JOURNAL OF NEMATOLOGY

VOLUME 39 DECEMBER 2007 NUMBER 4

Journal of Nematology 39(4):283–294. 2007.

The Future of Nematode Management in Cotton

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Abstract: The importance of plant-parasitic nematodes as yield-limiting pathogens of cotton has received increased recognition and attention in the United States in the recent past. This paper summarizes the remarks made during a symposium of the same title that was held in July 2007 at the joint meeting of the Society of Nematologists and the American Phytopathological Society in San Diego, California. Although several cultural practices, including crop rotation, can be effective in suppressing the populations of the important nematode pathogens of cotton, the economic realities of cotton production limit their use. The use of nematicides is also limited by issues of efficacy and economics. There is a need for development of chemistries that will address these limitations. Also needed are systems that would enable precise nematicide application in terms of rate and placement only in areas where nematode population densities warrant application. Substantial progress is being made in the identification, characterization and mapping of loci for resistance to *Meloidogyne incognita* and *Rotylenchulus reniformis.* These data will lead to efficient marker-assisted selection systems that will likely result in development and release of nematode-resistant cotton cultivars with superior yield potential and high fiber quality.

Cotton (*Gossypium hirsutum*) is the most important fiber crop in the world, and current lint production in the US accounts for nearly one quarter of world supply. The land devoted to cotton production in the US peaked in 1926 at approximately 18 million hectares. The advent of mechanized farming and the availability of effective, relatively low-cost fertilizers, pesticides and improved cotton cultivars after World War II allowed the production of significantly greater yields per unit area and total hectares planted declined. United States production of cotton lint in the past 5 years has varied from 3.0×10^9 kg to 4.4×10^9 kg from approximately 5 million hectares. Additionally, cotton seed is a valuable source of vegetable oil, ruminant animal feed and other feed products.

Since World War II, cotton cultivation has been increasingly dependent on inputs of pesticides for weed and insect control. Historically, the cotton boll weevil, *Anthonomus grandis*, was the most costly pest of cotton in the US. Until recently, the combination of crop loss due to this insect directly and the expense of insecticides for control amounted to several billion dollars annually. The success of the Boll Weevil Eradication Program coordinated by the US Department of Agriculture has resulted in a major reduction in insecticide usage and improved profitability for growers and has led to a resurgence of cotton production in the southeastern US. In addition, the widespread use of transgenic cotton cultivars (currently 92.7% of the crop) with resistance to herbicides and/or lepidopteran insects has further reduced total pesticide usage on the crop (USDA-Agricultural Marketing Service, 2007). Reductions in losses from weeds and insects as a result of the deployment of transgenic traits and the boll weevil eradication program have allowed the cotton industry to focus on other pest problems, especially nematodes.

Modern cotton production in the US is intensive, highly mechanized and dependent on a local infrastructure to support this industry. Equipment for cotton harvesting and lint processing, including cotton pickers, modules for storing seed cotton, and gins, are highly specialized and generally not used for other crops. The necessity of an exclusive infrastructure to support cotton production has two important implications: (i) cotton is frequently grown in monoculture, and (ii) cotton typically has a greater impact on local economies than grain crops because of the jobs created to serve the industry.

The damage potential of plant-parasitic nematodes to cotton has been recognized since the late 19th century. Classic work by Atkinson demonstrated the pathogenicity of *Meloidogyne incognita* to cotton and the role of this nematode in Fusarium wilt of cotton (Atkinson, 1892, 1899). Plant-parasitic nematodes, however, received only limited study as cotton pathogens until the 1950s. Currently, the four most damaging species of plant-parasitic nematodes affecting cotton in the US are the southern root-knot (*Meloidogyne incognita*), reni-

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Received for Publication November 19, 2007.

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This manuscript is a summary of information presented in a symposium at the joint APS/SON meetings in San Diego, CA 31 July 2007. The authors are grateful to all persons who have shared their data with us for presentation in that symposium and in this manuscript. This work was supported in part by cooperative research agreements from Cotton Incorporated (to AFR, PAR, JLS) and a University of California Discovery Grant (to PAR).

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This paper was edited by David Bird.

form (*Rotylenchulus reniformis*), Columbia lance (*Hoplolaimus columbus*) and sting (*Belonolaimus longicaudatus*) (Blasingame, 1993; Koenning et al., 1999; Starr et al., 2005; Blasingame, 2006). Estimated losses of cotton lint yield by these pathogens in the US have increased from 1% to 2% in the 1950s to more than 4% in 2000 (Blasingame, 2006). This increase in estimated losses due to plant-parasitic nematodes can be attributed to several factors: (i) the lack of resistant cultivars, (ii) limited use of crop rotation in many areas, (iii) increased awareness of pathogenic nematodes as production constraints, especially the reniform nematode, (iv) the loss of highly effective, low-cost, fumigant nematicides, and (v) a recent increase in cotton production in the southeastern US.

MANAGEMENT BY CULTURAL PRACTICES

In modern cotton production, cultural practices often have limited use in suppressing nematode population densities and minimizing yield losses. Crop rotation, growing non-host, resistant or antagonistic cover crops, incorporation of plant materials or animal manures, and destruction or removal of cotton stalks and roots to minimize nematode survival and reproduction have been investigated (Barker and Koenning, 1998; Davis et al., 2000, 2003; Koenning et al., 2003a, 2003b). Crop rotation, perhaps the most widely used cultural means of limiting nematode populations, requires sufficient suitable land for the production of alternate crops that are non- or poor hosts to the nematode species in question. For rotation crops to be practical, alternative crops also must provide an adequate income to the grower and result in sufficient yield increases in a subsequent cotton crop to justify removing land from cotton production. Selection of a crop for a rotation with cotton must be done on the basis of the nematode species that is present.

