STUDIES ON IDENTIFICATION AND HOST-PARASITE RELATIONSHIPS OF THE COMMON ROOT-KNOT NEMATODES (MELOIDOGYNE SPP.) WITH SPECIAL REFERENCE TO MARYLAND

By

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INTRODUCTION AND REVIEW OF LITERATURE

Root knot, a plant disease caused by nematodes of the genus *Meloidogyne*, Göldi, 1887,[1] was first reported by Berkeley (5)[2] in 1855 on cucumber roots taken from an English greenhouse. The first printed reference to root-knot in the United States is that of J. N. May (16) in which he states that he saw the disease on violets in 1876. Monographs of Neal (19) and Atkinson (2) in 1889, Stone and Smith (27) in 1898 and Bessey (4) in 1911[3] constitute the first extensive investigations on the disease in this country. These early American workers obviously recognized that nematodes causing root knot were obligate parasites since they recommended control by growing non-susceptible crops, and probably were the first to recommend crop rotation for control of this disease. The discovery, however, that root-knot nematodes are obligate parasites should be credited to Göldi (14) who in 1887 studied the embryology and development of a root-knot nematode infecting coffee in Brazil, which he called *Meloidogyne exigua*. He observed that young larvae would hatch in the laboratory but would not develop further. He knew, however, that they could complete their life cycle in roots of certain plants.

Various developmental stages in the life cycle of a root-knot

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[1]Nematodes of this genus were formerly grouped under the genus *Heterodera marioni* (Cornu, 1879) Goodey, 1932.

[2]Numbers in parentheses refer to literature cited (21).

[3]This was apparently the first published mention of occurrence of root knot in Maryland.

nematode are shown in Figures 1 and 2. Eggs (Fig. 1-A and B) laid by the adult female (Fig. 2) develop into larvae (Fig. 1-C) which migrate through the soil and enter roots of host plants. In the roots, the larvae migrate to a position near the axial cylinder and become sedentary. Here they begin to feed and rapidly become sausage-shaped (Fig. 1-D). At this point the last of four molts take place. Females become pear-shaped (Fig. 1-G and Fig. 2), while males are transformed into elongated eel-shaped worms about 1.3 mm. long (Fig. 1-E and F). The full grown females which measure about 0.8 mm. long by 0.5 mm. wide produce an average of 300 to 600 eggs which are deposited in a mass held together by a jelly-like substance (Fig. 2). Males are frequently found but there is some evidence that they are not necessary in the production of progeny (30).

Marcinowski (17) in 1909 prepared the first extended list of plants attacked by the root-knot nematode by listing 235 species. Subsequently in 1911, Bessey (4) enumerated about 480 susceptible plant species. In 1931, the Imperial Bureau of Agriculutral Parasitology, Winches Farm, St. Albans, England, issued a list containing 569 names of plants attacked. In 1933, Buhrer, Cooper and Steiner (6) and in 1938, Buhrer (7) listed a total of 1332 host plants. The present list (1952) maintained in the files of the Division of Nematology, U. S. Department of Agriculture, numbers 1865 species.

As the root-knot nematodes were more extensively studied, evidence was found that there were differences in the host preferences of these parasites from various locations. For example, Sherbakoff (24) in 1939 reported considerable root knot injury to cotton grown on land previously planted to cotton but observed no injury to cotton grown on land previously planted to tomatoes even though the tomatoes had been severely injured by root knot. Tyler (31) in 1941 compiled the available information on plant species and varieties that had been called either resistant or tolerant, revealing many inconsistences in host reactions to the root-knot nematode. The outstanding work of Christie and Albin (10) in 1944 and Christie (11) in 1946 established beyond all doubt that there were several strains or races of the root-knot nematode. These investigators demonstrated that differences in the host-parasite relationships of the different races may become manifest in at least two ways: (1) a plant may be susceptible to one race and resistant to another; or (2) a plant may be susceptible to each of two races but the type of root galling produced by one race may differ from that produced by the other. Chitwood (8) in 1949 after making a morphological study of the root-knot nematodes, removed them from the genus *Heterodera*, reassigning them to *Meloidogyne*. Five species and one variety were described by Chitwood at this time. Later (1952) he described another subspecies (9). In 1953, another new species was described from Ceylon by Loos (15).

The above work explains to a great extent why control of root knot by crop rotation (12, 22, 23, 32) has been successful in some instances and not in others. Root-knot nematodes being obligate parasites, depend upon suitable host plants for development and reproduction. Alternating immune or resistant crops with susceptible crops decreases the amount of reproduction of the nematodes and keeps the population at a low level. In selecting suitable crop plants to be used in rotation programs, it is necessary to know (1) the species of root-knot nematode present and (2) plant species which are immune, resistant or susceptible to that particular nematode species. It is also helpful to know if larvae enter the roots but fail to develop to maturity and reproduce. Plant species which the larvae enter but in which they fail to develop may be used to trap nematodes and such plants should be more efficient in a rotation program than plants which they fail to enter. Barrons (3) in 1939 while apparently working with a single species, or a mixture of two or more species, found no significant differences between the mean number of larvae entering the roots of resistant and susceptible plants when all were equally exposed to root knot inoculum. However, in 1946 Christie (11) working with several races of the nematode (later shown to be species) demonstrated that larvae of some races did not enter the roots of some plants as readily as did others.

The present research was undertaken with the following aims in view: (1) to determine susceptibility of important agronomic crops which might be used in rotation programs to control species of root-knot nematode known to occur in the eastern United States and (2) to determine the behavior of these nematodes in resistant plants. Other studies included a survey to determine which of the root-knot nematode species occur in Maryland and their approximate distribution within the state.

MATERIALS AND METHODS

A. Definitions

In literature relating to nematode diseases of plants in general and root knot in particular, numerous terms such as infection, resistance, susceptibility, tolerance, immunity and the like are used. These have been borrowed from related sciences and used with more or less diverse meanings according to the circumstances. In nematological literature, only a few authors have made an effort to define their terms exactly — Steiner (25) 1925, Barrons (3) 1939, and Tyler (31) 1944. Even where this has been done, there is little exact agreement between authors as to the meanings of certain terms. In addition, concepts have changed as additional information has been obtained. Usually the borrowed terms relate to somewhat parallel cases in other fields and are understandable from the context. Nevertheless, the relationships of root-knot nematodes to plants are often such that they cannot be fully understood by study of the definitions of terms in standard dictionaries or by reference to definitions such as those published by the Committee on Technical Words of the American Phytopathological Society (20). However, the relationships of nematodes to plants do not warrant the coining of new words to express these concepts. Rather, it seems best to define the terms as used in this thesis to facilitate an understanding of the problem. The following definitions are not intended to apply to the whole field of nematology, but only to root-knot nematodes and their relations to plants.

Infection is used to mean invasion of the plant by larvae of the root-knot nematode. It does not imply that the nematode is feeding on the plant tissue or even that it can live in plant tissue for more than a short time, but simply that the living nematode is in the plant tissue. To infect is to invade the plant; an infected plant is one that has been invaded, and infection is the process of invading the plant or the state of being in the plant.

An immune plant is one which is never invaded by the larvae of the root-knot nematode. Evidence for existence of immunity must necessarily rest on negative examinations and therefore there can always be some doubt that a plant is really immune. In practice, it means that nematodes were not found in the plant after a thorough examination.

Resistance to infection indicates that the plant is invaded by reduced number of nematodes, even in the presence of large numbers of larvae and under conditions where there is no apparent external circumstance which would prevent invasion of the plant. In practice, it would indicate that the plant had been subjected to experimental conditions favorable for infection similar to those in which another plant had been heavily infected. Resistance to infection is highly variable, ranging from near immunity to high susceptibility according to plant species and perhaps to other factors.

Susceptibility to infection is the opposite of resistance, and can be used interchangeably with resistance provided the sense of the modifying adjective is changed. A highly resistant plant has low susceptibility.

According to the definition of the Committee on Technical Words, a host is a "living organism harboring another organism or virus dependent on it for existence." If existence is defined as continued existence of the species and not merely temporary existence of the individual, a host would be a plant in which the nematodes can reproduce. A host plant of a root-knot nematode species is a plant in which the species can reproduce. Under this definition, infected plants may or may not be host plants. Host plants may be susceptible host plants in which nematodes reproduce freely or resistant host plants in which reproduction is inhibited. The important distinction between plants resistant or susceptible to infection and resistant or susceptible host plants is that reproduction takes place in host plants, but may or may not take place in plants resistant or susceptible to infection.

A useful antonym of host plant is non-host plant. This is a plant in which the nematodes are unable to reproduce. Non-host plants may range from immune to highly susceptible to infection, provided that there is no reproduction by the nematodes.

Tolerance is used in the meaning given by the Committee on Technical Words: "Ability of the infected organism to endure the operation of a pathogenic factor or invasion by a pathogenic organism or virus with little or no reaction, as shown by the more or less complete absence of symptom expression and damage." Tolerance relates to root knot as a plant disease.

B. Identification of the Root-Knot Nematodes (Meloidogyne spp.)

Before undertaking the investigations outlined in the introduction, it was necessary to become thoroughly familiar with the different root-knot nematode species to be used in the study and to be able to make species determinations rapidly and accurately. Since the characters used by Chitwood (8) in his differentiation of species were either variable or applied to the males which were not always readily available, under the microscope, using the oil immersion lens. Type material was also examined. Photomicrographs were made of many of the perineal patterns for further study and comparison. These were made with a Leitz "Makam" camera mounted on a Bausch and Lomb research microscope under the following conditions:

Magnification -- 666.

Objective -- Apochromatic 90X-2mm-1.30 N.A., oil immersion.

Ocular -- 8X periplanatic - tube length 160 mm.

Illumination and condenser -- Bausch and Lomb Panfocal Illuminator with permanently aligned integral achromatic condenser and light. N. A. of condenser was set at 1.0. Illumination consisted of a 6-8 volt bulb operated directly from 115 volt, 60-cycle A. C. line through adjustable transformer.

Filter -- None; stain; none.

Film -- Contrast process panchromatic 9X12 cm. cut film.

Exposure -- Variable depending on specimen; usually 10 sec.

Developer -- D-11 diluted 1:1 for recommended time-temperature development.

C. Isolation and Culture of the Root-Knot Nematode Species

Roots of several plant species severely infected with root-knot nematodes were collected in the fall of 1950 from several locations in Maryland. These were brought into the laboratory and all soil removed by washing. Individual egg masses which usually protrude from the roots, were removed from the female nematode with the aid of forceps and placed in a No. 00 gelatin capsule containing moist soil. Each capsule was numbered. The embedded female from which the egg mass came was then removed from the root tissue and preserved in five percent formaldehyde. Each female was given a number corresponding to the egg mass and later identified as to species. Several capsules were prepared as described above and taken to the greenhouse where single capsules were placed in 4-inch pots of steam sterilized soil with a tomato seedling which had been propagated in sterile soil. The pots were watered thoroughly and placed on greenhouse benches on inverted clay saucers. The purpose of the saucers was to prevent contamination from the greenhouse benches. Contamination by splashing water during watering was eliminated by wide spacing of the pots. Capsules containing eggs were found to dissolve in about 24 hours in moist soil. After about 30 days the root systems were examined for infection and nematode reproduction. Infected root systems which contained mature females with egg masses were then divided into several lots and used as inoculum for other pots also filled with sterile soil and planted with tomato seedlings grown in steam sterilized soil. By this procedure large quantities of inoculum from single female cultures were obtained in about four months for *Meloidogyne incognita* (Kofoid and White, 1919) Chitwood, 1949, *M. incognita* var. *acrita* Chitwood, 1949 and *M. hapla* Chitwood, 1949. Single female cultures of *M. arenaria* (Neal, 1889) Chitwood, 1949 and *M. javanica* (Treub, 1885) Chitwood, 1949, also used in this study were obtained from cultures maintained by the Division of Nematology, U. S. Department of Agriculture, Beltsville, Maryland. This was necessary since neither of these species were found in any of the collections obtained in Maryland. Rutgers tomato plants were used to maintain the cultures since this variety is highly susceptible to all the above root-knot nematode species. *M. arenaria* subspecies *thamesi*, Chitwood, 1952, and *M. brevicauda* Loos, 1953, had not been described when these investigations were begun and were not included in these studies. Neither was *M. exigua* Göldi, 1887, included since it has never been reported as occurring in the United States, except at the New York Botanical Gardens.

D. Studies on Susceptibility of Plant Species to Root-Knot Nematodes

Seed for most of the crop plants tested were obtained from a commercial seed producer[7] to insure that seed of high germination percentage and known origin were used in these tests. Seed for some of the crop plants not available from this source, were obtained either from the U. S. Department of Agriculture or from local reputable seed dealers. Seedlings of test plants were grown in flats of sterile soil and transplanted to thumb pots for about 10 days to permit growth of a good root system. In some of the tests, depending on the crop plant, the seed were sown directly into the inoculated soil.

