

Meloidogyne incognita Inoculum Source Affects Host Suitability and Growth of Yellow Nutsedge and Chile Pepper¹

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Abstract: *Meloidogyne incognita* (Mi) reproduction and host plant responses in chile pepper (*Capsicum annuum*) and yellow nutsedge (*Cyperus esculentus* = YNS) to three sources of inoculum obtained by rearing a single Mi population on chile, YNS, and tomato were evaluated in two factorial greenhouse experiments. The interactive effects of Mi inoculum source and crop-weed competition were determined. In the absence of YNS competition, chile growth was reduced less by Mi inoculum from chile than by inoculum from YNS or tomato. When YNS was present, chile root weight was not affected and shoot weight increased with Mi initial inoculation, regardless of inoculum source. Chile plants inoculated with Mi from tomato exhibited double the nematode reproduction observed with inoculum from chile or YNS. With chile present, Mi reproduction on YNS was nearly three times greater with inoculum from tomato, but reproduction was similar among inoculum sources when chile was absent. Reductions in YNS root mass due to competition from chile failed to reduce the total number of Mi eggs produced on YNS plants. Differences in total Mi reproduction among inoculum sources were not attributable to differences in root growth or plant competition. This study illustrates the influence of Mi-YNS interactions and previous hosts on severity of Mi infection.

Key words: *Capsicum annuum*, chile pepper, *Cyperus esculentus*, host-parasite relationship, inoculum source, interaction, *Meloidogyne incognita*, root-knot nematode, weed, yellow nutsedge.

Cash receipts from chile peppers (*Capsicum annuum* L., hereafter referred to as 'chile') provide the leading source of farm income from row crops grown in New Mexico (Gore et al., 1994). Two organisms that seriously damage chile production are the southern root-knot nematode (*Meloidogyne incognita* (Kofoid & White) Chitwood) and yellow nutsedge (*Cyperus esculentus* L.). More than two-thirds of the New Mexico chile hectareage is infested with *M. incognita* (Thomas, 1994), which can severely reduce yields in many pepper cultivars at low pre-plant populations (DiVito et al., 1985; Lindsey and Clayshulte, 1982; Thomas et al., 1995). Yellow nutsedge, a competitive perennial weed that reproduces vegetatively through basal bulbs, rhizomes, and tubers, often escapes economic weed control prac-

tices used in chile and other rotation crops and serves as an alternate host of *M. incognita* (Högger and Bird, 1976; Schroeder et al., 1993, 1994). Management of both root-knot nematodes and yellow nutsedge in New Mexico chile depends exclusively on pesticides at present (Schroeder et al., 1994; Thomas, 1994).

Hectareage suitable for chile production in New Mexico is limited by climate and availability of irrigation. Intense management of such land leads to recurring problems with root-knot nematodes and yellow nutsedge. Therefore, understanding the interactions among the pathogen, pest, and chile is necessary to develop production practices that minimize damage to chile and other rotation crops. Previous studies have demonstrated that *M. incognita*, yellow nutsedge, or purple nutsedge (*C. rotundus* L.), alone or in combination, reduce root weights of chile (Schroeder et al., 1993). When *M. incognita* was present with yellow or purple nutsedge, or when purple nutsedge occurred in the absence of root-knot nematodes, chile shoot weights also were reduced.

Further investigations of interactions involving chile, yellow nutsedge, and *M. incognita* indicated that both the nematode and the crop reduced yellow nutsedge growth

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and reproduction (Schroeder et al., 1994). The presence of chile reduced production and germination of yellow nutsedge tubers (the propagative units of yellow nutsedge), but *M. incognita* increased tuber production and had no effect on tuber germination. Yellow nutsedge plants established from tubers that were collected from *M. incognita*-infested soil developed nematode-infected roots and produced more tubers than plants established from tubers produced in the absence of nematodes (Schroeder et al., 1994). However, none of the studies addressed whether differences might exist in plant or nematode development as a result of the host species on which the root-knot nematodes had been produced.

The objective of this research was to evaluate nematode reproduction and host plant responses in chile and yellow nutsedge to three sources of inoculum obtained by rearing the same isolate of *M. incognita* on chile, yellow nutsedge, and tomato.

