PENETRATION RATES OF ROOT-KNOT NEMATODES INTO *CUCUMIS SATIVUS* AND *C. METULIFERUS* ROOTS AND SUBSEQUENT HISTOLOGICAL CHANGES

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ABSTRACT

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Root-knot nematode penetration and the histology of the infection sites were studied in selected susceptible and resistant *Cucumis*. *Meloidogyne arenaria* races 1 and 2, *M. incognita* race 3, *M. javanica* and *M. hapla* readily penetrated resistant and susceptible *Cucumis*. In *C. sativus* 'Sumter', all nematodes developed normally from J2 to J3 or J4 stages except for *M. hapla*. In *C. sativus* var *hardwickii* 'NC-42', infective stage 2 juveniles (J2s) of *M. arenaria* races 1 and 2, *M. javanica*, and *M. hapla* remained high at 15 days after inoculation, although some development to the J3 or J4 stage occurred for all species except *M. hapla*. For all root-knot nematodes evaluated, the development of J3s or J4s in 'NC-42' was lower than in 'Sumter'. In *C. metuliferus* PI 482454, high numbers of J2s for all root-knot nematodes were observed with few developing into later stages (J3s or J4s). The mechanism of resistance in 'Sumter' to *M. hapla*, 'NC-42' to *M. arenaria* races 1 and 2, *M. hapla*, and *M. javanica*, and *C. metuliferus* to *M. arenaria* races 1 and 2, *M. hapla*, *M. incognita* race 3, and *M. javanica* are similar. Reduced development of the nematodes is clearly one likely mechanism. Although not accounted for, other possible reasons for the reduced detection of J3 or J4 stages could be J2 death or emigration from roots. The histological evidence unequivocally demonstrated that resistance was not due to a hypersensitive reaction as giant cells are induced. Although giant cells develop after root-knot nematode penetration in resistant *Cucumis* roots, resistance is most likely associated with feeding site development as the giant cells in resistant roots tended to be elongated in shape. These sites probably result in abnormal nematode development as these parasites depend on the nutrient supply from fully developed giant cells to complete their life cycle.

Key words: African horned cucumber, cucumber, cucurbit, *Meloidogyne arenaria*, *M. hapla*, *M. incognita*, *M. javanica*, resistance.

RESUMEN

Walters, S. A., T. C. Wehner, M. E. Daykin, y K. R. Barker. 2006. Tasas de penetración de nematodos del nudo radical en raíces de *Cucumis sativus* y *C. metuliferus* y cambios histológicos asociados. Nematropica 36:231-242.

Se estudió la penetración e histología de los sitios de infección de nematodos del nudo radical en selecciones de *Cucumis* resistentes y susceptibles. *Meloidogyne arenaria* razas 1 y 2, *M. incognita* raza 3, *M. javanica* y *M. hapla* penetran con facilidad las selecciones de *Cucumis* resistentes y susceptibles. En *C. sativus* 'Sumter', todos los nematodos se desarrollaron normalmente de J2 a estadios J3 o J4, con excepción de *M. hapla*. En *C. sativus* var *hardwickii* 'NC-42', los estadios infectivos (J2) de *M. arenaria* razas 1 y 2, *M. javanica*, y *M. hapla* permanecieron en alto número 15 días después de la inoculación, aunque ocurrió algún desarrollo de estadios J3 o J4 en todas las especies excepto *M. hapla*. Para todos los nematodos del nudo radical evaluados, el desarrollo de J3 o J4 en 'NC-42' fue menor que en 'Sumter'. En *C. metuliferus* PI 482454, se observaron altas cantidades de J2 con todos los nematodos y

poco desarrollo de estadios subsiguientes (J3 o J4). Los mecanismos de resistencia de 'Sumter' a *M. hapla*, 'NC-42' a *M. arenaria* razas 1 y 2, *M. hapla*, y *M. javanica*, y de *C. metuliferus* a *M. arenaria* razas 1 y 2, *M. hapla*, *M. incognita* raza 3, y *M. javanica* son similares. Claramente, el menor desarrollo de los nematodos es un posible mecanismo. Otras posibles explicaciones para la menor detección de estadios J3 o J4 pueden ser muerte o emigración, aunque no poseemos datos para sustentar la ocurrencia de estos fenómenos. La evidencia histológica demuestra inequívocamente que la resistencia no se debió a una reacción hipersensible en el momento de inducir las células gigantes. Aunque hay desarrollo de células gigantes tras la penetración de nematodos del nudo radical en raíces de *Cucumis* resistentes, la resistencia probablemente está asociada al desarrollo de los sitios de alimentación dado que las células gigantes en raíces resistentes tendían a ser de forma elongada. Estos sitios probablemente causan desarrollo anormal, pues los parásitos dependen del suministro de nutrientes proveniente de células gigantes completamente formadas para completar su ciclo de vida.