Four-inch pots used in these experiments were partially filled with a sterile mixture of one part soil and one part sand. Approximately five grams of roots heavily infected with one of the root-knot nematode species being tested were then added to each pot and the pots filled with the sterile soil mixture. The various test plants were then planted. There were five replications for each test. For each series of plants tested, five pots each receiving approximately five grams of

[7]Supplied through the courtesy of Associated Seed Growers, Inc., New Haven, Connecticut.

infected roots from the same lot of inoculum were planted with Rutgers variety tomato seedlings. These served to indicate inoculum potential. Test plants and tomato indicator controls grew for periods of time ranging from 45 to 60 days, depending on the plant. The only exceptions to this were with woody-type plants which were allowed to grow for as long as six months. All tests were conducted in the greenhouse with temperatures of 65° F. or above. Adequate space was allowed between series of test pots involving different nematode species to prevent contamination from splashing. Furthermore, all pots were placed on inverted clay saucers to prevent possible contamination from the greenhouse benches. Whenever possible, tests for the various crop plants were conducted during the season of year in which they would normally grow in the field. Susceptibility of the test plants to the various root-knot nematode species was determined by carefully washing all soil from roots and observing the amount of infection and reproduction on the roots. Reproduction was assumed to have occurred only when egg masses were observed. Tomato indicator controls were also examined and unless these were severely galled the tests were repeated. A rating system with the following symbols and definitions was used to indicate the degree of infection: 0, no infection or if larvae entered the roots they did not develop into mature egg-laying females; 1, extremely light infection with only an occasional mature female with egg mass found; 2, light infection with mature females and egg masses easily seen with the naked eye; 3, moderate infection with full grown females and egg masses moderately abundant; 4, severe infection with mature females and egg masses very abundant.

In all cases in which infection could not be detected with the naked eye or by aid of the dissecting microscope, the roots of the test plants were stained with lacto-phenol-acid fuchin (18). After clearing, these were examined under the dissecting microscope for the presence of nematode infection. Tests yielding negative results were repeated except in a few cases in which it was not possible to obtain additional cuttings or seedlings for making the tests. In some cases where negative results were obtained for a given crop variety, additional varieties of that crop were tested, but only against the nematode species which gave negative results. For those crop species which were obviously infected, a small portion of the root system was preserved in five percent formaldehyde and a microscopic determination of the nematode species involved was made before the crop was recorded as a host.

E. Studies on Infection and Development of Root-Knot Nematodes in Resistant and Susceptible Plants

Inoculum for each of the nematode species used in these tests was prepared as follows: Roots of various plants severely infected with a single species of the root-knot nematode, were washed free of soil with a gentle stream of water. Infected roots with numerous egg masses protruding from them, were then cut into small pieces. Approximately five gram samples were then placed in a Waring Blendor with 80 ml. of water. The blendor was allowed to run for 10 seconds, and the contents then poured onto a three sieve combination consisting of a 30-mesh over a 100-mesh over a 325-mesh. A forceful spray of water was directed on the top sieve which washed the dislodged egg masses and larvae through onto the 100-mesh sieve. Root debris caught on the 30-mesh sieve was discarded. A gentle stream of water was then directed on the 100-mesh sieve which washed larvae and any eggs which had become detached from the egg mass, onto the 325-mesh sieve. Intact egg masses caught on the 100-mesh sieve were washed off with a small amount of water and again placed in the Waring Blendor. The blendor was run for 60 seconds to dislodge all eggs from the egg masses. This suspension of eggs was then poured into a large beaker. Eggs and larvae caught on the 325-mesh sieve were washed into the same beaker with a small amount of water. Several hundred milliliters of inoculum consisting of a suspension of eggs, larvae and root debris were prepared in this manner for each of the root-knot nematode species to be tested. Four-inch pots used in the experiments were prepared by partially filling with sterile soil. Inoculum was then added and the pots filled with sterile soil. Inoculum in the series of pots used for each species of nematode was equally divided among all the pots of that series but no effort was made to insure that pots in different series received equal amounts of inoculum. Plant species ranging from apparently immune to highly susceptible for the particular nematode species being tested, were planted in the pots. Five pots were used for each combination of nematode species and plant species, and the plants were allowed to grow for 20 days under greenhouse conditions. At the end of this period, the soil was carefully removed from the roots by washing, which also removed any nematodes which might be on the outside of the roots. Nematodes in the roots were freed from the root tissue by a modification of the technique described by Taylor and Loegering (29). Samples of approximately five grams of root cut into pieces not more than two cm. long were macerated in the Waring Blendor. The blendor was allowed to run for 20 seconds.

The macerated tissue and water was then poured onto a three sieve combination as previously described. A forceful stream of water was then used to wash the nematodes through the top two sieves onto the 325-mesh sieve. Most of the root tissue was caught on the top two sieves and discarded. The nematodes were removed from the 325-mesh sieve by placing it upside down at an angle of 45° with the edge on a 600 ml. beaker in such a manner that water poured on the bottom of the sieve ran into the beaker. About 40 ml. of water was used for this purpose. The water containing the nematodes was then poured into a 90 mm. petri dish. The number of nematodes in 20 fields of a dissecting microscope or 1/17th of the area of the petri dish was recorded in two groups. One group included nematodes showing obvious signs of development beyond the first parasitic stage and the other included nematodes showing no such development. The total number of nematodes which entered the root and the percentage showing development was then calculated.

F. Survey of Root-Knot Nematode Species in Maryland

In the fall of 1950 and the summer and fall of 1951 roots of various plants affected with root knot were collected from various areas of Maryland. Data recorded with each sample included host plant, location and date of collection. All samples were preserved in five percent formaldehyde for 24 hours or longer. Root-knot nematode species found in the root samples were identified by morphological characters in the manner described in section B.

EXPERIMENTAL RESULTS

A. Identification of the Root-Knot Nematode Species

Identification of root-knot nematode species used in these tests was based primarily on morphology of the perineal region of adult females. This character was found to be very reliable for species determination. It was observed that while perineal patterns of the females were as individual as human finger prints, which they somewhat resemble; like finger prints, they could be grouped in classes for each species. Sometimes the species could be determined by observing a single pattern. At other times, because of normal variations in perineal patterns, it was necessary to study a series of patterns. Some of these variations are shown in Figures 3 through 7. While each pattern differs, there is a close similarity between the four patterns of a given species as compared to patterns of different species. *Meloidogyne incognita* and *M. incognita* var. *acrita* were found to be very similar morphologically and at times it was difficult to distinguish between them by a study of the perineal pattern alone. All the species, aside from normal variation, apparently remained morphologically and physiologically stable throughout these tests. There was no evidence of influence of the host on morphology of the nematode.

B. Susceptibility of Plant Species to Root-Knot Nematodes

To determine susceptibility of various plant species to root knot caused by species of *Meloidogyne* experiments were conducted in which plants were inoculated with single female cultures of root-knot nematodes. Inoculated plants were allowed to grow 45 to 60 days under greenhouse conditions and then examined for nematode infection. Susceptibility ratings for all plants tested against _Meloidogyne_ spp. are shown in Tables I through V.

Fifty plant species and varieties were tested for resistance to the five root-knot nematodes. Fifteen or 30 percent were highly resistant to _M. incognita_; 14, or 28 percent were highly resistant to _M. incognita_ var. _acrita_; 23, or 46 percent were highly resistant to _M. hapla_; 16, or 32 percent were highly resistant to _M. javanica_ and 15, or 30 percent highly resistant to _M. arenaria_.

Table VI lists all plant species tested with ratings of susceptibility to all the nematode species. This table shows that some plant species were highly resistant to all the nematode species and others were highly susceptible to all the nematode species. The majority of plants tested, however, were found to be between these two extremes in susceptibility, i.e., resistant to some nematode species and susceptible to others.

Of the 50 plant species and varieties tested against the five root-knot nematodes, only eight were found to be highly resistant (i.e., ratings of 0 or 1) to all. These included oat, geranium (two varieties), azalea, common ragweed, _Strophanthus_ and two species of _Crotalaria_.

Nineteen plant species and varieties were found to be susceptible (i.e., ratings of 2, 3 and 4) to all the nematode species. These included eggplant, potato, tobacco (two varieties), alfalfa, bean (two varieties), garden pea, soybean (three varieties), cabbage, radish, beet, _Calendula_, muskmelon, carrot, sultan snapweed, and tomato.

Fourteen plant species and varieties were found to be susceptible to four of the root-knot nematodes and resistant to the other one.

TABLE I. Susceptibility ratings of plant species to *Meloidogyne incognita*.

Scientific name	Common name	Horticultural variety
SUSCEPTIBILITY RATING 0[a]		
Ambrosia artemisiifolia L.	common ragweed	-----
Arachis hypogaea L.	peanut	Spanish
Crotalaria mucronata Desv.	striped crotalaria	-----
Crotalaria spectabilis Roth	showy crotalaria	-----
(X *Fragaria ananassa* Duch.)	strawberry	Blakemore
(X *Fragaria ananassa* Duch.)	strawberry	Catskill
(X *Fragaria ananassa* Duch.)	strawberry	Premier
(X *Fragaria ananassa* Duch.)	strawberry	Temple
Gossypium hirsutum L.	upland cotton	Coker 100
Lycopersicon peruvianum (L.) Mill	-----	-----
Pelargonium sp.	geranium	John Doyle
Pelargonium sp.	geranium	Rosana
Rhododendron sp.	azalea	Glenn Dale Hybrid
SUSCEPTIBILITY RATING 1		
Avena sativa L.	oat	Arlington
Strophanthus sarmentosus DC.	arrowpoison strophanthus	-----
SUSCEPTIBILITY RATING 2		
Ipomoea batatas (L.) Lam.	sweet potato	Maryland Golden
SUSCEPTIBILITY RATING 3		
Capsicum frutescens L.	red pepper	California Wonder
Dianthus caryophyllus L.	carnation	Riviera Giant Mixed
Glycine max (L.) Merr.	soybean	Lincoln
Glycine max (L.) Merr.	soybean	Wabash
Hibiscus esculentus L.	okra	Clemson Spineless
Medicago sativa L.	alfalfa	Atlantic
Nerium oleander L.	common oleander	-----
Phaseolus sp.	bean	State Half Runner
Secale cereale L.	rye	Prolific
Zea mays L.	corn	Golden Cross Bantam
Zea mays L.	corn	Cogent Ill. 8 x 6

TABLE I. (Continued) Susceptibility ratings of plant species to *Meloidogyne incognita*.

Scientific name	Common name	Horticultural variety
	SUSCEPTIBILITY RATING 4	
Allium cepa L.	onion	Egyptian Winter
Amaranthus retroflexus L.	pigweed	-----
Beta vulgaris L.	beet	Detroit Dark Red
Brassica oleracea var. *capitata*	cabbage	Golden Acre
Calendula sp.	calendula	-----
Cucumis melo var. *reticulatus* Naud.	muskmelon	Jumbo Hale's Best
Cucumis sativus L.	cucumber	Marketer
Cucurbita maxima Duchesne	squash	Early Prolific Straightneck
Citrullus vulgaris Schrad.	watermelon	Dixie Queen
Daucus carota L.	carrot	Red Core Chantenay
Glycine max (L.) Merr.	soybean	Hawkeye
Hibiscus cannabinus L.	kenaf hibiscus	PI. 189208[b]
Hordeum vulgare L.	barley	Moore
Impatiens sultanii Hook. f.	sultan snapweed	-----
Lycopersicon esculentum Mill.	tomato	Rutgers
Nicotiana tabacum L.	tobacco	Maryland Mammoth
Nicotiana tabacum L.	tobacco	402
Phaseolus sp.	bean	Top Crop
Pisum sativum L.	garden pea	Thomas Laxton
Raphanus sativus L.	radish	Early Scarlet Globe
Solanum melongena L.	garden eggplant	Burpee's Black Beauty
Solanum tuberosum L.	potato	Irish Cobbler
Triticum aestivum L.	wheat	Coastal

[a]See section D of Materials and Methods for definitions of susceptibility ratings.

[b]Refers to U. S. Dept. of Agriculture plant introduction number.

TABLE II. Susceptibility ratings of plant species to *Meloidogyne incognita* var. *acrita*.

Scientific name	Common name	Horticultural variety
SUSCEPTIBILITY RATING 0		
Ambrosia artemisiifolia L.	common ragweed	-----
Arachis hypogaea L.	peanut	Spanish
Avena sativa L.	oat	Arlington
Crotalaria mucronata Desv.	striped crotalaria	-----
Crotalaria spectabilis Roth	showy crotalaria	-----
(X *Fragaria ananassa* Duch.)	strawberry	Blakemore
(X *Fragaria ananassa* Duch.)	strawberry	Catskill
(X *Fragaria ananassa* Duch.)	strawberry	Premier
(X *Fragaria ananassa* Duch.)	strawberry	Temple
Pelargonium sp.	geranium	John Doyle
Pelargonium sp.	geranium	Rosana
Rhododendron sp.	azalea	Glenn Dale Hybrid
SUSCEPTIBILITY RATING 1		
Nerium oleander L.	common oleander	-----
Strophanthus sarmentosus DC.	arrowpoison strophanthus	-----
SUSCEPTIBILITY RATING 2		
Capsicum frutescens L.	red pepper	California Wonder
Dianthus caryophyllus L.	carnation	Riviera Giant Mixed
Glycine max (L.) Merr.	soybean	Hawkeye
Ipomoea batatas (L.) Lam.	sweet potato	Maryland Golden
Lycopersicon peruvianum (L.) Mill.	-----	-----
Phaseolus sp.	bean	State Half Runner
Secale cereale L.	rye	Prolific
Triticum aestivum L.	wheat	Coastal
Zea mays L.	corn	Cogent Ill. 8 x 6
SUSCEPTIBILITY RATING 3		
Gossypium hirsutum L.	cotton	Coker 100
Hibiscus cannabinus L.	kenaf hibiscus	PI. 189208
Hordeum vulgare L.	barley	Moore
Medicago sativa L.	alfalfa	Atlantic
Solanum melongena L.	garden eggplant	Burpee's Black Beauty
Solanum tuberosum L.	potato	Irish Cobbler
Zea mays L.	corn	Golden Cross Bantam

TABLE II. (Continued) Susceptibility ratings of plant species to *Meloidogyne incognita* var. *acrita*.

