PATHOGENICITY AND HISTOPATHOLOGY OF *MELOIDOGYNE JAVANICA* AND *M. INCOGNITA* ON OLIVE AND TOMATO

BY

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Root-knot nematodes, Meloidogyne spp. Goeldi, 1887, are considered as a global menace to world agriculture (Sasser, 1980). In Jordan, Abu-Gharbieh (1982 a) refered to these nematodes as a real problem facing irrigated agriculture. Therefore, extensive research work has been done in Jordan on the biology (saleh, 1979), ecology (Abu-Gharbieh, 1982 b), and control (Abu-Gharbieh, 1962 and 1982 a; Sharawi,1982) of the root-knot nematodes. Most of the work, however, was concentrated on cultivated vegetable crops, particularly tomatoes, but very little was devoted to fruit trees. On a world-wide scale, also, studies on the root-knot nematodes of fruit trees seem to be relatively limited.

Olive, Olea europaea L., is the most wide-spread fruit tree crop cultivated in Jordan. In 1985, nearly 56% of the entire fruit tree area was found to be planted to olives (Department of Statistics). Olive seedlings produced in certain nurseries were reported to suffer extensive root-knot nematode infections (Abu-Gharbieh, 1962). In the mediterranean region, only scattered information on the effect of these nematodes on olives is available

(Diab and El-Eraki, 1968; Lamberti, 1968; Lamberti and Baines, 1969). And except the work of Sharawi (1982), very little work was done on the biology, ecology, and control of the root-knot nematodes on olive in Jordan.

While information on the histopathology of Meloidogyne spp. on fruit trees are meager, such information on olives are simply nonexistent. In the same time, quantitative histological studies, even on vegetables, are still very limited, and direct relationship between the plant cellular responses and nematode reproduction were not, until this work, well established.

This research work, therefore, was conducted to meet the following principal goals:

1 - To study the pathogenicity of the two major root-knot nematode species in Jordan, Meloidogyne javanica (Treub) Chitwood, 1949 and M. incognita (Kofoid and White) Chitwood, 1949, to the predominant local 'Nabali' and the introduced 'Grosa de Spain' olive cultivars.

2 - To study the histopathology of both nematode species on the above mentioned olive cultivars.

3 - And, to determine possible quantitative relationships between certain cellular responses and the nematode reproduction potential.

All these characteristics were also studied on the standard tomato cultivar 'Claudia Raf', since it is a well known vegetable host, susceptible to both nematode species (Abu-Gharbieh, et al, 1978)

REVIEW OF LITERATURE

The root-knot Nematodes

A. Occurance and economic importance:

Within the genus Meloidogyne there are two distinct survival groups: thermophils and cryophils (Guiran and Ritter, 1979, Van Gundy 1985). This gives the species of this genus the opportunity to have a world-wide distribution (Wang et al, 1975; Sasser, 1976). It is reasonably certain that most of the wide-spread economicaly important species, roughly in order of distribution and crop damage are: M. incognita, M. javanica, M. hapla, and M. arenaria (Taylor and Sasser, 1978; Sasser, 1980). These species account for more than 95% of root-knot nematodes in agricultural soils (Carter and Sasser, 1982). However, M. incognita and M. javanica are the most widespread root-knot species in areas with subtropical and mediterranean climates(Lamberti,1979) Meloidogyne incognita is unquestionably the most important species on a world-wide basis (Sasser, 1980). In Jordan, Abu-Gharbieh and Hammou (1970) reported two species of the genus Meloidogyne present in the country, namely M. javanica and M. incognita. Later, Abu-Gharbieh (1982) reported that

M. javanica predominates in the hot southern Jordan Valley area, while M. incognita predominates the milder irrigated highlands. The auther attributed this pattern of distribution to the fact that M. javanica has 4-5^{0}c higher optimum temperature than that of M. incognita.

The root-knot nematodes have an extensive host range, exceeding 2,000 plant species (Hussey, 1985). Collectively, the various species of Meloidogyne attack nearly every crop grown (Sasser, 1980). Vegetable crops, field crops, fruit trees, forest trees, forages and weeds are attacked by the roo-knot nematode species (Webster, 1972). In Jordan, root-knot nematodes have been reported on 20 vegetable crops, five fruit trees (Mamluk et al, 1984) and a large number of weed hosts (Abu-Gharbieh 1982 a). Meloidogyne incognita was reported on eggplant, sweet melon, pepper and tomato, while M. javanica on broadbean, cabbage, cucumber, eggplant, sweet melon, okra and tomato (Mamluk et al, 1984). Tomato seems to be one of the most seriously attacked vegetable crops. Hashim (1979) reported that in the irrigated low lands of Jordan, the vegetable crops tomato, eggplant, and cucumber appeared to be the most seriously affected by M. incognita and M. javanica; the latter more commonly. Experiments in Italy demonstrated that severe attack of M. incognita on canning tomato may

cause yield losses of about 50%. Also, in North Carolina, out door experiments showed that M. incognita can suppress yield of tomato by up to 85% in the coastal plains (Lamberti, 1979). In screening tomato cultivars for resistance to the root-knot nematodes, Abu-Gharbieh et al (1978) found about 90 out of 100 cultivars to be susceptible to either M.javanica or M.incognita or both.

Many fruit and forest trees were reported to be attacked by the root-knot nematodes. Cherry, pear , walnut , banana, strawberry, raspbery, blue berry and grape are known to be attacked by one or more of the Meloidogyne species (Webster, 1972). In the United States, root-knot nematodes were reported in association with redmapple, yellow poplar, American sycamore, riverbirch, and eastern cottonwood (Wang et al, 1975). Mamluk et al (1984) reported Meloidogyne species in association with banana, grape, walnut and olive trees in Jordan. Abu-Gharbieh (1962) stated that in olive nurseries whose soils were not fumigated, up to 90% of the seedlings were infected with the root-knot nematodes. Species of Meloidogyne occur in many olive growing regions of the world, the most frequently encountered being M. incognita and M. javanica (Hashim, 1982). Diab and El-Eraki (1968) reported that M. javanica decreased the growth of

olive seedlings in Egypt by 28%. However, parasitizing of olives in Jordan by either M. incognita or M. javanica was evident in nurseries and olive groves grown under irrigation (Hashim, 1982). Under rainfed conditions, however, the root-knot nematodes were unable to get established (Abu-Gharbieh, 1978). Meanwhile, more and more olive plantations are being established under irrigation, particularly in the eastern areas of Jordan (Abu-Gharbieh, personal communications).

Olive cultivars seem to differ in their response to Meloidogyne species. Weights of 'Ascolano' plants were significantly reduced by addition of 1,000 or more larvae of M. incognita, while weights of 'Manzanillo' plants were not reduced by addition of 65,000 larvae (Lamberti and lownsberg, 1968).

B. Reproduction.

Arens et al (1981) proposed three main factors controlling nematode reproduction: the nematode species or race, the plant cultivar, and the environmental conditions. Hence, under the same conditions, variability in reproduction of a nematode species is a host response. Wallace (1963) considered a well-growing host plant on which the nematode

reproduces well, to be tolerent; while resistant if the nematode reproduction on that host is poor. According to Bafokuzara (1983), the population densities of a nematode species are function of the reproductivity of that species, while, crop losses are usually function of the population densities. Investigators have reported many examples of differences in nematode reproduction on different hosts. Bafokuzara (1983) found that M. javanica produced more eggs per eggmass on tomato cv 'Monymaker' than on the cabbage cv 'Ashley'. Also, the number of galls per 50 cm of roots followed the same trend. This author concluded that host plants had a dominant influence on the survival and multiplication of root-knot nematodes, particularly under conditions of adequate soil moisture. Swanson and Van Gundy (1984) found variability in the reproduction rate of M. incognita on two soybean cultivars. Also on tomato roots, number of eggs per eggmass of M. javanica ranged from 120 to 880 in different dates throughout the season (Saleh, 1979). Significant differences were further observed in the growth and re production rates of M. javanica on different host plants under the same environmental conditions (Bird, 1974). Arens (1981) attributed the differences in pathogenicity of M. javanica, M. incognita and M. hapla on tobacco to the differences in their fecundity on that host.

C. Symptomology:

The most common symptom of Meloidogyne infections is the development of galls on the root system (Jenkins and Taylor, 1967; Taylor and Sasser, 1978; Dropkin 1980). In addition, host plants may exhibit one or more of the general symptoms which include growth retardation, stunting, loss of yield, reduction in quality of produce, severe deficiency symptoms of some elements - particulary nitrogen, incipient wilting during hot periods of the day, increased susceptibility to vascular wilts, and even loss of resistance to certain other pathogens (Wallace, 1963; Jenkins and Taylor, 1967). Not only Meloidogyne species induce root galling, but also species of Meloidodera induce rounded galls, Hypsoperine induce rather inconspieuous galls, and Hemicycliophora produce small-sized galls. The false root-knot nematode, Nacobbus, produces root galls similar to those caused by Meloidogyne species, and Xiphinema diversicaudatum induce curly-tip galls (Jenkins and Taylor, 1967). Recently, Globodera pallida was reported to induce unusual swelling of tomato roots (Vovlas et al 1986).

Gall formation is believed to be induced by nematode secretions ejected into the plant tissue (Endo, 1971). It

is suggested that Meloidogyne larvae respond to host plant stimulants to release the galling stimulus (Dropkin, 1972). This galling stimulus induces the adjacent host cells to undergo an increase in size, hypertrophy, or an increased rate of celldivision,hyperplasia, (Dropkin, 196 ; Bird, 1979). However, galling do not seem to be essential for the nematode growth and development (Webster, 1969; Bird, 1979).

Some plant species, however, respond to the attack by certain nematode species by an increased root growth in the form of root proliferation, i.e. more frequent lateral root development (Wallace, 1963). These lateral roots might arise from the infection site, the gall, or from any part of the infected root, depending on the parasite and the host. Trichodorus Christiei, Belonolaimus gracilis, Dolichodorus heterocephalus and Pratylenchus projectus, all induce root proliferation all over the root system (Wallace, 1963). On the other hand, Meloidogyne hapla is known to induce root proliferation (Wallace, 1963) from the gall, as on carrot roots (Carter and Sasser, 1982).

Other species of Meloidogyne are not reported to induce root proliferation except in a special host-parasite

relationship with olive (Lamberti and Baines, 1969; Sharawi, 1982).

Lamberti and Baines (1969) reported that a specific reaction of olive seedlings to infections with M. javanica or M. incognita resulted in the production of short stubby roots, while Diab and El-Eraki (1968) reported that the root system of olive seedlings were more dense and tended to form branches near the region of invasion, as a response to M. javanica infections.

The lateral root formation is stimulated by auxins and other growth regulators, but its suppression by endogenous inhibitors may be responsible for the frequency and distribution of laterals on the parent root (Esau, 1977). Treatments with exogenous indoleacetic acid (IAA) induced lateral roots, hypertrophy and hyperplasia in decapitated pea epicotyls (Dropkin, 1969).

On tomato roots, however, root galling, some times very extensive with an extremely malformed root system, seem to be the most known root symptom (Wallace, 1963; Jenkins and Taylor, 1967; Radewald, 1978).

D. Host cellular responses

1. Host cellular responses to sedentary endoparasitic nematodes.

Various genera of phytoparasitic nematodes have evolved intimate relationships with their hosts by the development of specialized feeding site within plant tissues (Jones, 1981 a). Cyst nematodes (Heterodera and Globodera), Reniform nematodes (Rotylenchulus reniformis) and false root-knot nematodes (Nacobbus spp.) induce the formation of a syncytium. i.e., a multinucleate mass of protoplasm formed by fusion of uninucleate cells (Dropkin, 1969; Sultan, 1976; Bird, 1979; Jones, 1981 a). Whilst the citrus nematode (Tylenchulus semipenetrans) induces the formation of nurse cells with normal sized cells whose nuclei and nucleoli undergo hypertrophy (Webster, 1969; Sultan, 1976; Bird, 1979). On the other hand, root-knot nematodes (Meloidogye spp.) induce a giant cell(s), which have multinucleate mass of protoplasm resulting from repeated mitotic divisions without cytokinesis (Bird, 1979; Jones, 1981 b; Huang, 1985)

2. Giant cells of Meloidogyne

a. General considerations:

As early as 1886, Treub described a group of enlarged cells surrounding the mouth of the root-knot nematode, now known as 'giant cells' (Bird, 1979). Giant cells are evidently sites of intense metabolic activity, specialized to take up solutes to supply nutrients to the nematodes, while at the same time maintaining functional integrity (Endo, 1971; Jones, 1981 a). These were recorded to initiate in the cortex, endodermis, pericycle, parynchyma cells of the central vascular strands and in the metaxylem, but msot commonly in the vascular tissue (Cole and Howard, 1958 ; Bhatti and Sasser, 1971; Jatala and Jensen, 1976). The giant cells vary in number from 3 up to 12, but most commonly around half a dozen (Dropkin, 1955; Webser, 1969).

The formation of giant cells seems to be associated with successful nematode growth and development (Wallace, 1963). Bird (1974) also considers that production of giant cells is the most important criterion for successful development of the nematode. However, the findings of Wang *et al* (1975) do not support this statement. After examining different forest trees for their reaction to

the root-knot nematodes, these investigators stated that "the absence of giant cells associated with development of adult male in china-fir and with females and males in scotch and jack pines (resistant forest trees) arises a question as to whether these cells are vital to full development". Several investigators, however, have indicated that root-knot nematodes feed in the intercellular spaces or on many kinds of thin-walled cells prior to giant cell formation (Endo and Veech, 1969; Huang and Maggenti, 1969; Endo, 1975). Wang's et al (1965) observations thus suggest that in some plants this type of feeding may be sufficient for complete development, while this remains an exception rather than the rule. On the other hand, when the giant cells are already established, the continuity of the nematode feeding is then vital. Bird (1974) demonstrated that if the nematode is removed or killed, the giant cells breakdown and are overwhelmed by the activity of normal cells. The nematode secretions therefore must continuously regulate the altered metabolism of its host's cells, the giant cells.

Galling, far on the other hand, is not essential for nematode growth and development, and can take place in plants in which the nematode does not become established (Bird, 1974 and 1979).

b. Mechanisms of host response:

The second stage larvae usually penetrate the cortex intercellularly (Endo, 1971; Bird, 1974). Throughout this pathway, larve may or may not feed, if they do, they receive their nutrients from the host through suction of plant substances that are deposited in the intercellular spaces between stimulated cells (Endo, 1975). In a resistant host, when larvae reach the vascular cylinder, they either fail to influence host cell nuclear division and growth to induce giant cells, or the host responds in a hypersensetive reaction. In both cases, larvae get starved to death or return back (Mcclure et al, 1974). In a susceptible host, however, cells around the nematodes lip undergo transformation to initiate the giant cells. Giant cells are formed through repeated endomitosis without cytokinesis, governed by the nematode secretions (Huang, 1985). There have been some arguments whether cell wall dissolution is involved in giant cell formation, but recent electron microscopy observations seem not to support this latter hypothesis (Jones and Payne, 1978; Huang, 1985).

Growth regulators have long been speculated to play a role in the induction of galls and giant cells and that the galled tissues contain more growth regulators than

healthy ones (Dropkin, 1972; Bird, 1979). Bird and Loveys (1980) for example, found marked differences in cytokinin content of root homogenates between infected and control plants. Yu and Viglierchio (Cited in Dropkin, 1972) found auxin activity in the extracts of M. hapla larvae. Webster (1975) suggested three mechanismsthat might explain the increased concentration of auxins in the nematode-infected plant tissue: 1) that the auxin increase is induced by nematode secretions releasing protein-bound auxin; 2) that the nematodes themselves release auxin; or 3) that the nematodes interfere with plant auxin synthesis. Sayre (cited in Endo, 1971) discussed the possibility of interactions of nematode secretions with plant hormones. He postulated that in the process of feeding, the nematode secretes proteolytic enzyme, which releases IAA or tryptophane, an IAA precursor, from protein chains in the tissue. The released IAA would then contribute to the galling and giant cell formation.

c. Nuclei and Nucleoli

Recently, Huang (1985) explained that mature giant cells are always multinucleate, due to the repeated endomytosis without cell wall formation, governed by the nematode parasite. Nuclei within a giant cell are highly

variable both in size and shape. According to Wang et al (1975), nuclei are round or elongate to spindle-shaped, and some are flattened or dish-shaped.. Webster (1969) described large, ovoid nuclei associated with a raptured nuclear membrance in tomato giant cells. Some are irregularly lobed and ameboid in form, thus with a tremendously increased surface area (Huang, 1985). According to Owens and Splecht (Cited in Endo, 1971), two types of nuclear responses were distinguished; a nucleus near the nematode stylet, which showed a hypertrophied size with apparent absence of nuclear membrance; and nuclei far from the stylet with various stages of membrance deterioration, and lobulated periphery. The increased size of nuclei, on the other hand, is attributed to the accumulation of chromosome sets (Huang and Maggenti, 1969). These authers also reported that a hypertropheid nucleus undergoes an increase in size of 10 to 12 folds than normal. During the interphase of an inact cell, the nucleus is usually roughly spherical in shape, about 10 μ in diameter and is chiefly consisted of nucleic acids and proteins (Hall et al, 1982) .

Nucleoli of the giant cell nuclei are also always hypertrophied. Nucleoli are rich in ribonucleoproteins and are intimately associated with the specific region of the

chromosomal DNA that codes for ribosomal RNA (Hopkins, 1978) A major role of the nucleoli also is that they are associated with the process of protein synthesis (Hall et al, 1982).

These structures of nuclei and nucleoli, accompanied with the tremendously increased surface area of lobed nuclei to facilitate more solute exchange, might explain the role of nuclei in the giant cells in supplying the nematode with its nutritional demands (Hussey, 1985).

d. Giant cell walls and wall ingrowths:

Giant cells have thickened, irregualr cell walls, while the stimulus for irregular deposition is unknown (Dropkin, 1972). But in general, wall thickening is due to the deposition of polysaccharides on the cell wall, as enhansed by the nematode secretions (Jones, 1981 a). Giant cell walls are lined with variable wall ingrowths. these are non lignified secondary wall deposits, composed of irregular cellulose microfibrils and matrix material. Ingrowths vary from finger-like projections to plates or flanges, and they can branch and anastomose to develop elaborate labyrinths (Jones, 1981 a). Giant cells with these ingrowths resemble the naturally occurring transfer

cells (Jones and Dropkin, 1976). Transfer cells are found where there is thought to be intensive solute exchange between the cell wall compartment and the cytoplasmic compartment . Ingrowths provide a marker for such sites (Jones, 1981 a). They increase surface area of the plasmalemma in a giant cell with an amplification factor which can reach more than 10 (Jones and Dropkin 1976). This increased area stimulates extensive solute flow (Jones and Dropkin, 1976) thus providing sufficient nutrients for the developing nematode.

e. The role of giant cells in host susceptibility and resistance:

One criterion of a susceptible host is its ability to support a good level of the parasite's reproduction; while a tolerent one, allows poor reproduction (Wallace, 1963). Taylor and Sasser (1978) related the status of giant cells to the level of nematode reproduction. These authers reported that a study of histopathological response of 19 cultivars of soybean Glycins max to M. incognita, produced three main types of responses: (1) large, thick-walled multinucleate giant cells, with granular, dense cytoplasm - this type of giant cells is optimum for nematode reproduction;

(2) large giant cells, but with thin walls and less dense cytoplasm - these giant cells are much less than optima for reproduction; and (3) small giant cells with inclusions such as strands or lobed matter - such cells are associated with very poor nematode reproduction.