Palabras clave: Cucumis sativus, *C. metuliferus*, cucurbitáceas, *Meloidogyne arenaria*, *M. hapla*, *M. incógnita*, *M. javanica*, pepino, resistencia.

INTRODUCTION

Of the more than 90 described species of root-knot nematodes, *Meloidogyne arenaria*, *M. incognita*, *M. javanica*, and *M. floridensis* are associated with cucumber (Sikora and Fernández, 2005). Penetration and reproduction by *Meloidogyne* have been documented in some species of *Cucumis* (Fassuliotis, 1970; Haynes and Jones, 1976; McClure and Viglierchio, 1966). Haynes and Jones (1976) found that fewer *M. incognita* juveniles penetrated bitter than non-bitter cucumber (*Cucumis sativus*) roots, which probably resulted from the cucurbitacins present in bitter roots repelling this nematode. Fassuliotis (1970) did not detect differences in root-knot nematode penetration between susceptible *Cucumis melo* and two resistant *Cucumis* species, *C. ficifolius* and *C. metuliferus*. Furthermore, Rohde (1972) and others (Herman *et al.*, 1991; Pedrosa *et al.*, 1996a) indicated that juveniles usually penetrate the roots of resistant plants as easily as susceptible ones, suggesting that resistance may be induced once infection occurs (Kaplan and Keen, 1980).

Two types of resistance responses are normally observed in nematode-resistant host plants (Trudgill, 1991). In one type, the plant responds to nematode infection by a rapid hypersensitive reaction; in the other, the feeding site does not develop properly for optimum nematode development. Hypersensitivity is usually controlled by one or a few genes (qualitative resistance) and usually governs resistance to one nematode species and/or race (Rhode, 1972). In contrast, poor feeding site development in resistant hosts is normally controlled by several genes (quantitative resistance) and may be the mechanism of resistance to several nematode species and/or races.

The hypersensitive reaction is a common resistance response in plants to pathogen attack including plant-parasitic nematodes (Fassuliotis, 1979). Hypersensitivity is characterized by the rapid cell death of infected tissues, which leads to isolation and eventual death of the pathogenic organism (Huang, 1985). In some plants that are resistant to certain species of endoparasitic nematodes, this reaction is characterized by the rapid necrosis of plant cells at the point of feeding site initiation (Trudgill, 1991), and usually results in arrested nematode development (Kaplan and Davis, 1987). The hypersensitive reaction is commonly associated with many nematode resistant cultivars of host

plant species including tomato (*Lycopersicon esculentum*) (Dropkin *et al.*, 1969), potato (*Solanum tuberosum*) (Giebel *et al.*, 1971; Wilski and Giebel, 1966), cotton (*Gossypium hirsutum*) (Brodie *et al.*, 1960), soybean (*Glycine max*) (Dropkin and Nelson, 1960) and tobacco (*Nicotiana tabacum*) (Sosa-Moss *et al.*, 1983). The alteration of the suitability of the feeding site is exemplified in resistant soybean and *Cucumis*. Pedrosa *et al.* (1996b) indicated that resistance to *M. arenaria* was expressed in soybean as small, poorly formed giant cells with limited hyperplasia and hypertrophy in the surrounding cells. Fassuliotis (1970) found a similar reaction in two resistant *Cucumis* species with the failure of giant cells to enlarge, thus restricting nematode development. In both cases, hypersensitivity was not observed.

The objectives of this research were to determine penetration rates and subsequent development of selected root-knot nematode species in resistant and susceptible *Cucumis*; and to determine if hypersensitivity was associated with the resistant reaction observed for *M. hapla* in *C. sativus* var. *sativus* 'Sumter' (Walters *et al.*, 1990), for *M. hapla*, *M. javanica*, and *M. arenaria* races 1 and 2 in *C. sativus* var. *hardwickii* line 'NC-42' (Walters *et al.*, 1996) and for these species and races plus *M. incognita* race 3 in *C. metuliferus* (Walters *et al.*, 1993).