Scientific name	Common name	Horticultural variety
	SUSCEPTIBILITY RATING 4	
Allium cepa L.	onion	Egyptian Winter
Amaranthus retroflexus L.	pigweed	-----
Beta vulgaris L.	beet	Detroit Dark Red
Brassica oleracea var. *capitata* L.	cabbage	Golden Acre
Calendula sp.	calendula	-----
Citrullus vulgaris Schrad.	watermelon	Dixie Queen
Cucumis anguria L.	gherkin	-----
Cucumis melo var. *reticulatus* Naud.	muskmelon	Jumbo Hale's Best
Cucumis sativus L.	cucumber	Marketer
Cucubita maxima Duchesne	squash	Early Prolific Straightneck
Daucus carota L.	carrot	Red Core Chantenay
Glycine max (L.) Merr.	soybean	Lincoln
Glycine max (L.) Merr.	soybean	Wabash
Hibiscus esculentus L.	okra	Clemson Spineless
Impatiens sultanii Hook. f.	sultan snapweed	-----
Lycopersicon esculentum Mill.	tomato	Rutgers
Nicotiana tabacum L.	tobacco	Maryland Mammoth
Nicotiana tabacum L.	tobacco	402
Phaseolus sp.	bean	Top Crop
Pisum sativum L.	garden pea	Thomas Laxton
Raphanus sativus L.	radish	Early Scarlet Globe

TABLE III. Susceptibility ratings of plant species to *Meloidogyne hapla*.

Scientific name	Common name	Horticultural variety
SUSCEPTIBILITY RATING 0		
Amaranthus retroflexus L.	pigweed	------
Ambrosia artemisiifolia L.	common ragweed	------
Avena sativa L.	oat	Arlington
Citrullus vulgaris Schrad.	watermelon	Dixie Queen
Crotalaria mucronata Desv.	striped crotalaria	------
Crotalaria spectabilis Roth	showy crotalaria	------
Gossypium hirsutum L.	cotton	Coker 100
Hibiscus cannabinus L.	kenaf hibiscus	------
Hibiscus esculentus L.	okra	Clemson Spineless
Hibiscus esculentus L.	okra	Spring Dwarf
Hordeum vulgare L.	barley	Moore
Nerium oleander L.	common oleander	------
Pelargonium sp.	geranium	John Doyle
Pelargonium sp.	geranium	Rosana
Rhododendron sp.	azalea	Glenn Dale Hybrid
Secale cereale L.	rye	Prolific
Strophanthus sarmentosus DC.	arrowpoison strophanthus	------
Triticum aestivum L.	wheat	Coastal
Zea mays L.	corn	Cogent Ill. 8 x 6
Zea mays L.	corn	Golden Cross Bantam
SUSCEPTIBILITY RATING 1		
Allium cepa L.	onion	Egyptian Winter
Citrullus vulgaris Schrad.	watermelon	Congo
Citrullus vulgaris Schrad.	watermelon	Hawkesbury
Cucumis sativus L.	cucumber	Cubit
Cucumis sativus L.	cucumber	Marketer
Cucurbita maxima Duchesne	squash	Black Zucchini
Cucurbita maxima Duchesne	squash	Butter Nut
Cucurbita maxima Duchesne	squash	Caserta
Cucurbita maxima Duchesne	squash	Early Prolific Straightneck
Dianthus caryophyllus L.	carnation	Riviera Giant Mixed
SUSCEPTIBILITY RATING 2		
Beta vulgaris L.	beets	Detroit Dark Red

TABLE III. (Continued) Susceptibility ratings of plant species to *Meloidogyne hapla*.

Scientific name	Common name	Horticultural variety
SUSCEPTIBILITY RATING 2		
Cucumis sativus L.	cucumber	A & C
Daucus carota L.	carrot	Red Core Chantenay
Glycine max (L.) Merr.	soybean	Wabash
Ipomoea batatas (L.) Lam.	sweet potato	Maryland Golden
Lycopersicon peruvianum (L.) Mill.	-----	-----
SUSCEPTIBILITY RATING 3		
Brassica oleracea var. *capitata* L.	cabbage	Golden Acre
Capsicum frutescens L.	red pepper	California Wonder
Impatiens sultanii Hook. f.	sultan snapweed	-----
Nicotiana tabacum L.	tobacco	Maryland Mammoth
Nicotiana tabacum L.	tobacco	402
Pisum sativum L.	garden pea	Thomas Laxton
Raphanus sativus L.	radish	Early Scarlet Globe
Solanum tuberosum L.	potato	Irish Cobbler
SUSCEPTIBILITY RATING 4		
Arachis hypogaea L.	peanut	Spanish
Calendula sp.	calendula	-----
Cucumis melo var. *reticulatus* Naud.	muskmelon	Jumbo Hale's Best
(X *Fragaria ananassa* Duch.)	strawberry	Blakemore
(X *Fragaria ananassa* Duch.)	strawberry	Catskill
(X *Fragaria ananassa* Duch.)	strawberry	Premier
(X *Fragaria ananassa* Duch.)	strawberry	Temple
Glycine max (L.) Merr.	soybean	Hawkeye
Glycine max (L.) Merr.	soybean	Lincoln
Lycopersicon esculentum Mill.	tomato	Rutgers
Medicago sativa L.	alfalfa	Atlantic
Phaseolus sp.	bean	State Half Runner
Phaseolus sp.	bean	Top Crop
Solanum melongena L.	garden eggplant	Burpee's Black Beauty

TABLE IV. Susceptibility ratings of plant species to *Meloidogyne javanica*.

Scientific name	Common name	Horticultural variety
	SUSCEPTIBILITY RATING 0	
Ambrosia artemisiifolia L.	common ragweed	-----
Arachis hypogaea L.	peanut	Spanish
Capsicum frutescens L.	red pepper	California Wonder
Capsicum frutescens L.	red pepper	Worldbeater
Crotalaria mucronata Desv.	striped crotalaria	-----
Crotalaria spectabilis Roth	showy crotalaria	-----
Cucumis anguria L.	gherkin	-----
(X *Fragaria ananassa* Duch.)	strawberry	Blakemore
(X *Fragaria ananassa* Duch.)	strawberry	Catskill
(X *Fragaria ananassa* Duch.)	strawberry	Premier
(X *Fragaria ananassa* Duch.)	strawberry	Temple
Gossypium hirsutum L.	cotton	Coker 100
Ipomoea batatas (L.) Lam.	sweet potato	Maryland Golden
Pelargonium sp.	geranium	John Doyle
Pelargonium sp.	geranium	Rosana
Rhododendron sp.	azalea	Glenn Dale Hybrid
Strophanthus sarmentosus DC.	arrowpoison strophanthus	-----
	SUSCEPTIBILITY RATING 1	
Avena sativa L.	oat	Arlington
	SUSCEPTIBILITY RATING 2	
Amaranthus retroflexus L.	pigweed	-----
Hordeum vulgare L.	barley	Moore
Lycopersicon peruvianum (L.) Mill.	-----	-----
Secale cereale L.	rye	Prolific
	SUSCEPTIBILITY RATING 3	
Allium cepa L.	onion	Egyptian Winter
Dianthus caryophyllus L.	carnation	Riviera Giant Mixed
Glycine max (L.) Merr.	soybean	Lincoln
Glycine max (L.) Merr.	soybean	Wabash
Hibiscus esculentus L.	okra	Clemson Spineless

TABLE IV. (Continued) Susceptibility ratings of plant species to *Meloidogyne javanica*.

Scientific name	Common name	Horticultural variety
	SUSCEPTIBILITY RATING 3	
Medicago sativa L.	alfalfa	Atlantic
Nerium oleander L.	common oleander	-----
Pisum sativum L.	garden pea	Thomas Laxton
Solanum tuberosum L.	potato	Irish Cobbler
Zea mays L.	corn	Golden Cross Bantam
Zea mays L.	corn	Cogent Ill. 8 x 6
	SUSCEPTIBILITY RATING 4	
Beta vulgaris L.	beet	Detroit Dark Red
Brassica oleracea var. *capitata* L.	cabbage	Golden Acre
Calendula sp.	calendula	-----
Citrullus vulgaris Schrad.	watermelon	Dixie Queen
Cucumis melo var. *reticulatus* Naud.	muskmelon	Jumbo Hale's Best
Cucumis sativus L.	cucumber	Marketer
Cucurbita maxima Duchesne	squash	Early Prolific Straightneck
Daucus carota L.	carrot	Red Core Chantenay
Glycine max (L.) Merr.	soybean	Hawkeye
Hibiscus cannabinus L.	kenaf hibiscus	PI. 189208
Impatiens sultanii Hook. f.	sultan snapweed	-----
Lycopersicon esculentum Mill.	tomato	Rutgers
Nicotiana tabacum L.	tobacco	Maryland Mammoth
Nicotiana tabacum L.	tobacco	402
Phaseolus sp.	bean	State Half Runner
Phaseolus sp.	bean	Top Crop
Raphanus sativus L.	radish	Early Scarlet Globe
Solanum melongena L.	garden eggplant	Burpee's Black Beauty
Triticum aestivum L.	wheat	Coastal

TABLE V. Susceptibility ratings of plant species to *Meloidogyne arenaria*.

Scientific name	Common name	Horticultural variety
	SUSCEPTIBILITY RATING 0	
Ambrosia artemisiifolia L.	common ragweed	-----
Crotalaria mucronata Desv.	striped crotalaria	-----
Crotalaria spectabilis Roth	showy crotalaria	-----
(X *Fragaria ananassa* Duch.)	strawberry	Blakemore
(X *Fragaria ananassa* Duch.)	strawberry	Catskill
(X *Fragaria ananassa* Duch.)	strawberry	Premier
(X *Fragaria ananassa* Duch.)	strawberry	Temple
Gossypium hirsutum L.	cotton	Coker 100
Ipomoea batatas (L.) Lam.	sweet potato	Maryland Golden
Pelargonium sp.	geranium	John Doyle
Pelargonium sp.	geranium	Rosana
Rhododendron sp.	azalea	Glenn Dale Hybrid
Strophanthus sarmentosus DC.	arrowpoison strophanthus	-----
	SUSCEPTIBILITY RATING 1	
Avena sativa L.	oat	Arlington
Cucumis anguria L.	gherkin	-----
Hibiscus esculentus L.	okra	Clemson Spineless
	SUSCEPTIBILITY RATING 2	
Dianthus caryophyllus L.	carnation	Riviera Giant Mixed
Hibiscus esculentus L.	okra	Spring Dwarf
Hordeum vulgare L.	barley	Moore
Secale cereale L.	rye	Prolific
Zea mays L.	corn	Golden Cross Bantam
	SUSCEPTIBILITY RATING 3	
Allium cepa L.	onion	Egyptian Winter
Amaranthus retroflexus L.	pigweed	-----
Capsicum frutescens L.	red pepper	California Wonder
Glycine max (L.) Merr.	soybean	Hawkeye
Glycine max (L.) Merr.	soybean	Lincoln
Glycine max (L.) Merr.	soybean	Wabash

TABLE V. (Continued) Susceptibility ratings of plant species to *Meloidogyne arenaria*.

Scientific name	Common name	Horticultural variety
	SUSCEPTIBILITY RATING 3	
Medicago sativa L.	alfalfa	Atlantic
Nerium oleander L.	common oleander	-----
Solanum melongena L.	garden eggplant	Burpee's Black Beauty
Solanum tuberosum L.	potato	Irish Cobbler
Triticum aestivum L.	wheat	Coastal
Zea mays L.	corn	Cogent Ill. 8 x 6
	SUSCEPTIBILITY RATING 4	
Arachis hypogaea L.	peanut	Spanish
Beta vulgaris L.	beet	Detroit Dark Red
Brassica oleracea var. *capitata* L.	cabbage	Golden Acre
Calendula sp.	calendula	-----
Citrullus vulgaris Schrad.	watermelon	Dixie Queen
Cucumis melo var. *reticulatus* Naud.	muskmelon	Jumbo Hale's Best
Cucumis sativus L.	cucumber	Marketer
Cucurbita maxima Duchesne	squash	Early Prolific Straightneck
Daucus carota L.	carrot	Red Core Chantenay
Hibiscus cannabinus L.	kenaf hibiscus	PI. 189208
Impatiens sultanii Hook. f.	sultan snapweed	-----
Lycopersicon esculentum Mill.	tomato	Rutgers
Lycopersicon peruvianum (L.) Mill.	-----	-----
Nicotiana tabacum L.	tobacco	Maryland Mammoth
Nicotiana tabacum L.	tobacco	402
Phaseolus sp.	bean	State Half Runner
Phaseolus sp.	bean	Top Crop
Pisum sativum L.	garden pea	Thomas Laxton
Raphanus sativus L.	radish	Early Scarlet Globe

TABLE VI. Susceptibility ratings of plant species to root-knot nematodes (*Meloidogyne* spp.).