Bird (1972) in his higtopathological studies found a possible relationship between the average section area of giant cells and the rate of reproduction of Meloidogyne species. Studies on the effect of hydroxyurea on giant cells and nematode development, revealed that hydroxyurea hampered giant cell formation, and the poorly developed giant cells inhibited the nematode maturation by 70-90% (Glazer and Orion, 1985). These authers, therefore, considered hydroxyurea to be an agent of induced resistance to the root-knot nematodes. Stender et al (1986) also concluded that the thin walls of giant cells, with less extensive ingrowths, and relatively small nuclei, contributed to the retardation of nematode growth and development.

It is assumed, therefore, that the status of giant cell structures, including their size, cytoplasmic density, size of nuclei and nucleoli, and thickness of cell walls

and ingrowths, play a major role in host resistance or susceptibility to the root-knot nematodes, which need to be more thoroughly investigated

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MATERIALS AND METHODS

A. Plant material:

1. Olives:-

Rooted cuttings (transplants) of 'Grosade Spain' and 'Nabali' olive cultivars were obtained from Al-Hussein Agricultural Station at Al-Baka' near Amman, on March 23, 1985. Rooting of these cuttings started in December 1984 when the basal ends of the cuttings were dipped for about 10 seconds in a solution containing 4000 part per million (PPM) indoleacetic acid (IAA). Rooting was accomplished in a mist chamber with the temperature kept at about 20^{0}C and 85-90% relative humidity.

At the campus of the University of Jordan in Amman, olive transplants were root-dipped in Zineb solution (2g/l) to inhibit growth of possible root-rot fungi. Transplants were then immediately planted in 15-cm diameter plastic pots. Each pot was filled with one liter soil mixture (50% methyl bromide-fumigated soil, 25% moss peat and 25% virgin sand).The planted pots were placed in a greenhouse until they become well established and the shoots started to

show conspicuous growth. At this stage, transplants of similar size and general condition were selected for experimentation. Throughout the experimental period, plants were regularly irrigated so that the soil moisture kept near the fieldcapacity. Olive plants were occasionally fertilized with the foliage fertilizer Nutrileaf (20,20,20) at the rate 4g/liter. At times when mites were observed on plants in the greenhouse, olive plants were sprayed with Fenpropathrin (Danitol 10 EC) at the rate 1 ml/l.

2. Tomato:

Seeds of tomato Lycopersicon esculentum Mill, cv. 'Claudia Raf'were sown in moss peat in propgation trays in the green house on September 5, 1985. At two true leaf stage, seelings were transplanted into potted soil mixture composed of 50% methylbromide-fumigated soil, 25% sterile moss peat and 25% agriperlite. Well established and uniform plants were selected for experimentation in the greenhouse.

Throughout the experimental period, temperature was recorded using a thermohydrograph (figure 1).The average monthly temperature ranged between 17^0C in December and 27^0C in August.

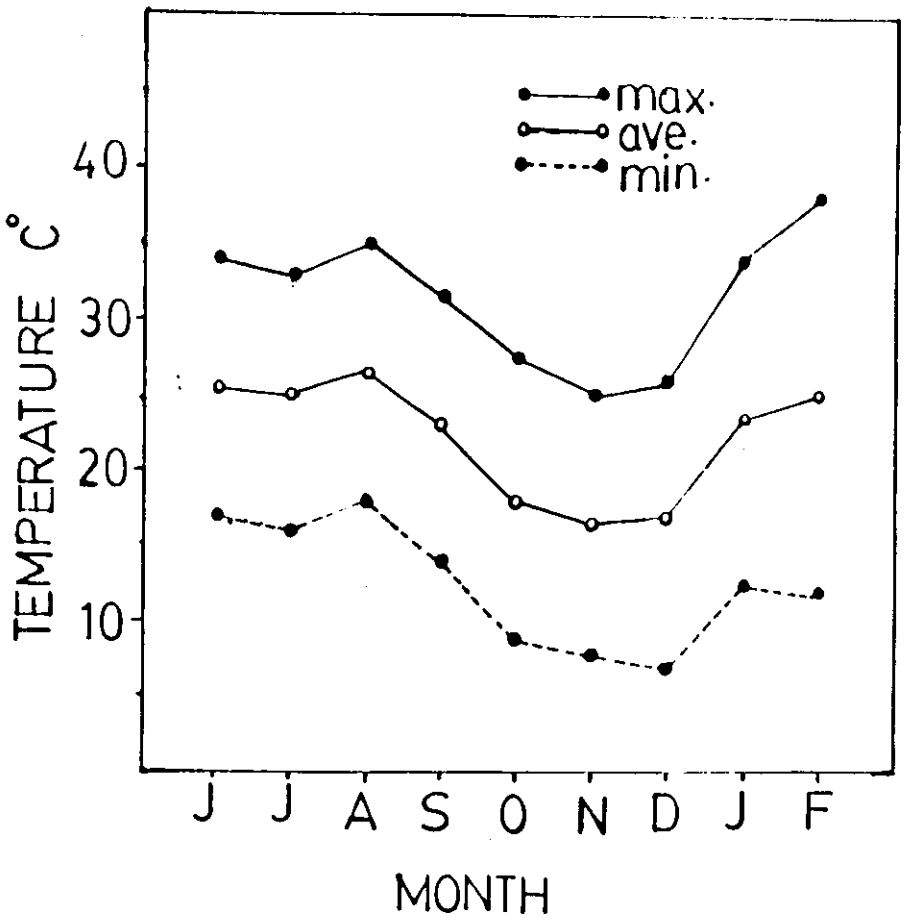

Figure 1: Monthly maximum, minimum and average daily temperatures during the experimental period (June, 1985 - February, 1986) in the greenhouse in which experiments were conducted.

B. Nemalode culturing and inoculation:

The root-knot nematode species used in this research, namely, Meloidogyne javanica (Treub) Chitwood, and M. incognita (Kofoid & White) Chitwood, race-2, were reared on 'Claudia Raf' tomato planted in potted fumigated soil in the greenhouse. Populations of the two nematode species were initiated from single eggmass cultures. The cultures were continuously renewed so as to remain viable, and to provide enough eggs for inoculation.

To prepare the inocula, six to twelve week-old infected tomato roots were pulled from the potted soil, washed, cut into 1-2 cm segments and vigorously shaked in 0.5% (a.i.) Sodiumhypochlorite (NaOCl) solution for about 3 minutes (Barker, 1985). Quickly the hypochlorite solution was passed through a 200-mesh sieve nested over a 500-mesh sieve to collect freed eggs. The 500-mesh sieve containing the eggs, was placed directly under a stream of cold water to remove residual hypochlorite. By taking alliquote samples, the number of eggs per unit volume of water suspension was standardized for inoculation.The two olive cultivars were inoculated separately with the two nematode species, on June 4, 1985. Three holes about five cm deep were dug around plant stems in the pot soil, through which the nematode inoculum was injected using a special inoculation syringe

(Macro-set Transfer Pipetting System, Oxford Laboratories). Holes were then immediately covered with fumigated soil and irrigated.

'Claudia Raf'tomatoes were inoculated in the same manner, on November 24, 1985.

To determine the race of M. incognita used in this research, the procedure described by Taylor and Sasser (1978), using the North Carolina Host Test, was followed. The nematodes were inoculated to tomato cv. 'Rutgers', cotton cv. 'Deltapine 16' and tobacco cv. 'NC95'. After 55 days, the nematode was found to react positively with tomato and tobacco, but negatively with cotton, and was thus defined as M. incognita, race-2.

C. The experiments, treatments and experimental design:

Two experimentas were undertaken in this research, one on olive and the other on tomato.

Experiment I on olive, comprised six treatments as follows:

Symbol	Treatment description	No.eggs/ pot
NJ	'Nabali' olive with M. javanica	5,000
NI	'Nabali' olive with M. incognita	5,000
NC	'Nabali' olive, noninoculated control	0
GJ	'Grosade Spain' olive with M.javanica	5,000
GI	'Grosade Spain' olive with M.incognita	5,000
GC	'Grosade Spain' olive, noninoculated control	0

Experiment II on tomato, comprised 3 treatments as follows:

Sympol	Treatment description	No.eggs/ pot
TJ	'Claudia Raf' tomato with M. javanica	5,500
TI	'Claudia Raf' tomato with M. incognita	5,500
TC	'Claudia Raf' tomato,noninoculated control	0

Treatments in the two experiments were replicated 8 times each, in a completely randomized design.

D. Data taking:

On March 1, 1986 (40 and 14 weeks after inoculation of olive and tomato, respectively), the two experiments were terminated, and the following parameters were recorded:

1. Effect of the nematodes on plant growth:

The effect of M.javanica and M. incognita on the examined host species and cultivars was recorded both quantitatively and qualitatively. Shoot fresh weights of the harvested individual olive and tomato plants from the point of soil surface, were recorded. For olives, the number of leaves per plant was also counted. The root systems of all plants were gently washed of soil, and weighed fresh. Roots of nematode - infected plants were further studied as to root galling and other symptoms. The root system of each infected plant was cut into small pieces, mixed well, and one-gram root fragments was taken so as to count the numberof galls per gram root and for further studies.

2. Nematode reproduction:

Reproduction of the two nematode species on the different host cultivars involved in this study was

determined. When plants were taken down, 100 ml soil were taken from each inoculated pot, and the second stage larvae in the soil samples were extracted using Baermann trays (Barker, 1985). The extracted nematodes were then concentrated through 325-mesh sieve, and counted on the binocular microscope in shallow dishes. On the other hand, one-gram fragmented root samples were stained red using phloxine B solution (0.15 g/L tap water) to get the eggmasses easily distingushed (Daykin and Hussey, 1985). The number of eggmasses per gram root was counted on the binocular microscope. Furthermore, twelve 10-eggmasses lots were taken from the infected plant roots of each treatment. The eggmasses were dissolved in 1% (a.i) Sodium hypochlorite solution for about 3 minutes with continous shaking to liberate the eggs. The number of eggs per eggmass was then determined by direct counting on the binocular microscope, using alliquot samples.

E. Histopathological studies:

Histological studies involving Meloidogyne aimed at the most to observe the giant cells. This requires the preperation of thin sections of infected root tissues with a minimum of distortion. The procedure

described by Daykin and Hussey (1985) was followed to prepare the thin sections. Galled root fragments roughly similar in diameter were slected from all the nematode - inoculated treaments of the two experiments together with healthy roots from the control treaments, and fixed in Formalin- Aceto-Alcohol (FAA). The dehydration schedule involving the Tertiary Butyl Alcohol (TBA) was followed, where the plant tissues were passed through the following gradiant of alcohols:

Step	% alcohol	time	Quantity (ml) needed for solution			
			Dist. H_2O	95% ethnol	Abs. ethnol	100% TBA
1	50	2 hr	50	40	0	10
2	70	over night	30	50	0	20
3	85	1.5 hr	15	50	0	35
4	95	1.5 hr	0	45	0	55
5	100	2.0 hr	0	0	25	75
6	100	2.0 hr	0	0	0	100
7	100	2.0 hr	0	0	0	100
8	100	over night	0	0	0	100

Alcohol in the tissues was then replaced with melted paraffin through a step of infiltration . Tissues were

then embedded in blocks of Paraplast ,a special type of paraffin especially made for histological use (Sherwood Medical Industries). Cross and longitudinal sections 10 micrometer (μ) thick were cut using a rotary microtome with steel knife. Ribbons were then mounted on glass microscope slides smeared with a drop of Haupt's adhesive. Then the tissues on slide were stained through the Triarch Quadraple Stain Schedule (Daykin and Hussey, 1985) involving these steps:

Step	Solution	Time
1	Xylene	5 min.
2	Xylene	5 min.
3	Xylene-absolute ethanol (1:1)	5 min.
4	95% ethanol	5 min.
5	70% ethanol	5 min.
6	1% safranin O in 50% ethanol	10 min.
7	distilled water, rinse	
8	1% aqueous crystal violet	1.5 min.
9	distilled water, rinse	
10	absolute ethanol	30 sec.
11	absolute ethanol	30 sec.
12	orange G-fast green (135ml-15ml)	3 min.
13	orange G-fast green (145ml-5ml)	2 min.

/ to be continued ....

Step	Solution	Time
14	orange G-fastgreen (148 ml-2ml)	2 min
15	orange G	2 min.
16	absolute ethanol	1 min.
17	Xylene	5 min.
18	Xylene	5 min.

Slides were mounted with DPX mountant (BDH Chemical LTD., Poole, England) just after the final step of the stain schedule. Coverslips 22 x 40 millimeter (mm) were then immediately placed-gently over the mountant. The slides were dried overnight on a hot plate set at 60^{0}C, to become ready for microscopic studies.

Specimens were studied under the microscope. Qualitative notes on the positions and shapes of giant cells, morphology and distribution of nuclei and the relative density of giant cell cytoplasm, were taken for each specimen. The number of giant cells, nuclei and nucleoli near the feeding sites were recorded. The average diameter of giant cells, nuclei and nucleoli were also measured using the microscope scale - from which the section area of each was calculated. Also, the giant cell wall thickness was measured in all cases. Data taken for each treatment were recorded from

7 different feeding sites (replicates) randomly chosen.

E. Statistical analysis:

Data on the horticultural parameters of olives and tomato were analyzed statistically for the analysis of variance, and the mean seperation was done, using Duncan's multiple range test as described by Little and Hills (1978). The same was done with the histological data on the numbers of giant cells, nuclei and nucleoli, the average section area of single and grouped giant cells, nuclei and nucleoli, and the average giant cell wall thickness. Data on the nematode reproduction and galling were transformed to $\sqrt{x + \frac{1}{2}}$ to reduce heterogeniety of variances and to overcome zero readings (steel and Torrie, 1960; Snedecor and Cochran, 1967). Transformed data were then statistically analyzed. Correlation and regression analysis of the number of eggs per eggmass, to the average section area of single and grouped giant cells, nuclei and nucleoli, and the giant cell wall thickness, were also made.

Plate 1. Effect of the root-knot nematode Meloidogyne incognita on the above ground parts of 'Grosa' olive transplants, 40 weeks after inoculation. Note the short internodes and small leaves.

Table 1. Effect of M. javanica and M. incognita on the growth of olive transplants, 40 week after inoculation.

Treatments	Shoot fresh wt. (g) (1) (2)	No. leaves /plant	Fresh wt. /leaf (10^{-2}g)	Root fresh wt. (g)
Nabali olive M. javanica	29.9 ab	110.8 a	25.9 b	17.0 ab
Nabali olive M. incognita	14.5 c	64.9 c	21.4 b	10.8 c
Nabali olive Control	27.4 ab	93.8 ab	27.1 b	13.8 bc
Grosa olive M. javanica	26.2 ab	98.8 ab	26.7 b	22.3 a
Grosa olive M. incognita	20.4 bc	79.3 bc	25.8 b	19.9 a
Grosa olive Control	33.1 a	92.6 ab	35.8 a	21.1 a

(1) All values are averages of eight replicates.

(2) Means within each column having the same letter do not differ significantly at P = 5% , according to Duncan's multiple range test.

reduced the number of leaves per plant significantly as compared to the control, except that M.incognita caused significant reduction on 'Nabali'. In relation to the average weight per fresh leaf, M. incognita and M. javanica caused significant reduction in 'Grosa ' by 28% and 25%, respectively, while in 'Nabali' did not cause significant effects.

2. Effect on the root system:

The roots, beside the extensive galling in most cases, have shown an increased rate of growth in the form of profound proliferation - development of more lateral roots from the site of infection-(Plate 2). Proliferation was highly prominent on the roots of 'Nabali' and 'Grosa' due to M. incognita and M. javanica infections.

Fresh weights of the infected roots were not reduced below the control treatments. In fact the root/shoot ratio increased in all the nematode-inoculated treatments over that of the control. The calculated root/shoot ratios showed that M. incognita and M. javanica on 'Nabali' and 'Grosa', respectively, were 0.74, 0.57, 0.98 and 0.85, while those of the control treatments were 0.50 and 0.65. respectively.

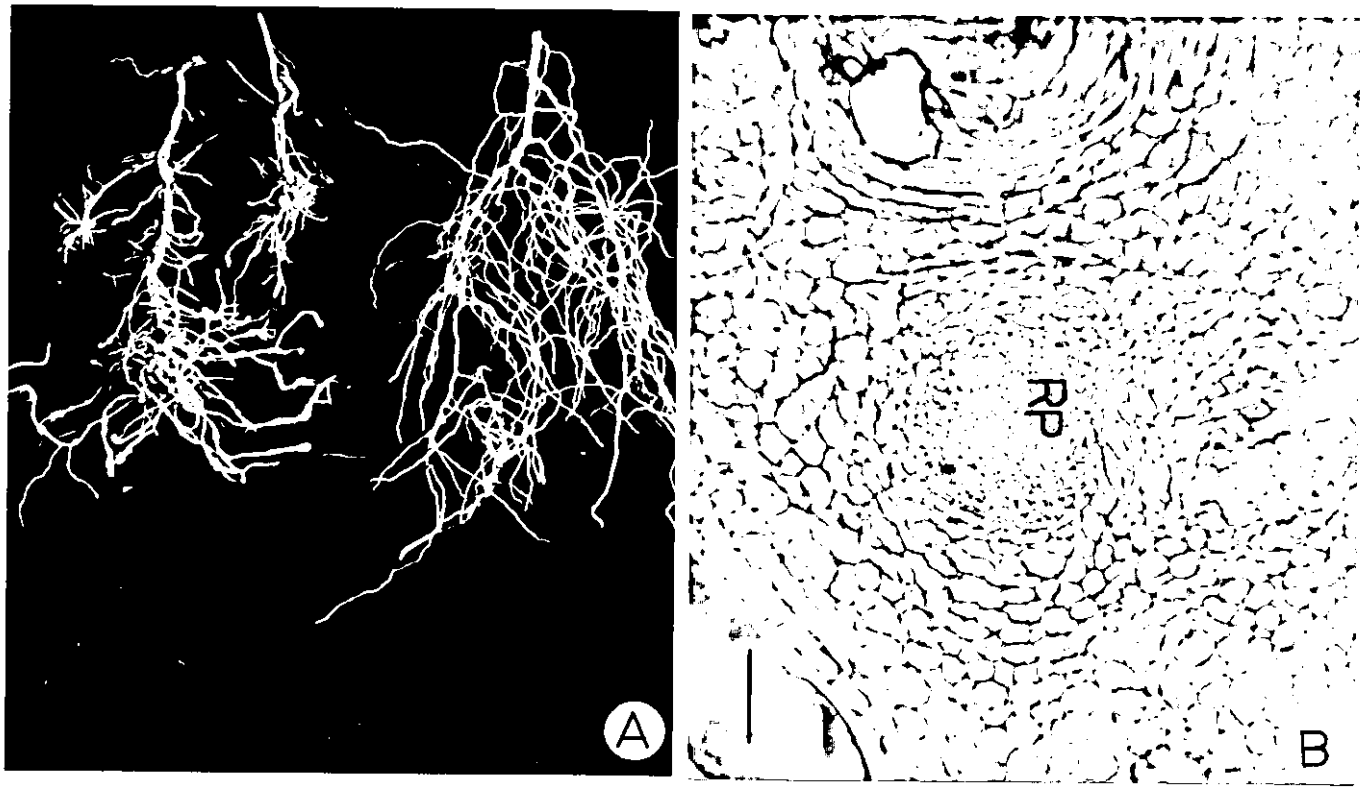

Plate 2. Root symptoms of the root-knot nematode infection on olive transplants. A) Root galling and proliferation from the gall, B) root primordium (RP) in a cross section through the gall. Bar = 40 μ.