MATERIALS AND METHODS

Root Penetration

A greenhouse experiment (3 × 5 × 3 factorial treatment arrangement in a randomized complete block design with three replications) was conducted to determine penetration of *Cucumis* by root-knot nematodes. Three *Cucumis* cultigens (*C. sativus* var. *sativus* 'Sumter', *C. sativus* var. *hardwickii* 'NC-42', and *C. metuliferus* PI 482454) were inoculated with 5,000 eggs suspended in 25-ml water of *M. arenaria* races 1 and 2, *M. hapla*, *M. incognita* race 3, and *M. javanica* with plant roots harvested at 5, 10, or 15 days after inoculation. A layer of approximately 13 mm of moist, sterilized, soil media was placed on the surface after inoculation to prevent desiccation of eggs. An experimental unit consisted of two seeds sown per 8-cm-diam (250 cm^3 volume) clay pot containing a steam-sterilized soil media composed of 85% sand, 10% silt, and 5% clay. At the cotyledon stage, plants were thinned to one per pot. The experiment was run at two different times.

Populations of *M. hapla*, *M. incognita* race 3, *M. javanica*, and *M. arenaria* races 1 and 2 were maintained in the greenhouse on 'Rutgers' tomato for production of inoculum. Eggs were extracted from egg masses collected from tomato roots with 1% NaOCl (Byrd *et al.*, 1972). Pots were watered daily and fertilized weekly with Peter's® 20-20-20 (N-P-K) nutrient solution (W.R. Grace & Co., Fogelsville, PA). Greenhouse temperatures ranged from 24-32°C (day) and 21-24°C (night).

At each harvest, roots were stained with acid fuchsin, cleared with glycerin (Byrd *et al.*, 1983), and examined to determine the number of juveniles that penetrated. These juveniles were then categorized for post-infection developmental stage. Nematode penetration counts were Log_{10} (x + 1) transformed for analysis, but the data is presented with non-transformed numbers. Mean penetration numbers were statistically compared using Fisher's LSD at $P \leq 0.05$. Since the timing of the experiments did not interact ($P > 0.05$) with *Cucumis* cultigens or root-knot nematodes for numbers of J2s, J3s, or J4s found in roots, data were analyzed based on six replications rather than three replications in each of the two experiments.

Post-penetration Survival

This test was conducted to determine the suitability of several *Cucumis* cultigens for post-penetration survival of several root-knot nematode species or races as assessed by enumeration of root-knot nematode juvenile developmental stages. The experimental design was similar to the root penetration experiment except that 20,000 eggs were gently mixed into 250-cm^3 of a sterilized soil media (as previously described). Eggs were allowed to hatch for five days in the soil. One *Cucumis* seedling at the cotyledon stage was then transplanted into each pot. Diurnal temperatures in the greenhouse were similar to the first experiment. Pots were fertilized at transplanting with Peter's® 20-20-20 (N-P-K) nutrient solution and watered daily.

Plants were harvested at 5, 10, and 15 days after inoculation. During the first harvest date, seedlings of plants designated for harvest at 10 and 15 days were also removed from the infested soil in pots, rinsed with water, and planted into pots containing sterilized soil media to assure that no additional penetration occurred. At each harvest date, roots were stained with acid fuchsin and cleared with glycerin (Byrd *et al.*, 1983). The number of juveniles that had penetrated the roots and their developmental stage were determined. Nematode penetration counts were Log_{10} (x +1) transformed. *Cucumis* means for root-knot nematode penetration were statistically compared using Fisher's LSD at $P \leq 0.05$.

Histopathology

An experiment was conducted to determine the root cellular response in root-knot nematode susceptible and resistant *Cucumis*. The experimental design was a 3 × 5 factorial treatment arrangement (with the same three *Cucumis* species and five root-knot nematodes used in the penetration tests) in a randomized complete block design with three replications. Plants at the first true-leaf stage were inoculated with 10,000 eggs. Temperatures in the greenhouse were also similar to that in the two previous experiments. Plants were watered daily to assure adequate soil moisture for optimum plant growth.

Roots were harvested at five days after inoculation. Root segments were fixed in formalin-propiono-propanol (FPP), dehydrated with isopropyl-alcohol (IPA) series, and embedded in paraffin (Daykin and Hussey, 1985). Transverse sections (12 µm thick) were cut with a rotary microtome, mounted on 75 mm × 25 mm glass slides with Haupt's adhesive and 3 to 5% formalin, and stained with Triach's quadruple stain (Hagquist, 1974).

RESULTS

Root Penetration

Based on number of J2 in roots at 5 days after inoculation, penetration of all *Cucumis* cultigen roots was similar for all species and races of *Meloidogyne* (Table 1). However, differences between *Cucumis* cultigens were detected with respect to root-knot nematode penetration and development in host roots over a 15-day period.

