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Variability in Reproduction of Four Populations of *Meloidogyne incognita* on Six Cultivars of Cotton

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Abstract: A range of virulence levels was found in four populations of *Meloidogyne incognita* collected from cotton fields of the Punjab region of Pakistan. The most virulent population was associated with development of larger gall size, larger giant cell formation and improved success of juveniles transitioning into reproducing adults. The most virulent nematode population, MI-78, emanated from cotton cultivar NIAB-78. This cotton cultivar also possessed the greatest level of resistance to the three other nematode populations evaluated in this study. The source of plant resistance was not evident during root penetration by second-stage juveniles (J2), but became apparent as nematode feeding was attempted. Although one other cotton cultivar, CIM-506, could also be designated as showing a level of resistance, none of the other cultivars reduced any nematode stage by more than 75% of that achieved on the best host. These data provide an example of a single cotton cultivar that could have short-term utility in field settings. The data also provide insight for future cotton breeding programs.

Key words: cotton, *Gossypium hirsutum*, populations of *Meloidogyne incognita*, reproduction potential, resistance.

Root-knot nematode, *Meloidogyne incognita*, is widespread and recognized as a major pathogen of cotton (*Gossypium hirsutum*) in cotton production regions of the world (Anwar and Khan 1973; Kinlock and Sprenkel, 1994; Martin et al., 1994; Baird et al., 1996; Bateman et al., 2000). This nematode induces extensive root galling which can alter uptake of water and nutrients, interferes with translocation of photosynthates (Bridge, 1992; Williamson and Hussey, 1996), and increases the incidence and severity of cotton wilt caused by *Fusarium oxysporum* f. sp. *vas infectum* (Anwar and Khan, 1973; Martin et al., 1994). The result is a reduction in yield that can range up to more than 75% (Orr and Robinson, 1984), depending on soil texture and prevailing weather conditions (Starr et al., 1993).

In Pakistan there has been minimal study of plant-parasitic nematodes as pathogens of cotton. The most damaging nematode parasites are southern root-knot nematode, *M. incognita*, reniform nematode, *Rotylenchulus reniformis*, Columbia lance nematode, *Hoplolaimus columbus*, and sting nematode, *Belonolaimus longicaudatus*. Four host races are recognized within *M. incognita* (Hartman and Sassar, 1985; Maqbool, 1992). Host races 3 and 4 are able to parasitize cotton (Starr and Veech, 1986). Race 3 has been found infecting cotton in Pakistan (Maqbool, 1992).

Several studies have demonstrated that resistance-breaking populations of *Meloidogyne* spp. can arise following continual exposure to plants referred to as resistant. This can occur in relatively few generations (Netscher, 1977; Bost and Triantaphyllou, 1982; Prot, 1984; McKenry, 1987; Carpenter and Lewis, 1991; Noe, 1992). In 1992, Noe characterized 13 populations of *M. arenaria* exhibiting variable rates of infection and reproduction on peanut, soybean and tomato. Four populations of *M. arenaria* have been differentiated on the basis of their reproduction and pathology on six soybean cultivars (Carpenter and Lewis, 1991).

Various races or populations of *Meloidogyne* spp. have been designated as virulent (aggressive) or avirulent (nonaggressive) based on their rate of reproduction (Swanson and Van Gundy, 1984; Starr and Veech, 1986; Windham and Barker, 1986; Carpenter and Lewis, 1991; Anwar and McKenry, 2000; Zhou et al., 2000). Roberts et al. (1995) reported significant variation in reproduction among isolates of *M. incognita* on cowpea genotypes with the *Pk* resistance gene. In tomato, the *Mi* gene provides resistance to *M. incognita, M. javanica* and *M. arenaria*. However, following widespread deployment of the *Mi* gene, aggressive isolates of *M. incognita* have developed and reproduced on plants containing the *Mi* gene (Kaloshian et al., 1996).