Peanut (*Arachis hypogaea*) is a nonhost for *H. columbus, M. incognita* and *R. reniformis* and provides an attractive rotational crop for managing these nematodes in parts of the US where peanut is grown (Koenning et al., 2004). Similarly, tobacco (*Nicotiana tobacum*) can be used effectively in rotation with cotton for suppression of *H. columbus* and *B. longicaudatus* population densities where this crop is economically feasible (Robbins and Barker, 1973; Fassuliotus, 1974). Corn (*Zea mays*) and grain sorghum (*Sorghum bicolor*) are generally susceptible to *M. incognita*, whereas soybean (*Glycine max*) cultivars vary from highly susceptible to immune (Hussey, 1977). Vegetable crops, in general, and tobacco should not be included in rotations with cotton where management of root-knot or reniform nematode is the primary objective. In contrast to *M. incognita, R. reniformis* has little or no reproduction on grain crops such as corn or grain sorghum (Robinson et al., 1997). Reniform nematode-resistant soybean cultivars and winter grain crops can be included in rotation with cotton to reduce the population density of *R. reniformis* and improve cotton yield (Fig. 1) (Davis et al., 2003). Rotation for suppression of reniform nematode with nonhost crops, however, is only effective for one year. Rotation is not generally an option in fields infested with *H. columbus* because many crops typically grown in the same region as cotton are susceptible to this nematode (Fassuliotus, 1974). All corn and soybean cultivars tested were excellent hosts for *H. columbus.* Peanut and tobacco can be used in rotation with cotton to achieve reductions in the population density of *H. columbus.* Only tobacco is considered to be resistant to *B. longicaudatus,* although some vegetables such as watermelon (*Citrullus vulgaris*) allow only limited reproduction. Populations of *B. longicaudatus* have been reported to vary in their ability to reproduce on peanut (Robbins and Barker, 1973). Vegetable or other crops may actually be grown in the same year as cotton in the southernmost areas of the US, and cotton is severely affected by *B. longicaudatus* in Florida following potato (*Solanum tuberosum*) (Crow et al., 2000).

Tillage has long been recommended as a means of incorporating crop residue and for destruction of residual roots. This may be especially important for cotton because it is a perennial that can support reproduction of plant-parasitic nematodes when soil temperatures remain above the nematode's activity threshold for extended periods following harvest of the crop. Destruction of cotton root systems or removal with a stalk puller, however, had only a minimal effect on population densities of *H. columbus* and did not increase the yield of subsequent cotton crops (Davis et al., 2000; Koenning et al., 2003a). In-row subsoiling and/or some other form of deep tillage appear to be necessary to optimize yields in fields infested with lance nematodes if a soil hardpan is present (Fig. 2) (Hussey, 1977). Deep tillage allows the tap roots to reach the clay layer where higher levels of water and nutrients are present than in the sandy top soils of the coastal plain. Many farmers, however, have adopted reduced tillage practices that eliminate or restrict routine subsoiling. The

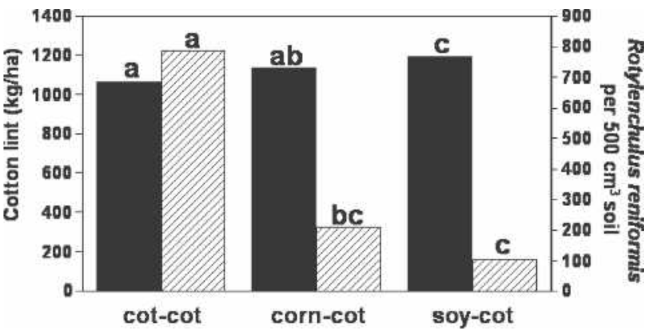

FIG. 1. Effects of rotation with a soybean cultivar resistant to *Rotylenchulus reniformis,* (soy-cot), non-host corn (corn-cot), or continuous cotton (cot-cot) on cotton lint yield and initial population densities of *R. reniformis* (Davis et al., 2003).

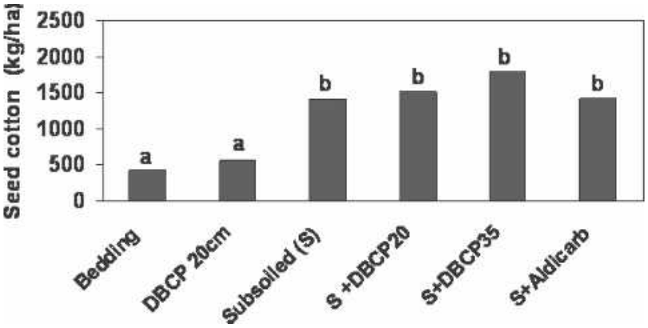

FIG. 2. Influence of tillage practices on cotton lint yield in the presence of *Hoplolaimus columbus* in field plots (Hussey, 1977). Bedding (conventional bed), 10 kg/ha 1, 2-dibromo-3chloropropane (DBCP) injected 20 cm deep, subsoiled (S), subsoiled plus DBCP injected 20 or 35 cm deep or aldicarb at 0.8 kg/ha (S + DBCP20, S + DBCP35, S+Aldicarb).

impact of reduced tillage practices on population densities of nematodes parasitic on cotton is not known.

Additional cultural practices that have been suggested for suppressing nematode population densities include planting date, the use of organic amendments, and cover crops. Unfortunately, little information is available on the effects of planting dates on cotton nematode populations. Later spring planting dates for Upland cotton in California were found to lessen the root-knot nematode infection potential and the extent of Fusarium wilt symptoms in infested fields (Jeffers and Roberts, 1993). Cotton planting date had no impact on *H. columbus* in North Carolina, and planting dates are not flexible enough in many areas because of the relatively long season needed to produce cotton (Koenning et al., 2003b). Application of poultry litter at rates suppressive to *M. incognita* or *H. columbus* may be impractical or exceed environmental regulations (Riegel et al., 1996; Koenning et al., 2003b). Winter cover crops, particularly the small grains wheat (*Triticum aestivu*m), rye (*Secale cereale*) and oats (*Avena sativa*), are commonly used in the southeast to prevent soil erosion, but their impact on plant-parasitic nematodes in cotton is controversial. Incorporation of cover crop residues improves water retention in sandy soils, and decomposing residues of rye may be toxic to nematodes (Barker and Koenning, 1998). However, many winter cover crops, including small grains, are hosts for *M. incognita*, *H. columbus* and *B. longicaudatus*, but generally not for *R. reniformis.* Winter wheat or rye cover crops had no impact on population densities of *H. columbus* in Georgia, and only limited information is available about the influence of small grains on southern root-knot and sting nematodes (Davis et al., 2000). A winter rye cover crop suppressed winter weeds in North Carolina that were hosts for *R. reniformis*, thus minimizing reproduction of this nematode during winter periods (unpublished, S. R. Koenning). Although small grain winter cover crops are hosts for many nematode species, in most instances nematode reproduction is suppressed by low soil temperatures. In California, wheat planted in soils with temperatures above 18°C supported reproduction of *M. incognita*, whereas the decline of this nematode did not differ between fallow soil and wheat planted after soil temperatures were below 18°C (Roberts et al., 1981). In the coastal plain soils of the eastern and gulf coast states where *H. columbus* and *B. longicaudatus* are most common, the impact of cover crops would be expected to have variable effects on nematode population densities based on local soil temperatures, sowing date and time of destruction of the cover crop.