For all nematodes except *M. hapla*, developmental progress normally resulted in higher numbers of J3s or J4s in 'Sumter' compared to either 'NC-42' or PI 482454 at 10 and 15 days after inoculation. For root penetration of 'Sumter' by *M. hapla*, most juveniles remained as J2s and did not develop into the later juvenile stages. Reduced J3 or J4 numbers of *M. hapla* in 'Sumter' showed a pattern similar to that of *M. hapla* in 'NC-42' and PI 482454. Furthermore, the J3s or J4s of *M. hapla* were not present in roots of 'NC-42' and only a

Table 1. Number of *Meloidogyne* juvenile stages detected in roots of selected *Cucumis* spp. at 5, 10, and 15 days after inoculation with 5000 eggs, and J3/4 development in roots as a percent of the susceptible cucumber 'Sumter'.[1]

Cultigen/ Nematode	5 days		10 days		15 days		J3/4 as % of 'Sumter' at 15 days
	J2s	J3/4s	J2s	J3/4s	J2s	J3/4s	
Cucumis sativus var. *hardwickii* 'NC-42'							
Ma1	76	0	75	16	53	25	7
Ma2	38	0	69	8	45	7	3
Mi3	21	0	25	7	41	27	13
Mj	75	0	167	21	87	21	5
Mh	52	0	212	1	182	0	0
Mean	52	0	110	11	82	15	5
LSD ($P \leq 0.05$)	NS	—	97	NS	84	19	6
Cucumis metuliferus (PI 482454)							
Ma1	82	0	92	3	97	13	4
Ma2	59	0	82	2	76	7	3
Mi3	21	0	24	2	50	4	2
Mj	51	0	89	5	93	7	2
Mh	85	0	96	3	63	11	42
Mean	70	0	77	3	76	8	10
LSD ($P \leq 0.05$)	NS	—	NS	NS	NS	NS	30
Cucumis sativus var. *sativus* 'Sumter'							
Ma1	195	0	105	121	36	347	100
Ma2	138	0	97	132	30	272	100
Mi3	103	0	27	91	36	205	100
Mj	127	0	96	292	51	435	100
Mh	114	0	184	26	226	26	100
Mean	109	0	102	132	76	257	100
LSD ($P \leq 0.05$)	NS	—	121	130	52	168	—

[1]Data are means of six replications of 1 plant each. Ma1 = *M. arenaria* race 1, Ma2 = *M. arenaria* race 2, Mi3 = *M. incognita* race 3, Mj = *M. javanica*, and Mh = *M. hapla*. NS = nonsignificant at $P \leq 0.05$.

few were detected in PI 482454 and 'Sumter' at 15 days after inoculation.

At 10 and 15 days after inoculation, few J2s of any *Meloidogyne* population were developing into later stage juveniles (J3 or J4) in 'NC-42' or PI 482454. Compared to the other root-knot nematodes tested, the J2 stage of *M. hapla* persisted at high numbers in 'Sumter' and 'NC-42' but not in PI 482454.

Differences between nematodes ($P \leq 0.05$) in both 'NC-42' and PI 482454 was recorded for numbers of J3s and J4s, expressed as a percentage of 'Sumter' 15

days after inoculation (Table 1). In all cases, more J3s or J4s were observed in 'Sumter' at 15 days than 'NC-42' or PI 482454. The percentage of J3s or J4s that developed in 'NC-42' compared to 'Sumter' for *M. arenaria* races 1 and 2, *M. javanica*, and *M. hapla* ranged from 0 to 7% (Table 1); this indicates that 'NC-42' was not a suitable host for these nematodes. However, host suitability of 'NC-42' to *M. incognita* race 3 was greater than all other nematodes at 13%. For all nematodes except *M. hapla*, the percentage of J3s and J4s in PI 482454 as compared to 'Sumter' ranged from 2 to 4%, which indicates non-suitability of PI 482454 as a host.

Post-penetration Survival

The three *Cucumis* cultigens ('NC-42', PI 482454, and 'Sumter') tested in this experiment were resistant to *M. hapla*, based on the low numbers of J3s or J4s in roots at 15 days after inoculation (Table 2). As in the penetration experiment, high numbers of *M. hapla* J2s were present in roots with few developing into later stages. 'Sumter' was an excellent host for the other species and races of *Meloidogyne* evaluated, similar to results for the penetration experiment. The J3 or J4 numbers of *M. javanica*, *M. incognita* race 3, and *M. arenaria* races 1 and 2 present in roots at 15 days were much higher in 'Sumter' than in the two other *Cucumis* cultigens evaluated (Table 2).

