NATURE OF THE ROOT-KNOT RESISTANCE INTRODUCED INTO *LYCOPERSICON ESCULENTUM* BY INTERSPECIFIC CROSSES WITH *LYCOPERSICON PERUVIANUM*

By

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INTRODUCTION

For the last two decades tomato breeders have introduced root-knot nematode resistance into Lycopersicon esculentum by interspecific hybridization with L. peruvianum. Breeding lines derived from the L. esculentum x L. peruvianum crosses have shown variations in the mode of inheritance of resistance to the root-knot nematodes since certain variables in the testing and classification of the plants interfered with an early determination of the number of genes involved. Resistance may be governed by the plant's anatomical characters that prevent the entrance of the larvae into the host tissues. Cases of resistance due to anatomical differences of the host preventing entrance by the parasite have been reported for other diseases in other crops. However, it is not yet known in tomato whether such histological variations are present in resistant and susceptible strains.

Therefore, this research deals with two objectives, namely: a) to determine the mode of inheritance in tomato to root-knot nematodes (Meloidogyne spp.) and the number of genetic factors controlling this resistance; and b) to investigate physiological and morphological host-parasite interactions of selected resistant and susceptible lines.

The root-knot nematode species used in this investigation are as follows:

Meloidogyne arenaria (Neal, 1889) Chitwood, 1949.

M. javanica (Treub, 1885) Chitwood, 1949.

M. hapla (Chitwood, 1949).

M. incognita (Kofoid & White, 1919), Chitwood, 1949.

M. incognita var. acrita (Chitwood, 1949)

REVIEW OF LITERATURE

Resistance to Root-Knot Nematodes in Tomatoes

Numerous workers (2, 3, 17, 19, 20, 53, and 56) have reported that L. peruvianum is resistant to root-knot nematodes. Romshe (46) suggested the use of Lycopersicon peruvianum as breeding stock to develop commercial varieties of tomatoes resistant to nematodes. Alexander, Lincon, and Wright (1) indicated that various strains of L. peruvianum are potentially valuable sources of resistance to mosaic, leaf mold, fusarium wilt, Septorial, and Alternaria leaf blights. Sasser (49) indicated that L. peruvianum is resistant to M. incognita but susceptible to M. incognita acrita and M. javanica. Houssry and Otelifa (29) found a high level of resistance in L peruvianum tomatoes to M. javanica, M. hapla, M. incognita, and M. incognita acrita. Giles and Hutton (24) successfully combined desirable horticultural characters with resistance to root-knot nematodes and fusarium wilt in tomatoes.

Host-Parasite Interactions

The researchers who worked on this problem found that the root-knot nematodes entered resistant plants just as freely as susceptible ones, but further penetration was checked because of the death of the larvae. Christie (8) studied the host-parasite relationship and found that the root-knot nematodes had freely entered roots of non-host plants as well as host plants. Liao (32) in studies of arrested invasion of L. peruvianum roots by the root-knot nematodes observed only a few nematodes had penetrated the root near its tip and these were located for the most part in the peripheral cells. In a second experiment he

found that all of the nematodes that had attacked the roots were clustered around the point of entry, and invasion of the tissue was arrested when approximately one-half of the worm had become embedded in the growing point of the young rootlet and that many of the larvae had died in this position. The presence of a chemical inhibitor in L. peruvianum is therefore suggested. Dean and Struble (12) observed that fewer larvae penetrated the roots of resistant L. peruvianum plants than the susceptible L. esculentum plants. Sasser and Taylor (48) stated that the larvae of root-knot nematodes showed the following reactions on the resistant plants: a) failure to enter, and b) entered in small numbers with little or no development and from none to a few individuals reaching maturity. Peacock (41) in his work found that the larvae of M. incognita are attracted to the root tips of both L. esculentum and L. peruvianum, but more strongly to L. esculentum than L. peruvianum. Riggs and Winstead (45) studied the nature of root-knot nematode resistance and found that the factors for resistance or susceptibility to M. incognita in tomato were located in both tops and roots and that the resistance factors were not translocated across a graft union. Larvae penetrated the roots of resistant plants as freely and as rapidly as they penetrated roots of susceptible plants; however, the invasion of resistant tissues resulted in the death of tissues around the invading larvae and the subsequent death of the larvae. Dropkin (14) concluded that both galling and egg mass production varied as parasite or host was changed.

Histology of Tomato Infested with Root-Knot

The histology of tomato in relation to root-knot nematodes has not been studied extensively. Christie (7) in his investigation stated that the reaction of the root tissues to the presence of the parasite often was very prompt. The first noticeable change was hypertrophy of the cortical cells. When several larvae entered tissue simultaneously, considerable area in the cortex often showed pronounced cellular hypertrophy. Histological studies of galls caused by Meloidogyne spp. have been made by many workers (6, 10, 11, 13, 15, 18, 31, 33, 35, 39, 40, 42, 43, 51) on several crops indicating that giant cell formation was a common response. Dean and Struble (12) reported that nematodes entering resistant tomato roots produced extensive necrosis of host tissues within 48 hours. Liao and Dunlap (32) reported similar results with tomato except that larvae were arrested half embedded in the tissues. Christie (9) found that some roots were not penetrated by root-knot nematode larvae while others were. He further found that necrosis developed when the roots of resistant plants were penetrated.

Breeding for Root-Knot Resistance

Porte and Walker (44) produced interspecific hybrids between Lycopersicon esculentum and L. peruvianum. Smith (51) similarly obtained interspecific hybrids between L. esculentum var. Michigan State Forcing and L. peruvianum (P.I. 128659) by using an embryo culture technique. Malloch (36) stated that useful varieties with resistance to root-knot nematodes were obtained only by crossing commercial varieties with resistant species. Ellis (17) mentioned that L. peruvianum had

considerable resistance to root-knot nematodes and for that reason it was used in breeding for that character. Sauer and Giles (50) reported that a derivative from a cross between L. peruvianum x L. esculentum, was highly resistant to M. javanica. Barham and Sasser (4) found one tomato line resistant to four Meloidogyne species. Gilbert, McGuire, and Tanaka (23) bred F_1 hybrids possessing resistance to eight tomato diseases including root-knot. Harrison (28) reported that commercial type tomatoes with resistance to fusarium wilt, Alternaria collar rot, and root-knot had been developed by using a combined technique. Gilbert and McGuire (21) discussed the possibility of using root-knot resistant lines to produce F_1 hybrids for commercial tomato production in Hawaii. McFarlane, Hartzler, and Frazier (37) successfully incorporated root-knot resistance and a desirable vitamin C content of the wild tomato species L. peruvianum into a commercial variety. Giles and Hutton (24) were successful in combining some good morphological characters with resistance to root-knot nematodes and fusarium wilt.

Tomato Genetics in Relation to Root-Knot Nematode Resistance

The genetics of resistance in tomato to the root-knot nematode has been studied by a number of scientists. Frazier and Denett (20) reported that resistance seemed to be dominant and controlled by a small number of factors. A similar report was published by McFarlane, Hattzler, and Frazier (37). Other workers (22, 57, 5, 55) suggested that resistance was governed by a single dominant gene; however, Barham and Winstead (5) stated that dominance was incomplete and that other factors may contribute to the resistance. This information indicates that resistance to severe root-knot galling in the tomato

caused by M. incognita, M. incognita acrita, M. javanica, and M. arenaria is governed by a single gene or by a block of genes that act as a unit plus some other unknown factors. Hare (25, 26) reported a similar situation in peppers in which a single dominant gene governed resistance to the same four species of Meloidogyne. Hare (27) reported a monofactorial dominant gene governing resistance in cowpeas to M. incognita.

In addition to these reports there have been innumerable studies by many research workers looking into the inheritance of specific characters. The results of these investigations are often of practical value to the plant breeders assigned the task of developing a new variety. A useful technical review of the literature by Young and MacArthur (60), in which 49 characters with named genes and 60 other characters without identified genes are described, gives an idea of the extensiveness of published information in this field.

MATERIALS AND METHODS

I. Genetic Study

Fifteen tomato varieties or breeding lines were collected from different sources and seed of each was planted in flats. When the seedlings were about one inch tall, they were transplanted into 3-inch peat pots which were arranged in flats. When the seedlings were about 9 inches high they were transplanted into a steam sterilized bed in the greenhouse. A night temperature of 70°F and a day temperature of 85°F with about 75% relative humidity was maintained. At the flowering stage, clusters of flower buds were covered with paper bags to prevent cross-pollination. (The tomato is normally a self-fertilized crop but crossing occasionally occurs at a low incidence in long style flowers). The bagged clusters were shaken daily at 8 a.m. to aid in pollination. The fruit when ripe was harvested and seed collected.

In another greenhouse room all 15 entries were tested for resistance to five species of root-knot nematodes namely, M. javanica. M. hapla, M. incognita, M. incognita var. acrita, and M. arenaria. Nematodes of these species were obtained from the Division of Nematology of the United States Department of Agriculture, Beltsville, Maryland. The inoculum of each species was increased prior to testing by growing a susceptible variety of tomato in 2 x 2 x 1/2 ft. wooden boxes. Five classes or types of infection were recognized as suggested by Wester (59), (Plates 1, 2, 3, 4, 5) and are described as follows:

Type 0 - No infection, or if larvae entered the roots, they did not develop into mature egg-laying females.

Type I - Extremely light infection with only an occasional mature, female with egg-mass.

Type II - Light infection with mature females and egg-masses easily seen with naked eye.

Type III - Moderate infection with full grown females and egg-masses moderately abundant.

Type IV - Severe infection with mature females and egg-masses very abundant.

One susceptible variety and four resistant breeding lines (Plate 6) were selected for genetic investigations. The resistant breeding lines were derived from crosses between L. esculentum and L. peruvianum. The entry numbers and the source of seed are given below.

V_1 = T60-32P_5 Tomato Green Leaf Alabama.

V_2 = T60-49P Tomato Green Leaf Alabama.

V_5 = HE 6819 (6769) from Dr. Gilbert, Hawaii.

V_{12} = Y23 (V_{16} in 1960) from Texas Agr. Expt. Sta., Yoakum.

V_{15} = Rutgers.

The characteristics of these parents are shown in Table 1.

A. Breeding Technique. Homozygous parents were planted in the greenhouse. When the plants flowered, the hybridization work was conducted as follows: The greenish stamens with anthers were removed from a selected bud one day before dehiscence with forceps sterilized in 95% ethanol. The emasculated bud was wrapped with a piece of sterile absorbent cotten, and covered with one-half of a gelatin capsule. A yellow tag containing the dates and times of emasculation and pollination, and varieties involved in the cross was tied to it. On the following day, at about 8 a.m., yellow matured stamens of the appropriate variety

involved in a cross were selected and pollen grains were collected in a petri-dish by slitting the stamens with a needle sterilized in 95% ethanol. Pollination was then accomplished by placing pollen grains on the stigmatic surface of the style of the appropriate emasculated bud, with a dry camel hair brush which was previously sterilized in 95% ethanol. The gelatin capsule was again placed over the pollinated bud. Three to four days after pollination and fruit set, the capsule was removed. Reciprocal crosses were made between the four resistant and one susceptible parents as follows:

C_1 = Resistant pistillate plant (V_1) X Susceptible staminate plant (V_{15})

C_5 = Susceptible pistillate plant (V_{15}) X Resistant staminate plant (V_1)

C_2 = Resistant pistillate plant (V_2) X Susceptible staminate plant (V_{15})

C_6 = Susceptible pistillate plant (V_{15}) X Resistant staminate plant (V_2)

C_3 = Resistant pistillate plant (V_5) X Susceptible Staminate plant (V_{15})

C_7 = Susceptible pistillate plant (V_{15}) X Resistant Staminate plant (V_5)

C_4 = Resistant pistillate plant (V_{12}) X Susceptible Staminate plant (V_{15})

C_8 = Susceptible pistillate plant (V_{15}) X Resistant Staminate plant (V_{12})

Several flower buds of each of the parents were bagged to get selfed homozygous seeds. These seeds and the F_1 seeds from the 8 reciprocal crosses were collected and planted again the next season. The F_1 seedlings with their respective parents were transplanted into greenhouse beds, where they were grown to maturity. Flower bud clusters were bagged and shaken each morning to induce fruit set. The F_1 population of all reciprocal crosses showed hybrid vigor. For all the characters, data were recorded and are presented in Table 6. From ripe selfed fruits, F_2 seeds were collected.

In another greenhouse room the F_1 population of the 8 reciprocal crosses was tested for resistance to the five species of root-knot nematodes. An individual F_1 plant of each cross was classified for resistance to each of the root-knot nematode species. The reactions of these plants were studied in relation to their parents. All F_1 plants were found to be resistant to M. javanica, M. incognita, and M. incognita var acrita, ranging in degree of infection from Type 0 to Type II. However, they segregated from Type I to Type IV when tested with M. hapla and M. arenaria.

B. F_2 Population Testing. Seedlings used in the previous experiments were started in flats containing a sterilized soil mixture composed of one-fourth peat, one-fourth sand and one-half top soil. The root medium was changed in this test because there was severe damping off in the boxes containing the nematode inoculum.

Sufficient quantities of F_2 seed from each of the F_1 plants were planted in flats containing a sterilized mixture composed of one-fourth top soil and three-fourths Weblite (58) which has the following chemical analysis:

Total silica as SiO_2, %	58.33
Total Aluminum as, Al_2O_3, %	25.22
Total Iron as Fe_2O_3, %	9.44
Total Calcium as, CaO, %	Nil
Total Magnesium as MgO, %	2.75
Total Sulphur as, SO_3, %	Nil
Total Sodium as Na_2O, %	0.08
Total Potassium as, K_2O, %	2.32
Loss of ignition, %	1.50

C. Method of testing F_2 population for resistance to five species of root-knot nematodes. Uniform seedling tests (with tomatoes) by Bailey (3) have been obtained in the greenhouse. Twenty wooden boxes each of 2' x 2' x 6" were made and arranged in two rows on a greenhouse bench. Two-thirds of each box was filled with a sterilized mixture of top soil and Weblite and a uniform one-inch layer of Weblite was used at the top in order to keep the surface dry. When the seedlings were about two and one-half inches high they were transplated into the boxes. In each box were four replications of four seedlings of each of the resistant and susceptible parents and 20 seedlings of each of the two reciprocal crosses. There were four boxes for each root-knot nematode species.

Inoculation. Inoculum of each of the root-knot nematode species was produced on susceptible Rutgers plants. Galled tomato roots were gently immersed in tap water and cleaned without disturbing the egg-masses and then washed with distilled water and placed into another container. Roots heavily infected with root-knot nematodes were

chopped into small pieces. About one-fourth gram of inoculum was placed directly in contact with the root of every seedling about one-half inch below the soil surface and covered with moist Weblite. After inoculation, seedlings were irrigated regularly. This method of inoculation was very laborious but gave better results than when the inoculum was mixed with soil.

Readings were made when the susceptible control seedlings were well galled, which was 50 days after inoculation in the winter. Variations in the severity of infection had been a problem in classifying seedlings accurately enough for genetic analysis. These variations in the inoculum from one root-knot nematode species to another was checked most easily by the use of both susceptible and resistant controls. Thus, misclassification of seedlings in segregating lines was usually avoided even when an exceptionally pathogenic species of M. hapla produced considerable minor galling in resistant plants or when light inoculum was added. The percentage of galling was arbitrarily scored from 0% to 75%.

One ground bed in the greenhouse was heavily infested with root-knot nematodes. Eight F_2 seedlings from each of the reciprocal crosses with their parents were planted for genetic and other studies. Observations were recorded for many characters. Perineal patterns of root-knot females taken from the soil in this bed showed that the species was probably M. incognita.

II. Histological Study

For histological studies on host-parasite reactions the roots of resistant and susceptible plants were killed and fixed in CRAF Solution

III (47). The roots were washed in running water overnight. The material was then dehydrated with the ethyl alcohol and the butyl alcohol series and after embedding and sectioning the material was stained with safranin and fast green as described by Johansen (30).

III. Root Penetration Study

The methods described by other workers (38, 45) to obtain "pure" inoculum for laboratory studies did not give satisfactory results. Many exploratory trials were conducted before a method of inoculum preparation was found that would give good results. The procedure adopted is described as follows. Susceptible seedlings of the tomato variety Rutgers were inoculated with larvae of each of the species of root-knot nematodes in flats containing Weblite as the root medium. After three months when numerous egg masses were visible on the roots, the plants were uprooted and the galled roots separated. The roots were first cleaned in tap water and then in distilled water. Debris and particles of Weblite were carefully removed without disturbing the egg-masses. About 3,000 egg-masses of each species were then picked up with sterilized forceps with the aid of dissecting microscope (low power, 15 x magnification) and placed in a sterilized petri-dish containing distilled water. Egg-masses were washed four times with distilled water in order to remove saprophagous nematodes and other impurities. From the petri-dish the egg-masses were transferred to a 100 ml beaker containing about 1 1/2 ml of distilled water (just enough to keep them moist and in aerobic condition). This small beaker was placed in a 150 ml beaker containing distilled water and then covered with a petri-dish to prevent drying of the inoculum and these were held at room

temperature (Plate 9). Egg-masses were washed daily with distilled water until saprophagous nematodes and protozoans completely disappeared. After about a week, the eggs started hatching, and gave about 4,000 to 6,000 fresh larvae per day for approximately a week. The larvae were held for three days in a refrigerator at 40°F. On the third day, the stored larvae and fresh larvae that had hatched later were mixed and the mixture used to inoculate test plants. The inoculum, thus prepared, was practically free of other organisms.

A. Growth regulating frames. The frames used in testing the penetration of seedlings by the five nematode species were 7.5 x 1 x 2.5 cm in size and were made from 10 inch long pot labels and 25 x 75 mm microscopic slides (Plate 10).