Scientific name	Common name	Horticultural variety	Susceptibility rating				
			M. incognita	*M. incognita* var. *acrita*	*M. hapla*	*M. javanica*	*M. arenaria*
Allium cepa L.	onion	Egyptian Winter	4	4	1	3	3
Amaranthus retroflexus L.	pigweed	------	4	4	0	2	3
Ambrosia artemisiifolia L.	common ragweed	------	0	0	0	0	0
Arachis hypogaea L.	peanut	Spanish	0	0	4	0	4
Avena sativa L.	oat	Arlington	1	0	0	1	1
Beta vulgaris L.	beet	Detroit Dark Red	4	4	2	4	4
Brassica oleracea var. *capitata* L.	cabbage	Golden Acre	4	4	3	4	4
Calendula sp.	calendula	------	4	4	4	4	4
Capsicum frutescens L.	red pepper	California Wonder	3	2	3	0	3
Capsicum frutescens L.	red pepper	Worldbeater	-	-	-	0	-
Citrullus vulgaris Schrad.	watermelon	Congo	-	-	1	-	-
Citrullus vulgaris Schrad.	watermelon	Dixie Queen	4	4	0	4	4
Citrullus vulgaris Schrad.	watermelon	Hawkesbury	-	-	1	-	-
Crotalaria mucronata Desv.	striped crotalaria	------	0	0	0	0	0
Crotalaria spectabilis Roth	showy crotalaria	------	0	0	0	0	0
Cucumis anguria L.	gherkin	------	-	4	-	0	1
Cucumis melo var. *reticulatus* Naud.	muskmelon	Jumbo Hale's Best	4	4	4	4	4
Cucumis sativus L.	cucumber	A & C	-	-	2	-	-
Cucumis sativus L.	cucumber	Cubit	-	-	1	-	-
Cucumis sativus L.	cucumber	Marketer	4	4	1	4	4
Cucurbita maxima Duchesne	squash	Black Zucchini	-	-	1	-	-
Cucurbita maxima Duchesne	squash	Butter Nut	-	-	1	-	-

TABLE VI. (Continued) Susceptibility ratings of plant species to root-knot nematodes (*Meloidogyne* spp.).

Scientific name	Common name	Horticultural variety	Susceptibility rating				
			M. incognita	*M. incognita* var. *acrita*	*M. hapla*	*M. javanica*	*M. arenaria*
Cucurbita maxima Duchesne	squash	Caserta	-	-	1	-	-
Cucurbita maxima Duchesne	squash	Early Prolific Straightneck	4	4	1	4	4
Daucus carota L.	carrot	Red Core Chantenay	4	4	2	4	4
Dianthus caryophyllus L.	carnation	Riviera Giant Mixed	3	2	1	3	2
(X *Fragaria ananassa* Duch.)	strawberry	Blakemore	0	0	4	0	0
(X *Fragaria ananassa* Duch.)	strawberry	Catskill	0	0	4	0	0
(X *Fragaria ananassa* Duch.)	strawberry	Premier	0	0	4	0	0
(X *Fragaria ananassa* Duch.)	strawberry	Temple	0	0	4	0	0
Glycine max (L.) Merr.	soybean	Hawkeye	4	2	4	4	3
Glycine max (L.) Merr.	soybean	Lincoln	3	4	4	3	3
Glycine max (L.) Merr.	soybean	Wabash	3	4	2	3	3
Gossypium hirsutum L.	upland cotton	Coker 100	0	3	0	0	0
Hibiscus cannabinus L.	kenaf hibiscus	PI. 189208	4	3	0	4	4
Hibiscus esculentus L.	okra	Clemson Spineless	3	4	0	3	1
Hibiscus esculentus L.	okra	Spring Dwarf	-	-	0	-	2
Hordeum vulgare L.	barley	Moore	4	3	0	2	2
Impatiens sultani Hook. f.	sultan snapweed	-----	4	4	3	4	4
Ipomoea batatas (L.) Lam.	sweet potato	Maryland Golden	2	2	2	0	0
Lycopersicon esculentum Mill.	tomato	Rutgers	4	4	4	4	4
Lycopersicon peruvianum (L.) Mill.	-----	-----	0	2	2	2	4

TABLE VI. (Continued) Susceptibility ratings of plant species to root-knot nematodes (*Meloidogyne* spp.).

Scientific name	Common name	Horticultural variety	Susceptibility rating[a]				
			M. incognita	*M. incognita* var. *acrita*	*M. hapla*	*M. javanica*	*M. arenaria*
Medicago sativa L.	alfalfa	Atlantic	3	3	4	3	3
Nerium oleander L.	common oleander	------	3	1	0	3	3
Nicotiana tabacum L.	tobacco	Maryland Mammoth	4	4	3	4	4
Nicotiana tabacum L.	tobacco	402	4	4	3	4	4
Pelargonium sp.	geranium	John Doyle	0	0	0	0	0
Pelargonium sp.	geranium	Rosana	0	0	0	0	0
Phaseolus sp.	bean	State Half Runner	3	2	4	4	4
Phaseolus sp.	bean	Top Crop	4	4	4	4	4
Pisum sativum L.	garden pea	Thomas Laxton	4	4	3	3	4
Raphanus sativus L.	radish	Early Scarlet Globe	4	4	3	4	4
Rhododendron sp.	azalea	Glenn Dale Hybrid	0	0	0	0	0
Secale cereale L.	rye	Prolific	3	2	0	2	2
Solanum melongena L.	garden eggplant	Burpee's Black Beauty	4	3	4	4	3
Solanum tuberosum L.	potato	Irish Cobbler	4	3	3	3	3
Strophanthus sarmentosus DC.	arrowpoison strophanthus	------	1	1	0	0	0
Triticum aestivum L.	wheat	Coastal	4	2	0	4	3
Zea mays L.	corn	Cogent Ill. 8 x 6	3	2	0	3	3
Zea mays L.	corn	Golden Cross Bantam	3	3	0	3	2

Sweet potato, okra and common oleander were susceptible to three of the nematode species and resistant to the other two. Only one (peanut) was susceptible to two of the nematode species and resistant to the other three. Strawberry and cotton were susceptible to one of the nematode species and resistant to the other four.

Varietal differences in susceptibility were not very great for those plant species in which more than one variety was tested. All were either highly resistant (ratings of 0 or 1) or highly susceptible (ratings of 2, 3, and 4) for the nematode species involved.

From the relatively small number of plants tested, it was difficult to correlate resistance with plant families, except in the case of M. hapla. Plant species tested in the families, Gramineae, Malvaceae and Cucurbitaceae, excepting muskmelon, were all highly resistant to Meloidogyne hapla.

C. Infection and Development of Root-Knot Nematodes in Resistant and Susceptible Plants

To compare infection and development of various species of Meloidogyne in resistant and susceptible plants, experiments were conducted in which both highly resistant and highly susceptible plants were inoculated with a single root-knot nematode species. Plants were allowed to grow for 20 days and the total number of larvae which entered the root system and the percentage showing development beyond the first parasitic stage was then determined. This was done for each of the nematode species. These data are shown in Tables VII through XI.

In general, resistant plants were not infected as readily as susceptible plants. An exception to this, in which a resistant plant was heavily infected was in the case of oat with M. incognita and M. arenaria.

TABLE VII. Infection and development of *M. incognita* in resistant and susceptible plants.

Test plant	Susceptibility ratings	Average No. larvae in roots[a]	% showing development
Lycopersicon peruvianum	0	58 ± 12*	0
Oat (Arlington)	1	999 ± 90*	0
Peanut (Spanish)	0	315 ± 8*	0
Rye (Prolific)	3	551 ± 37*	31
Strawberry (Blakemore)	0	42 ± 8*	0
Tomato (Rutgers)	4	756 ± 110	17

[a]The total number of larvae which entered each of five plants was averaged instead of calculating the number per gram of root. This method was found to more adequately express the data due to extreme variations in size of root systems of different plant species.

*Indicates a significant difference as compared with tomato.

TABLE VIII. Infection and development of *M. incognita* var. *acrita* in resistant and susceptible plants.

Test plant	Susceptibility ratings	Average No. larvae in roots	% showing development
Bean (State Half Runner)	2	326 ± 54*	66
Bean (Top Crop)	4	306 ± 65*	77
Lycopersicon peruvianum	2	58 ± 17*	0
Rye (Prolific)	2	64 ± 18*	21
Tomato (Rutgers)	4	166 ± 21	60

TABLE IX. Infection and development of *M. hapla* in resistant and susceptible plants.

Test plant	Susceptibility ratings	Average No. larvae in roots	% showing development
Oat (Arlington)	0	0*	0
Peanut (Spanish)	4	306 ± 38	30
Rye (Prolific)	0	0*	0
Strawberry (Blakemore)	4	289 ± 55	5
Watermelon (Dixie Queen)	0	195 ± 22*	7
Tomato (Rutgers)	4	265 ± 14	66

TABLE X. Infection and development of *M. javanica* in resistant and susceptible plants.

Test plant	Susceptibility ratings	Average No. larvae in roots	% showing development
Red pepper (California Wonder)	0	122 ± 30*	0
Strawberry (Blakemore)	0	115 ± 11*	0
Sweet potato (Maryland Golden)	0	683 ± 94*	0
Tomato (Rutgers)	4	1090 ± 112	5

TABLE XI. Infection and development of *M. arenaria* in resistant and susceptible plants.

Test plants	Susceptibility ratings	Average No. larvae in roots	% showing development
Oat (Arlington)	1	517 ± 85	0
Sweet potato (Maryland Golden)	0	217 ± 35*	0
Tomato (Rutgers)	4	419 ± 62	50

Cereal crops tested (oat and rye) apparently were not infected with *M. hapla*.

In resistant plants, although a considerable number of larvae entered the roots, there was practically no development of the larvae beyond the first parasitic larval stage. In other words, the larvae apparently had not begun to feed on the plant cells. This was true of all the nematode species tested. In susceptible plants, however, larvae had commenced feeding as evidenced by the percentage of those showing development beyond the first parasitic larval stage.

In summarizing the behavior of the different nematode species in regards to infection and development in all plants tested, four distinct conditions were observed: (1) no larvae were found in the roots; (2) larvae were found in reduced numbers in the roots, but there were few or none in an advanced stage of development; (3) larvae were found in large numbers in the roots, but there were few or none in the advanced stage of development; (4) larvae were found in the roots in large numbers and a considerable percentage were in the advanced stages of development. These types of nematode behavior, as well as species and plant involved are further shown in Table XII.

TABLE XII. Summarization of the behavior of *Meloidogyne* spp. in resistant and susceptible plants.

Nematode behavior	Nematode species	Plant species
No larvae were found in the roots.	*M. hapla*	Oat, rye
Larvae were found in reduced numbers.	*M. incognita*	Peanut, strawberry, *Lycopersicon peruvianum*
	M. incognita var. *acrita*	Rye, *Lycopersicon peruvianum*
	M. javanica	Strawberry, pepper
	M. arenaria	Sweet potato
Larvae were found in large numbers with little or no development.	*M. incognita*	Oat
	M. javanica	Sweet potato
	M. arenaria	Oat
Larvae were found in large numbers and developed normally.	All species tested	Tomato
	M. incognita	Rye
	M. incognita var. *acrita*	Bean (State Half Runner and Top Crop)
	M. hapla	Strawberry, peanut

D. Occurrence of Root-Knot Nematode Species in Maryland

During a partial survey two species and one variety of *Meloidogyne* were found to occur in Maryland. These were *M. incognita*, *M. incognita* var. *acrita*, and *M. hapla*. Approximate locations from which these species were collected are shown in Figure 8. Root knot was found in

12 of the 14 counties visited. M. hapla and M. incognita var. acrita were found much more frequently than M. incognita. In general root knot was more prevalent in the sandy loam type soils than in the heavier soil types.

Crop plants from which root samples were collected during the survey and the nematode species causing root knot on them are shown in Table XIII. Results of the survey with reference to susceptibility agree with greenhouse tests for the nematode and plant species concerned, although varieties of plant species collected in the survey were not determined.

TABLE XIII. Plants found infected with root-knot nematodes under natural conditions in Maryland, and the species of Meloidogyne involved.

M. incognita	M. incognita var. acrita	M. hapla
Beet	Bean (Lima)	Clover
Carrot	Bean (String)	Eggplant
Kale	Beet	Potato
Onion	Carrot	Strawberry
Potato	Kale	Sweet potato
Red pepper	Onion	Tobacco
Squash	Pigweed	Tomato
Sweet potato	Red pepper	
Tomato	Squash	
	Sweet potato	
	Tobacco	
	Tomato	

DISCUSSION

It has been known for many years that plants differ in their susceptibility to root knot and that nematode populations of the soil can be reduced by crop rotation. Growing susceptible crops year after year on infested soil permits the nematode population to build up to the point where severe damage or crop failure is almost certain to occur. On the other hand, the practice of alternating resistant or immune crops with susceptible ones, interrupts such rapid development of these parasites and greatly reduces losses due to root knot.