Selection of more virulent populations of *M. incognita* through continued planting of resistant cotton may have also occurred in California (Ogallo et al., 1997) and Texas (Zhou et al., 2000). In these cases, isolates with the highest level of reproduction on the resistant cultivar NemX were found in fields previously planted to this source of resistance. Zhou et al. (2000) reported substantial variation in root galling and reproduction by *M. incognita* isolates on resistant cotton genotypes.

Preliminary surveys of cotton fields in Pakistan by the senior author revealed substantial variability in gall incidence and size among various cotton cultivars developed at the Cotton Institute of Multan (CIM) when

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planted at various locations in the Punjab region. This prompted the hypothesis that variability in galling might be an indicator of differing virulence levels among populations of *M. incognita*, as previously described in California and Texas (Ogallo et al., 1997; Zhou et al., 2000). The objective of this research was to determine the level of variability in reproduction of four populations of *M. incognita* on six cotton cultivars commonly grown in the Punjab.

Materials and Methods

Nematode inoculum: Four populations, originally isolated from single egg masses, were increased on tomato (*Lycopersicon esculentum* Mill.) cv. Money Maker in a glasshouse. Eggs were collected from roots of tomato using 1% NaOCl (Hussey and Barker, 1973). Suspensions of eggs were stirred in tap water, and their counts adjusted to provide the desired inoculum density. For experiments 1 and 3, each 15-cm-diam. pot was infested with 5,000 eggs by distributing inoculum within two dibble holes (3-cm-deep) at the base of each plant 2 wk after planting and then covering with soil. For experiment 2, 17-cm-long, 5.5-cm-diam. growth tubes were planted with cotton cultivar NIAB-78. Each growth tube was inoculated with 500 J2.

For each of these experiments, the soil (85% sand, 10% silt, 5% clay) had been steam heated at 100°C for 6 hr to kill potential pathogens. Two seeds had been planted into each pot or growth tube, watered and then placed in a glasshouse that was maintained at 30°C ± 3°C. Two weeks after planting, cotton plants were thinned to one seedling and inoculated with either nematode eggs or second-stage juveniles. All treatments were replicated five times per experiment, and pots or growth tubes arranged in a completely randomized design on the glasshouse bench. Plants were fertilized every 2 wk with Hoagland's solution (Hoagland and Arnon, 1950).

Nematode reproduction on cotton: Three experiments were conducted. The first experiment compared reproduction of four populations of *M. incognita* on six Upland-type cotton cultivars including an advanced breeding line, CIM-534, as well as an F1 irradiated line, NIAB-78.

The second experiment, based on results of the first, compared the penetration, development and reproduction of four populations on the most resistant cotton cultivar, NIAB-78. Based on results of the first and second experiments, a third experiment was conducted to assess root galling, number of egg masses and total eggs per root system produced by two populations of *M. incognita* including MI-78 as the virulent and MI-534 as the avirulent. The root systems were rated for galling and egg mass presence on a 0 to 5 scale (Quesenberry et al., 1989) where 0 = no galls or egg masses, 1 = 1 or 2, 2 = 3–10, 3 = 11–30, 4 = 31–100, and 5 = > 100 galls or egg masses/root system.

The first experiment was terminated 60 d after inoculation. Five plants of each cultivar were available (5 reps). Plants were removed from their pots, and roots washed gently to remove soil. Root systems of the plants were stained with Phloxine B (Holbrook et al., 1983) and assessed for the presence of egg masses. Egg masses were hand picked from the galled roots. Eggs from individual egg masses were extracted by placing in 800-ml glass Mason jars with 1% NaOCl (Hussey and Barker, 1973), sealed and shaken for 4 min at 200 rpm on a rotary shaker (Eberbach, Ann Arbor, MI). Extracted eggs were rinsed thoroughly in tap water and counted at ×40 magnification.