B. Galling and reproduction:

Data on the number of galls and eggmasses per gram root, number of eggs/eggmass, and number of second stage larvae/100 ml soil are presented in Table 2.

1. Galling:

The two nematode species caused extensive root galling as compared with the noninoculated controls, which exhibited no galling. Within each of the two olive cultivars, M. incognita and M. javanica showed no significant variations in their galling rates, although M. incognita always produced galls more than M. javanica. On the other hand, galling rate of M. javanica on 'Grosa' was significantly higher than on 'Nabali'. Meloïdogyne incognita showed the same trend, but insignificantly so.

2. Reproduction:

Counts of the eggmasses produced on one gram root, indicated wide significant variations among the different combinations. On each of the two cultivars, M. incognita produced significantly more eggmasses than M. javanica. Meanwhile, M. incognita and M. javanica produced more

Table 2. Effect of olive transplants on galling and reproduction of M. javanica and M. incognita, 40 weeks after inculation.

Treatments	No. galls/ gram root	No. eggmasses/ gram root	No. eggs /egg mass	No. 2nd stage larvae/ 100 ml soil
	(1) (2)			
Nabali olive M. Javanica	7.6 b	2.8 c	8.3 c	5.2 bc
Nabali olive M. incognita	9.7 ab	5.5 b	11.4 b	10.3 b
Nabali olive Control	0.7 c	0.7 d	0.7 d	0.7 c
Grosa olive M. javanica	10.5 a	6.5 b	10.0 bc	17.7 a
Grosa olive M. incognita	11.3 a	10.0 a	13.5 a	22.7 a
Grosa olive Control	0.7 c	0.7 d	0.7 d	0.7 c

(1) Values, but number of eggs/egg mass (12 rep.), are averages of eight replicates. All are transformed to $\sqrt{X + 1/2}$ to overcome zero readings of the control.

(2) Means within each column having the same letter do not differ significantly at P = 5%, according to Duncan's multiple range test.

eggmasses on 'Grosa' than on 'Nabali. The average number of eggs per eggmass were counted for M. incognita and M. javanica on the two olive cultivars. Meloidogyne incognita produced significantly more eggs per eggmass on the two cultivars, than did M. javanica. Also, M. incognita produced more eggs per eggmass on "Grosa' than on 'Nabali'; M. javanica followed the same trend on the two cultivars but with no significance.

Mean numbers of second stage larvae per 100 ml soil, indicated that both M. incognita and M. javanica produced significantly more second stage larvae on 'Grosa' than on 'Nabali'. While no significant differences were detected between the two species within each of the two cultivars. Meloidogyne incognita, however, tended to produce more second stage larvae than M. javanica on each of the two cultivars, although not significantly so.

Experiment II: Pathogenicity of M. javanica and M. incognita on tomato.

A. Effect on the above ground plant parts:

Effects of M. javanica and M. incognita on the shoot and root of tomato plants (Table 3) did not differ significantly. Also, significant differences did not exist between the nematode-infected and nematode-free plants. The shoot weight in case of M. javanica, was even a little higher than that of the control.

B. Galling and reproduction:

Data on the number of galls and eggmasses per gram root, number of eggs per eggmass and number of second stage larvae per 100 ml soil are presented in Table 4.

Both M. incognita and M. javanica produced extensive galls and eggmasses which were significant over the control treatment - on which no root galls or eggmasses were detected. However, on tomato roots, M. incognita produced significantly more galls and eggmasses than M. javanica. The mean number of eggs per eggmass did not differ significantly between M. incognita and M. javanica,

Table 3. Effect of *M. javanica* and *M. incognita* on the growth of Claudia Raf tomato plants, 14 weeks after inoculation.

Treatments	Shoot fresh wt. (g) (1)	(2)	Root fresh wt. (g)	
M. javanica	73	a	33.4	a
M. incognita	57.2	a	34.8	a
Non-inoculated Control	64.3	a	35.2	a

(1) All values are averages of eight replicates.

(2) Means within each column having the same letter do not differ significantly at P = 5%, according to Duncan's multiple range test.

Table 4. Galling and reproduction of M. javanica and M. incognita on Claudia Raf tomato plants, 14 weeks after inoculation.

Treatments	No. galls /gram root (1)	(2)	No. eggmasses /gram root		No. eggs/ eggmass		No. 2nd stage larvae /100 ml soil	
M. javanica	6.8	b	4.7	b	21.1	a	22.4	b
M. incognita	9.7	a	9.4	a	22.6	a	43.5	a
Non-inoculated Control	0.7	c	0.7	c	0.7	b	0.7	c

(1) Values, but number of eggs/eggmass (12 Fep.), are averages of eight replicates. All are transformed to $\sqrt{X + 1/2}$ to overcome zero readings of the control.

(2) Means within each column having the same letter do not differ significantly at P = 5%, according to Duncan's multiple range test.

eventhough the former produced more. Also, the number of second stage larvae per 100 ml soil was significantly higher in M. incognita than in M. javanica. Meloidogyne incognita produced larvae 3.94 X as much as M. javanica.

Histopathology of M. incognita and M. javanica on olive and tomato.

A. Giant cells: position , number , shape , and section area:

Cross and longitudinal sections through the galls, indicated that the root-knot nematodes M. incognita and M. javanica produced giant cells on the 'Nabali' and 'Grosa' olive cultivars, as well as on tomato The giant cells were mostly located in the vascular cylinder, which was partially or completely distorted (Plate 3). In case of olive, giant cells were most frequently located in the phloem, while in case of tomato were either in pholem or in xylem or, not less frequently, both in phloem and xylem. One unusual case was found in the case of M. javanica on 'Nabali' olive, in which the giant cells were induced in the cortical region (Plate 4).

The nematodes seemed to have mostly intered the tissue intercellularly, and females developed always in the cortex, with the neck oriented toward the stele (Plate 5). Most of the cortical cells surrounding the neck of the nematode were mostly seen to have undergone hypertrophy. Hypertrophied cells are a little larger than others, with their nuclei

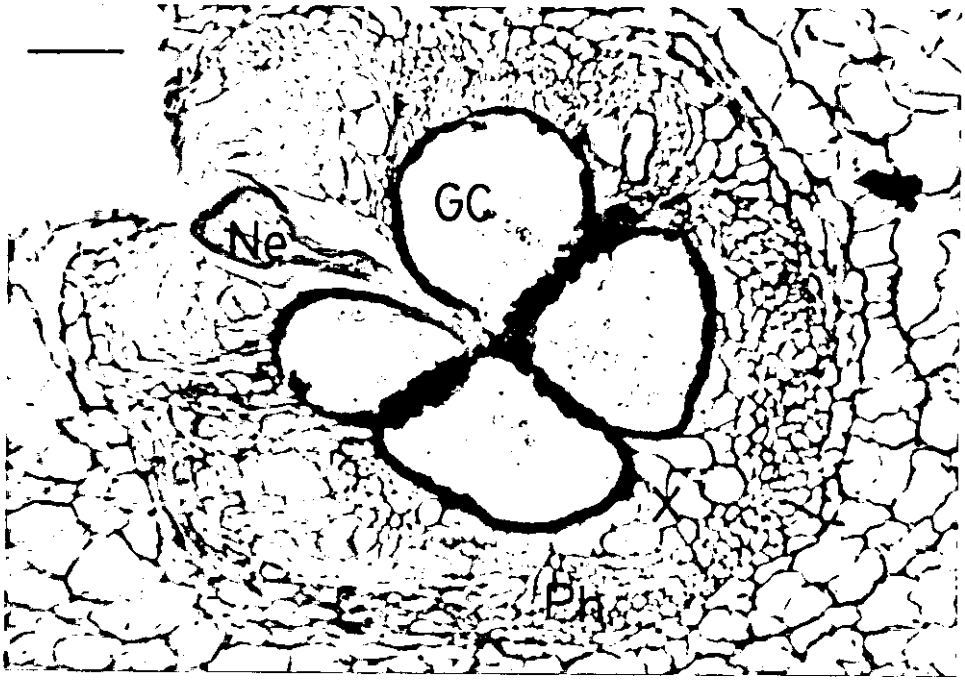

Plate 3. Giant cells (GC) in tomato roots associated with severely distroted vascular cylinder (Ph = phloem X = xylem), induced by the nematode (Ne) M. javanica . Bar = 40 μ.

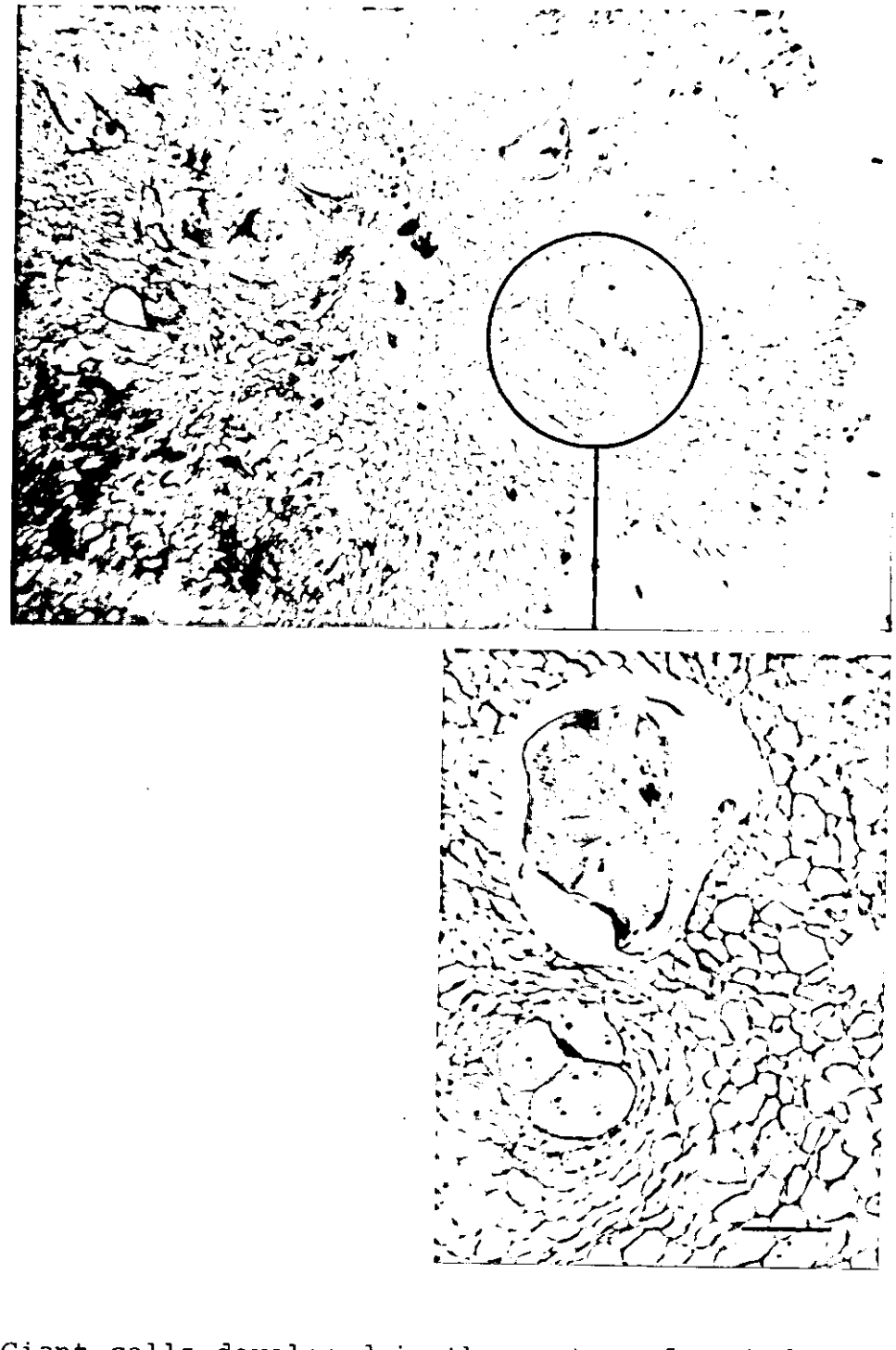

Plate 4. Giant cells developed in the cortex of 'Nabali' olive roots, induced by M. javanica (circle), with an enlarged view. Bar = 40 μ.

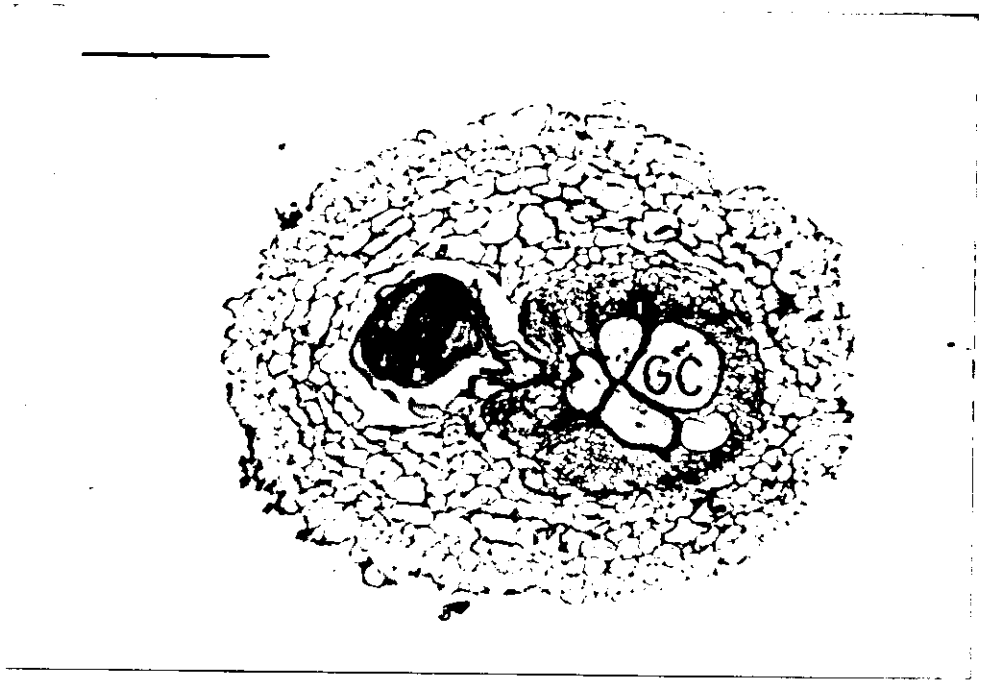

Plate 5. Female M. javanica in tomato root. The nematode (Ne) is located in the cortical tissue with its neck oriented towards the giant cells in the vascular cylinder. Bar = 40 μ.

and nucleoli were also hypertrophied (Plate 6). Around the giant cells, however, layers of small, highly compacted cells are present. These are expected to be hyperplastic cells (plate 6).

Number of giant cells per female, varied from three to seven both in olive and tomato. Among the six treatments, the mean number of giant cells did not differ significantly (Table 5). Shapes of the giant cells were highly variable. In tomato, most of the cells tended to be regularly hemispherical or pear-shaped. On the other hand, giant cells in olive were mostly regualr in shape. Cytoplasm of the giant cells were dense and granular, with its density being variable. Giant cells in tomato roots showed more densed and granulated cytoplasm, than in olive giant cells (plate 7).

The average section area per giant cell, and the total area of giant cells around a feeding site were significantly higher in tomato than in olive. In tomato, however, those induced by either M. incognita or M. javanica did not differ significantly. Thiswas also true on the two olive cultivars.

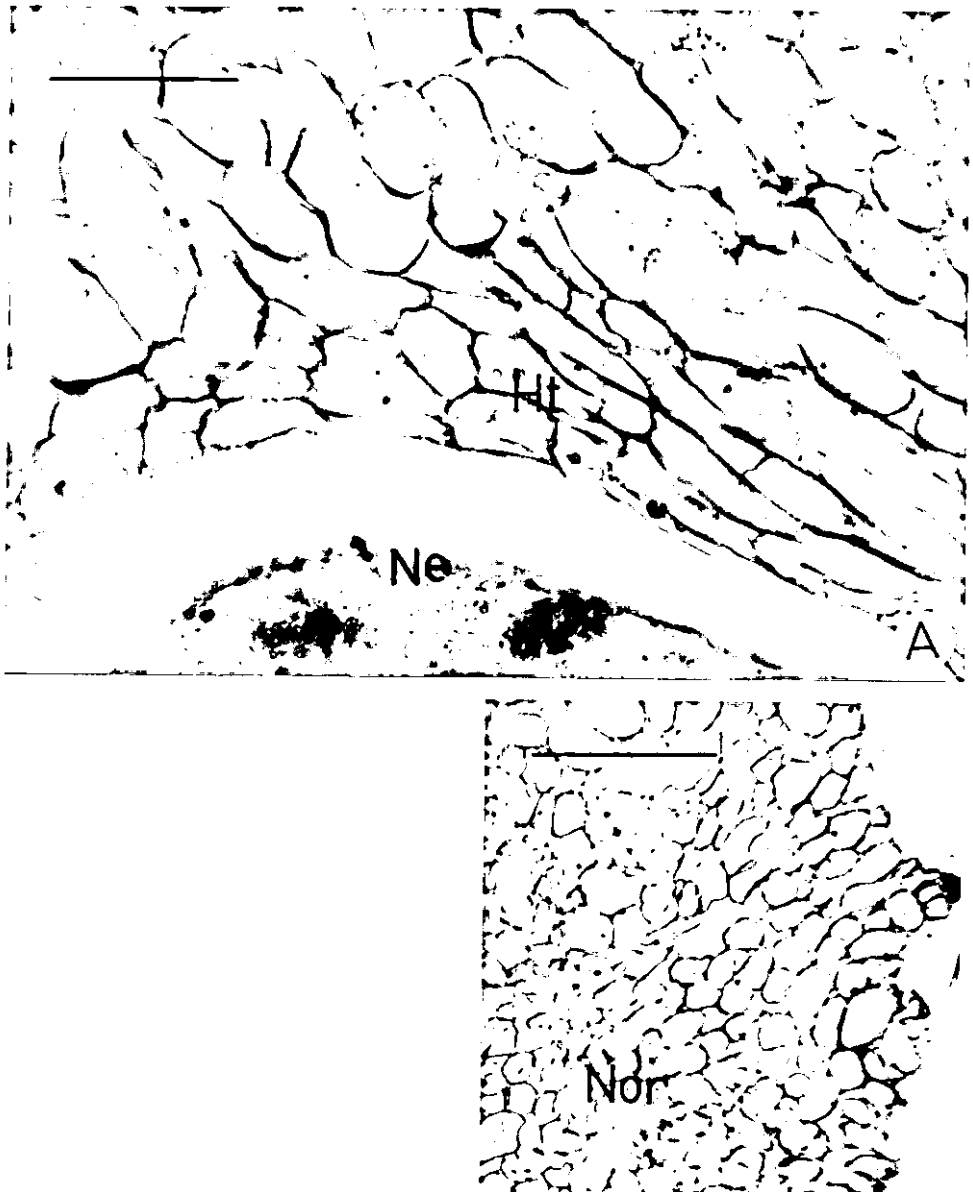

Plate 6. A) Hypertrophied (Ht) and normal (Nor) cortical cells, and B) Hyperplastic (Hp) pholem cells, associated with root-knot nematode infections to olive roots. Bars = 20 µ.