Application of this method of control has been handicapped largely because of the general belief that all nematodes causing root knot were the same species, and that any established host would be susceptible wherever root knot was present. As a result of this erroneous assumption, various host lists have included practically all economic crops and the possibility of control by rotation has not seemed practical because of the small number of resistant plants to choose from. The discovery, however, by Christie and Albin (10) that there were races of the root-knot nematode which differed from one another in their host preferences and the subsequent separation of the root-knot nematodes into several morphologically distinguishable species by Chitwood (8) has made it possible to study the host-parasite relationships of these species individually. These studies have provided information on resistance and susceptibility of various crop plants to each of the nematode species and not only provide a wider choice of crops to use in rotations, but permit the selection of crops best suited to control the particular nematode concerned. However, proper selection of the best crops to use, further depends upon (1) identification of the nematode species to be controlled and (2) a knowledge of the geographical distribution of the species since given areas usually are not infested with all the species but by only one, two or three. In areas where only one species is present, control by rotation is less difficult than in areas where several species are present. The presence of two or more species in an area reduces the number of crops which can be used. The present investigation is a step toward supplying the above information so far as Maryland is concerned.

The principal character used throughout this study for species determination has been the morphology of the perineal pattern of adult females. Allen (1), however, while studying perineal patterns from a single female population showed variations much greater than those encountered in the present study. Dropkin (13), on the other hand, studied perineal pattern variations in the offspring of single larvae of two species and showed statistically that the general shape and perhaps, some of the details of these patterns are under the control of heredity, and states that "not a single case has been observed in which a parent of one species produced offspring which could be classified as belonging to another species." Studies in preparation of the present paper support the view of Dropkin since single female cultures used in this work apparently remained morphologically stable and no particular difficulty was encountered in recognizing the various species. It is true that perineal patterns are variable and that the extremes of these variations can be mistaken for the pattern of an entirely different species. But if enough patterns from a given population are examined with the idea of finding similarities rather than differences, it is always possible to find a prepondrance of patterns obviously of the general type of pattern described for that species.

Variations in morphology make it apparent that identification of species by a study of the nematodes themselves will be a reliable method only in the hands of the specialist. The present study, however, has suggested that a simple and perhaps practical method of identification can be based on host reaction. Two types of host reaction can be used for this purpose: (1) susceptibility of certain plant species to various nematode species and (2) type of galls produced on the roots of infected plants. Several plant species which are highly resistant to at least one of the nematode species used in the present study but highly susceptible to the others are shown in Table XIV. A plus sign indicates susceptibility while a minus sign indicates resistance. For example, peanuts are susceptible to Meloidogyne hapla and M. arenaria, but resistant to the other nematode species. Watermelons, wheat, barley and corn are susceptible to M. arenaria but resistant or immune to M. hapla. Red pepper is resistant to M. javanica. Lycopersicon peruvianum is susceptible to M. incognita var. acrita but resistant to M. incognita (28).

Thus it should be possible to identify an unknown root-knot nematode population by using the four plant species -- peanuts, watermelon (or any of the cereals shown in Table XIV), red pepper, and Lycopersicon peruvianum, as shown in Figure 9. For example, should an unknown population not attack peanuts, the species present would be either M. javanica, M. incognita, or M. incognita var. acrita. If the population did not attack red pepper, the species present would be M. javanica,

TABLE XIV. Susceptibility of certain plant species to root-knot nematodes (*Meloidogyne* spp.).[a]

Meloidogyne species	Plant species[b]			
	Peanuts	Watermelon, wheat, barley or corn	Pepper	*Lycopersicon peruvianum*
M. hapla	+	-	+	+
M. arenaria	+	+	+	+
M. javanica	-	+	-	+
M. incognita	-	+	+	-
M. incognita var. *acrita*	-	+	+	+

[a]Plus indicates susceptibility; minus indicates resistance or immunity.

[b]Varieties used were: peanuts, Spanish; watermelon, Dixie Queen; wheat, Coastal; barley, Moore; corn, Golden Cross Bantam; pepper, California Wonder.

while a moderate to heavy infection would indicate either *M. incognita* or *M. incognita* var. *acrita*. The latter two species are further separated by testing the population against *L. peruvianum*. A moderate infection on *L. peruvianum* would indicate *M. incognita* var. *acrita* while negative results would indicate *M. incognita*. Should an unknown population infect peanuts, the species present would be either *M. hapla* or *M. arenaria*. These two species can be separated by testing the root knot population against watermelons or any of the cereal crops listed. Negative results would indicate that the species present was *M. hapla*, while positive results would indicate *M. arenaria*.

In these investigations, only *M. hapla* could be identified by the type of galling produced on host roots. Plants infected by this species were found to have very small galls and extensive root proliferation; the roots often forming a dense mat when infection was severe. This type of galling is shown in Figures 10, 11, 12, 14. Production of lateral roots just above the gall was found to be typical of plants infected with M. *hapla*. This effect is almost entirely absent in the case of the other species (Fig. 13 and 15).

It should be pointed out that this procedure for identification is applicable only to those species used in this study, though the general method can be used for identification of other species when the necessary data are collected.

The relatively small number of plants tested in these studies did not reveal any general pattern which would enable the prediction of resistance or susceptibility among plant species. The only indication of a correlation of resistance in plants with a nematode species was in the case of plant species of the families Cucurbitaceae (except cantaloup), Gramineae and Malvaceae which were resistant to M. *hapla*. Additional testing might show similar correlations between other root-knot nematode species and plant families, but in the meantime it appears necessary to test each nematode species and plant species and varieties separately.

Studies with the different nematode species, using both resistant and susceptible plants, revealed that infection and development of nematodes varied, depending upon the plant and the nematode. The different behaviors observed would indicate that resistance is not of the same nature in all plants. An explanation of resistance to root-knot nematodes has been that the larvae are not attracted to the roots of certain plants or are prevented from entering by the structural nature of the root. From the present study it is apparent that some very definite type of resistance exists in the cases of the plant and nematode species in which no larvae were found in the roots and perhaps also for those in which larvae were found in reduced numbers. The difference, however, between plants in which larvae were found in large numbers with little or no development and those in which larvae entered in large numbers and developed normally, obviously is not of this nature since large numbers of larvae entered the roots. Failure of nematodes to develop normally in those plants in which they entered freely, could only be due to some unknown physiological factor.

Practical use can be made of these observations. For the nematode species concerned, plants in which larvae do not enter and those in which larvae enter in reduced numbers, could be used in crop rotations designed to starve the nematodes. Plant which are highly susceptible to infection but resistant to development and reproduction of nematodes could be used to trap these organisms as suggested by Barrons (3).

The fact that those nematode species found in Maryland occurred rather generally throughout the state, would indicate that they have become well established. The other species probably are very rare or do not occur in Maryland since they were not found in any of the collections. Therefore, these need not be considered in designing rotation programs.

Practical significance of the work reported in this paper is that it provides a basis for scientific rotation of crops to control root knot. For purposes of crop rotation, the Maryland farmer has only two types of root-knot nematode to consider -- M. hapla and M. incognita var. acrita. In designing a rotation program, the first step would be to identify the nematode species present. This can be done by (1) a study of morphology, (2) by host tests or, (3) by observation of the type of gall produced. The host list can then be consulted for the purpose of finding crops which are immune or resistant to the nematode species present. From this list the crops most suitable for use in the farm program can be selected.

SUMMARY

Fifty plant species and varieties, consisting chiefly of agronomic crops commonly used in rotation programs in the southeastern United States, were tested for susceptibility to the root-knot nematodes, *Meloidogyne incognita*, *M. incognita* var. *acrita*, *M. hapla*, *M. arenaria* and *M. javanica*. Some plant species were found to be resistant to all the nematode species while others were susceptible to all. However, the majority of plants tested, were found to be between these two extremes in susceptibility, i.e., resistant to one or more of the nematode species and susceptible to the others. More plant species were resistant to *M. hapla* than any of the other nematodes.

Studies on infection and development of the different nematode species in resistant and susceptible plants revealed that in general resistant plants were not infected as readily as susceptible plants, when both were equally exposed to root knot inoculum. Larvae which entered roots of resistant plants showed little or no development beyond the first parasitic larval stage, while considerable development occurred in susceptible plants.

The principal character used for species determination was the perineal pattern of the adult female. Variations in morphology make it apparent that identification of species by a study of the nematodes themselves will be reliable only in the hands of specialists. The present study, however, suggested a simple and perhaps practical method of identification based on susceptibility of certain plant species to the various nematode species and type of galls produced on the roots of infected plants.

During a limited survey, two species and one variety of root-knot nematodes were found to occur in Maryland. These were *M. incognita*, *M. incognita* var. *acrita*, and *M. hapla*. The latter two were found more frequently. Occurrence of root knot was rather general throughout the state, having been found in 12 of the 14 counties visited. Severe infestations were more commonly found in the sandy loam type soils of the Eastern Shore than in the heavier type soil.

The practical significance of the work reported in this paper is that it provides a basis for scientific rotation of crops to control root knot.

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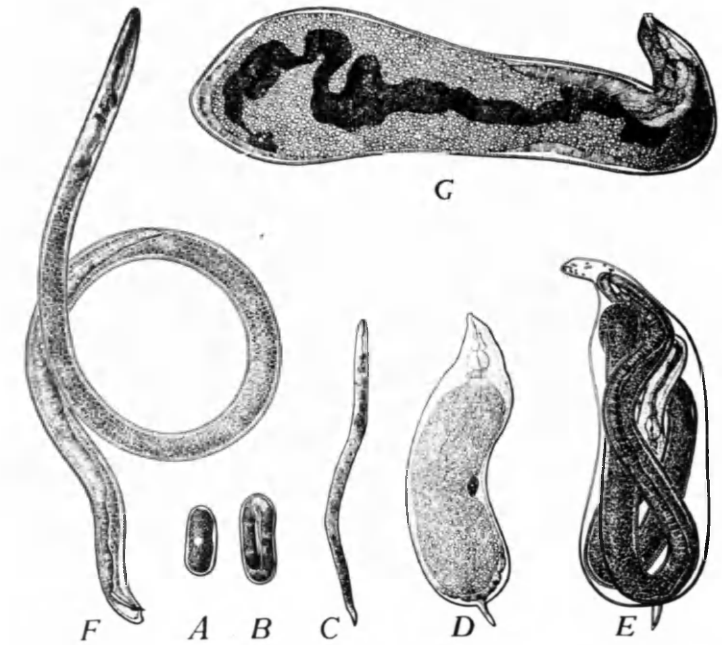
Figure 1. Drawings of various developmental stages of root-knot nematode. A. Unsegmented egg; B. egg, containing larva; C. migratory larva free in the soil; D. sausage-shaped sedentary in the root; E. larval molt containing fully developed male; F. adult male; G. young female. X100. (after Steiner, 1949).

Figure 2. Photomicrograph of a swollen root section of balsam plant (Impatiens balsamina) with adult females and egg masses of a root-knot nematode. X70. (after Steiner, 1949).


G
F
A
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E

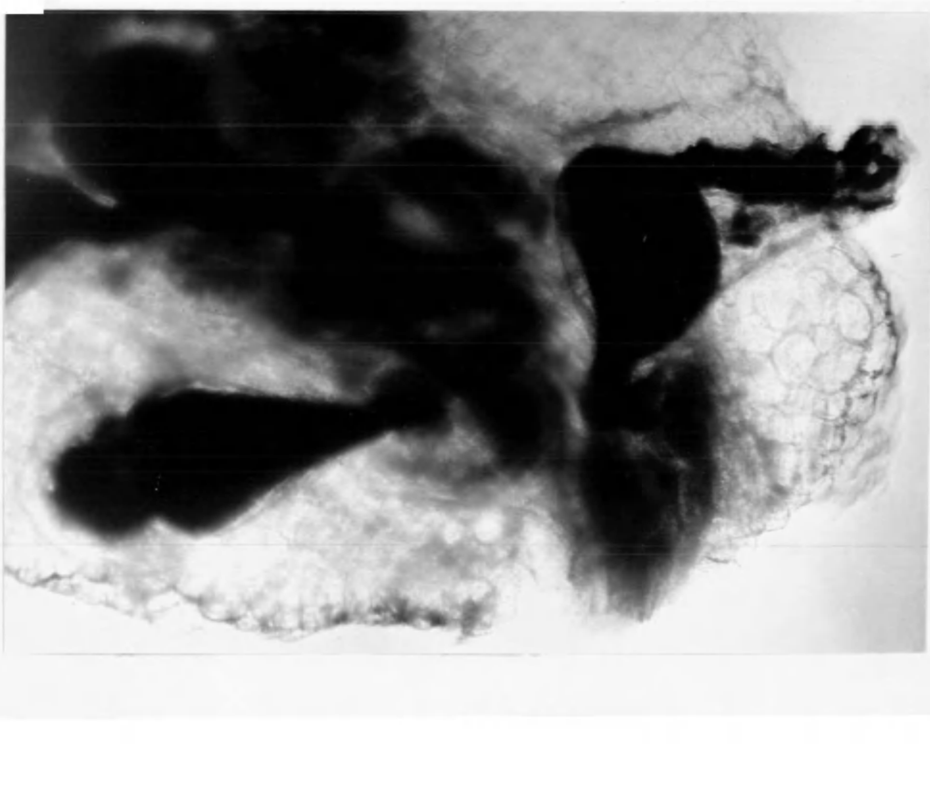

Figure 3. Some common variations found in perineal patterns of adult females of *Meloidogyne incognita*. The four specimens were taken from the following crop plants: A. tomato; B. tomato; C. alfalfa; D. cabbage.