At 10 and 15 days after inoculation, numbers of J3s or J4s of *M. hapla* and *M. arenaria* races 1 and 2 in 'NC-42' were significantly lower than those of *M. incognita* race 3. 'NC-42' was at least a moderately good host for *M. incognita* since development proceeded in a normal manner from J2 to J3 or J4 stages. Cultigen 'NC-42' was a poor host for *M. arenaria* races 1 and 2, *M. javanica*, and *M. hapla* judging from the relatively high numbers of J2s that remained in roots at 15 days after inoculation without subsequent development to the J3 or J4 stage.

Cultigen PI 482454 had a response similar to that observed in the penetration experiment with few J2s that penetrated roots developing into later stages. Although numbers of J3s or J4s of *M. arenaria* race 1 were significantly higher in roots of PI 482454 at 15 days after inoculation compared to the other root-knot nematodes evaluated (Table 2), most of the J2s of this nematode were not developing into the later stages.

For all root-knot nematodes, the percentage of J3s and J4s in PI 482454 compared to 'Sumter' ranged from 0 to 3%, indicating non-suitability of PI 482454 as a host. For *M. arenaria* races 1 and 2, *M. javanica*, and *M. hapla*, the percentage of J3s and J4s that developed in 'NC-42' compared to 'Sumter' ranged from 0 to 12% (Table 2). This agrees with the root penetration experiment indicating that 'NC-42' was not a suitable host for these nematodes. However, host suitability of 'NC-42' for *M. incognita* race 3 was fairly high at 25%, which was greater than for all other nematodes.

Histopathology

Juveniles of all root-knot nematode species and races tested penetrated and induced giant-cell formation in resistant and susceptible *Cucumis* by 5 days after inoculation. Hypersensitivity was not observed in the roots of resistant *Cucumis* infected with any of the five-root knot nematodes evaluated.

Infected roots of 'Sumter' had large, rounded, well defined giant cells by 5 days after inoculation (Fig. 1A-D), regardless of the root-knot nematode species. Several small nuclei were usually present in cross-sections of giant cells that developed in

Table 2. Number of *Meloidogyne* juvenile stages detected in roots of selected *Cucumis* spp. at 5, 10, and 15 days after inoculation with 20,000 eggs, and J3/4 development in roots as a percent of susceptible 'Sumter'.[1]

Cultigen/ Nematode	5 days		10 days		15 days		J3/4 as % of 'Sumter' at 15 days
	J2s	J3/4s	J2s	J3/4s	J2s	J3/4s	
Cucumis sativus var. *hardwickii* 'NC-42'							
Ma1	626	0	289	35	207	40	6
Ma2	337	0	335	25	139	51	8
Mi3	191	0	82	126	26	142	25
Mj	499	0	477	134	232	88	12
Mh	548	0	377	1	248	0	0
Mean	440	0	312	64	170	80	14
LSD ($P \leq 0.05$)	NS	—	163	95	165	76	14
Cucumis metuliferus (PI 482454)							
Ma1	760	0	201	17	199	21	3
Ma2	865	0	270	7	252	1	0
Mi3	413	0	305	0	69	1	0
Mj	714	0	255	0	363	9	1
Mh	634	0	205	0	48	0	0
Mean	677	0	247	5	186	6	1
LSD ($P \leq 0.05$)	152	—	85	6	59	8	1
Cucumis sativus var. *sativus* 'Sumter'							
Ma1	632	0	270	277	88	706	100
Ma2	673	0	236	405	101	666	100
Mi3	294	0	94	296	15	576	100
Mj	966	0	337	468	104	762	100
Mh	358	0	351	23	245	42	100
Mean	565	0	257	294	111	550	100
LSD ($P \leq 0.05$)	377	—	221	114	118	148	—

[1]Data are means of six replications of 1 plant each. Ma1 = *M. arenaria* race 1, Ma2 = *M. arenaria* race 2, Mi3 = *M. incognita* race 3, Mj = *M. javanica*, and Mh = *M. hapla*. NS = nonsignificant at $P \leq 0.05$.

'Sumter'. Although root-penetration data indicated that *M. hapla* did not develop normally in roots of 'Sumter' over a 15 day period (Tables 1 and 2), this parasite was able to induce the formation of giant cells in the root tissue of 'Sumter' by 5 days after inoculation (Fig. 1A).

