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Relationships Between Tolerance and Resistance to *Meloidogyne incognita* in Cotton[1]

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Abstract: The southern root-knot nematode, *Meloidogyne incognita,* is the most damaging pathogen of cotton in the United States, and both resistance and tolerance to *M. incognita* could be valuable management approaches. Our objectives were to evaluate advanced cotton breeding lines for resistance and tolerance to *M. incognita* and to determine if a relationship between resistance and tolerance exists. Reproduction of *M. incognita* was evaluated on 17 breeding lines, a susceptible control (Delta and Pine Land DP5415), and a resistant control (M-120) in two greenhouse trials with six replications in a randomized complete block design. Two-week-old seedlings were inoculated with 8,000 *M. incognita* eggs and assessed for egg production 8 weeks later. Reproduction on the resistant control was only 10% of that on the susceptible control. Eight breeding lines supported 45% to 57% less ($P \leq 0.05$) nematode reproduction than the susceptible control, and none of them were as resistant as M-120. Yield was determined in 2001 and 2002 in fumigated (1,3-dichloropropene at 56 liters/ha) and nonfumigated plots in a strip-plot design with three replications in a field naturally infested with *M. incognita.* Yield suppression caused by nematode infection differed among genotypes ($P \leq 0.05$ for genotype × fumigation interaction). Six genotypes in 2001 and nine in 2002 were tolerant to *M. incognita* based on no difference in yield between the fumigated and nonfumigated plots ($P \geq 0.10$). However, only three genotypes had no significant yield suppression in both years, of which two also were resistant to *M. incognita.* Regression analysis indicated that yield suppression decreased linearly as nematode resistance increased.

Key words: Gossypium hirsutum, Meloidogyne incognita, nematode management, southern root-knot nematode.

Resistance and susceptibility to plant-parasitic nematodes describe the effect of the plant on the nematode's ability to reproduce (Cook and Evans, 1987). Tolerance and intolerance describe the degree of damage, usually measured in terms of yield suppression, inflicted by the nematode on the plant (Cook and Evans, 1987). Both resistance and tolerance can be useful in managing plant-parasitic nematodes (McSorley, 1998; Potter and Dale, 1994; Reese et al., 1988; Seinhorst, 1970; Young, 1998). Resistance and tolerance may be expressed simultaneously, but they can be inherited and expressed independently resulting in plants that are resistant but intolerant or tolerant but susceptible (Barker, 1993; Boerma and Hussey, 1992; Cook and Evans, 1987; Evans and Haydock, 1990).

Tolerance to nematodes can be identified by comparing plant growth or yield in nematicide-treated and nontreated field plots (Cook and Evans, 1987). Tolerance to *Globodera pallida* and *G. rostochiensis* has been identified in potato, *Solanum tuberosum* (Arntzen and Wouters, 1994; Dale et al., 1988; Phillips et al., 1998; Trudgill and Coates, 1983; Trudgill et al., 1996), and nematode resistance and tolerance are inherited independently in potato (Arntzen et al., 1994; Evans and Haydock, 1990; Trudgill and Cotes, 1983). Tolerance to *Heterodera glycines* has been identified in soybean, *Glycine max* (Anand and Koenning, 1986; Boerma and Hussey, 1984; Hussey and Boerma, 1989; Miltner et al., 1991; Reese et al., 1988; Radcliffe et al., 1990), and it also shows independent inheritance from resistance (Boerma and Hussey, 1984; Boerma and Hussey, 1992). Tolerance to nematodes also has been identified in kenaf (*Hibiscus cannabinus*) (Cook and Mullin, 1994); pineapple (*Ananas comosus*) (Sipes and Schmitt, 1994); rice (*Oryza sativa*) (Soriano et al., 2000), *Prunus* spp. (Nyczepir, 1991); strawberry (*Fragaria* spp.) (Potter and Dale, 1994); and white clover (*Trifolium repens*) (Gibson, 1973). The tolerance observed in rice, pineapple, and kenaf appears to be independent of nematode resistance.