MANAGEMENT WITH NEMATICIDES

With only a limited number high yielding nematode-resistant cultivars available and the economic and practical limitations to crop rotation, nematicides continue to be the primary means of managing nematodes in cotton in the US. Practical use of nematicides actually began after WWI, driven by the need to dispose of large quantities of surplus chloropicrin that remained at the close of the war (Johnson and Godfrey, 1932). The concept of applying a volatile material such as chloropicrin to the soil for control of soilborne pests was targeted originally for high value crops, but the success of these treatments was instrumental in focusing attention on the importance of nematodes as plant pests (Johnson and Feldmesser, 1987). By the time the surpluses were exhausted, the concept of soil fumigation as a practical means of nematode control had become established, and a search for more effective and convenient materials was underway, leading to the discovery of the nematicidal properties of the mixture of 1,3-dichloropropene and 1,2-dichloropropane (Carter, 1943) and of ethylene dibromide (Christie, 1945). The discovery of 1,2-dibromo-3-chloropropane in 1954 (McBeth, 1954; Raski, 1954) increased the interest in the application of nematicides to cotton because it was less phytotoxic than other fumigants and was easier to apply.

Although fumigant nematicides were highly effective, the difficulty and expense required for application and safety and environmental concerns associated with their use limited their utility in cotton. During the 1960s, two new classes of chemicals, the organophosphates and the carbamates, were synthesized and screened primarily in a search for more effective insecticides. They were soon recognized as having nematicidal activity (Christie and Perry, 1958; Weiden et al., 1965). Many of the individual chemicals in both classes were much less phytotoxic than most fumigants, and they were active against nematodes in the soil either in their original form or initial degradation products. These insecticide/nematicides rapidly gained in popularity because they could be applied to the soil at planting using relatively simple equipment and they were considerably less expensive than soil fumigants. One of these materials, aldicarb, has been the most widely used nematicide in cotton in the US for more than 20 years (Koenning et al., 2004).

Currently, there are three basic strategies for nematode management using nematicides in the US (Koenning et al., 2004). The most widely used strategy consists of the application of aldicarb at rates of 0.8–1.2 kg/ha in the planting furrow. A second, more expensive strategy is preplant soil fumigation using either 1,3-dichloropropene or metam-sodium. A third strategy is the supplemental use (in addition to an at-planting application of aldicarb) of either aldicarb applied as a side-dress during the first third of the season, or a foliar application of the carbamate oxamyl (Lawrence and McLean, 2000, 2002). The popularity of these strategies varies across the country. At-planting application of aldicarb is perhaps the most universal nematicide strategy in the US and is applied on 20% to 30% of the cotton hectarage each year (Koenning, et al., 2004), whereas soil fumigation is most common in the southeastern states.

Recently, the concept of applying a low concentration of nematicides as a seed dressing has shown promise in protecting emerging roots from nematode infection for a limited period of time (Monfort et al., 2006). Abamectin, one of a number of avermectins produced by *Streptomyces avermictilus* (Putter et al., 1981), received registration for use on cotton in 2006. A second compound, thiodicarb, was registered for use as a seed-treatment nematicide in 2007. Protection of developing roots during the first few days or weeks after germination may be critical to the establishment of optimum yield potential (Penteado et al., 2005). However, seed treatment alone may not be sufficient to provide protection from nematode damage to cotton plants in fields with high population densities of economic nematode species.

Biorational approaches to nematode control have not been thoroughly explored in cotton production systems. Harpin, a protein from *Erwinia amylovora* (Wei and Beer, 1996) that may elicit a systemic acquired resistance (SAR) response in certain plants, has been suggested as a way to mitigate nematode infection in cotton. Although laboratory investigations have shown promise, yield in field trials has been disappointing (Bednarz et al., 2002). A second material, acibenzolar-S-methyl, also induces SAR and enhances resistance to certain fungal pathogens (Allen et al., 2004), but its efficacy against nematodes has not been studied.

In the absence of significant new chemical nematicides, improved precision in utilizing existing materials may enhance crop profitability and environmental stewardship. Of particular interest is the adaptation of precision agriculture technology to more effective placement of nematicide within fields rather than the current practice of applying a single rate of nematicide field-wide (Evans et al., 2002). Accurately determining the spatial variability of most nematode species of concern in cotton has been an impediment to practical adoption of this concept (Wheeler et al., 1999; Wrather et al., 2002; Wyse-Pester et al., 2002). However, ongoing investigations using aerial imagery and/or measurable edaphic factors, such as soil electrical conductivity, may lead to improved strategies both for mapping nematode population distribution within fields and in site-specific delivery of nematicides to specific problem areas (Wolcott et al., 2006; Monfort et al., 2007; Overstreet et al., 2007).

Until effective nematode-resistant cotton cultivars or other tools for mitigating nematode damage in cotton are available, nematicide application is likely to remain a cornerstone of nematode management in cotton in the US. Escalating production costs and heightened environmental and health concerns make it imperative that more sustainable and profitable strategies for nematode control with nematicides are developed.