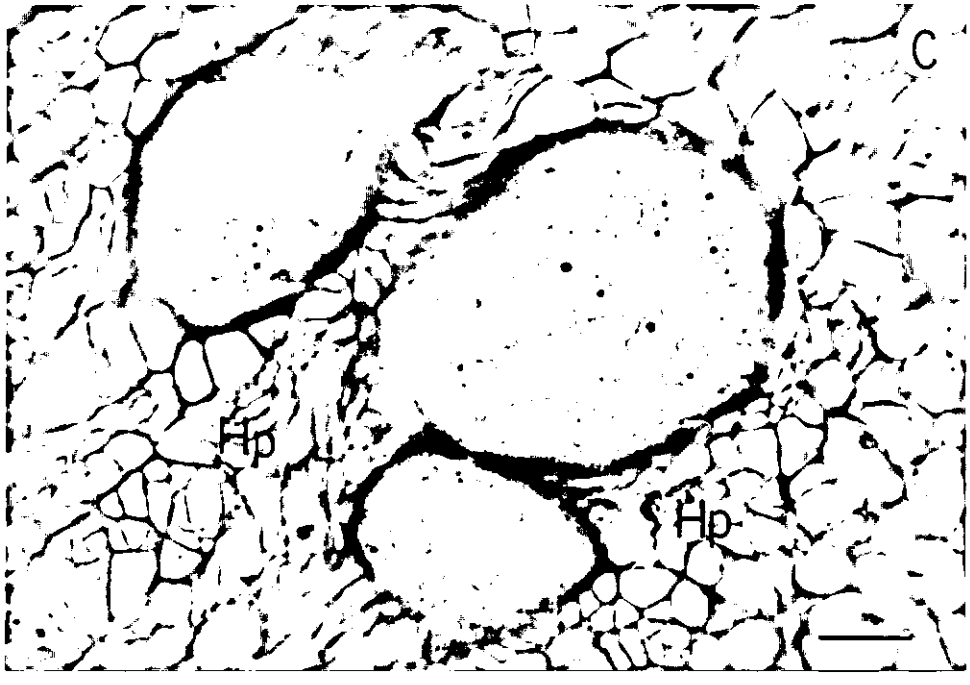

Plate 6 (Contd.)

Table 5. Cellular responses of olives and tomato to infections with *M. javanica* and *M. incognita*.

Treatments	No. giant cells/ feeding site (1)	(2)	Area/giant cell (10^3 μ^2)		Total area of giant cells ($10^3\mu^2$)		Giant cell wall thickness (μ)	
'Claudia Raf' tomato *M. javanica*	5.0	a	6.7	ab	31.7	a	7.4	a
'Claudia Raf' tomato *M. incognita*	5.1	a	7.9	a	36.7	a	6.5	a
'Nabali' olive *M. javanica*	4.9	a	1.8	c	8.3	b	2.4	b
'Nabali' olive *M. incognita*	4.3	a	4.7	bc	19.3	b	5.7	a
'Grosa' olive *M. javanica*	4.1	a	2.9	c	11.3	b	3.6	b
'Grosa' olive *M. incognita*	4.7	a	3.4	c	13.9	b	2.6	b

(1) All values are averages of seven replicates.

(2) Means within each column having the same letter do not differ significantly at P = 5%, according to Duncan's multiple range test.

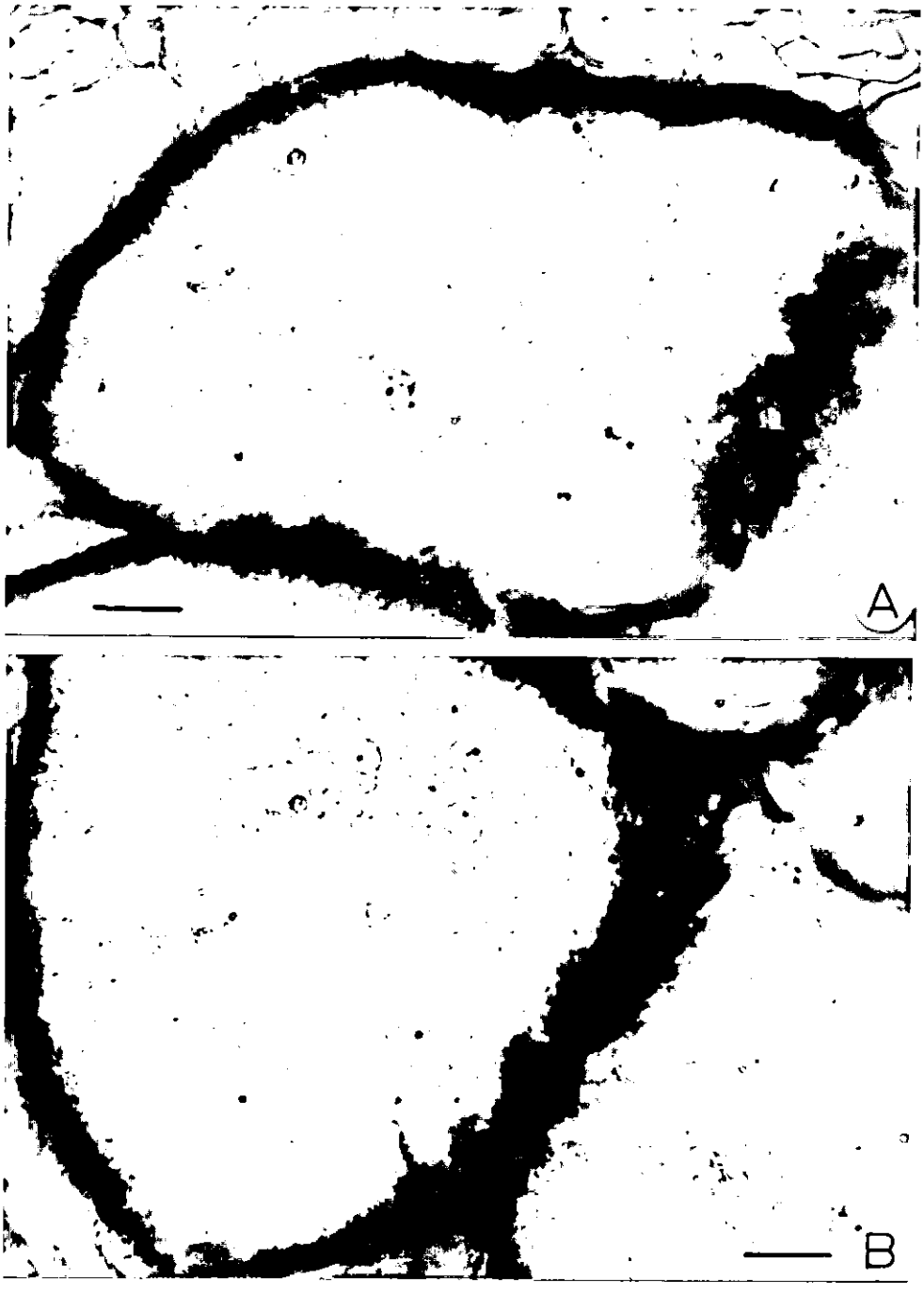

Plate 7. Variability in the density of giant cell cytoplasm: A) dense, granulated cytoplasm in tomato giant cells, B) less dense cytoplasm in olive giant cells. Bars = 20 μ.

Walls of giant cells were always thicker than those of the neighbouring cells. However, thinckness of the giant cell walls was highly variable for the different treatments 9plate 8). Wall ingrowths also varied in their shape and thickness. Cell walls of tomato giant cells both with M. incognita and M. javanica, were the thickest, with most extensive knob-like wall ingrowths. Cell walls were particularly thicker between giant cells than at the outer periphery (Plate 8). Many pit fields were mostly present in the walls between giant cell in tomato roots. 'Nabali' olive with M. javanica have shown regular wall thickness, with little wall ingrowths and no pit fields, while for 'Nabali' olve with M. incognita, heavy wall ingrowths especially between giant cells, and many pit fields were observed. 'Grosa' olve with M. javanica and M. incognita, seemed to have moderate to thick wall ingrowths, beeing more thick next to xylem.

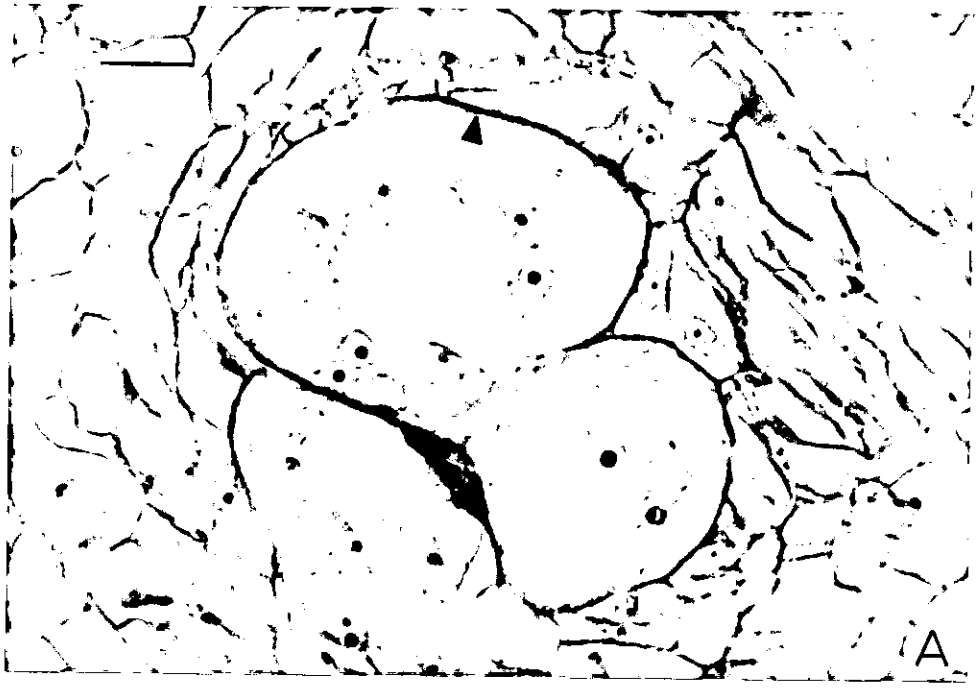

Plate 8. Patterns of giant cell walls: A) thin wall without wall ingrowths in giant cells of M. javanica in the root cortex of 'Nabali' olive; B) thick wall with little wall ingrowths in giant cells of M. javanica in the root of tomato; C) thick wall with extensive knob-like wall ingrowths (WI) in giant cells of M. incognita in the root of tomato; D) walls between giant cells (BW) thicker than outer walls (OW) in giant cells of M. javanica in the roots of tomato; and E) extensive pit fields (PF) in the walls between giant cells in a longitudinal section of 'Nabali' olive roots, parasitized by M. incognita. Bars = 20 μ.

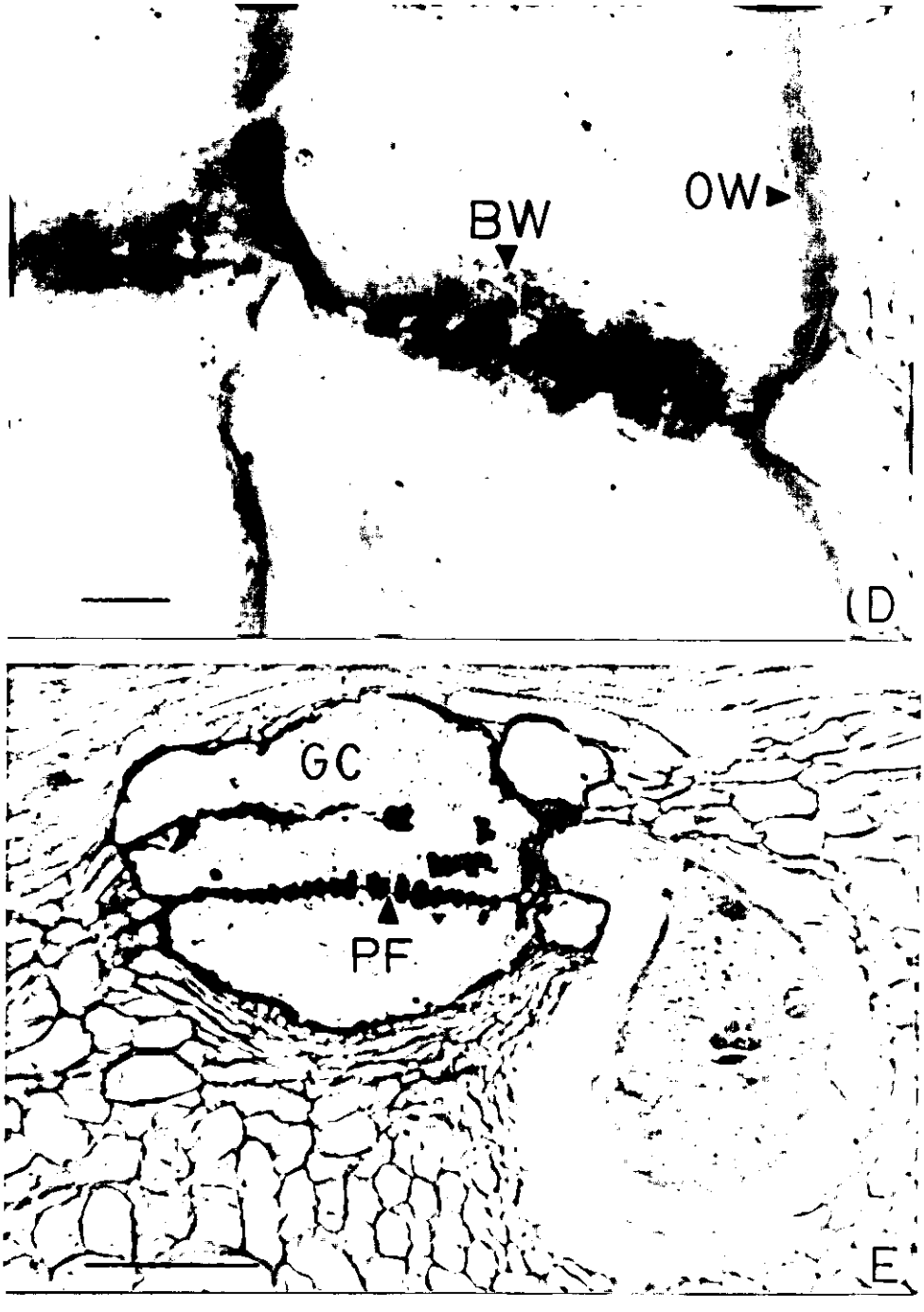

Plate 8 (Contd.)

B. Nuclei: number , distribution, shape , and section area.

Giant cells in all cases were multinucleate. Nuclei were highly variable in number, shape, size and pattern of distribution. The number of neclei present in the giant cells of a feeding site ranged between 10 to 97 throughout the six treatments, and averaged 45.2 and 39.2 in olive and tomato, respectively. The highest mean number of nuclei was recorded for 'Grosa' olive with M. incognita (58.9), which was significantly higher than that of M. javanica on the same cultivar (35.4). The two nematode species, however, did not cause significant differences in the number of nuclei both in tomato and 'Nabali' olive, although there was a general tendency of M. incognita producing nuclei in the giant cells more than M. javanica (Table 6).

Nuclei of giant cells were either uniformly distributed all over the area of the giant cell, or accumulated toward the center of the giant cell, or near the nematode head region. 'Nabali' olive with M. javanica , 'Nabali' with M. incognita and 'Grosa' with M. incognita seemed to show tendency toward the uniform distribution. On the other hand, in tomato with M. javanica and 'Grosa' olive with M. javanica , nuclei were concentrated in

Table 6. Cellular responses of olives and tomato to infections by M. javanica and M. incognita.

Treatments	No. nuclei / feeding site	Area/nucleus ($10\ u^2$)	Total area of nuclei ($10^2\ u^2$)	No. nucleoli /feeding site	Area/nucleolus (u^2)	Total area of nucleoli ($10\ u^2$)
'Claudia Raf' tomato	(1) (2)					
M. javanica	30.6 b	7.9 a	25.0 a	43.7 b	76. a	25.3 a
'Claudia Raf' tomato						
M. incognita	47.7 ab	4.8 b	22.4 ab	55.1 ab	3.1 b	15.5 b
'Nabali' Olive						
M. javanica	36.6 b	2.6 c	8.6 c	35.3 b	2.0 bc	5.4 cd
'Nabali' olive						
M. incognita	50.1 ab	3.3 bc	15.8 bc	56.6 ab	2.1 bc	13.1 bc
'Grosa' olive						
M. javanica	35.4 b	2.7 c	9.2 c	44.3 b	0.9 c	3.8 d
'Grosa' olive						
M. incognita	58.9 a	2.7 c	15.0 bc	71.9 a	1.9 bc	13.5 bc

(1) All values are averages of seven replicates.
(2) Means within each column having the same letter do not differ significantly at P=5%, according to Duncan's multiple range test.

