50% sand was used for all the experiments. Powdered fertilizer (Phostrogen) was added once a week.

### Nematode inoculum and inoculation

The infested roots of tomato plants from pure cultures of each isolate were first washed free of soil. Active Nacobbus juveniles were then obtained from egg-masses which were picked-off the roots and placed on small 90 μ nylon mesh sieves in watch glasses containing distilled water and the level of distilled water was adjusted until the surface of the sieve was immersed (Escobar, 1975). The egg-masses were kept at 27°C ± 2 in an incubator. Hatched juveniles,

after migrating through the sieves, were removed and kept in distilled water at room temperature until required. Only those juveniles which hatched in the first six days were used. The number of juveniles obtained was estimated by counting three 1 mil. aliquots of the agitated juvenile suspension.

Inoculation was achieved by injecting with a syringe a predetermined number of juveniles into a hole made in the moist soil. The tomato seedling was then planted in this hole.

Extraction and estimation of populations

Nematodes from roots and soil were extracted, counted, their development stages identified and, when required, their sex identified.

a) In roots

The whole root system (for life cycle experiments) or 1g. of roots for the other experiments, were washed free of soil, and then boiled in 0.1% lactophenol cotton blue for 3 minutes. The excess of stain was washed off in running tap water and the roots cleared in clear lactophenol. The nematodes were dissected from the roots using fine forceps and a scalpel with the aid of a stereoscopic microscope (Hooper, 1970a).

b) In soil

Two methods of extraction were used:

i. A modification of Cobb's decanting and sieving method (Cobb, 1918, cited by Flegg and Hooper, 1970).

This method was used in two life cycle experiments. The whole root system was gently washed with tap water in a bucket. The suspension was passed through a series of sieves (300, 90 and 53 µm aperture size). The residue from the last two sieves was washed into

a beaker and water added to give a final volume of 100 mls. A 10 ml. aliquot was removed, and the number of nematodes counted.

ii Tray modification of the Baermann funnel technique (Whitehead and Hemming, 1965).

All the soil from life cycle experiments or 100 $cm^3$ of soil from the other experiments was placed on tissue in a photographic tray containing approximately 800 ml. of water. This was left for 48 hours in a heated glasshouse. The suspension was collected in a beaker and left to stand for 24 hours. The supernatant was siphoned off (Bridge, 1971). The number of nematodes were estimated from a 5% aliquot of the suspension.

The stage and sex of the nematodes was determined by examination of gonad development in lactophenol microscope slide mounts (Clark, 1967) using a compound microscope.

# SECTION 3

## MORPHOLOGICAL STUDIES

### Introduction

In the genus Nacobbus, four species and one sub species have been described. N. aberrans (formerly Anguillulina aberrans, Thorne, 1935), Thorne and Allen, 1944. N. dorsalis, Thorne and Allen, 1944. N. batatiformis Thorne and Schuster, 1956. N. serendipiticus, Franklin, 1959, and the sub species N. serendipiticus bolivianus, Lordello, Zamith and Boock, 1961.

However, Sher (1970) reviewing the genus Nacobbus; proposed N. batatiformis, N. serendipiticus and N. serendipiticus bolivianus as synonyms of N. aberrans, leaving only two species N. aberrans and N. dorsalis.

N. aberrans is distinguished from N. dorsalis by the larger number of body annules between vulva and anus, the lower position of the vulva in the young female; and the shape and number of eggs retained in the mature female.

Twenty six populations of Nacobbus collected from Argentina, Bolivia, Ecuador, and Peru were examined morphologically for taxonomic identification by Jatala and Golden (1977). They found that, although there were differences in morpho metric details, the variations were within the limits proposed by Sher for N. aberrans.

The purpose of this study was to establish the taxonomic position of the Ecuadorian population of Nacobbus in comparison with the British isolate, originally described as N. serendipiticus (Franklin, 1959) from tomato roots in glasshouses.

## MATERIALS AND METHODS

Fresh hatched juveniles extracted from egg-masses, and other stages from infected tomato roots, were killed gently by heat and fixed in T.A.F. overnight. The nematodes were then stained in 0.1% lactophenol cotton blue, passed through Baker's solutions at 55°C and mounted finally in pure glycerol (Hooper, 1970b).

Twenty second stage juveniles, ten adult immature females, ten males and ten adult females were measured with the aid of a camera lucida for both isolates.

The following symbols have been used:

L = Total body length.

W = Greatest body width.

Spear = Spear length.

a = Total body length divided by greatest body width.

b = Total body length divided by distance from anterior end to junction of oesophagus and intestine.

b' = Total body length divided by distance from anterior end to posterior end of oesophageal gland (overlap).

c = Total body length divided by tail length.

c' = Total tail length divided by body width at anus or cloaca.

S = Spear length divided by body width at base of spear.

V = Distance of vulva from anterior end x 100 divided by body length.

O = Ovary length.

R Van = Annules between vulva and anus.

T = Distance from cloaca to anteriormost part of testis x 100 divided by body length.

Spicule = Spicule length.

Gubernaculum = Gubernaculum length.

# RESULTS

## Second stage juvenile measurements

British isolate n = 20. L = 0.35 mm. (0.31 - 0.37). W = 14 μ (13 - 19). Spear = 11 μ (10 - 12), a = 24.1 (19 - 27). b = 3.8 (3.3 - 4.5.). b' = 2.6 (2.3 - 3.0). c = 14.6 (13 - 18). c' = 2.6 (2.1 - 3.2). S = 1.1 ( 0.9 - 1.3 (Appendix A. Table 1).

Ecuadorian isolate n = 20. L = 0.32 mm (0.26 - 0.35). W = 13 μ (10 - 16). Spear = 12 μ (11 - 14). a = 24.7 (21 - 30). b = 3.5 (2.9 - 4.21). b' = 2.4 (2.1 - 2.7). c = 14.6 (13 - 17). c' = 2.6 (1.8 - 3.1). S = 1.2 (1.1 - 1.5) (Appendix A. Table 2).

## Description

The second stage juvenile has a lip region with three annules and an obvious cephalic framework. The tail is bluntly-rounded and the body cylindrical (resembling a young Pratylenchus). The excretory pore lies behind the hemizonid. Oesophagus extends dorsally over the intestine. The genital primordium appears as a single cell. Lateral field is formed of four bright lateral lines; phasmids present in the middle of the tail (Fig. 3.1).

Between isolates were found some morphometric characters that differed statistically. Highly significant were length of the body for the British isolate and spear length for the Ecuadorian isolate. There were also significant differences in greatest body width, b and b' for the British isolate.

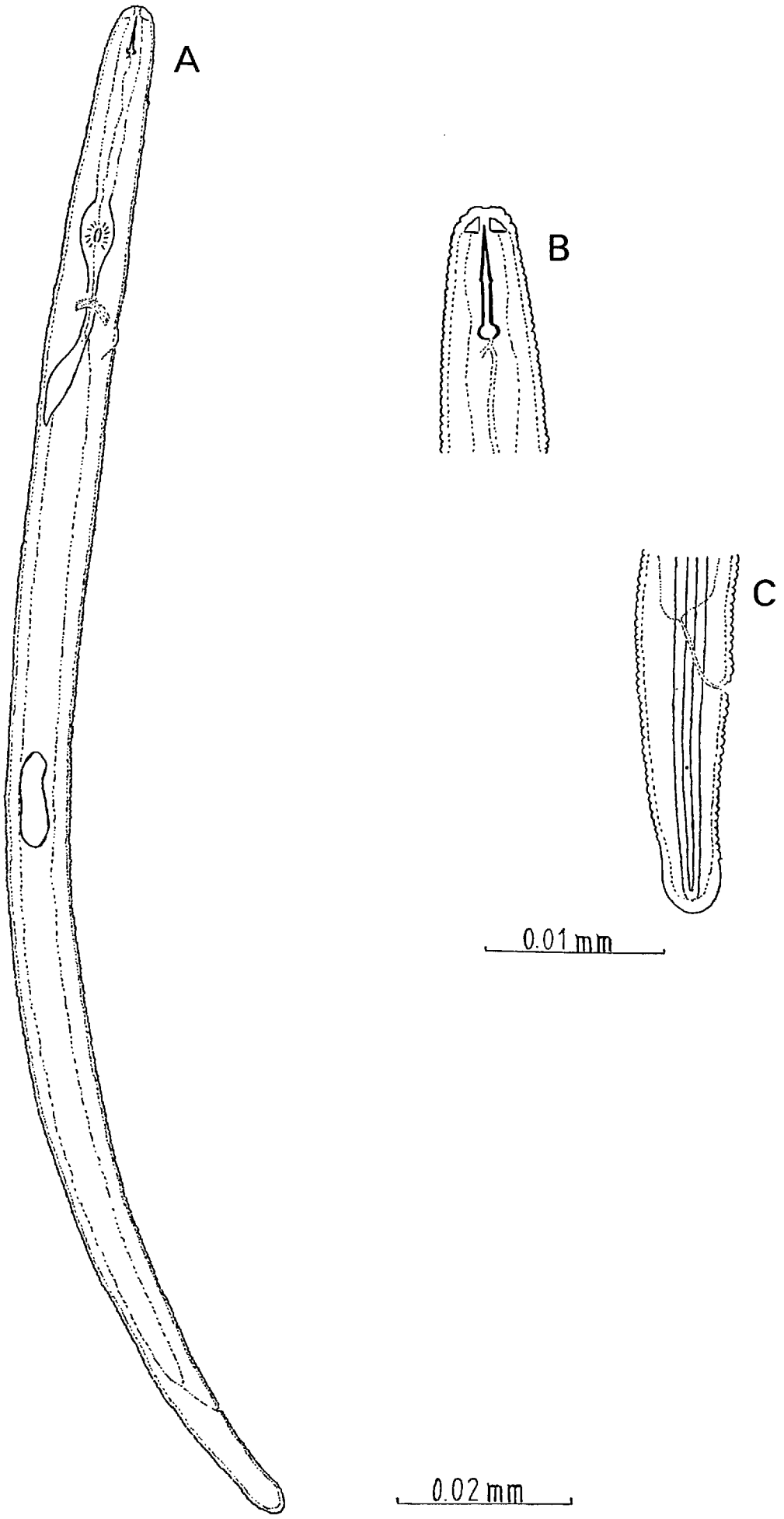



Fig. 3.1. Nacobbus aberrans. Second stage juvenile. (Ecuadorian isolate). A. Entire second stage juvenile. B. Head end. C. Tail end.

Sher (1970) did not show any descriptions relating to second stage juvenile, however in Table 3.1 is given the measurements, done by Lordello et al (1961) and Franklin (1959) and compared with those obtained in the present study.

Although Lordello et al's description is very short it agrees with Franklin in that Nacobbus $J_2$ has a lateral field marked by four lines and that a small phasmids are located in the middle of the tail. Franklin's descriptions are very detailed and are similar to those obtained in my study, despite the fact that I found statistical differences between isolates.

Immature female measurements

British isolate n = 10. L = 0.85 mm (0.68 - 1.05). W = 33 μ (25 - 41). Spear = 20 μ (17 - 22). a = 26 (22 - 32). b = 7.2 (5.6 - 8.7). b' = 4.2 (3.4 - 4.9). c = 32.8 (29 - 37). c' = 1.3 (1.1 - 1.5). S = 1.1 (0.9 - 1.2) V = 92.6% (91 - 94) O = 44.5 μ (29 - 61). R van = 20 (18 - 24). (Appendix A. Table 3.)

Ecuadorian isolate n = 10. L. = 0.92 mm (0.81 - 0.99). W = 30 μ (23 - 29). Spear = 20 μ (18 - 21). a = 31 (24 - 43). b = 7.7 (6.9 - 8.9). b' = 4.7 (4.0 - 5.4). c = 36 (29 - 47). c' = 1.3 (0.9 - 1.9). S = 1.1 (0.9 - 1.3). V = 92.5% (91 - 93). O = 42.8 μ (26 - 56). R van = 21 (17 - 25). (Appendix A. Table 4.).

Description

Body vermiform. Head sclerotized with 3 annules. Spear strong and typically tylenchid, with round knobs. Median bulb is quite well - developed with a large conspicuous valve (6.53 μ diameter), which is slightly bigger than males (4.03 μ diameter). The oesophageal

TABLE 3.1. MEASUREMENTS OF SECOND STAGE JUVENILE OF N. ABERRANS FROM DIFFERENT POPULATIONS DONE BY LORDELLO ET AL., 1961; FRANKLIN, 1959 AND THE AUTHOR.

| CHARACTER OF MEASUREMENTS | LORDELLO ET AL 1961 | FRANKLIN, 1959 | PRESENT RESULTS | |
|---|---|---|---|---|
| | BOLIVIA | ENGLAND | ENGLAND (20 $J_2$) | ECUADOR (20 $J_2$) |
| L | 0.30 - 0.36 mm | 0.33 mm (0.31 - 0.34) | 0.35 mm (0.31 - 0.37) | 0.32 µ (0.26 - 0.35) |
| W | 15.3 µ | 14µ(12 - 15) | 14 µ(13 - 19) | 13 µ (10 - 16) |
| Spear | 10.7 - 12.3 µ | 13µ | 11 µ(10 - 12) | 12 µ (11 - 14) |
| a | 19.5 - 23.8 | 23 (21 - 26) | 24.1 (19 - 27) | 24.7 (21 - 30) |
| b | 3.3 - 4.1 | 6 | 3.8 (3.3 - 4.5) | 3.5 (2.9 - 4.2) |
| b' | N.T. | N.T. | 2.6 (2.3 - 3.0) | 2.4 (2.1 - 2.7) |
| c | 9.7 - 13.0 | 13.4 (13 - 14) | 14.6 (13 - 18) | 14.6 (13 - 17) |
| c' | N.T. | N.T. | 2.6 (2.1 - 3.2) | 2.6 (1.8 - 3.1) |
| S | N.T. | N.T. | 1.1 (0.9 - 1.3) | 1.2 (1.1 - 1.5) |

lobe overlaps the intestine dorsally. Excretory pore lies behind the hemizonid. Orifice of dorsal oesophageal gland about 2 or 3 μ below spear base. Narrow isthmus. The single ovary does not show spermatheca. Four lines form the lateral field. Vulva close to the anus, with 21 annules between vulva and anus. The vulva position is 92 - 93% from anterior of the body. Phosmids are slightly behind the anus. Tail rounded (Fig. 3.2).

There were no statistical differences between isolates. The description of immature female in this study, is very closely similar to those of Franklin (1959), Sher (1970) and Lordello et al (1961). In general, there were no relevant morphological differences between populations, and the morphometric measurements given in Table 3.2, is evidence of this.

Male measurements

British isolate n = 10. L = 0.94 mm. (0.83 - 1.05). W = 40 μ (32 - 51). Spear = 21 μ (18 - 23). a = 24.1 (21 - 27). b = 7.9 (7.0 - 8.9). b' = 5.0 (4.3 - 5.7). c = 37.5 (28 - 42)- c' = 1.2 (1.0 - 1.5). S = 1.1 (0.9 - 1.3). Spicules = 26 μ (24 - 30). Gubernaculum = 7 μ (6 - 8). T = 66.7% (53 - 80). (Appendix A. Table 5.).

Ecuadorian isolate n = 10. L = 1.03 mm (0.76 - 1.24). W = 37 μ (25 - 48). Spear = 23 μ (22 - 24). a = 28.4 (23 - 42). b = 8.1 (6.7 - 9.1). b' = 4.6 (3.7 - 5.3). c = 39.4 (33 - 48). c' = 1.2 (1.0 - 1.4). S = 1.1 (0.9 - 1.6). Spicules = 31 μ (28 - 34). Gubernaculum = 8 μ (6 - 11). T = 67.3% (52 - 87). (Appendix A. Table 6.).

Description

Body is cylindrical, but an open 'c' shape when relaxed by gentle heat. Head sclerotized with 3 annules. Strong stylet and

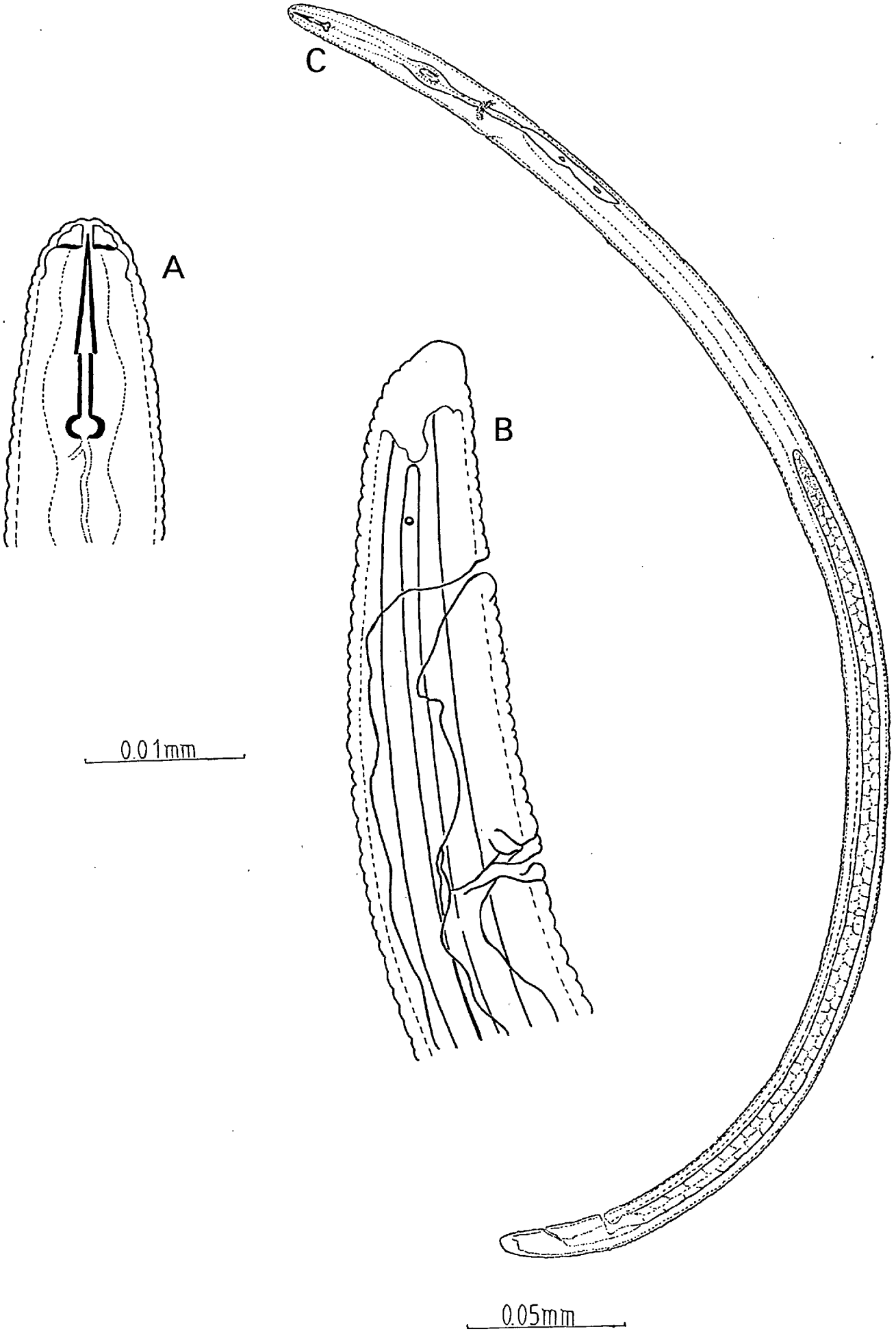



Fig. 3.2. Nacobbus aberrans. Immature female. (Ecuadorian isolate). A. Head end. B. Tail end. C. Entire vermiform immature female.

TABLE 3.2. MEASUREMENTS OF IMMATURE FEMALES OF N. ABERRANS FROM DIFFERENT POPULATIONS DONE BY SHER, 1970; LORDELLO ET AL., 1961; FRANKLIN, 1959 AND THE AUTHOR.

| CHARACTERS OF MEASUREMENTS | SHER, 1970 | | | LORDELLO ET AL 1961 | FRANKLIN 1959 | PRESENT RESULTS | |
|---|---|---|---|---|---|---|---|
| | TOPOTYPE (12 imm. ♀) | NEBRASKA (6 imm. ♀) | ENGLAND (10 imm. ♀) | BOLIVIA | ENGLAND | ENGLAND (10 imm. ♀) | ECUADOR (10 imm. ♀) |
| L | 0.84mm (0.71-0.93) | 0.78mm (0.74-0.84) | 0.71mm (0.60-0.78) | 0.77 mm | N.T. | 0.85mm (0.68-1.05) | 0.92mm (0.81-0.99) |
| W | N.T. | N.T. | N.T. | 26µ | N.T. | 33µ (25-41) | 30µ (23-39) |
| Spear | 23µ (21-25) | 21µ (20-23) | 20µ (19-21) | 16µ | N.T. | 20µ (17-22) | 20µ (18-21) |
| a | 27 (23-40) | 30 (27-32) | 28 (23-31) | 29.6 | N.T. | 26 (22-32) | 31 (24-43) |
| b | N.T. | 7.6 (7.0-9.3) | 5.4 (5.1-5.8) | N.T. | N.T. | 7.2 (5.6-8.7) | 7.7 (6.9-8.9) |
| b' | 3.8 (2.8-4.1) | 4.2 (4.1-4.5) | 3.3 (2.8-3.9) | N.T. | N.T. | 4.2 (3.4-4.9) | 4.7 (4.0-5.4) |
| c | 37 (24-40) | 34 (30-38) | 29 (23-32) | 25.9 | N.T. | 32.8 (29-37) | 36 (29-47) |
| c' | 1.2 (0.9-1.5) | 1.5 (1.3-2.0) | 1.5 (1.3-1.6) | N.T. | N.T. | 1.3 (1.1-1.5) | 1.3 (0.9-1.9) |
| S | N.T. | N.T. | N.T. | N.T. | N.T. | 1.1 (0.9-1.2) | 1.1 (0.9-1.3) |
| V | 93 (92-94) | 93 (92-94) | 92 (91-93) | 92.4 | 94 | 92.6 (91-94) | 92.5 (91-93) |
| O | N.T. | N.T. | N.T. | N.T. | N.T. | 44.5µ (29-61) | 42.8µ (26-56) |
| R van | 20 (15-24) | 22 (18-25) | 20 (16-24) | N.T. | N.T. | 20 (18-24) | 21 (17-25) |

round basal knobs, slightly bigger than female. Excretory pore lies behind the hemizonid. The oesophagus overlaps the intestine dorsally. The testes extend forward to a point two or four body - widths posterior to the oesophageal lobe. Spicules are typical tylenchid and the gubernaculum is simple. A narrow bursa envelopes the tail, which is blunt and slightly tapered. Lateral field shows four incisures. Phasmids are present, behind the spicules in the middle of the tail (Fig. 3.3).

Both the spear and spicule length of the Ecuadorian isolate, were significantly different to the British isolate (spear = 23 µ, spicules = 31 µ for the Ecuadorian population, and spear = 21 µ, spicules = 26 µ for the British population).

Sher (1970) described the male as similar to the immature female, except for sexual dimorphism. Franklin's description suggested that males have 4 annules on the head; in agreement, Lordello et al determined also the presence of 4 annules, which differed from my observations, where I found 3 annules. Morphometric measurements are shown in Table 3.3 for comparison.

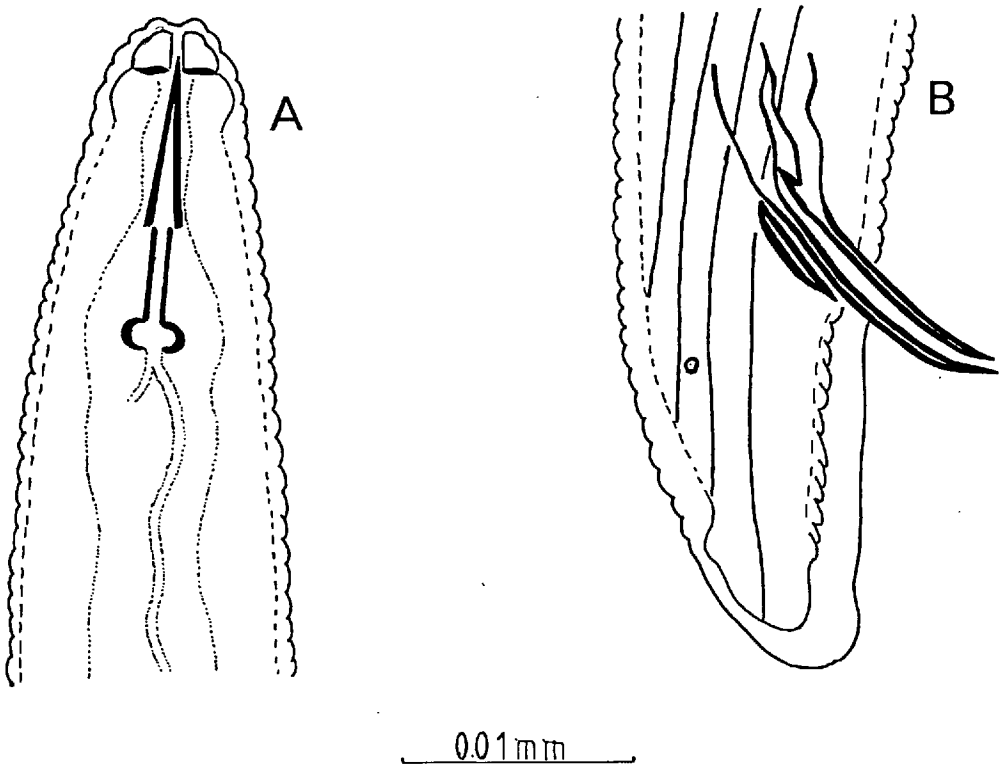
Mature female measurements

British isolate n = 10. L = 1.17 mm. (0.86 - 1.35). Spear = 20 µ (19 - 23). (Appendix A. Table 7.).

Ecuadorian isolate n = 10. L = 1.38 mm. (1.20 - 1.66). Spear = 20.7 µ (19 - 24). (Appendix A. Table 7).

Description

The body of mature female, typically is spindle - shaped, but variations occur, due apparently to the pressure of the root tissue. A narrow neck is present. The median bulb strongly developed, with conspicuous radial musculature. Excretory pore lies behind the



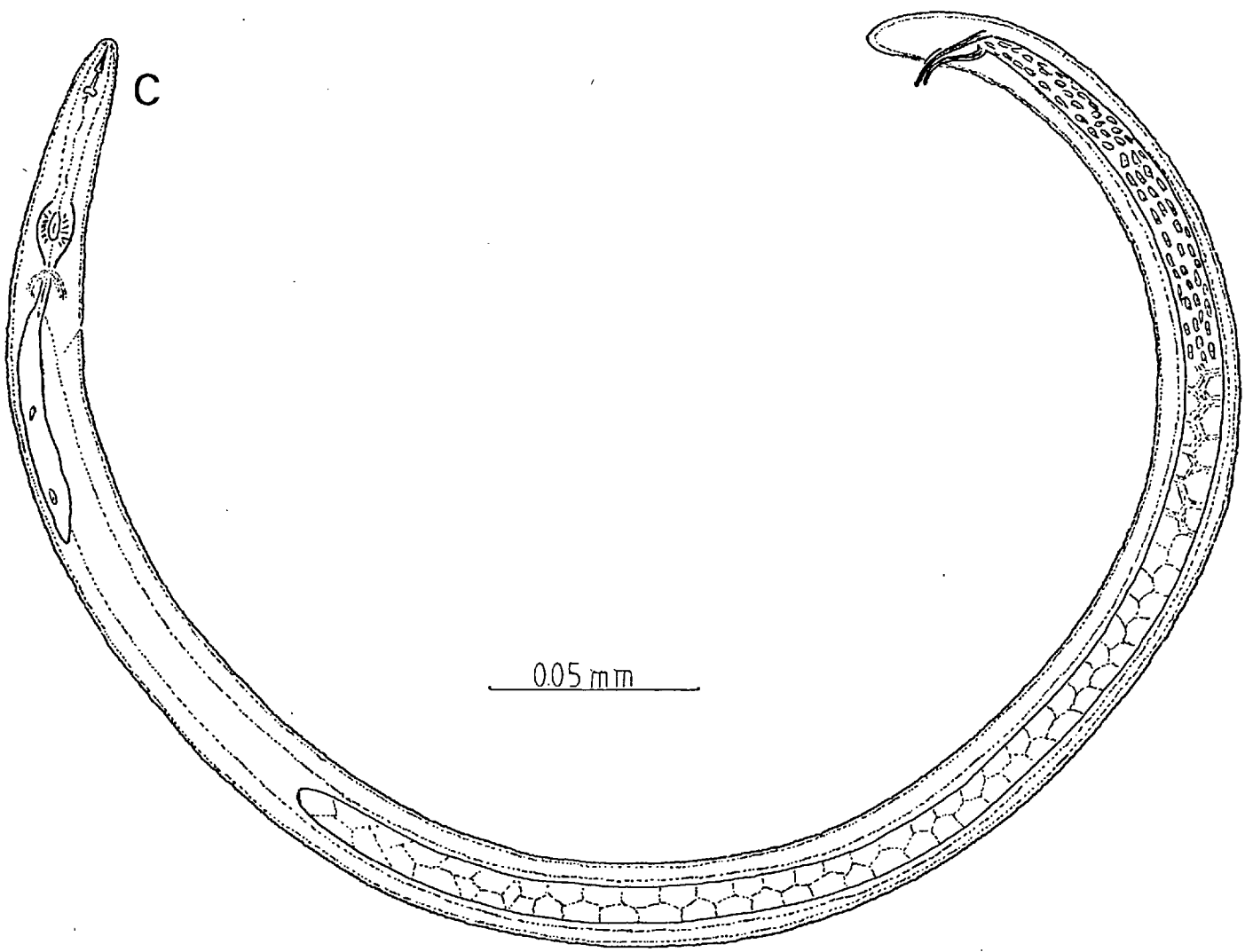




Fig. 3.3. Nacobbus aberrans. Male. (Ecuadorian isolate). A. Head end. B. Tail end.

TABLE 3.3. : MEASUREMENTS OF MALES OF N. ABERRANS FROM DIFFERENT POPULATIONS DONE BY SHER, 1970; LORDELLO et al., 1961; FRANKLIN, 1959 AND THE AUTHOR.

| CHARACTER OF MEASUREMENTS | SHER, 1970 | | | LORDELLO et al., 1961 | FRANKLIN, 1959 | PRESENT RESULTS | |
|---|---|---|---|---|---|---|---|
| | TOPOTYPE (7 ♂) | NEBRASKA (5 ♂) | ENGLAND (6 ♂) | BOLIVIA | ENGLAND | ENGLAND (10 ♂) | ECUADOR (10 ♂) |
| L | 0.86 mm (0.71-0.92) | 0.80 mm (0.68-0.88) | 0.78 mm (0.67-0.88) | 0.79- 0.90 mm | 0.83 mm (0.73-0.93) | 0.94 mm (0.83-1.05) | 1.03 mm (0.76-1.24) |
| W | N.T. | N.T. | N.T. | 35.2 -45.9 µ | 29 µ (25-30) | 40 µ (32-51) | 37 µ (25-48) |
| Spear | 25 µ (23-27) | 24 µ (23-27) | 25 µ (23-27) | 21.4 -22.9 µ | 25 µ (22-27) | 21 µ (18-23) | 23 µ (22-24) |
| a | 29 (24-31) | 33 (28-39) | 30 (24-32) | 18.8 -25.4 | 29 (23-32) | 24.1 (21-27) | 28.4 (23-42) |
| b | 7.0 (6.4-7.2) | 6.7 (6.5-8.3) | 6.1 (5.6-6.6) | 7.2 - 8.5 | 10 (6-13) | 7.9 (7.0-8.9) | 8.1 (6.7-9.1) |
| b' | 3.6 (3.4-4.0) | 4.3 (4.2-4.4) | 4.5 (3.5-5.4) | N.T. | N.T. | 5.0 (4.3-5.7) | 4.6 (3.7-5.3) |
| c | 38 (32-42) | 35 (33-36) | 34 (30-38) | 34.3 -46.8 | 40 (31-53) | 37.5 (28-42) | 39.4 (33-48) |

TABLE 3.3. : Continued.

| CHARACTER OF MEASUREMENTS | SHER, 1970 | | | LORDELLO et al., 1961 | FRANKLIN, 1959 | PRESENT RESULTS | |
|---|---|---|---|---|---|---|---|
| | TOPOTYPE (7 ♂) | NEBRASKA (5 ♂) | ENGLAND (6 ♂) | BOLIVIA | ENGLAND | ENGLAND (10 ♂) | ECUADOR (10 ♂) |
| c' | 1.3 (1.2-1.4) | 1.5 (1.3-1.7) | 1.2 (1.0-1.5) | N.T. | N.T. | 1.2 (1.0-1.5) | 1.2 (1.0-1.4) |
| S | N.T. | N.T. | N.T. | N.T. | N.T. | 1.1 (0.9-1.3) | 1.1 (0.9-1.6) |
| Spicules | 27 µ (21-30) | 28 µ (24-34) | 27 µ (26-32) | 26.0 -30.6 | 27 µ (24-29) | 26 µ (24-30) | 31 µ (23-34) |
| Gubernaculum | 7 µ (6-8) | 9 µ (7-11) | 8 µ (7-10) | 7.6 - 9.2 | N.T. | 7 µ (6-8) | 8 µ (6-11) |
| T | N.T. | N.T. | N.T. | N.T. | N.T. | 66.7 (53-80) | 67.3 (52-87) |

hemizonid. The oesophageal lobe overlaps the intestine dorsally. The ovary is coiled and may extend to reach the level of the isthmus or median bulb. The tail terminus has a special prominence like nipple - shape. (Fig. 3.4).

The length of the body in the Ecuadorian isolate was significantly longer than the British isolate (1.38 mm to 1.17 mm respectively).

The descriptions of Sher (1970), Franklin (1959) and Lordello et al (1961) with reference to mature female, are similar and agree with my observations. In Table 3.4 is given the morphometric measurements of each population for comparison.

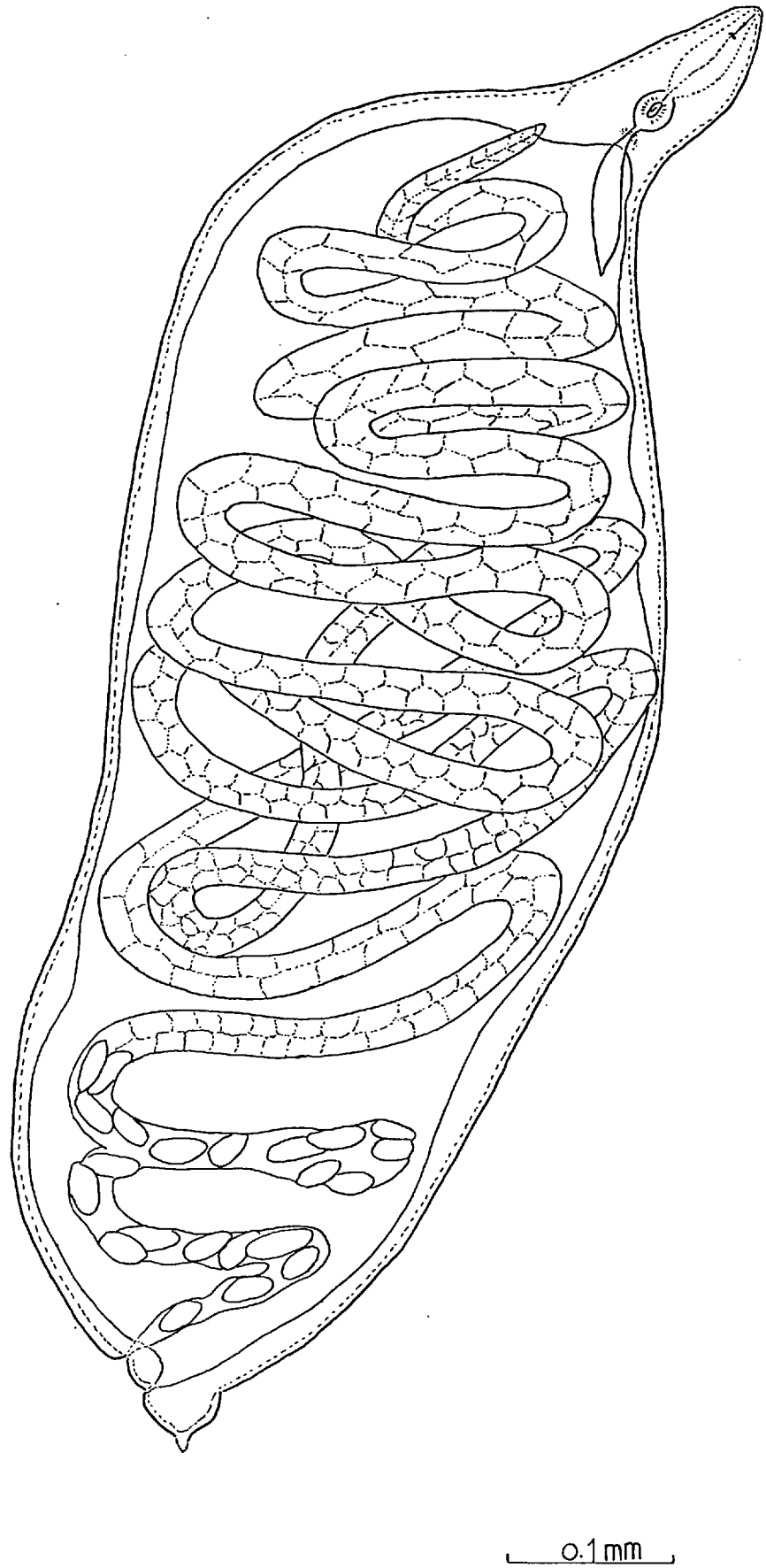



Fig. 3.4. Nacobbus aberrans. Mature female. (Ecuadorian isolate).

TABLE 3.4. : MEASUREMENTS OF MATURE FEMALES OF N. ABERRANS FROM DIFFERENT POPULATIONS DONE BY: SHER, 1970; LORDELLO et al., 1961; FRANKLIN, 1959 AND THE AUTHOR.

| CHARACTER OF MEASUREMENTS | SHER, 1970 | | | LORDELLO et al., 1961 | FRANKLIN, 1959 | PRESENT RESULTS | |
|---|---|---|---|---|---|---|---|
| | TOPOTYPE (6 mat. ♀) | NEBRASKA (6 mat. ♀) | ENGLAND (7 mat. ♀) | BOLIVIA | ENGLAND | ENGLAND (10 mat. ♀) | ECUADOR (10 mat. ♀) |
| L | 1.0 mm (0.8-1.2) | 1.1 mm (1.0-1.4) | 1.08 mm (0.91-1.45) | 1.08- 1.91 mm | 0.9-1.6 mm | 1.17 mm (0.86-1.35) | 1.38 mm (1.2-1.66) |
| W | N.T. | N.T. | N.T. | 465.0-542.5 µ | 260-420 µ | N.T. | N.T. |
| Spear | 22 µ (20-24) | 22 µ (20-24) | 22 µ (20-23) | 22 µ | 20.3 µ (19-22) | 20 µ (19-23) | 20.7 µ (19-24) |

## DISCUSSION

When Franklin (1959), described N. serendipiticus, she found that this new species was closest to N. batatiformis; however, slight differences were noted such as, N. serendipiticus female had a longer stylet than N. batatiformis; the males of N. batatiformis were a little longer and more slender than N. serendipiticus and finally that the larvae of N. batatiformis differed from N. serendipiticus in being more slender and having longer tails.

Lordello et al in 1961, discovered, what they called a new sub-species of N. serendipiticus, N. serendipiticus bolivianus. This new sub-species differed from Franklin's species in two features, a) the central ribbon of the lateral field was narrower than the outer ones, a characteristic shown particularly by first stage larvae and young female; and, b) wider males.

After comparing the British isolate with the Ecuadorian isolate of Nacobbus it was found that the second stage juvenile of the British isolate had a longer body, and other measurements such as, w, b, b' were significantly different from the Ecuadorian isolate. Also the second stage of the Ecuadorian isolate had a longer spear than the British isolate.

Differences between males, also were determined. The Ecuadorian isolate had longer spears and spicules than the British isolate; moreover, the length of the mature female of the Ecuadorian isolate differed significantly from that of the British isolate.

Sher considered males to be morphologically similar to females, except for sexual characters, but in this study was found that the valve diameter of the median bulb in immature females, was significantly larger than that of males in both isolates, which is a new

character distinguishing males from females.

The morphometric differences exhibited in this study for both isolates, however, did not differ in my opinion from the range of observations by Franklin (1959), Lordello et al (1961) and Sher (1970) for other populations of Nacobbus, that the latter synonimized with Nacobbus aberrans. Furthermore, the characters that Franklin used to differentiate N. serendipiticus from N. batatiformis, and Lordello et al N. serendipiticus bolivianus from Franklin's species, were not found in my observations, so that the variations found among populations in some cases, are inherent to each isolate. In agreement, Jatala and Golden (1977) studying the taxonomic status of 26 populations of Nacobbus sampled in Argentina, Bolivia, Peru and Ecuador, found that there were morphometric differences among the nematodes of these various populations but they were within the broad limits of the several populations described by Sher for N. aberrans.

Therefore, I agree with the Sher revision, and include the Ecuadorian isolate within the species Nacobbus aberrans Thorne, 1935 (Sher, 1970), but consider that N. aberrans has a series of biological forms.

# SECTION 4

## BIOLOGICAL STUDIES OF TWO ISOLATES OF NACOBBUS ABERRANS

### 4.1 LIFE CYCLE STUDIES

#### Introduction

Since the first description of the genus Nacobbus by Thorne and Allen (1944), few studies on the life history of this nematode have been done, and some confusion has occurred due to the lack of information. The biology of Nacobbus has been studied by Thorne and Schuster (1956) Schuster et al (1965), Clark (1967) and Prasad and Webster (1967).

Thorne and Schuster (1956) described the life cycle of N. aberrans on sugar beet and pointed out that larvae emerging from the eggs enter small roots. Two moults occur during this feeding period, the preadults then migrate into the soil, moult for the last time and became active males or immature females. The females invade other roots, became swollen, and their feeding produces galls. They extrude a gelatinous matrix into which eggs are discharged and males are often found entangled within this gelatinous matrix. The second larval stage has been termed the infective stage by Schuster et al (1965). They also presumed that the fourth stage larvae and adults were sedentary whilst the early third stage larvae are motile.

Clark (1967), studying the development and life history of N. aberrans also found that four moults occurred. The sex of the larvae can be determined at the end of the third stage by the development of the gonads. Prasad and Webster (1967), found that the generation time in Nacobbus from egg to egg is 36 days at 25°C and 43 days at 20° or 30°C. They also stated that the sex ratio was affected by temperature.

Temperature appears to be an important factor in the development of Nacobbus. It has been shown for other nematodes, such as Meloidogyne, that invasion, reproduction, pathogenicity, survival, resistance, etc., are related to temperature (Daulton and Nusbaum, 1961; Thomason, 1957; Davide and Triantaphyllou, 1967; Vrain, Barker and Holtzman, 1978).

The purpose of the present study was to observe and compare life cycles, and aspects of behaviour and development between two isolates of N. aberrans as influenced by temperature under different growing conditions.

## MATERIALS AND METHODS

In this series of biological observation, British and Ecuadorian isolates of N. aberrans were compared. Tomato seedlings (var. Money-maker), 15 days old, were inoculated with 100 second stage juveniles of N. aberrans in 4 in diameter plastic pots for both isolates.

Behavioural and developmental observations, mainly of invasion, migration, gall formation and egg-masses were done throughout the life cycles at ambient and constant temperatures.

It was not possible to keep a regular frequency of sampling among experiments because the life cycle was long, therefore the sampling frequency was adjusted to suit the different conditions.

### 4.1.1. LIFE CYCLE UNDER AMBIENT TEMPERATURES

#### A. During July to October 1978

Two groups of 10 tomato seedlings were individually inoculated with second stage juveniles of each isolate and placed in a heated glasshouse. As this experiment was done during the summer season, the pots were immersed in moist sand in order to reduce the temperature fluctuation.

One plant per isolate was sampled after 2, 6, 10, 14, 20, 35, 50 and 65 days. Nematodes were extracted by either dissecting out from roots or from soil by sieving and decanting (Section 2).

The soil temperature was recorded daily using a minimum/maximum soil thermometer, and ranged from $15^{o}$ to $34^{o}$C., minimum and maximum respectively.

B. During September to November 1978

Inoculated plants were grown under two sets of conditions in the glasshouse:

i) the pots were placed on the bench only.

ii) the pots were immersed in moist sand.

12 plants for each isolate and set of condition were used (total 48). One plant per isolate and set of conditionswes sampled after 2, 6, 10, 15, 20, 30, 40, 50 and 60 days. Nematodes were extracted from roots and soil as in the previous life cycle experiment. The soil temperatures were recorded daily at 8 a.m. and 3 p.m. over the 60 days., with the following range.

| CONDITION | TEMPERATURE | |
|---|---|---|
| | Minimum | Maximum |
| Pots | 15°C | 36°C |
| Pots immersed in sand | 17°C | 33°C |

4.1.2. LIFE CYCLE UNDER DIFFERENT CONSTANT TEMPERATURES

These studies were done in constant temperature rooms. (14°, 19° and 25°C). The C.T. rooms were provided with an adequate system of heating and ventilation in order to keep the temperature constant. The normal period of light was 16 hours per day, supplied by fluorescent light. To maintain the soil moisture, the pots were watered regularly.

A. At 14°C

Two groups of 8 tomato seedlings, were inoculated with second stage juveniles of each isolate of N. aberrans. One plant per isolate was sampled after 7, 14, 27, 42, 56, 76, 96 and 119 days. Nematodes were extracted by either dissecting out from roots, or from the soil by using a modification of the tray method (Section 2). Minimum

and maximum air temperatures were 11°C and 17°C, respectively. Temperature in soil was recorded at a constant of 14°C.

B. At 19°C

Two groups of 10 tomato seedlings were inoculated with each population. One plant per isolate was sampled after 7, 14, 21, 28, 35, 42, 49, 56, 70 and 83 days. Nematodes were extracted as above.

Minimum and maximum air temperatures were 15°C and 19°C, respectively. Soil readings remained at a constant of 19°C.

C. At 25°C

Two groups of 8 tomato seedlings were inoculated with each isolate of N. aberrans. One plant per isolate was sampled after 7, 14, 21, 28 and 35 days. Nematodes were extracted as before.

Minimum and Maximum air temperatures were 23°C and 28°C respectively. Soil remained at a constant of 25°C.

# RESULTS

## Ambient temperatures

Studies on the life-cycle of both isolates of N. aberrans revealed that maximum root population for the British isolate in the first ambient temperature experiment occurred 10 days after inoculation, and 20 days later for the Ecuadorian population (Fig. 4.1). In the second experiment (pots immersed in sand), 10 days post-inoculation the British isolate had the maximum root population; under other conditions and with the Ecuadorian isolate, the maximum number of nematodes in the roots was reached 15 days post-inoculation (Fig. 4.1).

Galling in the first experiment for both isolates was produced after 35 days (Table 4.1.1.), but egg-masses appeared 50 days after inoculation with the British isolate and 65 days in pots inoculated with the Ecuadorian isolate. In the second experiment, there were differences in time to galling between isolates. The Ecuadorian showed galling at 40 days and the British after 30 days. In the Ecuadorian isolate, 6 egg-masses were recorded 50 days after inoculation in pots immersed in sand and 5 egg-masses after 60 days in pots on the bench. However, in galled roots by the British isolate, 4 egg-masses for each condition were registered 40 days after inoculation.