MANAGEMENT WITH HOST RESISTANCE

Among the nematode management strategies in cotton, host-plant resistance has great potential to be an economic and highly effective approach. The use of resistant cultivars is easy to implement and risk-free to use compared to nematicides and more predictable in effect than cultural tactics such as multi-year rotations. Because resistance in cotton suppresses nematode reproduction resulting in reduced nematode population densities (Fig. 3), resistant cotton cultivars have the added advantage of being able to protect susceptible crops grown in rotation (Ogallo et al., 1999). A primary challenge for advancing nematode resistance implementation in cotton is introducing effective resistance into elite cotton cultivars. Cotton breeding programs have had only moderate success in attaining this goal, in large part because the genetics of the resistance is complicated and the phenotyping protocols are diffi-

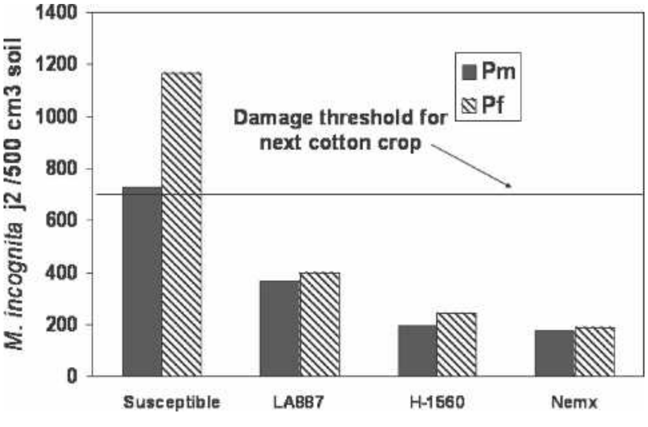

FIG. 3. Influence of resistant cotton cultivars Acala NemX, LA 887 and H1560 on midseason and final population densities of *M. incognita* compared to susceptible cotton cultivars Deltapine 90, Deltapine 51 and Suregrow 125 in North Carolina (Koenning et al., 2001).

cult, time-consuming and expensive. The heavy reliance on nematicides over the last several decades has also influenced priorities for cotton breeders. Consequently, many cotton improvement programs, especially in the private sector, have not placed emphasis on nematode resistance until recently. Further, no resistance to *B. longicaudatus* or *H. columbus* has been reported in cotton germplasm collections.

Resistance to Rotylenchulus reniformis: *Rotylenchulus reniformis* is an increasing problem in cotton production in the eastern half of the US cotton belt (Gaur and Perry, 1991; Lawrence and McLean, 2001; Starr et al., 2005). It is estimated to cause annual losses of approximately $130M, with major impact in the states of Mississippi, Louisiana and Alabama (Koenning et al., 2004; Blasingame, 2006; Robinson, 2007). Reniform nematode reproduction as a measure of resistance has been evaluated on more than 3,000 accessions of the genus *Gossypium* to discover sources of resistance (Carter, 1981; Yik and Birchfield, 1984; Beasley and Jones, 1985; Muhammad and Jones, 1990; Stewart and Robbins, 1995, 1996; Robinson and Percival, 1997; Robinson et al., 1999, 2001; Robinson, 2002; Robinson et al., 2004, 2006; Weaver et al., 2007). Only weak to moderate resistance has been reported in *G. hirsutum*, but high to very high levels of resistance have been found in other *Gossypium* species, including *G. anomalum*, *G. arboreum*, *G. barbadense*, *G. herbaceum*, *G. longicalyx*, *G. raimondii*, *G. somalense*, *G. stocksii* and *G. thurberi* (Yik and Birchfield, 1984; Stewart and Robbins, 1995; Robinson et al., 2004).

Reniform nematode resistance in accessions of *G. barbadense*, which hybridizes freely with *G. hirsutum*, usually suppresses nematode populations by approximately 70% to 90% (Robinson et al., 2004). In contrast, many accessions of *G. arboreum*, from which genes are introgressed via bridging species, are highly resistant to the reniform nematode (Stewart and Robbins, 1995), and the most resistant *G. arboreum* accessions suppress nematode reproduction by 95% or more compared to susceptible *G. hirsutum*. As the extreme case, *G. longicalyx*, from which genes can be transferred only with great difficulty, is virtually immune to *R. reniformis*. This apparent inverse relationship between compatibility with *G. hirsutum* and resistance within *Gossypium* greatly confounds strategies and funding for developing resistant cultivars.

About 20 *G. hirsutum* accessions with weak to moderate levels of resistance to the reniform nematode have been reported. Resistance within *G. hirsutum* appears highly sensitive to environment and/or nematode population. Resistance that was reproducible in one environment has not been observed consistently in a different environment or against a different population of reniform nematode. Seven accessions scored by Yik and Birchfield (1984) in replicated experiments as moderately resistant were later scored by Robinson et al. (1997) as susceptible, because in the latter study they supported 17- to 64-fold increases in nematode populations within a 7-week period. Of six primitive *G. hirsutum* accessions scored by Robinson et al. (2004) as moderately resistant, only TX1828 and TX 1586 also were classified by Weaver et al. (2007) as resistant. Of six accessions observed by Weaver et al. (2007) to consistently support lower nematode populations than the control, only TX 1565 had been scored as possibly resistant by Robinson et al. (2004). In some cases, moderately to highly resistant primitive accessions of *G. hirsutum* from the USDA Cotton Collection have been found to have flower and leaf traits similar to those of *G. barbadense*. Thus, the question remains as to whether some of the resistant accessions in this collection are *G. hirsutum* or *G. barbadense*. Nonetheless, several breeding efforts are in progress to develop cotton cultivars with improved levels of resistance to the reniform nematode from these various sources of resistance.

Comparison of reniform nematode reproduction on 850 accessions of *G. barbadense* and 1,419 of *G. hirsutum* (Robinson et al., 2004) clearly showed that although there is great variation in the ability of accessions in both species to support reniform nematode reproduction, susceptible *G. barbadense* accessions on average supported less reproduction than most *G. hirsutum* accessions and useful levels of resistance were more common in *G. barbadense*. In *G. barbadense*, 2.1% of the accessions supported less than one-third the reniform nematode reproduction of the susceptible cultivar Deltapine 16, compared with 0.4% of the *G. hirsutum* accessions (Fig. 4) (Robinson et al., 2004).