The second experiment was designed to assess penetration, development and reproduction of each *M. incognita* population on cotton cultivar NIAB-78. The first experiment had shown this cultivar to be a poor host for three populations of *M. incognita* but a good host for population MI-78. All experimental and environmental conditions were the same as in Experiment 1 except the number of individual plants available was 35 for each nematode population and the inoculation level was 500 J2/tube. Nematode penetration, development, reproduction and juvenile growth were assessed 2, 5, 12, 19, 33 and 44 d after inoculation. Five inoculated plants of each cultivar were available for assessment on each sample date, thus providing 5 reps for each time interval. Roots were washed free of soil, blotted onto paper to damp dry, and weighed. The whole root system of each plant at each harvest was stained with acid fuschin (Byrd et al., 1983). Each root system was spread in a film of glycerin between two glass plates, and nematode penetration and development within the roots determined under a dissecting microscope. The number of nematodes in each stained root system was recorded at each sampling date. Nematodes were classified into three developmental stages (Jenkins et al., 1995; Syndenham et al., 1996; Anwar and McKenry, 2000): Vermiform J2; globose J4 with spiked tail; and adult female. Nematode growth (= width) at the center of each developing juvenile was measured at each root harvest by using an ocular micrometer at ×100. Infection sites were also microscopically examined to assess the initiation and formation of giant cells.

The five remaining plants of each cotton cultivar were allowed to grow a total of 60 d.The entire root system of these plants was diced, and a 20 g composite root sample incubated in a mist chamber for 5 d to hatch the eggs (McKenry and Roberts, 1985). The number of J2 per root system was determined to assess the level of nematode reproduction on roots of each cultivar.

Based on results of the first and second experiments, a third experiment was conducted to assess root galling,

number of egg masses and total eggs per root system produced by two populations of *M. incognita* including MI-78 as the virulent and MI-534 as the avirulent. These populations were inoculated to roots of two cotton cultivars including NIAB-78 as resistant and CIM-534 as susceptible. All the experimental protocols and conditions were duplicated from the first experiment. Sizes of egg masses and galls were observed and quantified. The nematode-infected roots of each cultivar were microscopically examined to compare the occurrence of hyperplasia and hypertrophy of cells surrounding the feeding sites.

Data analysis: Data on egg masses per root system and eggs per egg mass were subjected to factorial analysis. An analysis of variance was performed on data from Experiment 1 and 2 using SAS. Significant differences in means of nematode reproduction were separated using Duncan's Multiple Range Test at ($P = 0.05$).

Results

Experiment 1—Nematode Reproduction: Reproduction of four populations of *M. incognita*, assessed as egg masses per root system and eggs per egg mass, was variable on roots of the six cotton cultivars (Table 1, 2). Three nematode populations, MI-534, MI-496 and MI-506, showed significantly higher reproduction ($P = 0.05$) on roots of CIM-534, CIM-496, CIM-506, CIM-499 and CIM-707 cotton cultivars compared to that of NIAB-78 cultivar.

Three cotton cultivars including CIM-534, CIM-496 and CIM-707 supported similar levels of egg masses per root system but significantly greater ($P = 0.05$) than that on three other cultivars when infected by the MI-78 population (Table 1). Four cotton cultivars, namely CIM-534, CIM-496, CIM-499 and CIM-707, produced similar numbers of eggs per egg mass but significantly greater ($P = 0.05$) than those on the other two cultivars when infected by the MI-78 population (Table 2).

Cotton cultivar NIAB-78 suppressed reproduction of all *M. incognita* populations except the MI-78 population. Cotton cultivars CIM-534, CIM-496, CIM-506, CIM-499 and CIM-707 exhibited variable numbers of egg masses of the MI-534 population, but significantly ($P = 0.05$) more than when exposed to the MI-78 population. With the MI-78 population, the number of eggs per egg mass was also variable among cotton cultivars. The level of reproduction by MI-534 was much lower than on other genotypes ($P = 0.05$).

The MI-496 population produced 38% more egg masses on CIM-534 cotton than on NIAB-78. Cotton cultivar CIM-707 had a significantly greater number of egg masses compared to CIM-506 but similar to CIM-496 and CIM-499 cotton cultivars. There was a significant difference among numbers of eggs per egg mass separated from roots of CIM-534, CIM-496, CIM-499 and CIM-707. These four cultivars supported significantly ($P = 0.05$) more egg masses than cotton cultivar NIAB-78. Eggs per egg mass on roots of CIM-506 were 66% more abundant than those on roots of NIAB-78.