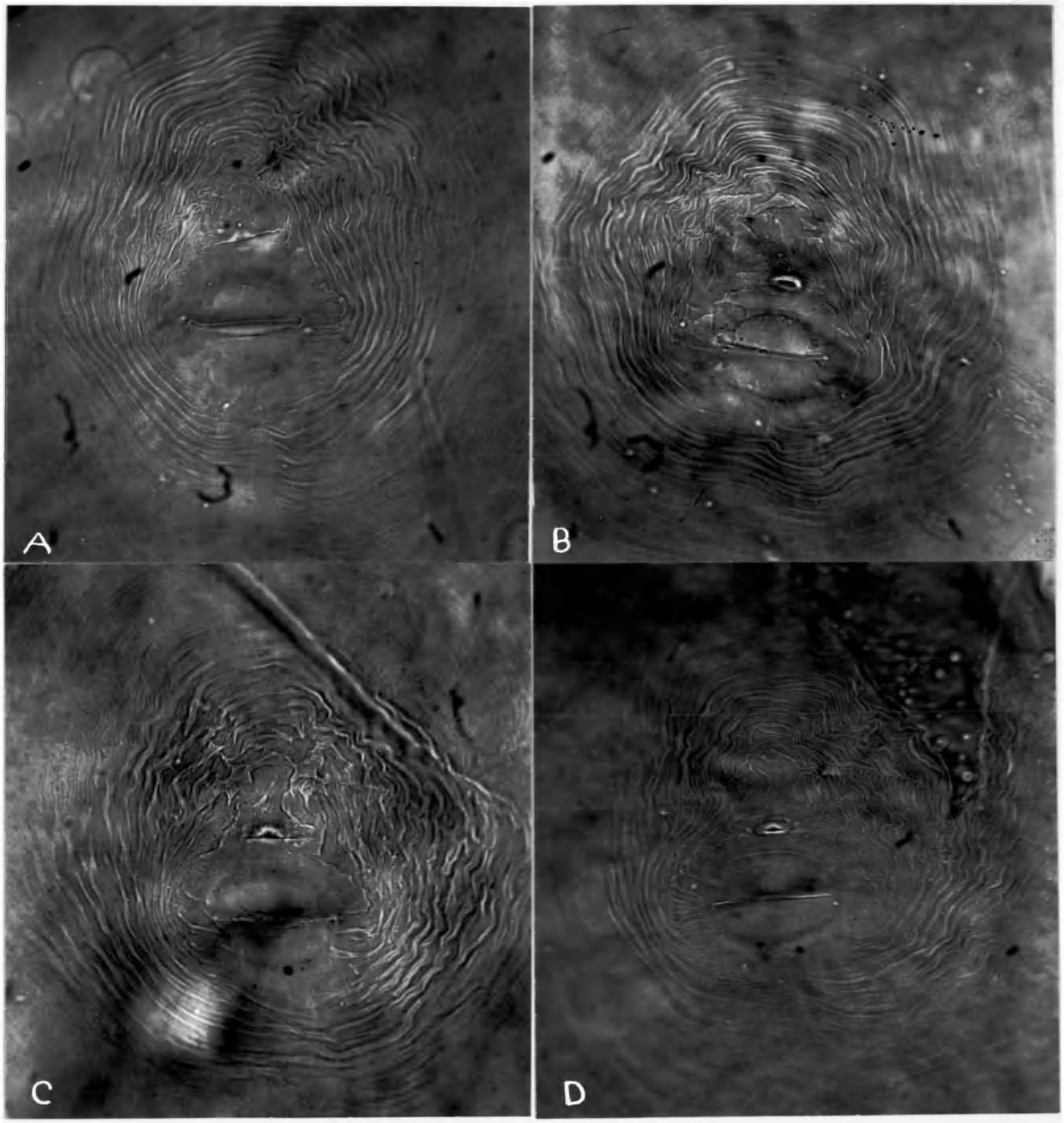
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Figure 4. Some common variations found in perineal patterns of adult females of *Meloidogyne incognita* var. *acrita*. The four specimens were taken from the following crop plants: A. wheat; B. pigweed; C. sweet potato; D. eggplant.

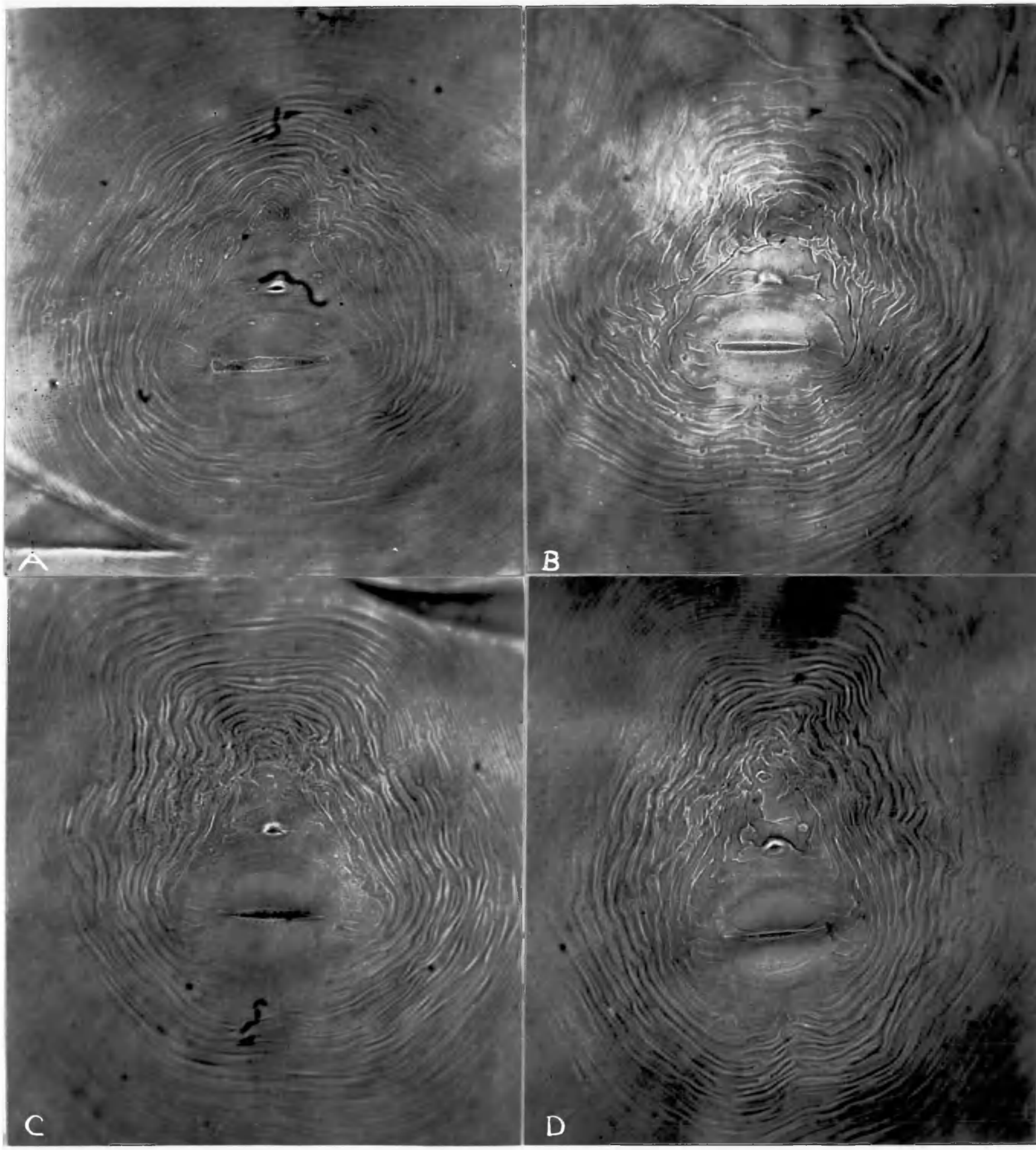
A
B
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Figure 5. Some common variations found in perineal patterns of adult females of *Meloidogyne hapla*. The four specimens were taken from the following crop plants: A. onion; B. onion; C. tomato; D. strawberry.

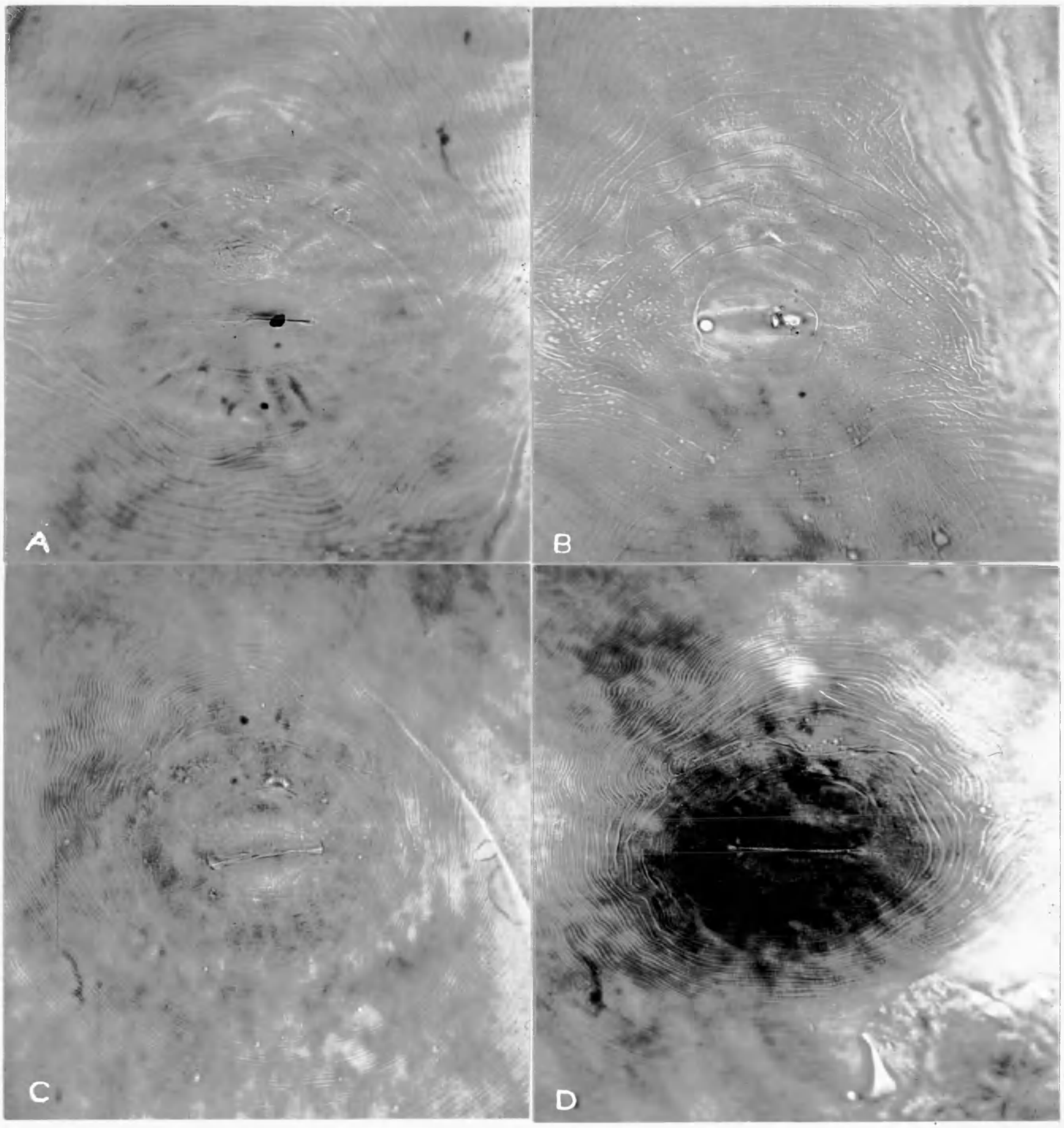
A
B
C
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Figure 6, Some common variations found in perineal patterns of adult females of *Meloidogyne javanica*. The four specimens were taken from the following crop plants: A. onion; B. carnation; C. wheat; D. alfalfa.

