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Plant-Parasitic Nematodes Attacking Cotton in the United States

Old and Emerging Production Challenges

Cotton is the most important fiber crop in the world, and current U.S. lint production accounts for nearly one quarter of the world supply. The unique role of cotton in world and American history is profound. Primitive cottons have been used in Africa, Asia, and the Americas for millennia. Domestic and international demand for cotton fiber contributed greatly to the westward expansion of the United States, the American Civil War, and the industrial revolution (81).

The land area devoted to cotton production in the United States peaked in 1926 with approximately 18 million hectares (Fig. 1). The advent of mechanized farming equipment 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 of land area, and hectareage declined. U.S. production of cotton lint in the past 5 years has varied from 3.0×10^9 to 4.4×10^9 kg produced on about 5 million hectares (147). Additionally, cotton seed is a valuable source of vegetable oil and protein used in animal feed, with production of 4.9×10^9 to 5.9×10^9 kg of cotton seed annually.

Since World War II, cotton cultivation was increasingly dependent on inputs of chemical pesticides for weed and insect

control. Historically, the cotton boll weevil, *Anthonomus grandis* Boheman, was the most costly pest of cotton in the United States. The combination of crop loss due to this insect directly and the expense for insecticides that was incurred by cotton growers attempting to control it amounted to several billion dollars annually until recently (130). The successful establishment of the Boll Weevil Eradication Program coordinated by the U.S. Department of Agriculture in many states in the eastern half of the country has resulted in a reduction in insecticide usage, improved profit-

ability for growers, and has led to a resurgence of cotton production in the Southeast (37). In addition, the current widespread use of transgenic cotton cultivars with resistance to herbicides and/or insects also has greatly reduced the need for inputs of pesticides. Currently, 71% of cotton grown in the United States is herbicide resistant, resistant to lepidopteran insects, or has resistance to both (3). Reductions in pest pressure from weeds and insects as a result of the deployment of transgenic resistance and the boll weevil eradication program have

Fig. 1. U.S. cotton production from 1866 to 2000: hectares of cotton harvested and lint yield per hectare (147).

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allowed the cotton industry to focus on other pest problems, including diseases and nematodes.

Modern cotton production in the United States is intensive, highly mechanized, and dependent on a local infrastructure to support this industry. Equipment for cotton harvest and lint processing, including cotton pickers, modules for storing seed cotton, and gins, is highly specialized and generally not adaptable to other farming uses (Fig. 2). 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.

Cotton was likely domesticated in four different world regions, with two species, *Gossypium hirsutum* L. and *G. barbadense* L., originating in the Yucatan Peninsula of Central America (137). Other species of cotton serve primarily as sources for germ plasm improvement. The primary species of cotton grown in the United States is *G. hirsutum*, also called upland cotton, although Pima cotton (a hybrid of *G. hirsutum* and *G. barbadense*), characterized by extremely long fibers (>4 cm), is also grown on limited hectareage. Pima cotton accounts for less than 5% of the total U.S. crop, and it is grown primarily in the western states of New Mexico, Arizona, and California. Cotton is a perennial plant that is generally grown as an annual in cotton production systems.

The damage potential of nematodes to cotton has been recognized since the late nineteenth century. Classic work by Atkinson demonstrated the pathogenicity of root-knot nematode to cotton and the role of this parasite in wilt disease of cotton (4,5). 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 United States are the southern root-knot (*Meloidogyne incognita*), reniform (*Rotylenchulus reniformis*), Columbia lance (*Hoplolaimus columbus*), and sting (*Belonolaimus longicaudatus*) (17,19,69,97, 119,131). Estimated losses of cotton lint yield by these pathogens in the United States have increased from 1 to 2% in the 1950s to more than 4% in 2000 (Fig. 3). 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, (iv) the emergence of the reniform nematode as an important cotton pathogen and its apparent spread, (v) the loss of highly effective, low-cost, fumigant nematicides, and (vi) a shift in cotton production from the western to the southeastern United States.

The Southern Root-Knot Nematode

The southern root-knot nematode is the only *Meloidogyne* species that is capable of appreciable reproduction on cotton in the United States. This nematode is found in all cotton production regions (Fig. 4) and is the most widely distributed economic nematode parasite of the crop (141). Across the U.S. Cotton Belt, approximately twice as much yield loss is attributed to root-knot nematode as to all other nematode parasites of the crop (18–20). The *M. incognita* species complex is characterized by considerable intraspecific variability in host specificity and patho-

genicity. Populations of root-knot nematode that parasitized cotton were commonly referred to as *M. incognita acrita* until synonymized with *Meloidogyne incognita* (145). The concept of host races of this pathogen was proposed by Sasser et al. shortly after *M. incognita* was recognized as a species. The North Carolina Differential Host Test utilizes six standard host plant species: cotton, tobacco, pepper, watermelon, peanut, and tomato to characterize parasitic variation within as well as among the major *Meloidogyne* species (118,139). Under this scheme, four “host races” can be described within the *M. incognita* species complex. Only two of these races (host races 3 and 4) are capable

Fig. 2. Module of seed cotton ready for transport to a cotton gin.