Giant cells that formed in roots of PI 482454 were generally elongated in shape (Fig. 2A-D), and were similar to those produced in 'NC-42' (Fig. 3A-D). The nuclei within these giant cells were easily observable in all cases. The feeding sites in PI 482454 and 'NC-42' appear to be abnor-

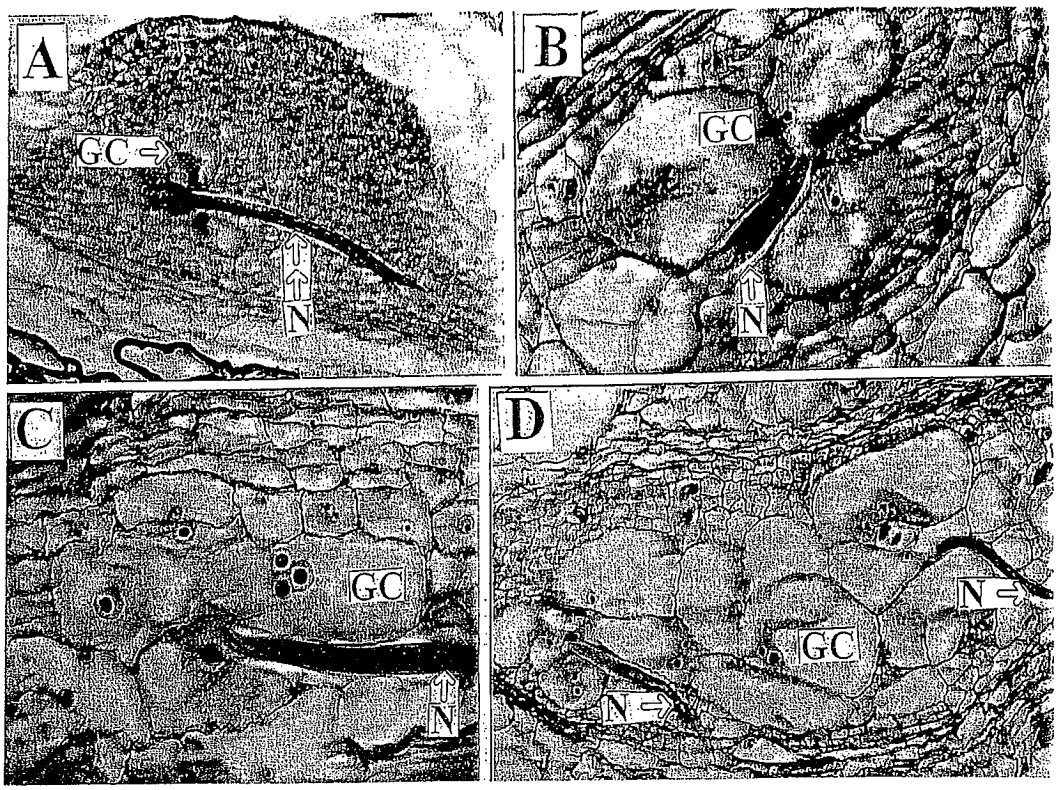

Fig. 1. Transverse sections of *Cucumis sativus* 'Sumter' infected with root-knot nematodes at 5 days after inoculation with eggs. A) *Meloidogyne hapla*, B) *M. javanica*, C) *M. arenaria* race 1, and D) *M. incognita* race 3. GC = giant cell and N = nematode.

mally developed compared to the large, rounded giant cells produced in 'Sumter'.

DISCUSSION

By 5 days after inoculation, a parasitic relationship was established between root-knot nematodes and the *Cucumis* cultigens, regardless of the level of resistance. However, resistance to certain *Meloidogyne* species and races was being expressed in the *Cucumis* cultigens evaluated which resulted in the delay or retardation of nematode development. The resistance to *M. hapla* in 'Sumter', *M. arenaria* races 1 and 2, *M. hapla*, and *M. javanica* in 'NC-42', and all root-knot nematodes evaluated in PI 482454 may be associated with feeding site development since no hypersensitivity was associated with the resistance. This agrees with Fassuliotis's (1970) conclusion in which no necrosis or hypersensitive reactions were observed with root-knot nematode invasion in resistant roots of *C. metuliferus*. This resistance was deemed to be associated with (a) hindrance of larval development beyond the J2, (b) delayed development of juveniles to adults, and (c) a high amount of sex reversal (increased stimulation of juveniles toward maleness).