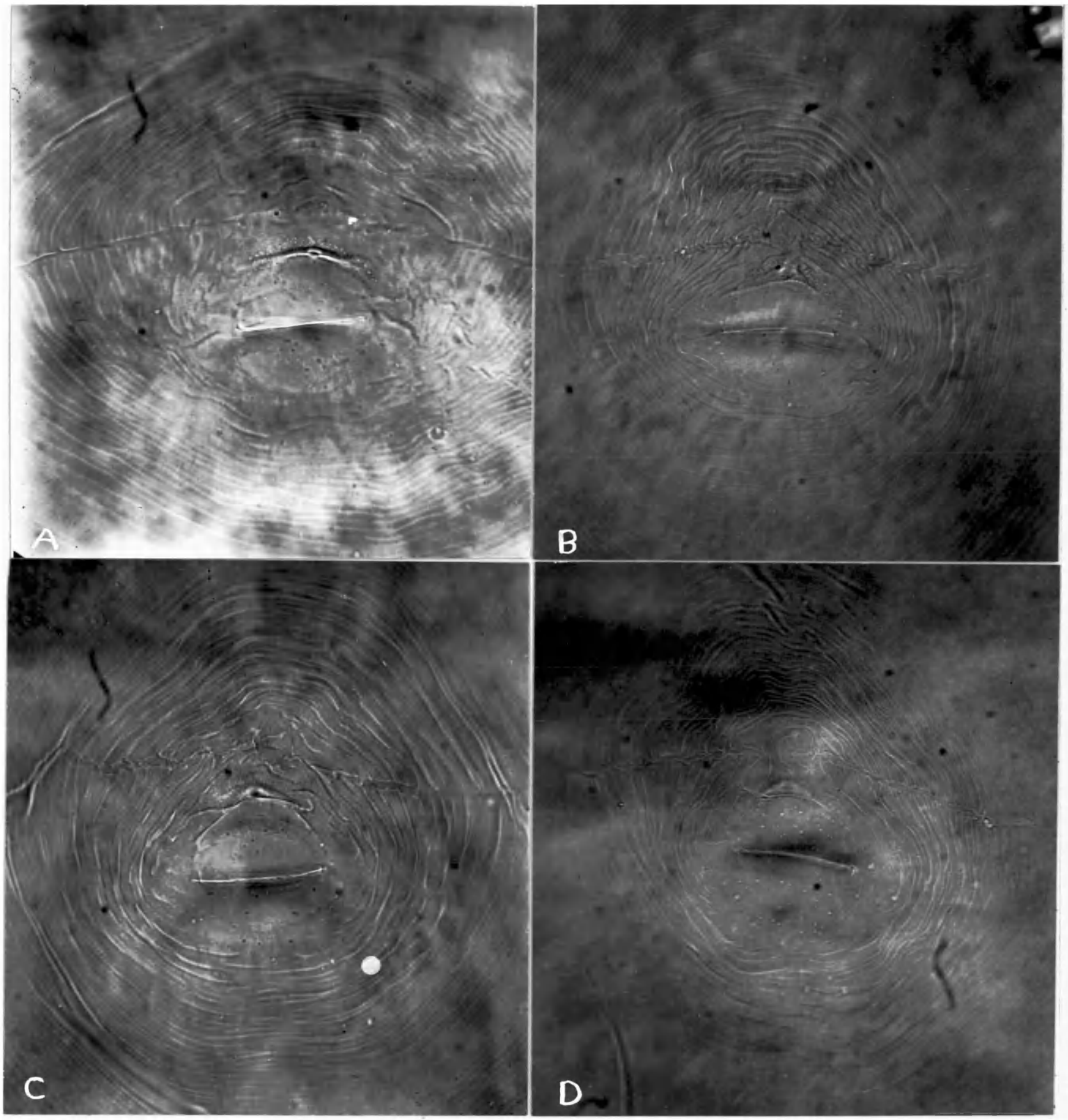

A
B
C
D

Figure 7. Some common variations found in perineal patterns of adult females of *Meloidogyne arenaria*. The four specimens were taken from the following crop plants: A. red pepper; B. common oleander; C. tobacco; D. watermelon.

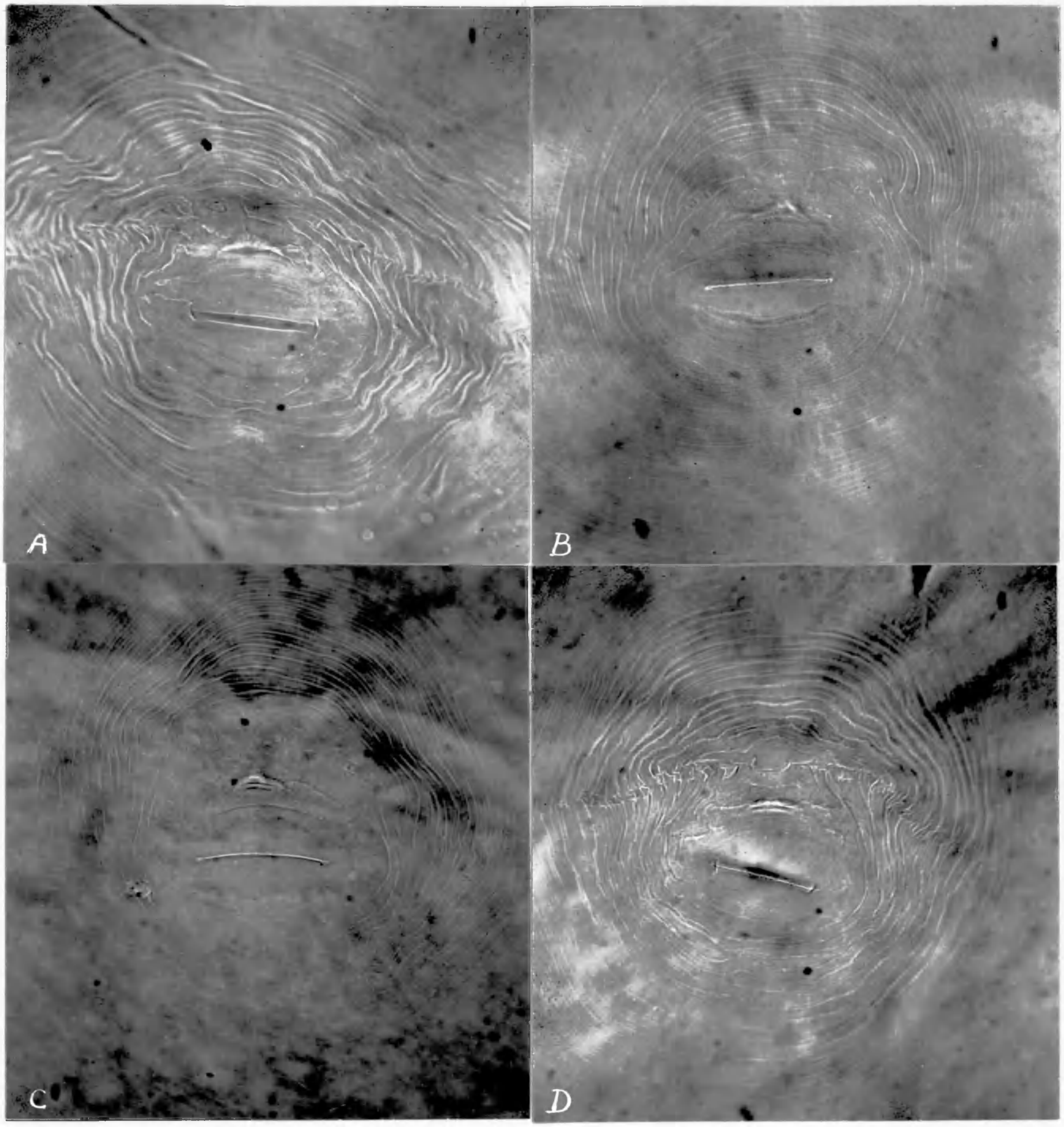
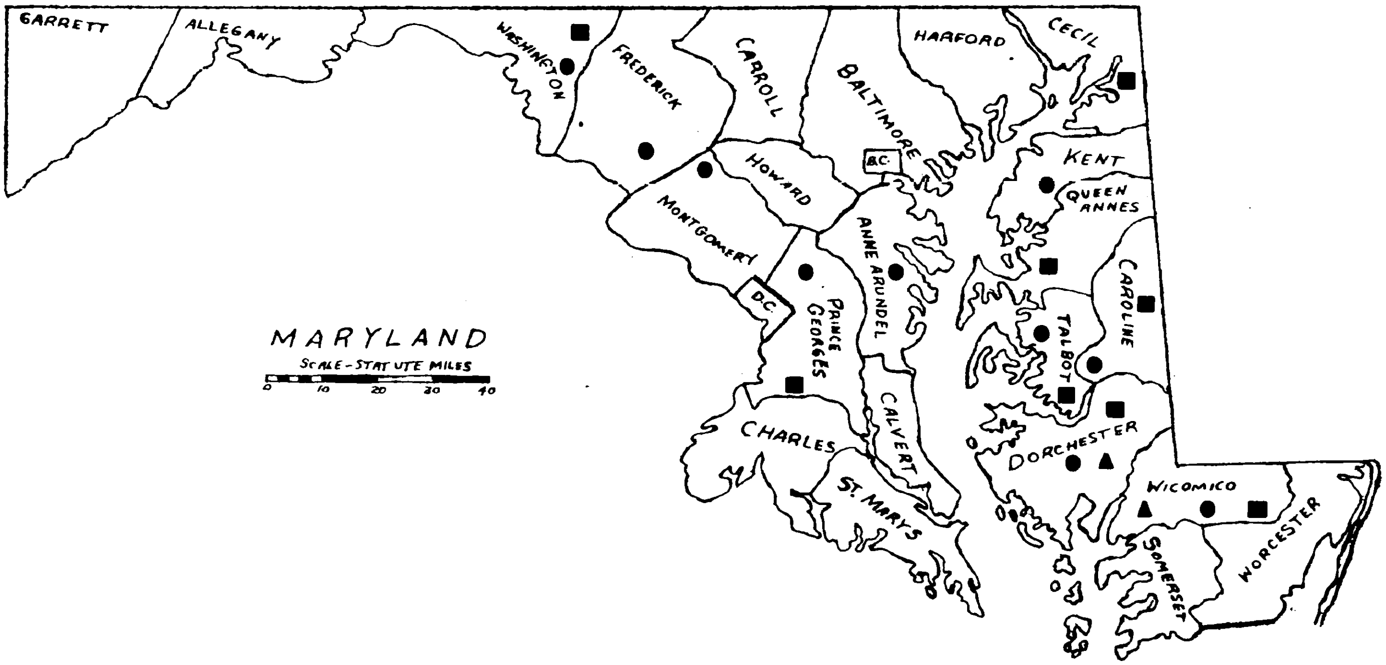

A
B
C
D

Figure 8. Approximate locations from which species of Meloidogyne were collected in Maryland. Meloidogyne incognita is designated by a triangle; M. incognita var. acrita by a square; M. hapla by a circle. Root knot was not found in Carroll or Howard Counties.

Figure 9. Identification of root-knot nematodes (Meloidogyne spp.) by host reaction. A plus sign indicates susceptibility to root knot; a minus sign indicates resistance to root knot.


GARRETT
ALLEGANY
WASHINGTON
FREDERICK
CARROLL
BALTIMORE
HARFORD
CECIL
B.C.
HOWARD
MONTGOMERY
KENT
QUEEN ANNES
ANNE ARUNDEL
CAROLINE
D.C.
PRINCE GEORGES
TALBOT
MARYLAND
SCALE - STATUTE MILES
0 10 20 30 40
CALVERT
CHARLES
DORCHESTER
ST. MARYS
WICOMICO
SOMERSET
WORCESTER

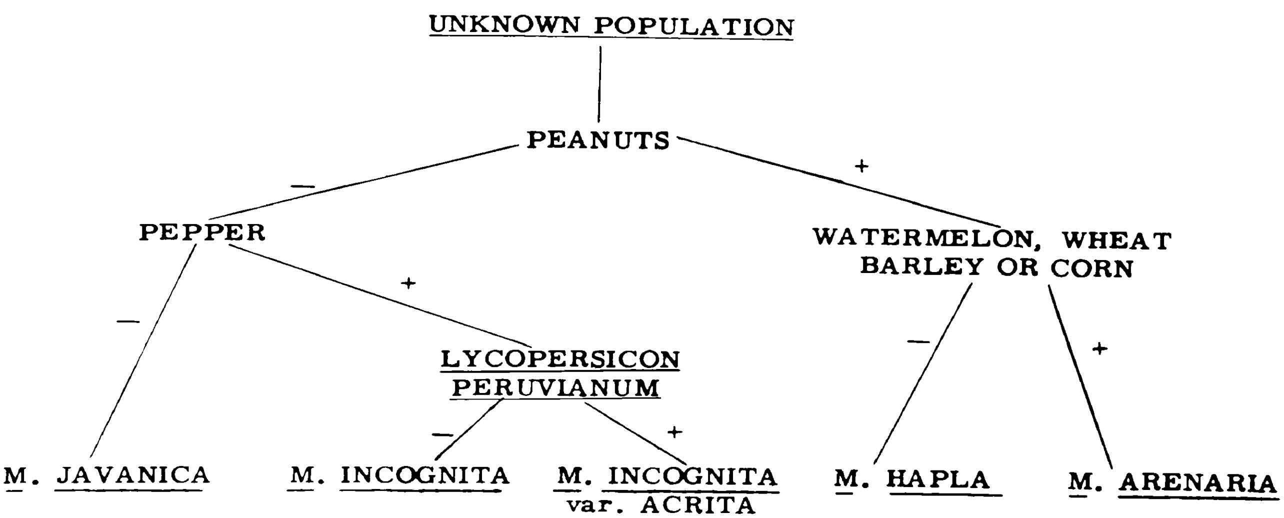
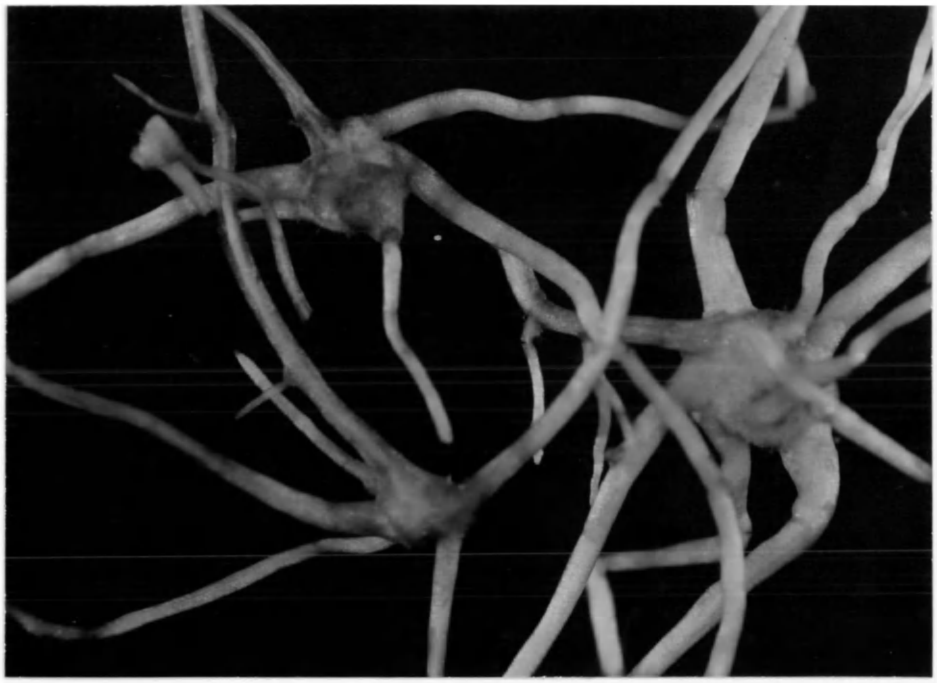