Fig. 3. Estimated percent cotton yield suppression due to plant-parasitic nematodes from 1952 through 2002, and percent cotton hectares treated with the nematocide/insecticide aldicarb from 1991 through 2001 (18,146).

of reproduction on cotton. Differences among individual populations of host races 3 and 4 have been reported on cotton (62,65), but distinct differences between race 3 and race 4 in virulence have not been found in either cotton, cowpea, or soybean (109,149,159). The North Carolina Differential Host Test, however, is more useful in discriminating between *Meloidogyne* species when combined with morphometric data than for characterizing differences between populations of *M. incognita* (109).

The southern root-knot nematode is a sedentary endoparasite that reproduces by mitotic parthenogenesis (144). Juveniles develop from eggs deposited in a gelatinous matrix on the surface of cotton roots. The life cycle of the nematode is characterized by four juvenile stages, the first developing inside the egg and the second (J2) emerging into the soil shortly after the first molt (Fig. 5). The J2 is the only infective stage of this nematode species. Juveniles preferentially penetrate developing cotton roots immediately behind the root cap, migrate intercellularly through the root cortex, and establish a permanent feeding site in the zone where the phloem and xylem tissues are differentiating (51). Developing parenchyma cells, and in some cases vascular cells, are penetrated by the stylet,

and secretions originating from the esophageal glands are injected (54). This process stimulates the formation of specialized, multinucleate feeding sites known as giant cells. Once feeding has begun and the J2 begins to develop toward the third juvenile stage, the nematode becomes permanently sedentary within the root. As development progresses through the third and fourth juvenile stages, the nematode takes on a rounded, slightly pear-shaped appearance. An outward symptom of giant cell enlargement and nematode development that is visible to the unaided eye within a few days after infection is the development of hyperplasia in root tissue resulting in the characteristic root galls that give the nematode its name.

The presence of root galls is the most diagnostic characteristic of an *M. incognita* problem in cotton (Fig. 6). Aboveground symptoms are nondescript and include suppressed plant growth, nutritional deficiency, temporary wilting during the heat of the day, and lower yields. Root galling with the accompanying physiological changes that occur due to nematode parasitism is not well understood. Root galling results in a disruption of the vessel elements that may alter nutrient and water flow in the vascular system of the plant. Water flow through intact roots of infected

cotton seedlings may be greatly suppressed by infection by *M. incognita* (61). In older plants, nematode infection may lower leaf transpiration rates and stomatal conductance, and increase leaf temperature (63). Both the maximum rate of water moving through intact roots and the cumulative flow over time are reduced in nematode-infected plants.

Soil temperature and texture are the most important factors in nematode survival and pathogenicity. The optimum temperature range for *M. incognita* is 25 to 30°C (140,148), and within this range, the life cycle can be completed in about 20 days. Egg hatch is restricted below 12°C and inhibited below 10°C (46). The climate and soil types where cotton is produced in the U.S. Cotton Belt provide an ideal environment for survival and reproduction of this nematode species. The southern root-knot nematode is adapted to a range of soil types, although coarse-textured soils appear to be conducive to severe infestations in cotton and crop damage (70,93,114,132,140,148,154) (Fig. 7). Reproduction of *M. incognita* was greater in soils ranging in sand content from 72 to 91% than in soil types with a greater clay content, and nematode migration decreased in soil as clay content approaches 30% (101). Soil texture as it relates to water holding capacity is likely a key factor in this association. At low water potentials, such as would be expected in soil types with greater clay content, decreased egg hatch and motility of juveniles of certain *Meloidogyne* species has been observed (11,143,153). Soil pH does not appear to appreciably affect *M. incognita* reproduction, although increased damage to tomato by the nematode has been observed in alkaline soils, presumably because of greater stress on the

Fig. 4. Distribution of the Columbia lance nematode, *Hoplolaimus columbus*, the root-knot nematode, *Meloidogyne incognita*, and the reniform nematode, *Rotylenchulus reniformis*, on cotton in the United States, courtesy of the Cotton Foundation (32).