The MI-506 population produced significantly ($P = 0.05$) more egg masses and eggs per egg mass on CIM-506 than any other MI population. This population also produced significantly ($P = 0.05$) more egg masses than MI-534 or MI-78 populations. The MI-78 population produced 13% more egg masses on roots of CIM-534 than it did on NIAB-78.

Experiment 2—Nematode Development: Development and reproduction of four populations were studied on the roots of NIAB-78, the poorest host for the four nematode populations (Table 3). Equivalent numbers of J2 penetrated roots of NIAB-78 regardless of the population evaluated. However, further development of J2 was significantly ($P = 0.05$) influenced, as greatest incidence of J4, adults, and reproduction occurred with the MI-78 population on NIAB-78. On NIAB-78, reproduction by the MI-534 population was suppressed 8, 10 and 19-fold as compared to reproduction by MI-496, MI-506 and MI-78 populations, respectively.

As indicated in Figure 1, the J2 of the virulent MI-78

Table 1. Number of egg masses per root system produced by four populations of *Meloidogyne incognita* (MI) on the roots of six cotton cultivars.

Cotton cultivars	Populations of *Meloidogyne incognita*			
	MI-534	MI-496	MI-506	MI-78
	Egg masses per root system*			
CIM-534	150 DE**	96 K	112 J	159 ABC
CIM-506	129 I	131 HI	153 BCDE	135 GHI
CIM-496	145 EF	138 FGH	151 CDE	153 BCDE
CIM-499	119 J	135 GHI	140 FG	135 GHI
CIM-707	165 A	140 FG	155 BCD	161 AB
NIAB-78	76 L	59 M	45 N	141 FG

* Each mean for egg masses per root system consists of an average of five root systems.

** Means within each column or row followed by the same letter are not significantly different according to Duncan's Multiple Range Test at $P = 0.05$.

Table 2. Number of eggs per egg mass produced by four populations of *Meloidogyne incognita* (MI) on the roots of six cotton cultivars.

Cotton cultivars	Populations of *Meloidogyne incognita*			
	MI-534	MI-496	MI-506	MI-78
	Eggs per egg mass*			
CIM-534	377 DEF**	355 FG	389 CDE	367 EFG
CIM-506	275 I	289 I	401 BCD	323 H
CIM-496	499 A	415 BC	399 BCD	379 DEF
CIM-499	369 EFG	421 B	397 BCD	385 DE
CIM-707	273 I	351 FG	361 EFG	376 DEF
NIAB-78	77 J	99 J	101 J	345 GH

* Each mean for eggs per egg mass is an average of 10 egg masses.

** Means within each column or row followed by the same letter are not significantly different according to Duncan's Multiple Range Test at $P = 0.05$.

TABLE 3. Development and reproduction of four populations of *Meloidogyne incognita* (MI) in roots of cotton cv. NIAB-78.

Nematode populations	Stages of development			Reproduction factor [P_f/P_i]
	J2	J4	Adult females	
MI-534	135 a	81 b	69 b	2.06 c
MI-496	141 a	72 b	57 b	13.96 b
MI-506	128 a	71 b	60 b	16.35 b
MI-78	151 a	139 a	131 a	39.04 a

* Means within a column followed by the same letter are not significantly different according to Duncan's Multiple Range Test at $P = 0.05$.

were wider in diameter ($P = 0.05$) than those of avirulent MI-534. The egg mass, galling and reproduction indices (Ri) [Ri = (P_f on resistant cv. NIAB-78 / P_f on susceptible CIM-534) × 100] (Shepherd, 1979) for MI-78 and MI-534 differed between resistant and susceptible cultivars (Table 4). Gall indices for the virulent population were usually ($P = 0.05$) highest whether it was feeding on a resistant or susceptible cultivar.