Fassuliotis and Dukes (1972) found that induction of galling does not always indicate successful root-knot nematode development. Although the galling response

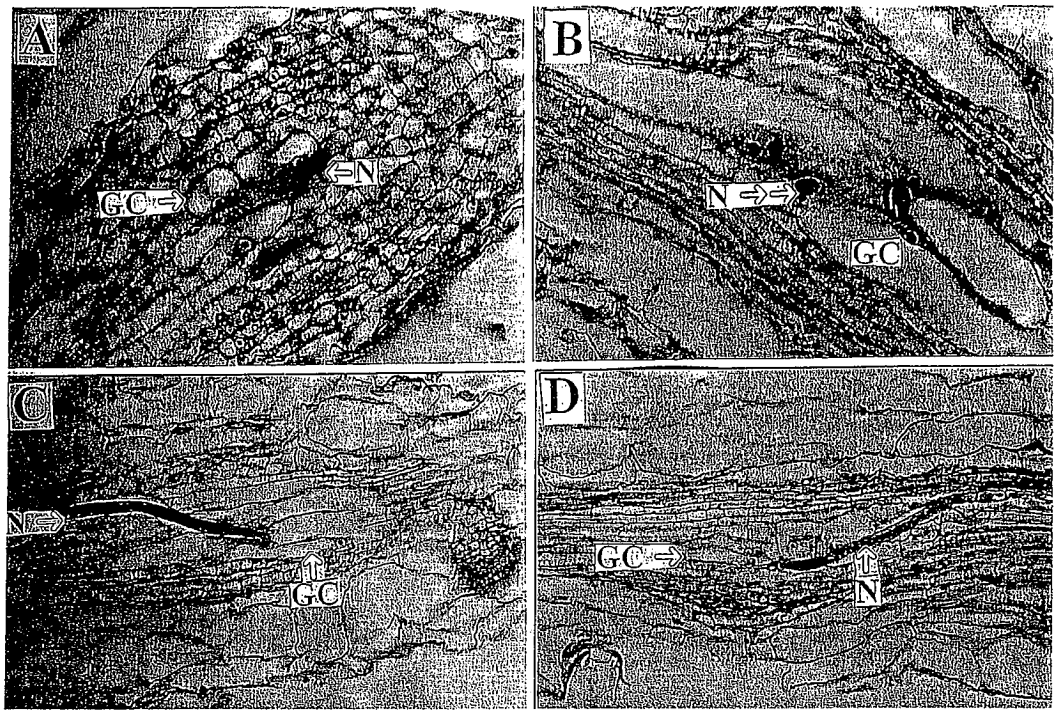

Fig. 2. Transverse sections of *Cucumis metuliferus* accession 482454 infected with root-knot nematodes at 5 days after inoculation with eggs. A) *Meloidogyne hapla*, B) *M. javanica*, C) *M. arenaria* race 1, and D) *M. incognita* race 3. GC = giant cell and N = nematode.

with giant cells is induced after penetration, it appears that the host fails to provide the necessary conditions for normal nematode development. Pedrosa *et al.* (1996b) indicated that giant cells induced by *M. arenaria* race 1 in resistant soybean genotypes were small and poorly developed, similar to those observed in resistant species of *Cucumis* when infected with root-knot nematodes (Walters *et al.*, 1990, 1993). Herman *et al.* (1991) and Pedrosa *et al.* (1996a) stated that root-knot nematode development was hindered in some manner in resistant soybean genotypes, resulting in fewer numbers of advanced stages of *Meloidogyne* juveniles, compared to those developing within susceptible genotype roots. This agrees with our findings in which few J3s or J4s were observed in resistant *Cucumis*. Possible explanations would include delayed development of nematodes, nematode death, or juvenile migration from roots.

The resistance in *C. sativus* var. *sativus* 'Sumter' to *M. hapla*, *C. sativus* var. *hardwickii* 'NC-42' to *M. arenaria* races 1 and 2, *M. hapla*, and *M. javanica*, and *C. metuliferus* PI 482454 to *M. arenaria* races 1 and 2, *M. hapla*, *M. incognita* race 3, and *M. javanica* is concluded to be due to reduced development of the root-knot nematodes. The resistance does not appear to be based on a hypersensitive reaction and is most likely associated with feeding site development as the giant cells in resistant roots tended to be elongated in shape. These sites probably result in abnormal nematode development as these parasites depend on