Current efforts (C. W. Smith and J. L. Starr, unpublished data) with progeny from a cross between root-knot nematode-resistant *G. hirsutum* M-315 RNR and reniform nematode-resistant *G. barbadense* TX 110 (Yik and Birchfield, 1984) show promise. Numerous F_1 plants tested separately against *M. incognita* and *R. reniformis* had resistance equivalent to the resistant parent, suggesting dominant inheritance of resistance to each nematode. Based on failure of an F_2 population to fit either a one- or a two-gene model, resistance to *R. reniformis* was assumed to be a polygenic trait. Using a pedigree breeding program, several lines were advanced to the F_7 generation with selection for nematode resistance in several generations. Three lines have resistance to both root-knot (data not shown) and reniform nematodes (Fig. 5A). In a single test for seed cotton yield, all of the nematode-resistant selections had yields that were slightly better than M-315 RNR but not equal to those of three high-yielding cultivars (Fig. 5B).

USDA scientists in Texas and Mississippi are working to introgress resistance from *G. barbadense* GB-713 into several root-knot nematode-resistant breeding lines as well as the once extensively planted susceptible cultivar Deltapine 16. GB-713 was by far the most resistant *G.*

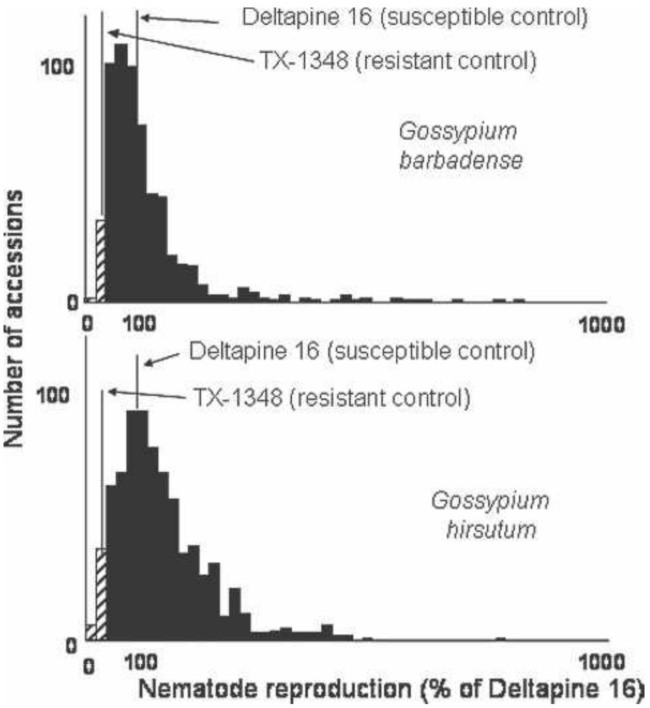

FIG. 4. Frequency of accessions with resistance to *Rotylenchulus reniformis* among accessions of *Gossypium barbadense* and *G. hirsutum* (Robinson et al., 2004).

barbadense accession identified in an extensive evaluation of *G. barbadense* in the USDA Cotton Collection (Robinson et al., 2004), consistently suppressing reniform nematode reproduction by 90% to 98% compared to Deltapine 16. Preliminary analysis of parental, F_1, F_2 and BC_1F_1 populations using SSR markers identified three markers linked to the resistance locus. Nematode reproduction on F_1 plants was uniform and intermediate between that on the two parents. Generation means analysis of nematode reproduction data from parents, F_1, F_2 and BC_1F_1 populations indicated genetic control by a single partially dominant gene with additive effects (Robinson, unpublished data). Thus inheritance indicated the trait was amenable to backcrossing into a root-knot nematode-resistant recurrent parent by selecting for resistance to reniform but not root-knot in progeny from each generation. It may be necessary to self the plants after each backcross and select for reniform nematode resistance in F_2 progeny, where highly resistant homozygous plants are expected.

A project under the direction of E. Sacks (pers. commun.) to introgress resistance to the reniform nematode from *G. arboreum* into cotton was initiated by crossing accession A2 190 (Burma C19) (Stewart and Robbins, 1995) with a $2[(AD_1)D_4]$ hexaploid bridging line named G 371. A single hybrid plant was obtained and was subsequently crossed with Deltapine 16 and MD51ne to develop pseudo-backcross populations for nematode screening. *Rotylenchulus reniformis* populations per gram soil from controlled environment tests confirmed that resistance in A2 190 was similar to that of *G. barbadense* GB-713. Nematode reproduction in the backcross population, expressed as a percentage of the controls, had a bimodal distribution, suggesting the action of a dominant gene. The peak of the resistant class of the backcross population (heterozygous for resistance) was at about 15% of the cultivar controls.

Virtual immunity to the reniform nematode in *G. longicalyx* (Yik and Birchfield, 1984) has been confirmed in various laboratories. Two tri-species hybrids of *G. hirsutum, G. longicalyx* and either *G. armourianum* or *G. herbaceum* (Bell and Robinson, 2004; also see Brown and Menzel, 1950 and Konan et al., 2007) were utilized as bridges to introgress this resistance from *G. longicalyx* into *G. hirsutum.* Introgression was accomplished by backcrosses to *G. hirsutum* with cytogenetic analysis of early backcross generations to assess progress toward the euploid state ($2n = 52$), selection for nematode resistance at each generation and examination of selfed progeny at the first, third, sixth and seventh backcross to identify and eliminate lineages with undesired recessive traits (Robinson et al., 2007). The resistance trait segregated (resistant:susceptible) in a 1:1 ratio in backcross progeny and 3:1 in self progeny from putatively heterozygous resistant plants. There was no obvious diminution of the resistance across backcross generations. Advanced backcross plants were indistinguishable from elite cotton genotypes under greenhouse conditions. Comparisons of 240 homozygous resistant BC_6S_2 plants with heterozygous, susceptible and recurrent parent plants in field plantings in 2006 showed normal lint quality and quantity. Two reniform nematode-resistant BC_7 lines, LONREN-1 and LONREN-2, were released by USDA in April of 2007. In multiple location field tests, these resistant breeding lines suppressed population densities of *R. reniformis* by 85% to 98% (Robinson, unpublished data).