The number of males and females of N. aberrans are shown in Table 4.1.2. To estimate the sex ratio, in the final observation, the number of males was divided by the number of females (juvenile and adult stages) present. In the first experiment the sex ratio was 0.26 for the Ecuadorian isolate and 0.36 for the British isolate. In the second experiment for pots immersed in sand, Ecuadorian 0.55

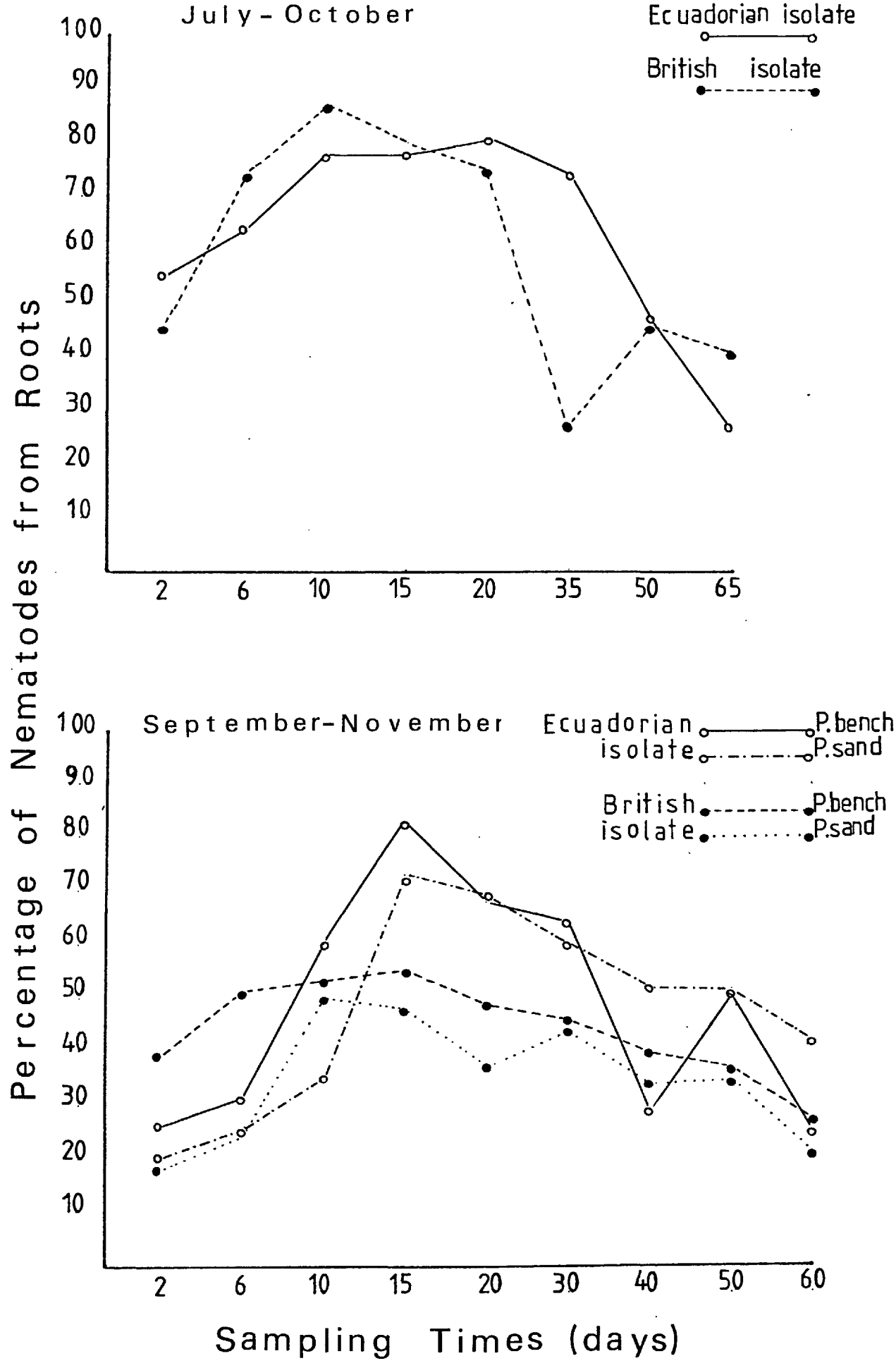



Fig. 4.1. Populations of two isolates of N. aberrans during their life-cycles at ambient temperatures in glasshouse.

TABLE 4.1.1. : DEVELOPMENT AND LIFE-CYCLE OF TWO ISOLATES OF N. ABERRANS IN TOMATO ROOTS AT AMBIENT TEMPERATURES IN THE GLASSHOUSE.

| DATE OF THE EXPERIMENTS | ISOLATES | TEMPERATURE | TIME IN DAYS PRESENCE OF DIFFERENT STAGES DETECTED | | | | | | | | TOTAL No. OF EGG-MASSES PRODUCED |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | $J_2$ | $J_3$ | $J_4$ | ♀ IMM. | ♀ without eggs | ♀ with eggs | ♂ | GALLING | |
| A. JULY-OCT. | ECUADORIAN | Min 15°C Max 34°C | 2-14 | 6-35 | 14-50 | 35-65 | 35-65 | 65 | 50-65 | 35 | 6 |
| | BRITISH | | 2-14 | 6-20 | 14-50 | 35-65 | 35-65 | 50 | 35-65 | 35 | 6 |
| B. SEPT.-NOV. 1. | ECUADORIAN POTS IMM. SAND | Min 17°C Max 33°C | 2-30 | 10-40 | 15-60 | 30-60 | 40-60 | 50 | 30-60 | 40 | 6 |
| | BRITISH POTS IMM. SAND | | 2-20 | 6-40 | 15-60 | 20-60 | 30-60 | 40 | 30-60 | 30 | 4 |
| 2. | ECUADORIAN POTS ON BENCH | Min 15°C Max 36°C | 2-30 | 10-40 | 15-60 | 30-60 | 40-60 | 60 | 40-60 | 40 | 5 |
| | BRITISH POTS ON BENCH | | 2-20 | 6-40 | 15-60 | 20-60 | 30-60 | 40 | 30-60 | 30 | 4 |

TABLE 4.1.2. : ESTIMATION OF THE NUMBER OF MALES AND FEMALES (JUVENILES AND ADULTS) OF TWO ISOLATES OF N. ABERRANS IN TOMATO ROOTS UNDER AMBIENT TEMPERATURE AT DIFFERENT SAMPLING TIMES.

| DATE OF THE EXPERIMENTS | ISOLATES | TEMPERATURE | SAMPLING TIMES (DAYS) | | | | | | | | | | | | | | | | | | SEX* RATIO ♂ x ♀ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | SEX | | | | | | | | | | | | | | | | | | |
| | | | 10 | | 15 | | 20 | | 30 | | 35 | | 40 | | 50 | | 60 | | 65 | | |
| | | | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | |
| A. JULY-OCT. | ECUADORIAN | Min 15°C | 27 | 31 | 21 | 33 | 30 | 36 | | | 22 | 46 | | | 20 | 27 | | | 4 | 18 | 0.26 |
| | BRITISH | Max 34°C | 30 | 32 | 26 | 34 | 27 | 41 | | | 5 | 22 | | | 12 | 34 | | | 11 | 30 | 0.36 |
| B. SEPT.-NOV. 1. | ECUADORIAN POTS IMM. SAND | Min 17°C | 4 | 8 | 18 | 26 | 21 | 35 | 22 | 35 | | | 24 | 28 | 21 | 31 | 15 | 27 | | | 0.55 |
| | BRITISH POTS IMM. SAND | Max 33°C | 8 | 17 | 7 | 21 | 15 | 20 | 15 | 29 | | | 12 | 22 | 14 | 21 | 6 | 15 | | | 0.40 |
| 2. | ECUADORIAN POTS ON BENCH | Min 15°C | 14 | 10 | 20 | 32 | 18 | 31 | 22 | 34 | | | 12 | 18 | 17 | 33 | 7 | 18 | | | 0.38 |
| | BRITISH POTS ON BENCH | Max 36°C | 1 | 6 | 12 | 34 | 11 | 35 | 16 | 30 | | | 11 | 29 | 10 | 27 | 13 | 14 | | | 0.92 |

* Calculated from the final observation.

and British 0.40. Pots on the bench, Ecuadorian 0.38 and British 0.92.

Constant temperatures

The percentage of nematodes recovered from roots for each isolate and regime of temperature is shown in Fig. 4.2. At 14°C, the Ecuadorian isolate reached the maximum root population 56 days after inoculation and the British 76 days after. Both isolates had maximum number of nematodes in the roots in 28 days at 19°C. When the life-cycle was done at 25°C, maximum root population was after 7 days for the Ecuadorian isolates and 28 days post-inoculation for the British isolate.

Galling was not recorded at 14°C in either isolate (Table 4.1.3.); stages of males and immature females were detected 96 - 119 days post-inoculation. At 19°C both isolates of N. aberrans caused galling of roots after 49 days, 3 egg-masses for the British isolate were detected at 70 days, and 2 egg-masses for the Ecuadorian at 83 days. The life-cycle at 25°C was shorter, with galls appearing after 21 days for both isolates, and 13 egg-masses were recorded in galled roots with the British isolate 28 days after inoculation. The Ecuadorian isolate produced 9 egg-masses 35 days post-inoculation (Table 4.1.3.).

In Table 4.1.4. is given the number of males and females in all stages under constant temperatures. The sex ratio was estimated by dividing the number of males by females (juvenile and adult stages) in the final observation. At 14°C, both isolates had a sex ratio of 0.50. The Ecuadorian isolate was 0.50 at 19°C and the British 0.71. However, at 25°C the number of males per females was lower, resulting for the Ecuadorian isolate 0.37 and for the British 0.13.

Fig. 4.2. Populations of two isolates of N. aberrans during their life-cycle at constant temperatures.

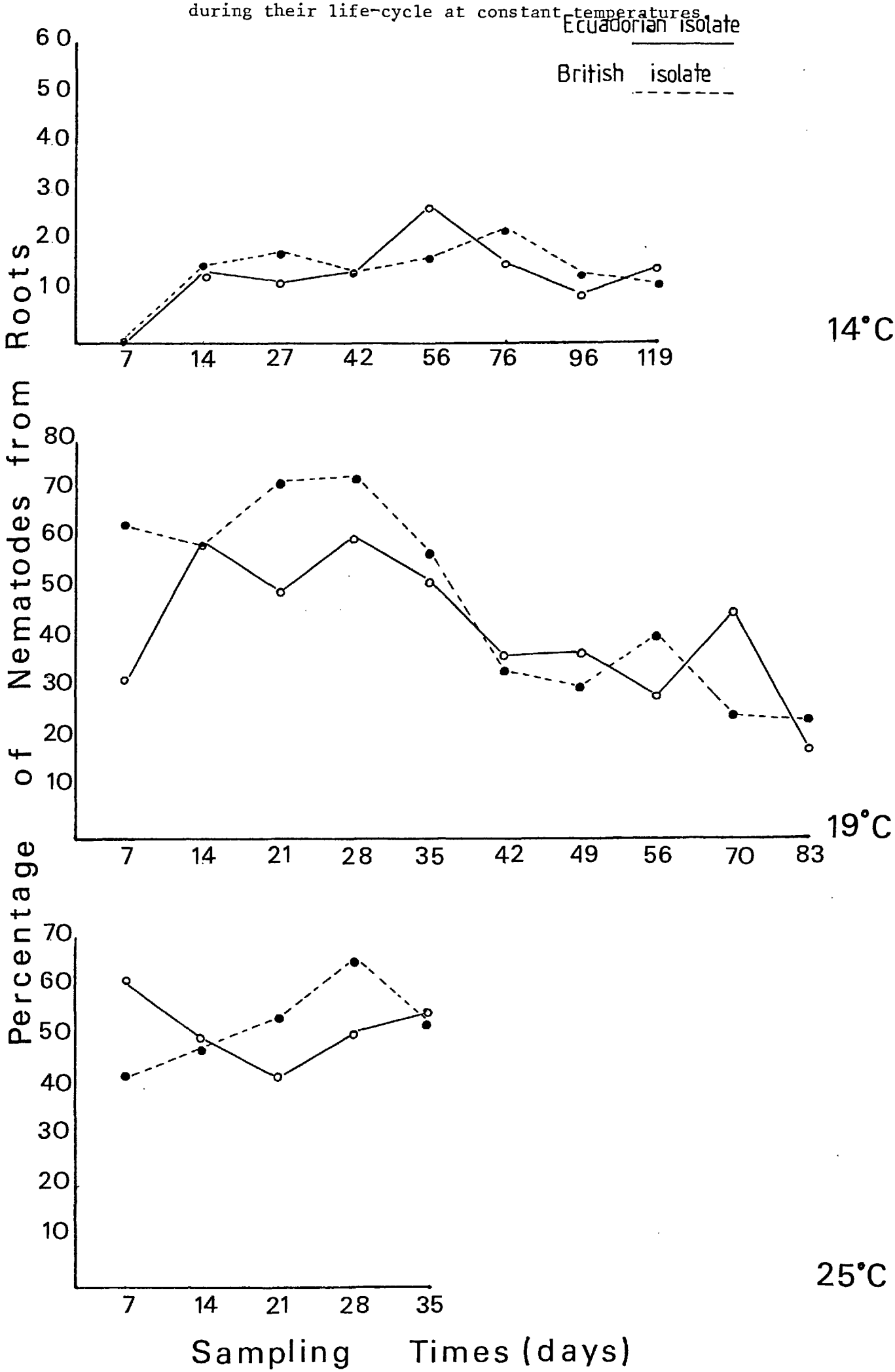


TABLE 4.1.3. : DEVELOPMENT AND LIFE CYCLE OF TWO ISOLATES OF N. ABERRANS IN TOMATO ROOTS UNDER CONSTANT TEMPERATURES.

| ISOLATES | TEMPERATURE | TIME IN DAYS PRESENCE OF DIFFERENT STAGES DETECTED | | | | | | | | TOTAL No. OF EGG-MASSES PRODUCED |
|---|---|---|---|---|---|---|---|---|---|---|
| | | $J_2$ | $J_3$ | $J_4$ | ♀ imm. | ♀ without eggs | ♀ with eggs | ♂ | GALLING | |
| ECUADORIAN | 14°C | 7-56 | 14-96 | 42-119 | 96-119 | 0 | 0 | 96-119 | 0 | 0 |
| BRITISH | | 7-56 | 14-96 | 27-119 | 96-119 | 0 | 0 | 96-119 | 0 | 0 |
| ECUADORIAN | 19°C | 7-28 | 14-42 | 21-83 | 35-83 | 49-83 | 83 | 42-83 | 49 | 2 |
| BRITISH | | 7-21 | 14-35 | 21-83 | 35-83 | 49-83 | 70 | 35-83 | 49 | 3 |
| ECUADORIAN | 25°C | 7-14 | 7-28 | 14-35 | 21-35 | 21-35 | 35 | 21-35 | 21 | 9 |
| BRITISH | | 7-14 | 7-21 | 14-35 | 14-35 | 21-35 | 28 | 21-35 | 21 | 13 |

TABLE 4.1.4. : ESTIMATION OF THE NUMBER OF MALES AND FEMALES (JUVENILES AND ADULTS) OF TWO ISOLATES OF N. ABERRANS IN TOMATO ROOTS UNDER CONSTANT TEMPERATURES AT DIFFERENT SAMPLING TIMES.

| ISOLATES | TEMPERATURE | SAMPLING TIMES (DAYS) | | | | | | | | | | | | | | | | | | | | SEX* RATIO ♂ x ♀ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | SEX | | | | | | | | | | | | | | | | | | | | |
| | | 7 | | 14 | | | | 28 | | | | 42 | | 56 | | 76 | | 96 | | 119 | | |
| | | ♂ | ♀ | ♂ | ♀ | | | ♂ | ♀ | | | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | |
| ECUADORIAN | 14°C | | | 1 | 2 | | | 1 | 3 | | | 2 | 7 | 11 | 16 | 7 | 9 | 4 | 6 | 5 | 10 | 0.50 |
| BRITISH | | | | 2 | 3 | | | 7 | 7 | | | 5 | 7 | 7 | 9 | 15 | 8 | 7 | 7 | 4 | 8 | 0.50 |

| | | 7 | | 14 | | 21 | | 28 | | 35 | | 42 | | 49 | | 56 | | 70 | | 83 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | |
| ECUADORIAN | 19°C | | | 4 | 11 | 17 | 20 | 24 | 34 | 23 | 29 | 18 | 19 | 18 | 20 | 13 | 16 | 20 | 26 | 6 | 12 | 0.50 |
| BRITISH | | | | 16 | 11 | 21 | 37 | 20 | 49 | 24 | 34 | 12 | 22 | 11 | 20 | 12 | 29 | 13 | 12 | 10 | 14 | 0.71 |
| ECUADORIAN | 25°C | 3 | 4 | 18 | 25 | 20 | 24 | 18 | 31 | 15 | 40 | | | | | | | | | | | 0.37 |
| BRITISH | | 1 | 2 | 17 | 23 | 17 | 34 | 15 | 51 | 6 | 45 | | | | | | | | | | | 0.13 |

* Calculated from the final observation.

In Fig. 4.3 is represented the sexual development of both sexes of the Ecuadorian isolate of N. aberrans. As described by Clark (1967) the sex of the juveniles could be distinguished from the third stage by the length and the position of the gonads. The developing gonads in the third stage females were longer (46.5 μ) than in third stage males (31,2 μ) and also more posteriorly placed near the tail. In fourth-stage females, the gonads grew forwards (129.4 μ) and remained longer than in males (83.3 μ) in which the gonads grew toward the tail.

It was noticed that populations of N. aberrans in both isolates began to decrease after that the highest peak was reached. Soil samples were examined to determine if migration occurred, which revealed that there was migration of nematodes out of the roots (Plate 2). Migration was mostly of $J_3$'s $J_4$'s and males, however, immature females were also observed less often.

Although time of life-cycle differed between isolates the development of N. aberrans in tomato roots was similar for both isolates. Second stage juveniles invaded the roots and became located in the cortex (Plate 1a). There, feeding began and caused necrotic areas. Inside the necrotic areas, nematodes remained coiled and developing (Plate 1b). Third stage juveniles in a few cases, but usually the fourth stages left the necrotic areas and migrated out of the roots into the soil (Plate 2). This migration also was observed to have occurred for males and immature females, although the immature females were more often found migrating within the same root (Plate 3a). The females became located along side the vascular system, feeding and producing root galling (Plate 3b).

The female's body became swollen and a gelatinous matrix

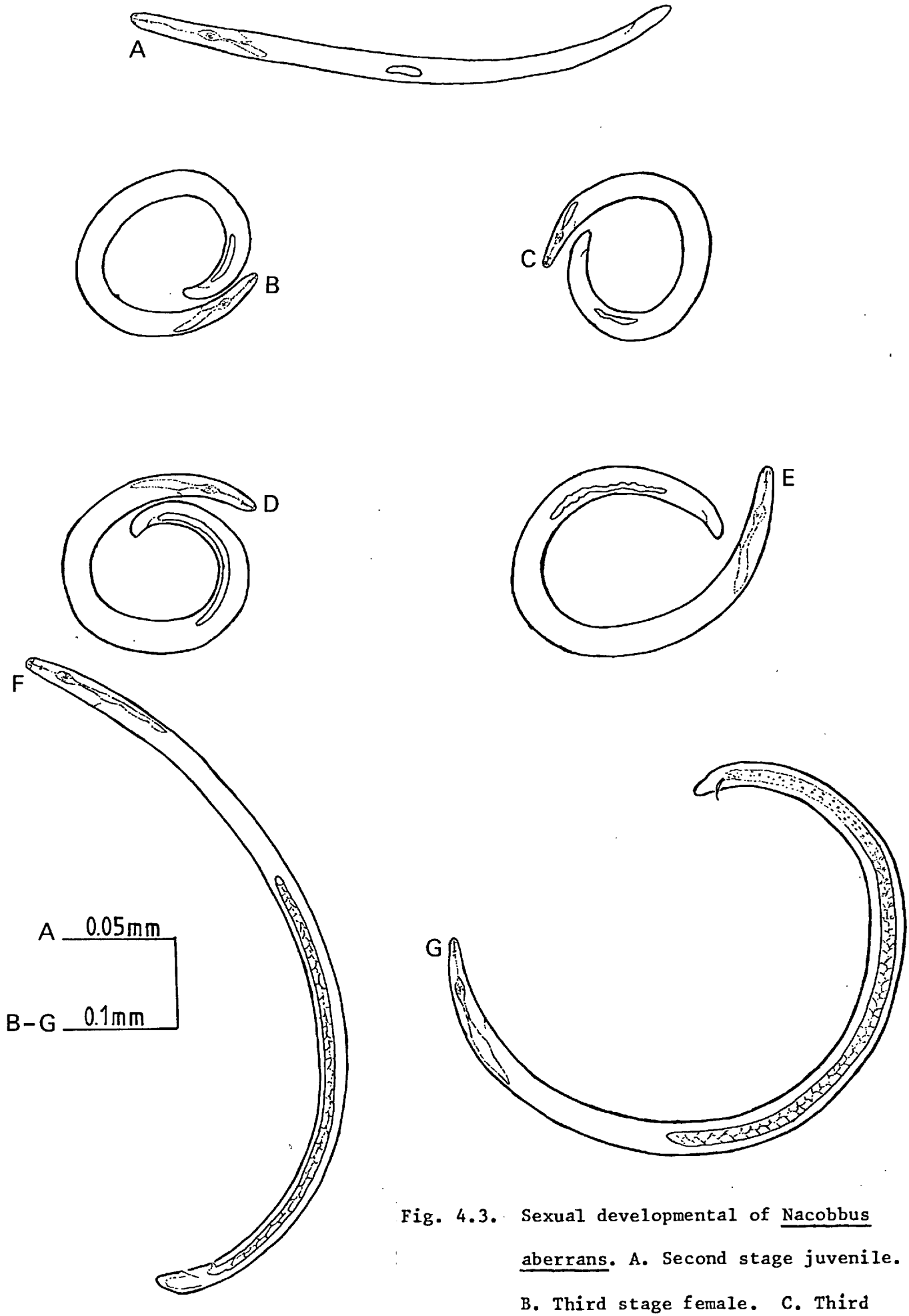



Fig. 4.3. Sexual developmental of Nacobbus aberrans. A. Second stage juvenile. B. Third stage female. C. Third stage male. D. Fourth stage female. E. Fourth stage male. F. Immature female. G. Male.

Plate 1

a. Second stage juvenile of N. aberrans in the cortex of tomato root (x 350)

c. cortex

e.p. epidermis

n. nematode

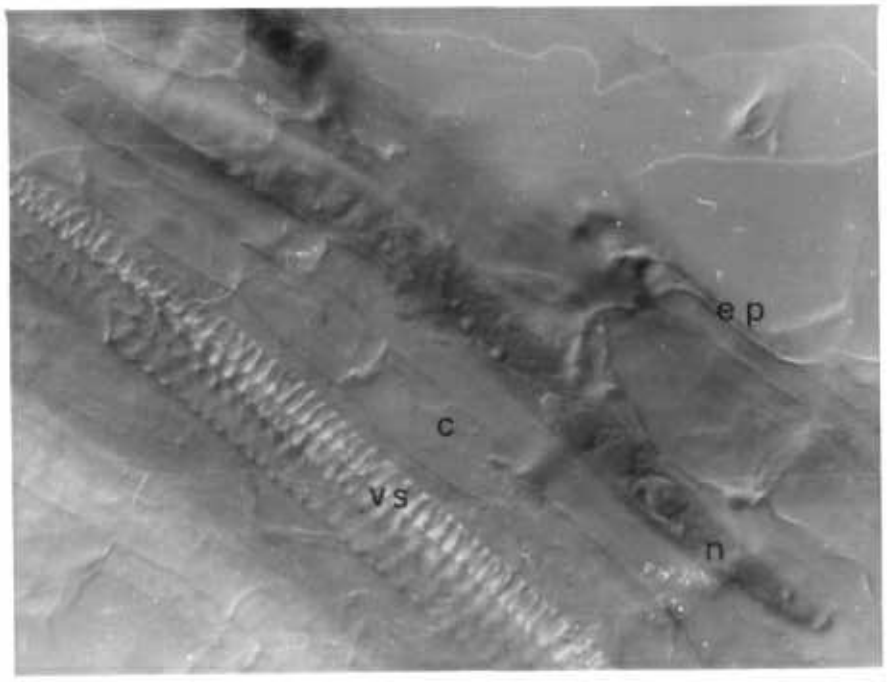
v.s. vascular system.

b. Necrotic area in the cortex caused by feeding of $J_2$. Note $J_3$ developing in the necrotic area (x 250).

n. nematode

n.a. necrotic area.

a




b

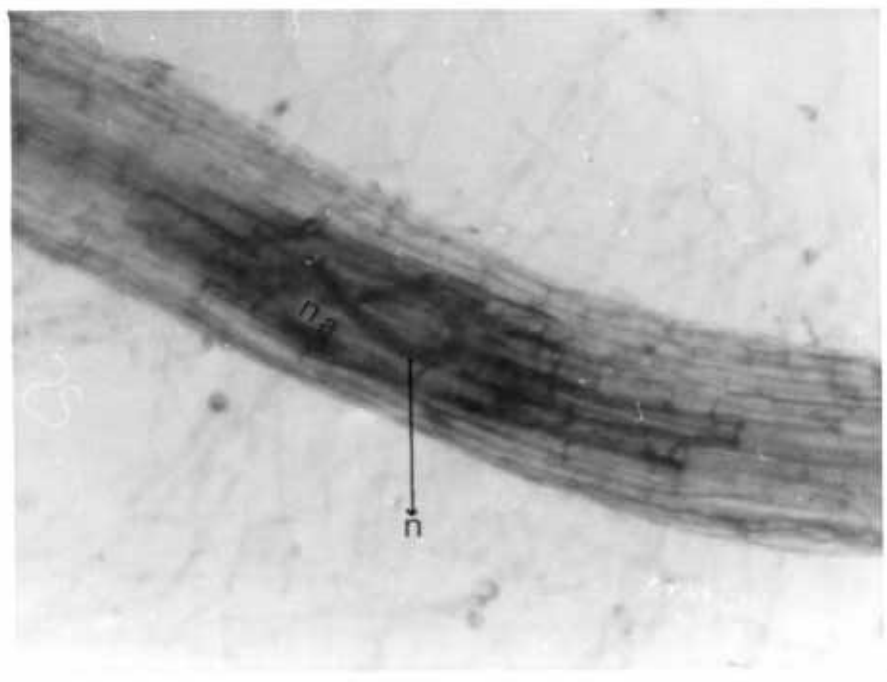
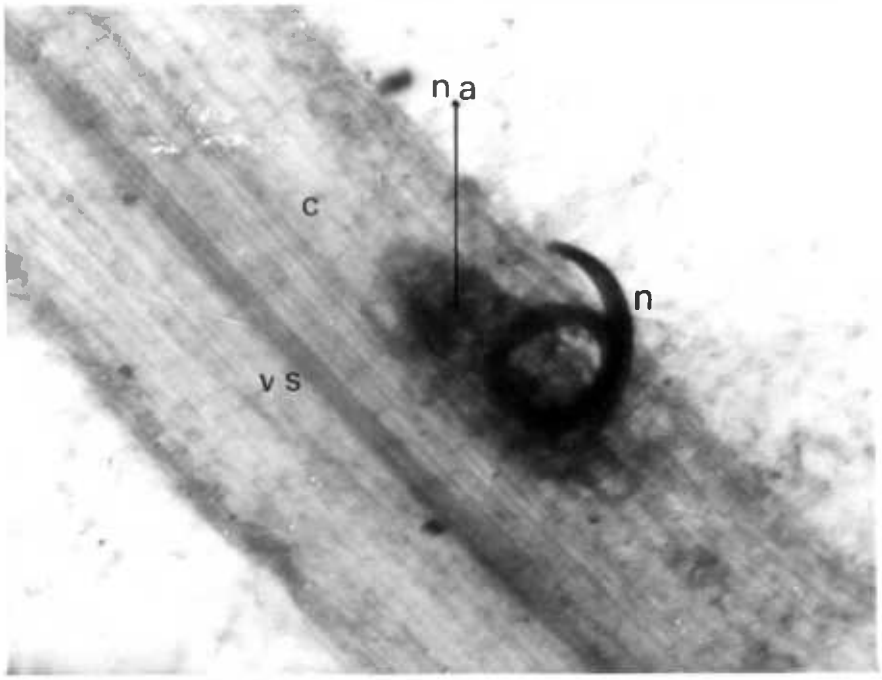


Plate 2.




Fourth stage juvenile leaving the necrotic feeding area of root out into the soil (x 300)

c. cortex

n.a. necrotic area

m. nematode

v.s. vascular system.

Plate 3.

a. Immature female migrating along the tomato root away from necrotic area to establish a new feeding site prior to becoming sedentary and swollen. Note position of immature female near the stale (x 300).

n. nematode

n.a. necrotic area

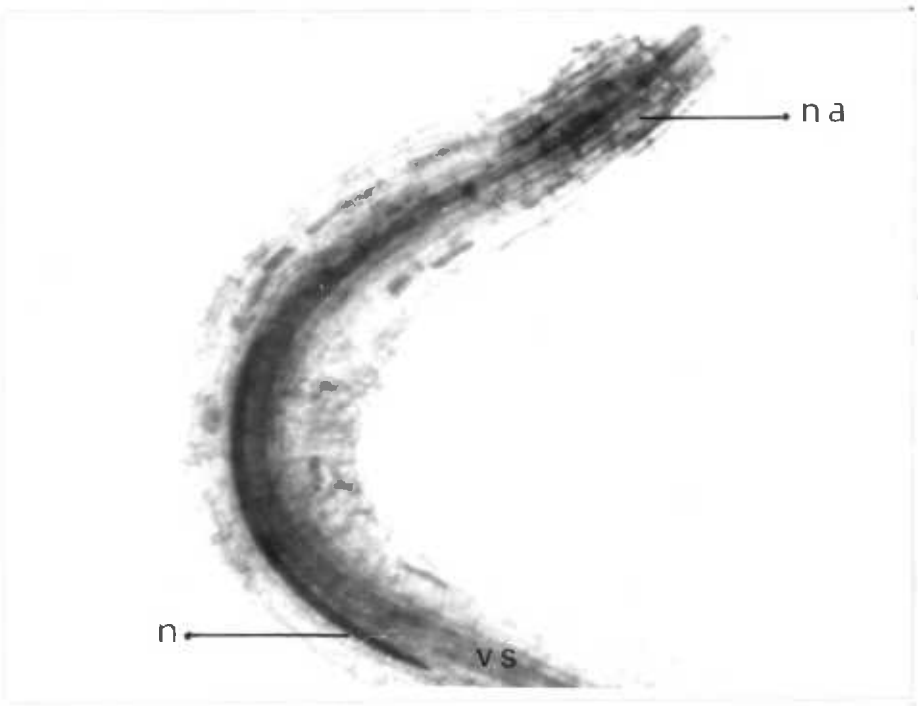
v.s. vascular system.

b. Female maturing at the new feeding site, where a syncytium is formed. Note nematode head in the stale (x 150).

n. nematode.

v.s. vascular system.

a

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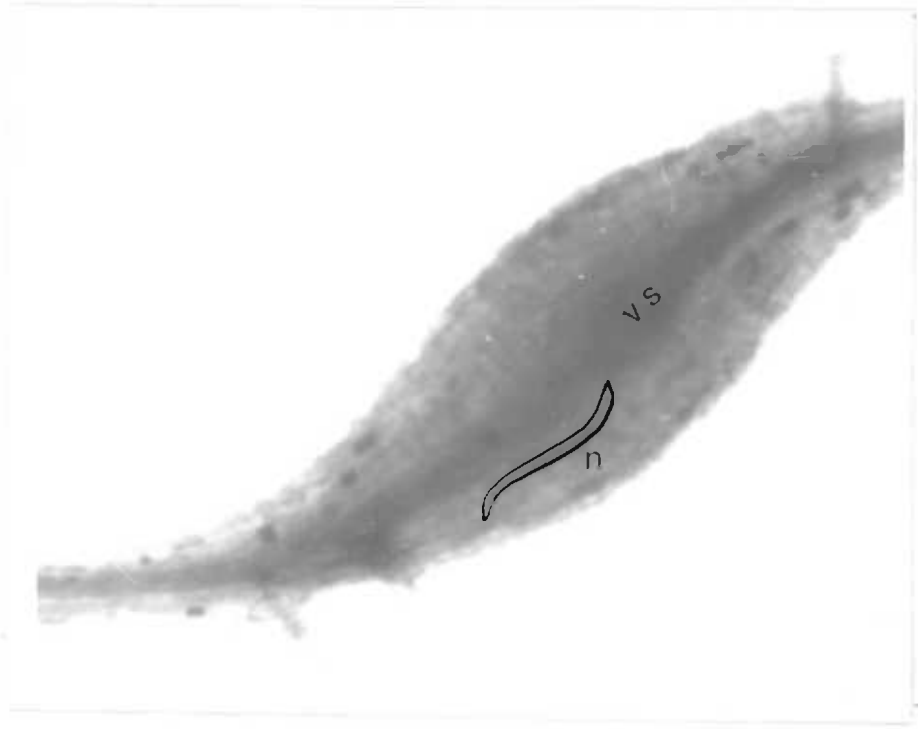


was produced into which were discharged the eggs. When the penetration of the females was deep, the eggs were found through the gall tissue and spread over the root surface; but when the female was closer to the root surface, the egg-masses appeared completely outside the gall, resembling those produced by some species of Meloidogyne. Males were often found entangled inside the gelatinous matrix, close to the vulva in the root cortex or on the root surface.

# DISCUSSION

Despite the fact that both isolates had similar life-cycles, there were differences in the time at which eggs were produced. In this aspect, the British isolate either under ambient temperatures or constant temperatures always completed its life-cycle in less time than the Ecuadorian isolate. This difference in time to complete the life-cycle, could be explained by the fact that both isolates had different origins and probably, as the British isolate has been cultured for almost 20 years on tomato, the host was an additional factor delaying the life-cycle of the Ecuadorian isolate. Johnson and Thames (1972) studying the biology of an unidentified population of Nacobbus in Texas, reported that optimum temperature for development was 20°C in spinach and 24°C in tomato, and no development occurred at temperatures above 28°C.

The origin of a population of the same species of nematode has a marked effect on its life-cycle, pathogenicity, survival etc. Dao (1970) determined that the minimum temperature required for a M. incognita population from the Netherlands to start infection and reproduction was about 5°C lower than for a Venezuelan population. Daulton and Nusbaum (1961) studying the survival of eggs among three isolate of M. javanica, found that a population from Rhodesia had a greater tolerance to high temperature and lower tolerance to low temperature than the population of the same species from Georgia and North Carolina.

Analysing the time required to complete the life-cycle, it was surprising to find that the greatest differences occurred at constant temperatures, independently of the isolates. At 14°C there

was no egg-production 119 days post-inoculation. Eggs were detected after 70 and 80 days at 19°C for the British and the Ecuadorian isolates respectively, while at 25°C, the cycle was much shorter and the British and the Ecuadorian isolates reached the major egg-mass production stage after 28 and 35 days respectively. Prasad and Webster (1967), who studied the life-cycle of N. aberrans in vitro, determined that at 15°C no female produced eggs even after 78 days, at 25°C from egg to egg the nematode took 35 days. However, they found that under 20° and 30°C the life-cycle was completed in 43 days.

Under ambient temperature on the whole, from $J_2$ to egg usually took 45 days for the British isolate and 60 days for the Ecuadorian population. This time required under glasshouse conditions is similar to that recorded by Jones (1965) who pointed out that Nacobbus completed its life cycle in 7 to 9 weeks. These present results have shown that the range of optima temperatures for Nacobbus activity is narrow. It would be interesting to observe the life-cycle of the Ecuadorian isolate under field conditions, as the nematodes may require fluctuating temperature for life-cycle and maximum reproduction, which are provided in nature by the normal weather fluctuations (Bird and Wallace, 1965).

The low root populations of both isolates even after high invasion is explained by Nacobbus migrating into the soil during the $J_3$, $J_4$, males and immature female stages of its development, above all after the emergence of males which are invariably migratory through the soil.

The behaviour of the nematodes through the life-cycle suggested the presence of two infective stages. The second stage juveniles and the immature females, with two different feeding habits. Second

stage juveniles invading the roots feed in the cortex, producing necrosis and cavities. The $J_3$ and $J_4$ stages remain developing inside the necrotic areas. After the last moult, the immature females mainly migrate in the same root or into the soil and re-enter a new root. They feed near the vascular system, where hypertrophy and hyperplasia are induced, resulting in gall formations. Males are migratory into the soil, and usually are found inside the galls, around the vulva of the female, suggesting that Nacobbus maybe amphimictic. Other authors have also mentioned the same idea (Thorne and Schuster, 1956; Clark, 1967; Prasad and Webster, 1967).

## 4.2 BEHAVIOURAL STUDIES OF NACOBBUS ABERRANS ON NUTRIENT WATER AGAR

### Introduction

Some aspects of the behaviour of the different stages of Nacobbus are not clear from the literature. It has been stated that this nematode has two parasitic stages, mainly the second juvenile stages and the immature females (Thorne and Schuster, 1956; Franklin, 1959).

Gall formation has been associated with certain stages of Nacobbus. Schuster and Sullivan (1960), found that the second stage of Meloidogyne incognita incognita, M. hapla and N. aberrans are capable of inducing root galling in tissue cultures. Prasad and Webster (1967) working with excised roots, determined that galling is caused by the third stage female. In contrast, Clark (1967) observed that immature females initiated gall formation on tomato roots.

With reference to reproduction, Thorne and Schuster (1956), pointed out that fertilization occurred in the gall, and that this

nematode has amphimictic reproduction. In agreement, Clark (1967) stated that fertilization probably occurred after the gall had been formed and not before.

Thorne and Schuster (1956) observed Nacobbus invasion and stated that larval penetration occurred behind the root tip, whilst Schuster et al (1965) observed that Nacobbus can invade any part of the root of sugar beet.

It is difficult to observe certain aspects of development and behaviour of plant-parasitic nematodes in soil. However, in vitro experiments have been used to investigate details of invasion, sex attraction, feeding, embryology, etc., (Green and Greet, 1972; Trudgill, 1967; Schuster and Sullivan, 1960; Jones, 1976).

To complement, and to reaffirm, the results obtained from the life-cycle studies, the investigation of the following in nutrient water agar were done: i) invasion, ii) gall formation, iii) role of individual Nacobbus stages, and iv) reproduction. At the same time, observations of the different stages of Nacobbus, were made in distilled water.

## MATERIALS AND METHODS

Tomato seeds were washed five times with sterile distilled water and then transferred into a 4 cm. deep, 8.5 cm. diameter plastic container lined with moist filter paper and allowed to germinate. When the first leaves appeared, the seedlings were removed and placed into square petri dishes (100 x 18 mm.) containing 80 ml. of nutrient water agar (3.5 g standard Davis agar, 0.5 g Phostrogen per litre of distilled water). A small cut was made in the side of the petri dishes to allow the growth of plants and watering.

Second stage juveniles for inoculation were obtained from egg-masses of N. aberrans (British isolate) (see Section 2.). The other stages for the same purpose were extracted from tomato roots, using a maceration-filtration technique (after Fallis, 1943 and Stemerding, 1964; Hooper, 1970a.). The nematodes were washed in at least five changes of sterile distilled water and were then ready for use as the inoculum.

The following inocula were used:

| | | |
|---|---|---|
| i | Juveniles in second stage | 100 |
| ii | Juveniles in third stage | 5 |
| iii | Juveniles in fourth stage | 10 |
| iv | Immature females | 3 |
| v | Males | 5 |

Each inoculum was replicated 3 times.

For the other part of the experiment, nematodes in different stages were placed in distilled water in 4.5 cm. diameter plastic

petri dishes. Using the following inocula:

| | | |
|---|---|---|
| i | Juveniles in second stage | 20 |
| ii | Juveniles in third stage | 5 |
| iii | Juveniles in fourth stage | 10 |
| iv | Immature females | 2 |
| v | Males | 5 |

Each inoculum was replicated 3 times.

Third and fourth stage nematode were distinguished by size, because in living nematodes it was difficult to observe the gonad development.

Invasion, development and survival were observed.

The petri dishes containing nutrient water agar were sealed with plastic tape and covered with aluminium foil to avoid algal development. Transplantation and inoculation was carried out in a sterile cabinet. Petri dishes with seedlings were tested in the laboratory in a lighted plastic growth cabinet with a day length of 16 hours. The minimum and maximum temperatures over two months were: $21^{o}$ and $27^{o}$C respectively.

Reproduction - To determine the type of reproduction of *N. aberrans*, a complementary experiment was carried out in the above growth cabinet. Individual vermiform immature females were inoculated singly and in combinations with males (12 per female) in a total of 15 replications per treatment. Tomato seedlings were grown in round petri dishes (8 cm diameter), containing approximately 50 ml. of nutrient water agar.

# RESULTS

In Table 4.2.1. and Appendix B Table 1 are given the percentage of invasion of different stages of N. aberrans inoculated around tomato roots on nutrient water agar. Second and third juvenile stages (although only a few of the latter invaded the roots), produced necrotic areas in the cortex without any galling. However, when the nematodes invaded the root tip, in rare cases, slight swollen, pendulum-like galls were observed (Plate 4.a.). As the apical meristem was affected, the root only grew a few centimeters and then root growth ceased.

All specimens of the immature females invaded the roots and induced the formation of typical galls (Plate 4.b.). A considerable percentage of third stage juveniles, all fourth stage juveniles and males were unable to invade the roots. The juvenile stages remained coiled and motionless in nutrient water agar, but the males moved around the roots until all the food reserves inside their bodies disappeared and they then died after 2 weeks.

The invasion of second stage juveniles occurred more in the secondary lateral roots than in the main lateral roots, with percentages of invasion of 67.7% and 32.3% respectively. The preferred sites of invasion were as follows: region of root elongation (56.8%), region of root hairs and mature root (30.9%) and root tip (12.3%) (Table 4.2.2. and Appendix B. Table 2.).

It was observed that after the nematodes invaded the roots, 27% of the nematodes migrated out of the roots as shown in Plate 5.a., Table 4.2.2.a, Appendix A. Table 2.1. This migration occurred as $J_3$'s and $J_4$'s and then these stages continued development in agar until they reached male or immature female stages.

TABLE 4.2.1. : INVASION AND DEVELOPMENT OF DIFFERENT STAGES OF N. ABERRANS IN TOMATO ROOTS ON NUTRIENT WATER AGAR AFTER 60 DAYS.

| No. NEMATODES AND STAGES INOCULATED | % NEMATODES ENDOPARASITIC* | % NEMATODES FORMING GALLS.* |
|---|---|---|
| 100 $J_2$ | 40.7 | 0 |
| 5 $J_3$ | 13.3 | 0 |
| 10 $J_4$ | 0 | 0 |
| 3 Imm. ♀ | 100 | 100 |
| 5 ♂ | 0 | 0 |

* Mean of 3 replicates.

TABLE 4.2.2. : INVASION SITES OF N. ABERRANS IN NUTRIENT WATER AGAR TOMATO CULTURES.

| TYPE OF ROOT INVADED \ REGION OF ROOT INVADED | ROOT TIP | | REGION OF ELONGATION | | REGION OF ROOT HAIRS AND MATURATION | | % OF TOTAL NEMATODES |
|---|---|---|---|---|---|---|---|
| | NO. NEMATODES | % OF TOTAL NEMATODES IN ROOTS | NO. NEMATODES | % OF TOTAL NEMATODES IN ROOTS | NO. NEMATODES | % OF TOTAL NEMATODES IN ROOTS | |
| MAIN LATERAL | 0.7 | 12.3 | 7.7 | 56.8 | 4.7 | 30.9 | 32.3 |
| SECONDARY LATERAL | 4.3 | | 15.3 | | 8.0 | | 67.7 |

* Mean of 3 replicates.

TABLE 4.2.2.a : DEVELOPMENTAL STAGES OF N. ABERRANS MIGRATING OUT OF ROOT ON NUTRIENT WATER AGAR TOMATO CULTURE INOCULATED WITH SECOND STAGE JUVENILES OF N. ABERRANS.

| NO. NEMATODES MIGRATING FROM ROOTS | % OF DIFFERENT DEVELOPMENTAL STAGES LEAVING ROOTS | | | | |
|---|---|---|---|---|---|
| | $J_3$ | $J_4$ | Imm. ♀ | Mat. ♀ | ♂ |
| 11 | 5.7 | 10.0 | 3.2 | 0 | 4.1 |

Plate 4.

a. Slight swollen root (pendulum like). Note evidence of hypertrophy (x300).

b. Typical Nacobbus gall induced by feeding of immature female (x100)

e. entrance of immature female.

a

b

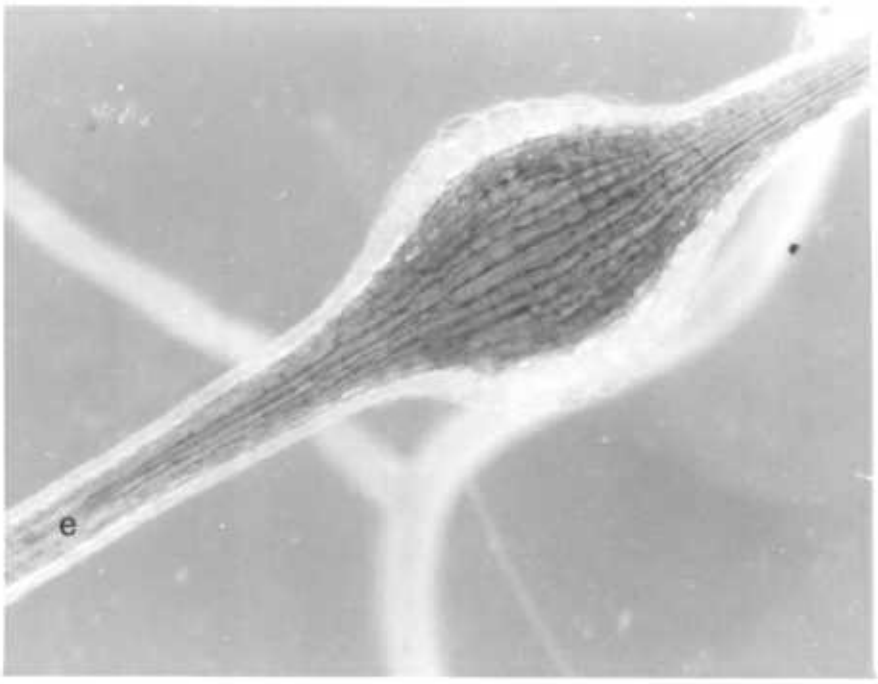
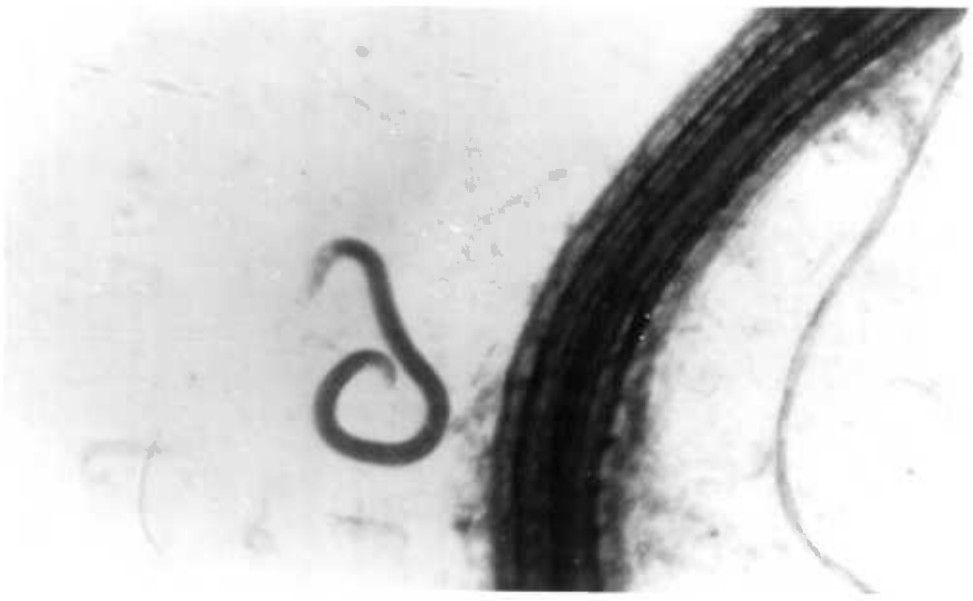


Plate 5.

a. $J_4$ stage migrating in water agar culture (x 400)

b. Fourth stage juvenile alive but quiescent after two months in water agar. Note the body contents (x 300).

a



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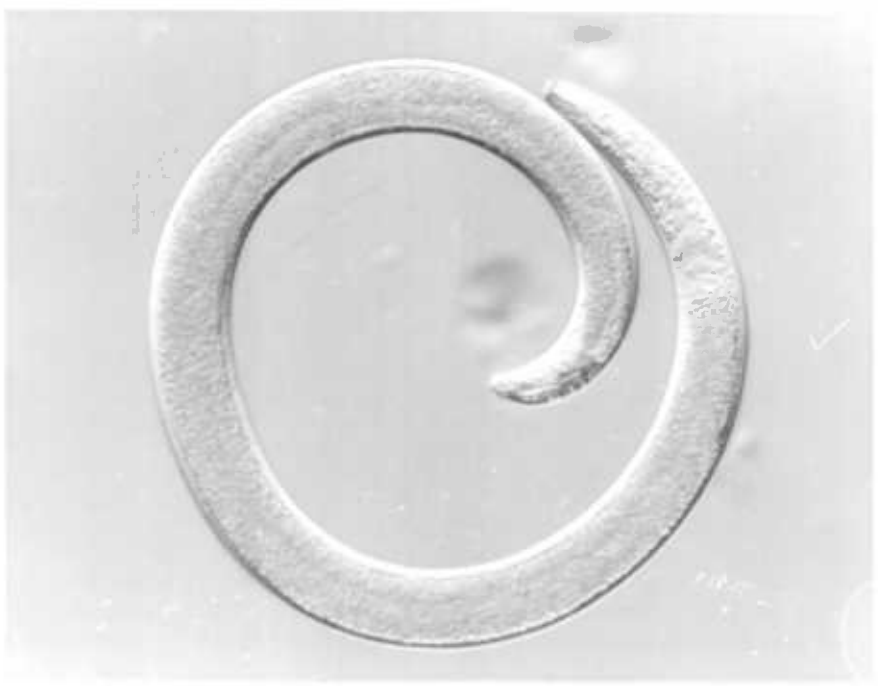


Other results in Table 4.2.3. and Appendix A. Table 3. show observations on development of different stages of N. aberrans inoculated on water agar alone. Second stage juveniles as well as immature females did not develop further and after 2 months all had died. When third stage juveniles were inoculated, there was development and they reached the $J_4$ stages, immature females and males, although 46.7% of the inoculum died. Also there was development to immature females and males of fourth stage juveniles, with higher percentage of development and less percentage of dead nematodes than in $J_3$ inocula. Moreover, 33% of the nematodes remained alive as $J_4$ stages even two months after inoculation, with a typical coiled shape and all with their bodies full of food reserves (Plate 5.b.). All males died during the period of observations.