Cotton (*Gossypium hirsutum*) breeding lines with significant levels of tolerance to *Rotylenchulus reniformis* have been identified, and at least some of the tolerant lines are susceptible (Cook et al., 1997; Koenning et al., 2000). Though much effort has been focused on resistance to *M. incognita* in cotton (Cook et al., 1997; Ogallo et al., 1997; Robinson et al., 1999; Robinson et al., 2001; Shepherd, 1974, 1983), little work has been done to identify differing levels of tolerance. Some cotton cultivars are considered to be tolerant of *M. incognita,* but moderately resistant cotton cultivars were shown to be no more tolerant of *Meloidogyne incognita* than susceptible cultivars (Koenning et al., 2001). Our objectives were to evaluate germplasm lines in the University of Georgia cotton breeding program to document (i) the level of resistance to *M. incognita,* (ii) the level of tolerance to *M. incognita,* and (iii) the relationship between resistance and tolerance to *M. incognita.*

Materials and Methods

Greenhouse experiments: Nineteen cotton genotypes were evaluated for resistance to *M. incognita* race 3 in two greenhouse trials. Each trial had six replications in a randomized complete block design. Soil temperatures in the pots varied between 24 °C and 35 °C during

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the study. Delta and Pine Land DP5415 was used as a susceptible control treatment, and M-120 was used as a resistant control. Cotton seeds were planted into 15-cm-diam. pots on 8 April 2002 for trial 1 and on 6 May 2002 for trial 2. Seedlings were thinned to one plant per pot.

Inoculum was collected from tomato roots (*Lycopersicon esculentum* 'Rutgers') by agitating roots in 0.5% NaOCl for 2 minutes (Hussey and Barker, 1973) approximately 1 hour before inoculation. Nematode inoculum of 8,000 *M. incognita* eggs/pot (approximately 800 eggs/150 cm^3 soil) was added on 22 April 2002 for trial 1 and on 20 May 2002 for trial 2. Inoculum was distributed into two holes approximately 2.5 cm deep and covered with soil. Pots were watered immediately following inoculation.

Nematode eggs were extracted from all roots in a pot on 18 June for trial 1 and on 15 July for trial 2 (57 and 56 days after inoculation, respectively). Roots were washed free of soil, weighed, cut into 5-cm pieces, and agitated in a 1% NaOCl solution in a 1-liter flask for 4 minutes. Eggs were collected and rinsed with tap water on nested 150- over 25-µm-pore sieves. Egg counts were subjected to a square-root transformation to equalize the error variances prior to statistical analysis. Data from the two trials were pooled for a combined analysis of variance and means separation by Fisher's protected least significant difference ($LSD_{0.05}$). A genotype was designated resistant if fewer eggs were recovered from it than from DP5415, the susceptible control genotype.

Field experiments: Tolerance to *M. incognita* was measured in 2001 and 2002 in field experiments with three replications in a strip-plot design at the University of Georgia Lang Farm in Tifton, Georgia. The soil type was a Dothan sandy loam (fine loamy, kaolinitic, thermic Plinthic Kandiudults). The field was naturally infested with *M. incognita,* had been planted to cotton for several years prior to initiation of this study, and was known to have a high damage potential though few nematodes were recovered from soil samples collected prior to fumigation. The horizontal factor was genotype, and the vertical factor was fumigation treatment (nonfumigated or 1,3-dichloropropene [Telone II®, Dow AgroSciences, Indianapolis, IN] at 56 liters/ha). Eighteen genotypes were evaluated each year, and 17 genotypes were common to both years and to the greenhouse evaluations of reproduction. Delta and Pine Land DP5415 was included as a susceptible and intolerant control. All plots were tilled with a single sub-soil chisel per row with disks creating a raised bed above the chisel trace. In fumigated plots, 1,3-dichloropropene was applied behind the sub-soil chisel approximately 35 cm deep. Subplots consisted of two 12.2-m rows spaced 91 cm apart. All genotypes were planted at a higher-than-desired seeding rate and hand-thinned to 5 plants/60 cm of row. Plots were sprayed as necessary with acephate (Orthene® 75, Valent USA Corp., Walnut Creek, CA) at 0.20 kg a.i./ha for thrips control. All plots received fertilizer, insecticide, and herbicide as recommended by the University of Georgia Cooperative Extension Service (Brown et al., 2000). All plots were managed identically except for the genotype planted, which varied by treatment. Irrigation was applied as needed. Yield data were collected at harvest on 28 September 2001 and on 25 September 2002. Seed cotton from each plot was harvested and weighed, and lint yield was determined by ginning a boll sample from each plot and using the percent lint in the subsample to calculate a lint yield for the plot. Yield data were analyzed by strip-plot analysis of variance. An LSD value appropriate for the experimental design was calculated so that lint yield of each genotype in fumigated and nonfumigated plots could be compared.