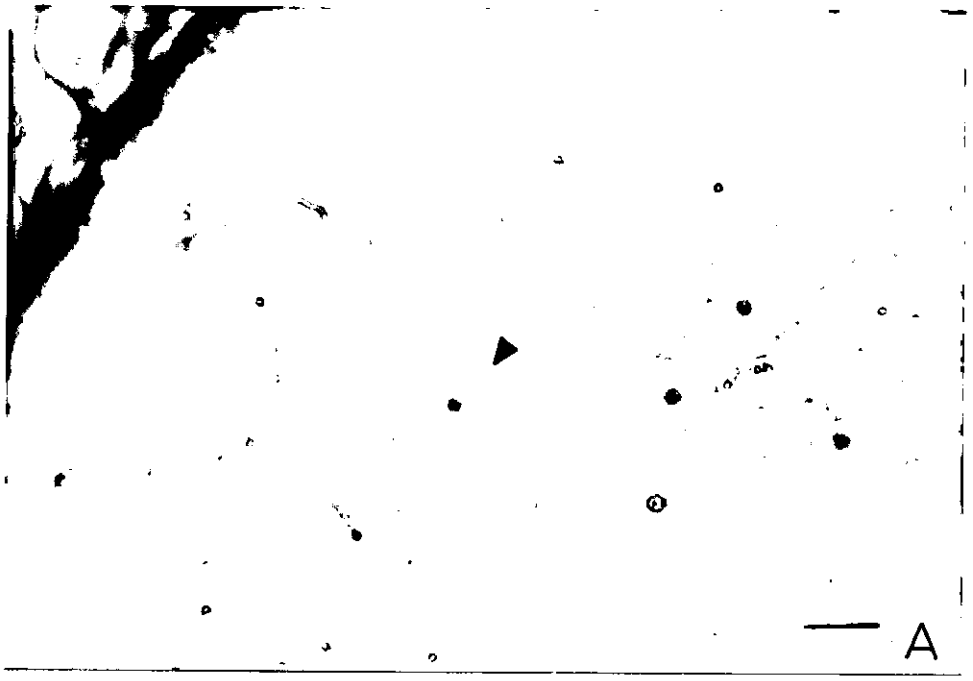

Plate 9. Peripheral morphology of nuclei in the giant cells (arrows): A) round nuclei with distinct nuclear membrane (M. javanica on 'Nabali' olive); B) oblong nuclei with indistinct nuclear membrane; and C) ameboid nuclei with indistinct nuclear membrane (B & C, Meloidogyne incognita on tomato) Bars = 10 μ.

Plate 9 (Contd.)

'Grosa' olive. Within same cultivar, effect of M. javanica and M. incognita on both parameters did not differ significantly except that the area per nucleus in which M. javanica significantly exceeded that of M. incognita (Table 6).

C. Nucleoli: morphology, number and section area:

Most of the nuclei in giant cells contained more than one hypertrophied nucleolus. Regardless of the outer morphology of the nucleus, nucleoli always assumed a round shape. Except for M. javanica on 'Nabali' olive, all treatments counted more nucleoli than nuclei, some times drastically. In general, nucleoli ranged between 8 and 112 in the six cases, and averaged 49.4 and 52.0 in tomato and olive, respectively. The least recorded number of nucleoli in a feeding site was, interistingly, accompanied with the absolutely largest section area of nucleoli (Plate 10), and was noticed in the unusual case when the giant cells developed in the cortical tissue.

Always, the mean number of nucleoli with M. incognita was more than that with M. javanica, but only on 'Grosa' olive differed significantly. However, between the three

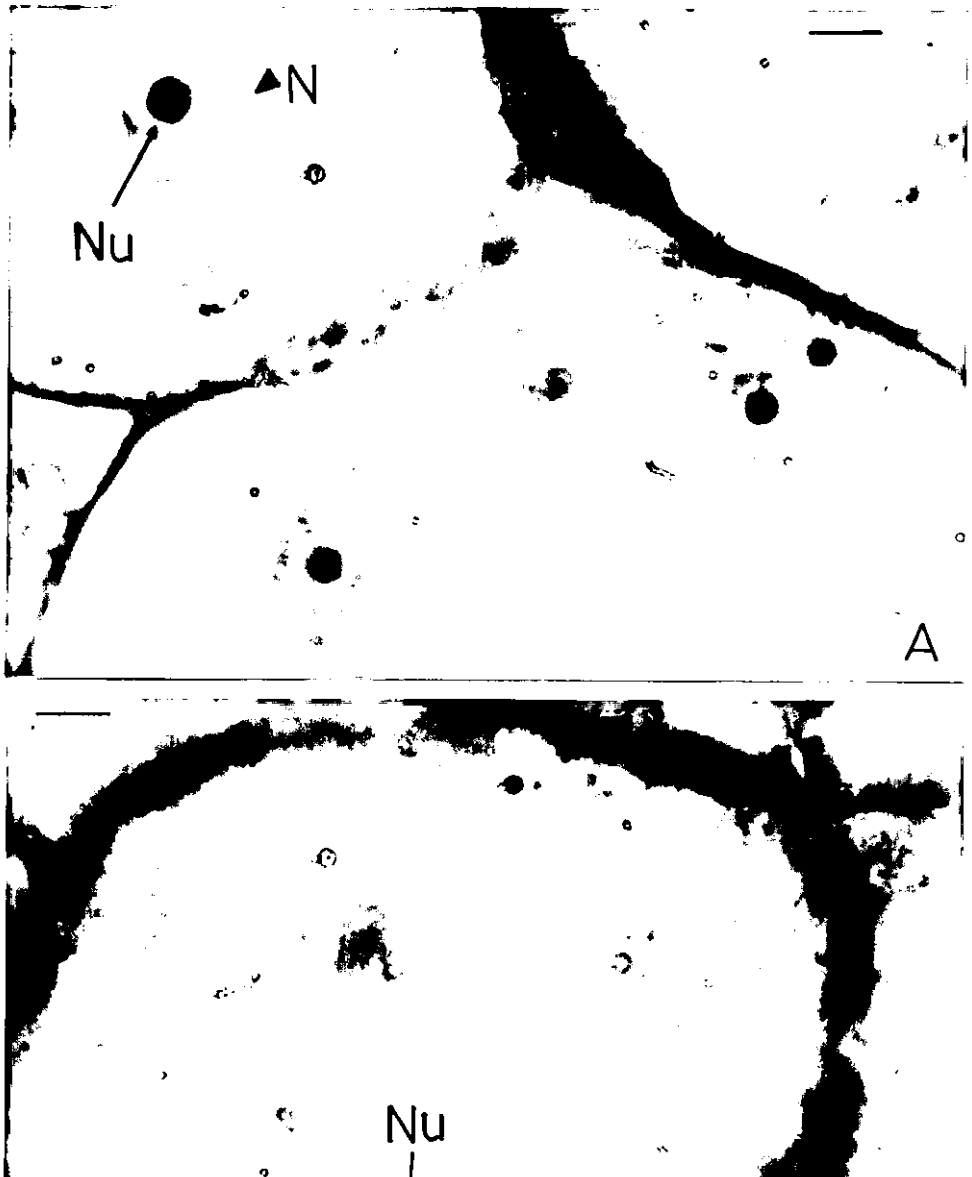

Plate 10. Hypertrophied nucleoli (Nu) in nuclei (N) of giant cells induced by M. javanica in 'Nabali' olive roots: A) extremely hyprotrophied nucleoli developed in the cortex; B) moderately hypertrophied nucleoli developed in vascular cylinder. Bars = 10 µ.

host cultivars, each nematode species did not show significant variations.

The average area of nucleolus and the average total area of nucleoli in a feeding site were significantly higher for tomato with M. javanica than all other treatments. Tomato with M. incognita had the same tendency, but insignificantly so. The two nematode species did nto show differences among each cultivar in the area per nucleolus, except on tomato. However, the total area of nucleoli of M. incognita on 'Grosa' olive and tomato was significantly more than of M. javanica (Table 6).

Relations of cellular responses to the reproduction of nematodes.

The area of single and grouped giant cells, nuclei and nucleoli and the giant cell wall thickness were tested for their possible correlation and regression to the number of eggs/ eggmass. The correlation coefficients of these factors to the corresponding number of eggs per eggmass are presented in Table 7. These coefficients indicate an appreciable tendency of all these cellular responses to be positively

Table 7. Correlation coeficients of the different Cellular responses, to the number of eggs/eggmass.

X	Y: No. eggs/ eggmass	
	r	p
X_1: Area/giant cell	0.9453	0.002
X_2: Area/nucleus	0.8228	0.022
X_3: Area/nucleolus	0.7482	0.044
X_4: Total area of giant cells	0.9671	0.001
X_5: Total area of nuclei	0.9333	0.003
X_6: Total area of nucleoli	0.7967	0.029
X_7: Giant cell wall thickness	0.8078	0.026

related to the number of eggs per eggmass. However, the average area per giant cell, the total area of giant cells per feeding site and the area of nuclei per feeding site, seemed to be the most related factors to the nematode reproduction. The total area of giant cells per feeding site is still the most prominent factor. The r^2 values tell that the values of number of eggs per eggmass can be predicted 94% from the values of total area of giant cells per feeding site; 89% from the area per giant cell; and 87% from the area of nuclei per feeding site. These three parameters therefore are the most important cellular responses that determine the rate of nematode reproduction. The numbers of giant cells, nuclei and nucleoli, however, seemed to have no relation with the nematode reproduction. Meanwhile, the giant cell wall thickness, area per nucleus, area per nucleolus and the area of nucleoli per feeding site were all correlated with the number of eggs per eggmass, but to a medium extent. The regression lines of all these factors, to the number of eggs per eggmass are constructed herein (Figure 2 to 8), to indicate the degrees of fitness of data to the regression line.

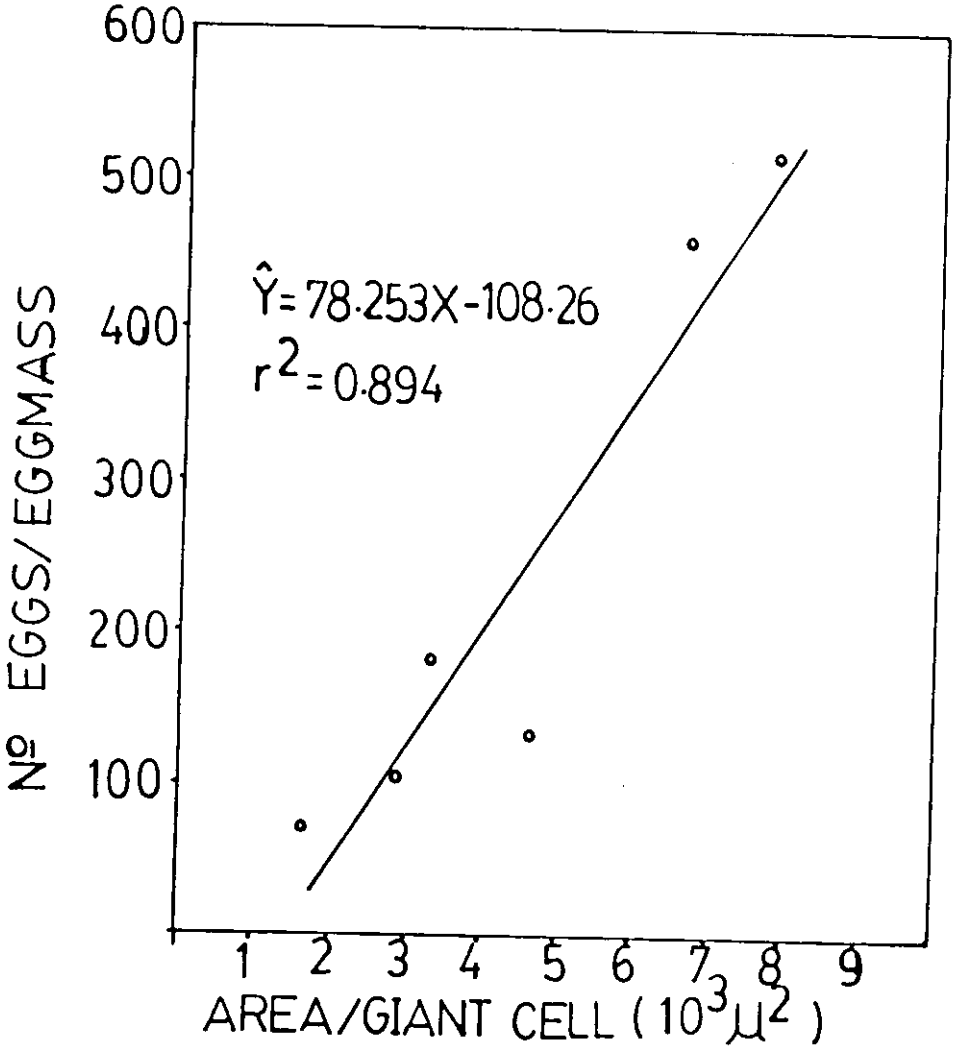

Figure 2. Regression line of number of eggs per eggmass, to area per giant cell.

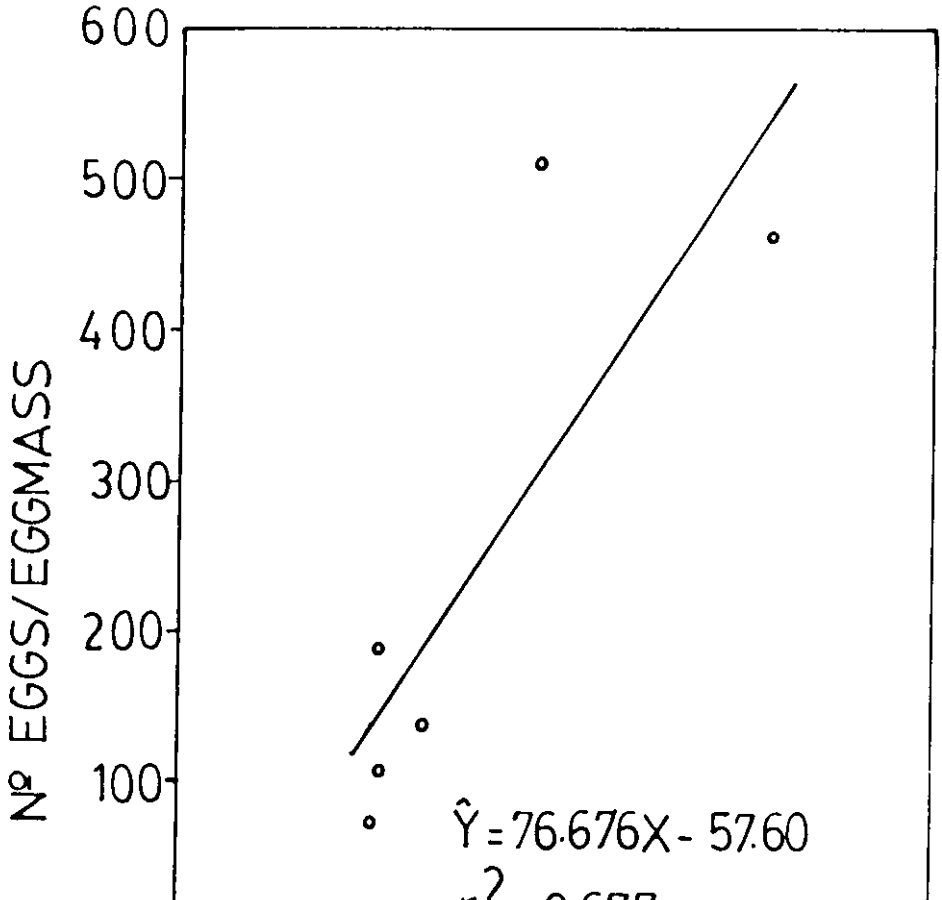

Figure 3. Regression line of number of eggs per eggmass, to area per nucleus.

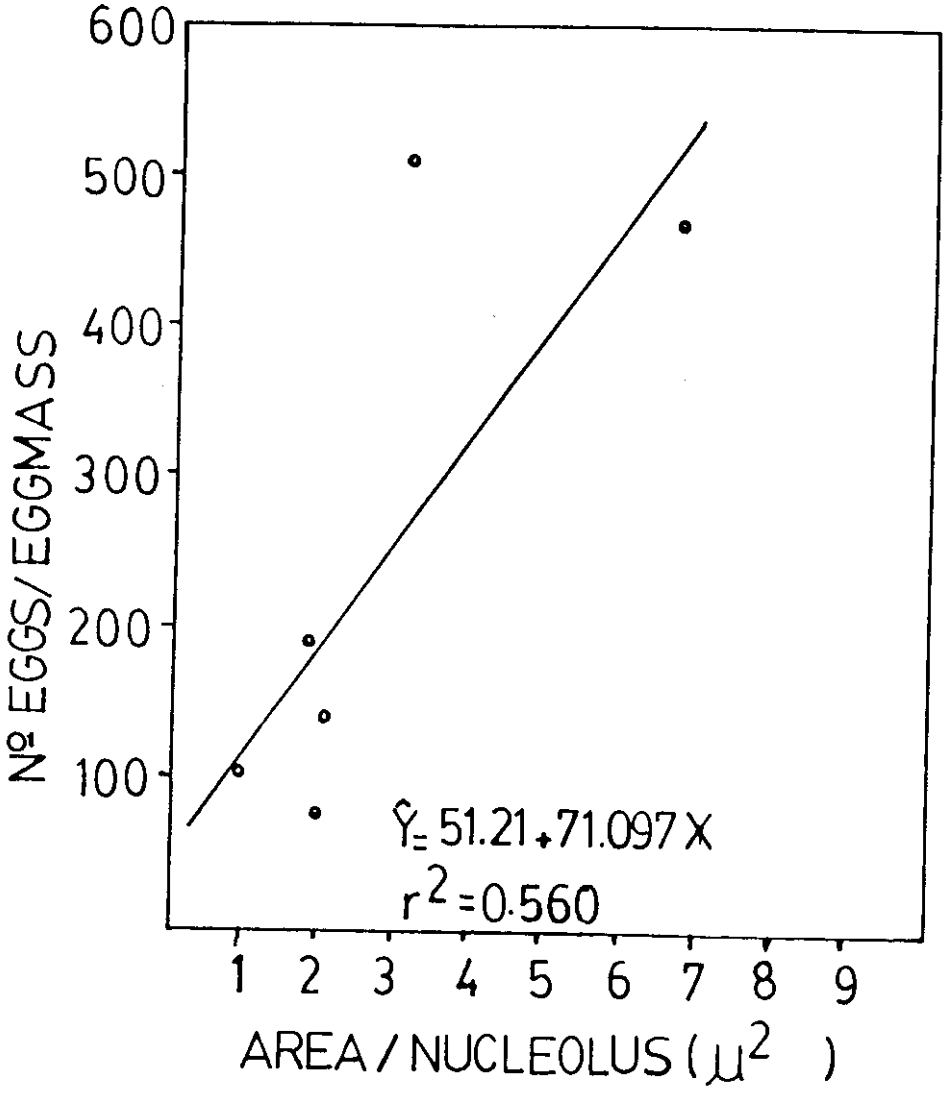

Figure 4. Regression line of number of eggs per eggmass, to area per nucleolus.