Fig. 5. Life cycle of the root-knot nematode, *Meloidogyne incognita*, courtesy of J. D. Eisenback.

plants in this environment due to increased uptake of sodium ions (38,148).

Survival of *M. incognita* for several months in the absence of a host is well documented, but survival in fallow soil beyond a year has not been demonstrated (148). During the growing season, eggs generally hatch immediately upon development, although environmental stresses, including declining soil temperature or dry soil may limit hatch (46). In Texas, nematode population densities in the soil from eight locations declined steadily after harvest with a mean of only about 9% of the population surviving in April the following year (133). In drying environments, the gelatinous matrix of the egg mass provides a barrier to water loss from eggs, and J2 of *Meloidogyne* species are known to enter a state of anhydrobiosis in dry soils (148). In cotton, both the J2 and the egg stage appear to be equally important in overwinter survival (46,133). During the growing season, the detectable population of *M. incognita* that is present in the soil is primarily eggs, because most J2 infect roots soon after they hatch. However, as the cotton crop reaches maturity, the popula-

tion density of J2 increases as the juveniles accumulate because of the decline in suitable roots to infect. J2 is the predominant life stage present in the soil during the late winter and early spring (133).

Crop-yield suppression due to root-knot nematodes varies according to soil type, population density of nematodes in the soil and their distribution in the field, crop-cultivar susceptibility, and the presence of other biotic and abiotic stresses that may also occur during the growing season. Cotton yield loss due to *M. incognita* across the U.S. Cotton Belt in 2002 has been estimated at about 10^8 kg (18). Although microplots have been used to examine the damage potential of *M. incognita* on cotton in different soil types, quantitative estimates of the degree of cotton lint suppression caused by the nematode have generally been obtained by comparing the yield of field plots treated with nematicides with yield from untreated control plots (58,59,65).

The Reniform Nematode

The reniform nematode, although recognized as a parasite of cotton in 1940, is an

emerging problem in cotton production across the southeast. Originally described in Hawaii (79), *R. reniformis* was found associated with *Pratylenchus pratensis* (probably *P. brachyurus*) in Georgia fields used in Fusarium wilt trials by Steiner and Smith (129). Subsequently, *R. reniformis* was identified as the causal agent for stunted cotton in Louisiana in the 1960s (12,14,55). Important studies on reniform nematode were conducted in Louisiana and Texas in the 1970s and 1980s, but only in the past decade has there been an increase in research effort and heightened awareness of the pathogenic ability of this nematode. Several factors contribute to the neglect of *R. reniformis* in the nematological literature. Its initial discovery in Hawaii and the southern United States resulted in its classification as a tropical or subtropical species of parasitic nematode; thus its importance to agriculture and potential for spread were not appreciated. This may have led to its being overlooked in many instances. Unlike many other species of plant-parasitic nematode, it reproduces readily and achieves very high population densities in fine-textured soils (Fig. 7). This factor has several implications: (i) symptoms caused by reniform nematode are often uniform across a field because the population density and associated stunting may vary little within a field, (ii) moisture stress in nonirrigated fine-textured soils is less evident, and (iii) symptoms are indistinct, with a limited amount of stunting, and suppressed root growth and yield. Still, cotton fields infested with the reniform nematode may experience considerable yield suppression as a result of nematode-induced nutritional deficiencies, fruit abortion, and abnormal maturation of the crop.

The life cycle of *R. reniformis* (Fig. 8) follows the basic pattern for plant parasitic nematodes, beginning with a one-celled egg. The egg is deposited in a gelatinous matrix and undergoes cell divisions that lead to the development of the first-stage juvenile (J1). The J1 molts to form a second-stage juvenile (J2) that hatches from the egg. The life cycle of the juvenile

Fig. 6. Galling of cotton root systems caused by the root-knot nematode, *Meloidogyne incognita* (race 4), (Clockwise from lower left) on susceptible cotton (DP 16 – cv. Deltapine 16), moderately susceptible cotton (DP 50 – cv. Deltapine 50), highly resistant cotton (AU 634 – breeding line Auburn 634), and moderately resistant cotton (LA 887 – cv. Louisiana 887), courtesy of K. R. Barker (65).