B. Root-medium. Weblite described previously was screened through a 30-mesh brass screen, washed with distilled water and dried at room temperature.

C. Seedlings and Inoculation. Seedlings of susceptible and resistant varieties were grown at room temperature on Whatman Filter Paper No. 3 in closed moistened petri-dishes. Generally the tomato seeds germinated in four days. At the end of this time, the primary root of the young seedlings was between one-fourth and one-half centimeter long. To check their vigorous growth the petri-dish cover was removed and the seedlings left uncovered for 3 days. The four day old seedlings, with tap roots 1 to 1 1/2 centimeters long were then inoculated with 2,000 larvae per seedling according to the inoculation technique described by Linford (34).

The progress of root penetration of resistant and susceptible seedlings by five species of root-knot nematodes was observed under the dissecting microscope in killed and stained seedlings removed at 18, 24, 36, 48, 60, 72, and 96 hour intervals after inoculation. The seedlings were killed in 4 1/2 percent formaldehyde solution and stained in boiling acidfuchsin-lactophenol (0.05 g/solution of lactophenol) for 1 minute. The seedlings were then cleared and mounted in lactophenol (glycerine, phenol, lactic acid, and distilled water, 2: 1: 1: 1) for microscopic examinations.

Photomicrographs of the nematodes inside and on the root surface were taken with a 35 mm camera, model 635, mounted on the trinocular Microstar, microscope manufactured by the American Optical Company.

EXPERIMENTAL RESULTS

I. Genetic Study.

The data on the characters studied in the F_1 generation are presented in Table 6. The fruits were harvested as they reached maturity and weighed. At the end of the test period the total weight of the harvested fruit was calculated and the data were statistically analyzed according to Duncan's multiple range test (16). The analysis of variance is shown in Table 2. All the hybrids gave higher yield than the control - V_{15} (Fig. 1). V_1 seems the poorest in combining ability with V_{15} since the reciprocal crosses, C_1 and C_5, gave lower yield than other reciprocal crosses. Specific combining ability for high yield was demonstrated by the reciprocal crosses C_3 and C_7 which were significantly higher in yield than any other hybrid in the test with one exception. This yield increase is of great interest since V_{15}, a standard variety, showed rather poor yielding ability. V_{15} gave 11.5 pounds of fruit per plant whereas the reciprocal crosses C_7 and C_3 gave 18.3 and 19.3 pounds of fruit per plant, respectively. V_5 was a heavy yielder and both of its reciprocal crosses gave high yields. This good performance of the hybrids suggests that the better yielding varieties will probably produce the better yielding hybrids.

The average fresh weight in pounds per plant for the F_1 hybrids and their parents with the analysis of variance is given in Table 3. V_{12}, a dwarf variety, gave the lowest weight per plant (Fig. 2). Although V_{15} was heavily infected with root-knot nematodes it produced higher weight per plant than any other parental variety with one exception. All the F_1 hybrid plants, with one exception, gave higher weight

per plant than the parental varieties. Reciprocal crosses C_3 and C_7 gave higher weight per plant than any other hybrid. V_5 was very vigorous in growth and produced extremely vigorous hybrid plants. V_2 was medium in vigor and its hybrids were also medium in vigor. This observation leads to the suggestion that vigorous tomato varieties will probably produce vigorous hybrids.

Data on plant height for the F_1 hybrids and the parental varieties and the analysis of variance are given in Table 4. V_{12}, a determinate dwarf variety, was very short (Fig. 3); however, it produced a hybrid which was taller than other hybrids with one exception. V_5 was the tallest variety and produced the tallest hybrid plants. V_1 and V_2 were medium tall varieties and produced hybrids slightly taller than the parental lines involved in the crosses.

The total number of fruits and their weight per plant were recorded for each harvest and when the final harvest was completed, the average weight in grams of an individual fruit was calculated. The analysis of variance of these data is shown in Table 5. V_2 was the largest fruited variety and V_{12} the smallest (Fig. 4). The fruit of V_{12} weighed only 97.8 grams. V_5 produced some of the largest individual fruits but they were not uniform in size and therefore the variety ranked second in average size. In crosses with the largest fruited varieties, V_2 and V_5, the hybrid means were substantially larger than combinations of the other parents. The hybrids from the reciprocal crosses of V_2 and V_5 with V_{15} as a common parent exceeded V_{15} in fruit weight, but neither hybrid exceeded V_2 and V_5 in fruit weight. These two hybrids were, therefore, intermediate to their parents in fruit weight and fruit size.

The hybrid between V_{12} and V_{15} gave similar results. The hybrid C_1 between V_1 and V_{15}, however, had a lower fruit weight than either of the parents. This result indicates that the specific combining abilities were not always uniform from one variety to another.

The F_1 seedlings of all reciprocal crosses and their respective parents were tested for resistance to Meloidogyne incognita, M. incognita var. acrita, M. javanica, M. arenaria, and M. hapla. All F_1 hybrids were resistant to M. javanica, M. incognita, and M. incognita var. acrita (Plates 7 and 8), but no variety or F_1 hybrid was highly resistant to M. hapla and M. arenaria. With both of the latter species, parents and F_1 hybrids appeared to segregate for resistance.

In another room in the greenhouse, the F_1 plants were selfed just before anthesis, to obtain F_2 generation seed. Back-crosses were not made due to the limitation of time. These F_2 populations were grown in a bed heavily infested with M. incognita where they segregated into 3:1 ratios for the important characters of the stem, leaf and inflorescence, shown in Table 6. Since the populations were small the data were not statistically analysed.

The type of infections on the F_2 seedlings by the five species of root-knot nematodes were studied on seedlings growing in soil infested with each species. The data on the type of infections are presented in Tables 7, 8, and 9. Tables 10, 11, and 12 show the results of the Chi-square test of these data. The very close fit to the expected 3:1 ratio in each reciprocal cross tested with M. javanica (Table 12) shows that resistance was dominant and controlled by a single pair of genes. The The symbol Mi is suggested for this gene. Table 10 presents the F_2 test

on the inheritance of resistance to M. incognita in the reciprocal crosses. These data indicate that the observed ratios were not significantly different from the expected ones and suggest that resistance to M. incognita in tomato is a monofactorial dominant.

Table 11 shows a summary of the classification of the reaction of the F_2 seedlings to M. incognita var. acrita, with Chi-square test for each cross. The reactions of the reciprocal crosses are very similar and fit very closely the expected 3:1 ratio. Those data indicate that resistance in tomato to M. incognita var acrita is dominant and controlled by one gene. Table 13 summaries the Chi-square analysis of the data presented in Tables 10, 11, and 12 and demonstrates that resistance to three species of root-knot nematodes is controlled by the same gene.

Most of the F_2 seedlings inoculated with M. arenaria were heavily galled. Very few seedlings showed Type I infection. Some seedlings were segregating with Type I to Type IV infection but very few showed Type 0 infection.

Phosphorous deficiency was observed in the seedlings growing in boxes infested with M. hapla and M. arenaria. The assumption was first made that the phosphorous deficiency was on susceptible seedlings which were heavily galled. When actual readings were taken, it was seen that both resistant as well as susceptible seedlings had phosphorus deficiency symptoms. The deficiency, however, was more pronounced on susceptible seedlings than on resistant ones. Phosphorus deficiency was severe on the seedlings inoculated with M. arenaria.

II. Histological Study

Microscopic examination of sectioned and stained roots of the different infection types revealed cytological and histological abnormalities when compared with noninfected roots (Plate 11). Root-knot formation was due to a hypertrophic response of cells in the cortex or stele (Plate 12) caused by the stimulation of the root-knot nematodes. In all infection types some degree of giant cell formation occured, but in Type I and Type II the giant cells were significantly smaller and fewer in number than in susceptible Type III and Type IV. There were no significant histological differences between Type I and Type II infections. In these resistant reactions, the parenchymatous cells in the cortex (Plate 19) and in the stele (Plate 13) were proliferated around the head of the nematode and ultimately around the giant cells. These proliferated cells formed a compact area around underdeveloped mature egg-laying females which occasionally laid a small egg mass on the surface of root but never in the cortex or in the vascular cylinder. In many cases, underdeveloped females did not lay eggs (Plate 15). Similar results were reported by Riggs and Winstead (45). In a resistant variety, two to six giant cells were generally observed around the head region of the nematode (Plates 15 and 22).

There were no significant histological differences between Type III and Type IV infections (Plates 12 and 17) caused by either of the five species of root-knot nematodes on susceptible seedlings. In both types hypertrophy was common. Larvae developed fully into mature egg-laying females with large egg masses on the surface of the roots as well as in the cortex and stele.

Longitudinal sections through galled roots revealed that giant cells in the vascular cylinder interrupted the continuity of some vessels and other vascular tissues (Plate 17). This interruption of tissues definitely would have affected the translocation of water and nutrients through the roots and thereby caused severe injury to plant growth.

Giant cells developed in the manner reported by Christie (7); i.e., from the dissolution of cell walls with subsequent deposition of a thick wall around the coalesced cytoplasms and nuclei (Plates 20, 21, and 22). The cytoplasm appeared granular in all giant cells. The nuclei varied in number (Plates 12, 14, 15, 17, 18, and 23) depending upon the region in which the cells were located and age of the cells. The nuclei varied in appearance even in adjacent giant cells (Plate 23). Nuclei of all giant cells were larger than normal and stained more deeply. In the cortex, young giant cells contained many nuclei (maximum of 22 observed) (Plate 15), whereas, within the stele the nuclei were less numerous and usually much larger (Plates 14 and 12). The number of nuclei observed in a single giant cell, probably, depended upon the number of cells which were involved in its formation. Christie (7) advanced this same hypothesis. In old giant cells the number of nuclei was observed to be either less than in young giant cells, or in some cases more, which appeared to have resulted from nuclei disintegrating or from coalescing of walls of young giant cells. The cell wall of young giant cells was thicker than that of old ones (Plate 18). Giant cell formation was quite varied around single females ranging from two to 14 in one Type IV infection (Plate 23). Generally giant cells were formed around the head region of the larvae (Plates 12 and 16).

The series of measurements were made to compare the thickness of cell walls of resistant and susceptible varieties. Healthy roots of five different sizes, i.e., diameters of .120 mm, .70 mm, 1 mm, 1.5 mm, and 2 mm, were selected for measurement and both epidermal and cortical cells were used. The data are presented in Fig. 5. No histological differences in the cell walls of resistant and susceptible plants were observed.

III. Root Penetration and Attraction Study

To determine the influence of age of seedling upon the attraction of larvae of M. javanica, seeds of V_{15} were germinated at one day intervals in petri-dishes and transferred into growth regulating frames. Germinating seed and seedlings ranging in age from one to five days were separately inoculated with 2,000 larvae of M. javanica per plant. Thirty-six hours after inoculation plant roots were killed with 4.5 formaldehyde solution and stained. It was observed in these preparations that the germinating seed did not attract a single larvae, the one day old seedling, 3 larvae; the two day old, 11 larvae; the three day old, 51 larvae; and the four and five day old seedlings attracted many larvae (Plate 26).

To test the attractiveness of roots of resistant and susceptible seedling to the different nematode species, four day old seedlings of V_2 and V_{15} were inoculated with 2,000 larvae per seedling. Roots were collected and killed at 18, 24, 36, 48, 60, 72, and 96 hours after inoculation. Larvae of the different nematode species were very sluggish for several hours but gradually became active approximately four hours after inoculation, and moved back and forth along the root-zone. After 12 hours,

many larvae were in contact with the roots of the susceptible seedlings and seemed not to leave them. After 18 hours many of them were massed near the growing point and root primordia. The zone of greatest attractivity appeared to lie just behind the root-cap, where penetration of the larvae occured most commonly. At the 18 hour interval many larvae had not generally penetrated the roots, but after 24 hours many larvae had entered the roots (Plate 24). The roots of resistant seedlings attracted a much smaller number of larvae and only a few penetrated the roots (Plate 25).

At 36 and 48 hour intervals (Plates 26 and 28) some larvae were completely embedded inside the roots of susceptible seedlings and others were partially embedded. In the roots of the resistant seedlings further penetration appeared to be checked (Plates 27 and 29). At 60, 72, and 96 hour intervals (Plates 30, 32, and 34), swelling of the roots was observed and the number of larvae inside the roots had increased considerably in susceptible and in resistant seedlings. In some resistant seedlings larvae remained half embedded (Plates 31, 33, and 35). The number of larval penetrations usually increased with time up to 96 hours; however, it was observed that occasionally there was no significant difference in the number of larvae which entered tomato roots at the different time intervals. This was apparently due to the variable concentration of the larvae on the root primordia and on the secondary roots which interfered with the migrating larvae toward the growing point (Plates 37, 38, and 39). When a small number of larvae of M. incognita, M. incognita var. acrita, and M. javanica were compared on resistant seedlings at 96 hours after inoculation (Plate 35) it was observed that penetration was not complete and the larvae

appeared to have only half penetrated the roots. When large numbers of larvae of M. incognita were introduced on the root of the resistant plants they appeared to enter as easily as they entered the roots of susceptible plants (Plate 36). Frequently it was observed that the larvae of the five species of nematodes had entered the root primordia of susceptible hosts while migrating toward growing points (Plates 38 and 39).

DISCUSSION OF RESULTS

I. Genetic Study

Hybrid vigor was exhibited by all F_1 plants for height, and increased fresh weight of stem, roots, and leaves. Fruit size was reduced but average yield was increased over the large fruited parent varieties. The F_2 plants segregated for the characters described in Table 6 in 3:1 ratios. These segregation ratios agree with the other tomato breeding reports (60). Since the plant population was small the data were not statistically analysed. When the F_1 plants and the F_2 plants along with their resistant and susceptible parents were grown for six months in a bed heavily infested with M. incognita, it was found that resistant parents and some other resistant lines had minor galling. Small egg-masses were occasionally found on the surface of the roots, of these resistant lines which supports the data of Riggs and Winstead (45).

The tests to obtain the inheritance data presented in the results were carried out with sufficient inoculum to minimize escapes, but some of the susceptible seedlings showed light infection of Type III. Also, some resistant seedlings showed Types I and II infections. The differences between seedlings in Types I, II, and III appeared to be largely a matter of chance variations in the concentration of nematode larvae at their roots. F_1 hybrids were resistant to M. javanica, M. incognita, and M. incognita var. acrita, but all F_1 hybrids were segregating with infection of Type I to IV to M. hapla and M. arenaria. These two species of root-knot nematodes had great ability to penetrate the tomato roots. V_{15} (Rutgers variety) was very susceptible to M. javanica and many seedlings died in the test.

The F_2 tests on the inheritance of resistance to M. incognita, M. incognita var. acrita, and M. javanica in the reciprocal crosses showed that the observed ratios were not significantly different from the 3:1 ratio. These results suggest that resistance in tomato to these three root-knot nematode species is completely monofactorial dominant and is controlled by the same gene. This opinion is in line with the report by Gilbert and McQuire (22) that resistance to M. incognita is dominant and is controlled by a single pair of genes. They had reported earlier similar conclusions for root-knot resistance in commercial type tomatoes. In their tests, most of the F_2 seedlings were found to be susceptible to M. hapla and M. arenaria.

Taylor, et al (54) in their investigations on root-knot nematodes showed that L. peruvianum was not resistant to M. hapla and M. arenaria. Since the root-knot resistant bred stock used in the present studies was developed from crosses between L. peruvianum and L. esculentum, F_2 seedlings would not be expected to show a high level of resistance to these two species of nematodes.

II. Histological Study

Sectioned and stained root-knot galls from resistant and susceptible tomato seedlings showed the presence of infections of M. arenaria, M. incognita, M. incognita var. acrita, M. hapla, and M. javanica. There was no anatomical difference between Type I and Type II infections caused by these five species of root-knot nematodes. Small egg masses were occasionally observed on the surface of roots but not in the cortex or vascular cylinder of resistant varieties. Larvae and underdeveloped females were

frequently observed in the stele of resistant varieties where the cells were small and compacted around the nematode and its giant cells. Thus, these compact cells might have hindered the development of the embedded larvae into mature females. The number and size of giant cells adjacent to the head region of the nematodes were smaller and appeared to have thicker walls than those formed in susceptible plants. This depressing of the nematode development may explain the reason for the minor galling observed in resistant varieties. Riggs and Winstead (45) in their investigation reported that very small egg-masses each containing approximately ten eggs were found on the surface of resistant tomato plants. In susceptible varieties the cells adjacent to the head region of larvae showed hypertrophy in the form of numerous thin walled giant cells. This observation agrees with one by Christie (7) that the immediate affect of larvae entering the roots was: hypertrophy of cells in the cortical region; slight hypertrophy of cells of the pericycle and endodermis when lying near the path of the parasites; and stimulation of cell division in the pericycle. In these investigations histological studies revealed that the nematode was generally located within the vascular cylinder or stele, but sometimes with the posterior part of their body extended into the parenchymatous cells of the cortex, particularly in young roots. Davis and Jenkins (10) working on roses infested with M. hapla reported the nematode was located in the cortex, stele, and root tip.

The larvae in penetrating either resistant or susceptible hosts seemed to pass between the cells. This information agrees with other reports (6, 9, 40, 43, 51) where larvae of Meloidogyne species were observed to pass between the cells. Giant cells developed near the head region

of the nematode and the cytoplasmic contents stained grey (14). Giant cells frequently developed extensively in the stele and thus caused a disruption of the conducting vessels which affected the translocation of water and nutrients through the roots. This disruption of the vessels may explain the reason for the death of V_{15} seedlings heavily infected with M. javanica.

III. Root Penetration Study

Penetration of the roots of tomato by larvae occured primarily behind the root-cap of either primary or secondary roots or where lateral roots were emerging from the main root. This agrees with the observations of Linford (34) and Christie (7) who reported similar results in their investigations.