The observations in distilled water (Table 4.2.4. and Appendix A. Table 4.) revealed that similar development occurred as in water agar; second stage juveniles and immature females died without any further development. In third stage juvenile inocula, there was development although a considerable, 66.7%, of the inocula died. More fourth stage juveniles developed than $J_3$'s and the number of dead nematodes was lower (26.7%). Also it was observed that some nematodes as fourth stage juveniles remained alive. After 2 months all males had died.

A further study to observe the type of reproduction of N. aberrans was started, but unfortunately, there was a contamination of poisonous gasses in the laboratory where the experiment was conducted. However, the plants were removed from the agar plates and transplanted in new nutrient water agar and inoculated. Although there was invasion of immature females, they failed to grow. The possible explanation is that there was a remnant of chemical in the roots which affected the nematodes.

TABLE 4.2.3. : DEVELOPMENT OF DIFFERENT STAGES OF N. ABERRANS ON NUTRIENT WATER AGAR ALONE.

| NO. NEMATODES AND STAGES INOCULATED | % OF DIFFERENT DEVELOPMENT STAGES FOUND AFTER TWO MONTHS* | | | | | | |
|---|---|---|---|---|---|---|---|
| | $J_2$ | $J_3$ | $J_4$ | Imm. ♀ | Mat. ♀ | ♂ | DEAD |
| 100 $J_2$ | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| 5 $J_3$ | 0 | 0 | 33.3 | 6.7 | 0 | 13.3 | 46.7 |
| 10 $J_4$ | 0 | 0 | 33.3 | 23.3 | 0 | 16.7 | 26.7 |
| 3 Imm. ♀ | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| 5 ♂ | 0 | 0 | 0 | 0 | 0 | 0 | 100 |

* Mean of 3 replicates.

TABLE 4.2.4. : DEVELOPMENT OF DIFFERENT STAGES OF N. ABERRANS IN DISTILLED WATER ALONE.

| NEMATODE STAGE INOCULATED | % OF DIFFERENT DEVELOPMENT STAGES FOUND AFTER TWO MONTHS* | | | | | | |
|---|---|---|---|---|---|---|---|
| | $J_2$ | $J_3$ | $J_4$ | Imm. ♀ | Mat. ♀ | o | DEAD |
| 20 $J_2$ | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| 5 $J_3$ | 0 | 0 | 13.3 | 6.7 | 0 | 13.3 | 66.7 |
| 10 $J_4$ | 0 | 0 | 16.7 | 26.7 | 0 | 30.00 | 26.7 |
| 2 Imm. ♀ | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| 5 ♂ | 0 | 0 | 0 | 0 | 0 | 0 | 100 |

* Mean of 3 replicates.

# DISCUSSION

Mainly second stage juveniles and immature females of N. aberrans invaded tomato roots in nutrient water agar culture, plus also a small percentage of third stage juveniles. The remaining third stage juveniles, all fourth stage juveniles and males, remained outside the roots and there was no evidence that they attempted to feed.

Clark (1967) reported that second and third stage juveniles were motile stages, and that the second and third moults occurred either in roots or in the soil. The fourth stage was parasitic in the cortex, where the final moult occurred. In agreement, Schuster et al (1965) pointed out that presumably the fourth and adult stages are sedentary, while the third stage is motile. However, from my observations in water agar and distilled water $J_2$'s and immature females failed to grow outside the host, while $J_3$'s and $J_4$'s did until they reached the stage of males or immature females. Although in both water agar and water alone the $J_3$ development was much less than $J_4$.

All these results can help to explain in part the behaviour of different stages of N. aberrans. It is clear that $J_2$ and possibly $J_3$ stages need to feed in the cortex of roots until they get sufficient food reserves to allow them to continue developing to the other stages. Second stage juveniles and immature females are the true but separate parasitic invasive stages of N. aberrans. Third stage juveniles will also invade roots after they have been excised from roots during their development.

Another important aspect is the migratory condition attributed to

Nacobbus. It seems to be that all the juvenile stages of N. aberrans normally remain endoparasitic within roots, however migration out of the roots was detected. This "migration" probably occurs accidentally due to the easy breakdown of the necrotic, fragile epidermal cells that surround the cavities and nematodes when nematode bodies increase in size in the cavities during development, especially in young roots or wherever the necrosis is near the root surface. This hypothesis is supported by the results showing that only a small percentage of juvenile nematodes migrate from the roots, and also when the second stage juveniles penetrated roots deeply, they remained inside the roots throughout their development. This reaffirms the idea that the host tissue, in this case tomato roots, is necessary for the development of all juvenile stages and that migration out of the roots is more accidental than behavioural. Therefore, the immature females and males must be considered as the only stages that deliberately migrate out of the roots.

The invasion of $J_2$'s was mainly in the secondary lateral roots rather than in the main lateral roots. Possibly this is because the young roots are more easily penetrated than the older roots. Also most invasion of juveniles occurred behind the root tip in the region of root elongation than in other parts of the root. This is probably due to the action of attractive root exudates in that area. Thorne and Schuster (1956) also observed that frequently larvae of N. aberrans preferred to invade the area slightly behind the sugar beet root tip.

The invasion of $J_2$'s in the root tip induced the formation of pendulum-like galls, due to hypertrophy, only in the apical meristem. This same phenomenon produced by $J_2$'s of N. aberrans on tomato, has been observed by Schuster et al (1965) on sugar beet

roots, more frequently in tissue culture than in soil grown roots, Clark (1967) observed on tomatoes slightly swollen roots as an effect of juvenile development; but she differentiated clearly these swollen roots from the typical galls induced by the immature females.

From my observations, after the final moult has occurred, immature females and males became migratory. The immature females can migrate in the same root (Section 4.1) or like males, migrate out into the soil. It is clear that immature females, which obligately need to feed to continue development, invade the roots and feed near the vascular system, where both hypertrophy and hyperplasia of cells is induced resulting in gall formation, in agreement with Clark's observations.

Schuster and Sullivan (1960) had determined that $J_2$'s induced root galling in excised tomato roots, and Prasad and Webster (1967) working also with excised tomato roots, said that galls are produced by "third stage females", obviously they were referring to the slightly swollen roots that differ completely from those produced by immature females.

Mature males seem to have only one function after emergence; reproduction. When inoculated around tomato roots on nutrient water agar without females, they moved for several days around the roots without feeding, spent all their food reserves, and then died.

An interesting feature is the survival of the $J_4$'s either in water agar or water. For two months, this stage remained alive, coiled and motionless in a quiescent state; with its food reserves

intact. This is similar to survival stages in other nematodes such as $J_4$'s in D. dipsaci, $J_2$'s in Anguina tritici, eggs within cysts in Heterodera spp., and egg within the egg-masses in Meloidogyne spp (Thorne, 1961; Cooper and Van Gundy, 1971) among others. Possibly both eggs and $J_4$'s of N. aberrans can survive adverse conditions. Clark (1967) studying survival of N. aberrans, said that "second stage larvae lay coiled within cells of dying tomato roots, they moved infrequently, uncoiling, stretching, giving a few spear thrusts and recoiling, but were never seen to feed." My observations showed that only $J_4$ stages became coiled within the roots and only $J_4$'s survived outside the host and I consider that the pre-adult juveniles are a true, and the only survival stage, apart from eggs, in N. aberrans.

## SUMMARY OF THE LIFE CYCLE AND BEHAVIOUR OF *NACOBBUS ABERRANS*

In Fig 4.4 is shown the diagramatic representation of the life-cycle of *N. aberrans* after the observations in soil grown roots and *in vitro*.

Second stage juveniles of *N. aberrans* leaving the eggs, are the first parasitic stages of the nematode capable of invading the roots of tomato, mainly in the region of root elongation, root hair zone and mature parts of roots. Feeding of the second stage juveniles in the cortical parenchyma induces necrotic reactions and cell wall breakdown producing cavities. The outer cells of the cavities have thickened cell walls and are enlarged. When the invasion of second stage juveniles occurs infrequently at the root tip, slightly swollen roots with pendulum-like galls are produced, which differ from the normal galls induced by feeding of the immature females.

The third and fourth stage juveniles are endoparasitic and remain coiled in the cavities of the necrotic areas in the cortex. However it was observed that some movement of $J_3$ and $J_4$ stages does occur out of the root, but this appears to be accidental as the necrotic, fragile epidermal cells of cavities in the outer cortex breakdown.

There was evidence that a small proportion of the $J_3$'s feed in the cortex, because reinvasion into the roots of some of these stages was detected. However, no $J_4$ stages were observed to feed, and both $J_3$'s and $J_4$'s are capable of developing to immature female or males outside the roots without feeding.

The emergence of males and immature females occurs after the fourth moult. The immature female is the second parasitic stage, that either migrates in the same root or out into the soil

and re-enters new roots. The immature females feed near the vascular system where they become swollen and sedentary and where syncytia and both hypertrophy and hyperplasia of the cells are induced, resulting in gall formation. Mature females extrude a gelatinous matrix in which eggs are laid. Eggs are found inside or outside the gall, depending on the depth of penetration, size of root and position of the female.

Mature males migrate out into the soil. They are commonly found entangled inside the gelatinous matrix near the posterior end of the female either on the root surface or within the root suggesting that mating occurs and that N. aberrans is amphimictic.

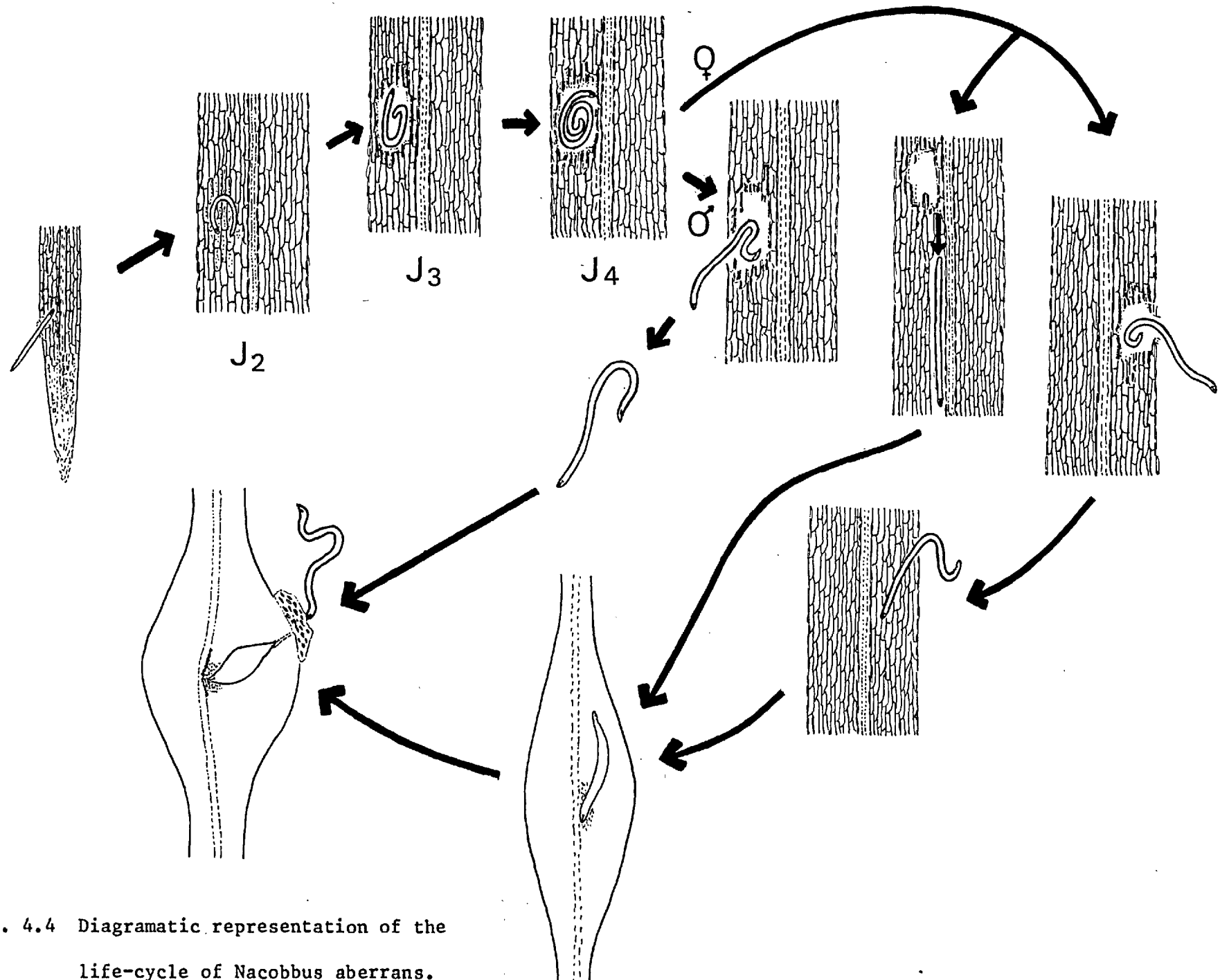



Fig. 4.4 Diagramatic representation of the life-cycle of Nacobbus aberrans.

TABLE 4.2.5. : COMPARISONS OF LIFE-CYCLE, BEHAVIOUR AND HOST-REACTION OF NACOBBUS ABERRANS WITH MELOIDOGYNE INCOGNITA.

| Nacobbus aberrans | | | Meloidogyne incognita | | |
|---|---|---|---|---|---|
| DEVELOPMENT STAGES | BEHAVIOUR | HOST-REACTION | DEVELOPMENT STAGES | BEHAVIOUR | HOST-REACTION |
| $J_2$ 's | First infective stage. Invade the roots, mainly in region of root elongation, root hair zone and mature roots. Feed in the cortex. | Necrosis, cavities and thickened cell walls in cortex. Invasion in root tip produce slight swellings in roots. No true galls. | $J_2$ 's | Infective stage. Invade the roots, mainly in region of root elongation and root hair zone. Feed in the vascular system. | Hypertrophy and hyperplasia. Start the formation of giant transfer cells and galls. |
| $J_3$ 's | Vermiform as an "open c", gradually become coiled. Sedentary endoparasites in the necrotic area or migratory into the soil accidentally. Evidence that some feed. Moult occurs. Increase in size. | Necrosis, cavities and thickened cell walls in cortex. If slight swelling roots present, they do not increase in size. No true galls. | $J_3$ 's | Swollen. Sedentary endoparasites. Do not feed. Moult occurs within the shed cuticle of the second moult. Increase in size. | Hypertrophy and hyperplasia. Increase in size of the giant transfer cells and galls. |
| $J_4$ 's | Vermiform and coiled. Sedentary endoparasites in the necrotic area or migratory into the soil accidentally. Do not feed. Moult occurs. Increase in size. | Necrosis, cavities and thickened cell walls in cortex. If slight swelling roots present, they do not increase in size. No true galls. | $J_4$ 's | Swollen. Sedentary endoparasites. Do not feed. Moult occurs within the shed cuticles of the second and third moult. No increase in size. | Hypertrophy and hyperplasia. Increase in size of the giant transfer cells and galls. |

TABLE 4.2.5. : Continued.

| Nacobbus aberrans | | | Meloidogyne incognita | | |
|---|---|---|---|---|---|
| DEVELOPMENT STAGES | BEHAVIOUR | HOST-REACTION | DEVELOPMENT STAGES | BEHAVIOUR | HOST-REACTION |
| Immature ♀ s | Second infective stage. Vermiform. Migratory in the roots or into the soil. Feed near the vascular system. | Begin hypertrophy and hyperplasia. Start the formation of syncytium and galls. | | NO EQUIVALENT STAGE | |
| Mature ♀ s | Spindle shape with tail. Sedentary endoparasites. Feed near the vascular system. Extrude a gelatinous matrix. Eggs within cortex or outside of galled roots, depending in female penetration and position and root size. | Hypertrophy and hyperplasia. Syncytium with enlarged no transfer cells. Galls and proliferation of secondary lateral roots from galls. | Mature ♀ s | Swollen. Sedentary endoparasites. Feed in the vascular system. Egg-laying in gelatinous matrix outside galled roots. | Hypertrophy and hyperplasia. Giant transfer cells (5 - 7). Galls. |
| Mature ♂ s | Vermiform. Migratory into the soil. Do not feed. Found normally entangled in the egg-masses, near posterior end of the females, or in soil. | | Mature ♂ s | Vermiform. Migratory into the soil. Do not feed. Found normally in soil or inside of old egg-masses (rare). | |

TABLE 4.2.5. : Continued.

| Nacobbus aberrans | | | Meloidogyne incognita | | |
|---|---|---|---|---|---|
| DEVELOPMENT STAGES | BEHAVIOUR | HOST-REACTION | DEVELOPMENT STAGES | BEHAVIOUR | HOST-REACTION |
| COMMENTS | Females and males have the same development and behaviour until $J_4$'s. Sex ratio influenced by the temperature. Low reproduction and possibly amphimictic. Eggs in egg-masses and $J_4$'s are the survival stages. | | COMMENTS | Females and males have the same development and behaviour until $J_4$'s. Although males require less food and space than females. Sex ratio depends on food available to the parasite. High reproduction and parthenogenetic. Eggs in egg mass are the survival stages. | |

## 4.3 RELATIONSHIP BETWEEN TEMPERATURE AND POPULATIONS OF TWO ISOLATES OF NACOBBUS ABERRANS ON TWO TOMATO VARIETIES.

### Introduction

It is obvious that the important role played by temperature needs to be considered when the activity of nematodes in general is investigated. Although temperature is a major factor affecting nematodes in their "niches", there are many other factors, such as rainfall, soil type, host, altitude, cultivation practices. Temperature affects directly or indirectly the life of all nematodes, in particular the plant parasite forms, especially the sedentary endoparasites, as temperature also has a marked effect on the growth of the plants.

N. aberrans has stages in the soil as well as parasitic stages on plant roots, and it has been shown that temperature affects infection and development of Nacobbus in sugar beet roots (Schuster et al., 1966). Similarly, temperature affects the life-cycle of Nacobbus on tomatoes (Prasad and Webster, 1967; and Section 4.1).

Effect of temperature has been studied in great detail with other nematodes. Bird and Wallace (1965) showed clearly how temperature regulates hatching, mobility, invasion and growth of M. hapla and M. incognita. The influence of the temperature in the development and reproduction of Meloidogyne spp. has also been studied by other workers (Wong and Mai, 1973; Thomason, 1957; Vrain et al, 1978; Daulton and Nusbaum, 1961). Temperature has also been observed to influence the sex ratio in nematodes (Davide and Triantaphyllou, 1967; Prasad and Webster, 1967). Furthermore, Alarcón and Jatala (1977) suggested that there might be a relationship between temperature

and resistance toward the false root-knot nematode in some potato varieties. They found galling occurred in a resistant variety under a high temperature regime. This observation agrees with that of Holtzmann (1965) and Grumdbacher and Stanford (1962), who showed that temperature affects the resistance of tomato to the root-knot nematode, and alfalfa to the stem nematode respectively.

In this study two tomato varieties were used. Jefferson, which is a traditional variety in the Ecuadorian valleys of the Andes mountains, and Moneymaker a well known tomato glasshouse variety in Great Britain. The idea was to observe both populations of N. aberrans on two different host varieties, in order to eliminate variations such as, adaptation to a particular variety that may have occurred with both populations.

The purpose of this study was two fold:

i) To determine how temperature affects the life-cycle of two populations of N. aberrans on two varieties of tomato (Jefferson and Moneymaker) and

ii) To evaluate galling and fecundity on the two varieties at different temperatures.

# MATERIALS AND METHODS

Tomato plants in 9 in. pots, were inoculated separately with 1,000 hatched larvae of each isolate and the nematode population allowed to increase over three months. The infected roots and soil obtained were then used as the inoculum for this experiment.

Two large box containers (96 x 80 x 30 cm) were partially filled with sterilized loam and sand (50 : 50) and placed on a bench in a heated glasshouse. In the middle of each container, in a rectangle of 70 x 50 cm, were placed chopped roots and infected soil arising from the above cultures, into which were planted tomato seedlings of each variety. One container was inoculated with the British isolate and the other with the Ecuadorian isolate, and two 15 days old tomato seedlings of each variety (Jefferson and Moneymaker) were planted in each container every two weeks, and then harvested after a six weeks growth period.

Nematodes from 1 g. of roots were counted and the different stages identified. The number of galls or knots and the presence of egg-masses were also noted.

Soil temperatures were recorded by a minimum/maximum soil thermometer from November 1978 to October 1979. Natural daylight was supplemented by artificial light during November 1978 to March 1979 to make a daylight of 12 hours.

# RESULTS

In Fig 4.5. Appendix C. Tables 1 and 2., is shown the variation in populations of N. aberrans in tomato var. Jefferson throughout the 11 months observations in relation to maxima and minima temperatures. Marked differences were apparent between the Ecuadorian and the British populations of the nematode.

During November and March when the minimum and maximum temperatures were $9^{o}$ and $24^{o}$C respectively, populations of the Ecuadorian isolate were much higher than those of the British isolate. However, after March, when temperatures were rising, populations of the British isolate increased at a greater rate than the Ecuadorian isolate to reach a peak of 240 nematodes per g. of roots, in June, July and August, when temperatures were $20^{o}$ and $38^{o}$C. (minimum and maximum range respectively), compared to populations of the Ecuadorian isolate of 122 nematodes per g. of roots in the same period.

The low temperatures also affected in different ways nematode development of both isolates. In the British isolate, the populations seemed to disappear in samples taken during January when temperatures were $9^{o}$ and $19^{o}$C (minimum and maximum range respectively), but nematodes were recovered from the Ecuadorian isolate, although populations were the lowest recorded over the sampling period.

Galling of roots also differed between isolates at the different temperatures. No galls were produced by the British isolate when minimum temperature dropped to $9^{o}$C during December to February with a mean of 13.5 and 18.2 (minimum and maximum respectively), whereas the Ecuadorian isolate produced some galls at these temperatures

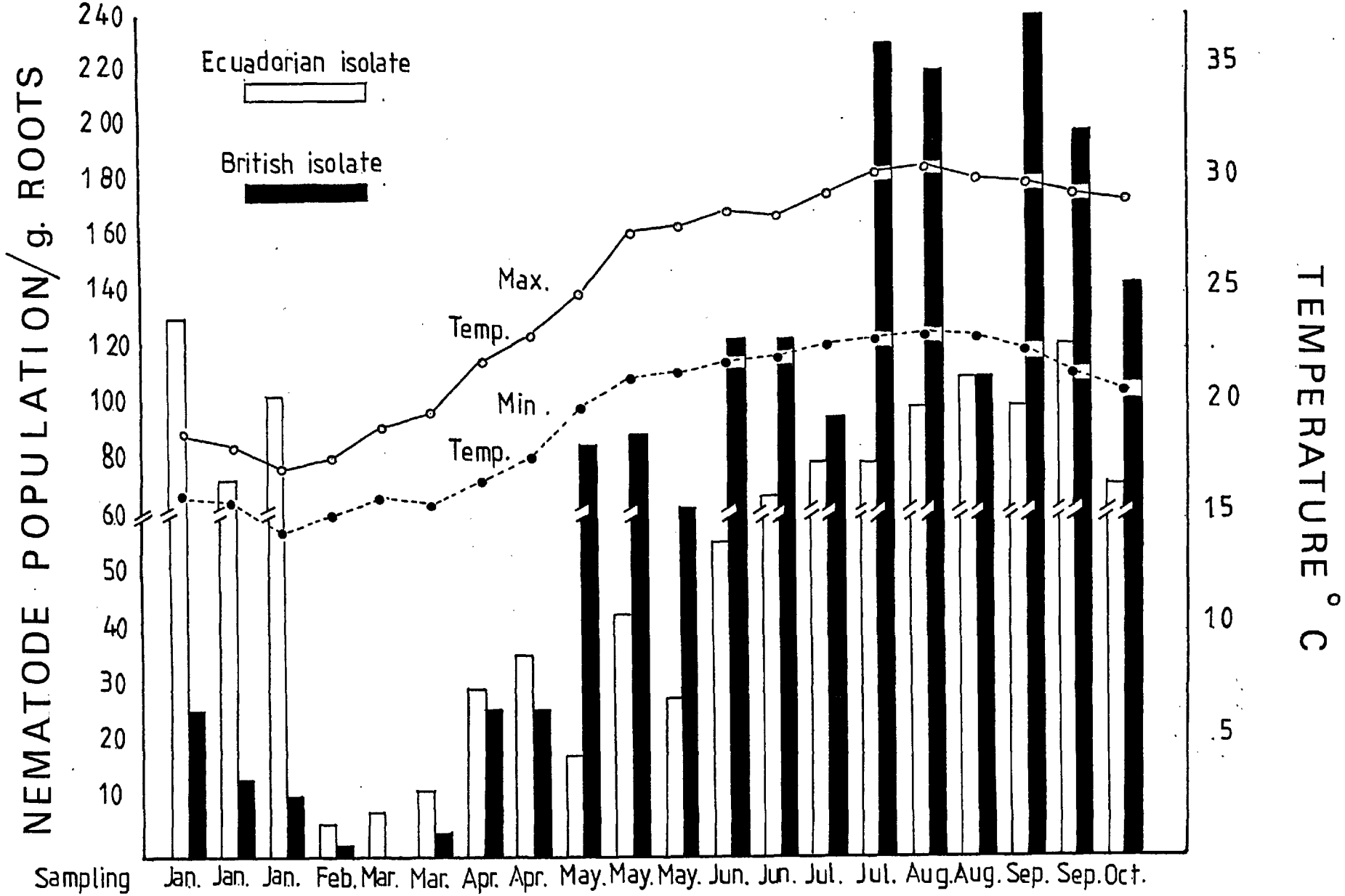



Fig. 4.5 Relationship between N. aberrans population on tomato var. Jefferson and temperature over 11 months.

(Fig. 4.6. Appendix C. Tables 1. and 2.). In contrast, the amount of galling produced by the British isolate exceeded that of the Ecuadorian isolate when temperatures increased to 20° and 38°C (minimum and maximum respectively) during June to August.

Despite the fact that nematodes of the Ecuadorian isolate developed and produced galls during the winter season at low temperatures, no eggs were produced until April when temperatures increased to 17° and 30°C (minimum and maximum respectively). The British isolate also did not produce eggs during the cold winter, but produced eggs sooner than the Ecuadorian isolate in March at temperatures of 13° and 27°C (minimum and maximum respectively). (Fig. 4.7. Appendix C. Tables 1. and 2.). The production of eggs may have been related to the presence of males which were recovered as soon as the egg-masses were detected in both isolates but not before (Appendix C. Table 1. and 2.)

In Figs. 4.8, 4.9 and 4.10 Appendix C. Tables 3. and 4. are included the populations of N. aberrans for both isolates on tomato var. Moneymaker, also the galling and number of egg-masses. The results are very similar with few differences from those obtained with var. Jefferson; maximum populations occurred in June but higher numbers were found with var. Moneymaker compared to Jefferson i.e. 400 nematodes per g of roots compared to 230 nematodes per g. roots respectively.

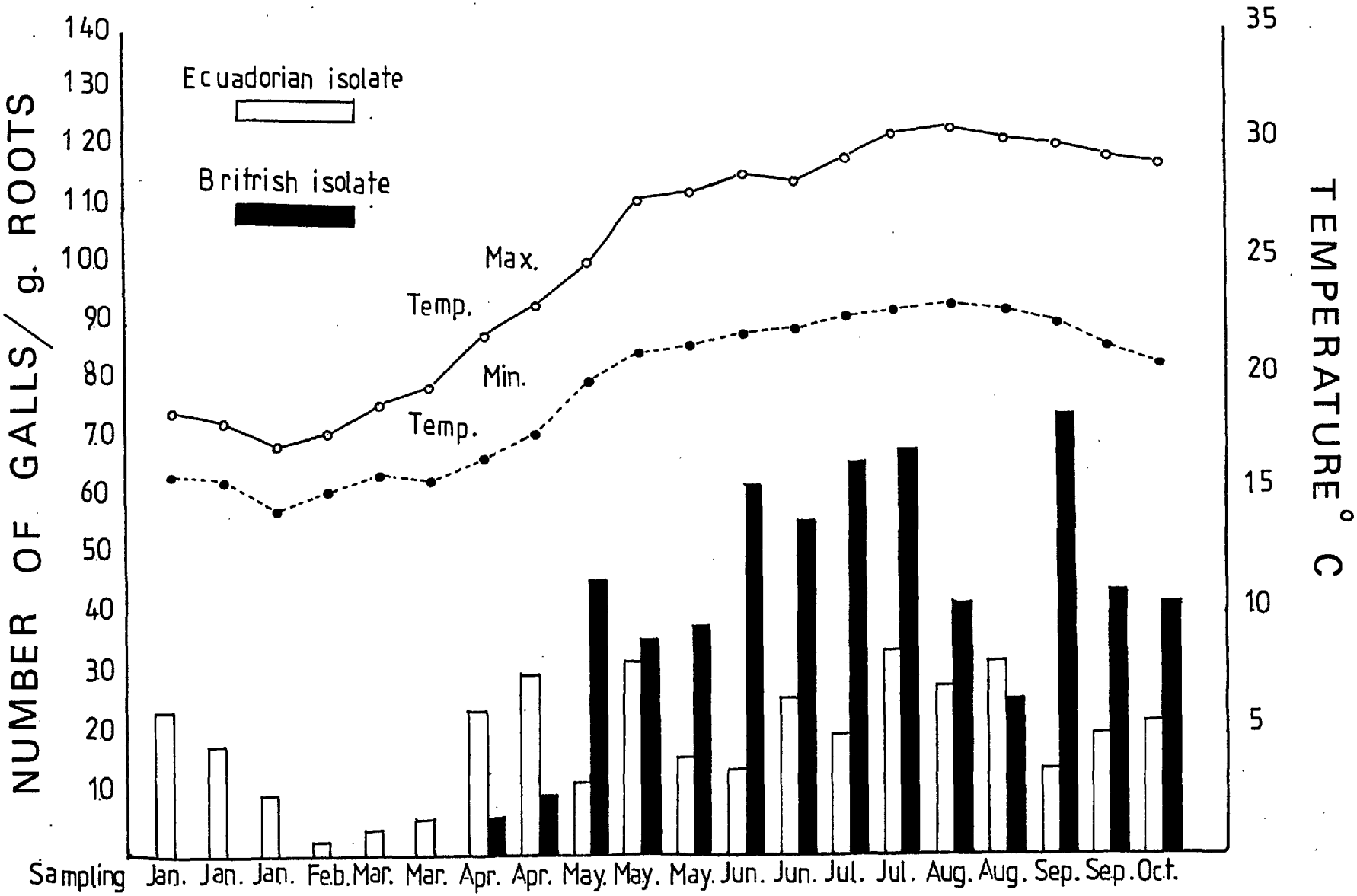



Fig. 4.6. Relationship between number of galls produced by N. aberrans on tomato var. Jefferson and temperature over 11 months.

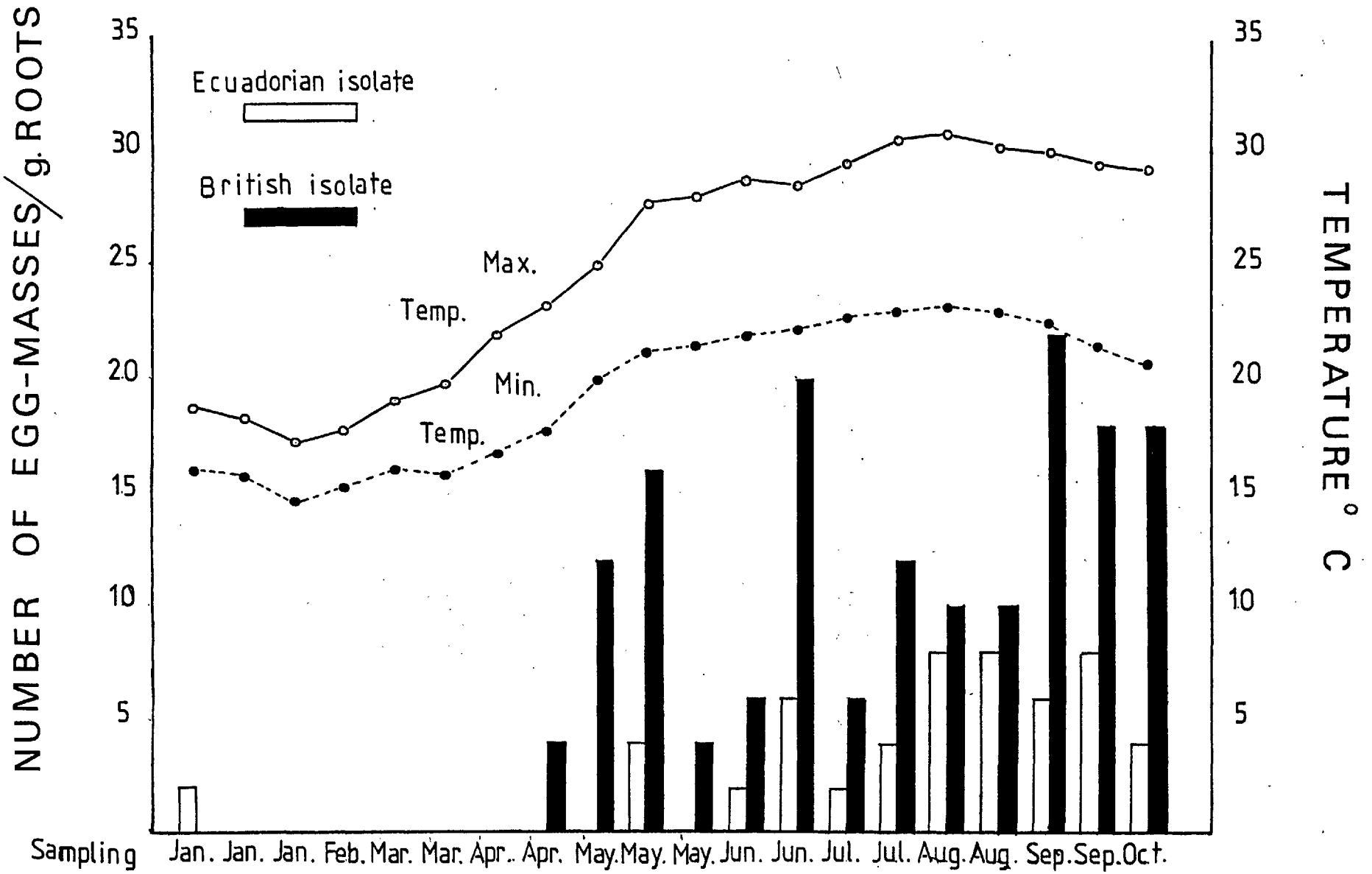



Fig. 4.7 Relationship between number of egg-masses of N. aberrans on tomato var. Jefferson and temperature over 11 months

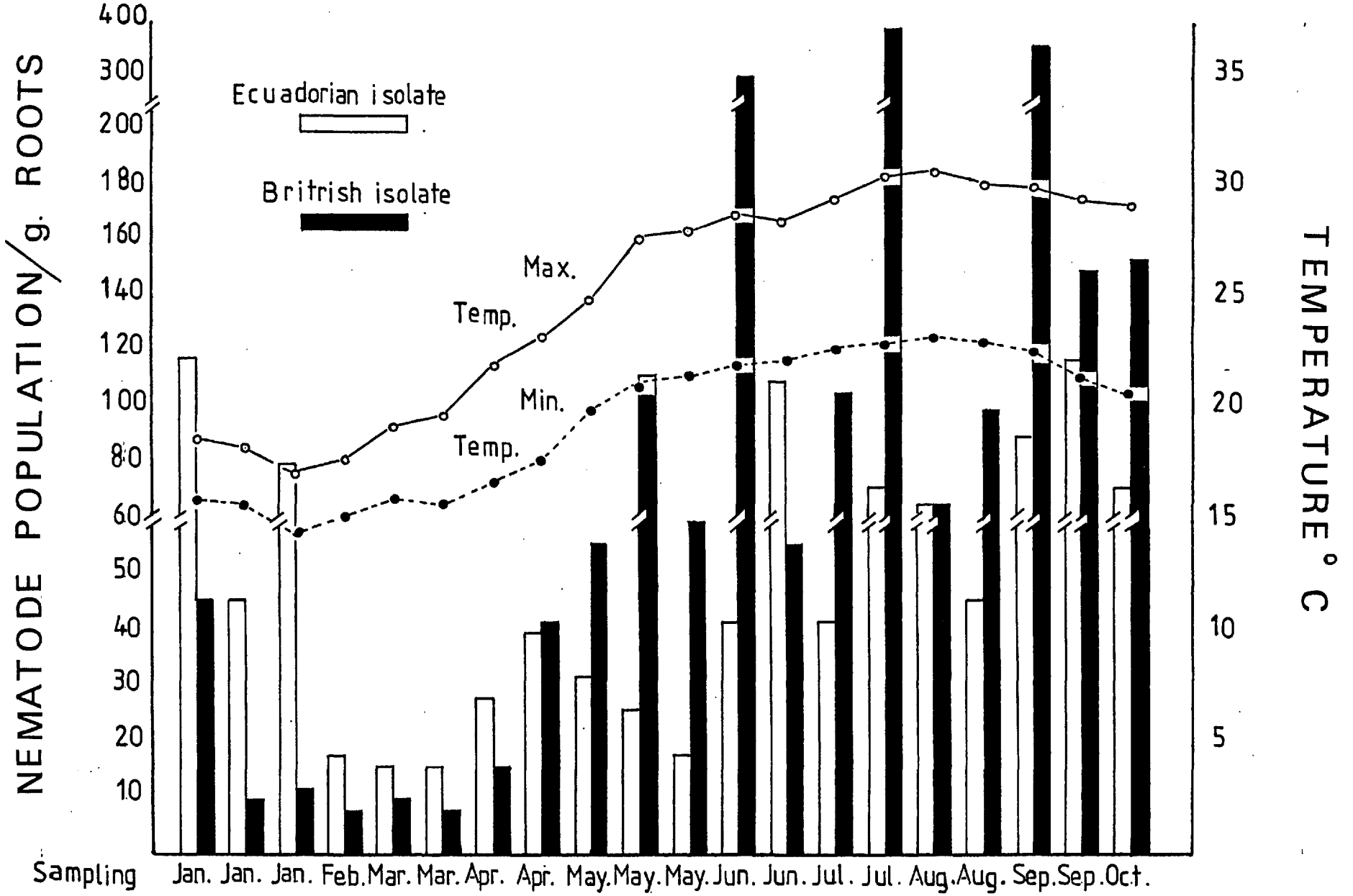



Fig. 4.8. Relationship between N. aberrans population on tomato var. Moneymaker and temperature over 11 months.

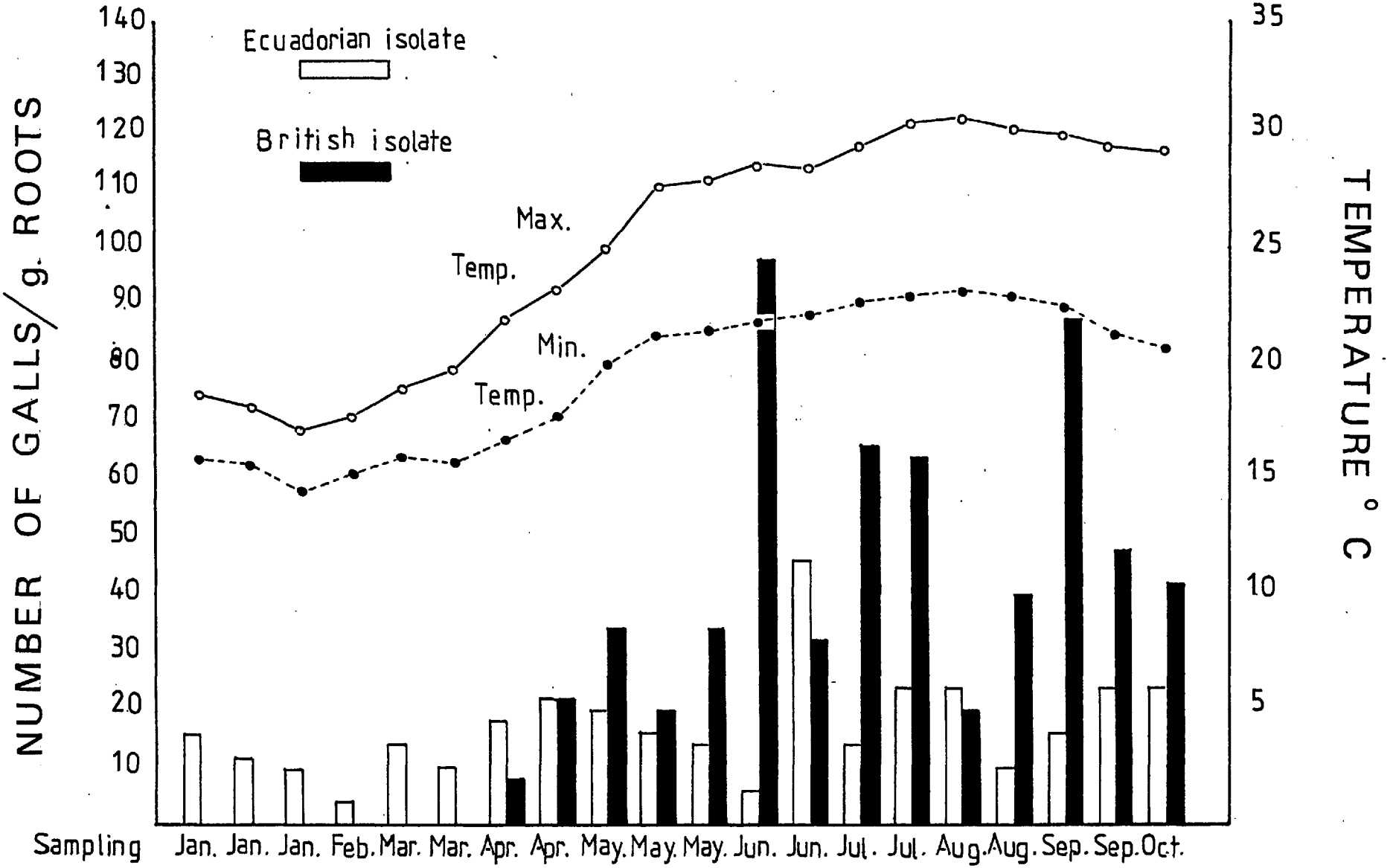



Fig. 4.9. Relationship between number of galls produced by N. aberrans on tomato var. Moneymaker and temperature over 11 months.

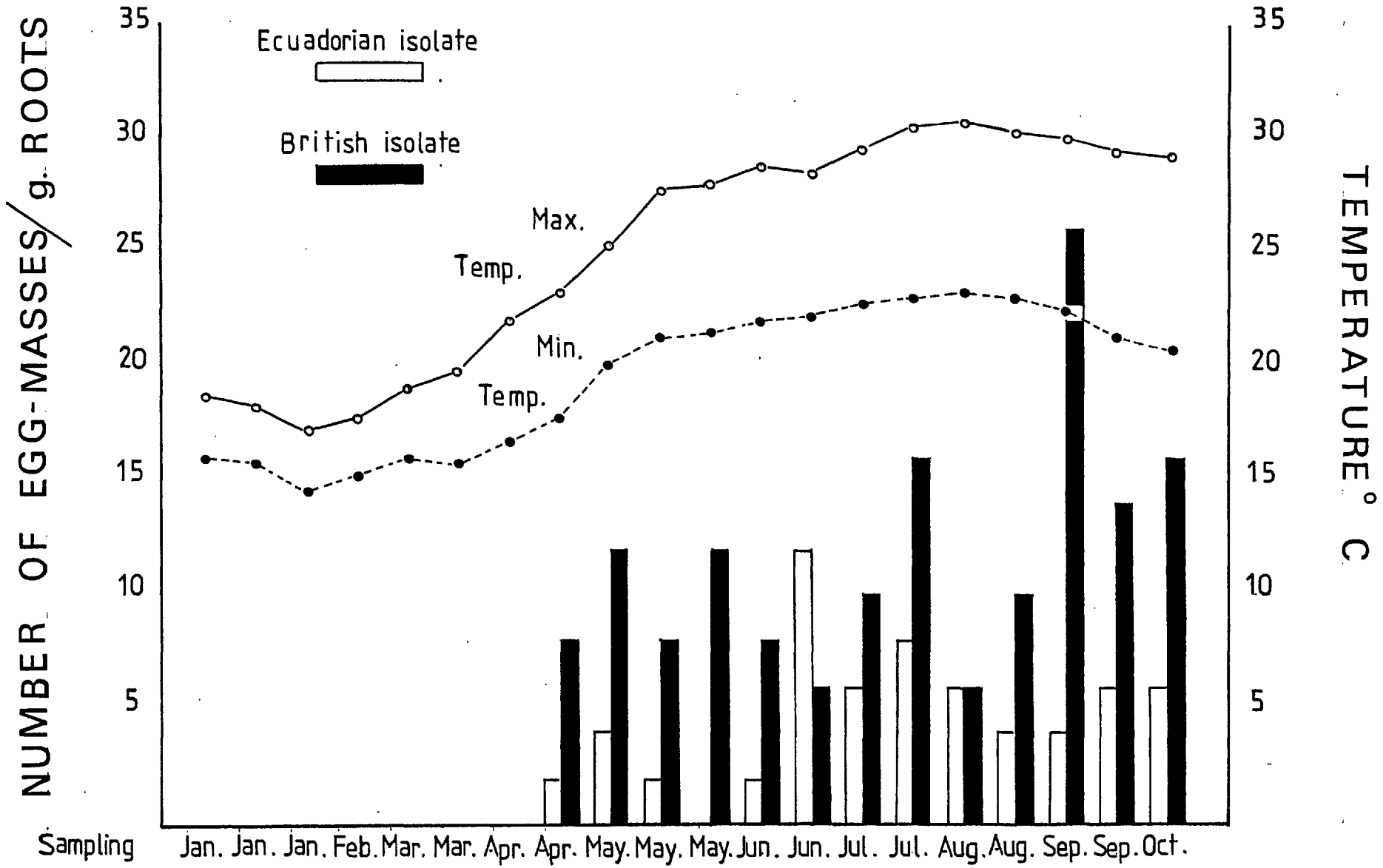



Fig. 4.10. Relationship between number of egg-masses of N. aberrans on tomato var. Moneymaker and temperature over 11 months.

# DISCUSSION

Temperature was a limiting factor in the normal activities of both isolates of N. aberrans. Thus, the population of the British isolate during the colder winter months decreased considerably, when neither galls nor eggs were produced. Although the Ecuadorian isolate could induce galling throughout the year, during winter there was no egg production. But when the temperature increased, the population of the Ecuadorian isolate only increased moderately in contrast to the British isolate which increased rapidly and reached higher levels.

The reason why the Ecuadorian isolate can tolerate the low temperatures better than the British isolate is probably related with the regime of temperature of the zone where it was sampled (Section 2.). Clark (1967) working with cultures of nematodes from which the British isolate was obtained, reported that galls were never found during winter months and it was only late in the summer when galls with egg-masses appeared. Schuster et al (1966) also observed the effect of temperature on infection and development of the formerly N. batatiformis. They found that few or no galls were evident at 10° and 15°C, however, with temperatures above 15°C, there was an increase in development and reproduction.

Other authors have reported the relationship that exists between temperature and nematode populations. Webster (1964), studying population increase of Ditylenchus dipsaci in narcisus, determined that a progressive increase of this nematode population in May/June was associated with a rise in temperature. Also, Thomason and Lear (1961), reported the influence of temperature on egg-mass production

of 6 populations of M. javanica and M. incognita acrita, 2 populations of M. hapla and 1 each of M. arenaria arenaria and M. arenaria thamesi, in which only a few egg-masses were produced at 15° - 16°C after 35 days, increasing rapidly at 20 - 21°C, and giving a maximum egg-mass production, for most of the species at 25 - 32°C.

Another interesting aspect was the relation between the presence of egg-masses and males in both isolates. Males were found as soon as egg-masses were detected, normally entangled inside the gelatinous matrix. Although the results of sex ratio from the life-cycle experiments were confused, Prasad and Webster (1967) pointed out that the sex ratio is influenced by temperature, with a large presence of males as the temperature increased to a maximum of 8 males to 1 female at 30°C. This observation strongly suggests that the presence of males is necessary for reproduction. However, this aspect must be studied to determine if N. aberrans has an amphimictic or parthenogenetic reproduction, or both as other nematodes such as T. semi penetrans (Dalmasso et al., 1973), and many Meloidogyne spp., e.g., M. graminicola and M. naasi (Triantaphyllou, 1969), M. graminis and M. ottersoni (Triantaphyllou, 1973).

It was also interesting to know that N. aberrans was able to survive under comparatively low temperature in the winter months, and that as soon as the minimum temperatures increased, the presence of nematodes was detected. Clark (1967) observed that Nacobbus successfully passed the exceptional hard winter of 1962-3 outdoors on winter-hardy lettuce, when the temperature ranged from -5°C to -10°C. Results from Section 4.2. suggests that both eggs and fourth stage juveniles survive adverse conditions.

As was mentioned in the introduction, despite the fact that temperature can affect directly nematode biology, it could also have an indirect effect on plant growth, and this effect on plant physiology may result in an abnormal nutrient supply for nematode development. However, the present results did not show any differences between varieties, so that apparently the varietal host did not have any influence on the development of either of the two isolates of N. aberrans used in this study.