MATERIALS AND METHODS

Nematode inocula: An isolate of *M. incognita* race 3 was initially collected from cotton in southern New Mexico and maintained and increased in the greenhouse on tomato (*Lycopersicon esculentum* Mill. 'Rutgers'). Six months before initiation of experiments, additional *M. incognita* cultures were established on yellow nutsedge (*Cyperus esculentus* L.) and chile pepper (*Capsicum annuum* L. 'New Mexico 6-4') using egg inoculum extracted from the tomato stock plants (Hussey and Barker, 1973). Yellow nutsedge tubers used to establish nematode cultures were obtained from greenhouse cultures of the weed that had been isolated from a clay loam soil adjacent to the Weed Science Field Laboratory at the Leyendecker Plant Science Research Center near Las Cruces, New Mexico, and were increased in 3.8-liter pots containing steam-sterilized soil. Pots were sampled periodically to ensure that nutsedge cultures were free of *M. incognita*. Nematode cultures on chile were subcultured as needed to maintain plant vigor. Subculturing of nematodes maintained on yellow nutsedge was not required.

General procedures: The experiment was conducted twice in the greenhouse as a factorial, randomized complete block design with six replications. Soil consisted of a 2:1 mixture by volume of sand and Maricopa fine sandy loam, which was heat-sterilized at 75 °C for 18 hours before use. Texture analysis of the mixture was a loamy sand (85% sand, 10% silt, 5% clay, pH 7.4, 0.4% organic matter). Experiments were conducted in a greenhouse maintained between 22 °C and 36 °C and with supplemental fluorescent lighting providing 340 $\mu\text{E} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$ to maintain the photoperiod at 14 hours. Plants were watered and fertilized, and insects were controlled with acephate or insecticidal soap as needed.

Yellow nutsedge plants used in the experiments were obtained by collecting tubers from pot cultures maintained in the greenhouse and determined to be free of plant-parasitic nematodes. Tubers were collected by removing the root mass from the pot, shaking soil from the root mass, and washing away the remaining soil with water. Tubers were separated from roots, rinsed in water, wrapped in moist paper towels, and stored at 2 °C for 1 week in sealed plastic bags. Following cold treatment, tubers wrapped in towels were placed in 2-liter glass jars in the greenhouse for 1 week. Tubers with 1-cm shoots were used in experiments.

Chile ('NM 6-4') seeds were sown in 3.8-liter pots, thinned to one plant per pot; 2 weeks later germinated nutsedge tubers were planted in appropriate pots. Approximately 4 weeks after planting, when chile plants reached the two-leaf stage, assigned pots were infested with 5,000 *M. incognita* eggs obtained from roots of the chile, yellow nutsedge, or tomato cultures. Egg inoculum was collected by means of an NaOCl (0.5%) extraction method (Hussey and Barker, 1973), and the egg suspension was divided among three 0.5 × 2.5-cm deep holes in the root zone of each plant or pair of plants. Treatments included combinations of chile (present or absent), yellow nutsedge (present or absent), and *M. incognita* (from chile, yellow nutsedge, tomato, or absent in the uninfested controls).

Data collection and analysis: Plants were harvested 16 weeks after chile was seeded (12 weeks after infestation). Chile and nutsedge plants were divided into above-ground (shoot) and below-ground (root) parts, dried at 70 °C, and weighed. Chile fruit also was weighed. Before drying, tubers from each pot were counted and 10 mature tubers were removed and tested for germination. Following cold treatment, tubers in the germination test were placed between two moist filter papers in covered petri dishes in the greenhouse at 22 °C to 36 °C for 1 week. Tubers with any root or shoot growth were considered to have germinated. Tubers used for the germination test were dried and the weights added to that of the appropriate nutsedge root system.