In determining whether larvae of the five species studied penetrated the roots of a resistant variety as rapidly and as easily as they invaded the roots of a susceptible variety, it was observed that larvae did not penetrate the roots of susceptible or resistant hosts at the 18 hour interval. At the 24 and 36 hour intervals many larvae were found half embedded in roots of susceptible hosts, but in the roots of the resistant hosts only a few were found and those were about one-third embedded. At the 48 hour interval, many larvae had entered completely the roots of susceptible plants and swelling was visible. The swelling was a result of the formation of giant cells as reported by Christie (7) and supported by Riggs and Winstead (45). At the 60, 70, and 96 hour intervals the swelling gradually became more pronounced as the formation of giant cells increased. At this time many larvae were completely embedded within the

96 hour interval. Occasionally, one or two larvae completely penetrated the resistant roots. Dean and Struble (12) reported similar results from their investigation, i.e., root systems of resistant tomatoes, L. peruvianum and L. peruvianum hybrid, were invaded by fewer larvae, usually half or less, than those of susceptible Marglobe tomatoes. Sasser and Taylor (48) working on the entry of larvae of root-knot nematodes into roots of susceptible and resistant plants showed various degrees of entry, i.e., in some plants larvae entered but did not fully develope. M. hapla and M. arenaria entered the roots of resistant hosts as freely as they entered the roots of susceptible hosts.

When the roots of resistant seedlings were inoculated with 8,000 larvae of the various root-knot species and exposed to invasion for 96 hours, it was found that they entered the roots as rapidly and as freely as they did susceptible roots. Similar results were obtained by Riggs and Winstead (45) in studies on resistance in tomato and on the occurence of pathogenic biotypes. As the density of the population of nematodes was increased the chance of invasion of resistant roots was increased.

SUMMARY

The two objectives of this investigation were to determine the morphological host-parasite interactions of selected resistant and susceptible lines of tomato to certain species of root-knot nematodes and to determine the mode of inheritance and the number of genetic factors controlling this resistance. Four varieties of tomato showing resistance to several root-knot species were crossed with one susceptible variety. The F_1 and F_2 populations were tested for resistance to M. arenaria, M. hapla, M. javanica, M. incognita, and M. incognita var. acrita.

The infections of plants were classified into five types based on the degree of root galling. Standard methods of microtechnique were used in preparing slides of longitudinal and cross sections of root-galls from resistant and susceptible plants. These anatomical studies showed there were several differences in development of infection on resistant and susceptible varieties. On roots of resistant plants, the larvae of M. incognita, M. incognita var. acrita and M. javanica stimulated new cell development around the area of penetration preventing normal development of the female. In these cases the females were smaller and produced small egg sacs, usually with 10 eggs or less near the surface of the roots but not in the cortex or stele as is normal in susceptible plants. In most cases only one underdeveloped female was seen in a root gall. Giant cells formed in resistant varieties were smaller in size and fewer in number than in susceptible varieties.

In the roots of susceptible varieties hypertrophy of cells occured around the head region of developing larvae and females laid large egg

masses in the cortex or on the surface. When the larvae entered the roots of susceptible hosts, the cells adjacent to the mouth parts of the larvae developed into giant cells which apparently arose from the dissolution of cell walls with a subsequent deposition of a thick cell wall around the coalesced cytoplasm and nuclei. Cross sections of susceptible and resistant ungalled roots of similar diameters did not show anatomical differences between the thickness of cell walls of cortical or epidermal cells.

In a root penetration and attraction study it was observed that when 2,000 larvae were used as inoculum, they freely penetrated the roots of susceptible plants whereas in resistant plants very few larvae entered and these remained half embedded in the roots even 96 hours after inoculation. When the concentration of inoculum was increased from 2,000 to 8,000 larvae per seedling, the larvae entered the roots of resistant seedlings as freely and as rapidly as they entered the roots of susceptible plants.

In a genetic study the F_1 population showed hybrid vigor for height, yield and fresh weight of roots, stems, and leaves. Resistance to M. javanica, M. incognita, and M. incognita var. acrita was dominant and susceptibility was recessive. The F_2 population segregated in a 3:1 ratio showing resistance is a monofactorial dominant character and controlled by a single gene.

The resistant parents and their F_1 and F_2 populations did not show resistance to M. hapla and M. arenaria. In this investigation, M. hapla and M. arenaria showed more ability to penetrate than the other three species of root knot nematode as they invaded roots of varieties resistant to M. incognita, M. incognita var. acrita, and M. javanica.

CONCLUSION

From the results obtained in this investigation it may be concluded that resistance in tomato to M. javanica, M. incognita, and M. incognita var. acrita is a monofactorial dominant character and controlled by a single gene. In the varieties tested the resistance to M. arenaria and M. hapla is unsatisfactory.

When high populations of M. incognita, M. incognita var. acrita and M. javanica are used, the roots of resistant varieties may be penetrated as quickly as those of susceptible plants.

In varieties carrying resistance to a given nematode species, penetration of the roots by the larvae is suppressed and the development of the nematode in the root is checked by some condition in the plant. The slight histological differences in cell development around the penetrating nematode in resistant and susceptible roots is not sufficient to account for the resistance.

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Table 1

Characteristics of the 5 parental tomato lines involved in the investigation

Characteristic	Variety				
	V_1	V_2	V_5	V_{12}	V_{15}
Stem					
Tall, dwarf, weak, or strong	Tall, strong	Tall, strong	Tall, strong	Dwarf, weak	Tall, strong
Thick, thin, or hairy	Thick, hairy	Thick, hairy	Thick, hairy	Thin, hairy	Thick, hairy
Pigmentation at seedling stage purple or green	Purple	Purple	Purple	Purple	Purple
Pigmentation at flowering stage purple or green	Green	Green	Green	Green	Green
Inflorescence					
Determinate or indeterminate	Indeterminate	Indeterminate	Indeterminate	Determinate	Indeterminate
Simple or compound	Simple	Simple	Simple	Compound	Simple
Length of style	Short	Short	Short	Short	Short
Leaf shape	Normal cut	Normal cut	Wilty leaf	Normal cut	Normal cut
Leaflet	Normal	Normal	Wilty	Normal	Normal
Leaflet color	Green	Green	Green	Yellowish	Green
Fruit					
Shape	Round	Round	Flat	Round	Round
Size	Medium	Large	Medium to large	Medium	Medium
Corky brown stem end ring size	Medium	Large	Medium to large	Small	Medium
Scar	Very small	Small to medium	Large	Very small	Very small
Shoulder	Medium smooth	Medium smooth	Medium smooth	Medium smooth	Medium smooth
Uniformity of fruit size	Uniform	Uniform	Not uniform	Uniform	Uniform
Bearing habit	Good	Good	Excellent	Good	Good
Root-knot nematode resistance	Resistant	Resistant	Resistant	Resistant	Susceptible

Table 2

Analysis of Variance
Yield in pounds per plant of F_1 hybrids and their parents

Variation due to	D. F.	S. S.	M. S. S.	F.
Replications	3	34.44	11.48	2.36
F_1 hybrids & parents	12	251.83	20.99	4.32 **
Error	36	174.83	4.86	
Total	51	461.10		

Significant at 1% level **

Duncan's Multiple Range Test.

V_{15}	C_1	V_1	C_5	V_2	C_2	C_8	V_{12}	V_5	C_6	C_4	C_7	C_3
11.5	12.2	12.6	13.2	14.0	14.6	14.7	15.0	15.0	15.6	16.8	18.3	19.3

Any two means underscored by the same line are not significantly different at 5% level.

Table 3

Analysis of Variance
Fresh weight in pounds per plant of F_1 hybrids and their parents

Variation due to	D. F.	S. S.	M. S. S.	F.	
Replications	3	2.37	.79	1.76	
F_1 hybrids & parents	12	68.47	5.71	12.69	**
Error	36	16.25	.45		
Total	51	87.09			

Significant at 1% level **

Duncan's Multiple Range Test.

2.00	2.19	2.88	2.88	3.13	3.31	3.69	4.19	4.38	4.50	5.25	5.44	5.56
V_{12}	V_1	V_2	V_{15}	C_1	V_5	C_5	C_6	C_8	C_2	C_4	C_7	C_3

Any two means underscored by the same line are not significantly different at 5% level.

Table 4

Analysis of Variance
Height in inches per plant of F_1 hybrids and their parents

Variation due to	D. F.	S. S.	M. S. S.	F.
Replications	3	1311	437	4.37 *
F_1 hybrids & parents	12	49980	4165	4.65 **
Error	36	3599	100	
Total	51	54890		

Significant at 5% level *
Significant at 1% level **

Duncan's Multiple Range Test.

60.25	126.50	133.75	136.25	144.00	148.50	148.75	152.75	153.50	166.25	166.75	184.25	191.25
V_{12}	V_1	V_{15}	C_5	V_2	C_1	C_6	C_2	C_8	V_5	C_4	C_7	C_3

Any two means underscored by the same line are not significantly different at 1% level.

Table 5

Analysis of Variance

Average weight in grams of fruit of F_1 hybrids and their parents

Variation due to	D. F.	S. S.	M. S. S.	F.
Replications	3	1021.91	340.64	1.33
F_1 hybrids & parents	12	33269.86	2772.48	10.84 **
Error	36	9206.19	255.73	
Total	51	43497.96		

Significant at 1% level **

Duncan's Multiple Range Test.

97.8	117.8	121.6	131.2	133.2	133.7	137.3	141.6	159.3	164.8	167.1	175.9	192.6
V_{12}	C_8	C_1	V_1	V_{15}	C_5	C_4	C_2	C_3	C_6	C_7	V_5	V_2

Any two means underscored by the same line are not significantly different at 1% level.

Table 6

Dominant and recessive characters of F_1 hybrids

Characters	Dominant	Recessive
Stem	Tall, thick, strong	Dwarf, thin, weak
Leaf color	Green	Yellow
Leaf size	Large	Small
Leaflet	Thick	Thin
Inflorescence	Indeterminate	Determinate
Inflorescence	Simple	Compound
Flower cluster	8 to 9 flowers	3 to 4 flowers
Corky brown stem end ring size	Large	Small
Root-knot resistance	Resistant	Susceptible

Table 7

Data for the type of infection of F_2 seedlings of reciprocal crosses inoculated with Meloidogyne incognita

Reciprocal Crosses*	Repetition	Number of F_2 seedlings with indicated type of infection							
		Resistant Seedlings				Susceptible Seedlings			
		Type 0	Type I	Type II	Total	Type III	Type IV	Total	Grand Total
C_1 ; C_5	R_1	28	2	1	31	2	6	8	39
	R_2	24	1	1	26	5	6	11	37
	R_3	29	2	0	31	0	8	8	39
	R_4	26	2	1	29	3	7	10	39
C_2 ; C_6	R_1	27	2	1	30	2	8	10	40
	R_2	26	4	1	31	2	7	9	40
	R_3	27	2	0	29	1	6	7	36
	R_4	21	6	1	28	3	6	9	37
C_3 ; C_7	R_1	27	2	0	29	2	8	10	39
	R_2	31	1	0	32	1	7	8	40
	R_3	25	3	0	28	2	9	11	39
	R_4	29	3	0	32	0	8	8	40
C_4 ; C_8	R_1	22	3	2	27	4	7	11	38
	R_2	28	1	1	30	0	8	8	38
	R_3	28	2	1	31	4	5	9	40
	R_4	27	1	0	28	4	7	11	39
Total		425	37	10	472	35	113	148	620

* See test for identification. Data from reciprocal crosses added together.

Table 8

Data for the type of infection of F_2 seedlings of reciprocal crosses inoculated with Meloidogyne incognita var. acrita

Reciprocal Crosses*	Repetition	Number of F_2 seedlings with indicated type of infection							
		Resistant Seedlings				Susceptible Seedlings			
		Type 0	Type 1	Type II	Total	Type III	Type IV	Total	Grand Total
C_1 ; C_5	R_1	18	9	1	28	3	7	10	38
	R_2	23	5	2	30	1	8	9	39
	R_3	21	9	3	33	2	3	5	38
	R_4	19	4	1	24	3	6	9	33
C_2 ; C_6	R_1	22	3	2	27	0	8	8	35
	R_2	18	3	3	24	0	10	10	34
	R_3	23	3	4	30	1	9	10	40
	R_4	25	3	3	31	0	8	8	39
C_3 ; C_7	R_1	16	2	5	23	2	5	7	30
	R_2	22	2	3	27	3	6	9	36
	R_3	23	3	2	28	4	5	9	37
	R_4	23	2	2	27	5	5	10	37
C_4 ; C_8	R_1	23	3	2	28	2	7	9	37
	R_2	24	4	2	30	3	8	11	41
	R_3	28	0	2	30	4	5	9	39
	R_4	26	3	1	30	3	10	13	43
Total		354	58	38	450	36	110	146	596

* See text for identification. Data from reciprocal crosses added together.

Table 9

Data for the type of infection of F_2 seedlings of reciprocal crosses inoculated with Meloidogyne javanica

Reciprocal Crosses*	Repetition	Number of F_2 seedlings with indicated type of infection							
		Resistant Seedlings				Susceptible Seedlings			
		Type 0	Type I	Type II	Total	Type III	Type IV	Total	Grand Total
C_1 ; C_5	R_1	24	5	0	29	5	4	9	38
	R_2	22	5	3	30	3	3	6	36
	R_3	18	6	2	26	3	7	10	36
	R_4	23	8	0	31	5	4	9	40
C_2 ; C_6	R_1	22	3	3	28	4	6	10	38
	R_2	18	10	4	32	5	3	8	40
	R_3	22	4	2	28	6	7	13	41
	R_4	22	5	3	30	5	3	8	38
C_3 ; C_7	R_1	21	5	2	28	4	3	7	35
	R_2	24	4	1	29	2	7	9	37
	R_3	22	3	2	27	5	5	10	38
	R_4	24	3	1	28	5	5	10	38
C_4 ; C_8	R_1	27	4	1	32	5	4	9	41
	R_2	20	2	3	25	3	5	8	33
	R_3	20	7	0	27	4	6	10	37
	R_4	22	6	4	32	2	8	10	42
Total		351	81	30	462	66	80	146	608

* See text for identification. Data from reciprocal crosses added together.

Table 10

A summary of the classification of the reaction of the F_2 seedlings to Meloidogyne incognita, with chi-square test for each cross

Cross	Resistant Seedlings	Susceptible Seedlings	Total	Ratio	X^2	P. Value
C_1	59	19	78	3:1	.017	.80 to .90
C_5	58	18	76	3:1	.070	.70 to .80
C_2	58	17	75	3:1	.217	.60 to .70
C_6	60	18	78	3:1	.154	.60 to .70
C_3	61	18	79	3:1	.206	.60 to .70
C_7	60	19	79	3:1	.038	.80 to .90
C_4	59	20	79	3:1	.004	.90 to .98
C_8	57	19	76	3:1	.000	0 to 1.0
Total	472	148	620		.706	

Table 11

A summary of the classification of the reaction of the F_2 seedlings to Meloidogyne incognita var. acrita, with chi-square test for each cross

Cross	Resistant Seedlings	Susceptible Seedlings	Total	Ratio	X^2	P. Value
C_1	56	16	72	3:1	.296	.50 to .70
C_5	59	17	76	3:1	.281	.50 to .70
C_2	56	20	76	3:1	.070	.70 to .80
C_6	56	16	72	3:1	.296	.50 to .70
C_3	55	18	73	3:1	.004	.90 to .98
C_7	50	17	67	3:1	.005	.90 to .98
C_4	60	20	80	3:1	.000	0 to 1.0
C_8	58	22	80	3:1	.266	.60 to .70
Total	450	146	596		1.218	

Table 12

A summary of the classification of the reaction of the F_2 seedlings to *Meloidogyne javanica*, with chi-square test for each cross

Cross	Resistant Seedlings	Susceptible Seedlings	Total	Ratio	X^2	P. Value
C_1	59	18	77	3:1	.108	.70 to .80
C_5	57	16	73	3:1	.369	.50 to .70
C_2	61	19	80	3:1	.066	.70 to .90
C_6	57	20	77	3:1	.039	.80 to .90
C_3	57	19	76	3:1	.000	0 to 1
C_7	55	17	72	3:1	.074	.70 to .80
C_4	60	18	78	3:1	.154	.60 to .70
C_8	56	19	75	3:1	.004	.90 to .98
Total	462	146	608		.814	

Table 13

A summary of the classification of the reaction of the F_2 seedlings to Meloidogyne incognita, M. incognita var. acrita and M. javanica, with chi-square test for all the seedlings inoculated with pure inoculum of each root knot nematode species

Root-Knot Nematode Species	Resistant Seedlings	Susceptible Seedlings	Ratio	X^2	P. Value
Meloidogyne incognita	472	148	3:1	.42	.50 to .70
Meloidogyne incognita var. acrita	450	146	3:1	.081	.70 to .80
Meloidogyne javanica	462	146	3:1	.32	.50 to .70