SECTION 5

# HISTOPATHOLOGICAL OBSERVATIONS

## Introduction

Plant parasitic nematodes cause damage to plants either by mechanical breakdown of cells or as a result of substances secreted during feeding. The injuries produced by nematodes are related to feeding habits. Kirkpatrick,Van Gundy and Mai (1964) grouped root parasitic nematodes into ectoparasites which remain outside the host tissue, except for the stylet; semi-endoparasites that bury the anterior portion of the body in the host tissue; and endoparasites that are entirely embedded in host tissue while feeding. All these various groupings can be further divided into either, i) migratory nematodes, which feed for a short time at one site and then move to another, or ii) sedentary nematodes which remain at a selected feeding site for a long period or permanently.

The relationship between the nematode and its host has been the subject of interesting studies on the histopathological effects of certain plant parasitic nematodes at both the gross morphological and ultrastructural levels. Schuster and Thorne (1956) were the first to observe the pathology of Nacobbus on sugar beet roots. Cellular alterations and gall formation have also been described by other workers (Schuster et al, 1964; Schuster et al, 1965). Clark (1967) observed galls produced by N. aberrans and found that within the gall (next to the stele) a spindle shaped structure was formed in which the female's head was buried.

More detailed studies on the structure and function of the syncytium induced by Nacobbus on tomato roots, were recently published

by Jones and Payne (1977a, 1977b). However, little attention has been paid to the histopathological effects of parasitism by the juvenile stages.

In this present study, the histopathological effects of N. aberrans were examined during all phases of parasitism.

## MATERIALS AND METHODS

For histopathological observations, 15 days-old tomato seedlings growing in a sterilised loam and sand soil in 7 in. pots, were inoculated separately with hatched juveniles of both isolates of Nacobbus and left in the glasshouse. Then, 25 and 65 days post-inoculation plants were removed from soil, roots washed carefully and then cut into small pieces (0.5 to 1 cm. long) prior to processing as follows:-

1. Fixed in F.A.A. for 48 hours

F.A.A. (Formalin/Acetic/Alcohol) contains:

| | |
|---|---|
| 95% alcohol | 20 ml. |
| Formalin | 6 ml. |
| Glacial acetic acid | 2.5 ml. |
| Distilled water | 40 ml. |

2. Dehydrated through an ethyl alcohol series, as follows:-

| | |
|---|---|
| 50% alcohol | 12 hours |
| 70% alcohol | 12 hours |
| 95% alcohol | 12 hours |
| 99.9% alcohol | 12 hours (2 changes) |
| 100% alcohol | 12 hours (2 changes) |

3. Embedded in:

| | |
|---|---|
| 50:50 xylene and butanol | 12 hours |
| pure xylene | 12 hours (2 changes) |
| 50:50 xylene and wax | 12 hours |
| 100% wax | 12 hours (2 changes) |

(Parafin wax m.p. 56 - 57°C)

Longitudinal and transverse serial sections, 12 µ

(for 25 days p.i. material) and 22 μ (for 65 days p.i. material), were cut on a rotating microtome and attached to slides using Glycerine - albumin as an adhesive.

The sections were stained with safranin and haematoxylin (Johansen, 1940), using the following procedure:

a. - Slides placed in xylene to remove the wax : 5 min (2 changes).

b. - Transferred to 99.9% alcohol 2 min.
95% alcohol 2 min.
70% alcohol 2 min.
50% alcohol 2 min.

c. - Stained in 0.5% paframin in 50% alcohol for 30 min.

d. - Rinsed in 50% alcohol.

e. - Stained in haematoxylin for 45 sec.

f. - Washed in running tap water for 5 min.

g. - Dehydrated in:

50% alcohol )
)
70% alcohol ) rapid
)
95% alcohol )

99.9% alcohol 2 min (2 changes).

h. - Transferred to xylene 5 min (2 changes).

i. - Mounted in Canada balsam.

# RESULTS

Twenty five days after inoculation the penetration of second stage juveniles of both isolates of N. aberrans alone or in large numbers, had produced an immediate reaction of the root tissue, expressed as necrosis (Plate 6.a.). Sections of these necrotic areas revealed that destruction of cell walls and the formation of cavities had occurred, where the nematodes remained coiled during development (Plate 6.b.). The cavities were located in the cortex, bounded by the endodermis, but the vascular system remained undamaged (Plate 7.a.).

Another interesting feature was the presence of cells with thickened cell walls surrounding the cavities. All $J_2$'s that invaded roots induced necrosis, cavities and thickened cell walls (Plate 7.b.).

In root material examined 65 days after nematode inoculation, the immature females of N. aberrans of both isolates, had left the necrotic areas and migrated within the roots or had moved out into the soil and re-invaded.

The immature females were located in a permanent site near the vascular system, with their entire bodies within the cortex. (Plate 8.a.), and had initiated the formation of syncytia and root galling, which contrasted with the normal tissue of a non-galled root (Plate 8.b.).

Females of N. aberrans induced hypertrophy and hyperplasia of the cortical tissue, resulting in the abnormal growth of the tissue and the formation of knots or galls. Modification and disorganization of the vascular elements around the syncytium was evident. Xylem

Plate 6.

a. Necrosis induced by the presence alone or in large number of juveniles of N. aberrans in the cortex of tomato var. Moneymaker (x 100).

b. Transverse section of tomato root infested with juveniles of N. aberrans (x 100).

a. necrotic area

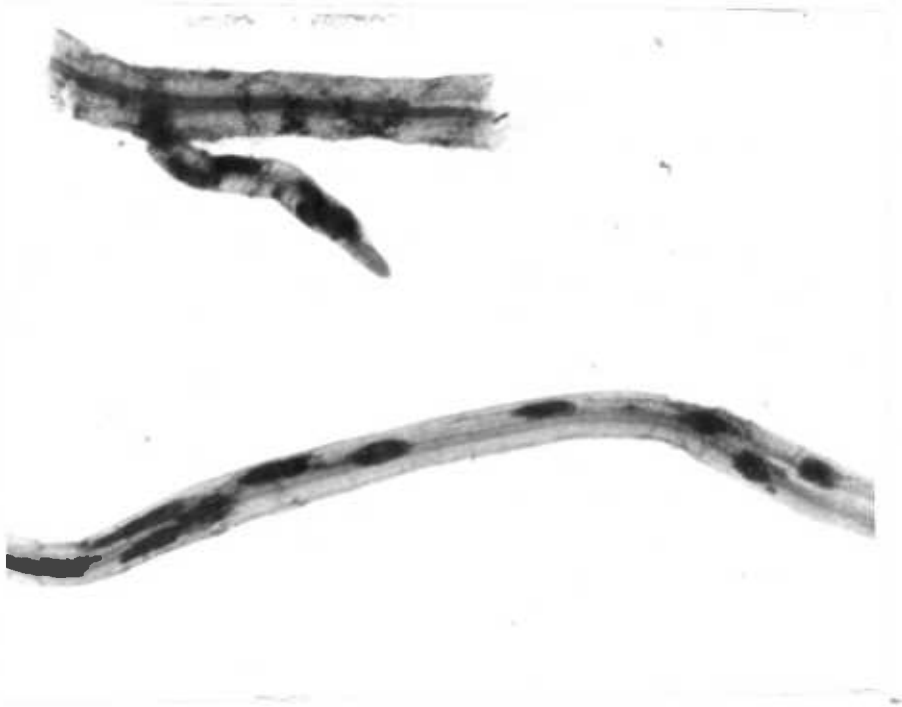
c. cortex

e.p. epidermis

n. sections of juvenile stage of N. aberrans

v.s. vascular system.

a



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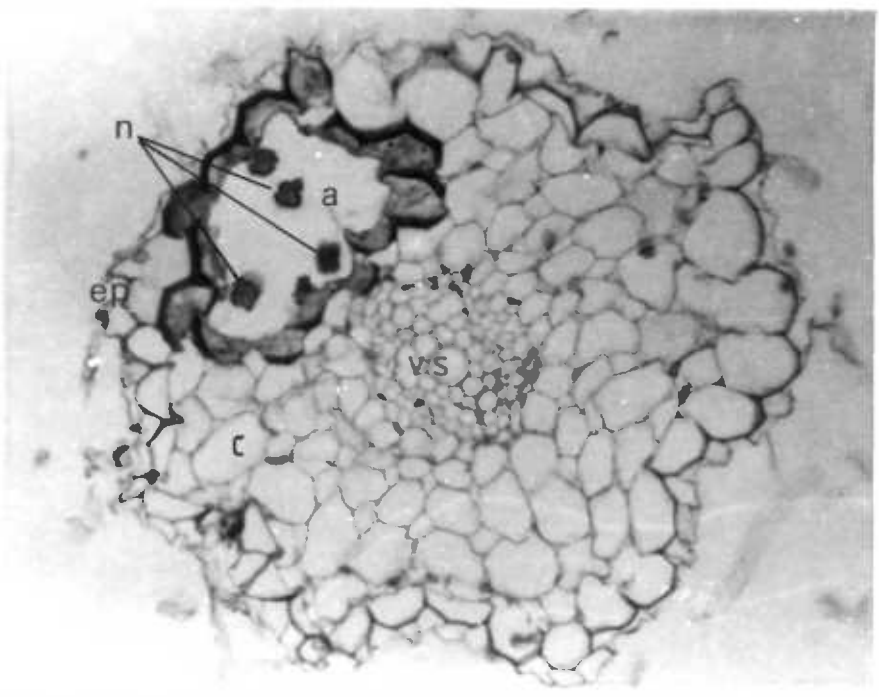


Plate 7.

a. Root cavity produced by juveniles of Nacobbus feeding in the cortex. Note thickened cell walls, and coiled nematode body (x 200).

a. necrotic area

c. cortex

e.n. endodermis

n. sections of nematode body.

v.s. vascular system.

b. Longitudinal section of tomato root with cavity produced by Nacobbus juveniles. Note thickened cell walls (x 200).

a. necrotic area

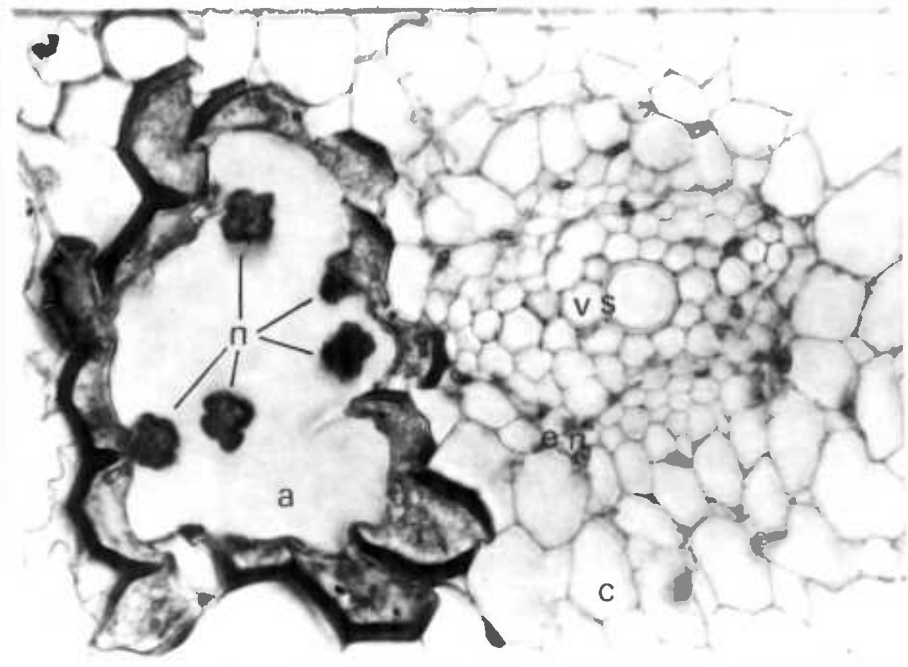
c. cortex

e.p. epidermis

n. nematode

v.s. vascular system

a

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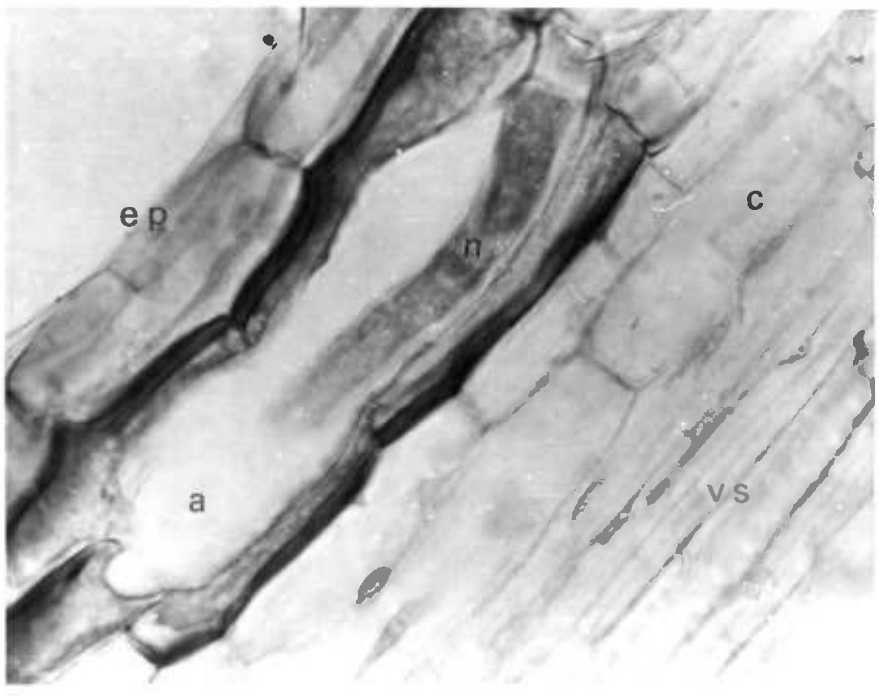


Plate 8.

a. General view of the gall induced by female of *N. aberrans*. Note the area affected by the syncytium (x 200).

e.n. endodermis

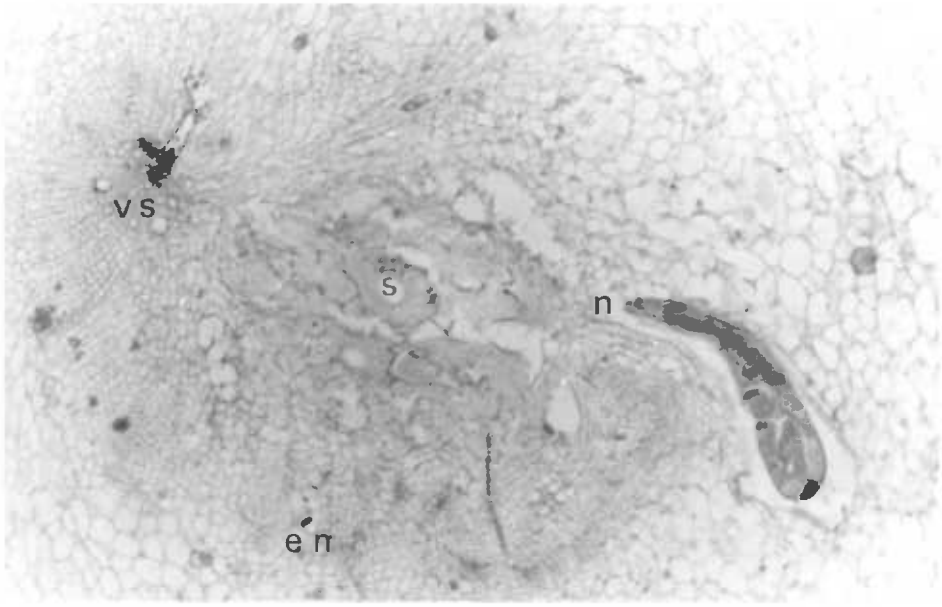
n. nematode

s. syncytium

v.s. vascular system

b. Transverse section of a normal root (x 400).

a

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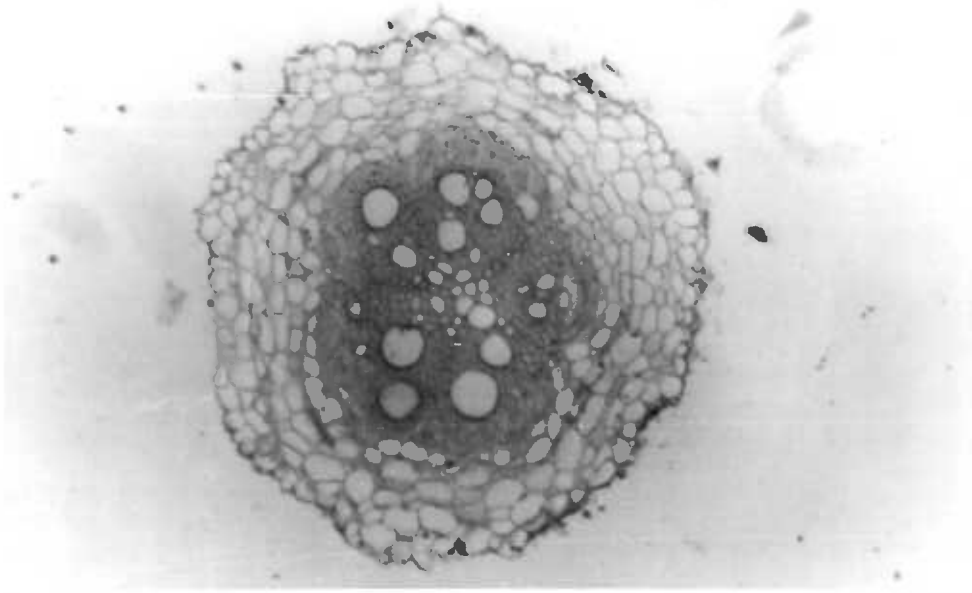


elements with abnormal shape grew inside the syncytium mass or surrounding the syncytium (Plates 9.a. b., and 10.b.).

The syncytium induced by the feeding of N. aberrans on tomato roots, was a spindle shaped mass of cells. There was a clear demarcation between cells which have been incorporated into the syncytium and those that remained outside (Plate 10.a.). Syncytial cells were either mono- or binucleate, and the nuclei were enlarged.

The presence of lateral roots emerging from galls was noticed either opposite the syncytial side (Plate 10.b.), or alongside the nematode feeding site (Plate 11.a.).

This study also revealed that the egg-mass produced by the female could be extruded directly out onto the root surface (Plate 11.b.), or if nematode was deep in the root, the eggs were released through a channel within the gall tissue.

Plate 9.

a. Nacobbus aberrans female with the head near syncytium (x 500).

n. nematode

s. syncytium

x. xylem

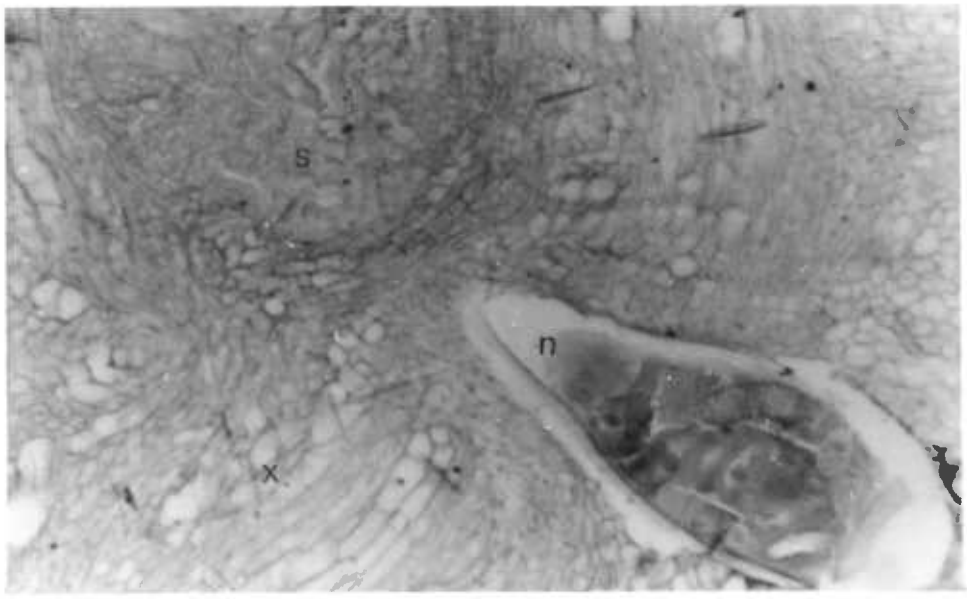
b. Nacobbus aberrans syncytium in the vascular system. Note the deformation of the xylem (x 400).

s. syncytium

v.s. vascular system

x.d. xylem deformed.

a

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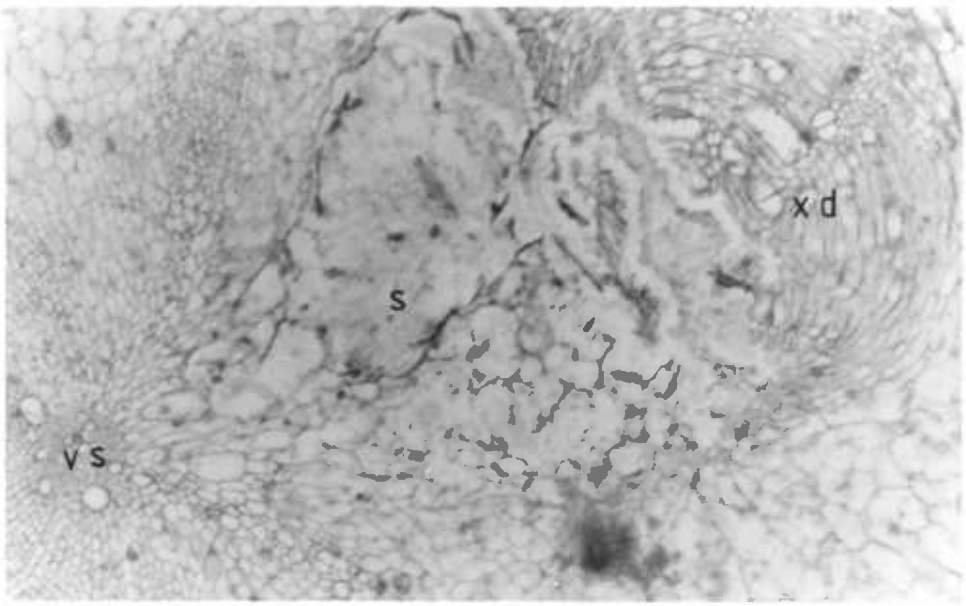


Plate 10.

a. View of the spindle-shaped syncytium. Note the enlarged cell within the syncytium and compared to the cells in the normal cortex (x 500).

c. cortex

s. syncytium.

b. Emergence of a lateral root opposite to the syncytium. Note the undamaged area of the vascular system and the area effected by the nematode (x 300).

c. cortex

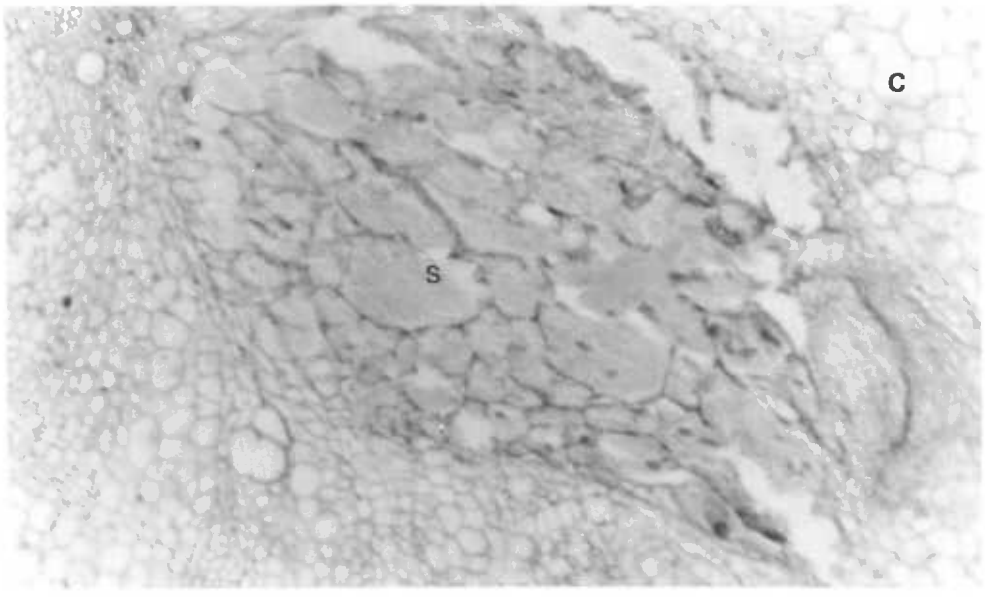
l.r. lateral root

n. nematode

s. syncytium

v.s. vascular system.

a

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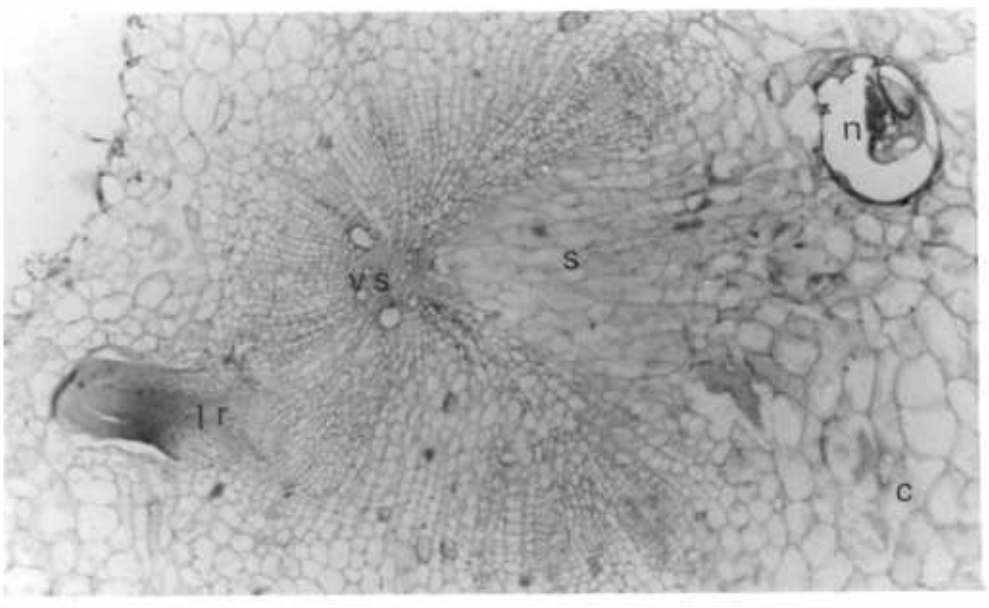


Plate 11.

a. Emergence of a lateral root alongside nematode body (x 400)

c. cortex

l.r. lateral root.

n. nematode

s. syncytium

v.s. vascular system

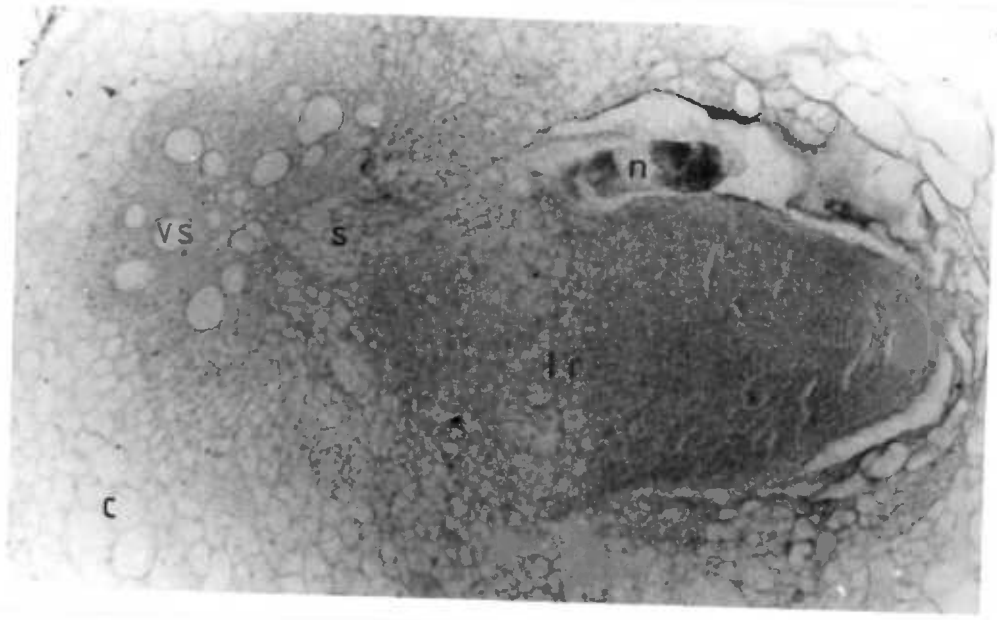
b. Nacobbus egg-mass on the gall surface (x 300).

e.m. egg-mass

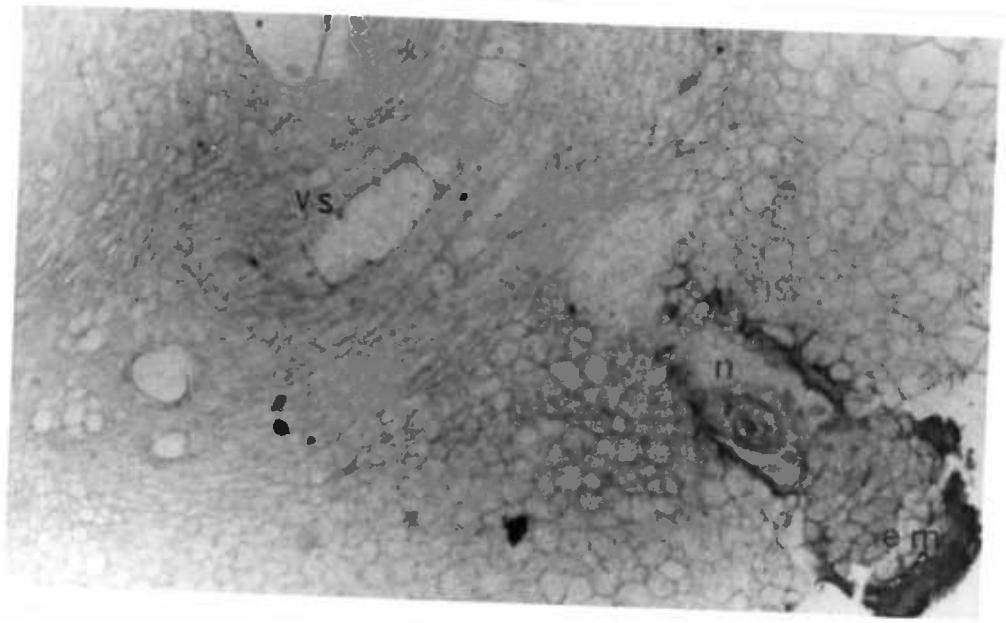
n. nematode

v.s. vascular system

a




b



# DISCUSSION

Observations from biological studies, revealed two parasitic stages of N. aberrans, the second stage juveniles and the immature females, and the results obtained in the histopathology study of these two stages reaffirmed the original idea. The present discussion includes some ideas from the first studies and it is orientated to compare some aspects of Nacobbus root-relationship with other nematodes, especially Meloidogyne.

The histopathology of N. aberrans has been observed on sugar beet. Schuster et al (1960) in roots grown in vitro, found that males as well as females were capable of inducing the formation of galls. Schuster et al (1965) also reported that, after penetration of the larvae, there was gall formation. Prasad and Webster (1967) pointed out that the "third stage female" induced gall formation in excised tomato roots. The present results disagree with these earlier observations because soon after the $J_2$'s invade the roots they lie exclusively in the cortex and begin feeding, producing necrosis and cavities, where they develop to immature females or mature males. Although slight like-pendulum galls were observed (Section 4.2.), these were produced when $J_2$'s invaded the root tip where the apical meristem and ground tissues were invaded and root growth ceased. These pendulum-like galls, have also been observed by other authors as induced by R. similis in citrus roots (Du Charme, 1959)- and in tomato by M. incognita (Christie, 1936).

Therefore, the first reaction of the root tissue to larval invation is similar to and typical of the Pratylenchid nematodes. Blake (1966), Du Charme (1959), Mountain and Patrick (1959), Babatola

and Bridge (1980), studying the histopathology of R. similis on bananas, R. similis on citrus, Pratylenchus penetrans on peach, and Hirschmanniella spp. on rice respectively, reported that the main effect after nematode invasion, was the destruction of cortical cells and cavity formations. In the case of N. aberrans, there are two differences compared to the Pratylenchid nematodes, i) Nacobbus juveniles remain coiled in one site and do not migrate through the cortical parenchyma, and ii) the presence of thickened cell walls surrounding Nacobbus cavities, have not been reported with the other nematodes.

Normally it is the immature females and not the advanced larval stages, as assumed by Schuster et al (1965), that leave the necrotic areas and either migrate within the same root from necrotic areas or leave the root and re-invade a new root from the soil, find a feeding site and induce the formation of syncytia and root galling.

The immature females feeding near the vascular system, produce a syncytium that starts in the cells near to nematode stylet and continue growing into the vascular tissue. It seems that the syncytium was being formed by the merging of protoplast due to the gradual dissolution of some cells. This observation is contrary to Schuster et al (1965) who said that usually the female does not affect the vascular tissue, and that the syncytium typically is located entirely within the cortex of the sugar beet root, or it is located very near the vascular system, the syncytium is crescent shaped in transverse section with the concave side toward the stele. However, my observations on tomato closely agree with those of Jones and Payne (1977b) who reported that transformed cells are placed in the stele.

The syncytium induced by Nacobbus resembles those of other endoparasites in that a large volume of cytoplasm with enlarged ameboid nucleus and nucleoli are present (Jones and Payne, 1977a; Jones and Payne, 1977b). However, among the endoparasites Meloidogyne, Heterodera and Rotylenchulus; Nacobbus induce external symptoms similar to Meloidogyne as both nematodes induce galls. However, juvenile stages of Meloidogyne spp., after invasion, incite giant cell formations (5-7 cells) (Paulson and Webster, 1970), while it is the immature female of Nacobbus which is associated with syncytium and gall formation. More abundant details and differences have been found with ultrastructural studies (Jones and Payne, 1977a; Jones and Dropkin, 1975; Jones and Payne 1977b).

In the first period of parasitism the damage is restricted to the cortical parenchyma, where only the presence of large quantities of nematodes, or the invasion of secondary organisms may cause considerable damage. The latter has been demonstrated in citrus with T. semipenetrans under field conditions (Cohn, 1965).

Syncytium and root galling induced by Nacobbus immature and mature females, in the second period of parasitism, will alter the translocation and conduction of nutrients and water through the vascular system, and stimulate the concentration of some elements in the root system, similar to the response to the presence of Meloidogyne spp. However, the alteration of root tissues by Nacobbus is probably not as severe because the syncytia are present only in a restricted part amounting to 20 - 40% of the stele area.

# SECTION 6

## HOST-PARASITE RELATIONSHIPS

### 6.1. PATHOGENICITY OF N. ABERRANS ON TOMATO

#### Introduction

For any plant parasitic nematode to be considered harmful or capable of causing economic losses, its pathogenicity must be demonstrated.

The injuries caused by nematodes to their hosts have been attributed mainly to reduced uptake and translocation of water and nutrients, metabolic disturbances and the association of nematodes with other pathogenic organisms. The net result is a reduction in plant growth and yield or, more rarely, the death of the host.

The pathogenicity of nematodes to the host is related to factors such as, age of the host, inoculum level, reproductive capacity, role of secondary invaders, temperature, host-status (Bergeson, 1968; Singh, 1975; Wong and Mai, 1973; Mayol and Bergeson, 1970).

The economic importance of Nacobbus has been little studied. This is perhaps due to the fact that Nacobbus has been mistaken for Meloidogyne spp. (Caveness, 1959), and control measures for root-knot disease have prevented the build up of Nacobbus populations (Franklin, 1959). However, studies of Nacobbus attacking sugar beet have shown its importance on this crop and have led to strict quarantine regulations being formulated in the U.S.A. (Weischer and Steudel, 1972). Furthermore, this nematode also has been affecting potatoes in western

South America and reducing their yield (Herrera, 1977).

Most of the estimates of damage by Nacobbus have been observed from field investigations (Schuster and Thorne, 1956; Gómez Tovar, 1973). Under glasshouse conditions, Sosa Moss and Muñoz (1973) studied the effects of different population levels of Nacobbus on tomatoes. At low population levels, the number of fruits increased, but plant height and weight of fruits were diminished at all population levels. The pathogenicity of Nacobbus to tomato and chilli pepper has been demonstrated by Bruijn and Stemerding (1968) and Sosa Moss and González,(1973) respectively. Besides the effects of temperature, pathogenicity of Nacobbus to sugar beet was investigated by Schuster et al (1966).

This study investigated the effects of three population levels of N. aberrans (British isolate) on tomato plants.

## MATERIALS AND METHODS

Second stage juveniles of the British isolate of N. aberrans were inoculated into sterilized soil to determine the effect of different nematode population on the growth of tomato var. Moneymaker. Four levels of inoculum were used originally: Control (no nematodes); 100; 1,000 and 5,000 nematodes per 5 kilos of soil in 9 in. plastic pots. The pots were arranged in a randomized block design with 3 replications.

Three crops were grown in the same soil: i) from October, 1978 to January, 1979; ii) January to May, and iii) May to July, 1979.

At the harvest of the first and the second crops, the stem was cut 3 cm. above the soil level, and the roots left in the soil, so that the nematodes were not disturbed, and a new tomato seedling was then planted in the pot. To assess the populations during these crops, the pots were sampled with an/in auger at three points around the plants, removing soil and roots.

For the third crop, all the root system was removed, weighed and the nematodes from root and soil counted. The number of galls, the amount of secondary lateral root proliferation and number of females per gall were also recorded. The population level from 1 g. of roots and 100 $cm^3$ of soil was measured (Section 2).

The effect of the different treatments on growth was assessed by measurements of plant height, after 20, 30, 45, 60 days and at harvest. Days to flowering and fruit formation, number of inflo rescences, number and weight of fruits and fresh shoot weight, were also recorded. The dry shoot weight for the final crop was noted.

The temperature was recorded daily using a soil thermometer, with the following ranges:

| CROPS | DATES | TEMPERATURE RANGES | |
|---|---|---|---|
| | | Minimum | Maximum |
| FIRST CROP | Oct. 1978 - Jan 1979 | 11 - 20 | 14 - 37 |
| SECOND CROP | Jan. 1979 - May 1979 | 9 - 24 | 15 - 35 |
| THIRD CROP | May. 1979 - July 1979 | 17 - 25 | 23 - 44 |

In the last crop there was a fungal infection of leaves and stems, and therefore a fungicide (Benlate) was applied to the foliage twice during growth of the plants.

## RESULTS

The inoculation of different population levels of N. aberrans on tomato did not alter the plant height during the first crop (Fig. 6.1 and Appendix D. Table 1.). However, in the second crop, was detected significance (P = 0.05) 60 days after transplanting, where plants with high inoculum level were shorter than non-inoculated, low and medium nematode levels. (Appendix D. Table 2.). In the third crop, plant height was depressed only at 45 days after transplanting, heights of plants inoculated with high and medium numbers of nematodes were different (P = 0.05) to non-inoculated plants, and low inoculum was similar to non-inoculated and the medium level (Appendix D. Table 3). In all the three successive crops, the final means of plant height were not significant.

The variables observed to assess nematode effect on tomato growth showed no differences between treatments during the first crop (Table 6.1.1. and Appendix D. Table 4.). Both the high and medium inoculum levels in the second crop delayed fruiting compared to nematode-free plants. (Appendix D. Table 5.). There were no other differences.

At high inoculum levd in the third crop (Appendix D. Table 6.), the number of inflorescences was reduced significantly (P = 0.05) when compared to other treatments. Fruiting was also delayed in pots containing high nematode inoculum. This same treatment also caused considerable reduction in tomato yield in the third crop with fewer fruits and yields were 21.8% of non-inoculated plants. Medium and low levels of nematodes reduced yields to 53.5% and 63% of the control. There were no differences between treatments when

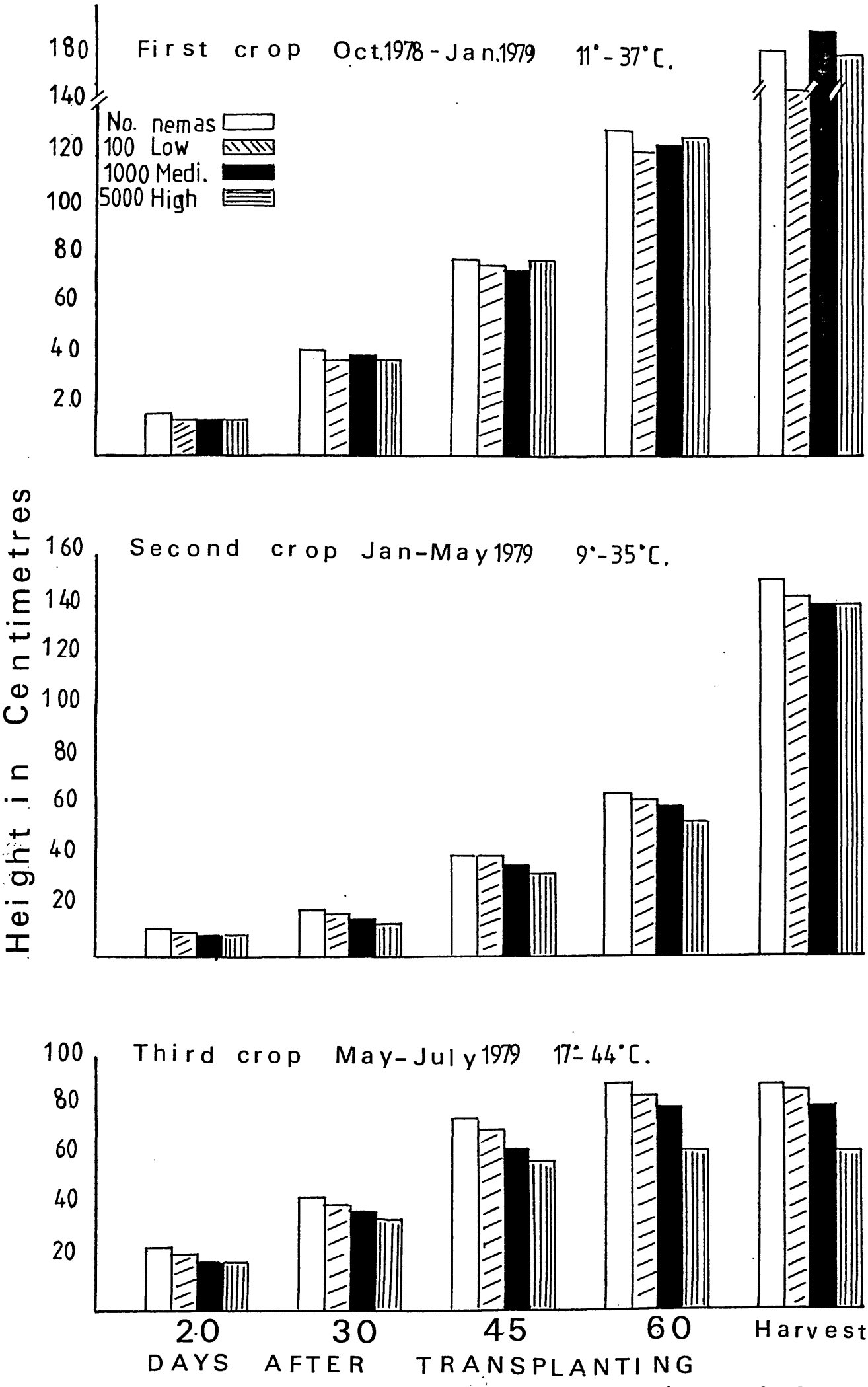



Fig. 6.1. Plant height at different sampling times during growth of three successive tomato crops.

TABLE 6.1.1. EFFECT OF N. ABERRANS ON GROWTH OF TOMATOES AT DIFFERENT POPULATION LEVELS IN THREE SUCCESSIVE CROPS*

| CROPS | NEMATODE POPULATIONS (TREATMENTS) | DAYS TO FLOWERING | NUMBER OF INFLORESCENCES | DAYS TO FRUITING | NUMBER OF FRUITS | WEIGHT OF FRUITS (g) | FRESH SHOOT WEIGHT (g) |
|---|---|---|---|---|---|---|---|
| FIRST CROP | 0 | 27.6[1] a | 8.3 a | 44.0 a | 6.0 a | 265.3 a | 234.0 a |
| | 100 | 30.6 a | 8.0 a | 45.3 a | 6.6 a | 241.6 a | 200.3 a |
| | 1,000 | 31.6 a | 8.3 a | 57.3 a | 5.3 a | 151.3 a | 250.6 a |
| | 5,000 | 30.0 a | 7.6 a | 50.6 a | 4.6 a | 179.3 a | 229.6 a |
| SECOND CROP | 0 | 50.6 a | 6.3 a | 58.3 b | 8.6 a | 297.7 a | 481.0 a |
| | LOW | 52.0 a | 5.3 a | 60.3 b | 8.3 a | 245.3 a | 409.0 a |
| | MEDIUM | 56.3 a | 6.6 a | 75.3 a | 7.6 a | 212.1 a | 322.6 a |
| | HIGH | 56.3 a | 5.6 a | 73.0 a | 6.6 a | 188.4 a | 313.3 a |
| THIRD CROP | 0 | 27.3 a | 7.6 a | 34.6 c | 7.3 a | 177.2 a | 196.2 a |
| | LOW | 30.3 a | 6.6 a | 42.6 b | 6.0 ab | 129.5 ab | 172.8 a |
| | MEDIUM | 30.0 a | 6.0 a | 39.3 bc | 4.3 ab | 94.8 ab | 139.9 a |
| | HIGH | 30.3 a | 4.3 b | 50.6 a | 3.3 c | 50.0 b | 114.0 a |

* Mean of 3 replicates.

[1] Averages followed by the same letter indicate no significant difference (P = 0.05) according to Duncan's Multiple Range Test.

fresh shoot weight was analysed (Table 6.1.1. Appendix. D. Table 6).

The effects of nematode inoculum on root growth were observed in the final crop (Table 6.1.2 and Appendix D. Table 7.), the means of root weight were not significant. Non-inoculated roots were significantly longer than high and low inoculum levels, but were similar to the medium nematode level. Other variables observed were the number of secondary lateral roots per root system; high number of nematodes produced significantly more lateral roots than other treatments. Medium and high treatments had more galls than the low inoculum level ($P = 0.05$). Number of galls did not differ significantly between treatments. Generally there were only two female Nacobbus per gall, even in heavily infested roots.

Nematode populations

During the first crop, the population of N. aberrans per g. of root increased to 40 for 1,000 and 165 for 5,000 nematode-inoculum respectively, which was significantly greater ($P = 0.05$) than the 100 nematode inoculum level of 25. In the second crop, there were no differences between populations, but the number of Nacobbus in the high and medium inoculum levels (453 and 431 respectively), were significantly increased compared to the low population level (130) in the final crop (Fig. 6.2. Appendix D. Tables 8, 9, 10).

When soil population alone was analysed, significant differences were only detected in the first crop between the higher inoculum (5,000 nematodes) and 100 and 1,000 nematode levels (Fig. 6.2. Appendix D. Tables 11, 12, 13).

N. aberrans caused typical rosary-like galling in all treatments inoculated with the nematodes (Plate 12.a, b, c, d.). Proliferation

TABLE 6.1.2. EFFECT OF N. ABERRANS ON ROOT GROWTH IN THE FINAL TOMATO CROP*

| NEMATODE TREATMENTS | FRESH TOTAL ROOT WEIGHT (g) | LENGTH OF ROOTS (cm) | NO. SECON. LATERAL ROOTS/ROOT SYSTEM | TOTAL NO. GALLS /ROOT SYSTEM | NO. SECON. LATERAL ROOTS/GALL | NO. ♀5/ GALL |
|---|---|---|---|---|---|---|
| NO NEMATODES | 26.56[1] a | 40.33 a | 1845.0 b | - | - | - |
| LOW | 29.60 a | 25.66 b | 1723.7 b | 394.0 b | 4.5 a | **1.9 a |
| MEDIUM | 40.70 a | 31.00 ab | 2671.0 b | 787.0 a | 3.7 a | 1.7 a |
| HIGH | 39.60 a | 28.66 b | 4893.7 a | 833.7 a | 5.8 a | 2.1 a |

* Mean of 3 replicates

** Mean of 29-37 galls per treatment

[1] Average followed by the same letter indicate no significant difference (P = 0.05) according to Duncan's Multiple Range Test.