Nematode counts were obtained for each pot by extracting *M. incognita* eggs from separate chile or nutsedge root systems with an NaOCl method (Hussey and Barker, 1973) prior to drying roots. Second-stage juveniles (J2) were extracted from a 500-cm³ subsample of soil from each pot by elutriation-centrifugal flotation (Byrd et al., 1976; Jenkins, 1964). Numbers of eggs per gram dry root and J2 per 100 cm³ soil were used to compare *M. incognita* population development. Nematode reproductive ratios (Pf/Pi) also were calculated for chile and yellow nutsedge by dividing the number of eggs collected per plant (Pf) by the inoculum level (Pi) (Oostenbrink, 1966). Composite nematode reproduction was calculated for each pot by dividing the number of J2 per pot by Pi and summing with the reproductive ratio from the chile and (or) nutsedge produced in the pot.

Data from the two experiments were combined after initial analysis indicated a lack of factor-by-experiment interactions. Dependent variables were subjected to analysis of variance, and means and standard errors were calculated for each factor. The treatment structure for chile variables was a two (nutsedge present or absent)-by-four (*M. incognita* from chile, from tomato, from nutsedge, or absent) factorial. The treatment structure for yellow nutsedge variables was similar, except for the plant factor (chile

present or absent). Nematode variables measured on either chile or nutsedge were analyzed as a three (*M. incognita* from chile, from tomato, or from nutsedge)-by-two (chile or nutsedge as hosts) factorial, except for composite nematode reproduction per pot, which consisted of the same three inoculum sources but contained three host combinations (chile, nutsedge, and chile plus nutsedge).

RESULTS AND DISCUSSION

The primary objective of the research was to determine whether nematode reproduction and plant responses involving chile and yellow nutsedge were influenced by the host source upon which *M. incognita* inoculum was produced. The experimental design and analysis focused on statistical interactions among the dependent variables rather than main effects. Therefore, the discussion will emphasize significant interactions that may elucidate the biological relationships among the weed, crop, and nematode.

Plant responses: Chile fruit dry weight was less when yellow nutsedge was present but was unaffected by *M. incognita* inoculum source, and there was no main effect interaction (Table 1). The nutsedge by nematode inoculum source interaction was significant for chile shoot and root dry weights. When chile was grown under greenhouse conditions in the absence of nutsedge, shoot weight was reduced in plants inoculated with *M. incognita* from nutsedge or tomato but not by *M. incognita* from chile, when compared to shoot weights of uninoculated plants. When chile and nutsedge were grown together, chile shoot weights of inoculated plants (regardless of *M. incognita* inoculum source) were at least 22% greater than shoot weights of uninoculated plants, and similar to shoot weights of uninoculated chile grown in the absence of nutsedge. Root weights of chile grown alone were reduced more (30% and 33%, respectively) by addition of *M. incognita* inoculum from nutsedge or tomato than by inoculum from chile (17% reduction) when compared to root weights of uninoculated plants. When

TABLE 1. Chile fruit, shoot, and root dry weight as affected by interactions between *Meloidogyne incognita* inoculum source and yellow nutsedge.^a

Inoculum source ^c	Nutsedge	Mean dry weight (g) ± SE ^b		
		Fruit	Shoot	Root
Uninoculated	Absent	11.43 ± 0.77	14.17 ± 0.86 ab	5.02 ± 0.29 a
Chile	Absent	10.12 ± 0.77	14.83 ± 0.86 a	4.17 ± 0.29 b
Tomato	Absent	11.28 ± 0.74	11.06 ± 0.83 de	3.36 ± 0.28 c
Nutsedge	Absent	10.89 ± 0.81	12.16 ± 0.91 cd	3.50 ± 0.31 c
Uninoculated	Present	9.61 ± 0.81	9.73 ± 0.86 e	3.07 ± 0.29 c
Chile	Present	6.72 ± 0.77	12.43 ± 0.91 bcd	3.21 ± 0.31 c
Tomato	Present	7.39 ± 0.77	13.27 ± 0.86 abc	3.42 ± 0.29 c
Nutsedge	Present	8.69 ± 0.77	12.43 ± 0.86 bcd	3.34 ± 0.29 c
		Nutsedge main effect ^d		
Absent		10.93 ± 0.38 a		
Present		8.10 ± 0.39 b		
		Inoculum source main effect ^e		
Uninoculated		10.52 ± 0.54		
Chile		8.42 ± 0.56		
Tomato		9.33 ± 0.53		
Nutsedge		9.79 ± 0.56		

^a Nutsedge by inoculum source interaction significance levels: fruit weight $P = 0.4925$, shoot weight $P = 0.0013$, root weight $P = 0.0039$.