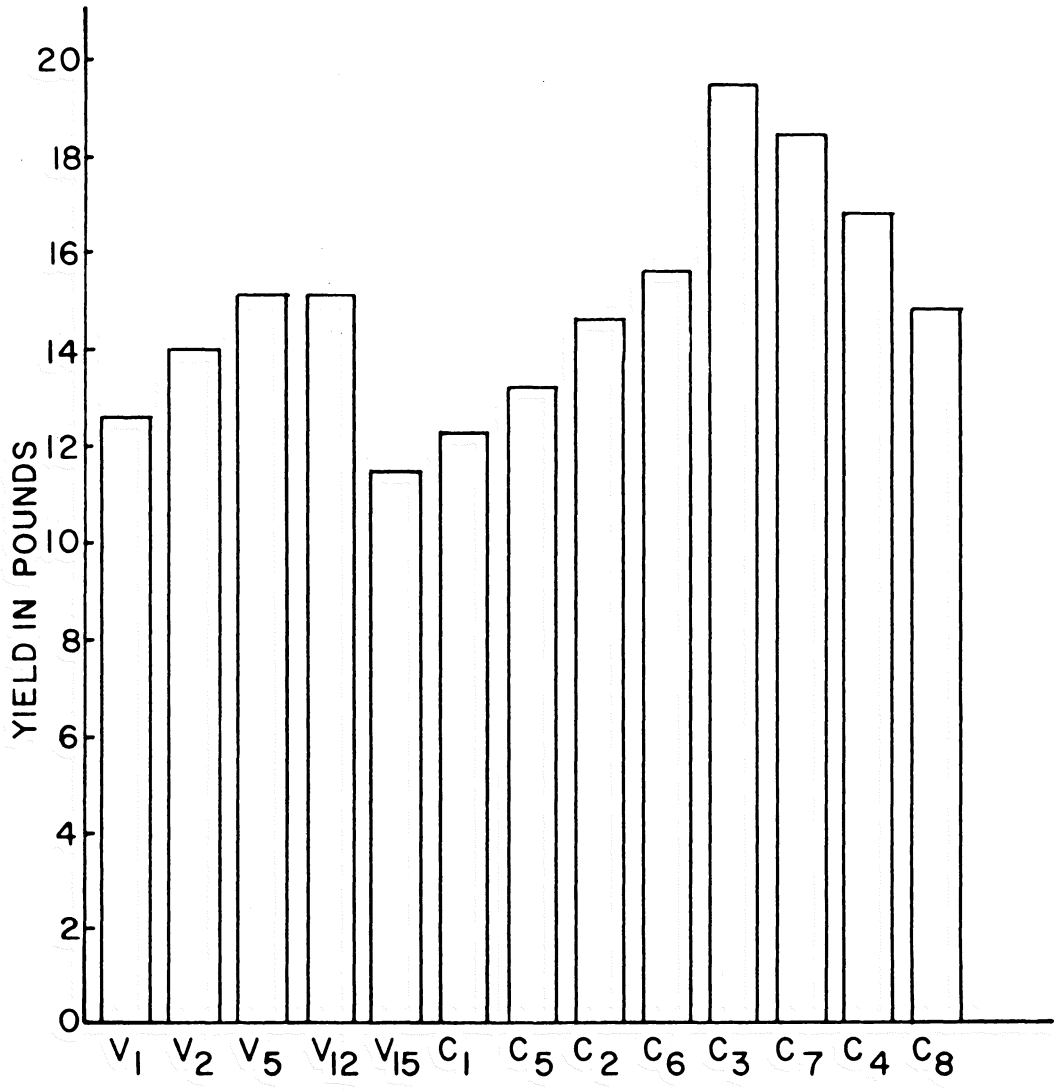


Fig. 1. — Yield of fruit in pounds per plant of F_1 hybrids and their parents.

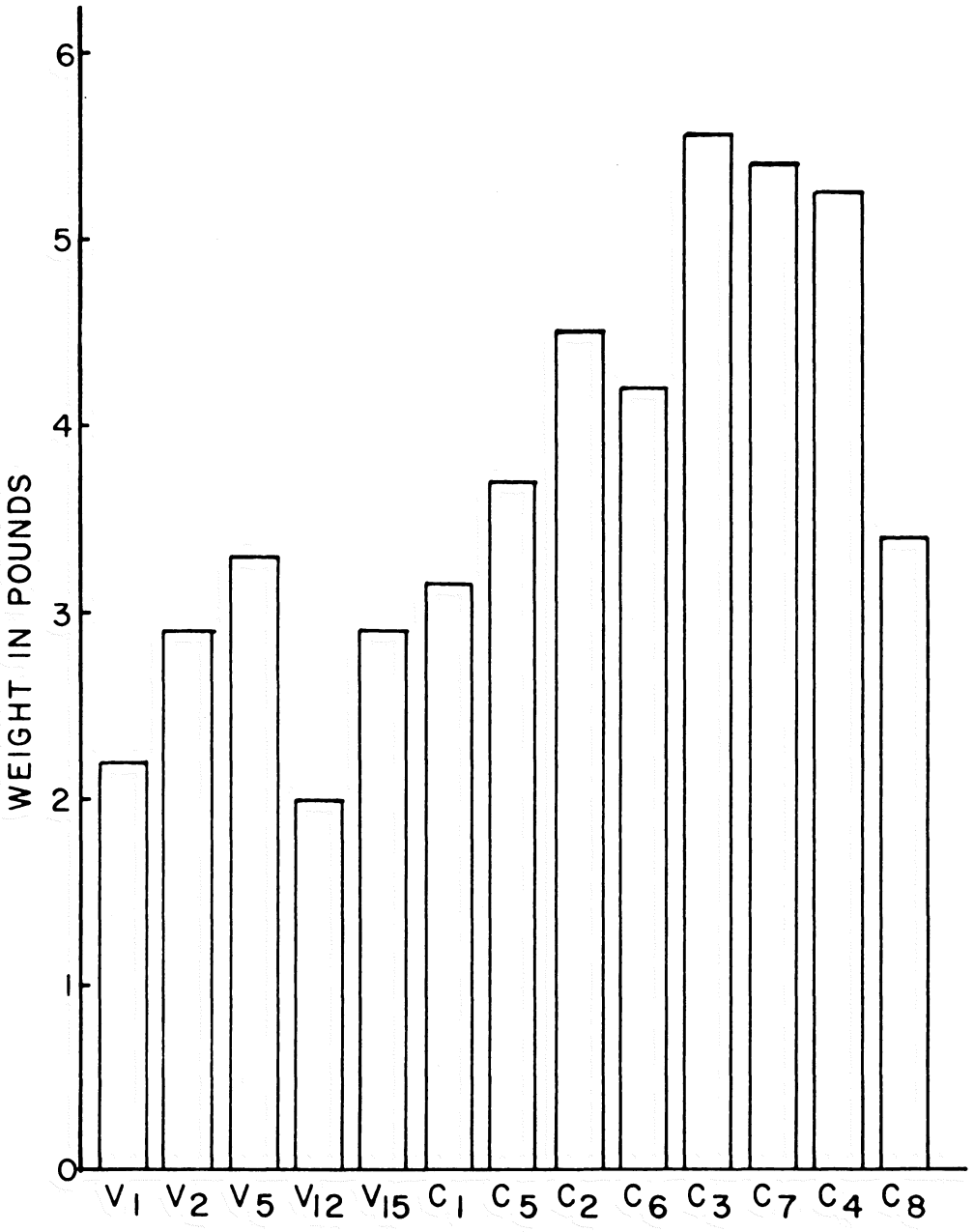


Fig. 2. — Fresh weight in pounds per plant (stem, roots, and leaves) of F_1 hybrids and their parents.

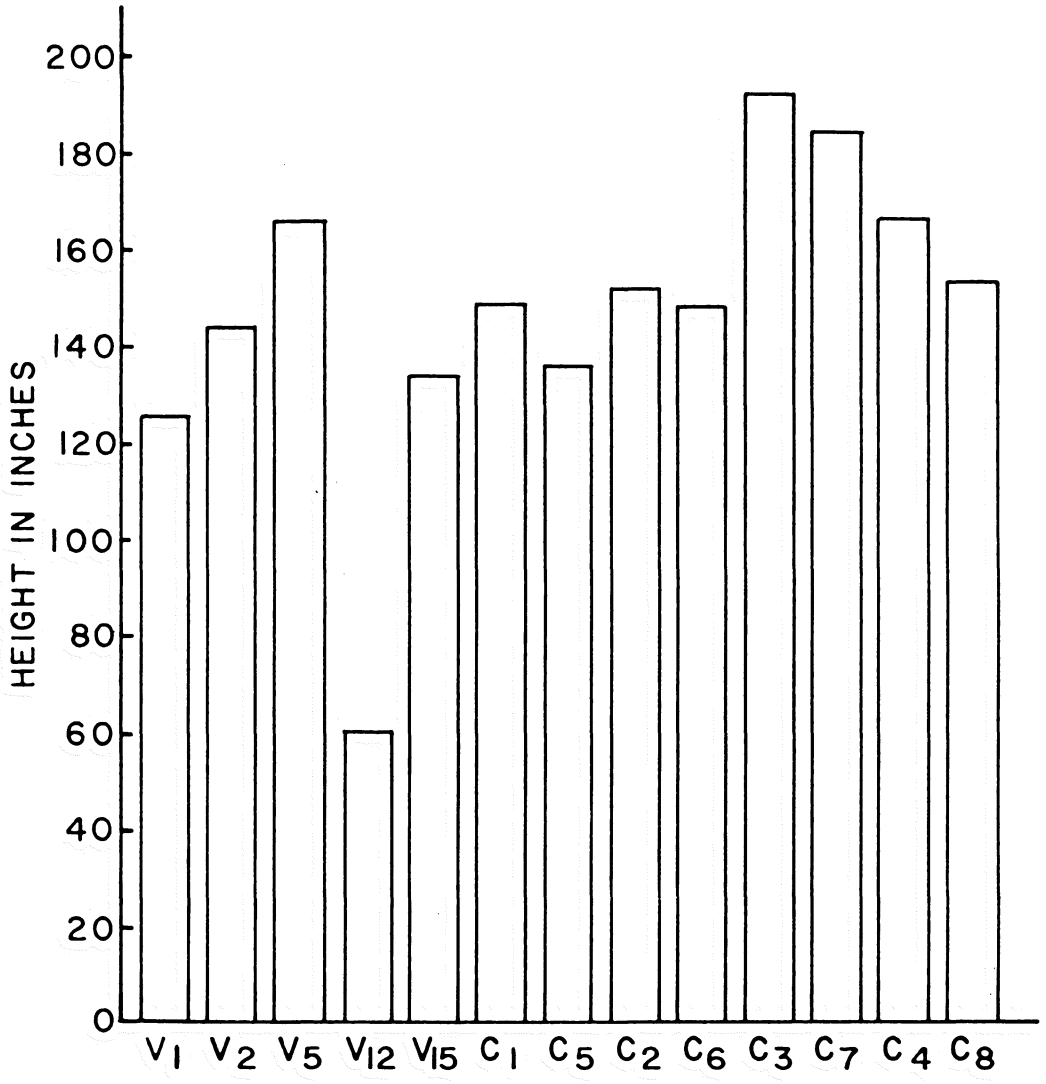


Fig. 3. — Height in inches per plant of F_1 hybrids and their parents.

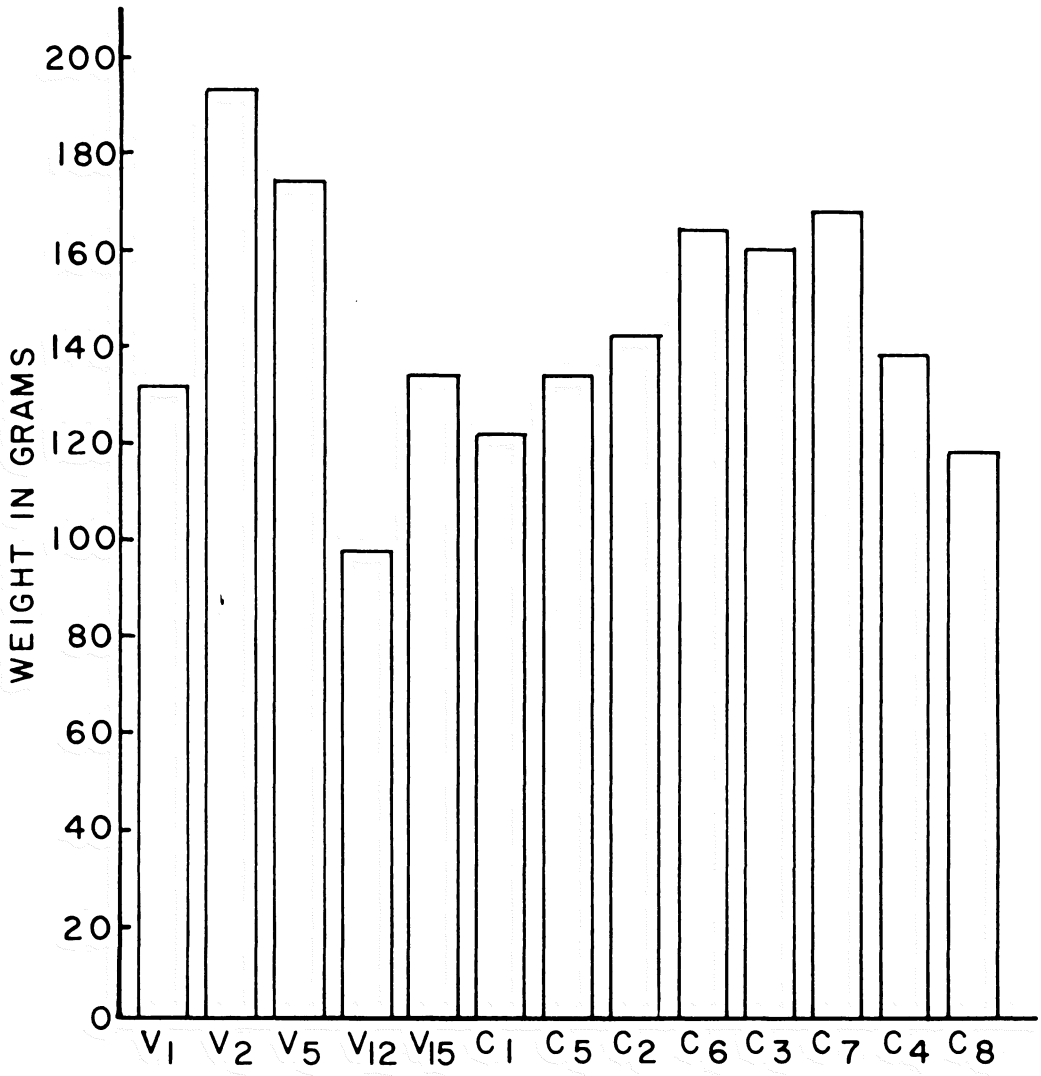


Fig.4.— Average weight in grams of fruit of F_1 hybrids and their parents.

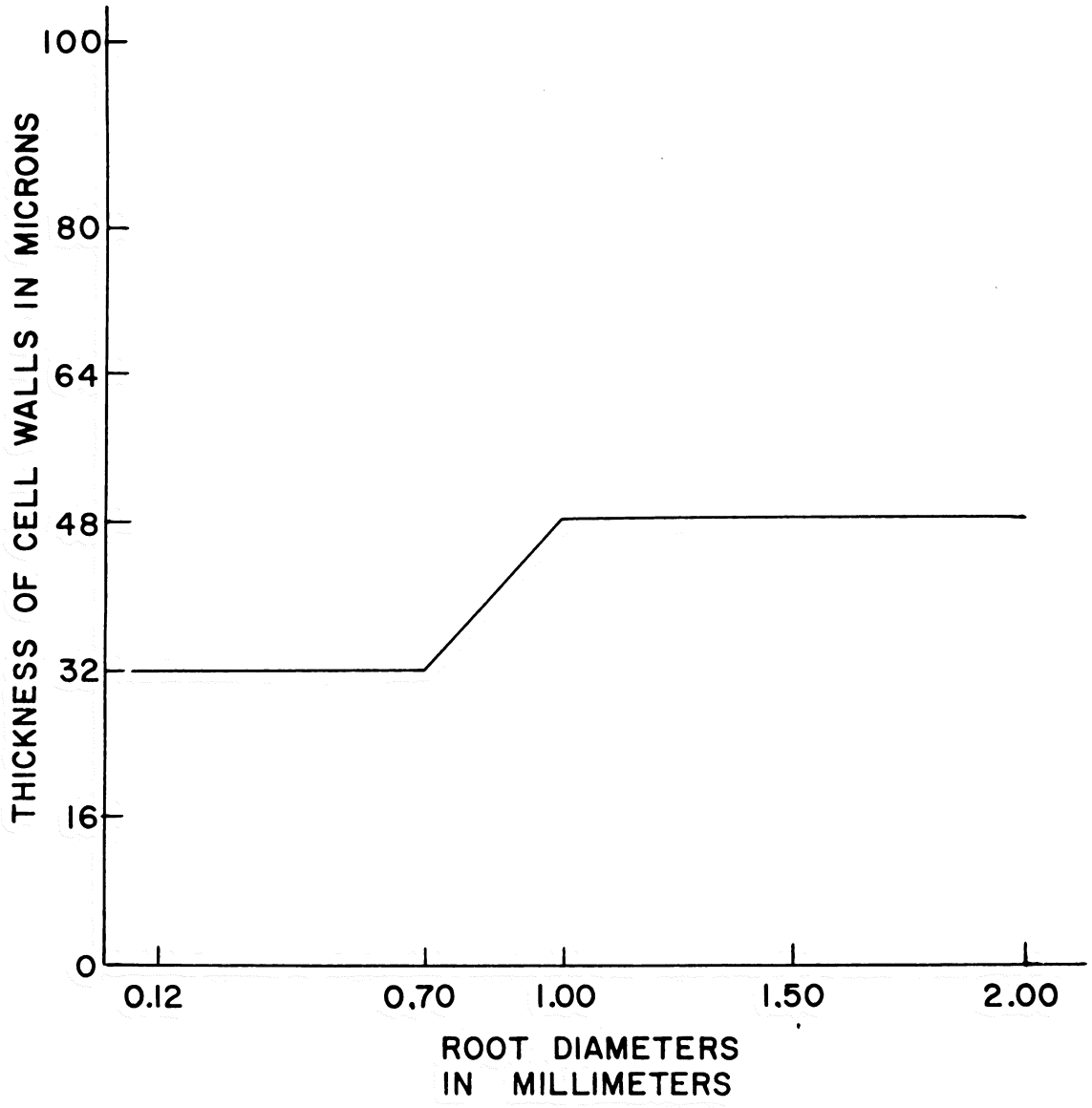


Fig. 5. — Comparison of cell wall thickness of susceptible and resistant tomato varieties of different root diameters. No measurable differences were observed in the cell wall thickness of resistant and susceptible varieties.