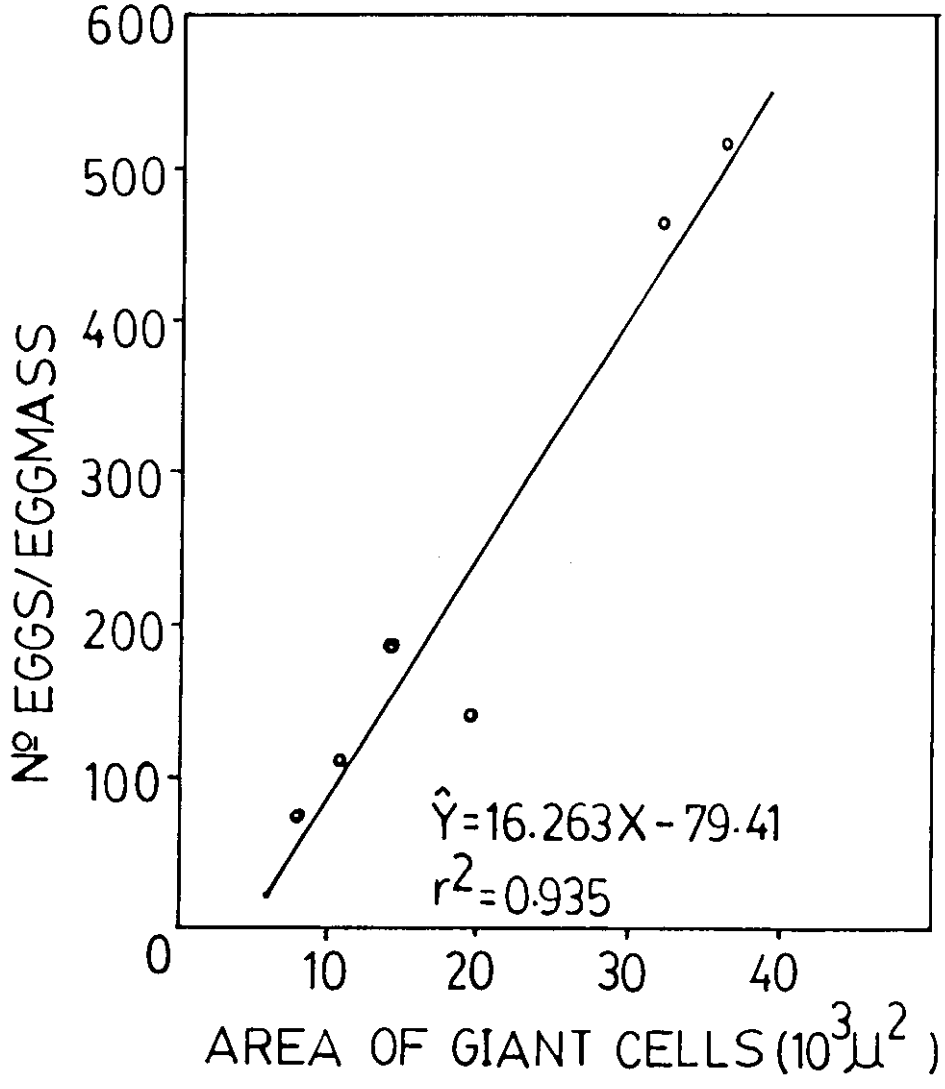

Figure 5. Regression line of number of eggs per eggmass, to the total area of giant cells per feeding site.

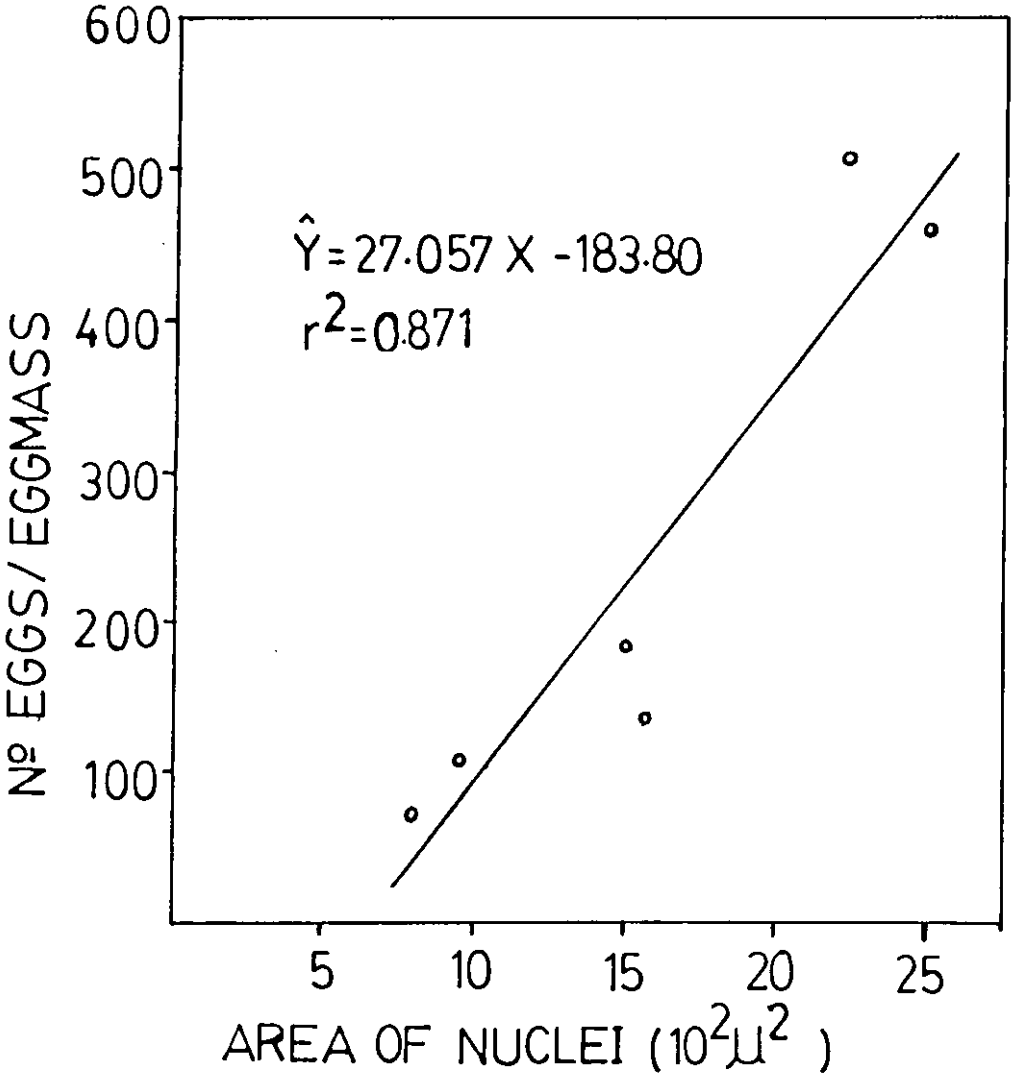

Figure 6. Regression line of number of eggs per eggmass, to the total area of nuclei per feeding site.

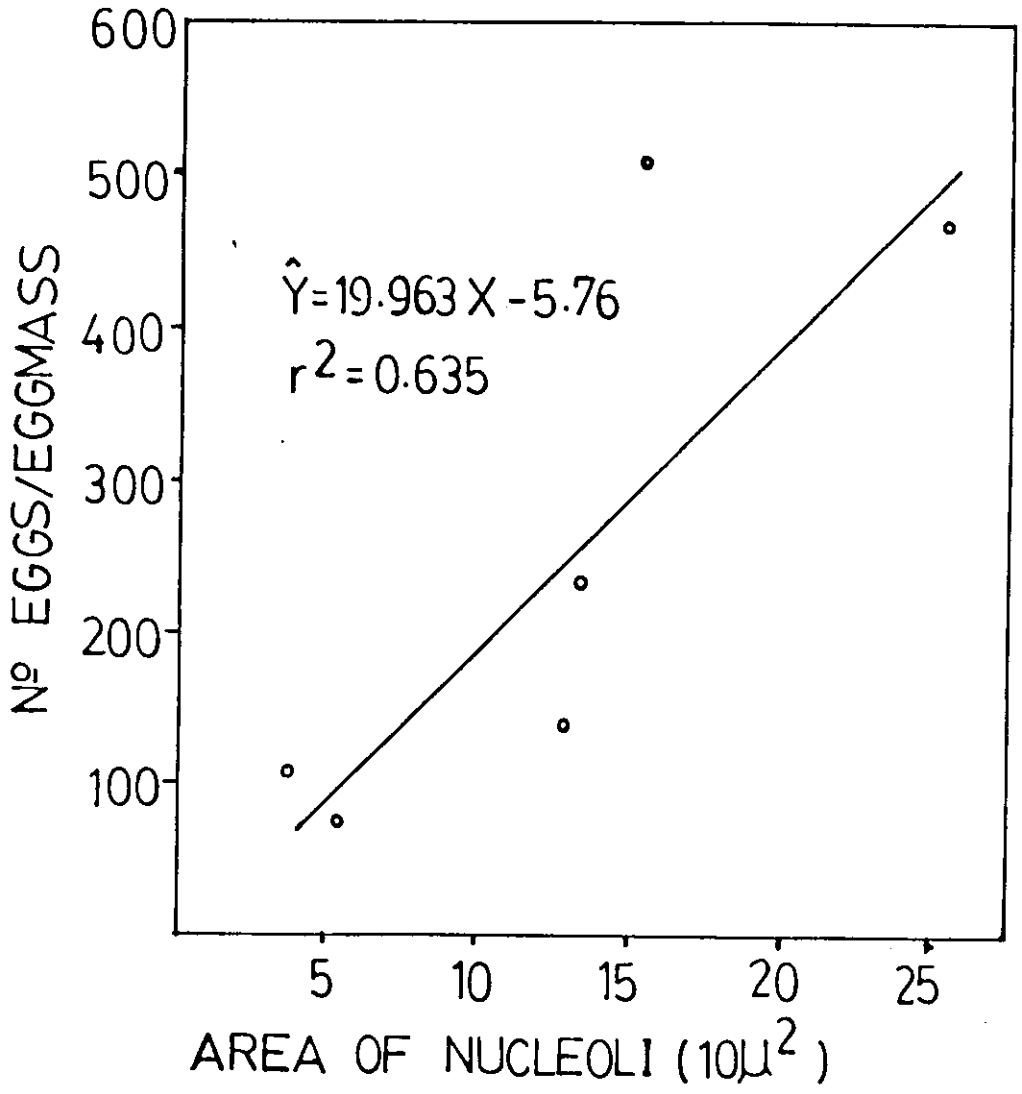

Figure 7. Regression line of number of eggs per eggmass, to the total area of nucleoli per feeding site.

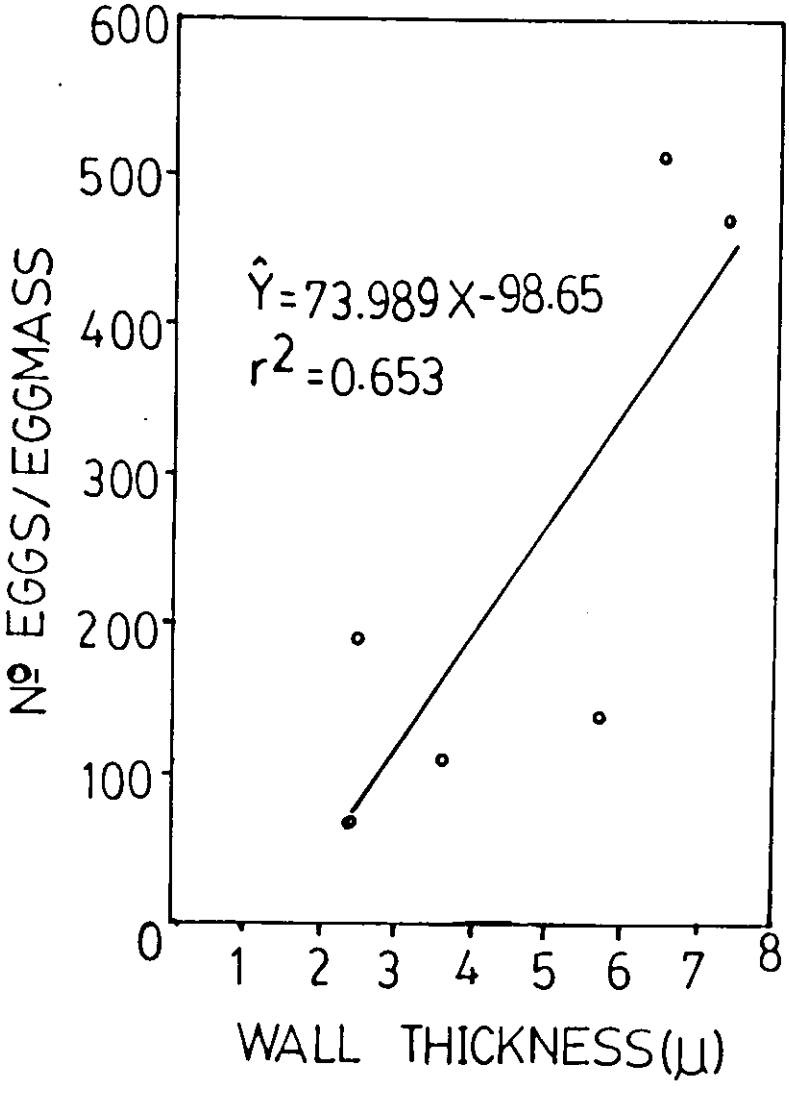

Figure 8. Regression line of number of eggs per eggmass, to giant cell wall thickness.

D I S C U S S I O N

A. Plant growth and nematode reproduction.

1 - Olive.

Olive cultivars differed in their response to the different Meloidogyne species. Meloidogyne javanica in these experiments did not cause significant effects on either of the two olive cultivars 'Nabali' and 'Grosa'; even a slight increase in the shoot weight over that of the control was detected in the 'Nabali'. Eventhough M. javanica reduced the growth of olive transplants by 28%, Diab and El-Eraki (1968) in Egypt, concluded that this species is probably not a destructive pathogen to olive, which may support a sizable population of nematodes without having its growth seriously affected. Lamberti (1968), however, found that after five months of inoculation, 1,000 larvae of M. javanica reduced the weights of 'Ascolano' olive plants significantly, while 'Manzanillo' olive plants were not affected by 65,000 larvae. Lamberti and Baines (1969) concluded that 'Ascolano' and 'Sevillano' olive trees were highly susceptible to M. javanica, while 'Manzanillo' trees were highly tolerent.

Results of this research work, on the other hand, showed that M. incognita significantly reduced the tops of both 'Nabali' and 'Grosa' olives by 47% and 38%, respectively. The general appearance of infected transplants was noticeably altered. The leaf size was generally reduced, the internodes were shortened, and the general plant vigor was retarded. Similarly, Lamberti and Baines (1967) found that the tops of "Ascolano' and 'Manzanillo' olive trees were significantly reduced months after inoculation with 1,000 and 10,000 larvae of M. incognita.The findings of Lamberti (1968) and Lamberti and Baines (1969) that 'Manzanillo' olive trees were significantly affected by M. incognita but not by M. javanica, might support our conclusion that the variations in the weights of tops of olives are due to the effect of nematode species but not the olive cultivars (appendix 1A). Sharawi (1982), however stated that the two root-knot nematode species M. javanica and M. incognita,did not significantly reduce the values of horticultural parameters of 'Nabali' olive, 9 months after inoculation with 10,000 and 8,000 eggs, respectively.

The two nematode species tested in this study, reproduced well, both on 'Nabali' and 'Grosa' olive transplants, but reproduced better on the latter. Meloidogyne incognita

produced galls, eggmasses, second stage larvae in the soil, and eggs per eggmass, more than M. javanica on each of the olive cultivars. At the same time, reproduction was higher on 'Grosa' than on 'Nabali' olive. This is in agreement with Sharawi (1982) who found that M. incognita reproduced better than M. javanica on the local 'Nabali' cultivar. It is obvious, therefore, that the local cultivar 'Nabali' and the introduced 'Grosa' were both susceptible to M. incognita, while tolerent to M. javanica.

The experimental results showed that the root weights of 'Nabali' and 'Grosa' were not reduced by any of the two nematode species, but on the contrary, they increased. This is generally known for Meloidogyne infections. Wallace (1963) reported that Meloidogyne species caused "increased root growth" in numerous hosts. Lamberti and Baines (1969) found that roots of 'Ascolano' olive trees inoculated with 1,000 or 10,000 M. incognita larvae per pot, weighed 67% and 89% more, respectively, than those of the non infested. The increased weight of roots is obviously attributed to root galling and proliferation.

Infected roots of 'Nabali' and 'Grosa' olives were highly proliferated from the galls incited by M. incognita

and M. javanica. This phenomenon was previously reported. Lamberti and Baines (1969) described short stubby roots of 'Ascolano' olive trees infected with M. javanica. Sharawi (1982) further stated that the root systems of 'Nabali' olive infected with either M. javanica or M. incognita were densed and tended to branch near the region of invasion. This auther suggested that this might explain the high degree of tolerence exhibited by the young olive plants to nematode infection under favorable conditions. To some extent, this seems true, since it is noticed here that although the 'Nabali' olive, for example, supported a sizable population of M. javanica with appreciable gallingg, plants were able to withstand this infection. On the other hand, 'Nabali' and 'Grosa' plants, eventhough their roots were highly proliferated, their vigor was significantly reduced by M. incognita. However, root proliferation either from the galls or elsewhere on the root system, was not previously recorded as a normal symptom of M. javanica and M. incognita infections, except on olive.

Lateral root development is generally governed by plant hormones (Leopold and Kriedemann, 1975; Salisbury and Ross, 1978), with the root apex performing an inhibitory action on root branching (Leopold and Kriedemann, 1975).

Esau (1977) stated that the lateral root formation is normally stimulated by auxins and other growth regulators. Meanwhile, the effect of endogenous growth inhibitors, governs the frequency and distribution of lateral roots. The process of lateral root initiation, therefore, seems to be governed by a state of balance between the growth regulators and growth inhibitors. Leopold and Kriedemann (1975) pointed out that when the effect of growth inhibitors is ceased by the removal of root apix, more laterals developed.

Root-knot nematodes, however, are known to alter the growth regulators' content in the infected tissue (Viglierchio and Yu, 1968; Bird and Loveys, 1980). According to Viglierchio and Yu (1968), it appears that plant growth regulators may characteristically be associated with a particular nematode species regardless of whether the healthy host normally contains auxins. Webster (1975) suggested that the nematodes interfere with plant auxin synthesis or inactivation, besides they might themselves release auxins.

From all these thoughts, one might suggest that due to a special host-parasite interaction of the root-knot

nematodes and olive; nematodes might inhance more auxin synthesis, or interfere to deminish the function of plant growth inhibitors at the site of infection, thus inducing the development of lateral roots. Meanwhile, this phenomenon is believed worthy to be studied histochemically, more throughly.