^b Means are not significantly different ($P = 0.05$) if followed by the same letter.

^c Nematode inoculum was extracted from roots of chile, tomato, or nutsedge ($n = 12$).

^d Nutsedge main effect significance level: fruit $P = 0.0001$, ($n = 48$).

^e Inoculum source main effect significance level: fruit $P = 0.0616$, ($n = 24$).

chile and nutsedge were grown together, chile root weight was not affected by *M. incognita*.

No significant chile by nematode inoculum source interactions occurred for nutsedge root or shoot weights, numbers of tubers produced, or tuber germination (data not presented). When yellow nutsedge and chile were grown together (data pooled across nematode effects), nutsedge shoot

and root dry weights were 69% and 59% less, respectively, and percentage germination of nutsedge tubers was 17% less compared to nutsedge grown alone (Table 2). Nutsedge root weights were approximately 50% less when *M. incognita* was present, but shoot weights were unaffected (data pooled across chile effects) regardless of the inoculum source. The reductions in nutsedge root growth due to *M. incognita* may have

TABLE 2. Nutsedge tuber number, tuber germination, and shoot and root dry weights as affected by *Meloidogyne incognita* inoculum source and chile.

Treatment	Tuber production ± SE ^a		Mean dry weight (g) ± SE ^a	
	Number	Germination (%)	Shoot	Root
		Chile main effect ^b		
Mi absent	17.56 ± 1.66	77 ± 4 a	10.79 ± 0.45 a	5.64 ± 0.46 a
Mi present	15.23 ± 1.66	66 ± 4 b	3.39 ± 0.45 b	2.29 ± 0.46 b
		Inoculum source main effect ^c		
Uninoculated	12.79 ± 2.35	70 ± 6	6.94 ± 0.64	6.70 ± 0.65 a
Chile	20.54 ± 2.35	72 ± 6	7.82 ± 0.64	3.53 ± 0.65 b
Tomato	16.42 ± 2.35	62 ± 6	7.13 ± 0.64	2.87 ± 0.65 b
Nutsedge	15.83 ± 2.35	81 ± 6	6.50 ± 0.64	2.76 ± 0.65 b

^a Means within main effects are not significantly different ($P = 0.05$) if followed by the same letter.

^b Chile main effect significance levels: tuber number $P = 0.3241$, tuber germination $P = 0.0494$, shoot $P = 0.0001$, root $P = 0.0001$ ($n = 48$).

^c Nematode inoculum was extracted from roots of chile, tomato, or nutsedge. Inoculum source main effect significance levels: tuber number $P = 0.1476$, tuber germination $P = 0.1162$, shoot $P = 0.5255$, root $P = 0.0001$ ($n = 24$).

reduced plant competition with chile and contributed to the increased chile shoot growth seen in Table 1. Though not significantly different from uninoculated plants, tuber production was always greater in nutsedge inoculated with *M. incognita*. Increased tuber production has been reported in yellow nutsedge plants infected with *M. incognita* (Schroeder et al., 1994).

Plant competition between chile and yellow nutsedge is most likely responsible for the differences observed in chile fruit weight, nutsedge tuber germination, nutsedge shoot and root weight effects, and reductions in chile shoot and root weights in the absence of nematodes. These results agree with previous studies where yellow nutsedge and purple nutsedge reduced chile root and shoot weights (Schroeder et al., 1993) and competition from chile reduced yellow nutsedge tuber germination and nutsedge shoot and root dry weights (Schroeder et al., 1994). Root-knot nematode inoculum produced on chile was less pathogenic to chile growing without nutsedge competition than was inoculum produced on yellow nutsedge or tomato. However, when plant competition occurred, *M. incognita* produced no additional suppression of chile root growth, and shoot growth was enhanced compared to uninoculated plants.