Plate 1. Infection Type 0. No infection or if larvae entered the roots, they did not develop into mature egg-laying females 50 days after inoculation.

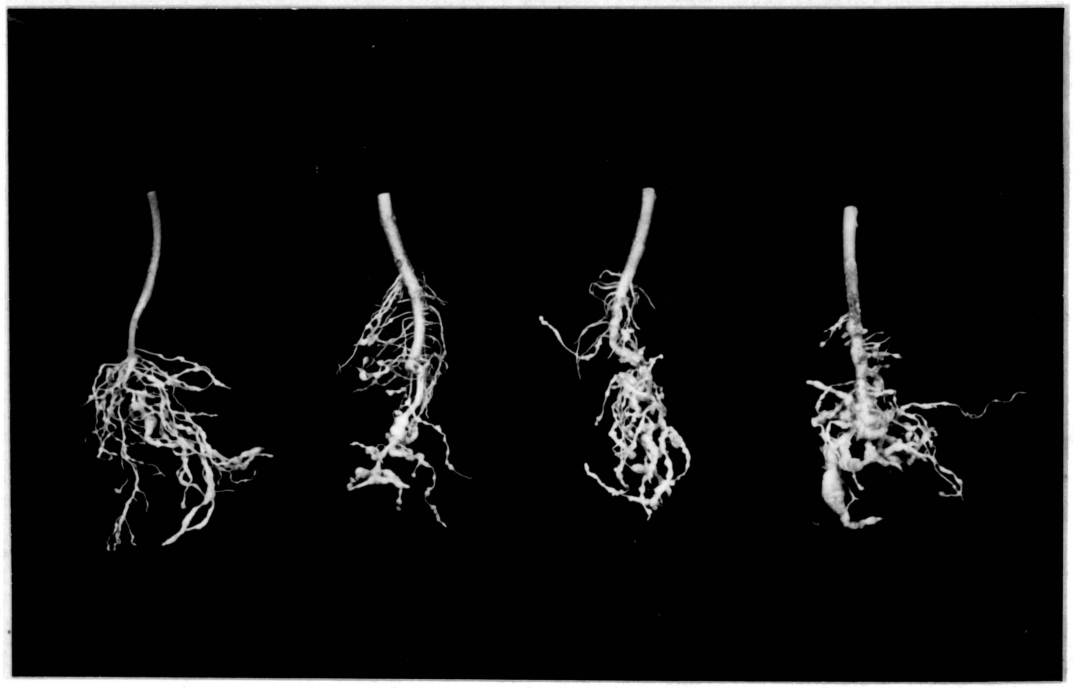
Plate 2. Infection Type I. Extremely light infection with only an occasional mature, female with egg-mass usually very small, laid on the surface of the roots 50 days after inoculation. Only a few tiny galls, usually on the secondary roots.

Plate 3. Infection Type II. Light infection with mature females and egg-masses easily seen with naked eye 50 days after inoculation. Several small galls, usually on the secondary roots but no large galls on secondary roots or on tap-root.

Plate 4. Infection Type III. Moderate infection with full grown females and egg-masses moderately abundant 50 days after inoculation. One or more galls somewhat larger than any in Type II infection but smaller than Type IV infection. Galls usually present on tap root.

Plate 5. Infection Type IV. Severe infection with mature females and egg-masses very abundant 50 days after inoculation.

Plate 6. V_1, V_2, V_5, V_{12}, and V_{15} are the parental varieties. V_1, V_2, V_5, V_{12} were resistant and V_{15} was susceptible to root-knot nematodes.



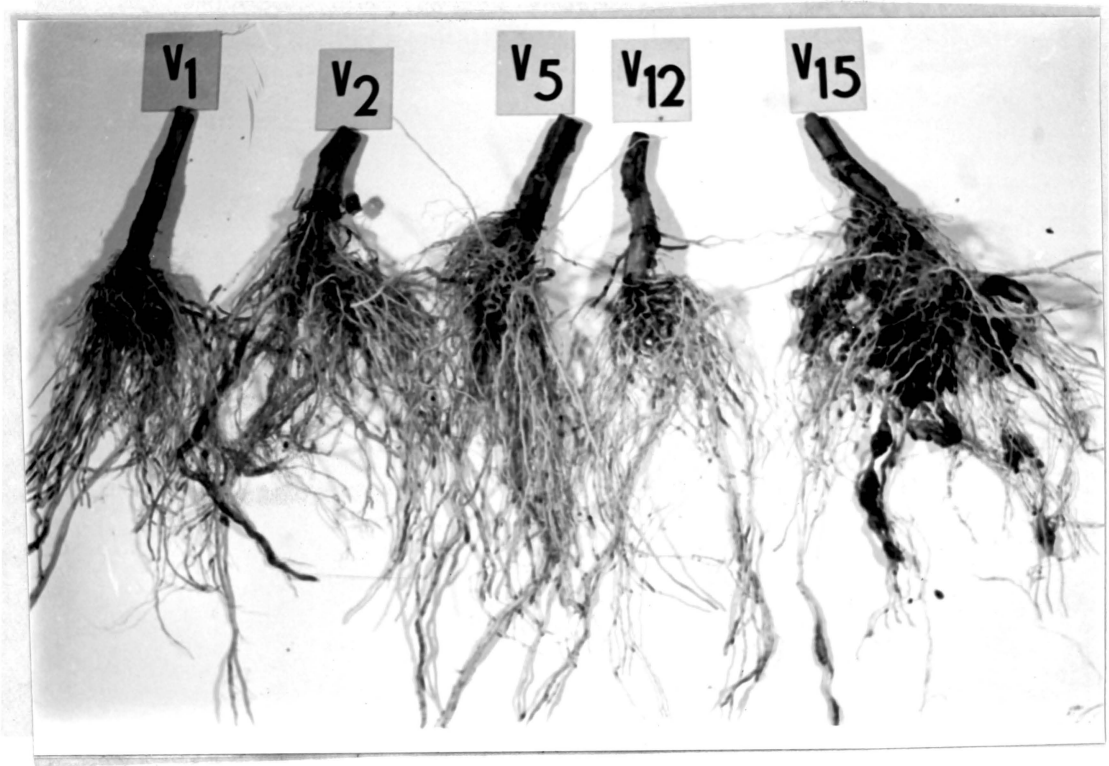
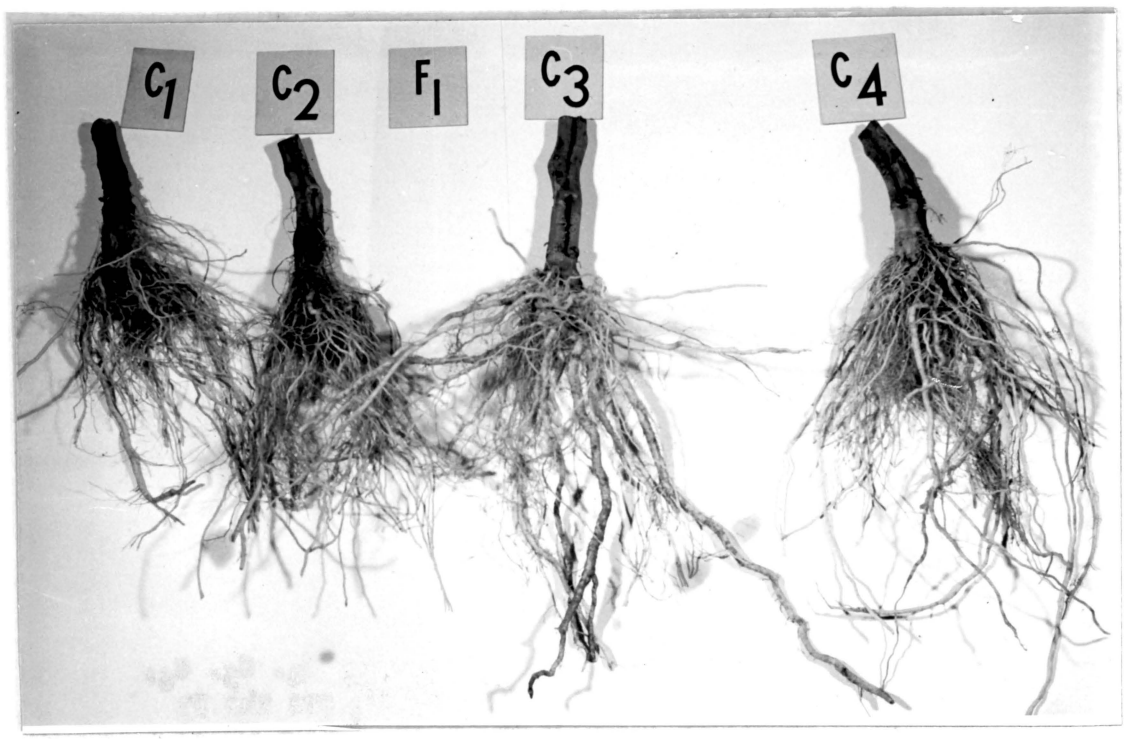

V1
V2
V5
V12
V15

Plate 7 and Plate 8. C_1, C_2, C_3, C_4, C_5, C_6, C_7, and C_8 are the F_1 hybrids of reciprocal crosses. All F_1 hybrids were resistant to M. incognita, M. incognita var. acrita, and M. javanica. No galling on roots.


C1
C2
F1
C3
C4

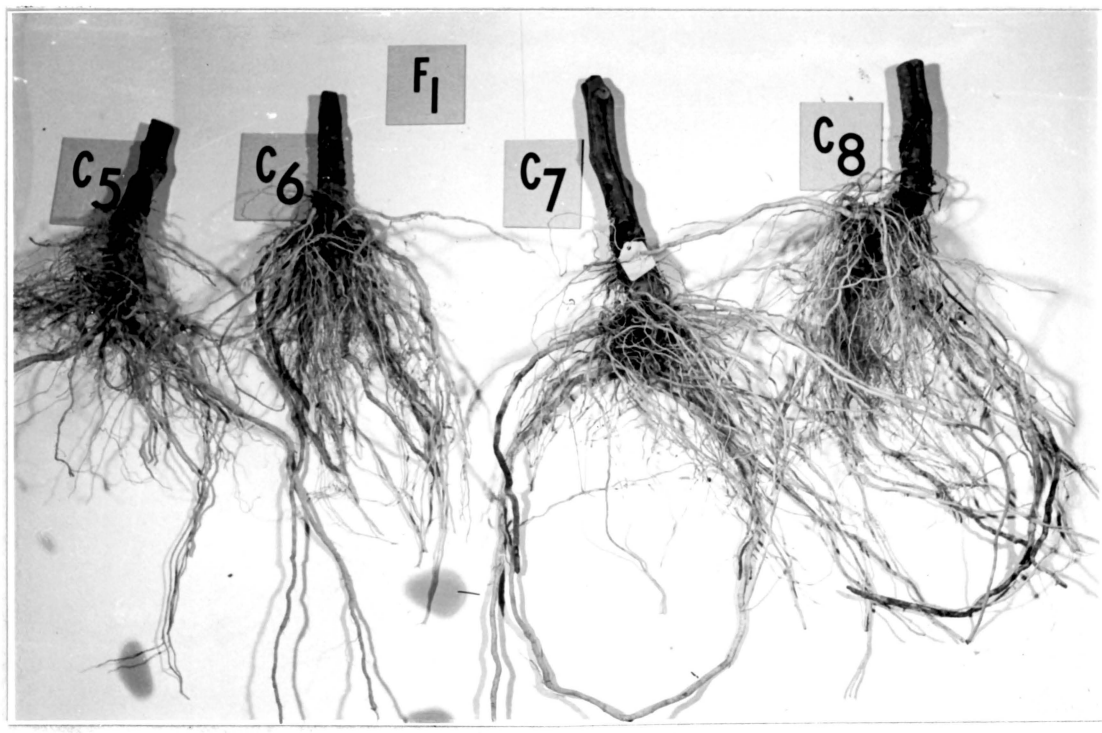

F1
C5
C6
C7
C8

Plate 9. A. 100 ml beaker containing egg-masses of M. arenaria in moist and in aerobic conditions, kept in a 150 ml beaker containing distilled water and covered with a Petri-dish in order to avoid drying of inoculum at room temperature. Eggs were being hatched.

B. Hypodermic needle used for placing inoculum on the roots of tomato seedlings.

C. Larvae of M. arenaria in distilled water suspension. Larvae were separated from egg-masses every 24 hours.

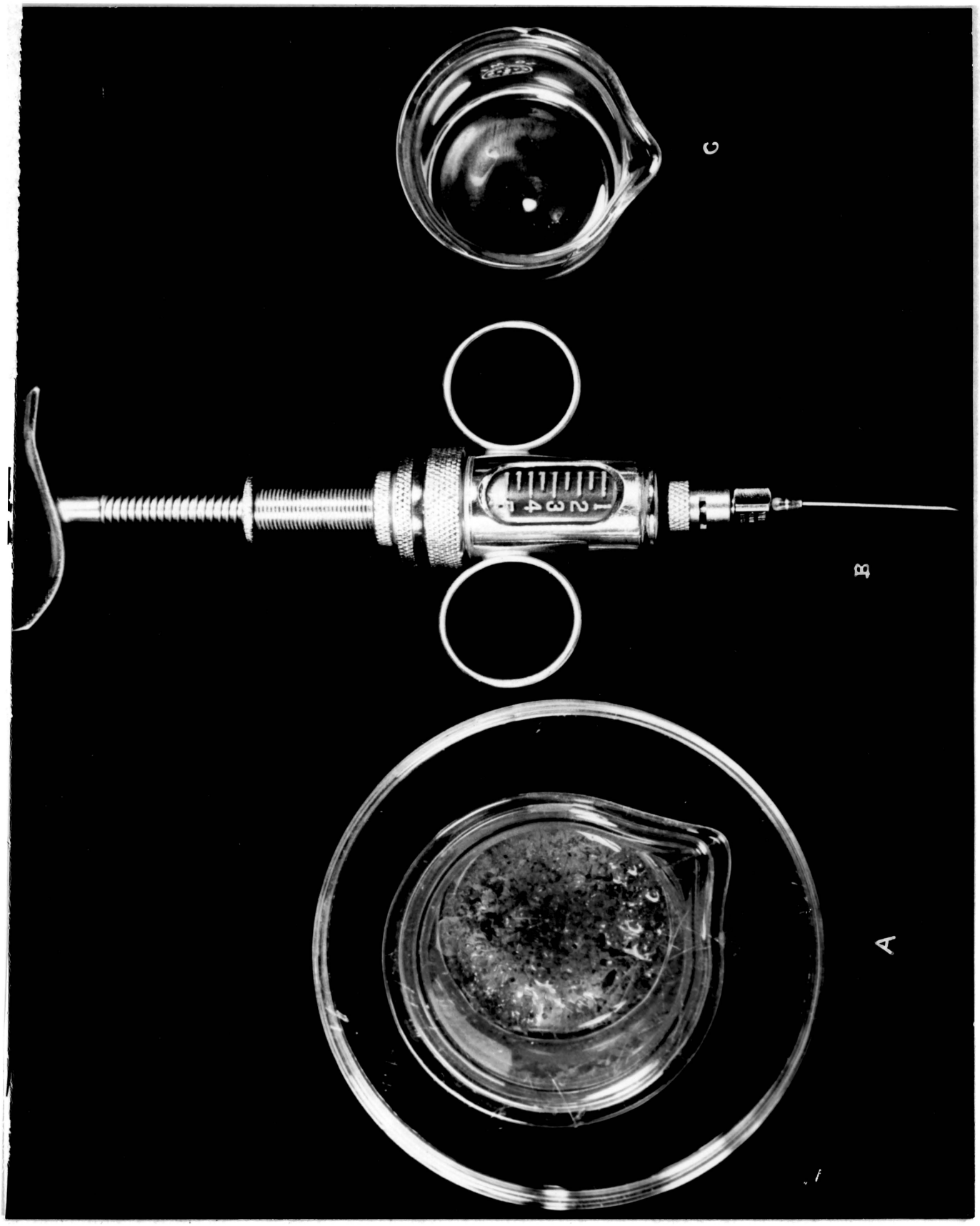

A
B
C

Plate 10. A, B, C, D, and E. The growth regulating frames in which V_{15} seedlings were inoculated with 2000 larvae of M. javanica. Roots were killed in 4.5% formaldehyde solution at 24, 36, 48, 60, and 72 hour intervals.

Plate 10. In F, G, H, I, and J. Growth regulating frames in which V_2 seedlings were inoculated with 2000 larvae of M. javanica. Roots were killed in 4.5% formaldehyde solution at 24, 36, 48, 60, and 72 hour intervals.