Root galling was evaluated at harvest in 2002. Ten root systems from each plot were carefully excavated and examined. Gall ratings were assigned to each plant, and the mean value for each plot was used for statistical analysis. A 0-to-10 scale was used in which 0 = no galling, 1 = 1–10% of the root system galled, 2 = 11–20% of the roots system galled, etc., with 10 = 91–100%.

Soil samples for nematode analysis were collected from the field trials at cotton harvest (2 October 2001 and 4 October 2002). Soil samples consisted of a composite of 8 to 10 cores/plot (2.5-cm diam. and approximately 20 cm deep) collected from the root zone. Nematodes were extracted from 150 cm^3 soil by centrifugal flotation (Jenkins, 1964). Least significant difference values appropriate for the experimental designs and comparisons of interest were calculated.

The relationship between resistance (reproduction) and tolerance (yield suppression) was evaluated by regression analysis. Reproduction for each genotype was standardized as mean percent of the susceptible control (DP5415) based on reproduction data from the two greenhouse evaluations (12 observations/genotype). Tolerance was calculated for each genotype as mean percent yield suppression (yield difference between fumigated and nonfumigated plots divided by yield of fumigated plots) based on data from the two field trials (6 observations/genotype). A single pair of resistance and tolerance means for each genotype was calculated for the analysis from all available data to provide the most accurate estimates possible.

Results

Greenhouse experiments: Reproduction assessed as numbers of eggs per pot and per gram fresh root showed that eight genotypes were resistant to *M. incognita* compared to the susceptible control, DP5415 (Table 1). Reproduction on the resistant control, M-120, was reduced 90% compared to DP5415. Reproduction on the resistant genotypes was reduced by 45% to 57%. The eight resistant genotypes had similar levels of *M. incognita* reproduction, and none of them were as resistant

TABLE 1. Numbers of *Meloidogyne incognita* eggs produced on selected cotton genotypes in greenhouse tests.

Genotype	Resistance rating[a]	Eggs per pot[b]	Eggs/g fresh root[c]
GA97-5	susceptible	183,100 a	16,698 a
DP5415	susceptible	145,350 ab	13,712 ab
GA95-138	susceptible	131,550 bcd	12,298 bcd
GA96-77	susceptible	130,350 ab	11,757 abc
GA97-9	susceptible	122,325 abc	11,628 abc
GA97-14	susceptible	115,450 abc	10,619 abcd
GA97-8	susceptible	114,800 abc	8,549 bcde
GA97-23	susceptible	109,800 bcd	10,271 bcde
GA95-74	susceptible	109,200 bcd	9,525 bcde
GA97-25	susceptible	96,950 bcde	9,516 bcde
GA95-137	resistant	80,000 cde	7,494 cdef
GA95-251	resistant	76,200 cde	7,346 cdef
GA95-88	resistant	73,150 cde	7,550 cdef
GA96-66	resistant	71,300 cde	7,506 cdef
GA95-155	resistant	68,983 e	4,306 fg
GA96-100	resistant	68,150 de	6,941 def
GA96-211	resistant	67,000 de	5,762 ef
GA96-54	resistant	62,100 e	5,974 ef
M-120	resistant	14,400 f	1,831 g

[a] Genotypes significantly different from DP5415 according to Fisher's Protected $LSD_{(0.05)}$ are designated resistant.

[b] The experiment was conducted twice with six replications per entry, and data are pooled from the two experiments. Means followed by the same letter are not significantly different according to Fisher's Protected $LSD_{(0.05)}$. Statistical analysis of eggs/pot was performed on square-root transformed data, but the means presented are untransformed.

[c] Statistical analysis of eggs/gram fresh root was performed on square-root transformed data, but the means presented are untransformed.

as M-120. Fresh root weight of 16 of the breeding lines and of M-120 did not differ from that of DP5415, but GA95-155 had greater fresh root weight ($P \leq 0.05$). Eggs per gram fresh root varied among genotypes (Table 1), with M-120 having the fewest and GA97-5 having the most. Analysis of eggs per gram fresh root identified the same eight resistant genotypes (compared to DP5415) as the analysis based on the total number of eggs produced.