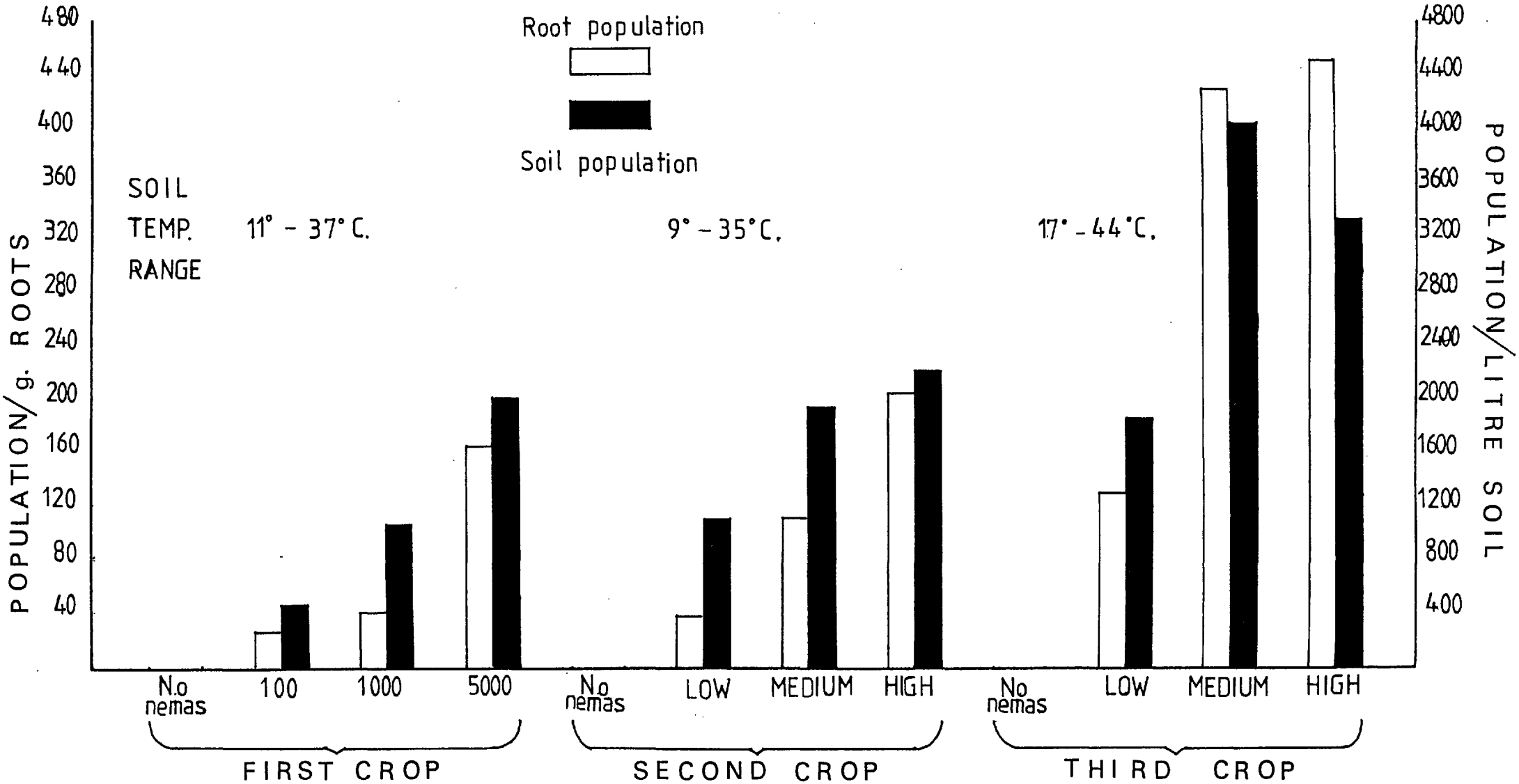



Fig. 6.2. Root and soil population for three successive tomato crops.

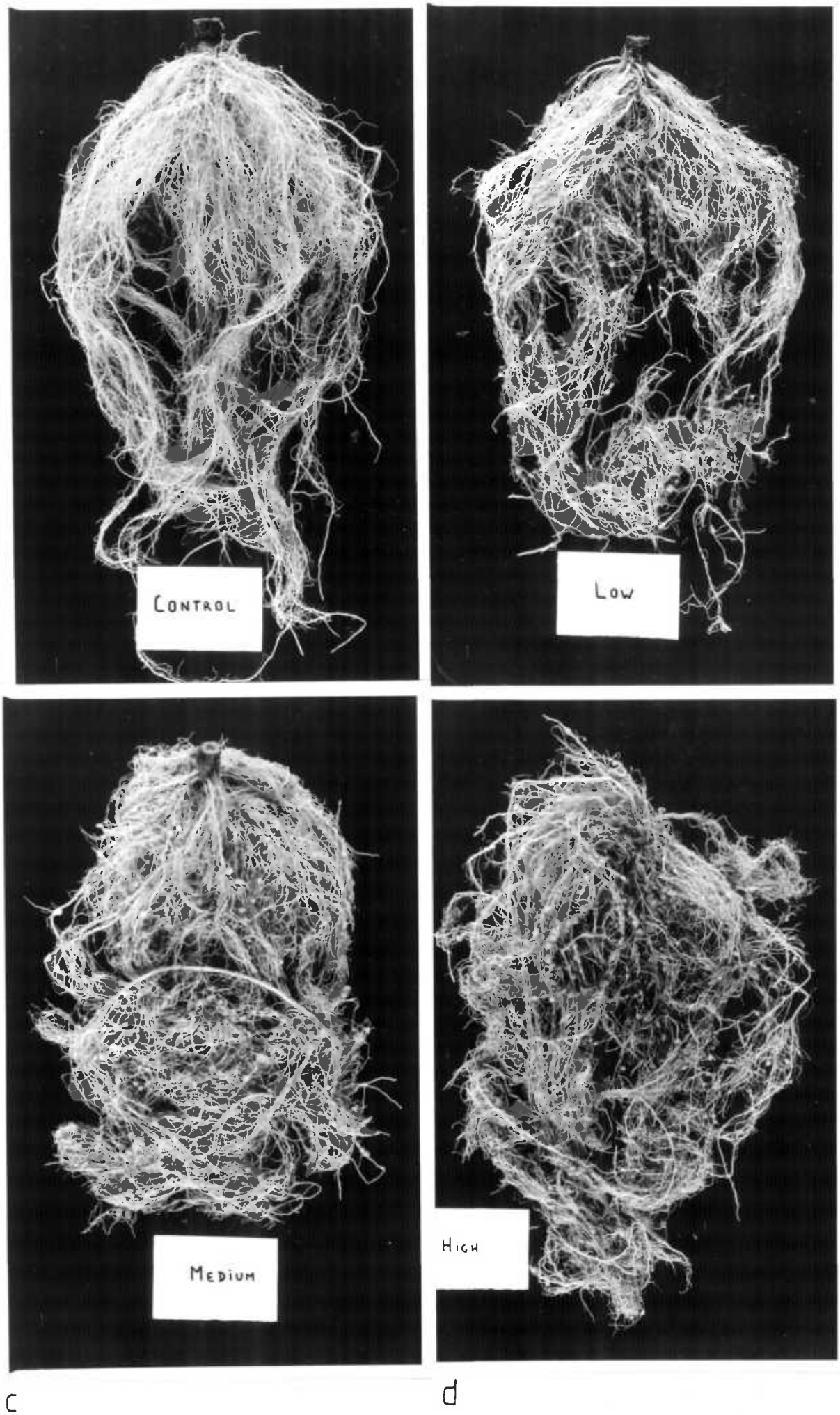
Plate 12

a. Root system of tomato var. Moneymaker (no nematodes)

b. Galled root system of tomato var. Moneymaker produced by low inoculum of *N. aberrans*.

c. Galled root system of tomato var. Moneymaker produced by medium inoculum of *N. aberrans*.

d. Galled root system of tomato var. Moneymaker produced by high inoculum of *N. aberrans*.


a
b
CONTROL
LOW
MEDIUM
HIGH
c
d

of secondary lateral roots from galls was also a common feature of Nacobbus infestation (Plate 13.).

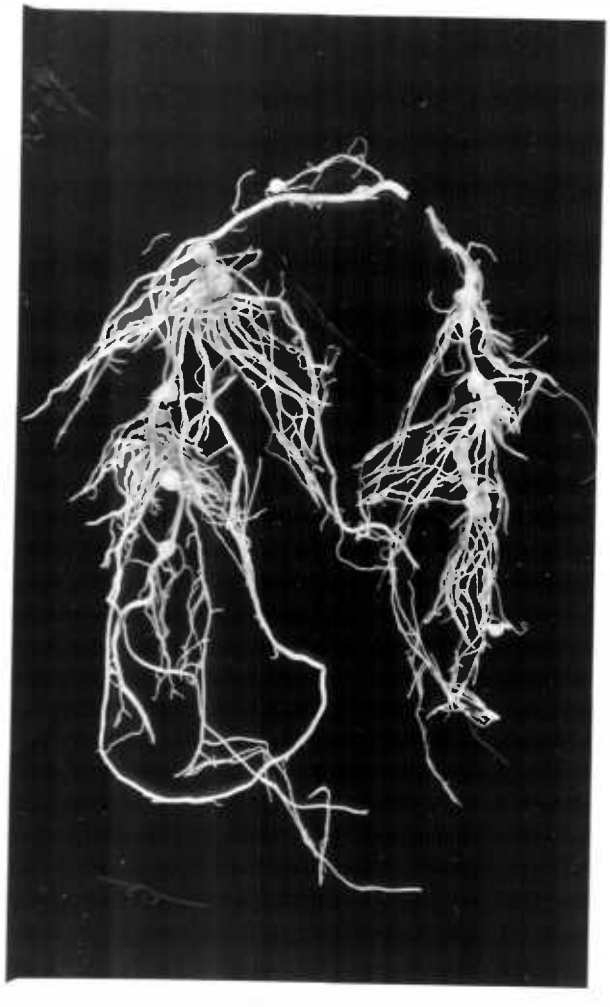


Plate 13. Close up observation of N. aberrans galling. Note the proliferation of secondary lateral roots from galls.

# DISCUSSION

Although N. aberrans, after three successive crops, was pathogenic to tomato, its pathogenicity must be analysed with regards to the conditions under which the experiment was done, and the effect that additional factors have in general.

Pathogenicity is related to population levels, but there is probably more than one factor involved in this relationship, as has been suggested by Wallace (1974). Nacobbus populations are affected mainly by temperature. Studying the effect of temperature on N. aberrans development through one year, between November and March, with temperature ranging 9° to 24°C (minimum and maximum respectively), the population fell considerably, and galls and egg-masses were not recorded for the British isolate (see Section 4.3). Therefore, although in the first crop (October 1978 - January 1979) 5,000 $J_2$'s were inoculated (high inoculum), there were no differences between inoculated and non-inoculated treatments. However, with low inoculum, there was a slight increase in the number of fruits. This observation agrees with those of Sosa Moss and Muñoz (1973), who reported that number of fruits seems to be increased by low population of N. aberrans on tomato.

During the second crop (January - May 1979), the Nacobbus populations did not increase as much as during the first crop, but an interesting aspect was revealed, time to fruiting in plants containing medium and high nematode inoculum levels, was significantly delayed than in non-inoculated plants and those inoculated with low inoculum; similarly plant height at 60 days was reduced between treatments. These results occurred more or less at the same time, just

when galling and reproduction was detected in the relationship between temperature and population experiment (Section 4.3). Nevertheless, plant heights at harvest were not significantly different.

When temperature increased during May to July in the third crop, Nacobbus pathogenicity on tomato was evident with significant decreases in plant growth and reduction in plant heights at 45 days between treatments. Populations in this crop in both roots and soil, were double those in the second crop.

N. aberrans, M. hapla and M. acronea, among other nematodes, cause increased production of lateral roots or rootlets in galled roots (Thorne and Schuster, 1956; Sasser, 1954; Bridge et al, 1976). This proliferation of secondary lateral roots might be considered as a source of compensation that would help the plants under certain conditions to recover from nematode damage. Under certain controlled conditions, where plants receive ideal watering and levels of fertilizer, these two factors plus the presence of extra roots, may compensate for the reduction in nutrient and water uptake caused by nematode root disruption. In relation to Nacobbus, this observation could explain why only at some sampling times for instance, plant height was reduced and apparently after that there were no differences. However, although in the third crop there was a higher proliferation of secondary lateral roots, these rootlets had limited space to grow, as the root length was shorter, and they were concentrated in the first 15 - 20 cm.

Another interesting point in discussion is the histopathology induced by feeding activities of N. aberrans. In the first parasitic stage, the concentration of juveniles in the cortex without burrowing activities, cause a limited damage to plants. During the second

parasitic stage, only a reduced area in the vascular system is affected, with more than 50% of the stele remaining undamaged, so that the normal functions of the roots would be only altered partially. This suggests that the damage produced by individual nematodes is limited, and only the presence of a large number of nematodes would induce serious damage. This explains why Nacobbus reduced tomato growth as temperature and populations increased.

In these present studies, N. aberrans was markedly affected by temperature and only developed within a limited temperature range. In conditions where optimum temperatures do not occur frequently this, together with its probable amphimictic reproduction, would produce a slow population increase. With this evidence the false root-knot nematode could be included within the group of nematodes that have severe limitations on rapid population increase, and as Jones (1979) said, would need several years to reach proportions that seriously diminish yields.

However, under certain field conditions, where the fluctuations of the temperature are not drastic and nematodes have become adapted to the normal daily variations, as in the valleys of the Andes mountain. Nacobbus can appear as a potential pest when a suitable host is present.

## 6.2 INTERACTION OF *N. ABERRANS* AND *M. INCOGNITA* ON TOMATO

### Introduction

It is well-known that nematodes can cause damage to plants. However, it is also well known that nematodes are part of the micro-environment, where mainly fungi, bacteria, viruses and other nematodes are present. Interactions between these various organisms can cause greater damage to the host than when the organisms act independently. These interactions are unpredictable and may affect the behaviour and reproduction of the organisms on the host.

One of the lesser studied fields in Nematology is the association of nematodes with other soil organisms. These disease complexes, as Powell *et al* (1971) called them, can be illustrated by several examples; the root-knot-Fusarium wilt interaction on tobacco (Meléndez and Powell, 1967). Bacterial wilt of alfalfa caused by *Corynebacterium insidiosum* and *Ditylenchus dipsaci* (Hawn, 1965), and the tobacco ring spot virus and the tobacco mosaic virus with *M. javanica* (Bird, 1969).

In relation to nematode-nematode interactions, Gay and Bird (1973) found that populations of *Pratylenchus brachyurus* on cotton were increased significantly in presence of either *M. incognita* or *M. arenaria*. Jatala and Jensen (1976) reported that there was a suppression of gall development of *M. hapla* in any treatment in which inoculations of *H. schachtii* preceded those of *M. hapla* by 10 days on sugar beet. Conversely, cyst development occurred when inoculation of *M. hapla* preceded that of *H. schachtii*. When both nematodes were inoculated simultaneously, there were no effects on populations of either. Other studies include those of Estores and Chen, 1972;

Sikora et al, 1972; Ferris et al, 1967; Chapman and Turner, 1975; Johnson and Nusbaum, 1970.

Nacobbus has been reported in sugar beet, potato, tomato and other crops of lesser economic importance and in native weeds (Thorne and Schuster, 1956; Lordello et al, 1961; Franklin, 1959; Schuster and Thorne, 1956). Nacobbus has been found in mixed population of Nacobbus mixed with Meloidogyne spp. and H. schachtii in some sugar beet fields in U.S.A. In potato fields it occurs with Heterodera (= Globodera) spp. (Cornejo, 1977a.).

Observations of galled roots that I received from Ecuador, revealed the occurrence of both N. aberrans and M. incognita. In view of the possibility of nematode-nematode interactions outlined above, the effects and population development of N. aberrans and M. incognita (British glasshouse isolates) in single and double inoculations were investigated.

## MATERIALS AND METHODS

Tomato seedlings var. Moneymaker were inoculated with second stage juveniles of the British glasshouse isolates of both N. aberrans and M. incognita, in 9 in. plastic pots. Five treatments were used: i) Control (no nematodes), ii) Nacobbus alone, iii) Meloidogyne alone, iv) Nacobbus and Meloidogyne, inoculated together, and v) Meloidogyne inoculated first and Nacobbus two weeks later. The pots were arranged in a fully randomized design with five replications in a heated glasshouse.

One thousand juveniles of each species were inoculated at transplantation (except treatment v, where Nacobbus was placed in holes made in the soil around the plant, two weeks after transplantation).

An early fungal infection of aerial parts of the plants prevented the use of parameters such as : height, fruit weight, days to flowering, etc; to assess plant growth. Fresh root weight and length, nematodes population levels and gall size were recorded two months after transplantation.

Daily soil temperatures were taken throughout the experiment and ranged from 16°C at 9 cm. to 36°C at 3 p.m.

## RESULTS

Tomato total root length was not altered by the presence of N. aberrans or M. incognita in single inoculations or when M. incognita inoculation preceded Nacobbus. However, when both species were inoculated together they significantly reduced total root length (Table 6.2.1. Appendix E. Table 1. and Plates 14. a, b, c, d, and 15. a, b, c, d.).

The presence of Meloidogyne alone or in combination with Nacobbus increased root weights, with averages highly significant compared to Nacobbus, alone and non-inoculated treatments (Table 6.2.1).

In roots from the Nacobbus/Meloidogyne treatment (inoculated at the same time), juvenile stages of both nematode genera occurred in the same root, but feeding at different sites (Plate 16.a.). Furthermore, the presence of a mature female of Nacobbus was usually surrounded by several juvenile stages of Meloidogyne in the gall originated by the first (Plate 16.b), and in rare cases the presence of a mature female of Meloidogyne was detected. Root galls in the treatment with both nematodes inoculated together were bigger than in any of the other treatments, as shown in Table 6.2.2.

The population levels of Nacobbus, when alone, increased four-fold, which was a significantly ($P = 0.01$) higher increase than in the mixed population with Meloidogyne (Table 6.2.3. Appendix E. Table 2.) Similarly, the greatest number of gravid females occurred when Nacobbus was in pure culture.

When Meloidogyne was inoculated together with Nacobbus, (treatment 4), the number of nematodes recovered (468), was significantly lower ($P = 0.01$) in relation to total population in treatment number 5

TABLE 6.2.1. : EFFECT OF *N. ABERRANS* AND *M. INCOGNITA* ON ROOT GROWTH.

| NEMATODE TREATMENTS | ROOT LENGTH (cm)* | | ROOT WEIGHT (g)* | |
|---|---|---|---|---|
| 1. No nematodes | 29.4† | a | 12.17 | b |
| 2. *Nacobbus* alone | 26.4 | a | 15.33 | b |
| 3. *Meloidogyne* alone | 25.2 | a | 37.81 | a |
| 4. *Nacobbus* + *Meloidogyne* (inocu. at the same time) | 18.6 | b | 39.89 | a |
| 5. *Meloidogyne* (inocu. first) + *Nacobbus* (inocu. 2 weeks later) | 24.8 | a | 43.33 | a |

* Mean of 5 replicates.

† Averages followed by the same letter indicate no significant difference (P = 0.01), according to Duncan's Multiple Range Test.

Plate 14.

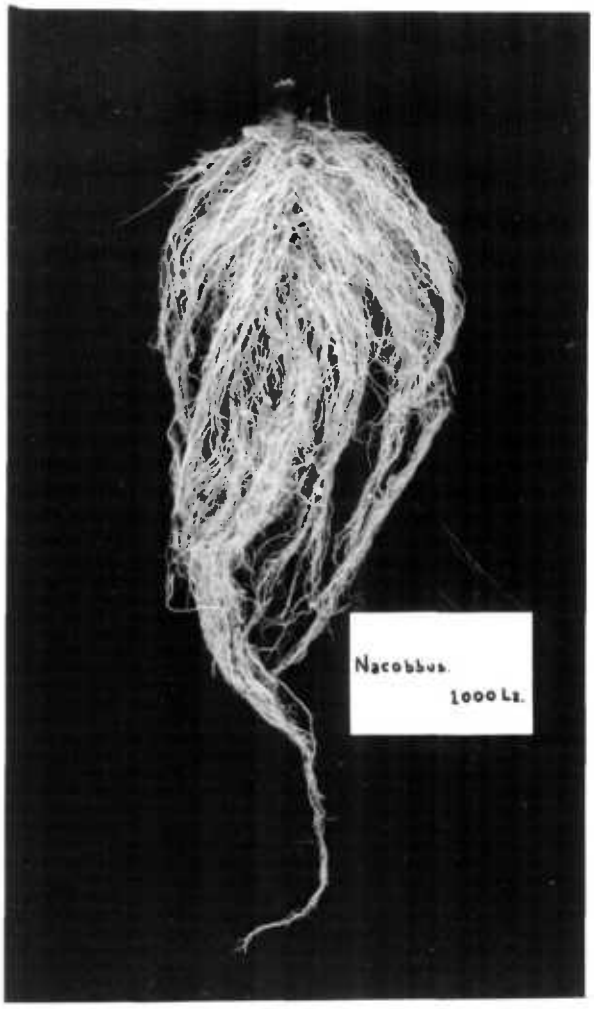
a. Galling produced on tomato roots var. Moneymaker by *N. aberrans*

b. Galling produced on tomato roots var. Moneymaker by *M. incognita*

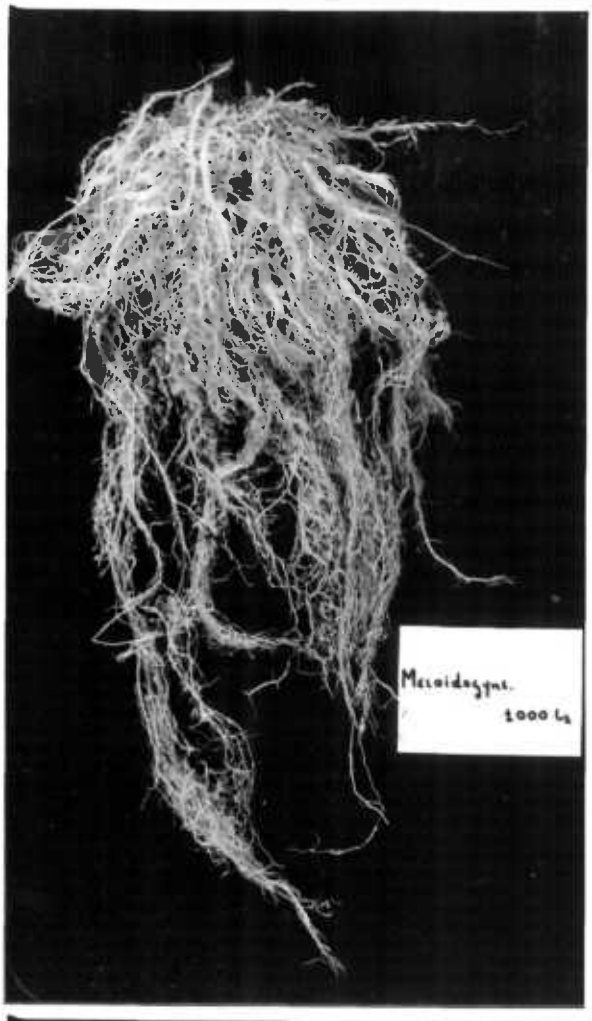
c. Galling produced on tomato roots var. Moneymaker by inoculation of *N. aberrans* and *M. incognita* together.

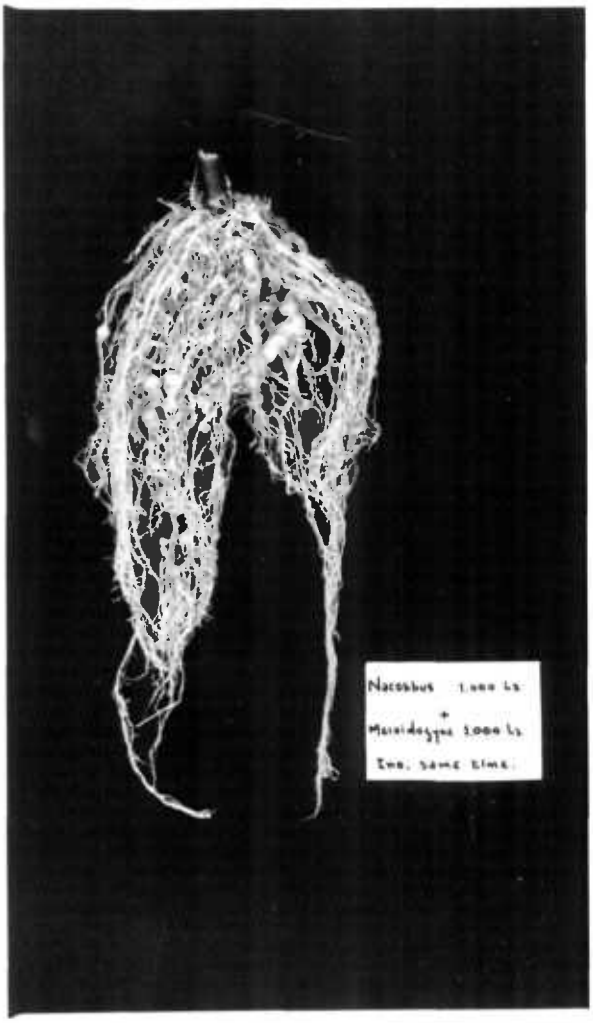
d. Galling produced on tomato roots var. Moneymaker by inoculation of *M. incognita* first and *N. aberrans* two weeks later.

a

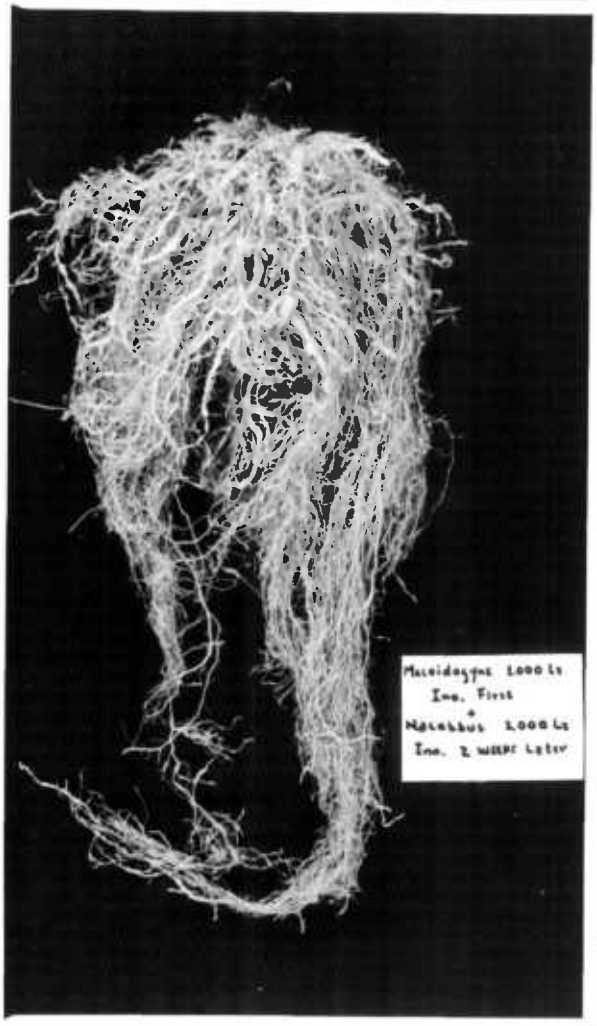

Nacobbus
1000 L2.

b


Meloidogyne
1000 L2


Nacobbus 1000 L2
+
Meloidogyne 1000 L2
Inc. same time.

c


Meloidogyne 1000 L2
Inc. First
+
Nacobbus 1000 L2
Inc. 2 weeks later

d

Plate 15.

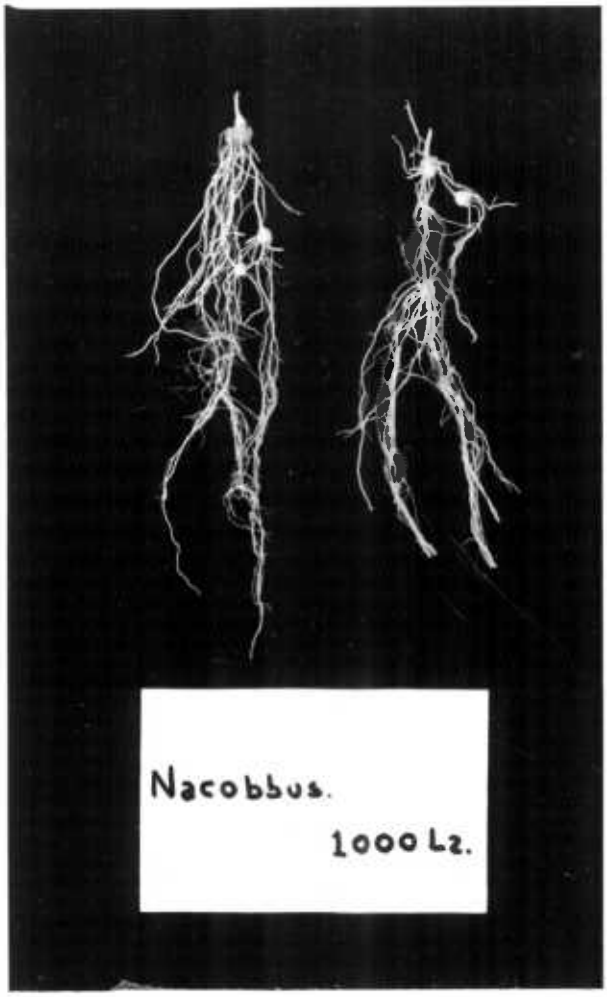
a. Close-up observation of N. aberrans galls. Note the proliferation of secondary lateral roots from galls.

b. Close up observation of M. incognita galls.

c. Close up observation of N. aberrans and M. incognita galls (inoculated together). Note the size of the galls and reduce proliferation of secondary lateral roots from galls.

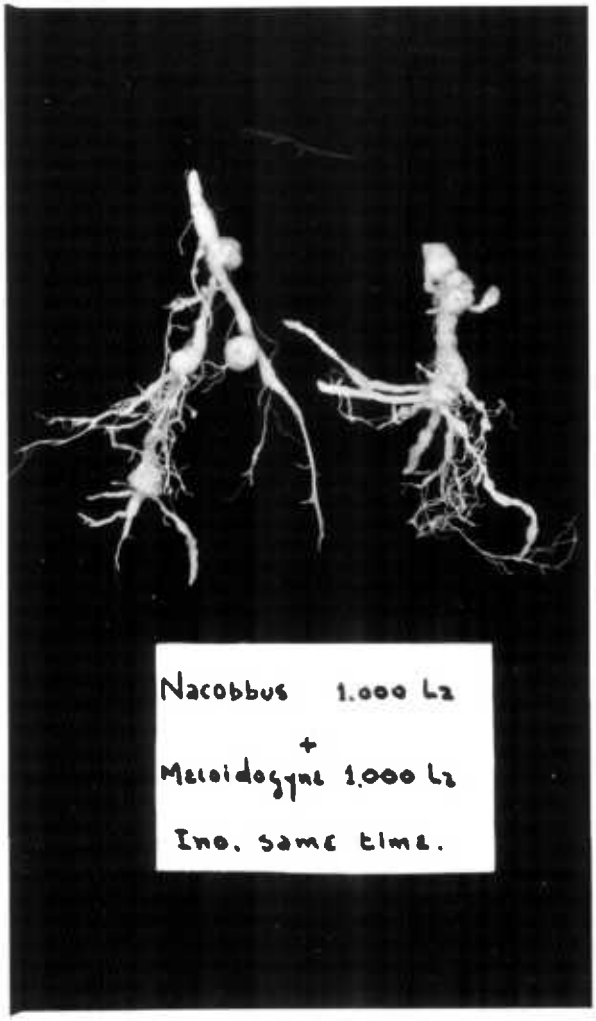
d. Close up observation of M. incognita and N. aberrans galls (inoculated first and two weeks later respectively).

a

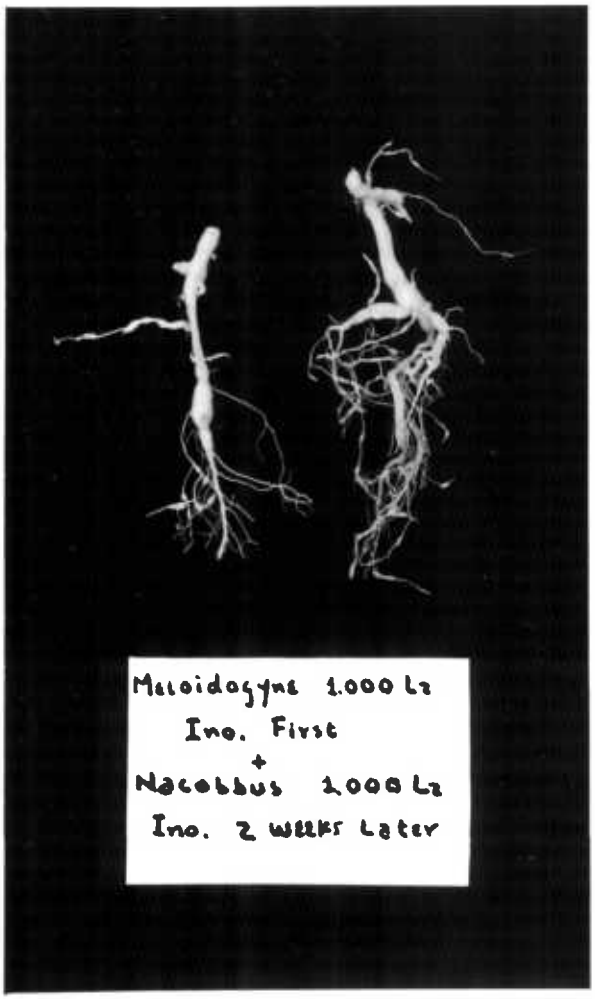

Nacobbus.
1000 L2.

b


Meloidogyne.
1000 L2


Nacobbus 1.000 L2
+
Meloidogyne 1.000 L2
Ino. same time.

c


Meloidogyne 1.000 L2
Ino. First
+
Nacobbus 1.000 L2
Ino. 2 weeks later

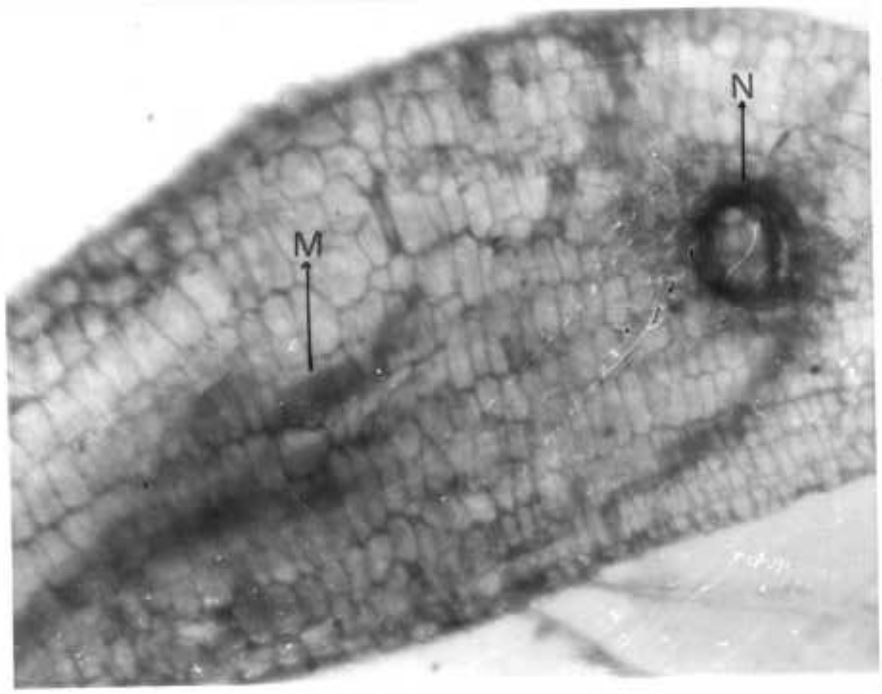
d

Plate 16.

a. Development of juvenile stage of N. aberrans (N.) inside the gall induced by feeding of juvenile stage of M. incognita (M.) Note the necrotic area. (x 500).

b. Mature female of N. aberrans (N.) surrounded by juvenile stages of M. incognita (M.) (x 100).

a




b

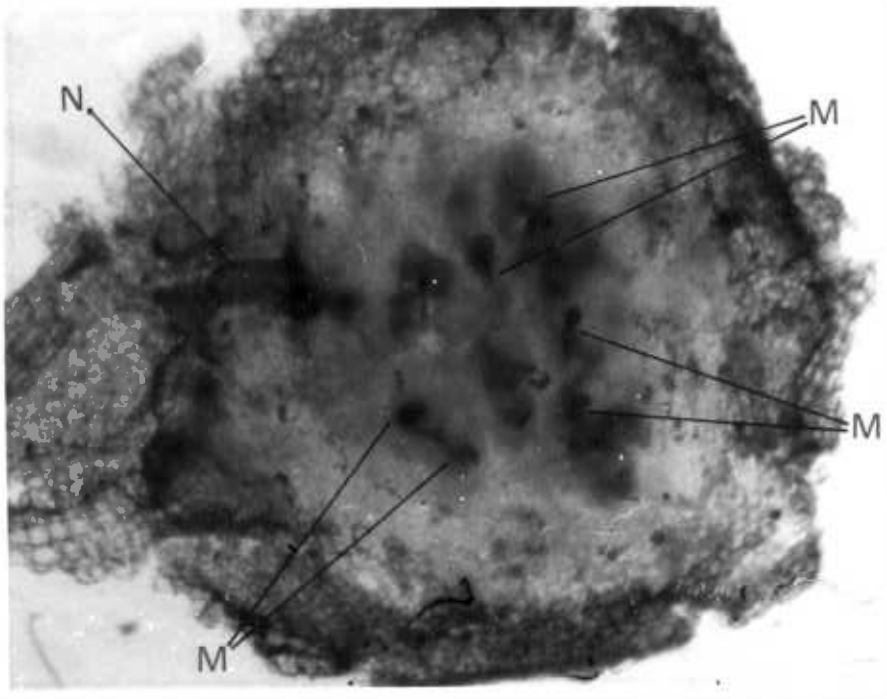


TABLE 6.2.2. : EFFECT OF *N. ABERRANS* AND *M. INCOGNITA* ON GALL SIZE.

| NEMATODE TREATMENTS | GALL DIAMETER* (cm) | |
|---|---|---|
| 1. No nematodes | 0 | |
| 2. *Nacobbus* alone | 0.34 (0.2 - 0.5)† | b |
| 3. *Meloidogyne* alone | 0.46 (0.3 - 0.6) | b |
| 4. *Nacobbus* + *Meloidogyne* (inocu. at the same time) | 0.94 (0.6 - 1.1) | a |
| 5. *Meloidogyne* (inocu. first) + *Nacobbus* (inocu. 2 weeks later) | 0.44 (0.3 - 0.6) | b |

* Mean of 40 galls.

† Averages followed by the same letter indicate no significant difference (P = 0.01), according to Duncan's Multiple Range Test.

TABLE 6.2.3. : DIFFERENT DEVELOPMENTAL STAGES OF N. ABERRANS AND M. INCOGNITA RECOVERED FROM ROOTS.

| NEMATODE TREATMENTS | NEMATODE POPULATION/g ROOT* | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | JUVENILES | | ♂ | | ♀ Imm. | ♀ without eggs | | ♀ with eggs | | TOTAL POPULATION | |
| | Nacobbus | Meloidogyne | Nacobbus | Meloidogyne | Nacobbus | Nacobbus | Meloidogyne | Nacobbus | Meloidogyne | Nacobbus | Meloidogyne |
| 1. NO NEMATODES | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2. Nacobbus alone | 227.6[1] a | - | 8.0 a | - | 3.8 a | 21.2 a | - | 6.8 a | - | 267.4 a | - |
| 3. Meloidogyne alone | - | 516.6 ab | - | 3.2 a | - | - | 116.2 a | - | 40.0 a | - | 676.0 ab |
| 4. Nacobbus + Meloidogyne (inocu. at the same time) | 20.2 b | 335.6 b | 5.2 a | 4.6 a | 3.4 a | 8.0 b | 91.4 a | 3.4 b | 36.0 a | 40.2 b | 468.0 b |
| 5. Meloidogyne (inocu. first) + Nacobbus (inocu. 2 weeks later) | 1.6 b | 589.2 a | 0 b | 4.8 a | 0 a | 1.4 b | 189.0 a | 0 c | 30.6 a | 3.0 b | 798.0 a |

* Mean of 5 replicates.

[1] Averages followed by the same letter indicate no significant difference (P = 0.01), according to Duncan's Multiple Range Test.

(Meloidogyne inoculated first and Nacobbus 2 weeks later) with 798 nematodes. However, Meloidogyne alone (676 nematodes) was no different to the other two treatments (Table 6.2.3. Appendix E. Table 2.). It was clear that the increase in population of 19, 35 and 25 fold respectively, was due mainly to the presence of juveniles stages, as the number of gravid females was not significantly increased.

Nacobbus populations from soil differed significantly between treatments. Higher numbers (560), were recovered from the treatment with Nacobbus alone, and lowest population (360) in the treatment with Nacobbus plus Meloidogyne inoculated together. No population was registered, when Nacobbus was inoculated 2 weeks after Meloidogyne.

The treatments with Meloidogyne alone and Nacobbus plus Meloidogyne (inoculated together), produced higher Meloidogyne populations (11,200 and 11,880 respectively) which were significantly more than in the treatment with Meloidogyne inoculated first and Nacobbus 2 weeks later (4560 nematodes) (Table 6.2.4. Appendix E. Table 3.).

TABLE 6.2.4. : POPULATIONS OF N. ABERRANS AND M. INCOGNITA RECOVERED FROM SOIL.

| NEMATODE TREATMENTS | NEMATODE POPULATION/L. SOIL* | | | | | | |
|---|---|---|---|---|---|---|---|
| | JUVENILES | | ♂ | | ♀ IMM. | TOTAL POPULATION | |
| | Nacobbus | Meloidogyne | Nacobbus | Meloidogyne | Nacobbus | Nacobbus | Meloidogyne |
| 1. NO NEMATODES | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2. Nacobbus alone | 560 | - | 0 | - | 0 | 560[1] a | - |
| 3. Meloidogyne alone | - | 11120 | - | 80 | - | - | 11200 a |
| 4. Nacobbus + Meloidogyne (inocu. at the same time) | 280 | 11720 | 80 | 160 | 0 | 360 b | 11880 a |
| 5. Meloidogyne (inocu. first) + Nacobbus (inocu. 2 weeks later) | 0 | 4560 | 0 | 0 | 0 | 0 c | 4560 b |

* Mean of 5 replicates.

[1] Averages followed by the same letter indicate no significant difference (P = 0.05), according to Duncan's Multiple Range Test.

# DISCUSSION

In nematode-nematode associations, the presence of one of the species could increase the reproduction of the other, or mutual inhibitory reproduction could occur. Gay and Bird (1973) reported that M. incognita or M. arenaria resulted in significant increase in population of P. brachyarus in roots of cotton. However, M. incognita suppressed P. brachyurus reproduction in roots of tomato. On the other hand. P. penetrans and M. incognita mutually inhibited populations when they coinhabited tomato roots (Estores and Chen, 1972).

In the present study, population increase of N. aberrans was normal when it was inoculated alone; when N. aberrans and M. incognita were inoculated together Nacobbus reproduction was inhibited, and no Nacobbus reproduction occured when it was inoculated after Meloidogyne. Meloidogyne reproduction in these experiments was low when Nacobbus and Meloidogyne were inoculated at the same time, but was statistically greater when Nacobbus was inoculated after Meloidogyne, although reproduction by Meloidogyne alone did not differ significantly from either of these two treatments. These results suggest that Meloidogyne incognita is the dominant species. They resemble those reported by other studies on concomitant nematode populations, as mentioned in the introduction, Jatala and Jensen (1976) observed a similar effect between H. schachtii and M. hapla. Populations of M. naasi at 6 months were lower when in combination with P. penetrans and Tylenchorhynchus dubius than when alone (Sikora et al, 1972). Johnson and Nusbaum (1970) also provided evidence of another interaction of nematodes, where M. incognita depressed the population of M. hapla in cultivars "NC 95" and "NC 2512" of tobacco. Dominance

of one species over another does occur in other sympatric nematode associations, for example, Acosta and Ayala (1976), studying the association of P. coffeae and Scutellonema bradys on yams (Dioscorea rotundata), demonstrated that the former species was dominant over the latter, either under greenhouse or field conditions.

Although the populations of Nacobbus and Meloidogyne were reduced compared to separate inoculations, when both nematodes were inoculated at the same time, root length was diminished significantly and the presence of both nematodes in roots caused increase in gall size, suggesting that there is a synergistic effect and that both nematodes may induce more damage to tomato when together than when alone.

An interesting feature determined here, was the comparison of reproductive capacity of both nematodes. Under the conditions of the experiment, Nacobbus showed a very low rate of reproduction in relation to Meloidogyne, when the number of egg-laying females and juveniles were analysed, independent of the different associations of the nematodes. Consequently the root-knot nematodes appeared as a more aggressive pathogen on tomato than the false root-knot nematode.

The presence mainly of juvenile stages of Meloidogyne in galls induced and inhabited by Nacobbus, could be explained by the attraction that Nacobbus feeding sites have for Meloidogyne. There is also the possibility that chemical modification of feeding sites by Nacobbus may attract Meloidogyne and there is evidence showing that Nacobbus can induce starch formation throughout its feeding processes (Schuster et al, 1965). Nacobbus is capable of inducing starch formation in different crops such as Beta vulgaris, Spinacia oleracea, Lycopersicon esculentum, Chenopodium album, Portulaca oleracea,

Opunitia tortispina, Kochia scoparia and Euphorbia maculata (Schuster et al, 1964). Jones and Payne (1977b.) found that accumulation of starch in the tissues around Nacobbus, is much more marked than in tissues transformed by Heterodera, Meloidogyne and Rotylenchulus, Cohn (1965) suggested that the preference of Tylenchulus semipenetrans for cortical tissues in feeding seems to be connected with the accumulation of storage products in cortical parenchyma, particularly of starch. With regards to Meloidogyne, Orion and Bronner (1973) working on the localization of starch, amylase and invertase in M. javanica galls, assumed that giant cells, or perhaps the parasites themselves, produce amylase which hydrolises the starch and produces soluble saccharides which diffuse into the giant cells. There, they are probably broken down to monosaccharides or to smaller molecules, and then consumed either by the nematode or during highly active giant cell metabolism, or both. It is possible that this feeding relationship, could explain in part the concentration of juveniles of Meloidogyne in Nacobbus galls and consequently the greater size of those galls.

The results of this research, although exploratory in nature, suggest that further research may produce some interesting facts concerning the host-parasite-parasite interaction between these two gall forming but different parasitic nematodes on tomato and other crops.

## 6.3. REPRODUCTION AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON ROOT-KNOT SUSCEPTIBLE AND RESISTANT TOMATO VARIETIES.

### Introduction

The tomato (Lycopersicon esculentum) is an important cash crop around the world and one of the main hosts for several species of Meloidogyne.

Since Smith (1944) produced a hybrid between L. peruvianum (root-knot resistant) and the commercial tomato L. esculentum (root-knot susceptible); the development of resistant varieties containing the Mi gene, has enabled the commercial growing of tomatoes in areas infested with root-knot; this being an inexpensive and effective control measure.

There are over 30 known varieties of tomato resistant to Meloidogyne (Fassuliotis, 1976). The resistance of these varieties is affected by several factors such as, temperature, (Holtzmann, 1965; Dropkin, 1969) and populations of Meloidogyne (Sikora et al, 1973; Netscher, 1976; Viglierchio, 1978). Investigations of the virulence of different populations of Meloidogyne has led to the recognition of different biotypes, for example M. incognita B (Riggs and Winstead, 1959; Winstead and Riggs, 1963).

The tomato plant is also an adequate host for Nacobbus and has been used for pathogenicity tests (Sosa Moss and Muñoz, 1973; Bruijn and Stemerding, 1968), but nematode resistant varieties have currently only been assessed against Meloidogyne spp.

As Nacobbus and Meloidogyne form very similar galls on tomato roots, the present study was done to observe the reaction of some root-knot susceptible and resistant tomato varieties in the presence of either N. aberrans (Ecuadorian isolate) or M. incognita (British isolate).

This experiment also comprised observations on pathogenicity, to compare how the two species of nematodes would affect plant growth and yield.

## MATERIALS AND METHODS

One thousand second stage juveniles of N. aberrans (Ecuadorian isolate) and M. incognita (British isolate) were inoculated individually in 8 in. plastic pots on 22 day-old seedlings of four root-knot susceptibles and eight resistant tomato varieties. Pots were arranged in a fully randomized design with three replications per treatment and a control (no nematodes) in a heated glasshouse.

The following varieties were used:

| ROOT-KNOT SUSCEPTIBLE | ROOT-KNOT RESISTANT |
|---|---|
| Harvester | Better Boy |
| Jefferson | Big Seven |
| Moneymaker | Bonus |
| Local variety from the Gambia | Red Glow |
| | Roma VFN |
| | Rossol |
| | VFN - 8 |
| | VFN - 662 |

500 nematodes were inoculated at transplantation, and five days later a further 500 nematodes were inoculated. Both reproduction and pathogenicity were observed in the same plants (except The Gambia variety, which was attacked by fungus.) Tomato plants were grown for 80 days before harvesting.

Nematode damage was assessed by measuring the plant heights after 20, 45 days and at harvest time, also days to flowering and fruit formation, number and weight of fruits, fresh shoot weight, and length and weight of the root.