UNKNOWN POPULATION
PEANUTS
—
+
PEPPER
WATERMELON, WHEAT BARLEY OR CORN
—
+
LYCOPERSICON PERUVIANUM
—
+
—
+
M. JAVANICA
M. INCOGNITA
M. INCOGNITA var. ACRITA
M. HAPLA
M. ARENARIA

Figure 10. Peanut roots showing early stages of infection with *Meloidogyne hapla*. The formation of lateral roots in the vicinity of the gall is typical for plants infected by this species. (about twice natural size)

Figure 11. Soybean roots infected with *Meloidogyne hapla*, showing extensive root proliferation.



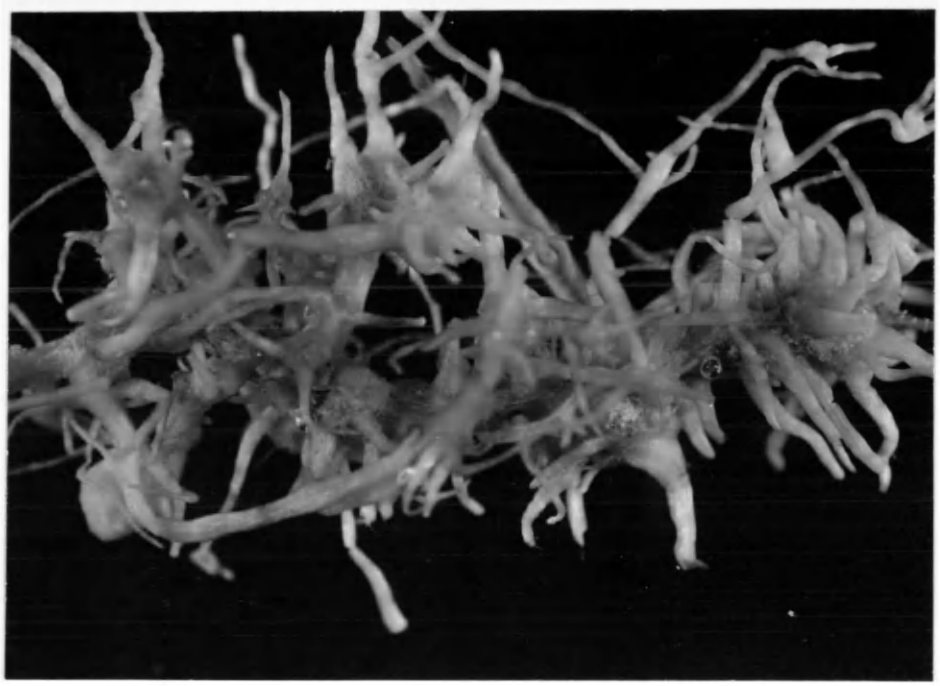
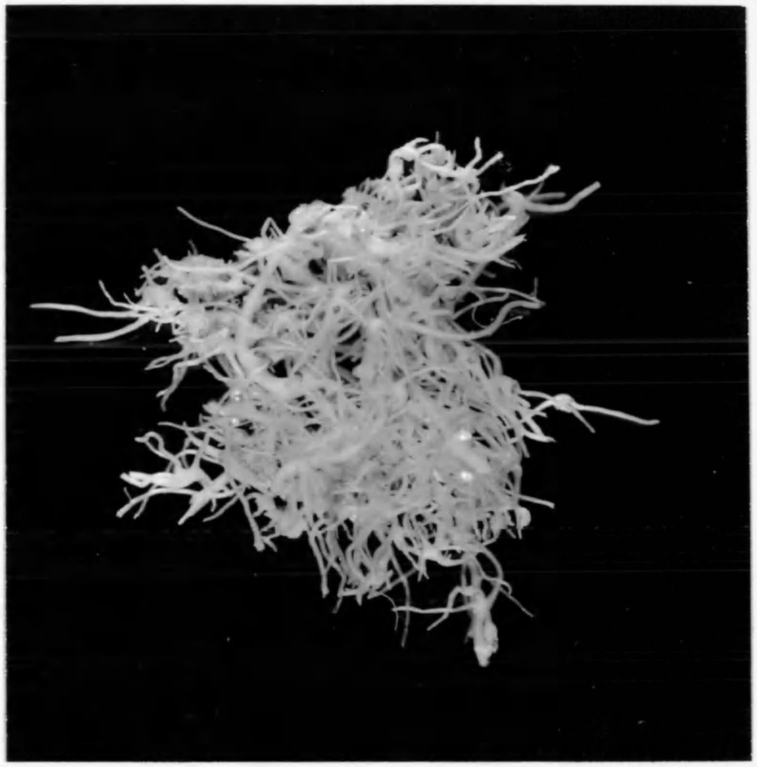


Figure 12. Tomato roots infected with *Meloidogyne hapla* showing small galls and matted root system.

Figure 13. Tomato roots infected with *Meloidogyne javanica*.



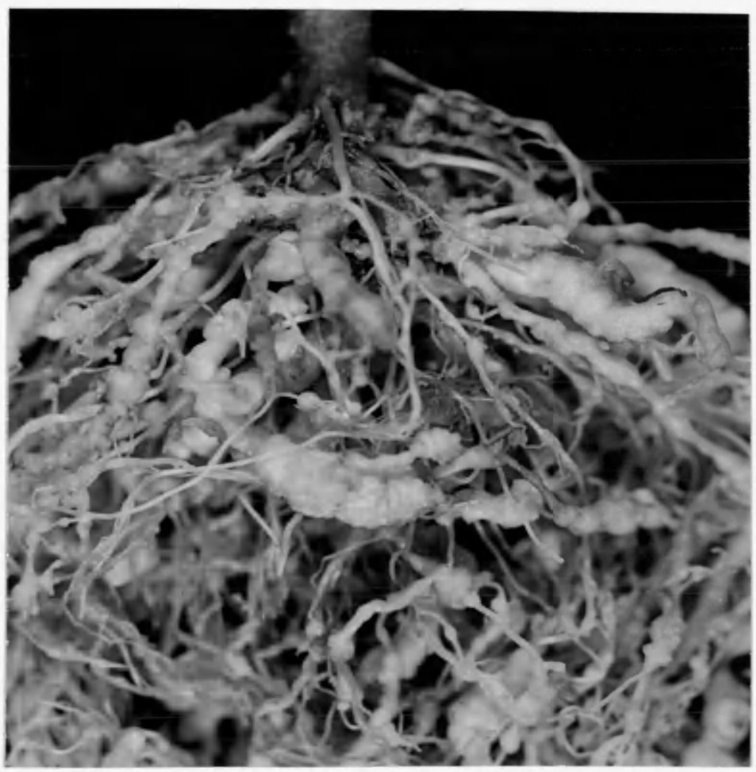
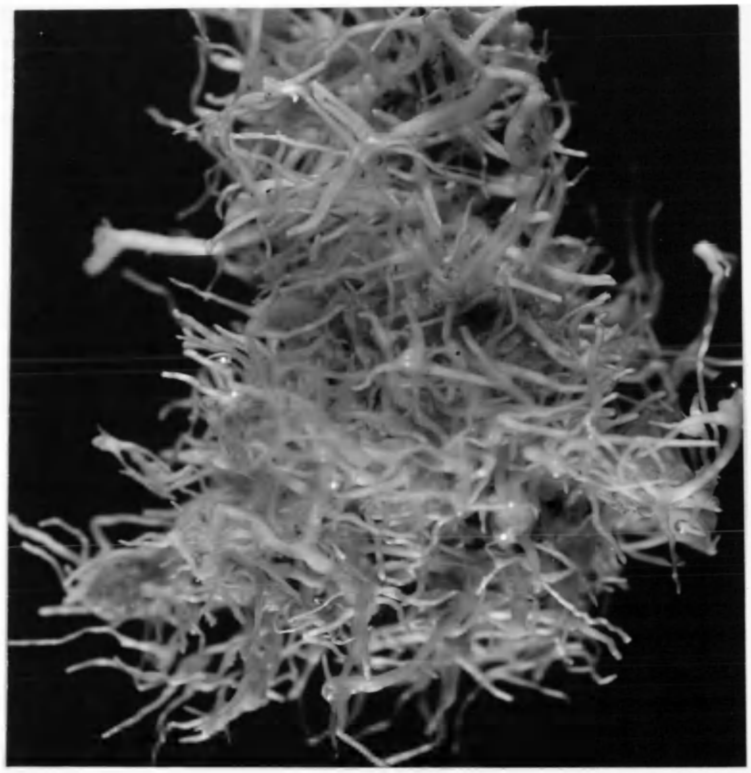
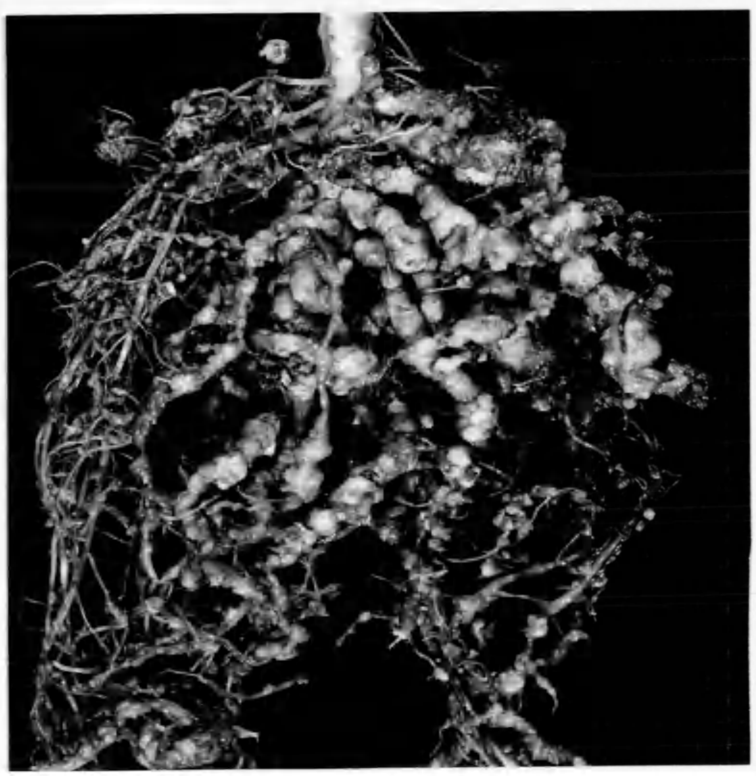


Figure 14. Snap beans infected with *Meloidogyne hapla*. Small galls are somewhat obscured by extreme proliferation of the root system.

Figure 15. Snap beans infected with *Meloidogyne incognita*. The galls are large and extensive proliferation of the root system as shown in Figure 14 is lacking.





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2. 1951. Studies on the control of Golden Nematode of potatoes with Systox spray (E-1059), an organic phosphate insecticide. U. S. Dept. Agr. Pl. Dis. Rptr. 35: 152-155. (with J. Feldmesser and G. Fassuliotis).

3. 1951. The use of gelatin capsules for making single egg-mass inoculations with the root-knot nematode (<u>Meloidogyne</u> spp.). (Abs.) Phytopathology 41: 564.

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5. 1952. Identification of root-knot nematodes (<u>Meloidogyne</u> spp.) by host reaction. U. S. Dept. Agr. Pl. Dis. Rptr. 36: 84-86.

6. 1952. Studies on the entry of larvae of root-knot nematodes into roots of susceptible and resistant plants. (Abs.) Phytopathology 42: 474. (with A. L. Taylor).

7. 1952. Observations on <u>Heterodera weissi</u> Steiner, 1949 (Heteroderidae, Nematoda). Proc. Helm. Soc. Wash. (in press). (Junior author with A. C. Tarjan).

8. 1952. The plant nematode problem on the Delmarva peninsula. Dept. of Hort., Univ. of Md., Misc. Pub. 131: 27-29.

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