Field experiments: Strip-plot analysis of variance of the 2001 yield data identified a genotype × fumigation interaction ($P = 0.039$), indicating that the magnitude of difference in yield between fumigated and nonfumigated plots varied among the genotypes. Genotypes differed in their yield ($P = 0.0004$), and fumigation increased yield ($P = 0.015$). In 2001, LSD comparisons appropriate for a strip-plot design did not identify differences in yield between the fumigated and nonfumigated plots for seven genotypes ($P \leq 0.05$); six genotypes did not differ with $P \leq 0.10$ (Table 2). In 2002, nine genotypes had no difference in yield between fumigated and nonfumigated plots at both $P \leq 0.05$ and $P \leq 0.10$. The relative yields of the genotypes in nonfumigated plots were unrelated to the level of resistance measured in greenhouse studies, with resistant genotypes being distributed randomly throughout the range of yields (Table 2).

Nematode population densities in the soil at harvest in fumigated plots with the breeding lines did not differ ($LSD_{0.05}$) in either year from the densities in fumigated plots of DP5415. In contrast, all breeding lines except GA97-8 and GA97-25 had lower population levels than DP5415 in the nonfumigated plots in 2001, and GA95-138, GA97-14, GA95-137, GA95-251, GA96-66, GA95-155, GA94-894, GA96-100, and GA96-211 were lower in 2002 (Table 2). However, there was no genotype × fumigation interaction for nematode population levels at harvest in 2001 ($P = 0.501$) or 2002 ($P = 0.317$). Root-gall ratings taken in 2002 (Table 2) generally were consistent with soil population density data. Fusarium wilt was not observed in this study.

Regression analysis revealed a significant relationship between mean percent reproduction and mean percent yield loss (% yield suppression = 0.0021 × (% reproduction) − 0.0253) ($R^2 = 0.297$, $P = 0.024$) (Fig. 1). Predicted yield loss (−2.5%) for plants supporting no nematode reproduction (the regression intercept) was not significantly different from zero ($P = 0.68$).

DISCUSSION

Fumigation with 1,3-dichloropropene at 56 liters/ha did not provide season-long nematode suppression in either year of this study. However, 1,3-dichloropropene at 56 liters/ha should minimize yield suppression, and the difference in yields observed between DP5415 in fumigated and nonfumigated plots indicated that yield suppression was greatly reduced. Although fumigation treatment to reduce nematode populations usually does not produce a nematode-free environment, it should be sufficient for estimating tolerance (Cook and Evans, 1987). If a nematode-free environment could have been maintained throughout the season, the difference in yield between fumigated and nonfumigated plots may have been larger than indicated in this study, but it is unlikely that the conclusions would be different.

The reduction of *M. incognita* reproduction by 45% to 57% on resistant breeding lines in this study should be considered moderate or partial resistance (Hussey and Janssen, 2002). The source of *M. incognita* resistance in the breeding lines in our study was the highly resistant germplasm Auburn 623 RNR. Jenkins et al. (1995) proposed that a moderately resistant breeding line, M-78, derived from Auburn 623 RNR was only partially resistant because it had only one of the two resistance genes found in Auburn 623 RNR. Similarly, the breeding lines in this study may have only one of the resistance genes, though it is not known if all of the moderately resistant genotypes in this study have the same resistance gene(s).

Plants highly resistant to nematodes are often tolerant to nematodes as well because they have to endure significantly less parasitism than susceptible plants when exposed to the same soil population densities of nematodes (Evans and Haydock, 1990). However, even highly resistant plants may be intolerant if the mecha-

TABLE 2. Mean numbers of *Meloidogyne incognita* in soil, root-gall ratings, and lint yields of selected cotton genotypes at harvest in two field tests.