For Meloidogyne the extent of the galling was assessed using a gall index (Bridge and Page, 1977), with the following scale:

0. - No galls
1. - Few small knots, difficult to find.
2. - Small knots only but clearly visible. Main roots clean.
3. - Some larger knots visible. Main roots clean.
4. - Larger Knots predominate, but main roots clean.
5. - 50% of roots infested. Knotting on parts of main roots. Reduced root system.
6. - Knotting on main roots.
7. - Majority of main roots knotted.
8. - All main root knotted. Few clean roots visible.
9. - All roots severely knotted. Plant usually dying.
10. - All roots severely knotted. No root system. Plant usually dead.

For Nacobbus, the assessment was done by counting the number of galls in the whole root system : Five grades of damage were used:

0. - No galls
1. - Less than 5 galls
2. - Very slight galling, 5 to 25 galls.
3. - Moderate galling 25 to 100 galls
4. - Heavy galling >100 galls

Temperatures in the glasshouse during the experiment were as follows: 9 a.m. (16$^{o}$C) and 3 p.m. (36$^{o}$C).

The plants were sprayed with Benlate twice.

## RESULTS

Observing the effect of M. incognita in root-knot susceptible and resistant tomato varieties, the susceptible varieties Moneymaker and Jefferson had a higher index of galling, 6.3 and 5.7 respectively (Table 6.3.1. Appendix F. Table 1.), which differed significantly from the var. The Gambia (4.7). Harvester with an index of 5.0, was similar to the other three varieties. In the group of root-knot resistant, Red Glow showed the higher galling index (4.3), being different in comparison to the lesser galling exhibited by var. Rossol, VFN-8, Roma VFN, Bonus and VFN-662, however it was similar to Better Boy and Big Seven. These last two varieties, with an index of 3.7, were different to Rossol, VFN-8 and Roma VFN, which showed lesser index of galling. 2.0; 2.3 and 2.3 respectively. Therefore, Red Glow, Better Boy and Big Seven exhibited moderate galling. In the root-knot resistant varieties necrosis was observed in the roots, as the typical reaction of these varieties to the presence of M. incognita.

Gall counts for N. aberrans (Table 6.3.1. Appendix F. Table 1), showed no marked differences between varieties, although Rossol gave the lesser number (44.7) and VFN662 the higher (109.7). In all the varieties, both root-knot susceptible and resistant, there was a moderate reproduction with juveniles and egg-masses in the roots. Root proliferation from galls was observed in both types of varieties. Some illustrations of galling induced by M. incognita and N. aberrans, in root-knot susceptible and resistant varieties, are shown in Plate 17. a.b.c.d. respectively.

Neither N. aberrans nor M. incognita had any effect on the final plant height of any of the tomato varieties (Table 6.3.2.

TABLE 6.3.1. : HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

A - Root galling*

| TOMATO VARIETIES | Nacobbus |
|---|---|
| | No. Galls/Root System |
| HARVESTER | 83.7 |
| JEFFERSON | 80.0 |
| MONEYMAKER | 74.3 |
| THE GAMBIA | 91.3 |
| BETTER BOY | 91.0 |
| BIG SEVEN | 94.3 |
| BONUS | 81.7 |
| RED GLOW | 94.3 |
| ROMA VFN | 73.0 |
| ROSSOL | 44.7 |
| VFN 8 | 93.0 |
| VFN 662 | 109.7 |

| TOMATO VARIETIES | Meloidogyne |
|---|---|
| | Index of Galling |
| HARVESTER | 5.0 |
| JEFFERSON | 5.7 |
| MONEYMAKER | 6.3 |
| THE GAMBIA | 4.7 |
| BETTER BOY | 3.7 |
| BIG SEVEN | 3.7 |
| BONUS | 2.7 |
| RED GLOW | 4.3 |
| ROMA VFN | 2.3 |
| ROSSOL | 2.0 |
| VFN 8 | 2.3 |
| VFN 662 | 3.0 |

* Mean of 3 replicates.

| | | | |
|---|---|---|---|
| L.S.D. | 0.05 | n.s. | 1.17 |
| | 0.01 | | 1.59 |

(Nematodes)

Plate 17.

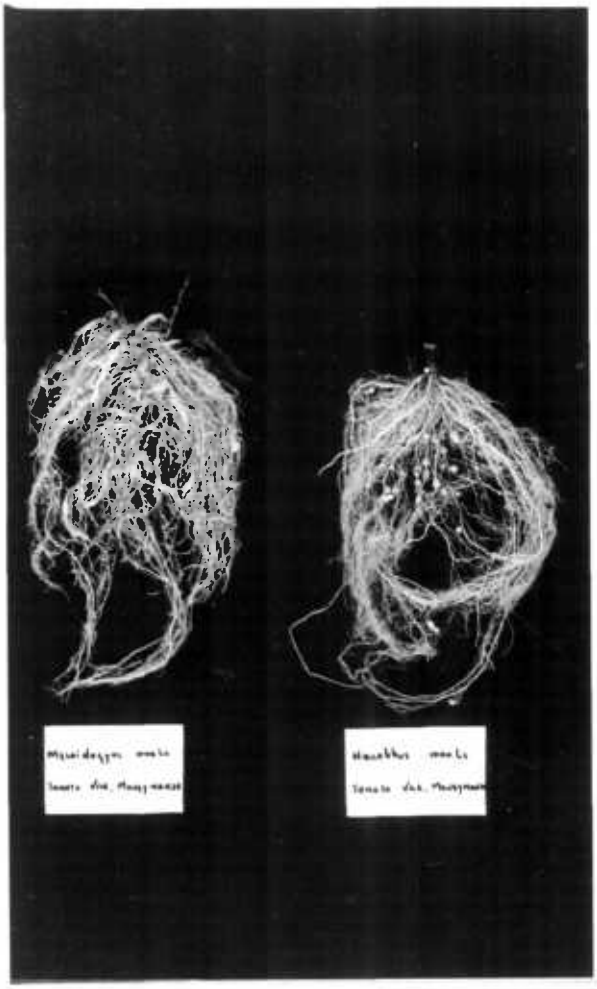
a. Galling of *M. incognita* and *N. aberrans* on root-knot susceptible tomato var. Moneymaker.

b. Galling of *M. incognita* and *N. aberrans* on root-knot susceptible tomato var. Jefferson.

c. Galling of *M. incognita* and *N. aberrans* on root-knot resistant tomato var. Big Seven.

d. Galling of *M. incognita* and *N. aberrans* on root-knot resistant tomato var. Rossol.

a



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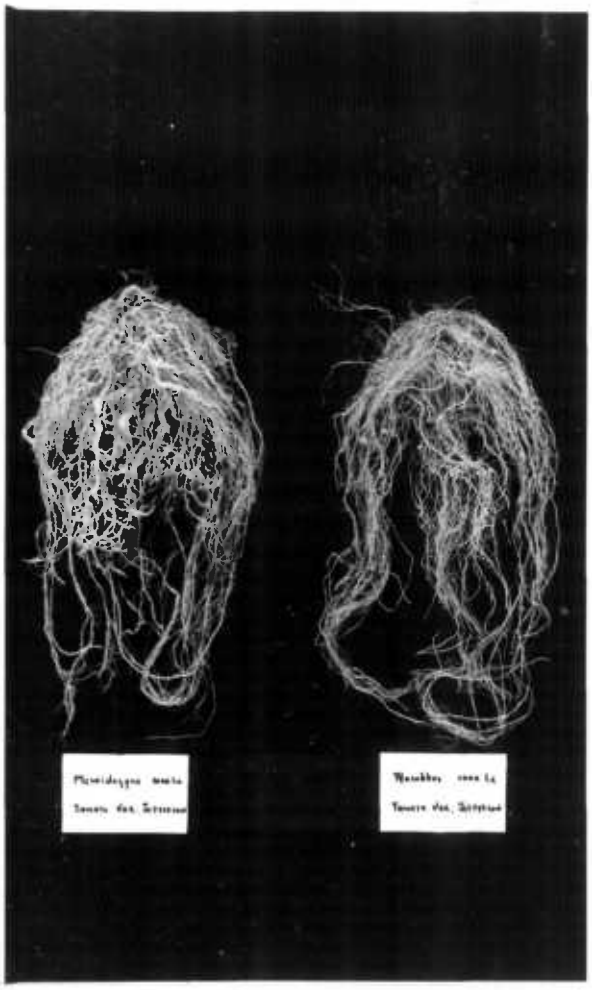

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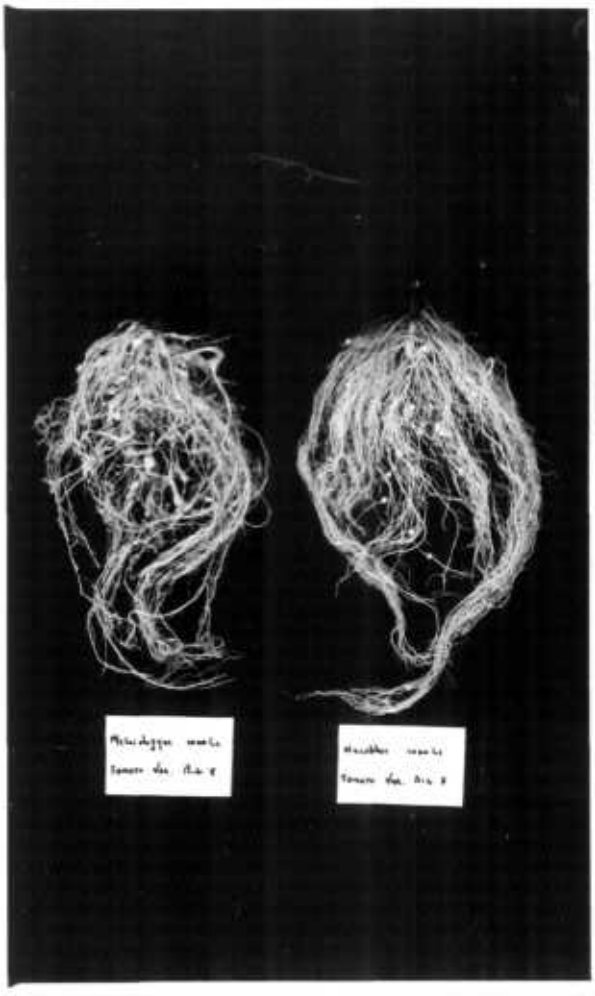

d

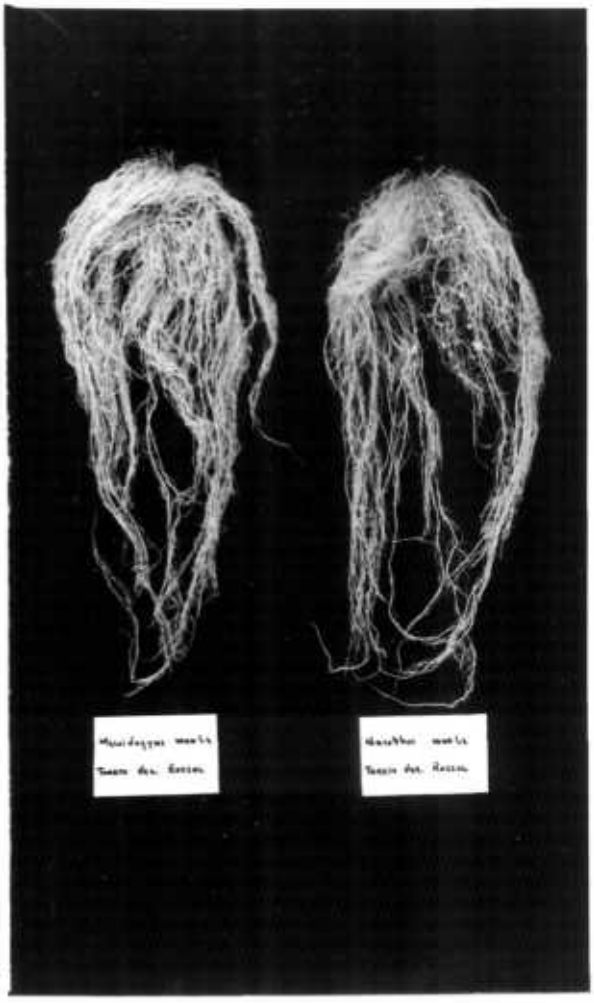

TABLE 6.3.2. : HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

B - Height of plants (in cm) at different sampling times*

| TOMATO VARIETIES | SAMPLING TIMES AFTER PLANTING | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 20 days | | | 45 days | | | 80 days (Harvest) | | |
| | No Nematodes | Nacobbus | Meloidogyne | No Nematodes | Nacobbus | Meloidogyne | No Nematodes | Nacobbus | Meloidogyne |
| HARVESTER | 28.33 | 28.66 | 25.66 | 90.66 | 102.00 | 87.33 | 125.33 | 146.66 | 116.00 |
| JEFFERSON | 26.33 | 20.66 | 24.33 | 72.33 | 61.00 | 82.33 | 78.00 | 65.66 | 83.00 |
| MONEYMAKER | 20.00 | 22.66 | 21.33 | 64.33 | 73.66 | 74.66 | 68.33 | 76.00 | 84.00 |
| BETTER BOY | 35.50 | 26.66 | 27.33 | 63.00 | 82.00 | 80.00 | 67.66 | 87.66 | 81.66 |
| BIG SEVEN | 23.00 | 21.00 | 21.66 | 54.00 | 67.66 | 61.66 | 71.66 | 70.33 | 63.00 |
| BONUS | 25.33 | 25.66 | 27.33 | 63.66 | 53.33 | 64.33 | 65.33 | 53.66 | 65.33 |
| RED GLOW | 25.66 | 24.00 | 25.33 | 70.33 | 52.66 | 70.33 | 78.66 | 55.66 | 71.33 |
| ROMA VFN | 23.00 | 22.33 | 23.33 | 50.66 | 69.33 | 69.66 | 53.33 | 80.00 | 70.66 |
| ROSSOL | 26.66 | 26.66 | 27.33 | 58.00 | 72.00 | 73.00 | 66.00 | 76.66 | 77.33 |
| VFN 8 | 24.00 | 24.66 | 22.00 | 63.33 | 67.66 | 59.00 | 69.66 | 67.66 | 64.00 |
| VFN 662 | 24.00 | 24.66 | 22.33 | 54.66 | 64.66 | 62.33 | 56.33 | 65.00 | 63.33 |

* Mean of 3 replicates.

L.S.D. 0.05 n.s. n.s. n.s.

0.01

Appendix F. Table 2.). Similarly, time to flowering was not different for any of screened varieties (Table 6.3.3. Appendix F. Table 3.). Meloidogyne on variety Jefferson, and both Meloidogyne and Nacobbus on var. VFN-8 significantly delayed time to fruiting.

When the number of fruits was analysed (Table 6.3.3. Appendix F. Table 3.), only var. Harvester was affected negatively by Nacobbus and Meloidogyne; the latter reduced the number of fruits to 55% compared to non-inoculated treatment. Although Harvester was affected in the number of fruits, the yield was not reduced significantly. Moneymaker only was affected by Meloidogyne, yielding 90.4 g in comparison to non-inoculated (152.2g) and Nacobbus (126.4 g). In the group of root-knot resistant varieties, N. aberrans and M. incognita produced some interesting results; both nematodes reduced yield in var. Better Boy (Nacobbus, 137.7g. and Meloidogyne 141.6g), compared with non-inoculated plant (194.3 g). There was a significant increase in yield by Nacobbus in Roma VFN (162.3 g), compared with non-inoculated plants, although Meloidogyne did not produce any significant difference. VFN-8 had more yield with Nacobbus inoculum (167 g.) than Meloidogyne (100.4 g), but non-inoculated was similar to the two treatments (142.3 g). In Red Glow, yields were significantly increased (219.5 g.) when Nacobbus was present in relation to non-inoculated and Meloidogyne treatments (130.7 g and 116.8 g. respectively). The results from fresh shoot weight were not significant.

Root length measurements showed slight differences, but they were not significant (Table 6.3.4. Appendix F. Table 4.). The root weights of all the susceptible varieties were increased significantly ($P = 0.01$), when M. incognita was present. Similarly, the root weight of Rossol and Red Glow, also was increased ($P = 0.05$) by the root-knot nematodes. Nacobbus did not cause any significant differences in root weight.

TABLE 6.3.3. : HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

C - Flowering and fruiting times, yield and fresh shoot weight*

| | | TOMATO VARIETIES | | | | | | | | | | | L.S.D. (Nematodes) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | HARVESTER | JEFFERSON | MONEYMAKER | BETTER BOY | BIG SEVEN | BONUS | RED FLOW | ROMA VFN | ROSSOL | VFN 8 | VFN 662 | 0.05 | 0.01 |
| DAYS TO FLOWERING | No Nematodes | 20.0 | 25.3 | 24.0 | 25.0 | 25.3 | 25.7 | 24.7 | 24.3 | 23.0 | 28.0 | 26.7 | n.s. | |
| | Nacobbus | 21.3 | 26.7 | 25.0 | 26.7 | 26.3 | 25.0 | 24.7 | 26.3 | 25.0 | 27.7 | 27.3 | | |
| | Meloidogyne | 22.0 | 26.3 | 26.0 | 25.7 | 26.7 | 25.0 | 27.0 | 25.7 | 26.0 | 30.7 | 29.3 | | |
| DAYS TO FRUITING | No Nematodes | 26.3 | 32.0 | 33.3 | 31.0 | 35.7 | 32.3 | 31.3 | 29.7 | 28.7 | 37.3 | 35.3 | 5.94 | 7.90 |
| | Nacobbus | 27.3 | 33.7 | 30.7 | 35.0 | 35.0 | 30.7 | 31.3 | 31.3 | 30.0 | 35.3 | 34.3 | | |
| | Meloidogyne | 28.7 | 39.7 | 32.3 | 34.0 | 35.0 | 31.7 | 37.3 | 30.7 | 32.0 | 42.3 | 38.7 | | |
| No. OF FRUITS | No Nematodes | 60.3 | 3.7 | 4.7 | 2.7 | 2.7 | 2.3 | 2.3 | 3.7 | 4.3 | 3.7 | 2.0 | 4.89 | 6.49 |
| | Nacobbus | 50.7 | 3.0 | 3.3 | 1.7 | 2.3 | 2.0 | 2.0 | 4.7 | 4.0 | 2.0 | 1.7 | | |
| | Meloidogyne | 33.3 | 2.7 | 3.3 | 2.0 | 2.3 | 2.0 | 2.3 | 4.3 | 4.0 | 3.3 | 1.0 | | |
| WEIGHT OF FRUITS | No Nematodes | 76.8 | 131.3 | 155.2 | 194.3 | 127.4 | 145.4 | 130.7 | 109.0 | 141.1 | 142.3 | 162.0 | 48.46 | 64.46 |
| | Nacobbus | 68.1 | 124.6 | 126.4 | 137.7 | 155.5 | 179.2 | 215.9 | 162.3 | 119.2 | 167.0 | 139.1 | | |
| | Meloidogyne | 46.8 | 97.8 | 90.4 | 141.6 | 128.0 | 147.6 | 116.8 | 138.3 | 130.6 | 100.4 | 113.9 | | |
| FRESH SHOOT WEIGHT | No Nematodes | 72.8 | 75.7 | 64.5 | 72.1 | 78.8 | 66.9 | 72.3 | 52.7 | 57.7 | 73.6 | 75.5 | n.s. | |
| | Nacobbus | 76.6 | 63.2 | 59.8 | 81.9 | 68.9 | 67.7 | 75.0 | 71.3 | 59.0 | 80.2 | 80.3 | | |
| | Meloidogyne | 69.1 | 82.5 | 82.2 | 76.8 | 72.4 | 75.5 | 75.3 | 62.4 | 68.1 | 73.0 | 92.5 | | |

* Mean of 3 replicates.

TABLE 6.3.4. : HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

D - Root length and fresh root weight*

| TOMATO VARIETIES | ROOT LENGTH (cm) | | | ROOT WEIGHT (g) | | |
|---|---|---|---|---|---|---|
| | No Nematodes | Nacobbus | Meloidogyne | No Nematodes | Nacobbus | Meloidogyne |
| HARVESTER | 44.3 | 47.7 | 44.7 | 41.0 | 49.3 | 83.9 |
| JEFFERSON | 30.7 | 30.0 | 26.7 | 14.4 | 18.0 | 41.5 |
| MONEYMAKER | 28.3 | 26.7 | 19.7 | 7.6 | 10.2 | 32.1 |
| BETTER BOY | 34.3 | 33.3 | 28.7 | 16.6 | 17.9 | 25.0 |
| BIG SEVEN | 33.3 | 32.3 | 30.0 | 14.4 | 17.9 | 21.9 |
| BONUS | 34.0 | 31.0 | 32.0 | 20.1 | 21.0 | 19.1 |
| RED GLOW | 30.3 | 29.0 | 27.7 | 13.1 | 22.2 | 28.6 |
| ROMA VFN | 36.7 | 42.3 | 41.3 | 24.9 | 29.4 | 27.0 |
| ROSSOL | 37.0 | 34.7 | 36.3 | 20.2 | 24.3 | 32.9 |
| VFN 8 | 32.7 | 33.3 | 31.3 | 13.7 | 24.3 | 20.8 |
| VFN 662 | 36.3 | 31.7 | 28.7 | 18.6 | 20.8 | 24.0 |

* Mean of 3 replicates

L.S.D. 0.05 n.s. 11.47

0.01 15.26

(Nematodes)

# DISCUSSION

The results and observations of the present study revealed interesting facts that help in our understanding of the host-reaction of root-knot susceptible and resistant tomato varieties to M. incognita and N. aberrans.

Where Nacobbus was inoculated, there were no significant differences between varieties, and all the varieties, both root-knot susceptible and resistant, showed a moderate galling. Egg-laying females and juveniles were always associated with galling in all the tomato varieties. In contrast, M. incognita behaved quite differently on the different varieties. All susceptible varieties showed a higher galling, while in the resistant group, Red Glow, Better Boy and Big Seven, had a moderate galling and in the rest, only slight galling occurred. This observation is in agreement with Rhodes (1965), who said that host reaction is specific enough in some cases to permit separations of sub species and races of nematodes; moreover, that the same host may react quite differently to various nematodes. Under the genetic aspect, Dropkin and Webb (1967) pointed out that resistance to a given species or biotype of nematode seems to be independent of resistance to other nematodes and to other pathogens we must assume a separate genetic mechanism for resistance to each pathogen.

So far as is known, all root-knot resistant tomato cultivars now in use derive their resistance from a single cross Lycopersicon esculentum (Michigan State Forcing ) X L. peruvianum (PI. 12B, 657) (Smith, 1944); considering the latter as the source of resistance. L. peruvianum which is indigenous to Peru and Ecuador, has been tested

against Nacobbus by Thorne and Schuster (1956) and Clark (1967) and shown to be susceptible, which could be one of the reasons why all the root-knot resistant tomato varieties were susceptible to N. aberrans.

Although nematodes are polyphagous there is selectivity for hosts, in the same way they have preference sites for invasion and feeding, being inherent in each species. Kirkpatrick, Van Gundy and Mai (1964) said that differences exist between nematodes due to the sites where they feed e.g. Belonolaimus longicaudatus and Xiphinema diversicaudatum prefer the root tip; Radopholus similis and Meloidogyne spp. prefer the region of root elongation and Rotylenchulus reniformis and Helicotylenchus dihystera the region of root maturation. With regards to N. aberrans and M. incognita, although they have the same preferred site for invasion, their life-cycles are different as well as their feeding habits. Juvenile stages of Nacobbus feed in the cortex, and the immature females which are migratory feed near the vascular system, where they become sedentary. Juveniles of Meloidogyne feed in the vascular system, establishing a definite feeding site as they are sedentary. Thus, the host reactions are different; the juveniles of Nacobbus first induce necrosis, cavities, and thickened cell walls, and the immature and mature females hypertrophy and hyperplasia, resulting in the formation of a syncytium and galls; Meloidogyne second stage juveniles from the beginning cause hypertrophy and hyperplasia, with the formation of giant cells and galls. So that, the only similarity found between these two genera is the induction of galls and the fact that both mature females discharge eggs in a gelatinous matrix. Although some other Meloidogyne spp. such as M. hapla and M. acronea produce secondary lateral roots from the galls as does N. aberrans. In my opinion, these differences in behaviour and host-reaction are related to the different nutrient requirements

of Nacobbus and Meloidogyne for the completion of their development, which are derived from different parts of the root. This would be another reason why N. aberrans can invade and reproduce normally in root-knot resistant tomato varieties.

Isolates of M. incognita can behave differently on different host varieties, however, the differences between N. aberrans and M. incognita in host-reaction and feeding habits can be applied to distinguish the false root-knot from any isolate of Meloidogyne.

In general, Meloidogyne showed a considerable effect on one of the susceptible varieties (Moneymaker), reducing its yield to 58% of the non-inoculated plant. The Meloidogyne population had been cultured for many years on the same variety Moneymaker. Even when, M. incognita was present in root-knot resistant varieties in varying levels, it was only capable of delaying time to fruiting in VFN-8 and decreasing yield in Better Boy to 73% of control.

Nacobbus, like Meloidogyne, delayed fruiting in VFN-8 and reduced yield in Better Boy. However, some other resistant varieties increased their yield in the presence of N. aberrans. Sosa Moss and Muñoz (1973) similarly observed that Nacobbus in low populations increased the number of fruits on tomato plants.

It has been already proved that resistant varieties are affected by populations of Meloidogyne spp. in several places. Sikora et al (1973) testing 10 root-knot resistant tomato varieties against an Indian population of M. javanica, found that VFN-8 and VFN-368 were heavily galled. Two populations of M. incognita from different areas in California were especially aggressive toward the resistant tomato cultivars VFN-8 and LA 1221 (Viglierchio, 1978). Myint (1978)

also reported the susceptibility of another root-knot resistant cultivar, Ronita, to isolates of M. incognita from Ecuador and El Salvador.

Other factors have been attributed for breaking resistance on tomato. Dropkin (1969) determined that at 28°C only 2% of the larvae of M. incognita acrita developed within the roots in contrast to 87% at 33°C. on resistant variety Nematex. Holtzmann (1965) also found that some root-knot resistant varieties and selections were relatively resistant at 20°C and 25°C; however, resistance was lower at 30°C and 34.5°C. Nevertheless, Netscher (1976) suggested that differences in the nature of the populations rather than environmental conditions are responsible for the attack of Meloidogyne on resistant tomatoes.

Galling induced by M. incognita in the present study was moderate in some root-knot resistant varieties such as Better Boy, Big Seven, and Red Glow, whose index of galling were from 3.7 - 4.3 as an evidence of the aggressiveness of I.C.I. population to root-knot resistant varieties and in agreement with Netscher's position.

The presence of necrotic areas in the resistant varieties, was evident after invasion by M. incognita. This has been demonstrated by other workers (Dropkin, 1969; Dropkin and Webb, 1967; Taylor, 1975), who observed that roots showed prominent brown discoloration a few hours after the invasion of Meloidogyne spp.

With any aspect, the interesting result from this experiment is that, despite the fact that both M. incognita and N. aberrans induce gall formation, their behaviour on the same tomato varieties is quite different.

## 6.4 HOST-RANGE OF N. ABERRANS ON TWELVE CROPS

### Introduction

The resistance or susceptibility of different crops to a particular nematode, can be investigated by its host-range.

N. aberrans (formerly N. batatiformis) has been studied on 74 plant species (Thorne and Schuster, 1956). All species of the Chenopodiaceae, Cruciferae, Cactaceae and Zygophyllaceae tested were susceptible. Those of the Gramineae, Liliaceae, Malvaceae, Iridiaceae and Convulvaceae were non-susceptible. While some species of Cucurbitaceae, Umbelliferae, Compositae and Solanaceae were resistant and others susceptible. Clark (1967) studied the host-range of N. aberrans (formerly N. serendipiticus) testing 25 plant species. A summary of both these investigations is given in Table (6.4.1.).

Cornejo (1977) also studied the host-range of Nacobbus aberrans in Peru, testing 21 crops and 10 species of weeds. The more efficient hosts were two species of potato, olluco (Ullucus tuberosus), and quinua (Chenopodium quinoa), and among the weeds, the Challamato (Calandria albis) and the Chinticoya (Physalis spp.).

Crop rotation has become a more important control method because of the expense of nematicides. It is therefore important to know the host-range of a nematode so that the correct rotation can be employed.

The host-range of N. aberrans (Ecuadorian isolate) was investigated, particularly to see if it could develop on two important Ecuadorian crops : Naranjilla (Solanum quitoense) and tree-tomato (Cyphomandra betacea), which are grown in some areas of the Andes mountains.

TABLE 6.4.1. : HOST RANGE OF N. ABERRANS (ACCORDING TO THORNE & SCHUSTER, 1956; CLARK, 1967).

| PLANTS | | HOST STATUS | |
|---|---|---|---|
| FAMILY | PLANT SPECIES | THORNE AND SCHUSTER | CLARK |
| CACTACEAE: | | | |
| | Mamillaria vivipara | + | N.T. |
| | Opuntia fragilis | + | N.T. |
| | O. tortispina | + | N.T. |
| CHENOPODIACEAE: | | | |
| | Beta vulgaris (early turnips) | + | N.T. |
| | B. vulgaris (sugar beet) | + | + |
| | B. vulgaris cicla | + | N.T. |
| | B. vulgaris macrorhiza | + | N.T. |
| | Chenopodium album | + | - |
| | Kochia scoparia | + | N.T. |
| | Solsola kali | + | N.T. |
| | Spinacia oleraceae | + | N.T. |
| CRUCIFERAE: | | | |
| | Brassica napobrassica | + | N.T. |
| | B. nigra | + | N.T. |
| | B. oleracea viridis | + | + |
| | B. oleracea botrytis | + | N.T. |
| | B. oleracea gemmifera | + | N.T. |
| | B. pekinensis | + | N.T. |
| | B. rapa | + | + |
| | Matthiola sp. | + | N.T. |
| | Raphanus sativus | + | N.T. |
| ZYGOPHYLLACEAE: | | | |
| | Tribulus terrestis | + | N.T. |
| COMPOSITAE: | | | |
| | Gaillardia pulchella | + | N.T. |
| | Lactuca sativa | + | + |
| | Tragopogon porrifolius | + | N.T. |
| | Senecio vulgaris | N.T. | - |

TABLE 6.4.1. : Continued.

| PLANTS | | HOST STATUS | |
|---|---|---|---|
| FAMILY | PLANT SPECIES | THORNE AND SCHUSTER | CLARK |
| | Carthamus tinctorius | - | N.T. |
| | Cichorium endivia | - | N.T. |
| | Helianthus annuus | - | N.T. |
| | Tagetes erecta | - | N.T. |
| | Zinnia elegans | - | N.T. |
| CUCURBITACEAE: | | | |
| | Cucurbita pepo | + | N.T. |
| | Cucumis sativus | + | larvae only |
| | Cucurbita maxima | - | - |
| | Cucumis melo | - | N.T. |
| | Citrullus vulgaris | - | N.T. |
| SOLANACEAE: | | | |
| | Lycopersicon esculentum | + | + |
| | L. peruvianum | + | + |
| | Solanum melongena | + | + |
| | Capsicum sp. | - | N.T. |
| | Solanum tuberosum | - | larvae only |
| | S. nigrum | N.T. | + |
| LEGUMINOSAE: | | | |
| | Pisum sativum | + | - |
| | Arachis hypogaea | - | - |
| | Glycine max | - | - |
| | Lathyrus odoratus | - | - |
| | Medicago sativa | - | - |
| | Melilotus officinallis | - | N.T. |
| | Phaseolus acutifolius latifolius | - | N.T. |
| | P. limensis | - | N.T. |
| | P. vulgaris | - | larvae only |
| UMBELLIFERAE: | | | |
| | Daucus carota | + | - |
| | Anethum graveolens | - | N.T. |

TABLE 6.4.1. : Continued.

| PLANTS | | HOST STATUS | |
|---|---|---|---|
| FAMILY | PLANT SPECIES | THORNE AND SCHUSTER | CLARK |
| AMARANTHACEAE: | | | |
| | *Amaranthus retroflexus* | - | N.T. |
| CONVOLVULACEAE: | | | |
| | *Ipomoea tricolor* | - | N.T. |
| GRAMINEAE: | | | |
| | *Avena sativa* | - | - |
| | *Hordeum vulgare* | - | larvae only |
| | *Secale cereale* | - | N.T. |
| | *Sorghum vulgare* | - | N.T. |
| | *Triticum vulgare* | - | N.T. |
| | *Zea mays* (pop corn) | - | N.T. |
| | *Z. mays* (sweet corn) | - | N.T. |
| IRIDACEAE: | | | |
| | *Gladiolus* sp. | - | N.T. |
| LILIACEAE: | | | |
| | *Allium cepa* | - | - |
| | *Asparagus officinalis* | - | N.T. |
| MALVACEAE: | | | |
| | *Hibiscus esculentus* | - | N.T. |
| | *Gossypium hirsutum* | - | N.T. |

\+ susceptible

\- non-susceptible

N.T. Not tested

## MATERIALS AND METHODS

The plants used in this experiment were as follows:-

| FAMILY | COMMON NAME | SCIENTIFIC NAME | VARIETY | COUNTRY OF ORIGIN |
|---|---|---|---|---|
| CUCURBITACEAE | Melon | *Cucurbita melo* | | IRAQ. |
| GRAMINEAE | Maize | *Zea mays* | | MALAWI |
| | Rice | *Oriza sativa* | INIAP-6 | ECUADOR |
| LEGUMINOSAE | Lucerne | *Medicago sativa* | CALIENTE | SULTANATE OF OMAN |
| | Soya | *Glycine max* | | BANGLADESH |
| | Winged-bean | *Psophocarpus tetragonolobus* | | NEW GUINEA |
| PEDALIACEAE | Sesame | *Sesamum indicum* | PORTOVIEJO I | ECUADOR |
| SOLANACEAE | Egg-plant | *Solanum melongena* | | IRAQ |
| | Naranjilla | *S. quitoense* | | ECUADOR |
| | Potato | *S. tuberosum* | PENTLAND CROWN | GREAT BRITAIN |
| | Tomato | *Lycopersicon esculentum* | MONEY-MAKER | GREAT BRITAIN |
| | Tree-tomato | *Cyphomandra betacea* | | ECUADOR. |

The inoculum used was infected soil from pure cultures of the Ecuadorian isolate of *N. aberrans*. Prior to planting, the number of nematodes per 100 $cm^3$ of soil was evaluated; using the modification of the tray method (Section 2) and found to be 200/100$cm^3$ soil.

Plastic pots (8 in. diameter) were partly filled with sterilized soil and a hole made in the centre. 200 $cm^3$ of infested soil, containing an estimated population of 400 nematodes, was added to the holes in each pot. Seedlings of each crop were planted in the infested soil.

Four replicates were used per crop in a fully randomized design in a heated glasshouse.

Population levels in roots and soil were measured, and observations were made on gall formation and presence of egg-masses after 10 weeks.

The soil temperature was recorded daily at 9 a.m. and 3 p.m. with the following ranges : 18°C and 34°C respectively.

## RESULTS

*N. aberrans* produced root galling within 10 weeks in four solanaceous crops: tomato, egg-plant, tree-tomato and naranjilla (Table 6.4.2. Appendix G. Table 1). Juvenile stages were recovered from potato, corn and rice, while in the other crops, sesame, soybean, lucerne, melon and winged-bean, no stages of the nematode were detected.

Although the four solanaceous crops showed galls, egg-masses were only produced in tomato, egg-plant and tree-tomato and not in naranjilla (Table 6.4.2. Appendix G. Table 1). However, in tree-tomato only a few were recorded. Potato, corn and rice showed necrotic areas typical of juvenile stage development. No symptoms of nematode damage were detected in the other crops.

The results from soil extractions are similar to those obtained in stained roots (Table 6.4.3. Appendix G. Table 2), because nematodes on tomato, egg-plant and tree-tomato produced egg-masses, the presence of juveniles in soil was recorded.

Gall size was measured in the four crops that showed galling slight differences were detected, although they were not significant (Table 6.4.4.).

TABLE 6.4.2. : GALLING AND DIFFERENT DEVELOPMENTAL STAGES OF N. ABERRANS RECOVERED FROM ROOTS OF TWELVE CROPS AFTER 70 DAYS.

| CROPS | No. NEMATODES/g ROOT* | | | | | No. galls/g root* |
|---|---|---|---|---|---|---|
| | JUVENILES | ♂ | ♀ without eggs | ♀ with eggs | TOTAL POPULATION | |
| CORN | 0.25 | 0 | 0 | 0 | 0.25 | 0 |
| EGG-PLANT | 12.25 | 2.25 | 8.75 | 2.75 | 26.00 | 11.25 |
| LUCERNE | 0 | 0 | 0 | 0 | 0 | 0 |
| MELON | 0 | 0 | 0 | 0 | 0 | 0 |
| NARANJILLA | 1.25 | 0 | 6.75 | 0 | 8.00 | 6.75 |
| POTATO | 1.25 | 0 | 0 | 0 | 1.25 | 0 |
| RICE | 0.50 | 0 | 0 | 0 | 0.50 | 0 |
| SESAME | 0 | 0 | 0 | 0 | 0 | 0 |
| SOYBEAN | 0 | 0 | 0 | 0 | 0 | 0 |
| TOMATO | 18.00 | 4.00 | 8.25 | 2.50 | 32.75 | 10.50 |
| TREE-TOMATO | 4.00 | 0.50 | 6.75 | 0.50 | 11.75 | 6.25 |
| WINGED-BEAN | 0 | 0 | 0 | 0 | 0 | 0 |

* Mean of 4 replicates.

L.S.D. 0.05 2.77

0.01 3.70

TABLE 6.4.3. : SOIL POPULATION OF N. ABERRANS FROM TWELVE CROPS AFTER 70 DAYS†.

| CROPS | POPULATION/L. SOIL* |
|---|---|
| CORN | 0 |
| EGG-PLANT | 350 |
| LUCERNE | 0 |
| MELON | 0 |
| NARANJILLA | 0 |
| POTATO | 0 |
| RICE | 0 |
| SESAME | 0 |
| SOYBEAN | 0 |
| TOMATO | 700 |
| TREE-TOMATO | 200 |
| WINGED-BEAN | 0 |

† Initial population: 400 nematodes.

* Mean of 4 replicates.

L.S.D. 0.05 298.7

TABLE 6.4.4. : GALL DIAMETER FOR FOUR CROPS. 70 DAYS AFTER NEMATODE INOCULATION.

| CROPS | EGG-PLANT | NARANJILLA | TOMATO | TREE-TOMATO |
|---|---|---|---|---|
| GALL DIAMETER* (cm) | 0.31 (0.2 - 0.4) | 0.30 (0.2 - 0.5) | 0.34 (0.3 - 0.5) | 0.29 (0.2 - 0.3) |

* Mean of 20 galls.

L.S.D. 0.05 n.s.

## DISCUSSION

The presence of N. aberrans in crops such as naranjilla and tree-tomato is important as these crops are grown in Ecuador in some valleys of the Andes mountains, where possibly N. aberrans is present or if transmitted may cause losses of importance.

Crops such as tomato and egg-plant, also have been reported as host of Nacobbus by Thorne and Schuster (1956) and Clark (1967) (Table 6.4.1.). However, potato, another solanacea, which is considered as a host of the false root-knot nematode in South America, was found to be resistant in these studies and only juvenile stages were detected in the roots after 70 days. In agreement with this observation, Clark (1967), reported that larvae were present in potato roots and Thorne and Schuster (1956), considered potato as a non-susceptible plant. Despite that, Gómez Tovar (1973), and Herrera (1977) among other authors, have demonstrated that N. aberrans is responsible for greater losses in some potato-growing areas in Peru. In a collecting expedition for Globodera species in Peru and Bolivia, Stone and Evans (1978) reported the presence of Cobb's nematode on some cultivated potatoes and wild tubers (Solanum spp.) in both countries.

This susceptibility and non-susceptibility showed by potato, possibly involve genetic aspects between potato varieties used in the host-range studies. However, other factors must be considered. Alarcón and Jatala (1977) testing a susceptible and a resistant potato variety to N. aberrans in Peru, found that the resistant variety showed considerable root galling when it was inoculated under a high regime of temperature ($18^{o}$ - $30^{o}$C.). They suggested that temperature is an important factor in the expression of resistance. The same aspect has been observed in root-knot resistant tomato varieties by

Dropkin (1969) and Holtzmann (1965) who found that resistance was lower as temperature increased with mean of 33°C and 30° to 34.5°C. respectively.

Similarly, in Mexico, Sosa Moss and González (1973) did a pathogenicity test with different levels of N. aberrans on three varieties of chilli peppers (Capsicum annum); however, Thorne and Schuster (1956) reported that Capsicum sp. was a non-host for Nacobbus, and from my own observation, when young seedlings of green pepper were planted in pots containing high populations of N. aberrans (British isolate), after 2 months only a few galls were detected.

It would be interesting under field conditions to observe the response of potato and green pepper to the presence of N. aberrans

Corn and rice had juvenile stages of N. aberrans in the roots, but no galling. Corn has been considered as a non-susceptible plant (Thorne and Schuster, 1956), however, Clark (1967) reported the presence of larvae in barley (Hordeum vulgare). This is not a consistent proof of susceptibility, but an indication that Nacobbus can invade these crops.

The low populations of N. aberrans in the present host-range test, are related to the amount of inoculum used, as this nematode has a low rate of reproduction.

# SECTION 7

## GENERAL DISCUSSION AND CONCLUSIONS

This project was initiated to investigate the biology, morphology and host-parasite relationships of an Ecuadorian isolate of Nacobbus sp. and compare it with a British isolate of N. aberrans (formerly N. serendipiticus. Franklin.).

In their biology, both isolates showed identical life-cycles with two well differentiated parasitic stages. They were different only in one aspect, the time to egg production, which either under ambient temperaturesor constant temperatures was 7 - 15 days shorter for the British isolate, than the Ecuadorian isolate. This difference in time to complete the life-cycle could be explained by the fact that both isolates have different origins and probably, as the British isolate has been cultured for almost 20 years on tomato, the host was an additional factor delaying the life-cycle of the Ecuadorian isolate. Johnson and Thames (1972) studying the biology of an unidentified population of Nacobbus in Texas, found that 20°C was the optimum temperature for the development in spinach and 24°C. in tomato, and no development occurred at temperatures above 28°C.

Despite the fact that some minor morphometric differences were found, mainly in second stage juveniles, comparisons of morphological characters of these two isolates with each other, revealed that both populations belong to the same species, Nacobbus aberrans Thorne, 1935 (Sher, 1970).

The life-cycle of N. aberrans, complemented by in vitro observations on tomato, revealed the presence of two parasitic stages with different habits. The first parasitic stage is the second stage

juvenile that invades the roots mainly in the region of root elongation, the root hair zone and also mature roots. It feeds in the cortical parenchyma, producing necrotic areas and cavities surrounded by cells with thickened cell walls. The nematodes remain inside the necrotic areas and develop in a coiled position. There is evidence that $J_3$'s might require to feed in order to obtain sufficient energy to continue their development, as a small percentage of this stage was observed re-invading the roots. Fourth stage juveniles do not feed, and $J_4$'s can develop outside the roots to males or immature females without feeding. This condition, exhibited mainly by the fourth stage and, in some cases, the third stage juveniles, is similar to those observed in other species of nematodes. Bird (1959) studying the development of M. javanica, pointed out that the energy necessary for the completion of the third and fourth moults must be obtained before the second moult, as the third and fourth stages are unable to feed. Similarly, Razak (1965) found that Rotylenchulus reniformis can grow from $J_2$'s to adult without feeding. Thus, feeding was observed to be essential for second stage and perhaps for the third stage juveniles of N. aberrans during this period of parasitism.

Although some migration of third and fourth stage juveniles was observed, it is concluded that these stages are mainly sedentary. This is because their migration is more accidental that behavioural; the necrotic epidermal cells that surround the cavities caused by feeding of $J_2$'s are easily broken down as the nematodes increase in size during development within the cavities, especially in young roots or wherever necrosis is near the root surface.

The behaviour exhibited by immature females and males differed completely from that of juvenile stages. The immature females, which are the second parasitic stage, migrate within the same root, or out

into the soil and re-enter new roots. They feed near the vascular system, inducing syncytia and both hypertrophy and hyperplasia of cells, resulting in gall formation without any necrosis. Mature females extrude a gelatinous matrix in which eggs are discharged, either inside or on the surface of galled roots. Males are migratory in the soil, and are found entangled in the egg-masses.

The presence of males in egg-masses, and the absence of eggs and males during the winter months, are two strong facts to suggest that this nematode has an amphimictic reproduction, as other workers have indicated (Clark, 1967; Prasad and Webster, 1967; Thorne and Schuster, 1956).

Temperature is a limiting factor on the life-cycle of both isolates of N. aberrans in tomato roots. When the life-cycle was studied at 14°C., only immature females and males were recovered from roots, and there was no gall formation. At 19°C the British isolate took 70 days from $J_2$ to egg, and the Ecuadorian isolate 80 days. These results contrasted with those obtained at 25°C., where the life-cycle was completed in 28 and 35 days for the British and the Ecuadorian isolates respectively. During July to November, with ambient temperatures ranging from 12°C. to 36°C., the life-cycle from $J_2$ to egg, took 45 and 60 days for the British and the Ecuadorian populations respectively. This indicates that the range of optimum temperature for N. aberrans activity is narrow and length of life-cycle increases at temperatures below 25°C. In agreement, Jones (1965) said that N. aberrans can complete the life-cycle later in the season, in 7 to 9 weeks.

The lower temperatures during winter months, ranging from 9° to 21°C., suppressed the development of the British isolate, when

neither galls nor egg-masses were detected. The Ecuadorian isolate could induce galling throughout the year, although during winter, there was no egg-production. N. aberrans appears to be a warm temperate nematode, and the diminished population during the cooler, winter months suggests that low temperature could be important in controlling the nematodes in areas such as the Andes in tropical South America. The apparent narrow range of optimum temperature at which this species can develop and reproduce is probably one of the reasons why N. aberrans has a limited distribution; the presence of geographical and climatic barriers could be limiting its dispersion.

N. aberrans rapidly increased its population after the winter months even after the population of the British isolate had practically disappeared. Knowing that this nematode has a long life-cycle (7-9 weeks) under warmer ambient temperatures, it implied that the nematode had a late juvenile survival stage.

The presence during the cooler period of $J_4$'s in root samples, their frequent occurrence in soil samples, and the fact that they remained alive for two months out of roots in a quiescent state with their food reserves intact, points to them being the overwintering, survival stage for N. aberrans. Cooper and Van Gundy (1971) said that eggs cointained in cysts of Heterodera, $J_4$'s in Ditylenchus dipsaci, $J_2$'s in Anguina tritici, among others, are the stages that survive adverse conditions and that as soon as normal conditions are restored, eggs hatch or juvenile stages continue their development. Thus, apart from the eggs, the $J_4$ stage is the main survival stage in N. aberrans.

The damage caused by N. aberrans to tomato roots has been differentiated clearly into two phases. The first, produced by the juveniles in the cortex has many similarities to the damage caused

by Pratylenchus spp. and other root lesion nematodes. The second caused by immature females feeding near the vascular system and forming galls is like Meloidogyne spp. The second stage juveniles feeding in the cortex, produce necrosis and cavities surrounded by enlarged cells with thickened cell walls. This reaction of tomato plants against the presence of $J_2$'s in the roots, is similar to the other members of the Pratylenchidae although, genera such as Pratylenchus and Radopholus do not remain confined to small necrotic areas and continue migrating through the roots. Moreover, the presence of thickened cell walls has not been reported with these nematodes (Du Charme, 1959; Mountain and Patrick, 1959; Blake, 1966). In addition the juvenile stages of N. aberrans remain sedentary and coiled inside the cavities made in the cortex, which is another major difference between N. aberrans and related genera of the Pratylenchidae.

Normally the immature females, leaving the necrotic areas, either migrate within the same root or leave the roots and re-invade new roots. They become located near the vascular system, enlarge into swollen females and then their feeding induces syncytia, hypertrophy and hyperplasia of the cells and consequently the formation of galls.

The syncytium induced by N. aberrans is spindle shaped, with enlarged cells, mono-or binucleate. The presence of the syncytium causes modification and disorganization of the vascular elements, and an abnormal proliferation of secondary lateral roots from the galls. In the formation of galls, Nacobbus resembles the root-knot nematodes, Meloidogyne spp. However, there are many differences in host-reaction, structure of the galls and behaviour between these two gall-forming, but different, nematode genera (See Table 4.2.5.).

The observations *in vitro* revealed that *N. aberrans* is a true plant pathogen since it causes necrosis in the absence of secondary invaders, and induces gall formation. Despite this, *N. aberrans* under good growing conditions for the host, such as when plants receive ideal levels of water and fertilizer, does not always cause severe damage to its host. The low reproduction rate, possibly because of the need of males, the comparatively long life-cycle, the limitations of temperature, and the proliferation of secondary lateral roots from galls, could all contribute to its reduced pathogenicity. In addition, the relatively small area of the vascular system that is affected by individual mature *N. aberrans* females (see Section 5) compared to *Meloidogyne* spp. will only have a limited effect on the translocation of water and nutrients. However after three successive tomato crops with high nematode infestation, fruiting was delayed and yields reduced significantly.

Necrotic areas caused by invasion of juvenile stages, could form an ideal infection site for many of the secondary invaders present in the soil. Mountain and Patrick (1959), reported that lesions originated by *P. penetrans* on peach roots, were invaded by fungi, and Blake (1966) observed that *Fusarium oxysporum* alone failed to cause lesions on *Musa* spp., but when *R. similis* was present in the cortex, the fungus colonised parenchyma cells. So that, although juvenile stages of *N. aberrans* can alone induce certain damage, they might also predispose the root to the invasion of other pathogens as an incitant organism. Mayol and Bergeson (1970) reported that secondary microbial invaders of the galled roots caused by *M. incognita* were the major cause of plant growth reduction. Thus, this would be another interesting aspect to study under controlled or field conditions.