Other research on the *G. longicalyx* source of reniform resistance has focused on mapping of the responsible gene(s) and identification of markers linked to resistance genes. Marker discovery initially emphasized representation of all A-subgenome linkage groups, a wide separation of loci and more than 1,000 phenotyped plants spanning seven backcross and three selfed generations (Dighe, 2007). Resistance was found to be linked to the SSR marker BNL1066 and linkage group A03 (chromosome 11), which led to testing of 14 additional markers from public maps of A03 and its homeolog, D02. The results indicated that markers BNL3279_114, BNL1066_156 and BNL836_215 mapped on one side of the resistance locus within 1.4, 2.0 and 4.4 cM, respectively, whereas Fz^{lon} mapped on the opposite side of the resistance locus with a linkage estimate of 4.5 cM (Dighe, 2007). Release of the resistant germplasm and marker information should facilitate incorporation of this trait into new cotton cultivars.

Resistance to M. incognita: Unfortunately, few root-

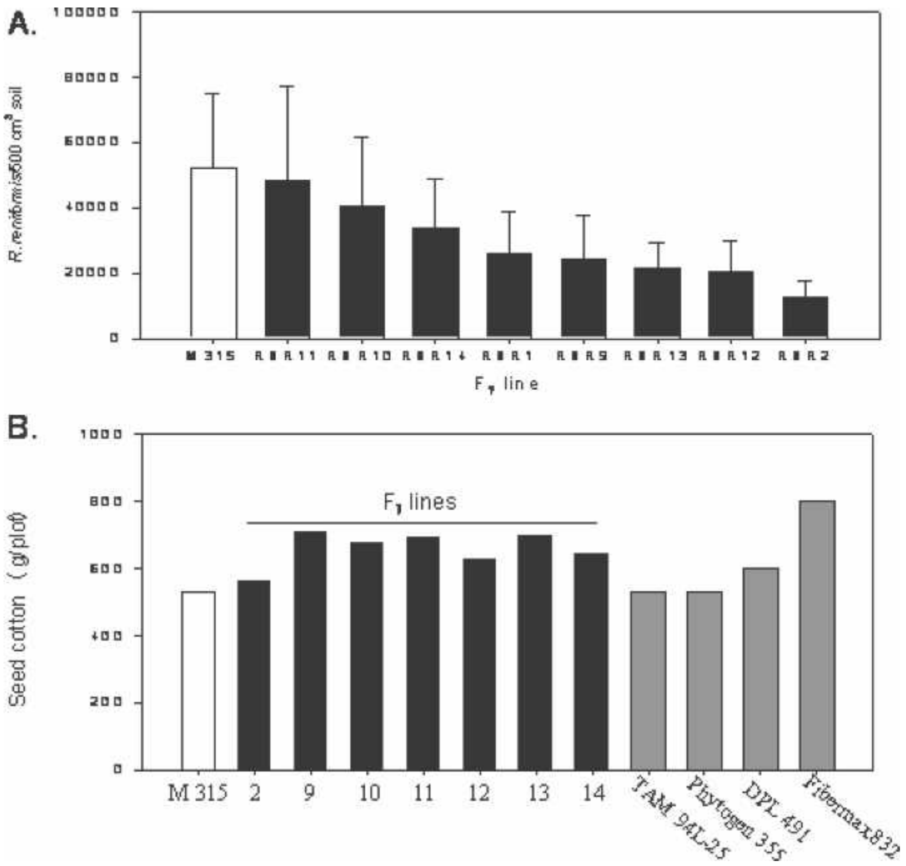

FIG. 5. Resistance to *Rotylenchulus reniformis* and yield potential of F$_7$ lines of cotton with resistance introgressed from *Gossypium barbadense* 'TX110'. A) Nematode reproduction on eight F$_7$ lines compared to reproduction on the susceptible parent M.315. B) Seed cotton yield in replicated, single-row plots (not infested with *R. reniformis*) of seven F$_7$ lines compared with M315 and four high-yielding cultivars.

knot resistant cotton cultivars with yield potential and fiber quality comparable to popular susceptible cultivars have been developed. Currently, the only root-knot nematode-resistant cotton cultivars available are Acala NemX, which is adapted to western cotton production areas, and Stoneville 5599BR. The obsolete cultivars LA 887 and H1560, which had levels of resistance comparable to NemX, had gained popularity and were grown in the southeastern US. Final nematode population densities following resistant cultivars in field trials were below the damage threshold for the next cotton crop (Fig. 1). Acala NemX provides increased yields in fields with moderate to severe infestations of *M. incognita* and suppresses nematode population densities (Ogallo et al., 1997). When Acala NemX was planted in the same infested plots for three consecutive years, the yield was stable, while the yield in plots planted to a root-knot susceptible cotton cultivar declined approximately 30% from the first year to the third year of the test (Ogallo et al., 1999). In addition to protecting the yield potential of the crop in infested fields, resistance to root-knot nematodes also suppressed final nematode population densities. The decline in nematode population densities after production of Acala NemX was beneficial for crops planted in the field after cotton. Yields of lima bean following 2 years of susceptible cotton in a field infested with *M. incognita* were only 25% of the yields following 2 years of the resistant Acala NemX (Ogallo et al., 1999). Nematode population densities in that study were about 4 times greater following the susceptible cultivar than following Acala NemX.

Despite these successes with cotton resistant to *M. incognita*, commercial seed producers have been reluctant to pursue the development of improved cultivars resistant to root-knot nematodes. Several recent advances have been made in nematode resistance genetics and gene mapping in cotton that should improve the efficiency and accuracy of incorporating resistance genes into elite cultivars. Further, such markers are highly informative in determining the uniqueness of and relationships between different resistance sources and in optimizing levels of resistance by combining resistance genes in various genetic backgrounds. It is anticipated that with these data, efficient marker-assisted selection systems will be used to develop a larger number of cultivars with high levels of resistance to *M. incognita*.