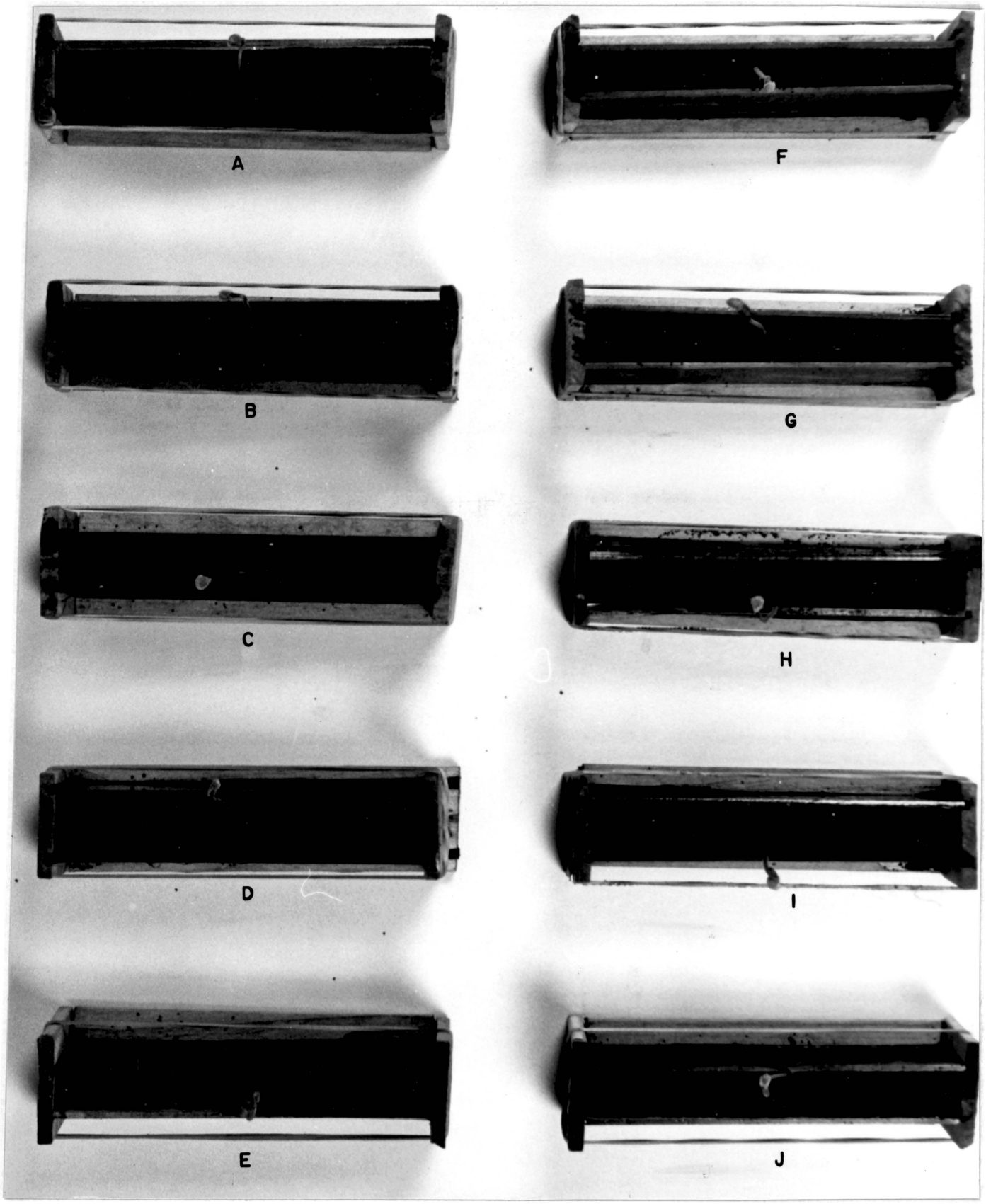
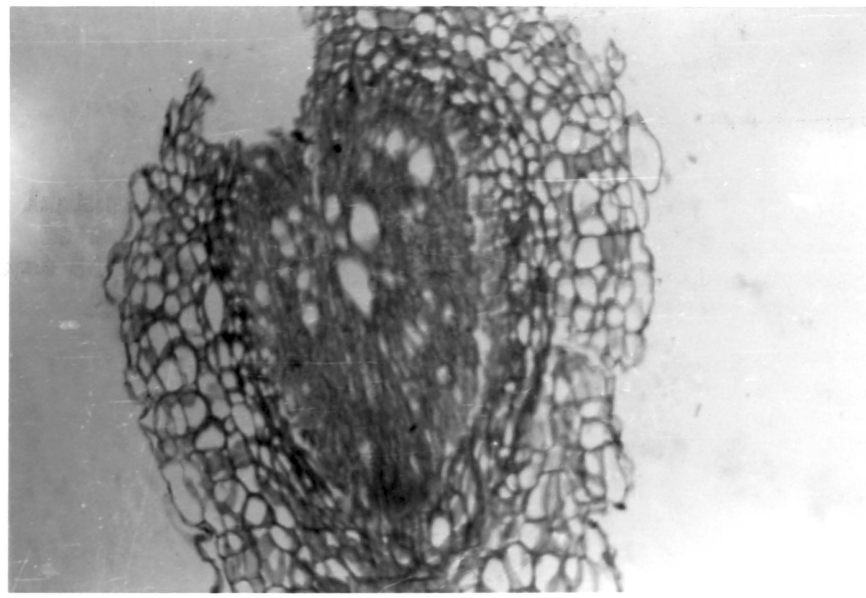

A
F
B
G
C
H
D
I
E
J

Plate 11. Type 0 infection. Longitudinal section of noninfected root of tomato seedling grown for 50 days in inoculum of M. incognita (X 100).

Plate 12. Type IV infection 50 days after inoculation. Longitudinal section of a susceptible tomato root infected with M. incognita var. acrita showing pronounced hypertrophy of the cells.

A. Head region of a larva.
B. Giant cells around the head region of the larva. (X 100).



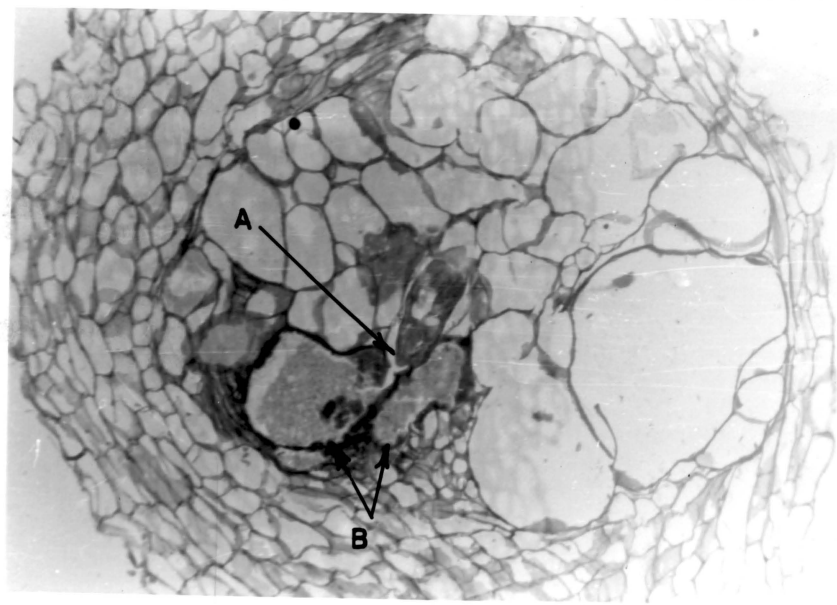
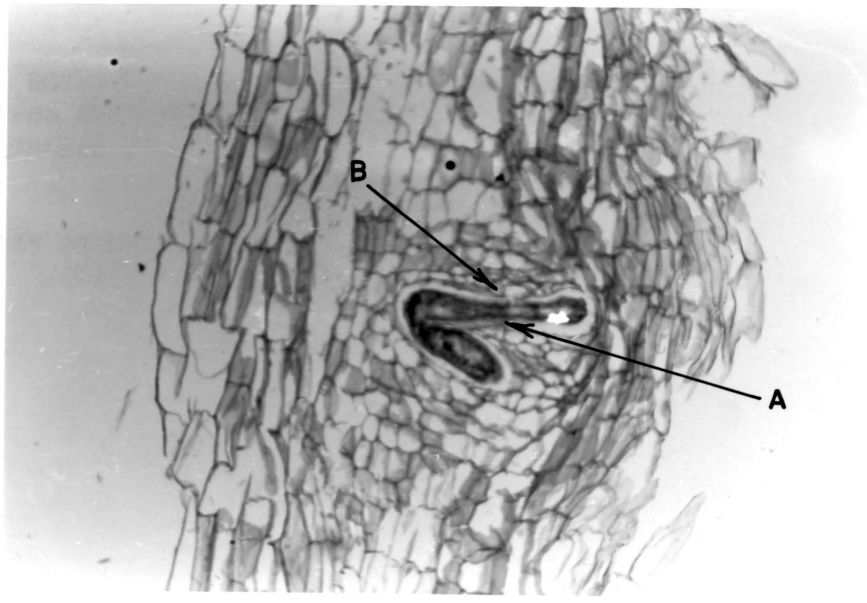

A
B

Plate 13. Type II infection 50 days after inoculation. A longitudinal section of a resitant tomato root infected with M. incognita.
A. Larva in the stele.
B. Proliferated cells around the body of the nematode. (X 100).

Plate 14. Type II infection 50 days after inoculation. Longitudinal section of a resistant tomato root infected with M. incognita var. acrita.
A. Adult female
B. Giant cells
C. Irregular xylem elements. (X 100).


B
A

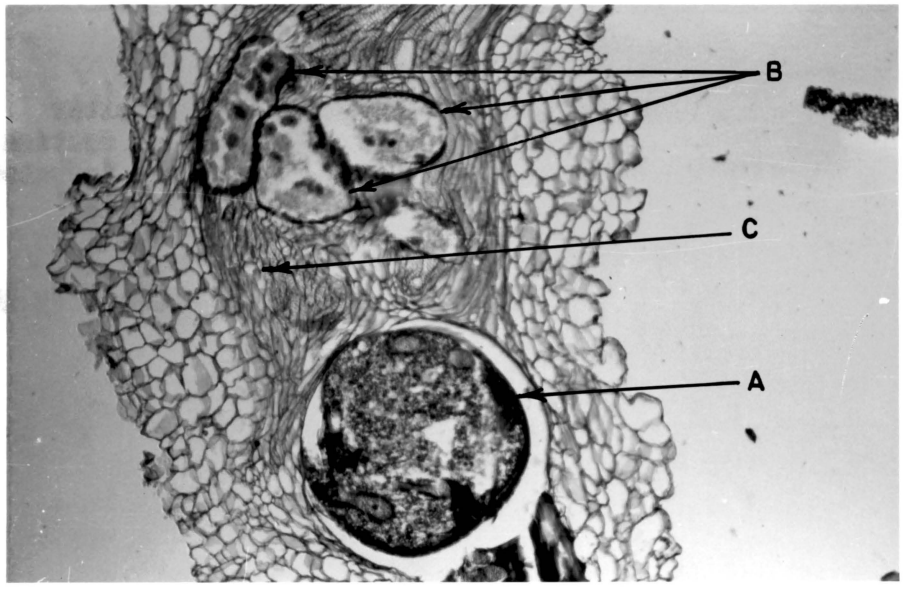
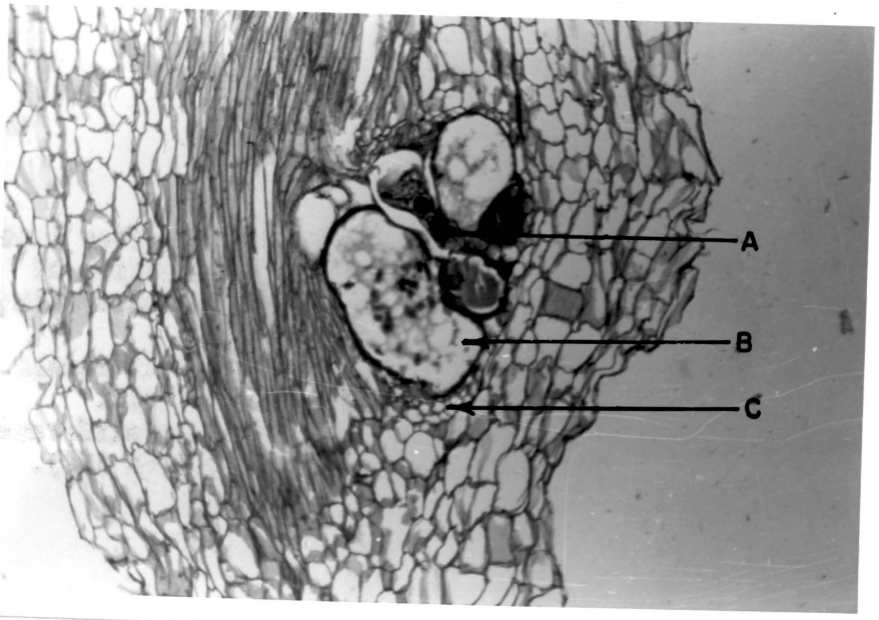

B
C
A

Plate 15. Type II infection 50 days after inoculation. A longitudinal section of resistant tomato root infected with M. arenaria.
A. Head region of the adult female.
B. 22 nuclei in a giant cell.
C. Parenchymatous cells proliferated around the giant cell (X 100).

Plate 16. Type IV infection 50 days after inoculation. Transverse section of susceptible tomato root infected with M. arenaria.
A. Head of a larva in the stele.
B. Giant cells clustered around the head region of larva. (X 430).


A
B
C

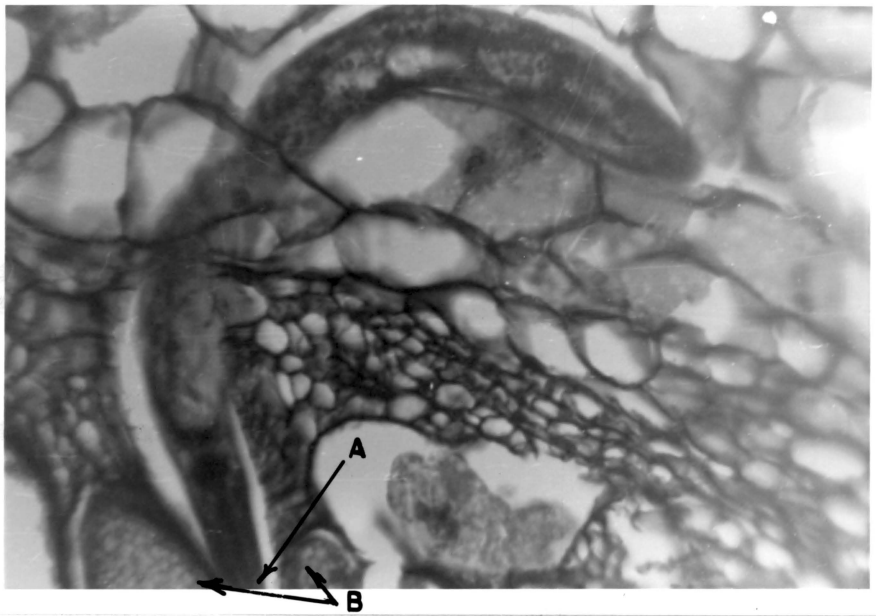
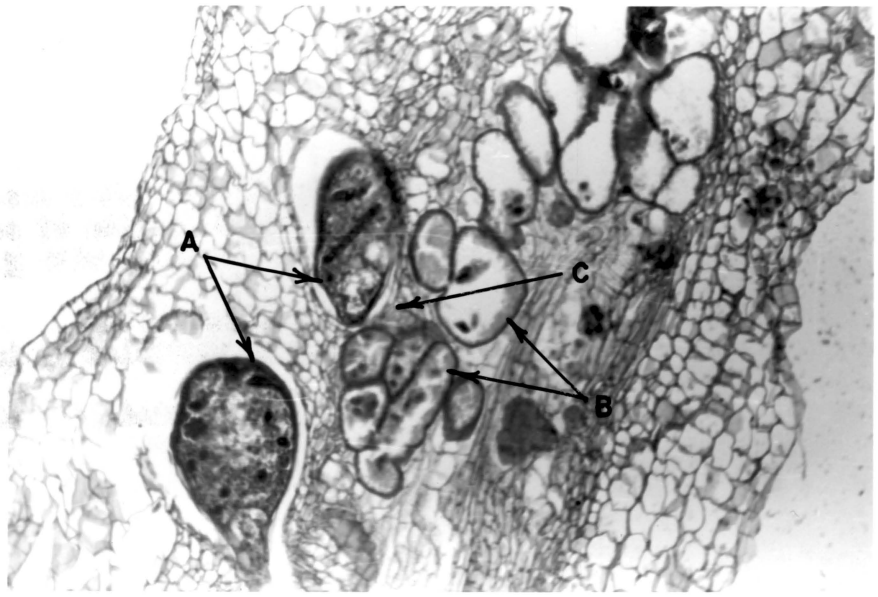

A
B

Plate 17. Type III infection 50 days after inoculation. A longitudinal section of susceptible tomato root infected with M. incognita var. acrita.
A. Adult females in the cortex.
B. Giant cells in the vascular cylinder.
C. Xylem elements dislocated. (X 100).

Plate 18. Type I infection 50 days after inoculation. A longitudinal section of resistant tomato root infected with M. incognita var. acrita.
A. A giant cell in the cortex with thick cell wall.
B. Large nuclei in the giant cell. (X 430).