It was suspected that, because *N. aberrans* and *Meloidogyne* spp.

are both gall-forming nematodes, the presence of Nacobbus under field conditions could easily be overlooked and mistaken for Meloidogyne especially when occurring sympatrically. Nacobbus on its own produces galls distinctly different from Meloidogyne galls, but when N. aberrans and M. incognita were inoculated together on tomato, they produced large, uneven galls that were indistinguishable from severe infestation by Meloidogyne alone. This result clearly adds weight to the suspicion that Nacobbus can easily be overlooked and it is obvious that a very detailed examination of galled roots is necessary to detect Nacobbus in Meloidogyne infested fields. In addition, the inoculation of both species together revealed that the root length was diminished significantly and gall size was increased, compared to single inoculations of either Nacobbus or Meloidogyne, suggesting that there is a synergistic effect, that is, N. aberrans and M. incognita may induce more damage when together than the combined damage when alone. From the practical point of view, this observation has been useful to demonstrate that the occurrence together of both species on certain crops and in environmental conditions suitable for both genera, could affect the crops severely.

More research is necessary to study the pathological effects produced by both nematodes in galled roots, and to support or refute the hypothesis related to the possible attraction that Nacobbus galls could have exerted upon juvenile stages of Meloidogyne.

Other evidence to differentiate further N. aberrans from M. incognita, was the reaction of root-knot susceptible and resistant tomato varieties in the presence of either species. Although the resistant varieties showed varying levels of galled roots caused by M. incognita, these were low indices compared with the severe galling produced in susceptible tomato varieties. The presence of egg-masses

and juvenile stages in some resistant varieties more than in others is evidence that resistance of tomato plants is related to the isolate of Meloidogyne present. Root-knot galling of resistant varieties has been reported by other authors (Netscher, 1976; Sikora et al, 1973; Viglierchio, 1978). N. aberrans induced the same amount of galling in all the tomato varieties screened, indicating that resistance in tomato is specific toward the root-knot nematodes. This different response of the tomato plant in the presence of N. aberrans and M. incognita is probably related to the different nutrient requirements exhibited by both nematodes involving different host-reaction during development.

The galling of root-knot resistant tomato varieties induced by N. aberrans opens up the possibility that in certain conditions, where both nematodes are present, the invasion of the false root-knot nematode in tomato resistant plants, could break down their resistance and thus become susceptible to the invasion of Meloidogyne spp.

The reproduction of N. aberrans in certain crops, such as the solanaceous ones, is possibly related to the distribution of this nematode in certain areas in the Andes, because the majority of the solanaceous plants originate from some countries in South America, such as Peru and Ecuador, where the nematode has been reported. From this study we must assume that different biotypes of N. aberrans exist. It was interesting to find that potato was a non-host in these studies, although potato is a susceptible crop for N. aberrans in South America (Gómez Tovar, 1973; Jatala and Scurrah, 1975; Herrera, 1977). However, Thorne and Schuster (1956) reported that of six varieties of potato tested, all were non-hosts for N. aberrans (formerly

N. batatiformis). Clark (1967) only found larvae in the roots of potato, working with N. aberrans (formerly N. serendipiticus), and in my host-range similarly, only juvenile stages of N. aberrans (Ecuadorian isolate), were detected in the roots of var. Pentland Crown. A screening test using potato varieties to test if some varieties carry resistant genes to N. aberrans would be useful information for some countries in South America where potato is a basic food-crop.

As N. aberrans caused root galling on naranjilla and tree-tomato, both crops of importance in Ecuador growing in areas where possibly the false root-knot nematode would be present, it has been useful to know their host-status with relation to N. aberrans for a future control programme.

The author's idea in these studies has been to increase our knowledge of the false root-knot nematode and to stimulate further studies of this singularly interesting nematode that perhaps is one of the most primitive of the gall inducing sedentary phytoparasites.

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# APPENDIX

APPENDIX A.

TABLE 1. MORPHOMETRIC MEASURES OF SECOND STAGE JUVENILE OF *N. ABERRANS* (BRITISH ISOLATE)

| | L(mm) | W(μ) | SPEAR (μ) | a | b | b' | c | c' | s |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.33 | 15 | 11 | 23 | 3.8 | 2.9 | 14 | 2.5 | 1.2 |
| 2 | 0.35 | 14 | 11 | 25 | 4.3 | 2.6 | 15 | 2.8 | 1.2 |
| 3 | 0.35 | 14 | 10 | 25 | 3.7 | 2.9 | 15 | 2.4 | 0.9 |
| 4 | 0.34 | 14 | 12 | 24 | 4.0 | 2.4 | 13 | 2.7 | 1.3 |
| 5 | 0.34 | 14 | 11 | 24 | 4.2 | 3.0 | 15 | 2.6 | 1.1 |
| 6 | 0.31 | 14 | 11 | 22 | 4.5 | 2.6 | 13 | 2.5 | 1.1 |
| 7 | 0.33 | 13 | 11 | 26 | 3.3 | 2.4 | 14 | 2.8 | 1.2 |
| 8 | 0.34 | 18 | 12 | 19 | 3.9 | 2.6 | 14 | 2.4 | 1.2 |
| 9 | 0.34 | 16 | 11 | 22 | 3.8 | 2.8 | 16 | 2.3 | 1.1 |
| 10 | 0.37 | 17 | 11 | 22 | 3.8 | 3.0 | 14 | 2.9 | 1.2 |
| 11 | 0.37 | 19 | 11 | 19 | 3.7 | 2.4 | 18 | 2.1 | 0.9 |
| 12 | 0.34 | 14 | 11 | 24 | 3.6 | 2.6 | 13 | 2.7 | 1.0 |
| 13 | 0.37 | 14 | 11 | 27 | 3.8 | 2.5 | 15 | 2.8 | 1.2 |
| 14 | 0.35 | 13 | 10 | 27 | 4.1 | 2.5 | 16 | 2.9 | 1.1 |
| 15 | 0.35 | 13 | 10 | 26 | 3.6 | 2.5 | 14 | 2.6 | 1.1 |
| 16 | 0.36 | 13 | 10 | 27 | 3.8 | 2.6 | 13 | 3.2 | 1.2 |
| 17 | 0.34 | 13 | 11 | 26 | 3.6 | 2.3 | 16 | 2.3 | 1.2 |
| 18 | 0.37 | 17 | 12 | 22 | 4.1 | 2.5 | 16 | 2.6 | 1.3 |
| 19 | 0.36 | 13 | 11 | 27 | 3.8 | 2.5 | 15 | 2.8 | 1.1 |
| 20 | 0.32 | 13 | 10 | 25 | 3.6 | 2.4 | 14 | 2.5 | 1.1 |
| Σ | 6.93 | 291 | 218 | 482 | 77 | 52 | 293 | 52.4 | 22.7 |
| $\bar{x}$ | 0.35 | 14.55 | 10.90 | 24.10 | 3.85 | 2.60 | 14.65 | 2.62 | 1.13 |

APPENDIX A

TABLE 2. MORPHOMETRIC MEASURES OF SECOND STAGE JUVENILE OF *N. ABERRANS* (ECUADORIAN ISOLATE).

| | L(mm) | W(μ) | SPEAR (μ) | a | b | b' | c | c' | s |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.32 | 14 | 12 | 23 | 3.7 | 2.3 | 14 | 2.6 | 1.3 |
| 2 | 0.31 | 15 | 12 | 21 | 3.6 | 2.4 | 14 | 2.3 | 1.1 |
| 3 | 0.35 | 16 | 13 | 22 | 3.5 | 2.6 | 17 | 1.8 | 1.2 |
| 4 | 0.31 | 13 | 13 | 23 | 4.0 | 2.5 | 13 | 2.6 | 1.3 |
| 5 | 0.34 | 15 | 13 | 22 | 3.9 | 2.7 | 13 | 3.0 | 1.1 |
| 6 | 0.34 | 15 | 13 | 23 | 3.9 | 2.6 | 14 | 2.7 | 1.2 |
| 7 | 0.31 | 14 | 12 | 22 | 3.8 | 2.7 | 14 | 2.4 | 1.1 |
| 8 | 0.32 | 14 | 14 | 22 | 3.6 | 2.4 | 14 | 2.6 | 1.3 |
| 9 | 0.32 | 13 | 12 | 24 | 3.7 | 2.7 | 14 | 2.8 | 1.3 |
| 10 | 0.31 | 14 | 13 | 22 | 3.6 | 2.6 | 15 | 2.5 | 1.5 |
| 11 | 0.32 | 15 | 14 | 22 | 3.3 | 2.4 | 14 | 2.8 | 1.3 |
| 12 | 0.33 | 12 | 12 | 29 | 4.2 | 2.4 | 17 | 2.6 | 1.4 |
| 13 | 0.32 | 11 | 13 | 29 | 2.9 | 2.1 | 14 | 2.9 | 1.3 |
| 14 | 0.34 | 11 | 12 | 30 | 3.3 | 2.3 | 14 | 2.6 | 1.4 |
| 15 | 0.35 | 12 | 13 | 29 | 3.8 | 2.6 | 16 | 2.8 | 1.4 |
| 16 | 0.26 | 10 | 12 | 26 | 3.3 | 2.1 | 14 | 2.9 | 1.4 |
| 17 | 0.33 | 13 | 12 | 24 | 3.3 | 2.2 | 15 | 2.5 | 1.4 |
| 18 | 0.35 | 13 | 11 | 27 | 3.4 | 2.2 | 13 | 3.1 | 1.1 |
| 19 | 0.33 | 11 | 11 | 28 | 2.9 | 2.1 | 16 | 2.8 | 1.3 |
| 20 | 0.30 | 11 | 11 | 27 | 3.4 | 2.2 | 17 | 2.4 | 1.3 |
| Σ | 6.46 | 262 | 248 | 495 | 71.10 | 48.10 | 292 | 52.70 | 25.7 |
| $\bar{x}$ | 0.32 | 13.10 | 12.40 | 24.75 | 3.55 | 2.40 | 14.60 | 2.63 | 1.28 |

TABLE 3. MORPHOMETRIC MEASURES OF IMMATURE FEMALE OF N. ABERRANS (BRITISH ISOLATE).

| | L(mm) | W(μ) | SPEAR (μ) | a | b | b' | c | c' | s | V(%) | O(%) | R Van |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.80 | 31 | 18 | 26 | 8.7 | 4.9 | 31 | 1.5 | 1.1 | 93 | 37 | 19 |
| 2 | 0.76 | 30 | 18 | 25 | 8.0 | 4.8 | 34 | 1.3 | 1.0 | 92 | 36 | 22 |
| 3 | 0.68 | 31 | 18 | 22 | 6.8 | 4.1 | 29 | 1.3 | 1.1 | 91 | 55 | 19 |
| 4 | 0.88 | 36 | 20 | 24 | 6.2 | 3.7 | 33 | 1.4 | 1.0 | 93 | 43 | 20 |
| 5 | 0.85 | 36 | 20 | 24 | 5.6 | 3.6 | 31 | 1.2 | 1.0 | 92 | 29 | 18 |
| 6 | 0.80 | 25 | 17 | 32 | 7.5 | 4.2 | 33 | 1.4 | 1.1 | 93 | 51 | 20 |
| 7 | 0.89 | 31 | 18 | 29 | 5.8 | 3.7 | 32 | 1.5 | 0.9 | 93 | 61 | 19 |
| 8 | 1.05 | 41 | 22 | 26 | 8.4 | 4.7 | 34 | 1.2 | 1.0 | 92 | 41 | 24 |
| 9 | 0.93 | 34 | 22 | 27 | 7.4 | 3.4 | 34 | 1.2 | 1.2 | 94 | 50 | 19 |
| 10 | 0.91 | 36 | 22 | 25 | 7.5 | 4.8 | 37 | 1.1 | 1.1 | 93 | 42 | 22 |
| Σ | 8.55 | 331 | 195 | 260 | 71.9 | 41.9 | 328 | 13.1 | 10.5 | 926 | 445 | 202 |
| $\bar{x}$ | 0.85 | 33.10 | 19.50 | 26.00 | 7.19 | 4.19 | 32.80 | 1.31 | 1.05 | 92.60 | 44.50 | 20.20 |

TABLE 4. MORPHOMETRIC MEASURES OF IMMATURE FEMALE OF N. ABERRANS (ECUADORIAN ISOLATE)

| | L(mm) | W (μ) | SPEAR (μ) | a | b | b' | c | c' | s | V(%) | O(%) | R. Van |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.99 | 23 | 20 | 43 | 8.1 | 5.1 | 40 | 1.6 | 1.3 | 93 | 56 | 20 |
| 2 | 0.90 | 29 | 19 | 31 | 8.0 | 4.6 | 47 | 0.9 | 1.2 | 93 | 53 | 22 |
| 3 | 0.97 | 28 | 21 | 35 | 7.2 | 5.2 | 29 | 1.9 | 1.3 | 92 | 47 | 20 |
| 4 | 0.95 | 39 | 20 | 24 | 7.0 | 4.7 | 30 | 1.6 | 1.0 | 92 | 38 | 25 |
| 5 | 0.82 | 33 | 18 | 25 | 7.3 | 4.1 | 33 | 1.3 | 0.9 | 91 | 37 | 25 |
| 6 | 0.98 | 31 | 21 | 32 | 8.2 | 4.3 | 42 | 1.2 | 1.1 | 93 | 26 | 19 |
| 7 | 0.91 | 27 | 21 | 34 | 8.2 | 4.0 | 36 | 1.3 | 1.2 | 93 | 55 | 21 |
| 8 | 0.95 | 34 | 21 | 28 | 8.9 | 5.2 | 32 | 1.3 | 1.1 | 93 | 52 | 22 |
| 9 | 0.97 | 29 | 19 | 33 | 7.7 | 5.4 | 37 | 1.2 | 1.0 | 93 | 30 | 17 |
| 10 | 0.81 | 32 | 18 | 25 | 6.9 | 4.4 | 34 | 1.3 | 1.0 | 92 | 34 | 20 |
| Σ | 9.25 | 305 | 198 | 310 | 77.5 | 47 | 360 | 13.6 | 11.1 | 925 | 428 | 211 |
| $\bar{x}$ | 0.92 | 30.50 | 19.80 | 31.00 | 7.75 | 4.70 | 36.00 | 1.36 | 1.11 | 92.50 | 42.8 | 21.1 |

TABLE 5. MORPHOMETRIC MEASURES OF MALE OF N. ABERRANS (BRITISH ISOLATE)

| | L(mm) | W(μ) | SPEAR (μ) | a | b | b' | c | c' | s | Spicule (μ) | Gubernaculun (μ) | T (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.86 | 38 | 18 | 23 | 7.0 | 4.6 | 28 | 1.5 | 1.0 | 26 | 7 | 62 |
| 2 | 0.83 | 34 | 19 | 25 | 7.2 | 5.2 | 32 | 1.3 | 1.0 | 24 | 7 | 72 |
| 3 | 0.93 | 37 | 20 | 25 | 7.1 | 4.3 | 42 | 1.3 | 1.0 | 26 | 7 | 53 |
| 4 | 0.84 | 32 | 20 | 27 | 8.9 | 5.3 | 36 | 1.3 | 1.1 | 28 | 7 | 80 |
| 5 | 0.96 | 45 | 20 | 21 | 8.5 | 5.7 | 40 | 1.0 | 0.9 | 30 | 7 | 64 |
| 6 | 1.05 | 51 | 22 | 21 | 8.5 | 5.1 | 38 | 1.4 | 1.1 | 28 | 7 | 73 |
| 7 | 0.96 | 41 | 21 | 24 | 7.5 | 4.7 | 40 | 1.2 | 0.9 | 26 | 7 | 66 |
| 8 | 1.02 | 38 | 22 | 27 | 8.4 | 5.2 | 36 | 1.2 | 1.0 | 24 | 6 | 66 |
| 9 | 0.97 | 41 | 22 | 24 | 8.6 | 5.0 | 42 | 1.2 | 1.3 | 26 | 8 | 70 |
| 10 | 0.98 | 41 | 23 | 24 | 7.9 | 4.9 | 41 | 1.2 | 1.2 | 27 | 7 | 61 |
| Σ | 9.40 | 398 | 207 | 241 | 79.60 | 50 | 375 | 12.60 | 10.5 | 265 | 70 | 667 |
| $\bar{x}$ | 0.94 | 39.80 | 20.70 | 24.10 | 7.96 | 5.0 | 37.50 | 1.26 | 1.05 | 26.50 | 7.00 | 66.70 |

TABLE 6. MORPHOMETRIC MEASURES OF MALE OF N. ABERRANS (ECUADORIAN ISOLATE).

| | L (mm) | W(μ) | SPEAR (μ) | a | b | b' | c | c' | s | Spicule (μ) | Gubernaculum (μ) | T(%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.91 | 39 | 22 | 23 | 7.2 | 4.2 | 35 | 1.2 | 0.9 | 30 | 9 | 69 |
| 2 | 1.24 | 43 | 24 | 29 | 8.8 | 4.9 | 42 | 1.1 | 0.9 | 34 | 8 | 59 |
| 3 | 1.11 | 45 | 22 | 24 | 6.9 | 4.7 | 38 | 1.1 | 0.9 | 32 | 8 | 78 |
| 4 | 0.99 | 33 | 23 | 30 | 7.9 | 4.9 | 40 | 1.3 | 1.1 | 29 | 11 | 79 |
| 5 | 0.91 | 33 | 23 | 28 | 8.3 | 4.9 | 48 | 1.0 | 1.2 | 30 | 8 | 63 |
| 6 | 1.11 | 45 | 24 | 25 | 9.1 | 4.8 | 38 | 1.2 | 1.0 | 32 | 6 | 52 |
| 7 | 1.15 | 48 | 22 | 24 | 8.6 | 4.6 | 44 | 1.0 | 0.9 | 32 | 6 | 65 |
| 8 | 0.76 | 29 | 24 | 26 | 6.7 | 3.7 | 33 | 1.2 | 1.6 | 30 | 8 | 87 |
| 9 | 1.16 | 35 | 22 | 33 | 8.8 | 5.3 | 37 | 1.4 | 1.2 | 33 | 8 | 62 |
| 10 | 1.04 | 25 | 22 | 42 | 9.1 | 4.9 | 39 | 1.4 | 1.3 | 28 | 7 | 59 |
| Σ | 10.39 | 375 | 228 | 284 | 81.4 | 46.9 | 394 | 11.9 | 11 | 310 | 79 | 673 |
| $\bar{x}$ | 1.03 | 37.50 | 22.80 | 28.40 | 8.14 | 4.69 | 39.40 | 1.19 | 1.1 | 31.00 | 7.90 | 67.3 |

APPENDIX A.

TABLE 7. MORPHOMETRIC MEASURES OF MATURE FEMALE OF N. ABERRANS (BRITISH AND ECUADORIAN ISOLATES)

A. BRITISH

| | L(mm) | SPEAR (μ) |
|---|---|---|
| 1 | 1.18 | 19 |
| 2 | 1.23 | 19 |
| 3 | 1.20 | 23 |
| 4 | 1.22 | 20 |
| 5 | 1.11 | 20 |
| 6 | 1.24 | 19 |
| 7 | 1.07 | 20 |
| 8 | 1.22 | 19 |
| 9 | 1.35 | 21 |
| 10 | 0.86 | 20 |
| Σ | 11.68 | 200 |
| $\bar{x}$ | 1.17 | 20.00 |

B. ECUADORIAN

| | L.(mm) | SPEAR (μ) |
|---|---|---|
| 1 | 1.32 | 20 |
| 2 | 1.45 | 20 |
| 3 | 1.30 | 20 |
| 4 | 1.43 | 22 |
| 5 | 1.66 | 19 |
| 6 | 1.28 | 20 |
| 7 | 1.27 | 22 |
| 8 | 1.40 | 19 |
| 9 | 1.49 | 24 |
| 10 | 1.20 | 21 |
| Σ | 13.8 | 207 |
| $\bar{x}$ | 1.38 | 20.70 |

APPENDIX B.

TABLE 1. INVASION OF DIFFERENT STAGES OF N. ABERRANS IN TOMATO ROOTS ON AGAR.

| NO. NEMATODES AND STAGES INOCULATED | REPLICATES | % NEMATODE ENDOPARASITIC | % NEMATODE FORMING GALLS |
|---|---|---|---|
| 100 $J_2$ | 1 | 49 | 0 |
| | 2 | 36 | 0 |
| | 3 | 37 | 0 |
| MEAN | | 40.7 | 0 |
| 5 $J_3$ | 1 | 0 | 0 |
| | 2 | 20 | 0 |
| | 3 | 20 | 0 |
| MEAN | | 13.3 | 0 |
| 10 $J_4$ | 1 | 0 | 0 |
| | 2 | 0 | 0 |
| | 3 | 0 | 0 |
| MEAN | | 0 | 0 |
| 3 Imm. ♀ | 1 | 100 | 100 |
| | 2 | 100 | 100 |
| | 3 | 100 | 100 |
| MEAN | | 100 | 100 |
| 5 ♂ | 1 | 0 | 0 |
| | 2 | 0 | 0 |
| | 3 | 0 | 0 |
| MEAN | | 0 | 0 |

TABLE 2. INVASION SITES OF N. ABERRANS IN WATER AGAR TOMATO CULTURES.

| TYPE OF ROOT INVADED / REGION OF ROOT INVADED | REPLICATES | NO. NEMATODES/AGAR PLATE | | | | | | % OF TOTAL NEMATODES |
|---|---|---|---|---|---|---|---|---|
| | | ROOT TIP | | REGION OF ELONGATION | | REGION OF ROOT HAIRS AND MATURATION | | |
| | | NO. NEMATODES | % OF TOTAL NEMATODES IN ROOTS | NO. NEMATODES | % OF TOTAL NEMATODES IN ROOTS | N. NEMATODES | % OF TOTAL NEMATODES IN ROOTS | |
| MAIN LATERAL | 1 | 0 | 0 | 9 | 18.4 | 6 | 12.2 | 10.2 |
| | 2 | 2 | 5.6 | 9 | 25.0 | 4 | 11.1 | 13.9 |
| | 3 | 0 | 0 | 5 | 13.5 | 4 | 10.8 | 8.1 |
| | MEAN | 0.7 | 1.9 | 7.7 | 19.0 | 4.7 | 11.4 | 32.3 |
| SECONDARY LATERAL | 1 | 6 | 12.2 | 18 | 36.7 | 10 | 20.4 | 23.1 |
| | 2 | 3 | 8.3 | 13 | 36.1 | 5 | 13.9 | 19.4 |
| | 3 | 4 | 10.8 | 15 | 40.5 | 9 | 24.3 | 25.2 |
| | MEAN | 4.3 | 10.4 | 15.3 | 37.8 | 8.0 | 19.5 | 67.7 |

TABLE 2.1 DEVELOPMENTAL STAGES OF N. ABERRANS THAT MIGRATED FROM WATER AGAR TOMATO CULTURES INOCULATED WITH $J_2$

| NO. NEMATODES MIGRATORY FROM ROOTS | REPLICATES | % OF DIFFERENT DEVELOPMENTAL STAGES | | | | |
|---|---|---|---|---|---|---|
| | | $J_3$ | $J_4$ | Imm. ♀ | Mat. ♀ | ♂ |
| 15 | 1 | 4.1 | 8.2 | 4.1 | 0 | 4.1 |
| 8 | 2 | 5.6 | 8.3 | 2.8 | 0 | 5.0 |
| 10 | 3 | 8.1 | 13.5 | 2.7 | 0 | 2.7 |
| MEAN | | 5.7 | 10.0 | 3.2 | 0 | 4.1 |

APPENDIX B.

TABLE 3. DEVELOPMENT OF DIFFERENT STAGES OF N. ABERRANS ON NUTRIENT WATER AGAR.

| NEMATODE STAGE INOCULATED | REPLICATES | % OF DIFFERENT DEVELOPMENT STAGES FOUND AFTER TWO MONTHS | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | $J_2$ | $J_3$ | $J_4$ | Imm ♀ | Mat ♀ | ♂ | DEAD |
| 100 $J_2$ | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| MEAN | | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| 5 $J_3$ | 1 | - | 0 | 20 | 0 | 0 | 40 | 40 |
| | 2 | - | 0 | 40 | 0 | 0 | 0 | 60 |
| | 3 | - | 0 | 40 | 20 | 0 | 0 | 40 |
| MEAN | | - | 0 | 33.3 | 6.7 | 0 | 13.3 | 46.7 |
| 10 $J_4$ | 1 | - | - | 40 | 20 | 0 | 20 | 20 |
| | 2 | - | - | 20 | 30 | 0 | 10 | 40 |
| | 3 | - | - | 40 | 20 | 0 | 20 | 20 |
| MEAN | | - | - | 33.3 | 23.3 | 0 | 16.7 | 26.7 |
| 3 Imm. ♀ | 1 | - | - | - | 0 | 0 | - | 100 |
| | 2 | - | - | - | 0 | 0 | - | 100 |
| | 3 | - | - | - | 0 | 0 | - | 100 |
| MEAN | | - | - | - | 0 | 0 | - | 100 |
| 5 ♂ | 1 | - | - | - | - | - | 0 | 100 |
| | 2 | - | - | - | - | - | 0 | 100 |
| | 3 | - | - | - | - | - | 0 | 100 |
| MEAN | | - | - | - | - | - | 0 | 100 |

APPENDIX B.

TABLE 4. DEVELOPMENT OF DIFFERENT STAGES OF N. ABERRANS ON DISTILLED WATER.

| NO. NEMATODES AND STAGES INOCULATED | REPLICATES | % OF DIFFERENT DEVELOPMENT STAGES FOUND AFTER TWO MONTHS | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | $J_2$ | $J_3$ | $J_4$ | Imm ♀ | Mat ♀ | ♂ | DEAD |
| 20 $J_2$ | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| MEAN | | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| 5 $J_3$ | 1 | - | 0 | 0 | 20 | 0 | 20 | 60 |
| | 2 | - | 0 | 20 | 0 | 0 | 0 | 80 |
| | 3 | - | 0 | 20 | 0 | 0 | 20 | 60 |
| MEAN | | - | 0 | 13.3 | 6.7 | 0 | 13.3 | 66.7 |
| 10 $J_4$ | 1 | - | - | 20 | 30 | 0 | 20 | 30 |
| | 2 | - | - | 10 | 40 | 0 | 40 | 10 |
| | 3 | - | - | 20 | 10 | 0 | 30 | 40 |
| MEAN | | - | - | 16.7 | 26.7 | 0 | 30.0 | 26.7 |
| 2 Imm. ♀ | 1 | - | - | - | 0 | 0 | - | 100 |
| | 2 | - | - | - | 0 | 0 | - | 100 |
| | 3 | - | - | - | 0 | 0 | - | 100 |
| MEAN | | - | - | - | 0 | 0 | - | 100 |
| 5 ♂ | 1 | - | - | - | - | - | 0 | 100 |
| | 2 | - | - | - | - | - | 0 | 100 |
| | 3 | - | - | - | - | - | 0 | 100 |
| MEAN | | - | - | - | - | - | 0 | 100 |

TABLE 1. RELATIONSHIP OF SOIL TEMPERATURE AND N. ABERRANS POPULATION (ECUADORIAN ISOLATE) ON TOMATO VARIETY JEFFERSON

| SAMPLING TIMES | TEMPERATURE | | NEMATODE POPULATION / g ROOT * | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | MIN | MAX | J2 | J3 | J4 | ♂ | Imm. ♀ | ♀ Without eggs | ♀ With eggs | TOTAL POPULATION |
| 22 Nov-2Jan | 15.96 | 18.88 | 30 | 24 | 42 | 8 | 0 | 26 | 2 | 132 |
| 6 Dec-16 Jan | 15.71 | 18.35 | 6 | 16 | 30 | 2 | 0 | 20 | 0 | 74 |
| 20 Dec-30 Jan | 14.71 | 17.53 | 2 | 22 | 70 | 0 | 0 | 10 | 0 | 104 |
| 10 Jan-21 Feb | 15.28 | 17.82 | 0 | 2 | 2 | 0 | 0 | 2 | 0 | 6 |
| 24 Jan-7 March | 16.02 | 19.23 | 0 | 2 | 0 | 0 | 0 | 6 | 0 | 8 |
| 7 Feb-21 March | 15.73 | 19.75 | 0 | 2 | 4 | 0 | 0 | 6 | 0 | 12 |
| 21 Feb-4 April | 16.73 | 22.01 | 0 | 2 | 2 | 0 | 0 | 26 | 0 | 30 |
| 7 Mar-18 April | 17.78 | 23.30 | 0 | 2 | 4 | 0 | 0 | 30 | 0 | 36 |
| 21 Mar-2 May | 20.11 | 25.19 | 0 | 2 | 0 | 4 | 0 | 12 | 0 | 18 |
| 4 Apr-16 May | 21.22 | 27.67 | 0 | 2 | 2 | 4 | 0 | 32 | 4 | 44 |
| 18 Apr-30 May | 21.48 | 28.13 | 0 | 2 | 8 | 0 | 0 | 18 | 0 | 28 |
| 2 May-13 June | 21.84 | 28.98 | 12 | 12 | 10 | 4 | 2 | 14 | 2 | 56 |
| 16 May-27 June | 22.28 | 28.66 | 0 | 8 | 22 | 6 | 2 | 24 | 6 | 68 |
| 30 May-11 July | 22.88 | 29.76 | 0 | 18 | 34 | 6 | 2 | 18 | 2 | 80 |
| 13 Jun-25 July | 23.07 | 30.42 | 8 | 16 | 20 | 8 | 2 | 22 | 4 | 80 |
| 27 Jun-8 Aug | 23.26 | 30.76 | 6 | 14 | 34 | 14 | 2 | 22 | 8 | 100 |
| 11 Jul-22 Aug | 23.19 | 30.16 | 22 | 14 | 14 | 20 | 0 | 32 | 8 | 110 |
| 25 Jul-5 Sept | 22.69 | 30.09 | 8 | 38 | 24 | 14 | 0 | 10 | 6 | 100 |
| 8 Aug-19 Sept | 21.57 | 29.64 | 4 | 14 | 46 | 36 | 0 | 14 | 8 | 122 |
| 22 Aug-3 Oct | 20.78 | 29.21 | 2 | 10 | 24 | 10 | 4 | 18 | 4 | 72 |

* Mean of two samples.

APPENDIX C.

TABLE 2. RELATIONSHIP OF SOIL TEMPERATURE AND N. ABERRANS POPULATION (BRITISH ISOLATE) ON TOMATO VARIETY JEFFERSON.

| SAMPLING TIMES | TEMPERATURE | | NEMATODE POPULATION / g ROOT * | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | MIN | MAX | J2 | J3 | J4 | ♂ | Imm. ♀ | ♀ Without eggs | ♀ With eggs | TOTAL POPULATION |
| 22 Nov-2Jan | 15.96 | 18.88 | 8 | 8 | 8 | 0 | 2 | 0 | 0 | 26 |
| 6 Dec-16 Jan | 15.71 | 18.35 | 2 | 6 | 6 | 0 | 0 | 0 | 0 | 14 |
| 20 Dec-30 Jan | 14.71 | 17.53 | 0 | 6 | 6 | 0 | 0 | 0 | 0 | 12 |
| 10 Jan-21 Feb | 15.28 | 17.82 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| 24 Jan-7 March | 16.02 | 19.23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 7 Feb-21 March | 15.73 | 19.75 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 4 |
| 21 Feb-4 April | 16.73 | 22.01 | 4 | 8 | 6 | 0 | 0 | 8 | 0 | 26 |
| 7 Mar-18 April | 17.78 | 23.30 | 0 | 2 | 2 | 12 | 0 | 8 | 2 | 26 |
| 21 Mar-2 May | 20.11 | 25.19 | 2 | 0 | 2 | 26 | 0 | 44 | 12 | 86 |
| 4 Apr-16 May | 21.22 | 27.67 | 0 | 14 | 10 | 26 | 2 | 22 | 16 | 90 |
| 18 Apr-30 May | 21.48 | 28.13 | 0 | 16 | 22 | 8 | 0 | 14 | 4 | 64 |
| 2 May-13 June | 21.84 | 28.98 | 52 | 26 | 8 | 16 | 0 | 16 | 6 | 124 |
| 16 May-27 June | 22.28 | 28.66 | 0 | 8 | 20 | 32 | 4 | 40 | 20 | 124 |
| 30 May-11 July | 22.88 | 29.76 | 0 | 4 | 4 | 18 | 2 | 62 | 6 | 96 |
| 13 Jun-25 July | 23.07 | 30.42 | 62 | 44 | 26 | 24 | 0 | 62 | 12 | 230 |
| 27 Jun-8 Aug | 23.26 | 30.76 | 18 | 56 | 60 | 18 | 4 | 54 | 10 | 220 |
| 11 Jul-22 Aug | 23.19 | 30.16 | 4 | 20 | 28 | 26 | 0 | 22 | 10 | 110 |
| 25 Jul-5 Sept | 22.69 | 30.09 | 38 | 40 | 22 | 38 | 4 | 76 | 22 | 240 |
| 8 Aug-19 Sept | 21.57 | 29.64 | 14 | 18 | 52 | 54 | 2 | 40 | 18 | 198 |
| 22 Aug-3 Oct | 20.78 | 29.21 | 18 | 24 | 26 | 28 | 2 | 28 | 18 | 144 |

* Mean of two samples.

APPENDIX C.

TABLE 3. RELATIONSHIP OF SOIL TEMPERATURE AND N. ABERRANS POPULATION (ECUADORIAN ISOLATE) ON TOMATO VARIETY MONEYMAKER.

| SAMPLING TIMES | TEMPERATURE | | NEMATODE POPULATION / g ROOT * | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | MIN | MAX | J2 | J3 | J4 | ♂ | Imm. ♀ | ♀ Without eggs | ♀ With eggs | TOTAL POPULATION |
| 22 Nov-2Jan | 15.96 | 18.88 | 8 | 38 | 48 | 4 | 0 | 20 | 0 | 118 |
| 6 Dec-16 Jan | 15.71 | 18.35 | 0 | 8 | 22 | 0 | 2 | 14 | 0 | 46 |
| 20 Dec-30 Jan | 14.71 | 17.53 | 0 | 10 | 58 | 0 | 0 | 12 | 0 | 80 |
| 10 Jan-21 Feb | 15.28 | 17.82 | 2 | 6 | 4 | 0 | 2 | 4 | 0 | 18 |
| 24 Jan-7 March | 16.02 | 19.23 | 0 | 0 | 2 | 0 | 0 | 14 | 0 | 16 |
| 7 Feb-21 March | 15.73 | 19.75 | 0 | 4 | 2 | 0 | 0 | 10 | 0 | 16 |
| 21 Feb-4 April | 16.73 | 22.01 | 2 | 2 | 4 | 2 | 0 | 18 | 0 | 28 |
| 7 Mar-18 April | 17.78 | 23.30 | 0 | 0 | 2 | 16 | 0 | 20 | 2 | 40 |
| 21 Mar-2 May | 20.11 | 25.19 | 0 | 0 | 2 | 10 | 0 | 16 | 4 | 32 |
| 4 Apr-16 May | 21.22 | 27.67 | 0 | 0 | 2 | 6 | 0 | 16 | 2 | 26 |
| 18 Apr-30 May | 21.48 | 28.13 | 0 | 0 | 4 | 0 | 0 | 14 | 0 | 18 |
| 2 May-13 June | 21.84 | 28.98 | 2 | 12 | 20 | 2 | 0 | 4 | 2 | 42 |
| 16 May-27 June | 22.28 | 28.66 | 2 | 10 | 26 | 20 | 4 | 36 | 12 | 110 |
| 30 May-11 July | 22.88 | 29.76 | 8 | 4 | 4 | 10 | 0 | 10 | 6 | 42 |
| 13 Jun-25 July | 23.07 | 30.42 | 18 | 10 | 8 | 10 | 0 | 18 | 8 | 72 |
| 27 Jun-8 Aug | 23.26 | 30.76 | 6 | 6 | 22 | 8 | 0 | 18 | 6 | 66 |
| 11 Jul-22 Aug | 23.19 | 30.16 | 2 | 12 | 12 | 8 | 0 | 8 | 4 | 46 |
| 25 Jul-5 Sept | 22.69 | 30.09 | 4 | 12 | 42 | 12 | 2 | 14 | 4 | 90 |
| 8 Aug-19 Sept | 21.57 | 29.64 | 6 | 22 | 42 | 20 | 2 | 20 | 6 | 118 |
| 22 Aug-3 Oct | 20.78 | 29.21 | 6 | 10 | 20 | 10 | 0 | 20 | 6 | 72 |

* Mean of two samples.

APPENDIX C.

TABLE 4. RELATIONSHIP OF SOIL TEMPERATURE AND N. ABERRANS POPULATION (BRITISH ISOLATE) ON TOMATO VARIETY MONEYMAKER.

| SAMPLING TIMES | TEMPERATURE | | NEMATODE POPULATION / g ROOT * | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | MIN | MAX | J2 | J3 | J4 | ♂ | Imm. ♀ | ♀ Without eggs | ♀ With eggs | TOTAL POPULATION |
| 22 Nov–2Jan | 15.96 | 18.88 | 8 | 16 | 22 | 0 | 0 | 10 | 0 | 46 |
| 6 Dec–16 Jan | 15.71 | 18.35 | 2 | 2 | 6 | 0 | 0 | 0 | 0 | 10 |
| 20 Dec–30 Jan | 14.71 | 17.53 | 0 | 6 | 6 | 0 | 0 | 0 | 0 | 12 |
| 10 Jan–21 Feb | 15.28 | 17.82 | 0 | 4 | 4 | 0 | 0 | 0 | 0 | 8 |
| 24 Jan–7 March | 16.02 | 19.23 | 0 | 4 | 6 | 0 | 0 | 0 | 0 | 10 |
| 7 Feb–21 March | 15.73 | 19.75 | 0 | 2 | 6 | 0 | 0 | 0 | 0 | 8 |
| 21 Feb–4 April | 16.73 | 22.01 | 0 | 4 | 4 | 0 | 0 | 8 | 0 | 16 |
| 7 Mar–18 April | 17.78 | 23.30 | 0 | 0 | 4 | 12 | 0 | 18 | 8 | 42 |
| 21 Mar–2 May | 20.11 | 25.19 | 0 | 0 | 0 | 14 | 0 | 30 | 12 | 56 |
| 4 Apr–16 May | 21.22 | 27.67 | 0 | 64 | 30 | 6 | 2 | 12 | 8 | 112 |
| 18 Apr–30 May | 21.48 | 28.13 | 2 | 4 | 8 | 12 | 0 | 22 | 12 | 60 |
| 2 May–13 June | 21.84 | 28.98 | 2 | 52 | 84 | 34 | 4 | 120 | 8 | 304 |
| 16 May–27 June | 22.28 | 28.66 | 0 | 2 | 4 | 14 | 4 | 26 | 6 | 56 |
| 30 May–11 July | 22.88 | 29.76 | 4 | 6 | 6 | 20 | 4 | 56 | 10 | 106 |
| 13 Jun–25 July | 23.07 | 30.42 | 108 | 104 | 66 | 32 | 2 | 64 | 16 | 392 |
| 27 Jun–8 Aug | 23.26 | 30.76 | 10 | 10 | 22 | 4 | 0 | 14 | 6 | 66 |
| 11 Jul–22 Aug | 23.19 | 30.16 | 6 | 14 | 16 | 18 | 2 | 34 | 10 | 100 |
| 25 Jul–5 Sept | 22.69 | 30.09 | 16 | 60 | 70 | 54 | 2 | 132 | 26 | 360 |
| 8 Aug–19 Sept | 21.57 | 29.64 | 24 | 18 | 24 | 30 | 0 | 40 | 14 | 150 |
| 22 Aug–3 Oct | 20.78 | 29.21 | 20 | 30 | 32 | 24 | 4 | 28 | 16 | 154 |

* Mean of two samples.

APPENDIX D.

TABLE 1. MEANS OF PLANT HEIGHT (IN CMS) AT DIFFERENT SAMPLING TIMES IN THE FIRST CROP.

| NEMATODE TREATMENTS \ SAMPLING TIMES AFTER PLANTING | | 20 | 30 | 45 | 60 | 104 (HARVEST) |
|---|---|---|---|---|---|---|
| NO NEMATODES | 1 | 14.5 | 39.0 | 76.0 | 130.0 | 160.0 |
| | 2 | 17.0 | 42.5 | 82.0 | 135.0 | 176.0 |
| | 3 | 18.0 | 45.0 | 78.0 | 125.0 | 212.0 |
| MEAN | | 16.5 | 42.1 | 78.6 | 130 | 182.6 |
| 100L2 | 1 | 16.5 | 44.0 | 90.0 | 133.0 | 158.0 |
| | 2 | 14.0 | 36.0 | 72.0 | 112.0 | 137.0 |
| | 3 | 13.5 | 36.5 | 67.0 | 118.0 | 171.0 |
| MEAN | | 14.6 | 38.8 | 76.3 | 121 | 155.3 |
| 1000L2 | 1 | 12.5 | 36.0 | 70.0 | 115.0 | 215.0 |
| | 2 | 16.5 | 43.0 | 80.0 | 138.0 | 217.0 |
| | 3 | 14.0 | 41.0 | 74.0 | 121.0 | 138.0 |
| MEAN | | 14.3 | 40.0 | 74.6 | 124.6 | 190 |
| 5000L2 | 1 | 14.5 | 39.5 | 77.0 | 130.0 | 208.0 |
| | 2 | 15.0 | 40.0 | 83.0 | 135.0 | 201.0 |
| | 3 | 14.5 | 37.0 | 74.0 | 117.0 | 128.0 |
| MEAN | | 14.6 | 38.8 | 78. | 127.3 | 179. |

APPENDIX D

TABLE 2. MEANS OF PLANT HEIGHT (IN CMS) AT DIFFERENT SAMPLING TIMES IN THE SECOND CROP.

| NEMATODE TREATMENTS \ SAMPLING TIMES AFTER PLANTING | | 20 | 30 | 45 | 60 | 110 (HARVEST) |
|---|---|---|---|---|---|---|
| NO NEMATODES | 1 | 12 | 20 | 42 | 62 | 150 |
| | 2 | 11 | 19 | 40 | 66 | 153 |
| | 3 | 9 | 17 | 38 | 66 | 152 |
| MEAN | | 10.7 | 18.7 | 40.0 | 64.7 | 151.7 |
| LOW | 1 | 9 | 16.5 | 41 | 63 | 160 |
| | 2 | 11 | 19 | 44 | 65 | 146 |
| | 3 | 8 | 15 | 35 | 60 | 128 |
| MEAN | | 9.3 | 16.8 | 40.0 | 62.7 | 144.7 |
| MEDIUM | 1 | 7 | 13.5 | 33 | 61 | 152 |
| | 2 | 9 | 17 | 37 | 57 | 140 |
| | 3 | 8 | 15 | 37 | 62 | 131 |
| MEAN | | 8.0 | 15.1 | 35.7 | 60.0 | 141.0 |
| HIGH | 1 | 7 | 12.5 | 33 | 56 | 152 |
| | 2 | 8 | 12 | 32 | 55 | 140 |
| | 3 | 9 | 15 | 35 | 51 | 131 |
| MEAN | | 8.0 | 13.1 | 33.3 | 54.0 | 141.0 |

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TABLE 3. MEANS OF PLANT HEIGHT (IN CMS) AT DIFFERENT SAMPLING TIMES IN THE FINAL CROP

| NEMATODE TREATMENTS \ SAMPLING TIMES AFTER PLANTING | | 20 | 30 | 45 | 60 | 67 (HARVEST) |
|---|---|---|---|---|---|---|
| NO NEMATODES | 1 | 24 | 45 | 79 | 92 | 93 |
| | 2 | 28 | 47 | 69 | 72 | 72 |
| | 3 | 21 | 40 | 77 | 103 | 104 |
| MEAN | | 24.33 | 44.00 | 75.00 | 89.00 | 89.66 |
| LOW | 1 | 20 | 41 | 71 | 84 | 86 |
| | 2 | 22 | 43 | 72 | 94 | 100 |
| | 3 | 21 | 40 | 69 | 76 | 77 |
| MEAN | | 21.00 | 41.33 | 70.66 | 84.66 | 87.66 |
| MEDIUM | 1 | 20 | 41 | 69 | 85 | 87 |
| | 2 | 20 | 40 | 60 | 68 | 69 |
| | 3 | 18 | 33 | 61 | 85 | 86 |
| MEAN | | 19.33 | 38.00 | 63.33 | 79.33 | 80.66 |
| HIGH | 1 | 22 | 43 | 57 | 62 | 64 |
| | 2 | 19 | 35 | 62 | 65 | 65 |
| | 3 | 16 | 30 | 56 | 60 | 61 |
| MEAN | | 19.00 | 36.00 | 58.33 | 62.33 | 63.33 |

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TABLE 4. EFFECTS OF N. ABERRANS ON GROWTH OF TOMATOES AT DIFFERENT POPULATION LEVELS IN THE FIRST CROP.

| NEMATODE TREATMENTS. | | DAYS TO FLOWERING | NUMBER OF INFLORESCENCE | DAYS TO FRUITING | NUMBER OF FRUITS | WEIGHT OF FRUITS | FRESH SHOOT WEIGHT |
|---|---|---|---|---|---|---|---|
| NO NEMATODES | 1 | 30 | 9 | 44 | 8 | 378 | 222 |
| | 2 | 28 | 7 | 51 | 5 | 199 | 248 |
| | 3 | 25 | 9 | 37 | 5 | 229 | 232 |
| MEAN | | 27.6 | 8.33 | 44 | 6 | 265.3 | 234 |
| 100L2 | 1 | 28 | 8 | 44 | 6 | 244 | 153 |
| | 2 | 30 | 7 | 44 | 9 | 335 | 204 |
| | 3 | 34 | 9 | 48 | 5 | 164 | 244 |
| MEAN | | 30.6 | 8.00 | 45.3 | 6.6 | 241.6 | 200.3 |
| 1,000L2 | 1 | 37 | 10 | 63 | 5 | 125 | 227 |
| | 2 | 28 | 8 | 51 | 5 | 104 | 304 |
| | 3 | 30 | 7 | 58 | 6 | 225 | 221 |
| MEAN | | 31.6 | 8.33 | 57.3 | 5.3 | 151.3 | 250.6 |
| 5,000L2 | 1 | 30 | 9 | 51 | 4 | 157 | 271 |
| | 2 | 30 | 7 | 51 | 5 | 178 | 206 |
| | 3 | 30 | 7 | 50 | 5 | 203 | 212 |
| MEAN | | 30 | 7.66 | 50.6 | 4.6 | 179.3 | 229.6 |

TABLE 5. EFFECTS OF N. ABERRANS ON GROWTH OF TOMATOES AT DIFFERENT POPULATION LEVELS IN THE SECOND CROP.

| NEMATODE TREATMENTS | | DAYS TO FLOWERING | NUMBER OF INFLORESCENCE | DAYS TO FRUITING | NUMBER OF FRUITS | WEIGHT OF FRUITS | FRESH SHOOT WEIGHT |
|---|---|---|---|---|---|---|---|
| NO NEMATODES. | 1. | 42 | 7 | 48 | 10 | 364.86 | 469 |
| | 2 | 55 | 5 | 60 | 6 | 313.31 | 502 |
| | 3 | 55 | 7 | 67 | 10 | 215.20 | 472 |
| MEAN | | 50.66 | 6.33 | 58.33 | 8.66 | 297.79 | 481.0 |
| LOW | 1 | 56 | 6 | 62 | 4 | 149.07 | 349 |
| | 2 | 43 | 5 | 56 | 9 | 199.60 | 429 |
| | 3 | 57 | 5 | 63 | 12 | 387.26 | 449 |
| MEAN | | 52.00 | 5.33 | 60.33 | 8.33 | 245.31 | 409 |
| MEDIUM | 1 | 58 | 5 | 76 | 6 | 240.03 | 486 |
| | 2 | 54 | 8 | 74 | 5 | 117.78 | 245 |
| | 3 | 57 | 7 | 76 | 11 | 278.65 | 237 |
| MEAN | | 56.33 | 6.66 | 75.33 | 7.66 | 212.15 | 322.6 |
| HIGH | 1 | 56 | 6 | 66 | 7 | 239.41 | 458 |
| | 2 | 55 | 6 | 77 | 10 | 218.93 | 245 |
| | 3 | 58 | 5 | 76 | 3 | 107.11 | 237 |
| MEAN | | 56.33 | 5.66 | 73.00 | 6.66 | 188.48 | 313.3 |

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TABLE 6. EFFECTS OF N. ABERRANS ON GROWTH OF TOMATOES AT DIFFERENT POPULATION LEVELS IN THE FINAL CROP.