Nematode reproduction: Chile plants inoculated with *M. incognita* from tomato yielded more than twice as many eggs per gram of root and demonstrated reproductive ratios that were twice as great as chile plants receiving the same amount of inoculum from yellow nutsedge or chile (Table 3). Nematode reproduction on chile was not affected by the presence of yellow nutsedge plants nor by interactions between nutsedge and root-knot nematode inoculum sources. Differences in nematode reproductive ratios among sources of inoculum were proportional to differences in egg production per gram of chile root, indicating that changes in root mass associated with plant competition had no effect on *M. incognita* reproduction per unit of chile root weight. Nematode reproductive ratios on all chile plants were

TABLE 3. *Meloidogyne incognita* reproduction on chile as affected by inoculum source and yellow nutsedge.

Treatment	Eggs/g chile root (in thousands) ^a	Pf/Pi ^b
Inoculum source main effect ^c		
Chile	196 ± 53 b	134 ± 40 b
Tomato	544 ± 48 a	372 ± 36 a
Nutsedge	254 ± 52 b	178 ± 39 b
Host plant main effect ^d		
Chile	315 ± 41	227 ± 31
Chile + nutsedge	348 ± 42	230 ± 31

^a Mean ± SE for egg numbers (in thousands) per gram dry chile root. Means followed by the same letter are not significantly different ($P = 0.05$).

^b Ratio of *M. incognita* eggs collected from inoculated chile (Pf) to inoculum level (Pi).

^c Nematode inoculum was extracted from the roots of chile, tomato, or nutsedge ($n = 24$). Inoculum source main effect significance levels: egg per gram chile root $P = 0.0001$, Pf/Pi on chile roots $P = 0.0001$.

^d Host plant combinations include chile growing alone and chile growing with nutsedge ($n = 36$). Host plant main effect significance levels: egg per gram chile root $P = 0.0934$, Pf/Pi on chile roots $P = 0.9460$.

relatively large and confirm that *C. annuum* is highly susceptible to *M. incognita* (DiVito et al., 1985; Lindsey and Clayshulte, 1982; Thomas et al., 1995).

The chile by nematode inoculum source interaction was significant for *M. incognita* egg production per gram nutsedge root (Table 4). When yellow nutsedge was grown in the absence of chile, nematode reproduction was similar, regardless of the inoculum source. With chile present, nematode reproduction on nutsedge was nearly three times greater when nematode inoculum came from tomato as when chile or yellow nutsedge was the inoculum source. Despite a 59% reduction in nutsedge root weight due to competition with chile, no corresponding reduction in nematode reproduction (Pf/Pi) was observed in nutsedge plants. It is not known if the increase in egg production per unit weight of nutsedge root resulted from the reduction in root mass attributed to competition or was due to an increase in secondary infection from the adjacent chile roots. Mean reproductive ratios indicated a 16-fold to 56-fold increase (80,000 to 280,000 eggs per plant) in *M. incognita* numbers on yellow nutsedge during the 12-week duration of these studies, supporting previ-

TABLE 4. *Meloidogyne incognita* reproduction on yellow nutsedge as affected by interactions between inoculum source and chile.^a

Inoculum source ^b	Chile	Eggs/g nutsedge root (in thousands) ^c		Pf/Pi ^d
Chile	Absent	18.2 ± 25.1 b	20 ± 13	
Tomato	Absent	22.1 ± 26.5 b	20 ± 13	
Nutsedge	Absent	23.6 ± 25.1 b	22 ± 13	
Chile	Present	31.6 ± 25.1 b	16 ± 13	
Tomato	Present	172.1 ± 25.1 a	56 ± 13	
Nutsedge	Present	62.3 ± 26.5 b	22 ± 13	
Inoculum source main effect ^e				
Chile			18 ± 9 b	
Tomato			38 ± 9 a	
Nutsedge			22 ± 9 ab	
Host plant main effect ^f				
Nutsedge			21 ± 7	
Nutsedge + chile			32 ± 7	

^a Inoculum source by chile interaction significance levels: eggs per gram nutsedge $P = 0.0243$, Pf/Pi $P = 0.2254$.

^b Nematode inoculum was extracted from the roots of chile, tomato, or yellow nutsedge ($n = 12$).

^c Mean ± SE for eggs collected (in thousands) per gram dry nutsedge root. Means are not significantly different ($P = 0.05$) if followed by the same letter.