At 5 d after inoculation, there was no observable variation in size of galls or giant cell formation regardless of the population inoculated. At later sampling dates, variability was noted in size of galls and giant cell formation when four different populations were inoculated to NIAB-78 (Table 4). Roots infected by the virulent MI-78 population developed larger galls, whereas those initiated by three other populations remained small throughout the duration of the experiment. Feeding sites within roots inoculated with the MI-78 population exhibited well developed giant cells. Feeding sites resulting from the MI-534 population were visibly underdeveloped, whereas sites infected by the other two populations were intermediate in size.

DISCUSSION

Root galling indices have been used to assess resistance of annual and perennial crops to root-knot nematodes (Marull et al., 1994; Stirling and Cirami, 1998, Zhou et al., 2000). However, root galling is not a satisfactory indicator of the durability of root-knot nematode resistance (McClure et al., 1974; Hussey and Boerma, 1981; Reed and Schneider, 1992; Zhou et al., 2000; Anwar and McKenry, 2002). In this experiment, we used egg mass number and number of eggs per egg mass to evaluate cotton cultivars against infection by four populations of *M. incognita*. These two parameters are better indicators of nematode reproduction than root galling (Luzzi et al., 1987; Hirunsalee et al., 1995; Jenkins et al., 1995; Ornat et al., 2001).

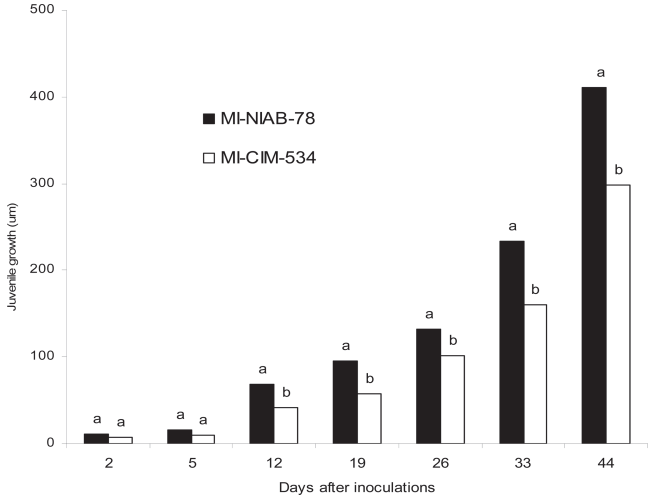

FIG. 1. Juvenile growth of two populations of *Meloidogyne incognita* (MI) on cotton cv. NIAB-78 at 2 to 44 days after inoculation. Data are means of 15 replications. Means on a given day after inoculation followed by the same letter are not different ($P \leq 0.05$).

Although similar numbers of J2 of MI-534, MI-496, MI-506 and MI-78 populations penetrated the roots of resistant NIAB-78 cotton, their further development from J2 to reproducing females was significantly limited (Table 4). Tang et al. (1994) reported that development of adult females depends on the ability of the penetrated J2 to initiate giant cells and stimulate formation of root galls. The presence of small giant cells and galls on roots of NIAB-78 infected by populations MI-534, MI-496 and MI-506 might be the result of arrested development, as the size of giant cells is related to the amount of food available. Similar numbers of J2 in roots of resistant and susceptible cotton cultivars indicate that genetically controlled barriers to root penetration had failed to halt the entry of J2 into the roots of resistant NIAB-78 cultivars. This also agrees with McClure et al. (1974) for investigations with Clevewilt-6–3-5, a source of moderate resistance.

Variability in reproduction among *M. incognita* populations on supposedly resistant cotton has already been documented (Ogallo et al., 1997; Zhou et al., 2000). In this study, the Mi-78 population multiplied equally well on all the cotton cultivars; however, three other populations, Mi-534, Mi-496 and Mi-506, did not reproduce well on NIAB-78 cotton. These latter three populations did, however, reproduce at high levels on the cotton cultivars with which they were originally associated in agricultural settings. This suggests that feeding history of each population is important. Similar observations have been reported among various populations of *Heterodera trifolii* (Wang and Riggs, 1999).