Previous and current resistance breeding work in cotton indicates a rich source of *M. incognita*-resistance genes present among *Gossypium* germplasm, especially in the allotetraploid species *G. hirsutum* and *G. barbadense* and in the A$_2$ genome donor diploid species *G.*

arboreum (Robinson et al, 2001; P. Roberts, M. Ulloa and C. Wang, unpublished). Several highly resistant breeding lines have been made available for cotton breeders, including Auburn 623 RNR (*G. hirsutum*), a transgressive segregant for resistance from a cross of Clevewilt 6–3-5 and Wild Mexico Jack Jones (Shepherd, 1974), and Auburn 634 RNR, developed from the cross Auburn 623 RNR × Auburn 56, which was used to develop the M-line series (M-120 RNR, M-315 RNR, etc.) of resistant genotypes (Shepherd, 1982; Shepherd et al., 1988; 1996). Resistant breeding lines including LA RN 4–4 and LA RN 1032 and the released cultivar Stoneville LA 887 were developed from crosses emanating from Clevewilt 6 as the likely resistance donor (see Robinson et al., 2001). In California, Acala NemX (Oakley, 1995) and Acala NemX HY (Anonymous, 2005) were released, with resistance derived from line N6072 for which the pedigree source of the resistance is not clear (Hyer and Jorgenson, 1984; Oakley, 1995; Robinson et al., 2001).

Genetic analysis of root-knot nematode resistance in these materials indicated the presence of multiple genes, both dominant and additive, and the occurrence of transgressive segregation for resistance (Shepherd, 1974). McPherson et al. (2004) reported a two-gene model for resistance in M-315 RNR derived from Auburn 623 RNR, and one recessive gene was indicated for moderate resistance in 'Clevewilt 6-1' (Bezawada et al., 2003). The first major resistance determinant to be mapped in cotton, *rkn1* in Acala NemX, is a single, incompletely recessive gene identified using both SSR (Wang et al., 2006c) and AFLP and CAPS markers (Wang and Roberts, 2006). These markers, tightly linked to *rkn1*, are informative for comparing resistant genotypes, and the same molecular patterns were amplified with SSR marker CIR316 and CAPS marker GHACC1 in resistant Acala NemX, Clevewilt 6, Auburn 623 RNR, Auburn 634 RNR, M-120, M-315, LA RN 4-4 and LA RN 1032 (Wang and Roberts, 2006). These results suggested that Acala NemX may have the same resistance source as Clevewilt 6, and a more detailed account of these germplasm source relationships is provided in Roberts et al. (2007). The SSR marker CIR316 is especially useful because its co-dominance enables the differentiation of heterozygous from homozygous individuals in progeny screening and selection (Wang et al., 2006c).

In the gene mapping strategy for *rkn1* in Acala NemX using existing SSR markers placed throughout the cotton genome, SSR markers linked to *M. incognita* resistance were identified using segregating progenies and recombinant inbred lines from intraspecific (*G. hirsutum*) crosses and an interspecific cross with *G. barbadense* Pima S-7 (Wang et al., 2006a, 2006c). The *rkn1* gene mapped to cotton LG A03 (Wang et al., 2006c), and A03 was subsequently assigned to chromosome 11 (Wang et al., 2006b). Markers CIR316 and BNL1231 in particular were highly informative for mapping, with CIR316 within 2–4 cM of *rkn1* depending on the population used (Wang et al., 2006c). AFLP markers were found linked to *rkn1*, and one was converted to a CAPS marker (GHACC1) and ultimately a SNP marker for high-throughput screening (Wang and Roberts, 2006). These and other markers linked to *rkn1* on chromosome 11 are shown in Figure 6A. Subsequently, Shen et al. (2006) reported that one major dominant resistance gene in M-120 RNR (ex., Auburn 634 RNR) was also linked to SSR marker CIR316 on chromosome 11 (Fig.

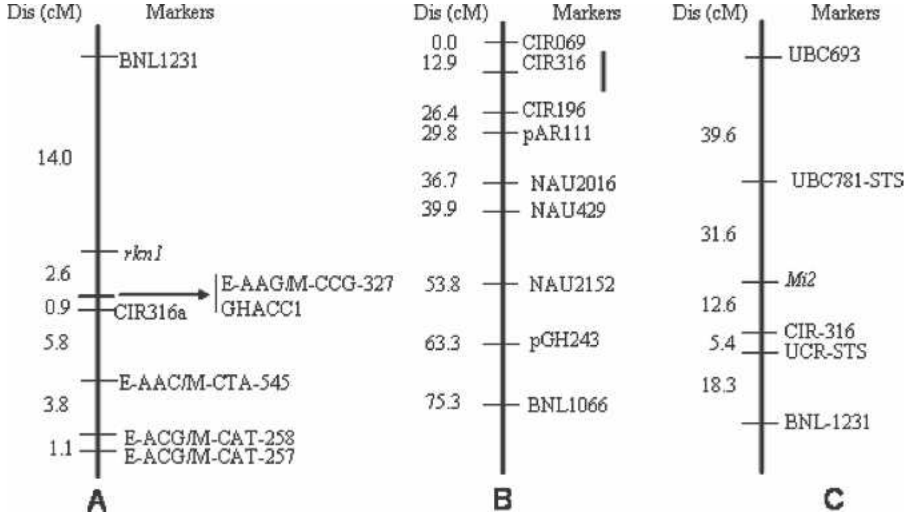

FIG. 6. Location of root-knot nematode resistance genes on cotton chromosome 11. A) the resistance gene *rkn1* in Acala NemX on chromosome 11 relative to four AFLP, one CAPS (GHACC1) and two SSR markers (CIR316a and BNL1231) in an $F_{2:7}$ (Acala NemX × Acala SJ-2) segregating RIL population (from Wang and Roberts, 2006); B) location of a QTL for resistance (vertical bar) from the Auburn-634 RNR source in the vicinity of marker CIR316 in a combined F_2 (M-120 RNR × Pima S-6) (from Shen et al., 2006); C) a resistance gene (putatively *Mi2*) from Auburn 634 RNR mapped to the CIR316 and UCR-STS (GHACC1 in Fig. 1A) marker region in a F_2 (ST 474 × Auburn 634 RNR) (from Nui et al., 2007). Distances are reported in Kosambi cM..