A
C
B

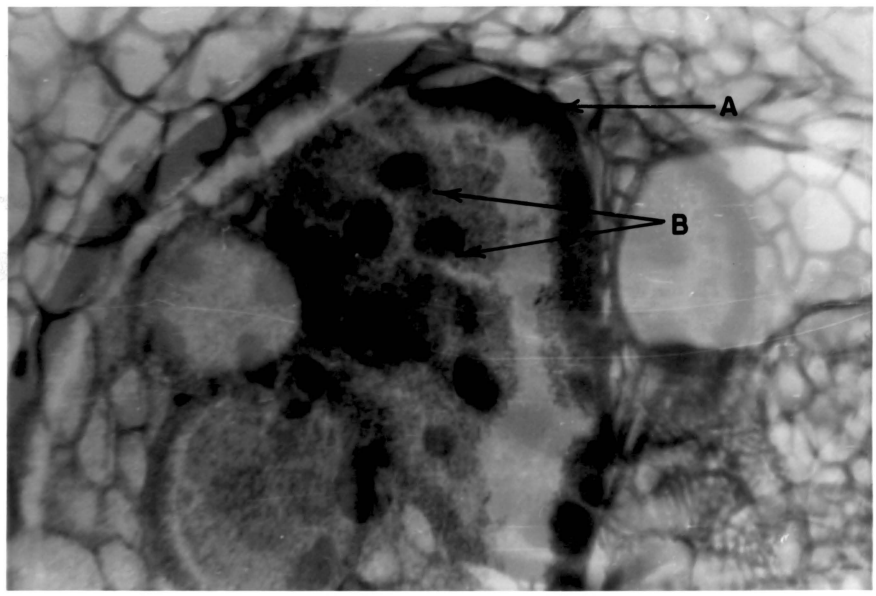

A
B

Plate 19. Type I infection 50 days after inoculation. A longitudinal section of resistant tomato root infected with M. arenaria.
A. Head of a larva.
B. Proliferated cells in the cortex around the head region of a larva. (X 430)

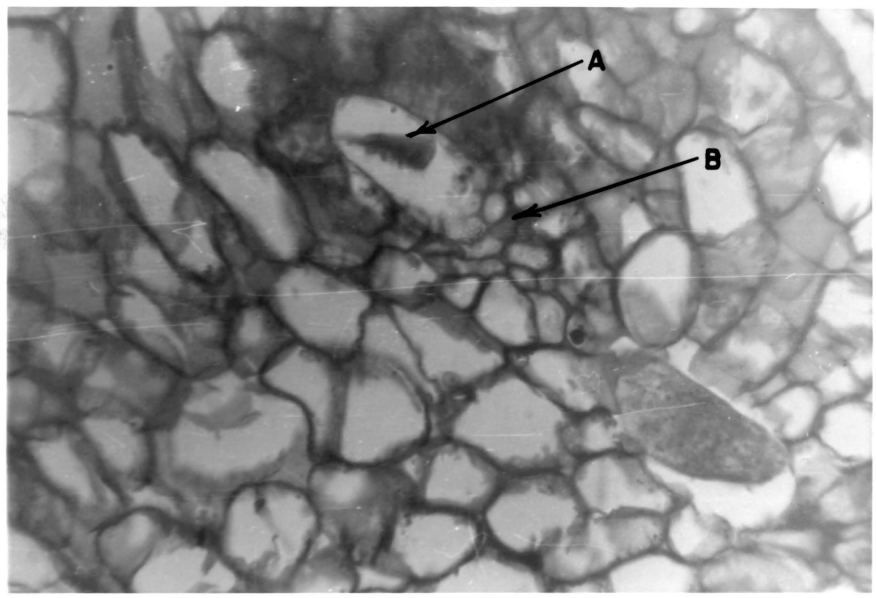
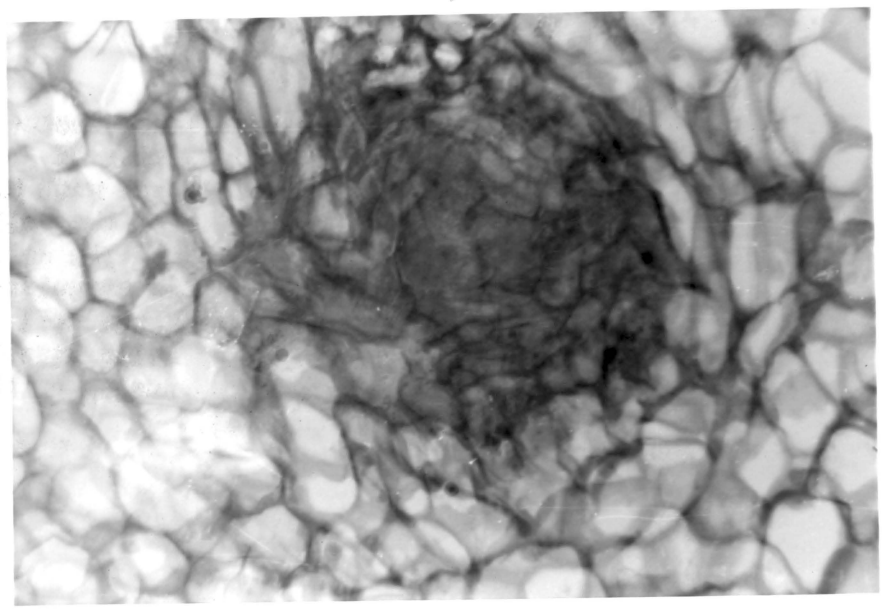

A
B

Plate 20. Type I infection 50 days after inoculation. A longitudinal section of resistant tomato root infected with M. arenaria shows a condition of the cells before giant cell formation. The cells were proliferated due to the stimulation of the larva and ultimately the cell walls of the proliferated cells dissolved. Protoplasmic contents and nuclei of the cells coalesced. (X 430).

Plate 21. Type I infection 50 days after inoculation. A longitudinal section of resistant tomato root infected with M. arenaria showing the formation of a giant cell.

A. Two giant cells formed.
B. Nuclei.
C. Proliferated cells around the giant cells. (X 430).



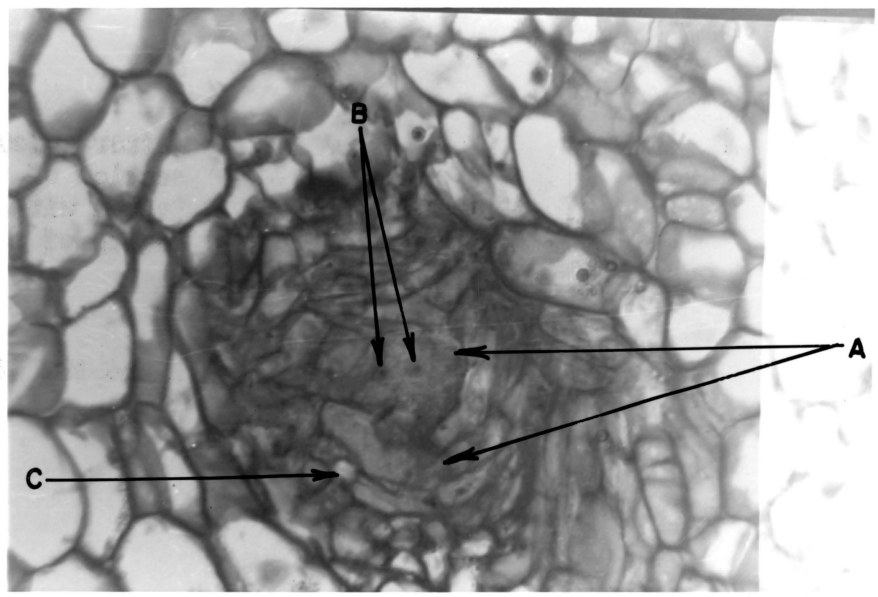
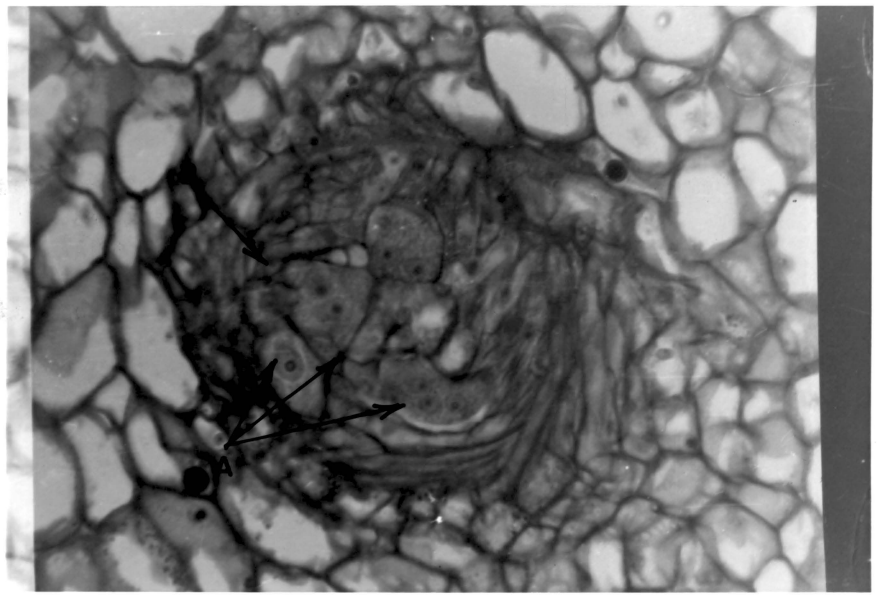

B
A
C

Plate 22. Type I infection 50 days after inoculation. A longitudinal section of resistant tomato of a giant cell.
A. Newly formed giant cells.
B. Giant cells surrounded by proliferated cells. (X 430).

Plate 23. Type IV infection 50 days after inoculation. Transverse section of susceptible tomato infected with M. hapla showing 14 giant cells clustered around the head of a larva. (X 100).


A

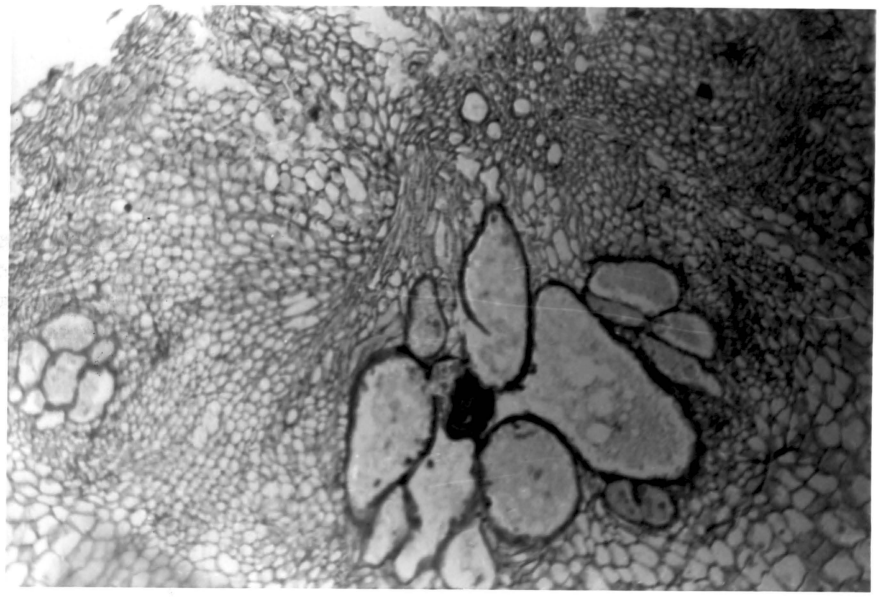
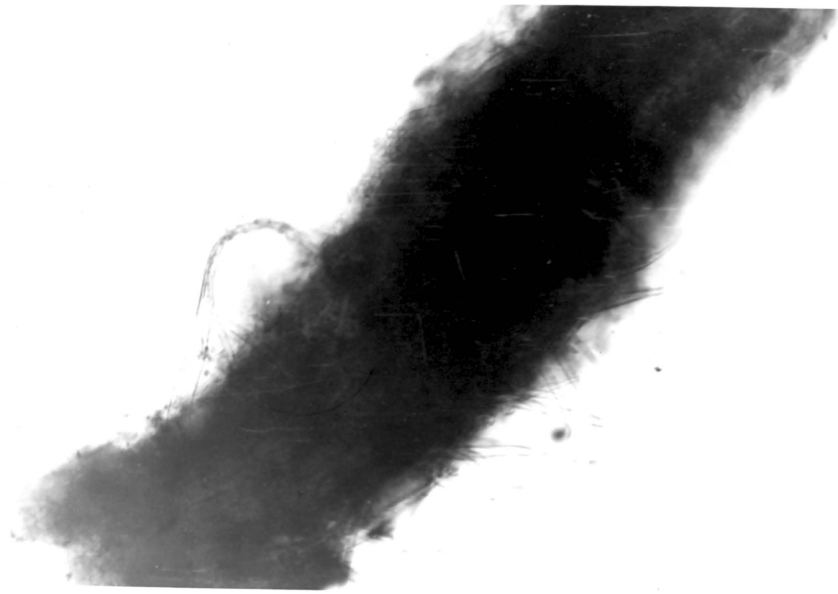


Plate 24. A susceptible (V_{15}) tomato root 24 hours after inoculation with 2000 larvae of M. incognita. Many larvae penetrated the root. (X 100).

Plate 25. A resistant (V_2) tomato root 24 hours after inoculation with 2000 larvae of M. incognita. Only two larvae penetrated the root. (X 100).



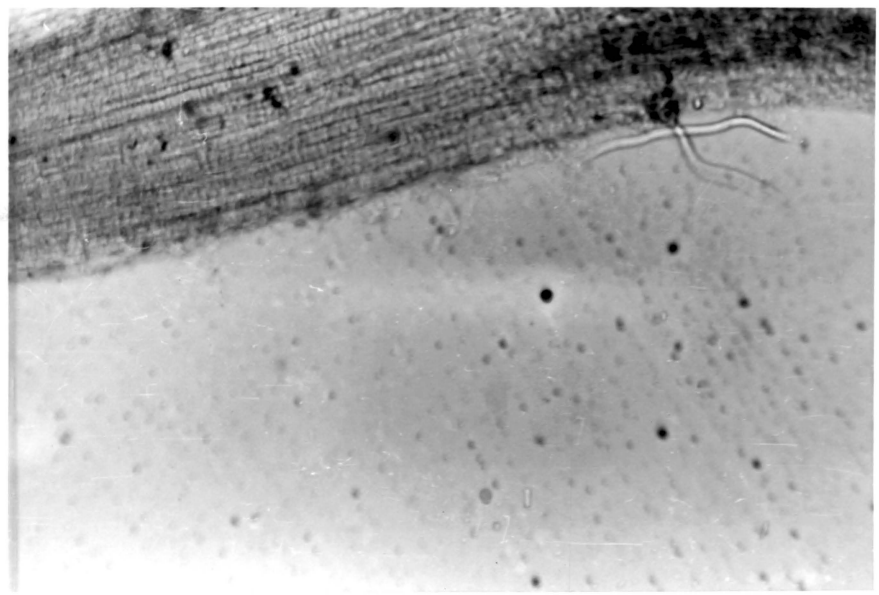
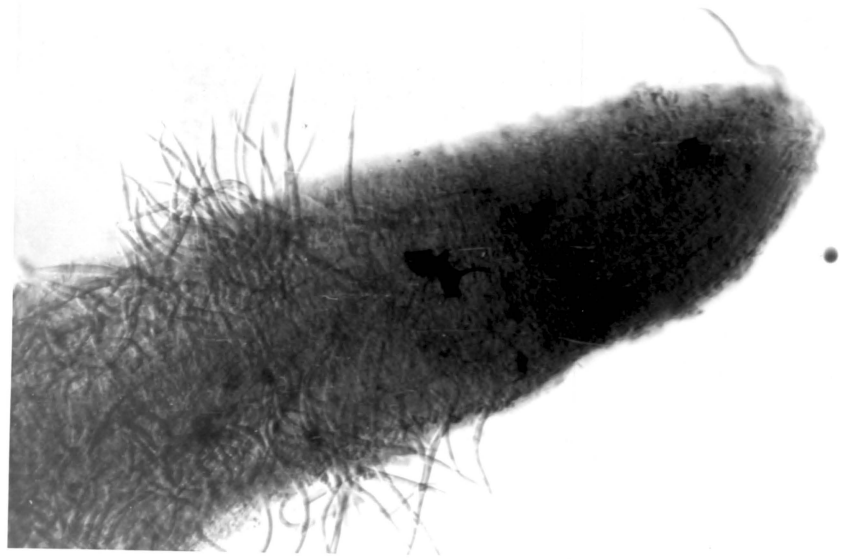


Plate 26. A susceptible (V_{15}) tomato root 36 hours after inoculation with 2000 larvae of M. javanica. Some larvae are embedded inside the root and many of them are half embedded. One larva is attached to the root tip. Larvae penetrated the root behind the root cap. (X 100).

Plate 27. A resistant (V_2) tomato root 36 hours after inoculation with 2000 larvae M. javanica. Some larvae penetrated root and others remained partially embedded. (X 100).