In this study, the MI-78 population exhibited the greatest virulence of the four populations and therefore provides a useful tool in our search for new, resistant cotton cultivars. Attributes of virulence within this population include the ability to develop greater numbers of females, higher fecundity rates (Table 3), better J2 growth (Fig. 1) and a higher reproduction index (Table 4).

Even on the most resistant of these cotton cultivars, there continues to be nematode feeding, giant cell formation, galling and reproduction. The fact that each of these populations was able to reproduce to some extent on each of the cotton cultivars deters us from concluding that any of them is resistant to root-knot. They sim-

TABLE 4. Reproduction of two populations of *Meloidogyne incognita* (MI) on roots of susceptible cotton cv. CIM-534 and resistant cv. NIAB-78.

M. incognita populations	Resistant cv. NIAB-78*			Susceptible cv. CIM-534			Reproduction index** [%]
	Eggs per root system	Index		Eggs per root system	Index		
		Egg-mass	Gall		Egg-mass	Gall	
Avirulent							
MI-534	2,378 b	1.5 b	1.6 b	55,751 a	5.0 a	5.0 a	4.3 b
Virulent							
MI-78	49,867 a	4.5 a	4.8 a	61,904 a	5.0 a	5.0 a	80.6 a

* Means within a column followed by the same letter are not significantly different according to Duncan's Multiple Range Test at $P = 0.05$.
** Reproduction index = P_f on resistant cv. NIAB-78 ÷ P_f on susceptible CIM-534) × 100.

ply exhibit significantly differing levels of resistance. We have also demonstrated in this study that in the short-term view there will be value to coupling the resistance in NIAB-78 with resistance sources that exhibit active resistance mechanisms as J2 enter root systems.

For the longer view, the search in Pakistan must be for broad and durable resistance to root-knot nematode. Breadth and durability of resistance being unavailable, a second option is to identify two or three completely different sources of resistance that can be rotated annually or biannually. In California, the value of NemX cotton has been that its resistance mechanisms have enough durability to last three successive years without rotation (Ogallo et al., 1999). The example of NemX cotton in California and elsewhere indicates the value of resistance mechanisms with durability. However, in the final analysis it is acceptable yields and resistance durability plus improved rotation strategies that will provide a sustainable agriculture.

LITERATURE CITED

Anwar, S. A., and Khan, I. U. 1973. Some studies on cotton wilt complex. Journal of Agricultural Research 11:94–98.

Anwar, S. A., and McKenry, M. V. 2000. Penetration, development and reproduction of *Meloidogyne arenaria* on two new resistant *Vitis* spp. Nematropica 30:9–17.

Anwar, S. A., and McKenry, M. V. 2002. Developmental response of a resistance-breaking population of *Meloidogyne arenaria* on *Vitis* spp. Journal of Nematology 34:28–33.

Baird, R. E., Davis, R. F., Alt, P. J., Mullinix, B. G., and Padgett, G. B. 1996. Frequency and geographical distribution of plant-parasitic nematodes on cotton in Georgia. Supplement to Journal of Nematology 28:661–667.

Bateman, R. J., Kirkpatrick, T. L., Robbins, R. T., and Lorenz, G. 2000. The distribution of root-knot and reniform nematodes in Arkansas, 1990–1999. Pp. 171 *in* Proceedings Beltwide Cotton Conference, San Antonio, TX, 5–8 January 2000. Cotton Council of America, Memphis, TN.

Bost, S. C., and Triantaphyllou, A. C. 1982. Genetic basis of the epidemiologic effects of resistance to *Meloidogyne incognita* in the tomato cultivar Small Fry. Journal of Nematology 14:540–544.

Bridge, J. 1992. Nematodes. Pp. 331–353 *in* R. J. Hillocks, ed. Cotton diseases. Walling Ford, UK: CSB International.