| NEMATODE TREATMENTS | | DAYS TO FLOWERING | NUMBER OF INFLORESCENCE | DAYS TO FRUITING | NUMBER OF FRUITS | WEIGHT OF FRUITS | FRESH SHOOT WEIGHT | DRY SHOOT WEIGHT |
|---|---|---|---|---|---|---|---|---|
| NO NEMATODES | 1 | 28 | 9 | 38 | 9 | 141.42 | 227.08 | 35.14 |
| | 2 | 24 | 7 | 30 | 6 | 253.28 | 145.41 | 21.70 |
| | 3 | 30 | 7 | 36 | 7 | 137.06 | 216.29 | 40.12 |
| MEAN | | 27.33 | 7.66 | 34.66 | 7.33 | 177.25 | 196.26 | 32.32 |
| LOW | 1 | 31 | 7 | 42 | 6 | 169.15 | 186.18 | 27.69 |
| | 2 | 30 | 7 | 42 | 7 | 148.31 | 191.25 | 29.94 |
| | 3 | 30 | 6 | 44 | 5 | 71.22 | 141.11 | 20.84 |
| MEAN | | 30.33 | 6.66 | 42.66 | 6.00 | 129.56 | 172.84 | 26.15 |
| MEDIUM | 1 | 31 | 7 | 40 | 4 | 79.18 | 111.32 | 14.22 |
| | 2 | 27 | 5 | 33 | 5 | 145.19 | 117.14 | 12.25 |
| | 3 | 32 | 6 | 45 | 4 | 60.29 | 191.26 | 29.76 |
| MEAN | | 30.00 | 6.00 | 39.33 | 4.33 | 94.88 | 139.90 | 18.74 |
| HIGH | 1 | 29 | 4 | 52 | 2 | 17.75 | 105.62 | 13.23 |
| | 2 | 31 | 4 | 49 | 4 | 63.06 | 131.30 | 16.64 |
| | 3 | 31 | 5 | 51 | 4 | 69.31 | 105.18 | 12.36 |
| MEAN | | 30.33 | 4.33 | 50.66 | 3.33 | 50.04 | 114.03 | 14.24 |

TABLE 7. EFFECT OF *N. ABERRANS* ON ROOT GROWTH IN THE FINAL CROP.

| NEMATODE TREATMENTS | | FRESH TOTAL ROOT WEIGHT | LENGTH OF ROOTS | NO. SECON. LATERAL ROOTS/ROOT SYSTEM | TOTAL NO. GALLS /ROOT SYSTEM | NO. SECON. LATERAL ROOTS/GALL | NO. ♀ S./ GALL |
|---|---|---|---|---|---|---|---|
| | 1 | 31.36 | 39 | 1881 | 0 | 0 | 0 |
| NO NEMATODES | 2 | 22.32 | 45 | 1527 | 0 | 0 | 0 |
| | 3 | 26.00 | 37 | 2127 | 0 | 0 | 0 |
| MEAN | | 26.56 | 40.33 | 1845.00 | 0 | 0 | 0 |
| | 1 | 24.30 | 22 | 1125 | 405 | 2.77 | 1.33 |
| LOW | 2 | 26.11 | 28 | 1856 | 316 | 5.87 | 1.12 |
| | 3 | 38.41 | 27 | 2190 | 461 | 4.75 | 3.25 |
| MEAN | | 29.60 | 25.66 | 1723.66 | 394 | 4.46 | 1.90 |
| | 1 | 38.87 | 38 | 2525 | 680 | 3.71 | 1.64 |
| MEDIUM | 2 | 33.86 | 25 | 1736 | 868 | 2.80 | 1.50 |
| | 3 | 49.39 | 30 | 3752 | 813 | 4.61 | 2.15 |
| MEAN | | 40.70 | 31.00 | 2671.00 | 787 | 3.70 | 1.76 |
| | 1 | 32.80 | 29 | 3052 | 496 | 6.15 | 2.30 |
| HIGH | 2 | 52.45 | 28 | 4356 | 886 | 4.92 | 2.16 |
| | 3 | 33.56 | 29 | 7273 | 1119 | 6.50 | 1.90 |
| MEAN | | 39.60 | 28.66 | 4893.66 | 833.66 | 5.85 | 2.12 |

TABLE 8. DIFFERENT DEVELOPMENTAL STAGES OF N. ABERRANS RECOVERED FROM ROOTS IN THE FIRST CROP.

| NEMATODE TREATMENTS | | NO. NEMATODES / g ROOTS | | | | | | | TOTAL POPULATION |
|---|---|---|---|---|---|---|---|---|---|
| | | ♀ EGGS | ♀ | ♀ (imm) | ♂ | JUVENILES 2 | JUVENILES 3 | JUVENILES 4 | |
| NO NEMATODES | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| MEAN | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 100 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 5 | 7 |
| | 2 | 0 | 6 | 2 | 0 | 0 | 3 | 7 | 18 |
| | 3 | 4 | 7 | 1 | 8 | 0 | 18 | 14 | 52 |
| MEAN | | 1.33 | 4.33 | 1.0 | 2.66 | 0 | 7.66 | 8.66 | 25.67 |
| 1,000 | 1 | 3 | 9 | 0 | 7 | 2 | 5 | 9 | 35 |
| | 2 | 2 | 10 | 0 | 5 | 1 | 7 | 12 | 37 |
| | 3 | 5 | 11 | 1 | 7 | 0 | 12 | 16 | 52 |
| MEAN | | 3.33 | 3.00 | .33 | 6.33 | 1.0 | 8.00 | 12.33 | 41.23 |
| 5,000 | 1 | 4 | 16 | 2 | 10 | 0 | 4 | 11 | 47 |
| | 2 | 5 | 25 | 4 | 15 | 5 | 28 | 109 | 191 |
| | 3 | 6 | 15 | 1 | 14 | 7 | 35 | 181 | 259 |
| MEAN | | 5.00 | 18.66 | 2.33 | 13.00 | 4.0 | 22.33 | 100.33 | 165.67 |

TABLE 9. DIFFERENT DEVELOPMENTAL STAGES OF N. ABERRANS RECOVERED FROM ROOTS IN THE SECOND CROP.

| NEMATODE TREATMENTS | | NO. NEMATODES / g ROOTS | | | | | | | TOTAL POPULATION |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | JUVENILES | | | |
| | | ♀ EGGS | ♀ | ♀ (imm) | ♂ | 2 | 3 | 4 | |
| | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NO NEMATODES | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| MEAN | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 1 | 0 | 3 | 0 | 0 | 0 | 2 | 4 | 9 |
| LOW | 2 | 3 | 5 | 0 | 13 | 0 | 2 | 11 | 34 |
| | 3 | 5 | 18 | 2 | 7 | 0 | 14 | 27 | 73 |
| MEAN | | 2.66 | 8.66 | .66 | 6.66 | 0 | 6.00 | 14.00 | 38.67 |
| | 1 | 2 | 9 | 0 | 0 | 0 | 4 | 6 | 21 |
| MEDIUM | 2 | 3 | 7 | 1 | 6 | 0 | 1 | 2 | 20 |
| | 3 | 22 | 35 | 4 | 27 | 0 | 57 | 151 | 296 |
| MEAN | | 9.00 | 17.00 | 1.66 | 11.00 | 0 | 20.66 | 53.00 | 112.33 |
| | 1 | 22 | 65 | 6 | 50 | 10 | 72 | 162 | 387 |
| HIGH | 2 | 7 | 37 | 2 | 13 | 0 | 20 | 41 | 120 |
| | 3 | 16 | 21 | 2 | 23 | 0 | 11 | 32 | 105 |
| MEAN | | 15.00 | 41.00 | 3.33 | 28.66 | 3.33 | 34.33 | 78.3 | 204.00 |

TABLE 10. DIFFERENT DEVELOPMENTAL STAGES OF N. ABERRANS RECOVERED FROM ROOTS IN THE FINAL CROP.

| NEMATODE TREATMENTS | | NO. NEMATODES / g ROOTS | | | | | | | TOTAL POPULATION |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | JUVENILES | | | |
| | | ♀ EGGS | ♀ | ♀ (imm) | ♂ | 2 | 3 | 4 | |
| NO NEMATODES | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| MEAN | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LOW | 1 | 7 | 31 | 0 | 8 | 4 | 7 | 10 | 67 |
| | 2 | 3 | 12 | 3 | 5 | 1 | 10 | 8 | 42 |
| | 3 | 8 | 64 | 1 | 28 | 41 | 72 | 67 | 281 |
| MEAN | | 6.00 | 35.66 | 1.33 | 13.66 | 15.33 | 29.66 | 28.33 | 130.00 |
| MEDIUM | 1 | 18 | 102 | 25 | 54 | 79 | 217 | 212 | 707 |
| | 2 | 27 | 81 | 10 | 37 | 47 | 62 | 71 | 335 |
| | 3 | 14 | 55 | 4 | 34 | 37 | 46 | 63 | 253 |
| MEAN | | 19.66 | 79.33 | 13.00 | 41.66 | 54.33 | 108.33 | 115.33 | 431.66 |
| HIGH | 1 | 20 | 97 | 14 | 43 | 75 | 139 | 193 | 581 |
| | 2 | 14 | 70 | 9 | 29 | 88 | 102 | 138 | 450 |
| | 3 | 15 | 68 | 8 | 39 | 46 | 43 | 108 | 327 |
| MEAN | | 16.33 | 78.33 | 10.33 | 37.00 | 69.66 | 94.66 | 146.33 | 452.66 |

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TABLE 11. SOIL POPULATION OF N. ABERRANS FROM THE FIRST CROP.

| NEMATODE TREATMENTS | | POPULATION / 100 $CM^3$ | | | | | POPULATION/ L. OF SOIL |
|---|---|---|---|---|---|---|---|
| | | ♀ | ♂ | JUVENILES 2 | 3 | 4 | |
| NO NEMATODES | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| MEAN | | 0 | 0 | 0 | 0 | 0 | 0 |
| 100L2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2 | 0 | 0 | 20 | 0 | 0 | 200 |
| | 3 | 0 | 0 | 120 | 0 | 0 | 1200 |
| MEAN | | 0 | 0 | 46.66 | 0 | 0 | 466.66 |
| 1,000L2 | 1 | 0 | 0 | 60 | 0 | 0 | 600 |
| | 2 | 0 | 0 | 100 | 0 | 0 | 1000 |
| | 3 | 0 | 0 | 160 | 0 | 0 | 1600 |
| MEAN | | 0 | 0 | 73.33 | 0 | 0 | 1066.66 |
| 5,000L2 | 1 | 0 | 0 | 140 | 20 | 0 | 1600 |
| | 2 | 0 | 0 | 220 | 0 | 0 | 2200 |
| | 3 | 0 | 0 | 220 | 0 | 0 | 2200 |
| MEAN | | 0 | 0 | 193.33 | 6.66 | 0 | 2000 |

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TABLE 12. SOIL POPULATION OF N. ABERRANS FROM THE SECOND CROP.

| NEMATODE TREATMENTS | | POPULATION / 100 $CM^3$ | | | | | POPULATION / L OF SOIL |
|---|---|---|---|---|---|---|---|
| | | ♀ (imm) | ♂ | JUVENILES 2 | 3 | 4 | |
| NO NEMATODES | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| MEAN | | 0 | 0 | 0 | 0 | 0 | 0 |
| LOW | 1 | 0 | 0 | 20 | 0 | 20 | 400 |
| | 2 | 0 | 0 | 20 | 0 | 0 | 200 |
| | 3 | 0 | 0 | 280 | 0 | 0 | 2800 |
| MEAN | | 0 | 0 | 106.66 | 0 | 6.66 | 1133.31 |
| MEDIUM | 1 | 0 | 0 | 80 | 0 | 0 | 800 |
| | 2 | 0 | 0 | 20 | 0 | 20 | 400 |
| | 3 | 0 | 20 | 380 | 40 | 20 | 4600 |
| MEAN | | 0 | 6.66 | 160.00 | 13.33 | 13.33 | 1933.33 |
| HIGH | 1 | 20 | 20 | 320 | 0 | 20 | 3800 |
| | 2 | 0 | 0 | 120 | 0 | 0 | 1200 |
| | 3 | 20 | 0 | 100 | 20 | 20 | 1600 |
| MEAN | | 13.33 | 6.66 | 180.00 | 6.66 | 13.33 | 2200 |

APPENDIX D.

TABLE 13. SOIL POPULATION OF N. ABERRANS FROM THE FINAL CROP.

| NEMATODE TREATMENTS | | NO. NEMATODES / 100 $CM^3$ | | | | | POPULATION/ L. OF SOIL |
|---|---|---|---|---|---|---|---|
| | | | | JUVENILES | | | |
| | | ♀ (imm) | ♂ | 2 | 3 | 4 | |
| NO NEMATODES | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| MEAN | | 0 | 0 | 0 | 0 | 0 | 0 |
| LOW | 1 | 0 | 0 | 100 | 0 | 0 | 1000 |
| | 2 | 20 | 0 | 60 | 0 | 0 | 800 |
| | 3 | 0 | 100 | 220 | 20 | 40 | 3800 |
| MEAN | | 6.66 | 33.33 | 126.66 | 6.66 | 13.33 | 1866.66 |
| MEDIUM | 1 | 0 | 80 | 600 | 20 | 40 | 7400 |
| | 2 | 0 | 40 | 240 | 0 | 20 | 3000 |
| | 3 | 20 | 20 | 100 | 20 | 20 | 1800 |
| MEAN | | 6.66 | 46.66 | 313.33 | 13.33 | 26.66 | 4066.66 |
| HIGH | 1 | 20 | 40 | 220 | 20 | 40 | 3400 |
| | 2 | 0 | 40 | 380 | 40 | 20 | 4800 |
| | 3 | 20 | 40 | 100 | 20 | 0 | 1800 |
| MEAN | | 13.33 | 40.00 | 233.33 | 26.66 | 20.00 | 3333.33 |

APPENDIX E.

TABLE 1. EFFECT OF N. ABERRANS AND M. INCOGNITA ON ROOT GROWTH.

| NEMATODE TREATMENTS | REPLICATES | ROOT LENGTH (CM) | ROOT WEIGHT (g) |
|---|---|---|---|
| | 1 | 30 | 12.29 |
| | 2 | 36 | 10.72 |
| NO NEMATODES | 3 | 25 | 8.75 |
| | 4 | 29 | 10.81 |
| | 5 | 27 | 18.29 |
| MEAN | | 29.4 | 12.17 |
| | 1 | 26 | 9.95 |
| | 2 | 27 | 11.61 |
| NACOBBUS ALONE | 3 | 26 | 21.23 |
| | 4 | 29 | 14.82 |
| | 5 | 24 | 19.04 |
| MEAN | | 26.4 | 15.33 |
| | 1 | 24 | 25.73 |
| | 2 | 26 | 43.10 |
| MELOIDOGYNE ALONE | 3 | 20 | 38.40 |
| | 4 | 28 | 56.60 |
| | 5 | 28 | 25.22 |
| MEAN | | 25.2 | 37.81 |
| | 1 | 20 | 31.29 |
| NACOBBUS | 2 | 22 | 39.75 |
| + INO.TOGETHER | 3 | 18 | 43.55 |
| MELOIDOGYNE | 4 | 16 | 58.41 |
| | 5 | 17 | 26.47 |
| MEAN | | 18.6 | 39.89 |
| | 1 | 26 | 36.85 |
| MELOIDOGYNE INO.FIRST | 2 | 27 | 34.98 |
| + | 3 | 23 | 38.82 |
| NACOBBUS | 4 | 26 | 57.88 |
| INO. 2 WEEKS LATER | 5 | 22 | 48.13 |
| MEAN | | 24.8 | 43.33 |

TABLE 2. DIFFERENT DEVELOPMENTAL STAGES OF N. ABERRANS AND M. INCOGNITA RECOVERED FROM ROOTS.

| NEMATODE TREATMENTS | REP. | NEMATODE POPULATION/g ROOT | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | JUVENILES | | ♂ | | ♀ Imm. | ♀ WITHOUT EGGS | | ♀ WITH EGGS | | TOTAL POPULATION | |
| | | Nacobbus | Meloidogyne | Nacobbus | Meloidogyne | Nacobbus | Nacobbus | Meloidogyne | Nacobbus | Meloidogyne | Nacobbus | Meloidogyne |
| | 1 | 133 | - | 12 | - | 2 | 32 | - | 9 | - | 188 | - |
| | 2 | 172 | - | 1 | - | 0 | 19 | - | 5 | - | 197 | - |
| NACOBBUS | 3 | 319 | - | 6 | - | 0 | 13 | - | 4 | - | 342 | - |
| ALONE | 4 | 154 | - | 6 | - | 3 | 24 | - | 8 | - | 195 | - |
| | 5 | 360 | - | 15 | - | 14 | 18 | - | 8 | - | 415 | - |
| MEAN | | 227.6 | - | 8.0 | - | 3.8 | 21.2 | - | 6.8 | - | 267.4 | - |
| | 1 | - | 464 | - | 1 | - | - | 150 | - | 20 | - | 645 |
| | 2 | - | 438 | - | 4 | - | - | 81 | - | 29 | - | 552 |
| MELOIDOGYNE | 3 | - | 530 | - | 6 | - | - | 66 | - | 39 | - | 641 |
| ALONE | 4 | - | 622 | - | 2 | - | - | 158 | - | 37 | - | 819 |
| | 5 | - | 519 | - | 3 | - | - | 126 | - | 75 | - | 723 |
| MEAN | | - | 514.6 | - | 3.2 | - | - | 116.2 | - | 40.0 | - | 676.0 |
| | 1 | 12 | 285 | 2 | 4 | 3 | 8 | 61 | 2 | 33 | 27 | 383 |
| NACOBBUS | 2 | 24 | 274 | 10 | 8 | 3 | 10 | 100 | 7 | 29 | 54 | 411 |
| + | 3 | 27 | 372 | 6 | 3 | 2 | 7 | 60 | 3 | 28 | 45 | 463 |
| MELOIDOGYNE | 4 | 18 | 314 | 5 | 1 | 5 | 8 | 133 | 3 | 31 | 39 | 479 |
| INO.TOGETHER | 5 | 20 | 433 | 3 | 7 | 4 | 7 | 103 | 2 | 59 | 36 | 602 |
| MEAN | | 20.2 | 335.6 | 5.2 | 4.6 | 3.4 | 8.0 | 91.4 | 3.4 | 36.0 | 40.2 | 468.0 |

TABLE 2. DIFFERENT DEVELOPMENTAL STAGES OF N. ABERRANS AND M. INCOGNITA RECOVERED FROM ROOTS (CONTINUED)

| NEMATODE TREATMENTS | REP. | NEMATODE POPULATION/g ROOT | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | JEVENILES | | ♂ | | ♀ Imm. | ♀ WITHOUT EGGS | | ♀ WITH EGGS | | TOTAL POPULATION | |
| | | Nacobbus | Meloidogyne | Nacobbus | Meloidogyne | Nacobbus | Nacobbus | Meloidogyne | Nacobbus | Meloidogyne | Nacobbus | Meloidogyne |
| | 1 | 1 | 487 | 0 | 6 | 0 | 1 | 134 | 0 | 13 | 2 | 640 |
| MELOIDOGYNE | 2 | 0 | 434 | 0 | 3 | 0 | 0 | 118 | 0 | 16 | 0 | 555 |
| + | 3 | 1 | 731 | 0 | 3 | 0 | 1 | 286 | 0 | 21 | 2 | 1041 |
| NACOBBUS | 4 | 2 | 717 | 0 | 5 | 0 | 2 | 165 | 0 | 68 | 4 | 895 |
| INO.FIRST INO.2 WEEKS | 5 | 4 | 577 | 0 | 7 | 0 | 3 | 242 | 0 | 35 | 7 | 861 |
| MEAN LATER | | 1.6 | 589.2 | 0.0 | 4.8 | 0.0 | 1.4 | 189.0 | 0.0 | 30.6 | 3.0 | 798.0 |

TABLE 3. POPULATION OF *N. ABERRANS* AND *M. INCOGNITA* RECOVERED FROM SOIL.

| NEMATODE TREATMENTS | REPLICATES | NEMATODE POPULATION/L. SOIL | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | JUVENILES | | ♂ | | ♀ IMM. | TOTAL POPULATION | |
| | | NACOBBUS | MELOIDOGYNE | NACOBBUS | MELOIDOGYNE | NACOBBUS | NACOBBUS | MELOIDOGYNE |
| NACOBBUS ALONE | 1 | 600 | - | 0 | - | 0 | 600 | - |
| | 2 | 800 | - | 0 | - | 0 | 800 | - |
| | 3 | 400 | - | 0 | - | 0 | 400 | - |
| | 4 | 600 | - | 0 | - | 0 | 600 | - |
| | 5 | 400 | - | 0 | - | 0 | 400 | - |
| MEAN | | 560 | - | 0 | - | 0 | 560 | - |
| MELOIDOGYNE ALONE | 1 | - | 14000 | - | 0 | - | - | 14000 |
| | 2 | - | 4200 | - | 200 | - | - | 4400 |
| | 3 | - | 7000 | - | 0 | - | - | 7000 |
| | 4 | - | 13600 | - | 200 | - | - | 13800 |
| | 5 | - | 16800 | - | 0 | - | - | 16800 |
| MEAN | | - | 11120 | - | 80 | - | - | 11200 |

TABLE 3. POPULATION OF N. ABERRANS AND M. INCOGNITA RECOVERED FROM SOIL (CONTINUED)

| NEMATODE TREATMENTS | REPLICATES | NEMATODE POPULATION/L. SOIL | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | JUVENILES | | ♂ | | ♀ IMM. | TOTAL POPULATION | |
| | | NACOBBUS | MELOIDOGYNE | NACOBBUS | MELOIDOGYNE | NACOBBUS | NACOBBUS | MELOIDOGYNE |
| | 1 | 400 | 14600 | 200 | 0 | 0 | 600 | 14600 |
| NACOBBUS | 2 | 200 | 10600 | 0 | 0 | 0 | 200 | 10600 |
| + | 3 | 200 | 16400 | 0 | 400 | 0 | 200 | 16800 |
| MELOIDOGYNE | 4 | 400 | 4600 | 200 | 400 | 0 | 600 | 5000 |
| INO.TOGETHER | 5 | 200 | 12400 | 0 | 0 | 0 | 200 | 12400 |
| MEAN | | 280 | 11720 | 80 | 160 | 0 | 360 | 11880 |
| | 1 | 0 | 2200 | 0 | 0 | 0 | 0 | 2200 |
| MELOIDOGYNE | 2 | 0 | 5000 | 0 | 0 | 0 | 0 | 5000 |
| INO. FIRST + | 3 | 0 | 4200 | 0 | 0 | 0 | 0 | 4200 |
| NACOBBUS | 4 | 0 | 2000 | 0 | 0 | 0 | 0 | 2000 |
| INO.2 WEEKS LATER | 5 | 0 | 9400 | 0 | 0 | 0 | 0 | 9400 |
| MEAN | | 0 | 4560 | 0 | 0 | 0 | 0 | 4560 |

APPENDIX F

TABLE 1. HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

D. ROOT GALLING OF M. INCOGNITA.

| TOMATO VARIETIES | REPLICATES | GALL INDEX |
|---|---|---|
| HARVESTER | 1 | 5 |
| | 2 | 5 |
| | 3 | 5 |
| JEFFERSON | 1 | 5 |
| | 2 | 6 |
| | 3 | 6 |
| MONEYMAKER | 1 | 6 |
| | 2 | 7 |
| | 3 | 6 |
| THE GAMBIA | 1 | 5 |
| | 2 | 5 |
| | 3 | 4 |
| BETTER BOY | 1 | 4 |
| | 2 | 3 |
| | 3 | 4 |
| BIG SEVEN | 1 | 5 |
| | 2 | 3 |
| | 3 | 3 |

| TOMATO VARIETIES | REPLICATES | GALL INDEX |
|---|---|---|
| BONUS | 1 | 3 |
| | 2 | 2 |
| | 3 | 3 |
| RED GLOW | 1 | 4 |
| | 2 | 4 |
| | 3 | 5 |
| ROMA VFN | 1 | 2 |
| | 2 | 2 |
| | 3 | 3 |
| ROSSOL | 1 | 1 |
| | 2 | 3 |
| | 3 | 2 |
| VFN 8 | 1 | 3 |
| | 2 | 1 |
| | 3 | 3 |
| VFN 662 | 1 | 3 |
| | 2 | 3 |
| | 3 | 3 |

APPENDIX F.

TABLE 1. HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

D. ROOT GALLING OF N. ABERRANS

| TOMATO VARIETIES | REPLICATES | NO. GALLS/ ROOT SYSTEM. |
|---|---|---|
| HARVESTER | 1 | 84 |
| | 2 | 71 |
| | 3 | 96 |
| JEFFERSON | 1 | 69 |
| | 2 | 86 |
| | 3 | 85 |
| MONEYMAKER | 1 | 73 |
| | 2 | 70 |
| | 3 | 80 |
| THE GAMBIA | 1 | 92 |
| | 2 | 118 |
| | 3 | 64 |
| BETTER BOY | 1 | 72 |
| | 2 | 130 |
| | 3 | 71 |
| BIG SEVEN | 1 | 173 |
| | 2 | 78 |
| | 3 | 132 |

| TOMATO VARIETIES | REPLICATES | NO. GALLS/ ROOT SYSTEM. |
|---|---|---|
| BONUS | 1 | 99 |
| | 2 | 25 |
| | 3 | 121 |
| RED GLOW | 1 | 143 |
| | 2 | 55 |
| | 3 | 85 |
| ROMA VFN | 1 | 46 |
| | 2 | 109 |
| | 3 | 64 |
| ROSSOLL | 1 | 34 |
| | 2 | 35 |
| | 3 | 65 |
| VFN 8 | 1 | 102 |
| | 2 | 59 |
| | 3 | 118 |
| VFN 662 | 1 | 120 |
| | 2 | 64 |
| | 3 | 145 |

TABLE 2. HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

A. HEIGHT OF PLANTS (IN CM) AT DIFFERENT SAMPLING TIMES.

| TOMATO VARIETIES | REPLICATES | SAMPLING TIMES AFTER PLANTING | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 20 DAYS | | | 45 DAYS | | | 80 DAYS (HARVEST) | | |
| | | NO NEMATODES | NACOBBUS | MELOIDOGYNE | NO NEMATODES | NACOBBUS | MELOIDOGYNE | NO NEMATODES | NACOBBUS | MELOIDOG |
| HARVESTER | 1 | 28 | 33 | 21 | 83 | 104 | 64 | 120 | 148 | 77 |
| | 2 | 27 | 26 | 29 | 74 | 112 | 106 | 94 | 138 | 140 |
| | 3 | 30 | 27 | 27 | 115 | 90 | 92 | 162 | 154 | 131 |
| JEFFERSON | 1 | 27 | 24 | 24 | 84 | 47 | 83 | 84 | 48 | 85 |
| | 2 | 28 | 19 | 21 | 93 | 74 | 83 | 110 | 81 | 83 |
| | 3 | 24 | 19 | 28 | 40 | 62 | 81 | 40 | 68 | 81 |
| MONEYMAKER | 1 | 20 | 21 | 22 | 67 | 74 | 76 | 72 | 75 | 87 |
| | 2 | 20 | 24 | 25 | 50 | 77 | 69 | 50 | 80 | 75 |
| | 3 | 20 | 23 | 17 | 76 | 70 | 79 | 83 | 73 | 90 |
| BETTER BOY | 1 | 22 | 25 | 27 | 54 | 77 | 90 | 54 | 79 | 91 |
| | 2 | 22 | 24 | 29 | 52 | 78 | 75 | 53 | 90 | 78 |
| | 3 | 27 | 31 | 26 | 83 | 91 | 75 | 96 | 94 | 76 |
| BIG SEVEN | 1 | 23 | 22 | 24 | 33 | 69 | 61 | 72 | 71 | 63 |
| | 2 | 23 | 20 | 20 | 67 | 76 | 58 | 69 | 82 | 60 |
| | 3 | 23 | 21 | 21 | 62 | 58 | 66 | 74 | 58 | 66 |
| BONUS | 1 | 29 | 28 | 26 | 72 | 54 | 51 | 72 | 54 | 53 |
| | 2 | 25 | 25 | 28 | 50 | 53 | 74 | 50 | 53 | 75 |
| | 3 | 22 | 24 | 28 | 69 | 53 | 68 | 74 | 54 | 68 |

TABLE 2. HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

A. HEIGHT OF PLANTS (IN CM) AT DIFFERENT SAMPLING TIMES. (CONTINUED)

| TOMATO VARIETIES | REPLICATES | SAMPLING TIMES AFTER PLANTING | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 20 DAYS | | | 45 DAYS | | | 80 DAYS (HARVEST) | | |
| | | NO NEMATODES | NACOBBUS | MELOIDOGYNE | NO NEMATODES | NACOBBUS | MELOIDOGYNE | NO NEMATODES | NACOBBUS | MELOIDOGYNE |
| RED GLOW | 1 | 23 | 22 | 27 | 78 | 53 | 76 | 78 | 53 | 76 |
| | 2 | 27 | 30 | 25 | 73 | 60 | 74 | 98 | 66 | 77 |
| | 3 | 27 | 20 | 24 | 60 | 45 | 61 | 60 | 48 | 61 |
| ROMA VFN | 1 | 22 | 24 | 21 | 48 | 64 | 67 | 49 | 65 | 68 |
| | 2 | 25 | 23 | 26 | 65 | 82 | 85 | 72 | 113 | 86 |
| | 3 | 22 | 20 | 23 | 39 | 62 | 57 | 39 | 62 | 58 |
| ROSSOL | 1 | 25 | 30 | 30 | 62 | 65 | 64 | 73 | 66 | 64 |
| | 2 | 27 | 26 | 26 | 55 | 95 | 76 | 60 | 108 | 86 |
| | 3 | 28 | 24 | 26 | 57 | 56 | 79 | 65 | 56 | 82 |
| VFN 8 | 1 | 22 | 25 | 23 | 39 | 70 | 52 | 40 | 70 | 54 |
| | 2 | 27 | 27 | 19 | 94 | 67 | 75 | 97 | 67 | 87 |
| | 3 | 23 | 22 | 24 | 57 | 66 | 50 | 57 | 66 | 51 |
| VFN 662 | 1 | 29 | 23 | 18 | 67 | 52 | 40 | 67 | 52 | 41 |
| | 2 | 22 | 23 | 24 | 48 | 65 | 70 | 50 | 66 | 72 |
| | 3 | 21 | 28 | 25 | 49 | 77 | 77 | 52 | 77 | 77 |

TABLE 3. HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

B. FLOWERING AND FRUITING TIMES, AND NUMBER OF FRUITS.

| TOMATO VARIETIES | REPLICATES | DAYS TO FLOWERING | | | DAYS TO FRUITING | | | NO. OF FRUITS | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | NO NEMATODES | NACOBBUS | MELOIDOGYNE | NO NEMATODES | NACOBBUS | MELOIDOGYNE | NO NEMATODES | NACOBBUS | MELOIDOGYNE |
| HARVESTER | 1 | 20 | 22 | 25 | 26 | 27 | 32 | 48 | 52 | 32 |
| | 2 | 19 | 23 | 20 | 26 | 28 | 27 | 70 | 39 | 31 |
| | 3 | 21 | 19 | 21 | 27 | 27 | 27 | 63 | 61 | 39 |
| JEFFERSON | 1 | 26 | 23 | 27 | 33 | 30 | 35 | 3 | 3 | 2 |
| | 2 | 25 | 29 | 27 | 31 | 37 | 52 | 6 | 3 | 3 |
| | 3 | 25 | 28 | 25 | 32 | 34 | 32 | 2 | 3 | 3 |
| MONEYMAKER | 1 | 24 | 27 | 23 | 37 | 31 | 29 | 5 | 3 | 2 |
| | 2 | 22 | 23 | 24 | 38 | 29 | 30 | 4 | 3 | 3 |
| | 3 | 26 | 25 | 31 | 35 | 32 | 33 | 5 | 4 | 5 |
| BETTER BOY | 1 | 25 | 25 | 26 | 30 | 32 | 37 | 2 | 2 | 1 |
| | 2 | 24 | 29 | 26 | 30 | 40 | 32 | 2 | 1 | 3 |
| | 3 | 26 | 26 | 25 | 33 | 33 | 33 | 4 | 2 | 2 |
| BIG SEVEN | 1 | 26 | 24 | 23 | 36 | 32 | 30 | 3 | 2 | 1 |
| | 2 | 26 | 28 | 27 | 41 | 38 | 35 | 3 | 4 | 2 |
| | 3 | 24 | 27 | 30 | 30 | 35 | 40 | 2 | 1 | 4 |
| BONUS | 1 | 25 | 25 | 25 | 31 | 32 | 31 | 2 | 2 | 2 |
| | 2 | 26 | 25 | 24 | 33 | 30 | 32 | 2 | 2 | 2 |
| | 3 | 26 | 25 | 26 | 33 | 30 | 32 | 3 | 2 | 2 |

TABLE 3. HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

B. FLOWERING AND FRUITING TIMES, AND NUMBER OF FRUITS (CONTINUED).

| TOMATO VARIETIES | REPLICATES | DAYS TO FLOWERING | | | DAYS TO FRUITING | | | NO. OF FRUITS | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | NO NEMATODES | NACOBBUS | MELOIDOGYNE | NO NEMATODES | NACOBBUS | MELOIDOGYNE | NO NEMATODES | NACOBBUS | MELOIDOGYNE |
| RED GLOW | 1 | 27 | 24 | 27 | 35 | 32 | 37 | 2 | 2 | 2 |
| | 2 | 24 | 24 | 27 | 30 | 29 | 41 | 2 | 2 | 3 |
| | 3 | 23 | 26 | 27 | 29 | 33 | 34 | 3 | 2 | 2 |
| ROMA VFN | 1 | 24 | 26 | 27 | 28 | 31 | 32 | 4 | 4 | 5 |
| | 2 | 26 | 27 | 27 | 32 | 32 | 32 | 3 | 4 | 4 |
| | 3 | 23 | 26 | 23 | 29 | 31 | 28 | 4 | 6 | 4 |
| ROSSOL | 1 | 24 | 22 | 24 | 30 | 27 | 29 | 5 | 5 | 5 |
| | 2 | 23 | 29 | 29 | 29 | 35 | 37 | 4 | 3 | 3 |
| | 3 | 22 | 24 | 25 | 27 | 28 | 30 | 4 | 4 | 4 |
| VFN 8 | 1 | 26 | 27 | 29 | 38 | 36 | 36 | 5 | 2 | 2 |
| | 2 | 29 | 27 | 35 | 36 | 32 | 52 | 1 | 2 | 5 |
| | 3 | 29 | 29 | 28 | 38 | 38 | 39 | 5 | 2 | 3 |
| VFN 662 | 1 | 24 | 26 | 30 | 32 | 32 | 38 | 2 | 2 | 1 |
| | 2 | 29 | 27 | 29 | 37 | 36 | 38 | 2 | 2 | 1 |
| | 3 | 27 | 29 | 29 | 37 | 35 | 40 | 2 | 1 | 1 |

TABLE 3. HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

B. WEIGHT OF FRUITS AND FRESH SHOOT WEIGHT.

| TOMATO VARIETIES | REPLICATES | FRUIT WEIGHT (g) | | | FRESH SHOOT WEIGHT (g) | | |
|---|---|---|---|---|---|---|---|
| | | NO NEMATODES | NACOBBUS | MELOIDOGYNE | NO NEMATODES | NACOBBUS | MELOIDOGYNE |
| HARVESTER | 1 | 60.09 | 67.42 | 34.03 | 65.53 | 84.35 | 80.40 |
| | 2 | 94.64 | 49.34 | 52.11 | 64.74 | 77.36 | 74.83 |
| | 3 | 75.78 | 87.54 | 54.19 | 90.08 | 68.09 | 52.03 |
| JEFFERSON | 1 | 145.15 | 69.96 | 85.46 | 88.57 | 36.25 | 80.60 |
| | 2 | 155.83 | 159.23 | 79.51 | 90.49 | 91.32 | 80.62 |
| | 3 | 92.81 | 144.51 | 128.48 | 48.15 | 61.87 | 86.28 |
| MONEYMAKER | 1 | 123.56 | 114.35 | 107.27 | 65.72 | 57.89 | 93.33 |
| | 2 | 158.72 | 120.87 | 91.62 | 57.84 | 69.60 | 58.00 |
| | 3 | 183.35 | 144.00 | 72.24 | 84.92 | 51.88 | 95.14 |
| BETTER BOY | 1 | 154.00 | 151.86 | 100.14 | 49.90 | 62.74 | 73.78 |
| | 2 | 242.19 | 113.40 | 175.28 | 82.76 | 95.71 | 80.00 |
| | 3 | 186.72 | 148.00 | 149.44 | 83.54 | 87.31 | 76.27 |
| BIG SEVEN | 1 | 95.53 | 164.73 | 100.23 | 81.69 | 75.88 | 54.53 |
| | 2 | 102.49 | 184.10 | 155.40 | 85.33 | 62.59 | 88.41 |
| | 3 | 184.09 | 117.80 | 128.48 | 69.34 | 64.25 | 74.14 |
| BONUS | 1 | 158.90 | 157.18 | 157.91 | 64.45 | 74.64 | 81.52 |
| | 2 | 120.03 | 176.97 | 140.66 | 82.85 | 55.95 | 85.02 |
| | 3 | 157.15 | 203.32 | 144.14 | 53.40 | 72.41 | 59.93 |
| RED GLOW | 1 | 172.69 | 195.97 | 109.19 | 86.43 | 78.47 | 87.85 |
| | 2 | 141.86 | 233.27 | 139.63 | 73.84 | 71.39 | 73.03 |
| | 3 | 77.62 | 218.34 | 101.55 | 56.72 | 75.16 | 65.00 |

TABLE 3. HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

B. WEIGHT OF FRUITS AND FRESH SHOOT WEIGHT (CONTINUED).

| TOMATO VARIETIES | REPLICATES | FRUIT WEIGHT (g) | | | FRESH SHOOT WEIGHT (g) | | |
|---|---|---|---|---|---|---|---|
| | | NO NEMATODES | NACOBBUS | MELOIDOGYNE | NO NEMATODES | NACOBBUS | MELOIDOGYNE |
| ROMA VFN | 1 | 99.48 | 160.04 | 135.30 | 45.15 | 75.46 | 62.37 |
| | 2 | 113.67 | 145.54 | 151.59 | 68.81 | 79.95 | 72.66 |
| | 3 | 114.45 | 181.37 | 127.92 | 44.15 | 58.49 | 52.17 |
| ROSSOL | 1 | 165.94 | 126.01 | 111.97 | 65.92 | 47.65 | 62.54 |
| | 2 | 149.01 | 140.44 | 111.02 | 58.21 | 76.18 | 70.85 |
| | 3 | 108.40 | 91.13 | 168.94 | 49.58 | 53.14 | 71.00 |
| VFN 8 | 1 | 164.00 | 157.83 | 108.25 | 48.99 | 78.65 | 62.53 |
| | 2 | 121.11 | 177.96 | 65.66 | 89.02 | 78.08 | 111.00 |
| | 3 | 141.96 | 165.27 | 127.22 | 82.83 | 84.00 | 45.50 |
| VFN 662 | 1 | 186.68 | 140.94 | 79.86 | 81.81 | 77.31 | 73.00 |
| | 2 | 88.00 | 122.70 | 143.44 | 62.26 | 77.12 | 94.57 |
| | 3 | 211.25 | 153.60 | 118.28 | 82.48 | 86.49 | 110.00 |

TABLE 4. HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

C. ROOT LENGTH AND FRESH ROOT WEIGHT.

| TOMATO VARIETIES | REPLICATES | ROOT LENGTH (CM) | | | ROOT WEIGHT (g) | | |
|---|---|---|---|---|---|---|---|
| | | NO NEMATODES | NACOBBUS | MELOIDOGYNE | NO NEMATODES | NACOBBUS | MELOIDOGYNE |
| HARVESTER | 1 | 53 | 45 | 47 | 34.12 | 50.23 | 102.49 |
| | 2 | 43 | 45 | 45 | 41.64 | 45.18 | 65.27 |
| | 3 | 37 | 53 | 42 | 47.13 | 52.42 | 84.00 |
| JEFFERSON | 1 | 31 | 29 | 33 | 12.43 | 17.42 | 34.03 |
| | 2 | 31 | 28 | 24 | 14.51 | 16.85 | 47.26 |
| | 3 | 30 | 33 | 23 | 16.21 | 19.39 | 43.34 |
| MONEYMAKER | 1 | 26 | 24 | 17 | 8.49 | 10.73 | 25.17 |
| | 2 | 31 | 26 | 20 | 5.78 | 9.02 | 35.03 |
| | 3 | 28 | 30 | 22 | 8.39 | 10.88 | 36.00 |
| BETTER BOY | 1 | 34 | 36 | 29 | 14.80 | 16.78 | 18.64 |
| | 2 | 37 | 31 | 28 | 20.07 | 18.46 | 16.31 |
| | 3 | 32 | 33 | 29 | 15.05 | 18.36 | 40.03 |
| BIG SEVEN | 1 | 26 | 28 | 24 | 11.43 | 15.94 | 25.37 |
| | 2 | 36 | 32 | 30 | 15.38 | 9.87 | 20.61 |
| | 3 | 38 | 37 | 36 | 16.54 | 27.80 | 19.72 |
| BONUS | 1 | 44 | 30 | 36 | 16.80 | 20.65 | 23.00 |
| | 2 | 26 | 34 | 29 | 26.94 | 17.86 | 14.86 |
| | 3 | 32 | 29 | 31 | 16.44 | 24.53 | 19.51 |

TABLE 4. HOST STATUS AND PATHOGENICITY OF N. ABERRANS AND M. INCOGNITA ON DIFFERENT TOMATO VARIETIES.

C. ROOT LENGTH AND FRESH ROOT WEIGHT. (CONTINUED)

| TOMATO VARIETIES | REPLICATES | ROOT LENGTH (CM) | | | ROOT WEIGHT (g) | | |
|---|---|---|---|---|---|---|---|
| | | NO NEMATODES | NACOBBUS | MELOIDOGYNE | NO NEMATODES | NACOBBUS | MELOIDOGYNE |
| RED GLOW | 1 | 29 | 25 | 30 | 13.43 | 24.83 | 14.22 |
| | 2 | 31 | 28 | 29 | 15.16 | 18.15 | 20.88 |
| | 3 | 31 | 34 | 24 | 10.65 | 23.49 | 50.74 |
| ROMA VFN | 1 | 31 | 55 | 56 | 23.19 | 39.16 | 24.00 |
| | 2 | 38 | 33 | 34 | 25.95 | 29.00 | 26.73 |
| | 3 | 41 | 39 | 34 | 25.46 | 20.15 | 29.97 |
| ROSSOL | 1 | 39 | 29 | 31 | 17.95 | 20.42 | 23.30 |
| | 2 | 34 | 48 | 37 | 21.29 | 20.92 | 45.00 |
| | 3 | 38 | 27 | 41 | 21.39 | 31.43 | 30.34 |
| VFN 8 | 1 | 32 | 33 | 36 | 11.07 | 21.76 | 27.82 |
| | 2 | 36 | 32 | 34 | 15.01 | 22.36 | 20.53 |
| VFN 662 | 3 | 30 | 35 | 24 | 14.86 | 28.86 | 14.10 |
| | 1 | 36 | 34 | 31 | 17.23 | 26.26 | 22.67 |
| | 2 | 35 | 31 | 28 | 17.80 | 15.36 | 29.90 |
| | 3 | 38 | 30 | 27 | 20.84 | 20.84 | 19.34 |

APPENDIX G.

TABLE 1. GALLING AND DIFFERENT DEVELOPMENTAL STAGES OF N. ABERRANS RECOVERED FROM ROOTS OF TWELVE CROPS AFTER 70 DAYS.

| CROPS | REPLICATES | NO. NEMATODES/g ROOT. | | | | | NO. GALLS/g ROOT |
|---|---|---|---|---|---|---|---|
| | | JUVENILES | ♂ | ♀ WITHOUT EGGS | ♀ WITH EGGS | TOTAL POPULATION | |
| CORN | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 1 | 0 | 0 | 0 | 1 | 0 |
| | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| MEAN | | 0.25 | 0 | 0 | 0 | 0.25 | 0 |
| EGG-PLANT | 1 | 9 | 2 | 9 | 3 | 23 | 11 |
| | 2 | 22 | 2 | 14 | 3 | 41 | 17 |
| | 3 | 11 | 3 | 7 | 3 | 24 | 10 |
| | 4 | 7 | 2 | 5 | 2 | 16 | 7 |
| MEAN | | 12.25 | 2.25 | 8.75 | 2.75 | 26.0 | 11.25 |
| LUCERNE | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| MEAN | | 0 | 0 | 0 | 0 | 0 | 0 |
| MELON | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| MEAN | | 0 | 0 | 0 | 0 | 0 | 0 |

APPENDIX G.

TABLE 1. GALLING AND DIFFERENT DEVELOPMENTAL STAGES OF N. ABERRANS RECOVERED FROM ROOTS OF TWELVE CROPS AFTER 70 DAYS.

(CONTINUED)

| CROPS | REPLICATES | NO. NEMATODES/g ROOT. | | | | | NO. GALLS/g ROOT |
|---|---|---|---|---|---|---|---|
| | | JUVENILES | ♂ | ♀ WITHOUT EGGS | ♀ WITH EGGS | TOTAL POPULATION | |
| | 1 | 2 | 0 | 8 | 0 | 10 | 8 |
| NARANJILLA | 2 | 0 | 0 | 5 | 0 | 5 | 5 |
| | 3 | 1 | 0 | 8 | 0 | 9 | 8 |
| | 4 | 2 | 0 | 6 | 0 | 8 | 6 |
| MEAN | | 1.25 | 0 | 6.75 | 0 | 8.0 | 6.75 |
| | 1 | 2 | 0 | 0 | 0 | 2 | 0 |
| POTATO | 2 | 1 | 0 | 0 | 0 | 1 | 0 |
| | 3 | 1 | 0 | 0 | 0 | 1 | 0 |
| | 4 | 1 | 0 | 0 | 0 | 1 | 0 |
| MEAN | | 1.25 | 0 | 0 | 0 | 1.25 | 0 |
| | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| RICE | 2 | 1 | 0 | 0 | 0 | 1 | 0 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| MEAN | | 0.50 | 0 | 0 | 0 | 0.50 | 0 |
| | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| SESAME | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| MEAN | | 0 | 0 | 0 | 0 | 0 | 0 |

APPENDIX G

TABLE 1. GALLING AND DIFFERENT DEVELOPMENTAL STAGES OF N. ABERRANS RECOVERED FROM ROOTS OF TWELVE CROPS AFTER 70 DAYS.

(CONTINUED)

| CROPS | REPLICATES | NO. NEMATODES/g ROOT. | | | | | NO. GALLS/g ROOT |
|---|---|---|---|---|---|---|---|
| | | JUVENILES | ♂ | ♀ WITHOUT EGGS | ♀ WITH EGGS | TOTAL POPULATION | |
| | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| SOYBEAN | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| MEAN | | 0 | 0 | 0 | 0 | 0 | 0 |
| | 1 | 2 | 4 | 9 | 2 | 17 | 11 |
| TOMATO | 2 | 38 | 3 | 4 | 3 | 48 | 7 |
| | 3 | 17 | 4 | 9 | 3 | 33 | 12 |
| | 4 | 15 | 5 | 11 | 2 | 33 | 12 |
| MEAN | | 18.0 | 4.0 | 8.25 | 2.50 | 32.75 | 10.50 |
| | 1 | 5 | 1 | 6 | 1 | 13 | 6 |
| TREE-TOMATO | 2 | 5 | 0 | 9 | 0 | 14 | 8 |
| | 3 | 3 | 1 | 7 | 1 | 12 | 6 |
| | 4 | 3 | 0 | 5 | 0 | 8 | 5 |
| MEAN | | 4.0 | 0.50 | 6.75 | 0.50 | 11.75 | 6.25 |
| | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| WINGED BEAN | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 4 | 0 | 0 | 0 | 0 | 0 | 0 |

APPENDIX G

TABLE 2. SOIL POPULATION OF N. ABERRANS FROM TWELVE CROPS.

| CROPS | REPLICATES | POPULATION/ L. SOIL | CROPS | REPLICATES | POPULATION/ L. SOIL |
|---|---|---|---|---|---|
| | 1 | 0 | | 1 | 0 |
| CORN | 2 | 0 | RICE | 2 | 0 |
| | 3 | 0 | | 3 | 0 |
| | 4 | 0 | | 4 | 0 |
| MEAN | | 0 | MEAN | | 0 |
| | 1 | 0 | | 1 | 0 |
| EGG-PLANT | 2 | 800 | SESAME | 2 | 0 |
| | 3 | 200 | | 3 | 0 |
| | 4 | 400 | | 4 | 0 |
| MEAN | | 350 | MEAN | | 0 |
| | 1 | 0 | | 1 | 0 |
| LUCERNE | 2 | 0 | SOYBEAN | 2 | 0 |
| | 3 | 0 | | 3 | 0 |
| | 4 | 0 | | 4 | 0 |
| MEAN | | 0 | MEAN | | 0 |
| | 1 | 0 | | 1 | 1400 |
| MELON | 2 | 0 | TOMATO | 2 | 400 |
| | 3 | 0 | | 3 | 0 |
| | 4 | 0 | | 4 | 1000 |
| MEAN | | 0 | MEAN | | 700 |
| | 1 | 0 | | 1 | 200 |
| NARANJILLA | 2 | 0 | TREE-TOMATO | 2 | 200 |
| | 3 | 0 | | 3 | 0 |
| | 4 | 0 | | 4 | 400 |
| MEAN | | 0 | MEAN | | 200 |
| | 1 | 0 | | 1 | 0 |
| POTATO | 2 | 0 | WINGED BEAN | 2 | 0 |
| | 3 | 0 | | 3 | 0 |
| | 4 | 0 | | 4 | 0 |
| MEAN | | 0 | MEAN | | 0 |