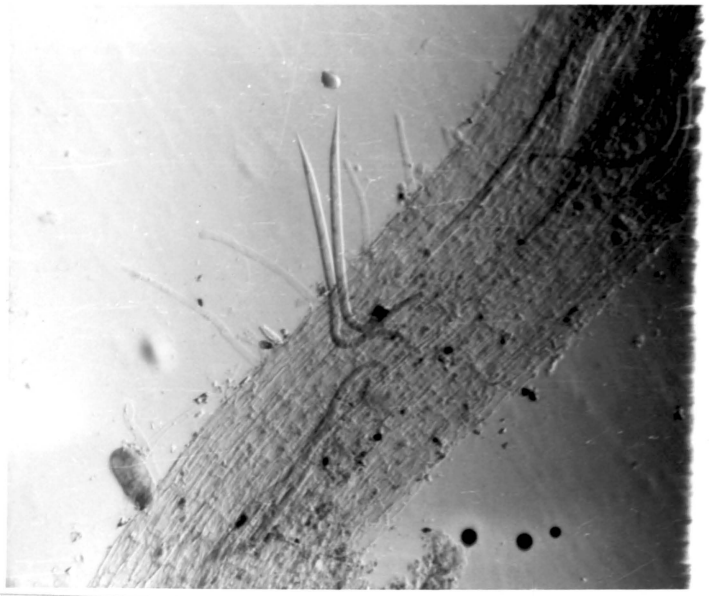
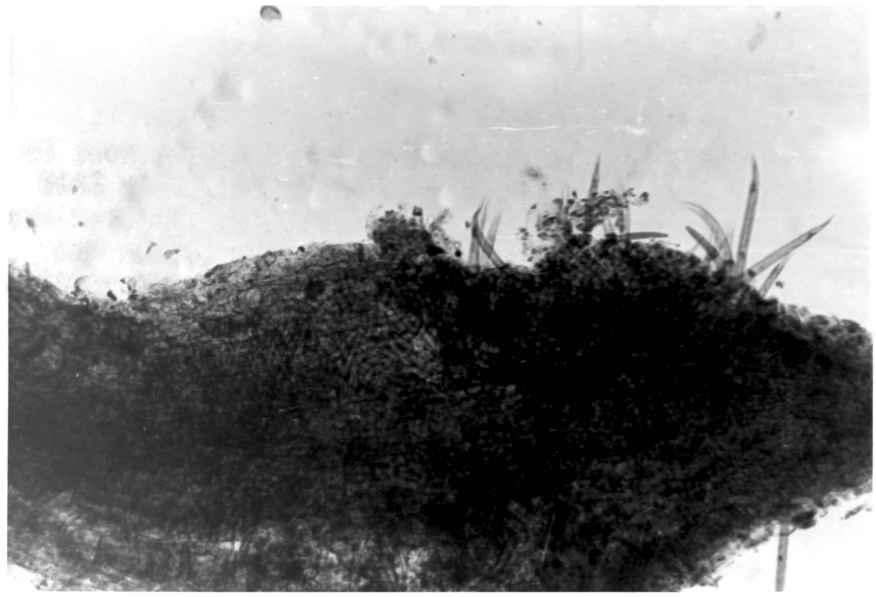


Plate 28. A susceptible (V_{15}) tomato root 48 hours after inoculation with 2000 larvae of M. incognita var. acrita. Many larvae are completely embedded inside the root while others were partially embedded. Swelling became pronounced above the root-cap. (X 100).

Plate 29. A resistant (V_2) tomato root 48 hours after inoculation with 2000 larvae of M. incognita var. acrita. A few larvae penetrated the root and others remained half embedded. (X 100).

Plate 30. A susceptible (V_{15}) tomato root 60 hours after inoculation with 2000 larvae of M. javanica. Most of the larvae are completely inside the root with only a few larvae partially inside. Swelling is prominent. (X 100).

Plate 31. A resistant (V_2) tomato root 60 hours after inoculation with 2000 larvae of M. javanica. A few larvae penetrated the root and others remained half embedded. No swelling of the root occurred. (X 100).



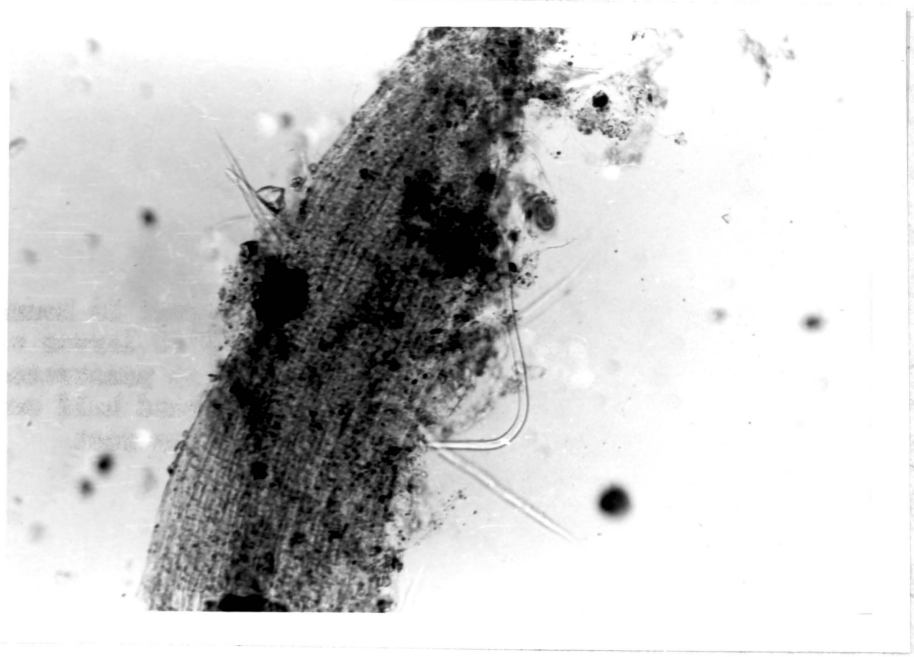
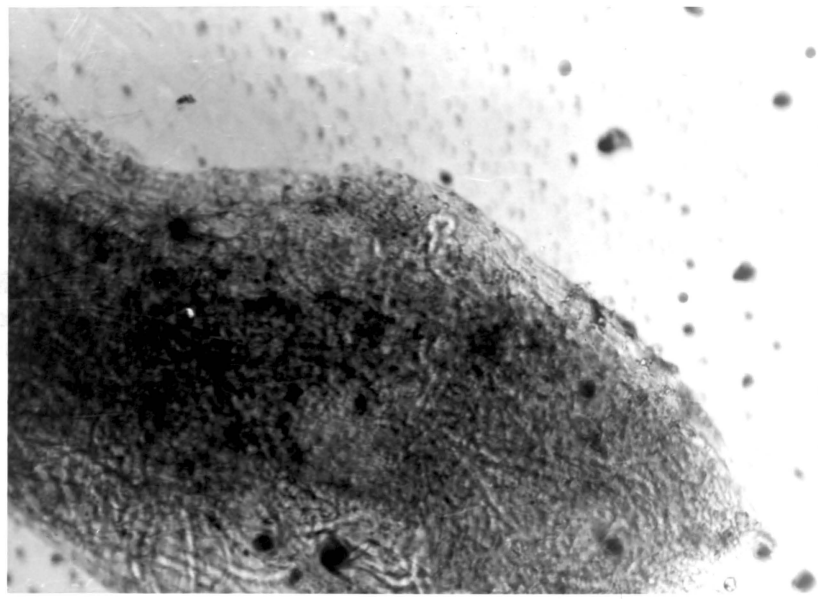


Plate 32. A susceptible (V_{15}) tomato root 72 hours after inoculation with 2000 larvae of M. incognita. All larvae penetrated the root. Root became considerably swollen (X 100).

Plate 33. A resistant (V_2) tomato root 72 hours after inoculation with 2000 larvae of M. incognita. Two larvae have partially penetrated the root. No swelling occurred. (X 100).



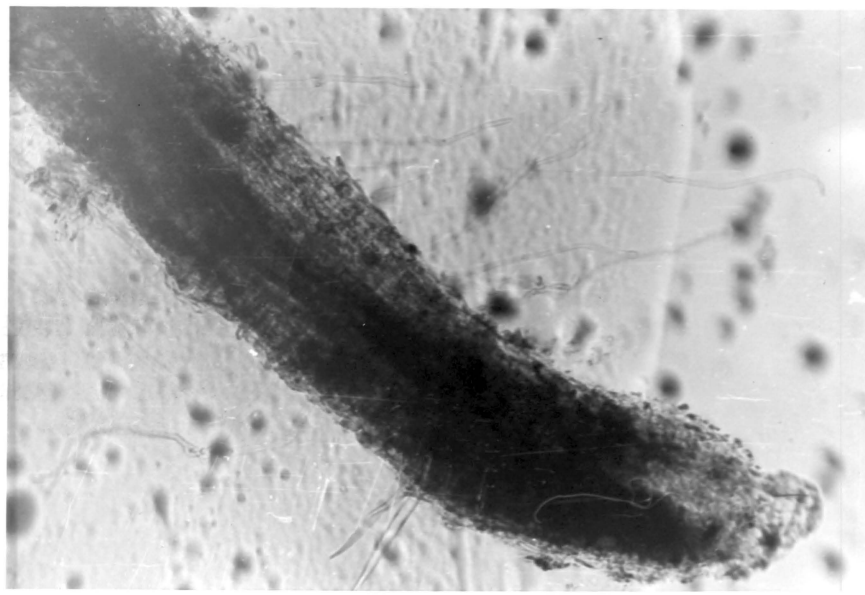
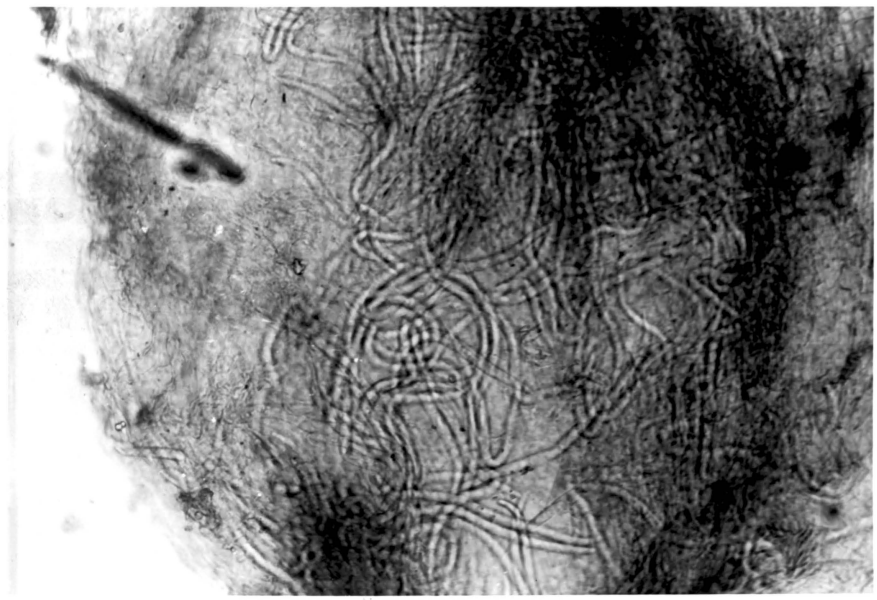


Plate 34. A susceptible (V_{15}) tomato root 96 hours after inoculation with 2000 larvae of M. javanica. A pronounced swelling resulted as many larvae penetrated the root. (X 100).

Plate 35. A resistant (V_2) tomato root 96 hours after inoculation with 2000 larvae of M. javanica. Many larvae only partially embedded. No swelling of the root. (X 100).



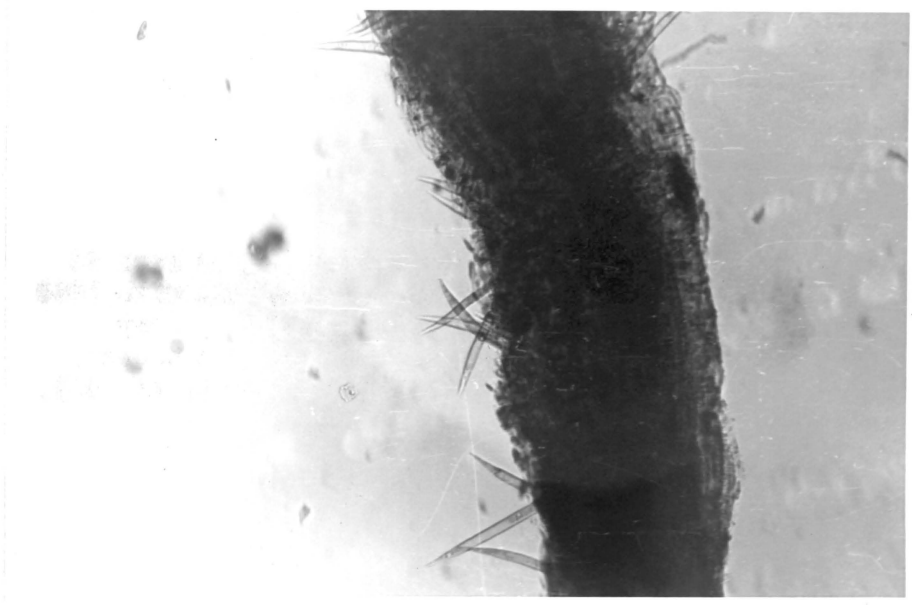


Plate 36. A resistant (V_2) tomato root 96 hours after inoculation with 8000 larvae of M. incognita. Many larvae have penetrated the root. The resistant seedling appeared to be susceptible when high concentration of inoculum was used. (X 100).

Plate 37. A susceptible (V_{15}) tomato secondary root 60 hours after inoculation with M. incognita. Many larvae entered the secondary root while migrating toward the growing point. (X 100).

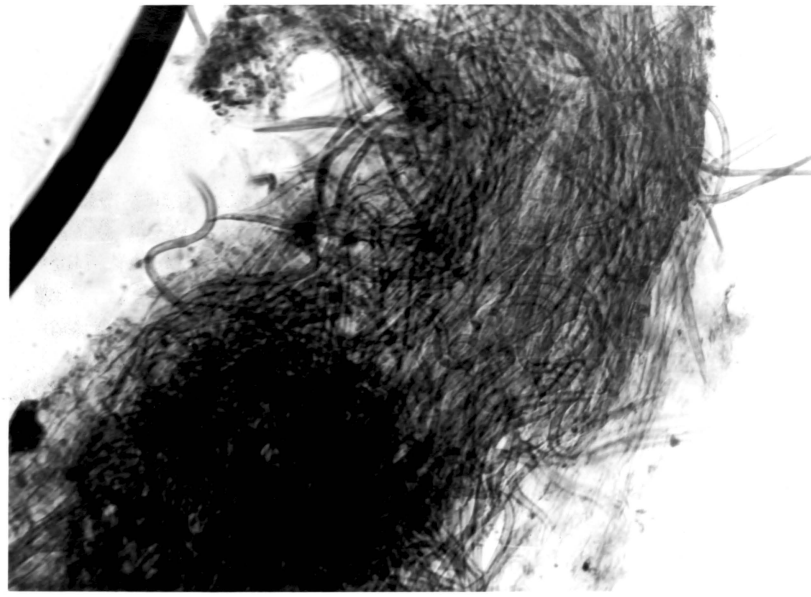
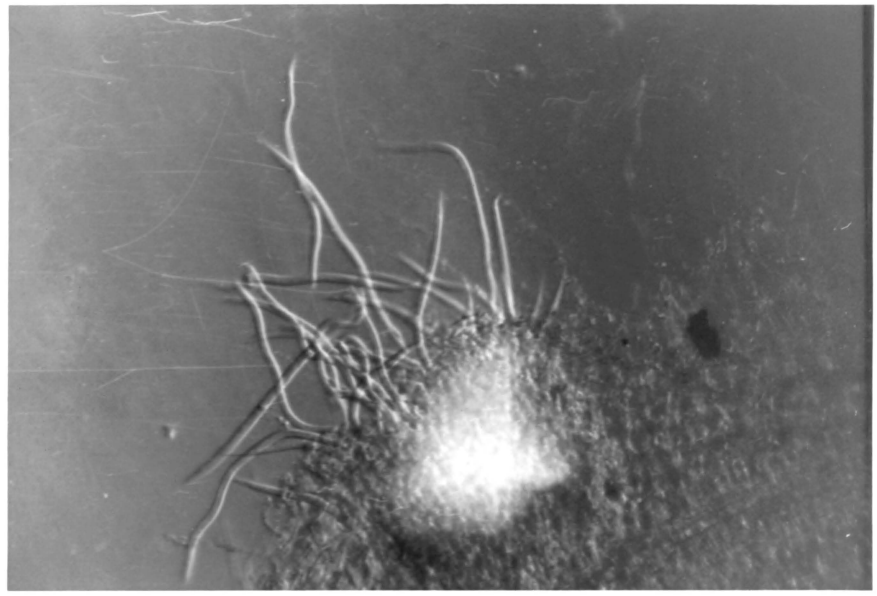


Plate 38. A susceptible (V_{15}) tomato root primordium 60 hours after inoculation with 2000 larvae of M. javanica. Shows larvae penetrating the root primordium (X 100).

Plate 39. A susceptible (V_{15}) tomato root primordium 48 hours after inoculation with 2000 larvae of M. incognita var. acrita. Larvae are grouped around the area of lateral root emergence. (X 100).



ABSTRACT

A study was undertaken to investigate the morphological host-parasite interactions of selected resistant and susceptible lines of tomato to Meloidogyne incognita, M. incognita var. acrita, M. javanica, M. hapla and M. arenaria and to determine the mode of inheritance of nematode resistance and the number of genetic factors controlling resistance to the root-knot nematodes.

Four resistant varieties of tomato were crossed with one susceptible variety. The F_1 populations showed hybrid vigor for height, yield, and fresh weight of roots, stems, and leaves. Resistance to M. javanica, M. incognita, M. incognita var. acrita was dominant and susceptibility was recessive. The F_2 populations segregated in a 3:1 ratio showing resistance is a monofactorial dominant character and controlled by the same gene. The resistant parents, and the F_1 and F_2 populations did not show resistance to M. hapla and M. arenaria.

Anatomical studies showed that there were some slight differences between resistant and susceptible varieties. In resistant varieties a compact layer of cells was formed around the body of the nematode which may have caused the noticeable reduction in nematode development and egg-formation. Giant cells formed in resistant varieties were much smaller and fewer in number than in susceptible varieties. The contrast between these two reactions by the resistant and the susceptible hosts suggests that resistance is related to the cellular response of the host to the parasite. In the root penetration and attraction study it was observed that when 2000 larvae were used as inoculum, they freely penetrated the

roots of susceptible seedlings whereas in resistant roots very few larvae entered and most remained half embedded in the roots even at the 96 hour interval after inoculation. When the concentration of the larvae inoculum was increased from 2000 to 8000 per seedling, the larvae entered the roots of resistant seedlings as freely and as rapidly as they entered the roots of susceptible ones, demonstrating that the concentration of inoculum is an important factor in penetration.