Byrd, D. P., Kirkpatrick, Jr., T., and Barker, K. R. 1983. An improved technique for clearing and staining plant tissues for detecting of nematodes. Journal of Nematology 15:142–143.

Carpenter, A. S., and Lewis, S. A. 1991. *Meloidogyne arenaria* populations on soybean. Supplement to Journal of Nematology 23:639–645.

Hartman, K. M., and Sasser, J. N. 1985. Identification of *Meloidogyne* species on the basis of differential hosts test and perineal pattern morphology. Pp. 69–77 *in* K. R. Barker, C. C. Carter, and J. N. Sasser, eds. An Advanced Treatise on *Meloidogyne*. Raleigh, NC: North Carolina State University Graphics.

Hirunsalee, A., Barker, K. R., and Beute, M. K. 1995. Infection, reproduction potential, and root galling by root-knot nematode species and concomitant populations on peanut and tobacco. Journal of Nematology 27:172–177.

Hoagland, D. R., and Arnon, D. I. 1950. The water-culture method for growing plants without soil. California Agricultural Experiment Station Circular 347:1–32.

Holbrook, C. C., Knauft, D. A., and Dickson, D. W. 1983. A technique for screening peanut for resistance to *Meloidogyne incognita*. Plant Disease 57:957–958.

Hussey, R. S., and Barker, K. R. 1973. Comparison of methods for collecting inocula of *Meloidogyne* spp., including a new technique. Plant Disease Reporter 57:1025–1028.

Hussey, R. S., and Boerma, H. R. 1981. A greenhouse screening procedure for root-knot nematode resistance in soybean. Crop Science 21:794–796.

Jenkins, J. N., Greech, R. G., Tang, B., Lawrence, G. W., and McCarty, J. C. 1995. Cotton resistance to root-knot nematode: II. Post-penetration development. Crop Science 35:369–373.

Kaloshian, I., Williamson, V. M., Miyao, G., Lawn, D. A., and Westerdahl, B. B. 1996. "Resistance-breaking" nematodes identified in California tomatoes. California Agriculture 50:18–19.

Kinlock, R. A., and Sprenkel, R. K. 1994. Plant-parasitic nematodes associated with cotton in Florida. Supplement to Journal of Nematology 26:749–752.

Luzzi, B. M., Boerma, H. R., and Hussy, R. S. 1987. Resistance to three species of root knot nematode in soybean. Crop Science 27: 258–262.

Maqbool, M. A. 1992. Distribution and host association of plant-parasitic nematodes in Pakistan. National Nematological Research Centre, University of Karachi, Karachi, Pakistan. Pp. 215.

Martin, S. B., Mueller, J. D., Saunders, J. A., and Jones, W. I. 1994. A survey of South Carolina cotton fields for plant-parasitic nematodes. Plant Disease 78:717–719.

Marull, J., Pinochet, J., Felipe, A., and Cenis, L. 1994. Resistance verification in *Prunus* selections to mixtures of thirteen *Meloidogyne* isolates and resistance mechanisms of a peach-almond hybrid to *M. javanica*. Fundamentals of Applied Nematology 17:85–92.

McClure, M. A., Ellis, K. C., and Nigh, E. L. 1974. Post-infection development and histopathology of *Meloidogyne incognita* in resistant cotton. Journal of Nematology 1:21–26.

McKenry, M. V. 1987. Control strategies in high-value crops. Pp. 329–349 *in* R. H. Brown and B. R. Kerry, eds. Principles and practice of nematode control in crops. Orlando: Florida Academic Press.

McKenry, M. V., and Roberts, P. A. 1985. Phytonematology Study Guide. University of California, Division of Agriculture and Natural Resources. Publication 4045.

Netscher, C. 1977. Observations and preliminary studies on the occurrence of resistance-breaking biotypes of *Meloidogyne* spp. on tomato. Cahiers ORSTOM Series Biologie 11:173–178.

Noe, J. P. 1992. Variability among populations of *Meloidogyne arenaria*. Journal of Nematology 24:404–414.