2. Tomato.

Pathogenicity tests on 'Claudia Raf' tomato have shown that neither the shoot nor the root weights were significantly affected by any of the root-knot species tested. But still tomato supported the highest numbers of second stage larvae and eggs per eggmass than any of the olive treatments. However, tomato is generally known to be one of the most suitable and most seriously affected host crops by the root-knot nematodes (Lamberti, 1979). Bafokuzara (1980) found that tomato, out of six examined hosts, supported the highest nematode population both in soil and roots. In the present work , tomato was inoculated with the nematodes in a relatively cool period. During the first two months after nematode inoculation, the night temperatures in the greenhouse were relatively low, averaging 8.6 C, with an average day temperatures of 18.8 C (Figure 1). This might

have caused a low rate of population build-up during the first two months, which did not significantly affect the growth of infected plants. Later on, the population build-up increased well, but did not have the chance to cause significant effects on the general conditions of the already established plants. Nevertheless, and as compared with olives the tomato supported higher nematode populations both on the roots and in the rhizosphere. The number of second stage larvae in the soil, and the number of eggs per egg-mass, drastically exceeded those produced on olives. This is in accordance with Bird's (1972) hypothesis in which he stated that the growth of the parasite is greatest on the host whose roots grew most rapidly, and least on the host whose roots grew most slowly.

B. Cellular response .

In general, giant cells incited by the root-knot nematodes tested in this study developed in the vascular system of the tested host plants. Such reaction was also reported by Dropkin (1972). The exception reported here on the development of giant cells in the cortex, was also previously reported by Dropkin (1972) who stated that only cells from stele were transformed, but giant cells can

also develop from cortical cells. Moreover, Sosa-Moss et al (1983) found that in the resistant NC-89 tobacco cultivar, M. incognita produced 2-5 oval or pear-shaped giant cells in the cortical tissue instead of the vascular cylinder, which were small in size. In the present study, giant cells developed in the cortex were exceptionally small, few in number, round in shape, and without any ingrowths lining their walls. This is expected, because the cortical cells do not naturally function as transfer cells (Gunning, 1977). Since cortical cells are far from the active solute flow routes, they might not be able to develop efficient wall ingrowths.

The number of nuclei and nucleoli were highly variable in these experiments. These parameters seem to have no direct effect on the parasite, although Narayana and Reddy (1980) found that the susceptible tomato produced 4 times the number of nuclei as much as the resistant one. The mean numbers of both nuclei and nucleoli were higher in olives than in tomato, while the parasite reproduced appreciably more on the latter. On the other hand, the total section area of giant cells, nuclei and nucleoli seemed to be important indicators to the nematode reproduction. In the present study, the nematodes

reproduced significantly more on tomato than on olives, where the total area of giant cells, nuclei and nucleoli were significantly more in the former. The area of grouped giant cells was the largest on tomato, and was more on 'Grosa' olive than on 'Nabali'. Also, the area of grouped giant cells produced by M. incognita were always larger than those produced by M. javanica. The pathogenicity of the two species followed the same trend on the three host cultivars.

Tests for correlation and regression indicated that the section area of giant cells around the feeding site was the most important factor determining the number of eggs per eggmass ($r = 0.9671$, $p = 0.001$). Such findings were not previously explored. This seems to be logical since the giant cells are the reservoir of nutrients consumed by the nematode. Thus, the area of giant cells presumably determines the amount of available nutrients. Bird (1972) found that the area of giant cells, area of nuclei, and mass of DNA were more in beans than in tomato than in cabbage, while the nematode growth was the most on beans, and the least on cabbage. Narayana and Reddy (1980) measured the diameters of giant cells in susceptible and resistant tomato to M. javanica. Giant cells on the susceptible

cultivar attained wider diameter (119 x 80 u) and higher total area of feeding site (9821 u^2) than the resistant cultivar whose giant cell diameters were (64 x 42 u) and the area of feeding site (2750 μ^2). Glazer and Orion (198) and Stender (1986) examined the effects of Hydroxyurea on the giant cells. These authors found that this compound hampered the giant cell formation and reduced their final size. Glazer (1985) further indicated that only 20% of the females feeding on these hampered cells reached maturity as compared to those feeding on the non-treated control. This auther considered that as a means of induced resistance to the root-knot nematodes. Therefore, the reduced giant cell area might be a true indicator of host resistance or tolerence to the root-knot nematodes.

Tht total area of nuclei and nucleoli in a feeding site seemed to be proportional to that of the giant cells. However, the area of nuclei was more correlated ($r = 0.943$, $p = 0.002$) with total giant cells area than the area of nucleoli ($r = 0.7873$, $p = 0.032$). These parameters, therefore, contribute in the final effect of the giant cells on the reproductivity potential of the nematode.

The outer morphology of the nuclei periphery seemed

also vital to the activity of the parasite, since it determines the degrees of solute exchange with the surroundings. The raptured nuclear membrane (Webster, 1969); the invaginations of giant cells' nuclei (Paul and Goff, 1973) the ameboid shapes of nuclei which provide tremendous surface area (Huang, 1985); or even the complete absence of the nuclear membrane (Endo, 1971), all are signs of high solute exchange between the nucleus and outside. Wang et al (1975) distinguished nuclei with definite membranes and others with indistinct membranes. The present results were in line with these findings. For instance, nuclei of tomato giant cells were mostly ameboid, or irregular in shape, with mostly indistinct nucler membranes. Those of olive varied, but in the M. javanica on 'Nabali' treatmet , the nuclei were mostly round with distinguished nuclear membrane. These variations in the peripheral morphology of nuclei seemed to be also related to the nematode reproduction accompanied the most lobulated nuclei with extensive invaginations, which might allow more solute exchange with the outside.

Wall ingrowths lining the giant cell walls play a major role in the solute flow from the symplast to the apoplast (Gunning, 1977). Jones (1981 b) suggested that these

ingrowths provide a selective and active solute flow into and between giant cells. Being more extensive on walls between giant cells, with many pit fields (Huang, 1985), that allow all giant cells to act as a single unit (Jones and Dropkin, 1976; Jones, 1981a). The thickness of wall ingrowths is proportional to the solute movement and seem consequently to be a function of the nematode growth and reproduction. Wall ingrowths in the present study were more extensive in tomato than in olive. This is being correlated to the nematode reproduction ($r = 0.8078$, $p = 0.026$). Moreover, pit fields between tomato giant cells were more frequent than in olive giant cells.

In summary, the area of giant cells, nuclei, and nucleoli; thickness of giant cell walls and wall ingrowths, characteristics of nuclear memberanes, and position of giant cells, all contribute in determining the reproduction potential of the parasite. However, variability in all these parameters seemed to be governed by a host response, or an interaction between the host and the parasite.

C O N C L U S I O N S

Under the conditions of the experiments, the root-knot nematodes, Meloidogyne incognita and M. javanica, proved parasitic to young olive trees of the local cultivar 'Nabali' and, to a greater extent, the introduced 'Grosa de Spain'. Meloidogyne incognita was more pathogenic to both olive cultivars than M. javanica; whereby the olive young transplants were able to support sizable populations of M. javanica without being much adversely affected. This may lead to the conclusion that both'Nabali' and 'Grosa de Spain' olives are susceptible to M. incognita, but tolerent to M. javanica (according to the definitions of Wallace, 1963). Both nematode species were also parasitic to the tomato cultivar 'Claudia Raf', but were unable to significantly cause deleterious effects.

Reproduction of the two root-knot nematode species proved to be higher on tomato than on olive, while on 'Gasa de Spain' more than on the 'Nabali' olive cultivar.

Numbers of giant cells, and numbers of nuclei and nucleoli near the feeding sites of the root-knot species did not seem to be important indicators to the reproduction

potential of the nematodes tested. On the other hand, the area per giant cell, the total section area of giant cells, and area of nuclei and nucleoli were intercorrelated, and seemed to be major indicators to the reproduction potential of the root-knot nematodes tested. The more the section area, the higher the rate of nematode reproduction. But the parameter related to the section area of the giant cells, was the most pronounced in this aspect. This factor determined 94% of the number of eggs per eggmass.

Thickness of the giant cell walls and wall ingrowths were also positively correlated to the nematode growth and reproduction.

These correlations and regressions, as far as known, have not been previously explored. This work is believed to be the first quantitative assessment of cellular responses in relation to nematode reproduction.

S U M M A R Y

The pathogenicity and histopathology of the root-knot nematodes Meloidogyne javanica and M. incognita on olive and tomato grown in 15 cm pots, were studied under greenhouse conditions at the campus of the University of Jordan, during 1985-1986.The olive experiment consisted of six treatments comprising inoculation with 5,000 eggs of each of the two nematode species on each of the olive cultivars 'Nabali' and 'Grosa de Spain', along with a noninoculated control treatment of each cultivar. The tomato cv 'Claudia Raf' experiment, consisted of three treatments comprising inoculation with 5,500 eggs of each of the nematode species and a noninoculated control. In the olive and tomato experiments, treatments were replicated eight times and each experiment was arranged in a completely randomized design.

Inoculated olive transplants and tomato seedlings were left to grow 40 and 14 weeks, respectively, then plants were taken down. The shoots and roots were separately weighed fresh, the number of galls and eggmass per gram was recorded, and the number of second stage larvae extracted from 100 ml pot soil was counted. In addition, number of leaves per plant and weight per fresh leaf, were recorded for olive.

Upon termination of experiments on March 1, 1986, numbers of eggmasses were taken to determine the number of eggs per eggmass. In addition, small galled secondary roots with mature eggmasses were taken and fixed in Formalin - Aceto - Alcohol (FAA) for histopathological studies. These root parts were processed as described by Daykin and Hussey (1985), Thin sections were studied under the microscope and qualitatively described. Quantitatively, numbers of giant cells, and number of nuclei and nucleoli per feeding site was recorded. The average diameter of giant cells, nuclei, and nucleoli was measured' from which the section area was calculated, and the average thickness of giant cell walls and wall ingrowths were also recorded.

Pathogenicity results indicated that both 'Nabali' and 'Grosa' olive cultivars were parasitized by both Meloidogyne javanica and M. incognita. However, M. incognita significantly reduced the weights of tops of both 'Nabali' and 'Grosa de Spain', but M. javanica did not. The weight per leaf was also significantly reduced by M. incognita on the two olive cultivars. The two nematode species induced considerable gall formation and eggmass production on roots of the two cultivars. 'Nabali' and 'Grosa de Spain' olive cultivars were considered tolerent

to M. javanica but susceptible to M. incognita infections.

None of the nematode species caused significant effect on the vegetative growth of tomato, possibly due to the non favourable temperature conditions at the beginning of the experiment. However, the two nematode species reproduced much better on tomato than on olive. In addition, the number of eggs per eggmass was significantly higher on tomato than on olive, and more on 'Grosa de Spain' than on the 'Nabali' olive cultivar. Meloidogyne incognita always produced more eggs per eggmass than M. javanica.

Histopathological studies showed that the number of giant cells, nuclei and nucleoli were significantly more in tomato than in olive roots. In olive, however, those caused by M. incognita were significantly more than those of M. javanica. Cell walls of the giant cells were also thicker in tomato than in olives. Nuclei of tomato giant cells were irregular in shape, mostly ameboid with indistinct nuclear membrane, while those of olive were mostly round with distinct membranes.

The average section area per giant cell, total area of grouped giant cells, and total area of nuclei were highly

correlated to the number of eggs/eggmass (i.e. reproduction) potential in the six treatments. The section area of the grouped giant cells were the major factor, whereby the regression test have indicated that the average section area of grouped giant cells, determines 94% of the number of eggs/eggmass.

ملخص باللغة العربية

تمت دراسة العلاقه التطفليه لنوعي نيماتود تعقد الجذور Meloidogyne javanica والسلالة رقم -٢ من M. incognita على صنفي الزيتون نبالي وجروساوي اسبانيا ،وصنف البندورة كلوديا راف ،المزروعة في قوارير قطرها ١٥ سم تحت ظروف البيت الزجاجي في حرم الجامعة الاردنيه في عمان خلال الفترة ١٩٨٥ - ١٩٨٦ .

اشتملت تجربة الزيتون على ست معاملات تضمنت العدوى بـ ٥٠٠٠ بيضه للقوار من كلّ من نوعي النيماتود على صنفيّ الزيتون ،اضافة الى معاملة الشاهد غير المعديّه من كل صنف . أما تجربة البندورة فقد استملت على ثلاث معاملات تضمنت العدوى بـ ٥٥٠٠ بيضه للقوار من كلّ من نوعيّ النيماتود ،اضافة الى معاملة الشاهد غير المعديّه . كررت المعاملات ثماني مرات في كلّ من التجربتين وقد صممت التجربتان بحيث كانت تامة العشوائيه .

بعد ٤٠ و ١٤ اسبوعا من تاريخ عدوى الزيتون والبندورة ،على التوالي خلعت نباتات الزيتون والبندوره واخذت عليها القراءات التاليه : الوزن الطري للمجموع الخضري، الوزن الطري للمجموع الجذري ،وكذلك عدد يرقات الطور الثاني للنيماتود والمعزوله من ١٠٠ مل من تربة كل قوار . أما في حالة الزيتون فقد سجّل ايضا عدد الاوراق على النبات الواحد ومعدل وزن الورقه الواحده .

ولدى انهاء التجربتين في الاول من آذار عام ١٩٨٦ ،اخذت اعداد كافيه من اكياس البيض تامة النضج من كل النباتات المعديه بالنيماتود ،لتحديد معدل عدد البيوض في كيس البيض الواحد وفي نفس الوقت اخذت مجاميع جذور ثانويه من الزيتون والبندورة تظهر عليها العقد الجذريه واكياس البيض تامة النضج وتم تثبيتها كيميائيا باستخدام محلول فورمالين - استيو - الكحول ،حتى تتم عليها الدراسات التشريحيه، حيث عوملت هذه الجذور بطريقة Daykin& Haussy (١٩٨٥) . تمت دراسة القطاعات الرقيقه تحت المجهر حيث سجّلت الملاحظات والقراءات عن اعداد الخلايا العملاقه واخذت الملاحظات الوصفيه لها .

اظهرت النتائج ان نوعيّ نيماتود تعقد الجذور M. javanica و M. incognita يتطفلان على كل من صنفيّ الزيتون نبالي المحلّي وجروسادى اسبانيا المدخل للاردن حديثا

اظهرت النتائج ان نوعيّ نيماتود تعقد الجذور M. javanica و M. incognita يتطفلان على كل من صنفي الزيتون نبالي المحلي وجروسادى اسبانيا المدخل للاردن حديثا ،كما اظهر نوع النيماتود M. incognita قدرة على خفض النمو الخضري لكلا الصنفين بدرجة معنوية كما احدث تراجعا في معدل وزن الورقه لكل من الصنفين في حين ان النوع M. javanica لم يحدث اضرارا معنويه بأي من الصنفين .

وبناء على ذلك يمكن اعتبار صنفي الزيتون المذكورة عوائل حساسه للاصابه بنوع نيماتود تعقد الجذور M. incognita بينما هي اكثر تحملا للاصابه بنوع النيماتود M. javanica كما تبين ان M. incognita اكثر قدرة على التكاثر من M. javanica على صنفي الزيتون ،في حين ان النوعين يتكاثران بدرجة اكبر على صنف جروسادي اسبانيا منها على صنف نبالي . اما على البندورة فلم يحدث أي من نوعي النيماتود نقصا معنويا في الوزن الخضري او وزن الجذور الطري ،ربما لعدم مناسبة الظروف الحراريه داخل البيت الزجاجي في بداية فترة التجربه .

هذا في حين ان كلا النوعين اظهر قدره على التكاثر على البندورة اعلى بكثير منها على الزيتون .

كذلك اظهرت نتائج الدراسات التشريحيه ان معدل القطاع في الخلايا العملاقه ومساحات الانويه والنويات كانت في جذور البندورة المصابه اكبر منها في جذور الزيتون ،في حين كانت المساحات المشار اليها اكبر في جذور الزيتون المصابه بالنوع M. incognita من تلك المصابه بالنوع M. javanica.بينت النتائج كذلك ان اعداد الخلايا العملاقه واعداد الانويه والنويات داخل الخلايا المصاحبه لانثى النيماتود الواحده قد اظهرت اختلافات معنويه في بعض الحالات ،الا انها لم ترشد الى اية استنتاجات ذات معنى.

من جهة اخرى اظهرت جدر الخلايا العملاقه ميلا لان تكون اكثر سمكا في خلايا البندوره منها في خلايا الزيتون . اما انوية الخلايا العملاقه فقد كانت تميل الى الشكل غير المنتظم او الاميبي مع عدم وضوح الغشاء النووي في خلايا البندورة ،بينما كانت اقرب الى الانتظام والدائريه مع وضوح الغشاء النووي في خلايا الزيتون .

بيّن التحليل الاحصائي ان معدل مساحة قطاع الخليه العملاقه الواحده وقطاع مجموعه الخلايا العملاقه ومجموع مساحة الانويه ،مرتبطه بمعامل ارتباط عال مع معدل عدد البيوض في كيس البيض الواحد (اي المقدره على التكاثر) مع ان معدل مساحة قطاع مجموعة الخلايا العملاقه كانت العامل الاكثر اهمية ،حيث تبيّن معاملات الارتباط ان معدل مساحة القطاع في الخلايا العملاقه قد تدخّل في تحديد عدد البيوض في كيس البيض الواحد بدرجه تصل الى ٩٤ ٠/٠ .

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Appendix 1.A.1. Shoot fresh weight (g) of olive transplants, 40 weeks after inoculation with *M. javanica* and *M. incognita*.

Treatments	Replicates R1	R2	R3	R4	R5	R6	R7	R8	Mean
'Nabali' *M. javanica*	44.7	19.4	61.5	20.5	38.8	11.5	19.7	23.4	29.9
'Nabali' *M. incognita*	10.6	7.4	16.0	5.6	17.9	31.1	18.2	9.3	14.5
'Nabali' Control	13.0	21.6	36.5	34.4	24.9	26.2	29.2	33.6	27.4
'Grosa' *M. javanica*	25.9	30.5	20.2	27.0	19.2	23.9	23.8	38.7	26.2
'Grosa' *M. incognita*	6.2	14.9	35.5	20.9	21.8	24.9	15.8	27.7	20.4
'Grosa' Control	33.4	27.4	34.7	41.7	37.4	22.9	42	25	33.1

1.A.2. Analysis of Variance

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	47	5846.5				
Treatments	5	1820.8	364.2	3.80		3.49
N	2	1498.0	749.4	7.81		5.15
H	1	79.3	79.3	0.83	4.07	
N x H	2	242.7	121.4	1.27	3.22	
Error	42	4025.7	95.9			

(1) N = Nematode species, H = Host cultivar.

Appendix 1.B.1. Root fresh weight (g) of olive transplants, 40 weeks after inoculation with M. javanica and M. incognita.