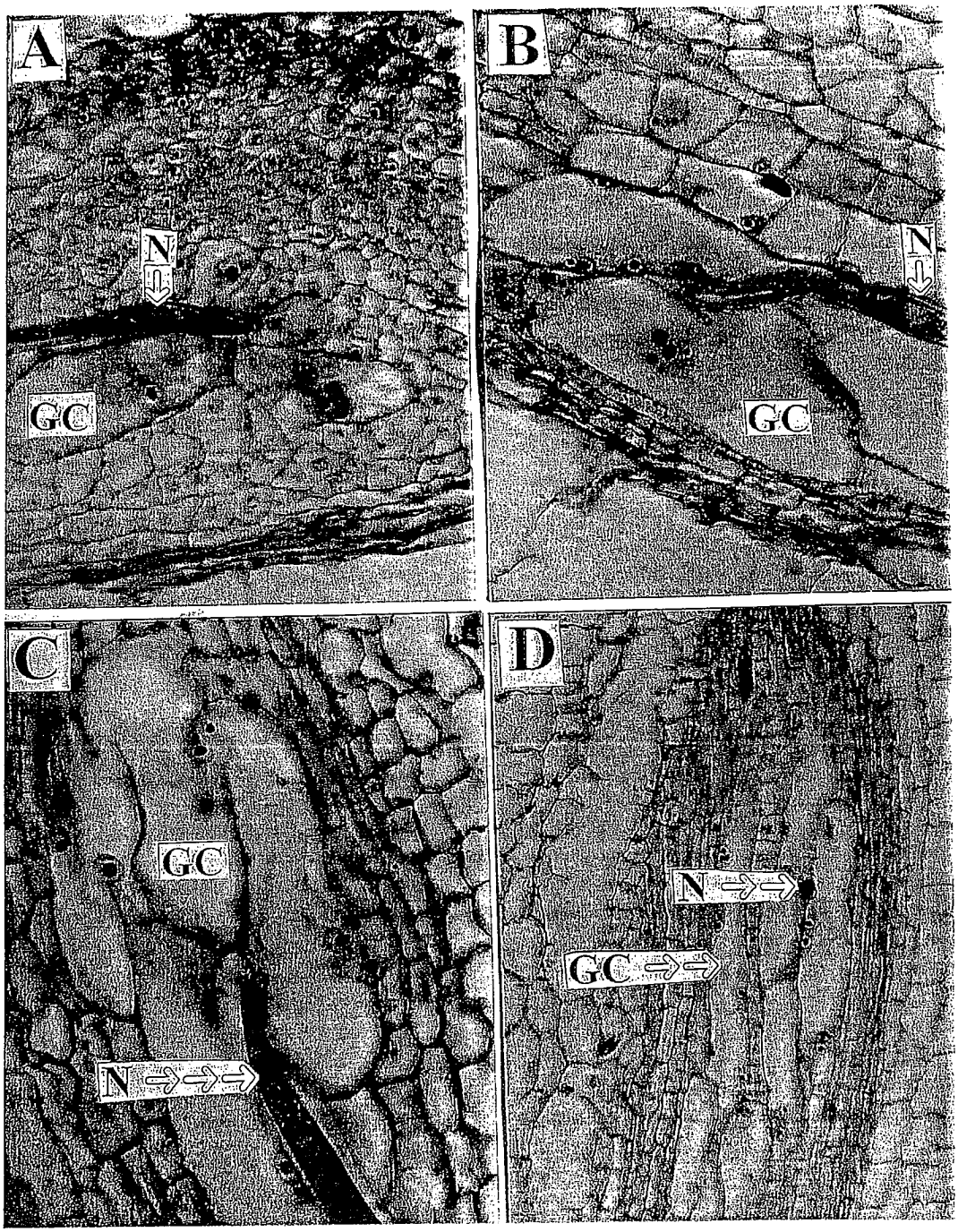

Fig. 3. Transverse sections of *Cucumis sativus* var. *hardwichii* 'NC-42' infected with root-knot nematodes at 5 days after inoculation with eggs. A) *Meloidogyne hapla*, B) *M. javanica*. C) *M. arenaria* race 1, and D) *M. incognita* race 3. GC = giant cell and N = nematode.

the nutrient supply from fully developed giant cells to complete their life cycle.

Although there are root-knot nematode resistant cultivars for many different vegetable crops (Fassuliotis, 1979), little progress has been made in selecting and breeding cucumber (*C. sativus* var. *sativus*) resistant to root-knot nematodes (Walters et al., 1993). The resistance in 'NC-42' could be used in developing cucumbers resistant to root-knot nematodes since it is cross-compatible with *C. sativus* var. *sativus* (Deakin *et al.*, 1971). The development of cultivars resistant to one of more *Meloidogyne* species would be an important step in the management of root-knot nematodes in cucumber.

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