Ogallo, J. L., Goodell, P. B., Eckert, J., and Roberts, P. A. 1997. Evaluation of NemX, a new upland cotton cultivar with high resistance to *Meloidogyne incognita*. Journal of Nematology 29:531–537.

Ogallo, J. L., Goodell, P. B., Eckert, J., and Roberts, P. A. 1999. Management of root-knot nematodes with resistant cotton cv. NemX. Crop Science 39:418–421.

Ornat, C., Verdejo-Lucas, S., and Sorribas, F. J. 2001. Population of *Meloidogyne javanica* in Spain virulent to the *Mi* resistance gene in tomato. Plant Disease 85:271–276.

Orr, C. C., and Robinson, A. F. 1984. Assessment of cotton losses in western Texas caused by *Meloidogyne incognita*. Plant Disease 68:284–292.

Prot, J. C. 1984. A naturally occurring resistance-breaking biotype of *Meloidogyne arenaria* on tomato. Reproduction and pathogenicity in tomato cultivars: Roma and Rossol. Revue de Nematologie 7:23–28.

Quesenberry, K. H., Baltensperger, D. D., Dunn, R. A., Wilcox, C. J., and Hardy S. R. 1989. Selection for tolerance to root-knot nematodes in red clover. Crop Science 29:62–65

Reed, S. M., and Schneider, S. M. 1992. Evaluation of *Nicotiana otophora* as a source of resistance to *Meloidogyne incognita* Race 4 for tobacco. Journal of Nematology 24:253–256.

Roberts, P. A., Frate, C. A., Matthews, W. C., and Osterli, P. P. 1995. Interactions of virulent *Meloidogyne incognita* and *Fusarium* wilt on resistant cowpea genotypes. Phytopathology 85:1288–1295.

Shepherd, R. L. 1979. A quantitative technique for evaluating cotton for root-knot nematode resistance. Phytopathology 69:427–430.

Starr, J. L., Heald, C. M., Robinson, A. F., Smith, R. M., and Krause, J. P. 1993. *Meloidogyne incognita* and *Rotylenchulus reniformis* and associated soil texture from some cotton production areas of Texas. Supplement to Journal of Nematology 25:895–899.

Starr, J. L., and Veech, J. A. 1986. Comparison of development, reproduction and aggressiveness of *Meloidogyne incognita* races 3 and 4 on cotton. Journal of Nematology 18:413–415.

Stirling, G. R., and Cirami, R. M. 1998. Resistance and tolerance of grape rootstocks to South Australian populations of root-knot nematode. Australian Journal of Experimental Agriculture and Husbandry 24:277–282.

Swanson, T. A., and Van Gundy, S. D. 1984. Variability in reproduction of four races of *Meloidogyne incognita* on two cultivars of soybeans. Journal of Nematology 16:368–371.

Syndenham, G. M., McSorley, R., and Dunn, R. A. 1996. Effects of resistance in *Phaseolus vulgaris* on development of *Meloidogyne* species. Journal of Nematology 28:485–491.

Tang, B., Lawrence, G. W., Greech, R. G., Jenkins, J. N., and McCarty, J. C. 1994. Post-infection development of *Meloidogyne incognita* in cotton roots. Mississippi Agriculture and Forestry Experiment Station Technical Bulletin no. 195.

Wang, S., and Riggs, R. D. 1999. Variations in host preference among and within populations of *Heterodera trifolii* and related species. Journal of Nematology 31:407–417.

Williamson, V. M., and Hussey, R. S. 1996. Nematode pathogenesis and resistance in plants. Plant Cell 8:1735–1745.

Windham, G. L., and Barker, K. R. 1986. Relative virulence of *Meloidogyne incognita* host races on soybean. Journal of Nematology 18:327–333.

Zhou, E., Wheeler, T. A., and Starr, J. L. 2000. Root galling and reproduction of *Meloidogyne incognita* isolates from Texas on resistant cotton genotypes. Supplement to Journal of Nematology 32:513–518.