^d Ratio of *M. incognita* eggs collected from inoculated nutsedge (Pf) to inoculum level (Pi).

^e Inoculum source main effect significance level: Pf/Pi $P = 0.0188$ ($n = 24$).

^f Host plant main effect significance level: Pf/Pi $P = 0.2970$ ($n = 36$).

ous reports in which yellow nutsedge was a good host for *M. incognita* (Schroeder et al., 1993, 1994).

Composite *M. incognita* reproduction was

affected by interactions between sources of inoculum and host plant combinations (Table 5). At harvest, numbers of J2 were greatest where chile alone had been inoculated with *M. incognita* from tomato, compared to all other combinations of plants and sources of nematode inoculum. The composite nematode reproductive index and numbers of J2 extracted from soil were generally less when only nutsedge was present, regardless of the nematode inoculum source. The composite nematode reproductive ratios on chile and the chile-nutsedge combination were similar when plants received inoculum from chile or yellow nutsedge, but generally twice as great when inoculum was produced on tomato. Composite nematode reproductive ratios were normalized for differences in root growth and the effects of plant competition by dividing Pf/Pi by total root and tuber weights from each pot (Table 5). Differences in composite reproductive ratios and normalized reproductive ratios were proportional to one another within inoculum sources, indicating that differences in total nematode reproduction are not directly attributable to differences in root growth or plant competition.

In summary, plant responses and *M. incognita* reproduction were both affected by the

TABLE 5. Composite *Meloidogyne incognita* reproduction as affected by interactions between host plant combinations and inoculum source.^a

Inoculum source ^b	Host ^c	J2 per 100 cm ³ soil ^d	Pf/Pi ^e	
			Composite ^f	Per gram root ^g
Chile	Chile	1,649 ± 358 bc	152 ± 45 b	40 ± 12 b
Chile	Chile + nutsedge	1,183 ± 358 cd	159 ± 45 b	31 ± 12 bc
Chile	Nutsedge	113 ± 358 ef	21 ± 42 c	4 ± 12 d
Tomato	Chile	3,463 ± 346 a	402 ± 41 a	117 ± 11 a
Tomato	Chile + nutsedge	2,081 ± 358 b	440 ± 42 a	100 ± 11 a
Tomato	Nutsedge	64 ± 358 f	30 ± 45 c	7 ± 12 cd
Nutsedge	Chile	794 ± 377 def	172 ± 45 b	44 ± 12 b
Nutsedge	Chile + nutsedge	813 ± 358 de	237 ± 47 b	45 ± 12 b
Nutsedge	Nutsedge	89 ± 358 f	22 ± 42 c	5 ± 11 d

^a Host plant by inoculum source interaction significance levels: J2 per 100 cm³ soil $P = 0.0080$, Pf/Pi overall $P = 0.0135$, Pf/Pi per gram host root $P = 0.0060$.

^b Nematode inoculum was extracted from roots of chile, tomato, or nutsedge ($n = 12$).

^c Host plant combinations included chile and nutsedge growing alone or together.

^d Mean ± standard error of the mean. Means followed by the same letter are not significantly different ($P = 0.05$).

^e Ratio of *M. incognita* extracted per pot from soil and roots (Pf) to inoculum level (Pi).

^f Composite reproductive ratio = (Pf/Pi on chile + Pf/Pi on nutsedge) + (J2 per pot/Pi).

^g Composite Pf/Pi divided by total root dry weight per pot.

host source from which nematode inoculum was obtained in this research. Chile plants were less damaged by inoculum from chile in the absence of nutsedge competition, and *M. incognita* reproduction was often lower when both inoculum source and inoculum recipient were the same plant species. This research indicates that hosts may exert a qualitative as well as quantitative effect on root-knot nematodes that remains evident in the population considerably past the first generation of nematodes. Also, reductions in yellow nutsedge root mass failed to reduce the number of nematodes produced on nutsedge plants. Further research is needed to simultaneously determine the relationships among weeds, plant-parasitic nematodes, and crops in order to characterize factors affecting pathogen and pest severity. This research emphasizes the need for multidisciplinary and integrated approaches in field crop management.

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