		2001		2002		
Genotype[a]	Nematicide treatment[b]	Lint (kg/ha)[c]	*M. incognita* (J2/150 cm^3 soil)	Lint (kg/ha)	*M. incognita* (J2/150 cm^3 soil)	Root-gall rating (0–10 scale)[d]
Susceptible						
GA97-5	Non-treated	1,050	369	1,398	203	6.4
GA97-5	Fumigated	1,335	243	1,675	27	4.1
DP5415	Non-treated	744	663	1,308	283	9.2
DP5415	Fumigated	922	287	1,641	170	5.6
GA95-138	Non-treated	935	261	1,380	100	3.4
GA95-138	Fumigated	1,174	155	1,691	70	1.6
GA96-77	Non-treated	1,102	40	1,258	267	9.3
GA96-77	Fumigated	1,313	149	1,411	177	5.1
GA97-9	Non-treated	1,211	285	1,043	150	7.8
GA97-9	Fumigated	1,465	329	1,539	160	3.2
GA97-14	Non-treated	1,093	199	1,294	93	6.4
GA97-14	Fumigated	1,209	199	1,563	93	3.7
GA97-8	Non-treated	832	427	1,372	143	6.9
GA97-8	Fumigated	1,165	505	1,394	43	4.5
GA97-23	Non-treated	1,126	280	1,363	120	6.5
GA97-23	Fumigated	1,320	496	1,474	100	5.8
GA95-74	Non-treated	1,131	173	1,253	120	5.5
GA95-74	Fumigated	1,373	67	1,522	67	6.4
GA97-25	Non-treated	1,108	399	1,262	147	6.9
GA97-25	Fumigated	1,193	180	1,246	80	5.0
Resistant						
GA95-137	Non-treated	1,143	127	1,321	60	2.2
GA95-137	Fumigated	1,284	92	1,081	47	2.0
GA95-251	Non-treated	1,078	187	1,210	37	4.7
GA95-251	Fumigated	1,136	57	1,600	110	2.6
GA95-88	Non-treated	851	164	1,129	193	4.5
GA95-88	Fumigated	1,034	132	1,373	13	2.3
GA96-66	Non-treated	1,317	204	1,183	67	3.3
GA96-66	Fumigated	1,363	176	1,478	27	1.2
GA95-155	Non-treated	—[e]	–[e]	1,325	27	1.8
GA95-155	Fumigated	—[e]	—[e]	1,306	40	0.8
GA94-894	Non-treated	1,035	340	—[e]	—[e]	—[e]
GA94-894	Fumigated	1,409	225	—[e]	—[e]	—[e]
GA96-100	Non-treated	1,258	141	1,269	67	4.9
GA96-100	Fumigated	1,329	61	1,295	140	1.4
GA96-211	Non-treated	1,113	182	1,390	80	3.3
GA96-211	Fumigated	1,038	132	1,387	43	1.8
GA96-54	Non-treated	1,106	167	1,277	127	2.5
GA96-54	Fumigated	1,536	152	1,329	120	0.9
	$LSD_{(0.05)}$	152.0[f]	281.3[h]	209.6	164.0	3.74
	$LSD_{(0.10)}$	117.4[g]	233.0[i]	161.8	135.7	3.09

[a] Genotypes ranked according to egg production levels in Table 1.
[b] Non-treated or fumigated with 1,3-dichloropropene at 56 liters/ha.
[c] Actual lint yield after ginning.
[d] 0 = no galling, 1 = 1–10% of root system galled, 2 = 11–20% galled, etc., 10 = 91–100% galled. Gall ratings are for 2002 only.
[e] Not tested.
[f] $LSD_{(0.05)}$ for comparing the fumigated and non-fumigated means from three replications of a single genotype.
[g] $LSD_{(0.10)}$ for comparing the fumigated and non-fumigated means from three replications of a single genotype.
[h] $LSD_{(0.05)}$ for comparing two genotype means from three replications within a fumigation treatment.
[i] $LSD_{(0.70)}$ for comparing two genotype means from three replications within a fumigation treatment.

nism of resistance is a strong, localized hypersensitive response that causes root necrosis (Roberts, 1992), as is the case with sugar beet (*Beta vulgaris*) with resistance to *H. schachtii* derived from *B. procumbens* (McFarlane et al., 1982). Intolerant plants may appear to be resistant if nematode feeding reduces the amount of root tissue, thereby reducing potential nematode feeding sites (Young, 1998). Because host plant resistance can affect plant tolerance to nematodes, resistant plants should be evaluated for nematode tolerance (Roberts, 1992). The mechanism of resistance in the breeding lines in our study may be the same as in Auburn 623 RNR, but it is not clear if the mechanism of resistance imparted by genes from Auburn 623 RNR is a hypersensitive response (Jenkins et al., 1995). There was no indication in our study of significant root deterioration or reduc-