6B), and one minor gene influencing resistance mapped to chromosome 7. In one cross within *G. hirsutum* of resistant (from Auburn 634 RNR) × susceptible near-isolines, Ynturi et al. (2006) used SSR markers to identify one additive and dominant gene on chromosome 14 and an additive gene on chromosome 11 contributing to *M. incognita* resistance. These studies are consistent with the RAPD and STS marker associations with Auburn 634 RNR-derived resistance on chromosome 11 determined by Nui et al. (2007) (Fig. 6C). In addition, there is evidence that at least one transgressive factor interacting with *rkn1* also maps to this same region (Wang et al., 2007).

The emerging picture is the identification of a suite of genes for root-knot resistance, several of which map to the same region of chromosome 11, although their relationships to one another are unclear. Work is in progress to map BAC-end sequence-derived SSR markers into the chromosome 11 map, providing a good start to saturation mapping and providing a physical map for this region. Chromosome 11 is especially interesting because it also contains other resistance genes. Three large-effect QTL for resistance to Verticillium wilt were mapped to chromosome 11 (Bolek et al., 2005) in an interspecific cross with Acala 44. The reniform nematode (*R. reniformis*) resistance from *G. longicalyx* introgressed into upland cotton by Robinson et al. (2007) also is based on a trait that maps to chromosome 11 (Dighe, 2007), and Fusarium wilt resistance also maps to this chromosome (Roberts, unpublished data). Thus chromosome 11 represents a rich resource for resistance gene exploitation.

Higher levels of *M. incognita* resistance in cotton resulting from transgressive segregation were first reported by Shepherd (1974) and can be obtained with factors contributed by susceptible parents in intraspecific and interspecific crosses (Roberts et al., 2007; Wang et al., 2008). Transgressive segregation for resistance was found in a RIL population of the cross Acala NemX x Acala SJ-2, in which susceptible Acala SJ-2 contributed to the level of resistance (Wang et al., 2006a). In this example (Fig. 7), galling reaction phenotypes of the individual RIL form resistant and susceptible classes based on presence and absence of gene *rkn1*, respectively, and also form 'Acala NemX equivalent' and 'higher than Acala NemX' resistant sub-classes due to absence/presence of the transgressive factor from Acala SJ-2. Analysis of the *rkn1* gene in interspecific crosses between Acala NemX and susceptible *G. barbadense* Pima S-7 also revealed transgressive segregation (Wang et al., 2007). The F_1 plants were much more resistant than the resistant Acala NemX parent, and distinct transgressive segregants with resistance phenotypes beyond the range of the parent were found in test-crosses and advanced segregating progenies (Wang et al., 2007). The transgressive segregation effects on cotton nematode-resistance traits present a valuable resource for cotton improvement because extreme genotypes beyond the parent range are generated, and these can be selected in breeding programs, especially with markers available for the trait determinants.

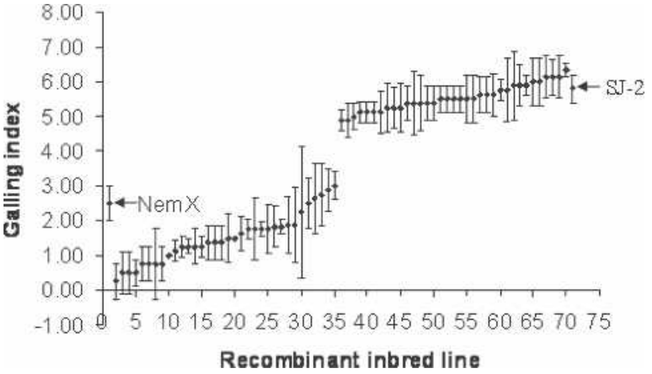

FIG. 7. Distribution of different classes of RKN resistance reaction of $F_{2:7}$ RIL (Acala NemX × Acala SJ-2) based on galling index. Mean values of four plants per line plus SD bar. Mean scores of the resistant (Acala NemX) and susceptible (Acala SJ-2) parents are indicated (Wang et al., 2006a). Galling index: 0 to 10 scale; 0 = no galling, and 10 = severe galling.

CONCLUSIONS

Plant-parasitic nematodes are increasingly recognized as economically important pests of cotton. Research and development efforts, in both the public and private sectors, to improve management of these pathogens have increased substantially since 1990. Because the economics of cotton production rather than ability to suppress nematode population densities largely govern the strategies used by most growers, many effective approaches to nematode management are underutilized. As evidenced by the emphasis in this review, there is much hope that the development and deployment of high-quality cotton cultivars with effective levels of genetic resistance will find widespread acceptance among growers and reduce the impact of *M. incognita* and *R. reniformis* on cotton yields. Further, it is generally acknowledged that greater effort on the part of private sector breeders for nematode resistance will be dependent on development of efficient, high-throughput marker-assisted selection protocols. However, in the final analysis it will likely be the yield potential and fiber quality of these resistant cultivars, rather than the level of resistance itself, that will determine grower acceptance and whether host resistance plays a more important role in future nematode management systems in cotton than it does today.

Recent advances in engineered resistance to *M. incognita* in Arabidopsis based on RNA interference (Huang et al., 2006) and the recent announcement by a company that it was working to develop RNA interference technology to engineer nematode resistance in corn (http://www.divergence.com/press/

20070917.html) bring the hope of additional sources of resistance to several nematodes.

New, more efficacious and environmentally safe nematicides are needed along with technologies for more efficient application. The clustered distribution of most nematodes within a field poses a serious challenge to efficient placement of nematicides. Cotton production in the US is an intensive production system with narrow profit margins. Corn and soybean have traditionally had even lower profit margins, thus nematode management using rotation with either of these crops is likely to be limited. An increase in the economic value of these or other potential rotation crops would affect the use of rotation as a management tactic. Regardless, such practices as crop rotations or organic soil amendments will be used profitably by some producers.

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