	Replicates								
Treatments	R1	R2	R3	R4	R5	R6	R7	R8	Mean
'Nabali' M. javanica	17.0	11.6	32.0	16.0	17.4	7.6	13.4	21.0	17.0
'Nabali' M. incognita	8.6	6.3	8.6	6.3	15.8	18.3	13.7	8.8	10.8
'Nabali Control	11.9	17.0	17.5	12.6	14.1	13.5	10.0	13.5	13.8
'Grosa' M. javanica	21.4	26.6	15.7	20.5	14.7	24.9	28.0	26.4	22.3
'Grosa' M. incognita	9.5	22.0	25.2	22.3	20.7	9.1	23.7	26.3	19.9
'Grosa' Control	21.3	15.7	20.3	25.4	28	15.8	24.0	18	21.1

I.B.2. Analysis of Variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	Tabulated F 1%
Total	47	2002.1				
Treatments	5	800.9	160.2	5.6		3.49
N	2	148.9	74.5	2.6	3.22	
H	1	623.6	623.6	21.8		7.25
N x H	2	28.5	14.3	0.5		
Error	42	1201.2	28.6			

(1) N = Nematode species, H = Host cultivar.

Appendix 1.C.1. Number of leaves / olive transplant, 40 weeks after inoculation with *M. javanica* and *M. incognita*

Treatments	Replicates R1	R2	R3	R4	R5	R6	R7	R8	Mean
'Nabali' *M. javanica*	150	91	185	95	139	45	90	91	110.8
'Nabali' *M. incognita*	58	39	75	49	60	94	98	46	64.9
'Nabali' Control	61	103	113	107	91	100	81	88	93.8
'Grosa' *M. javanica*	89	123	72	82	90	88	106	140	98.8
'Grosa' *M. incognita*	50	61	96	79	98	59	106	85	79.3
'Grosa' Control	100	101	91	90	107	66	109	77	92.6

1.C.2. Analysis of variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	47	37610				
Treatments	5	10199.3	2039.9	3.1	2.44	3.49
N	2	8791.6	4395.8	6.7	3.22	
H	1	2.1	2.1	0.003	4.07	
N x H	2	1405.6	702.8	1.08	3.22	
Error	42	27410.8	652.6			

(1) N = Nematode species, H = Host cultivar.

Appendix 1.D.1. Fresh weight (10^{-2} g) / leaf of olive transplants, 40 weeks after inoculation with *M. javanica* and *M. incognita*.

Treatments	Replicates R1	R2	R3	R4	R5	R6	R7	R8	Mean
'Nabali' *M. javanica*	29.8	21.3	33.2	21.6	27.9	25.5	21.9	25.7	25.9
'Nabali' *M. incognita*	18.3	19.0	21.3	11.4	29.8	33.1	18.6	20.0	21.4
'Nabali' Control	20.6	23.5	31.7	31.9	27.1	26.6	25.9	29.4	27.1
'Grosa' *M. javanica*	29.1	24.8	28.1	32.9	21.3	27.1	22.5	27.6	26.7
'Grosa' *M. incognita*	13.0	24.4	36.9	26.4	22.2	42.2	14.9	26.7	25.8
'Grosa' Control	33.2	27.4	38.2	47.1	35.0	34.9	38.7	31.5	35.8

1.D. 2. Analysis of Variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	47	2476.4				
Treatments	5	884.8	177	4.7		3.49
N	2	505.5	252.8	6.67		5.15
H	1	255.7	255.7	6.75		7.25
N x H	2	123.6	61.8	1.63	3.22	
Error	42	1591.6	37.9			

(1) N = Nematode species, H = Host cultivar.

Appendix 1.E.1 Number [1] of galls/gram root of olive transplants, 40 weeks after inoculation with M. javanica and M. incognita.

Treatments	Replicates R1	R2	R3	R4	R5	R6	R7	R8	Mean
'Nabali' M. javanica	0.7	8.1	7.8	9.2	6.3	9.5	8.1	11.1	7.6
'Nabali' M. incognita	7.4	11.2	7.8	8.9	13.5	10.3	9.9	8.4	9.7
'Nabali Control	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7
'Grosa' M. javanica	12.2	10.2	10.1	12.0	9.8	11.0	10.4	8.1	10.5
'Grosa' M. incognita	3.3	8.1	15.6	9.5	14.1	14.1	13.4	11.9	11.3
'Grosa' Control	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7

(1) Data transformed to $\sqrt{X + \frac{1}{2}}$.

1.E.2. Analysis of Variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	47	1159.7				
Treatments	5	932.9	186.6	34.6		3.49
N	2	889.9	445	82.4		5.15
H	1	26.4	26.4	4.9		7.25
N x H	2	16.6	8.4	1.55	3.22	
Error	42	226.8	5.4			

(1) N = Nematode species, H = Host cultivar.

Appendix 1.F.1. Number[1] of eggmasses / gram root of olive transplants, 40 weeks after inoculation with *M. javanica* and *M. incognita*.

	Replicates								
Treatments	R1	R2	R3	R4	R5	R6	R7	R8	Mean
'Nabali' *M. javanica*	0.7	5.1	1.6	1.2	5.0	3.1	3.5	2.1	2.8
'Nabali' *M. incognita*	2.1	6.0	3.9	5.3	10.7	4.2	5.1	6.3	5.5
'Nabali' Control	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7
'Grosa' *M. javanica*	4.3	7.3	6.2	7.8	7.0	3.1	8.3	7.8	6.5
'Grosa' *M. incognita*	3.1	12.7	6.3	12.1	11.3	12.5	12.6	9.6	10.0
'Grosa' Control	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7

(1) Data transformed $\sqrt{X + \frac{1}{2}}$

1.F.2. Analysis of Variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	Tabulated F 1%
Total	47	711.5				
Treatments	5	536.1	107.2	25.5		3.49
N	2	398.0	199	47.4		5.15
H	1	91.0	91	21.7		7.25
N x H	2	47.1	23.6	5.6		5.15
Error	42	175.4	4.2			

(1) N = Nematode species, H = Host cultivar.

Appendix 1. G. 1. Number (1) of eggs/ eggmass, produced by M. javanica and M. incognita on olive roots.

Treatments	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	R11	R12	Mean
'Nabali' olive M. javanica	4.8	8.1	11.1	10.2	7.9	5.1	9.1	8.5	6.8	9.9	7.5	10.7	8.3
'Nabali' olive M. incognita	10.2	19.0	10.8	10.9	7.8	7.8	10.5	13.1	16.7	8.6	9.7	11.0	11.4
'Nabali' olive Control	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7
'Grosa' olive M. javanica	8.2	12.5	7.9	8.7	10.5	13.1	16.7	8.6	7.0	9.0	9.7	8.6	10.0
'Grosa' olive M. incognita	10.9	14.0	14.5	13.3	14.2	12.3	11.5	9.0	14.8	19.1	11.0	16.9	13.5
'Grosa' olive Control	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7

(1) Data transformed to $\sqrt{X + \frac{1}{2}}$

1. G. 2. Analysis of Variance

Source of Variation (1)	df.	SS	MS	Calculated F	Tabulated F 5%	Tabulated F 1%
Total	71	2142.3				
Treatments	5	1719.4	359.9	69.2	3.31	
N	2	1754.9	877.4	168.7	4.95	
H	1	29.5	29.4	5.6	3.99	7.04
N x H	2	15.4	7.7	1.5	3.4	
Error	66	342.6	5.2			

(1) N = Nematode species, H = Host cultivar

Appendix 1.H.1. Number [1] of second stage larvae / 100 ml soil around olive transplants, 40 weeks after inoculation with *M. javanica* and *M. incognita*.

Treatments	Replicates R1	R2	R3	R4	R5	R6	R7	R8	Mean
'Nabali' *M. javanica*	0.7	4.6	4.6	5.3	5.4	8.0	9.9	3.4	5.3
'Nabali' *M. incognita*	4.6	9.6	24.8	5.3	6.4	8.0	5.7	17.8	10.3
'Nabali' Control	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7
'Grosa' *M. javanica*	10.6	8.4	41.5	8.4	27.1	21.5	18.5	5.3	17.7
'Grosa' *M. incognita*	18.7	24.4	20.2	42.1	19.8	15.4	19.1	22	22.7
'Grosa' Control	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7

(1) Data transformed to $\sqrt{X + \frac{1}{2}}$

1.H.2. Analysis of Variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	47	5258.9				
Treatments	5	3315.2	663.0	14.3		3.49
N	2	824.2	412.1	8.9		5.15
H	1	2078.9	2078.9	44.9		7.25
N x H	2	413.0	206.5	4.46	3.22	5.15
Error	42	1943.7	46.3			

(1) N = Nematode species, H = Host cultivar.

Appendix 2.A.1. Shoot fresh weight (g) of 'Claudia Raf' tomato plants, 18 weeks after inoculation with M. javanica and M. incognita.

	Replicates								
Treatments	R1	R2	R3	R4	R5	R6	R7	R8	Mean
M. javanica	80.8	63.3	50.4	44.0	65.4	97.9	78.8	102.9	73.0
M. incognita	71.0	37.3	71.0	51.6	56.4	72.1	61.4	36.7	57.2
Noninoculated control	70.8	41.0	59.5	70.4	54.7	55.5	90.5	72.3	64.3

2.A.2. Analysis of Variance.

Source of variation	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	23	7128.4				
Treatments	2	993.6	496.8	1.7	3.47	
Error	21	6134.8	292.1			

Appendix 2.B.1. Root fresh weight (g) of 'Claudia Raf' tomato plants, 18 weeks after inoculation with M. javanica and M. incognita.

	Replicates								
Treatments	R1	R2	R3	R4	R5	R6	R7	R8	Mean
M. javanica	39.0	37.9	27.9	19.2	25.1	34.4	39.7	43.9	33.4
M. incognita	33.4	27.8	49.8	38.4	34.3	33.0	30.3	31.2	34.8
Noninoculated control	40.4	29.7	37.4	34.8	39.5	37.7	29.8	32.1	35.2

2.B.2 Analysis of Variance.

Source of variation	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	23	948.2				
Treatments	2	14.0	7.0	0.16	3.47	
Error	21	934.2	44.5			

Appendix 2. E. 1. Number (1) of eggs/ eggmass, produced by *M. javanica* and *M. incognita* on

Treatments	Replicates												
	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	R11	R12	Mean
M. javanica	12.1	25.4	20.6	22.6	20.3	20.0	25.9	22.3	22.6	21.6	22.5	21.2	21.4
M. incognita	19.1	18.7	25.8	19.6	23.5	26.7	24.6	22.8	22.1	22.6	24.4	21.7	22.6
Control	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7

(1) Data transformed to $\sqrt{x + \frac{1}{2}}$

2. E. 2 Analysis of Variance:

Source of Variation	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	35	3852.4	1824.2			
Treatments	2	3648.3	6.38	285.9		5.29
Error	33	204.1				

Appendix 3.A.1 Number of giant cells/feeding site, induced by *M. javanica* and *M. incognita* in olive and tomato roots.

Treatments	Replicates R1	R2	R3	R4	R5	R6	R7	Mean
Tomato *M. javanica*	4	6	4	8	4	5	4	5
Tomato *M. incognita*	4	6	5	6	6	3	6	5.1
'Nabali' olive *M. javanica*	7	4	3	3	6	5	6	4.9
'Nabali' olive *M. incognita*	6	4	3	4	5	4	4	4.3
'Grosa' olive *M. javanica*	3	5	3	5	6	4	3	4.1
'Grosa' olive *M. incognita*	4	4	3	4	7	6	5	4.7

3.A. 2. Analysis of variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	41	69.0				
Treatments	5	5.57	1.11	0.63	2.48	
N	1	0.05	0.05	0.03	4.11	
H	2	3.21	1.61	0.91	3.26	
N x H	2	2.31	1.61	0.66		
Error	36	63.43	1.76			

(1) N = Nematode species, H = Host cultivar or species.

Appendix 3.B.1. Number of nuclei/feeding site, induced by *M. javanica* and *M. incognita* in olive and tomato roots.

Treatments	Replicates R1	R2	R3	R4	R5	R6	R7	Mean
Tomato *M. javanica*	22	29	43	39	28	25	28	30.6
Tomato *M. incognita*	72	62	35	55	42	33	32	47.7
'Nabali' olive *M. javanica*	24	61	18	10	65	28	50	36.6
'Nabali' olive *M. incognita*	38	54	80	50	26	67	36	50.1
'Grosa' olive *M. javanica*	32	40	25	27	50	43	31	35.4
'Grosa' olive *M. incognita*	17	97	37	55	68	50	88	58.9

3.B.2 Analysis of variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	41	16249.1				
Treatments	5	4042.8	808.6	2.39	2.49	
N	1	3420	3420.0	10.09		7.42
H	2	448.5	224.3	0.66	3.26	
N x H	2	174.3	87.3	0.26		
Error	36	12206.3	339.0			

(1) N = Nematode species, H = Host cultivar or species.

Appendix 3.C.1. Number of nucleoli/feeding site, induced by *M. javanica* & *M. incognita* in olive and tomato roots

Treatments	Replicates R1	R2	R3	R4	R5	R6	R7	Mean
Tomato *M. javanica*	22	45	49	50	53	53	34	43.7
Tomato *M. incognita*	83	75	42	69	50	37	30	55.1
'Nabali' olive *M. javanica*	29	70	8	10	71	37	22	35.3
'Nabali' olive *M. incognita*	47	56	87	50	32	83	41	56.6
'Grosa' olive *M. javanica*	41	57	40	27	59	51	35	44.3
'Grosa' olive *M. incognita*	24	112	39	63	93	68	104	71.9

3.C.2. Analysis of Variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	41	23209.1				
Treatments	5	5797.4	1159.9	2.40	2.49	
N	1	4240	4240	8.77		7.42
H	2	1093.8	546.9	1.13	3.26	
N x H	2	463.6	231.8	0.48	3.26	
Error	36	17411.7	483.7			

(1) N = Nematode species, H = Host cultivar or species.

Appendix 3.D.1. Area ($10^3 \mu^2$)/ giant cell, induced by M. javanica and M. incognita in olive and tomato roots

Treatments	Replicates R1	R2	R3	R4	R5	R6	R7	Mean
Tomato M. javanica	6.6	4.0	8.4	5.9	8.4	9.5	3.8	6.7
Tomato M. incognita	10.4	5.5	9.5	9.3	4.8	14.2	1.3	7.9
'Nabali' olive M. javanica	0.6	3.2	1.0	1.8	2.4	1.8	1.6	1.8
'Nabali' olive M. incognita	4.5	8.2	8.0	3.7	1.0	4.6	3.2	4.7
'Grosa' olive M. javanica	4.2	3.2	2.0	2.6	1.5	2.7	3.7	2.9
'Grosa' olive M. incognita	0.8	3.6	6.1	8.1	1.4	1.2	2.9	3.4

3.D.2 Analysis of variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	41	425.9				
Treatments	5	192.1	38.4	5.91		3.59
N	1	25.6	25.6	3.94	4.12	
H	2	155.3	77.7	12.00		5.27
N x H	2	11.5	5.8	0.89	3.27	
Error	36	233.5	6.5			

(1) N = Nematode species, H = Host cultivar or species.

Appendix 3.E.1. Area (10 μ^2) / nucleus, induced by *M. javanica* and *M. incognita* in olive and tomato roots.

Treatments	Replicates							
	R1	R2	R3	R4	R5	R6	R7	Mean
Tomato *M. javanica*	7.9	6.2	12.5	6.4	10.2	6.4	5.7	7.9
Tomato *M. incognita*	4.4	4.3	3.6	3.4	7.5	6.0	4.5	4.9
'Nabali' olive *M. javanica*	1.9	2.1	2.5	4.1	2.4	2.9	2.1	2.6
'Nabali' olive *M. incognita*	6.5	4.0	3.0	1.6	2.9	2.3	2.7	3.3
'Grosa' olive *M. javanica*	4.0	1.8	3.1	3.0	2.1	2.7	2.1	2.7
'Grosa' olive *M. incognita*	1.1	1.8	6.5	2.2	3.0	2.1	2.1	2.7

3. E. 2. Analysis of variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	Tabulated F 1%
Total	41	245.4				
Treatments	5	153.2	30.6	11.77		3.59
N	1	6.6	6.6	2.5	4.12	
H	2	118	59.0	22.7		5.27
N x H	2	28.6	14.3	5.5		
Error	36	92.2	2.6			

(1) N = Nematode species, H = Host cultivar or species.

Appendix 3.G.1. Total rea ($10^3 \mu^2$) of giant cells/ feeding site, induced by M. javanica and M. incognita in olive and tomato roots.

Treatments	Replicates R1	R2	R3	R4	R5	R6	R7	Mean
Tomato M. javanica	26.4	24	33.6	47.2	33.6	19.0	38.0	31.7
Tomato M. incognita	41.6	33.0	47.5	55.8	28.8	42.6	7.8	36.7
'Nabali' olive M. javanica	4.2	12.8	3.0	5.4	14.4	9.0	9.6	8.3
'Nabali' olive M. incognita	27.0	32.8	2.8	14.8	5.0	18.4	12.8	19.3
'Grosa' olive M. javanica	12.6	16.5	6.0	13.0	9.0	10.8	11.1	11.3
'Grosa' olive M. incognita	3.2	12.0	18.3	32.4	9.8	7.2	14.5	13.9

3.G.2. Analysis of Variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	41	7897.8				
Treatments	5	4659	931.8	10.35		3.57
N	1	403	403	4.48	4.11	7.4
H	2	4128.9	2064.5	22.9		5.25
N x H	2	127	63.5	0.71	3.26	
Error	36	3238.8	90.0			

(1) N = Nematode species, H = Host cultivar or species.

Appendix 3.I.1. Total area ($10\mu^2$) of nucleoli / feeding site, induced by M. javanica and M. incognita in olive and tomato roots.

Treatments	Replicates							
	R1	R2	R3	R4	R5	R6	R7	Mean
Tomato M. javanica	20.0	17.1	39.2	24.5	29.2	20.1	27.2	25.3
Tomato M. incognita	12.5	18.8	9.7	15.9	22.5	19.6	9.3	15.5
'Nabali' olive M. javanica	3.8	6.3	1.0	6.2	9.2	9.3	1.8	5.4
'Nabali' olive M. incognita	9.3	15.7	42.6	3.0	4.8	10.8	5.3	13.1
'Grosa' olive M. javanica	5.3	6.3	3.2	2.2	4.7	3.1	2.1	3.8
'Grosa' olive M. incognita	1.4	14.6	12.1	8.2	28.8	15.6	13.5	13.5

3.I.2. Analysis of Variance.

Source of Variation (1)	df	SS	MS	Calculated F	Tabulated F 5%	1%
Total	41	4218.6				
Treatments	5	2100.2	420	7.1		3.5
N	1	65.2	65.2	1.11	4.11	
H	2	1228.3	614.2	10.45		5.2
N x H	2	806.7	403.4	6.86		
Error	36	2118.4	58.8			

(1) N = Nematode species, H = Host cultivar or species.