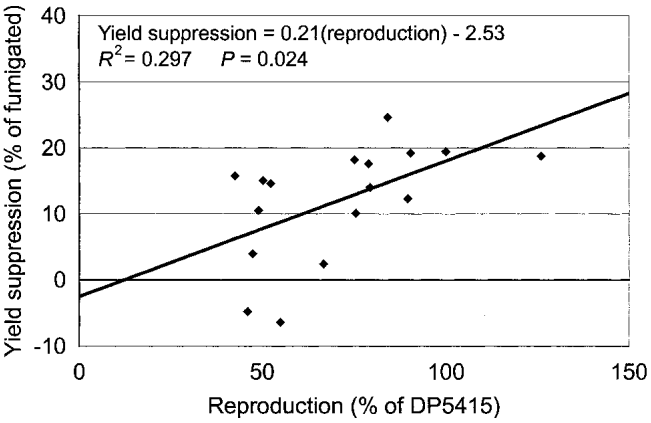

FIG. 1. Relationship of yield suppression and *Meloidogyne incognita* reproduction on selected cotton genotypes. Each data point is a mean value for a single genotype from two tests (12 observations for reproduction and 6 observations for yield suppression).

tion in the amount of root tissue, so it is unlikely that resistance resulted in intolerance or that intolerance caused the observed resistance.

Regression analysis in our study indicated that as the level of resistance increases and fewer nematodes are able to complete their life cycle, the level of nematode tolerance increases. This relationship between resistance and tolerance may be considered analogous to a damage function relating nematode population density and damage. However, a low R^2 value (0.297) suggests that other factors were also affecting the level of tolerance exhibited. Though there was a linear relationship between resistance and tolerance in the genotypes studied, there was a wide range of tolerance expressed among the moderately resistant genotypes. Such variability in tolerance might be influenced by host plant genetics or by variation in nematode population densities, environmental stress, soil fertility, or other factors that can affect yield. Tolerance levels of genotypes with similar gall ratings and resistance levels could differ if galling on one genotype were somehow more disruptive of root function. The mechanism of *Meloidogyne* tolerance in cotton is not known beyond that which can be predicted by nematode resistance.

From a practical cotton-breeding perspective, selecting lines that have the lowest percent yield suppression in field trials will probably select plants that express *M. incognita* resistance. However, this method may not lead to selection of the lines that have the highest level of resistance. In our study, GA97-25 had consistently low yield suppression even though other genotypes had higher levels of resistance. Selecting genotypes that have the highest yield in infested fields instead of selection based on percent yield suppression probably would not select either resistant or tolerant genotypes. In both years of the field study in Tifton, mean yield in nontreated plots had no relation to the level of resistance or tolerance. Therefore, a breeding program to select resistant and tolerant genotypes must actually measure resistance and tolerance and cannot base selection solely on yield potential in infested fields.

Nematode population densities in the soil at harvest generally were consistent with root-gall ratings, but designating genotypes as resistant based on gall ratings is faster, easier, and probably more accurate. Gall ratings are used widely as an initial screen in breeding programs and should identify the most resistant and susceptible genotypes, but designations based on galling should be verified in more precisely controlled greenhouse studies.

Nematicide use may still be beneficial with moderately resistant cotton cultivars when nematode population levels are above the damage threshold (Koenning et al., 2001). Yield of the moderately resistant cotton cultivar Stoneville LA 887 was increased by nematicide application in an *M. incognita*-infested field (Colyer et al., 1997). Some of the moderately resistant breeding lines in our study had improved yields when a nematicide was used, but more tolerant breeding lines such as GA97-25, GA96-100, and GA96-211 consistently showed no increase when treated with nematicides at the nematode densities encountered in this study. Incorporating that level of tolerance into cultivars should result in improved profits for growers. However, even moderately resistant genotypes would be expected to have suppressed yields at higher nematode population densities or if Fusarium wilt is present. Use of resistant and tolerant varieties may require modification of existing damage thresholds.

Moderate nematode resistance should contribute to nematode management, especially when combined with nematode tolerance. For example, two alfalfa germplasms were released that exhibited superior performance in *Pratylenchus penetrans*-infested fields; the germplasms supported 20% to 30% fewer nematodes per gram of fresh root (moderate resistance) and exhibited tolerance (Barnes et al., 1990). Moderately resistant cultivars may be most valuable if they reduce nematode reproduction enough to affect the residual nematode population density in a field. The benefits of crop rotations that include *Meloidogyne*-resistant cotton have been shown previously (Ogallo et al., 1999). Cotton often is grown without crop rotation for many years, and growth of cultivars with moderate resistance for several consecutive years may affect the nematode damage potential in such fields.

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