Fig. 7. Influence of soil texture on final population density of the root-knot nematode, *Meloidogyne incognita*, and the reniform nematode, *Rotylenchulus reniformis* (70).

stages diverges from that of many plant-parasitic nematodes in that the J2 through J4 stages are fairly immobile and do not feed (16,45,115,128). Also, the J3 and J4 remain inside the cuticles from previous molts (16). Adult males and immature females emerge from the cuticles, and vermiform females penetrate roots to establish a feeding site in the stele. The females are sedentary semiendoparasites during the remainder of their life cycle, with the anterior portion of the female on the root surface. The reproductive system of the female continues to develop after initiating a feeding site, and egg production begins within 1 to 2 weeks depending on temperature. Typically, about 60 eggs are found in an egg mass. The optimum temperature for reproduction is about 30°C, with no development at 16 or 36°C (16). The ratio of males to females is approximately 1:1, and reproduction is by amphimixis. However, some populations may reproduce parthenogenetically, in which case males are rare or absent (115). The males of *R. reniformis* are not parasitic, and the stylet and esophageal glands are much less developed than in the female.

Several aspects of the population biology of reniform nematode have contributed to its emergence as a major pathogen of cotton. This parasite has a broad host range, including hundreds of dicotyledonous plants and several grasses, making control by crop rotation difficult (13,14,115). Important crop species in the Continental United States susceptible to this nematode include cotton, soybean, tobacco, most vegetable crops, and many common weed species. Certain cultivars of some crops such as soybean, however, may be resistant to this nematode (107). A second important aspect of *R. reniformis* biology is its ability to enter an anhydrobiotic state wherein desiccated stages may remain viable for long periods. This arrested stage of development may extend the life cycle for up to 2 years, facilitating survival in the absence of a host (15). Recent research indicates that *R. reniformis* infests the soil profile to a depth of more than 1 m (75,88). High population densities of this nematode persist at these depths even in the presence of a nonhost such as corn (75). The high reproductive rate of this nematode combined with its

ability to recolonize the plow layer from depths below the effective range of nematicide treatment means that long-term plans for management are required.

The ability of this nematode to survive in a dormant state probably has contributed to its recent spread to other areas of the Cotton Belt. It was not detected in South Carolina and Mississippi until the 1960s, North Carolina in 1982 (J. L. Imbriani, *personal communication*, although reported as 1962 [48] it was used in research in North Carolina [24] and was not natural infestation), Arkansas in 1988, Missouri in 1994, Tennessee in 1992, and Virginia in 2002 (J. E. Eisenbach, *personal communication*) (48,88,161). Although it appears that the reniform nematode has increased its range within the United States, spreading to previously uninfested areas, several factors may have prevented its detection in these locales earlier. Obviously, awareness about reniform nematode and its distribution pattern within fields may have limited detection of this pathogen. Similarly, clay and silty loam soils, which favor high densities of this nematode, are not routinely sampled for plant-parasitic nematodes. In

Fig. 8. Life cycle of the reniform nematode, *Rotylenchulus reniformis*, originally published in *Nematropica* (115). (A) Cotton plant. (B) Vermiform female reniform nematode penetrates cotton root and establishes a feeding site. (C) Male reniform nematode. (D) Female reniform nematode becomes swollen after feeding and fertilization of oocytes. (E) Fecund female deposits eggs in a gelatinous matrix and egg undergoes cell divisions that lead to development of first-stage juvenile (J1) that molts to form a second-stage juvenile (J2) that hatches from the egg. (F) J2 through J4 stages are fairly immobile and do not feed (J3 and J4 remain inside the cuticles from previous molts).

addition, during much of this period, soybean production and concern with the soybean cyst nematode in southeastern states received much of the attention in nematological research and extension programs through the 1960s to the 1980s. The widespread adoption of soybean cultivars with resistance to *Heterodera glycines*, derived from Peking, that were also resistant to reniform nematode may have contributed to a lack of its detection earlier (107). Resistant soybean cultivars may have suppressed population densities of this nematode below detection limits in many areas. Through the 1990s, soybean production in the southeastern states has declined, while the production of cotton in many of these areas has increased. In recent years, soybean cyst nematode (SCN) resistance derived from Peking has been largely replaced with resistance from PI (Plant Introduction) 88788. Although PI 88788 is resistant to reniform nematode, most cultivars derived from this source are not (107). Still, a likely reason for spread of this nematode is the movement of farm equipment from infested areas to noninfested areas with increased cotton production in more northerly areas.

The Columbia Lance Nematode

Lance nematodes are among the least studied of the parasitic-nematode species attacking cotton. Only the Columbia lance nematode, *H. columbus*, causes significant yield losses. The Columbia lance nematode was first identified in the late 1960s near Columbia, SC (127). This nematode occurs primarily in the coastal plains soils of Georgia, North Carolina, and South Carolina, although isolated fields infested with *H. columbus* also have been detected in Alabama, Florida, and Louisiana (three parishes, C. Overstreet, *personal communication*) (6,60,69). The most recent surveys conducted in South Carolina found *H. columbus* in over 60% of all cotton fields and above damage thresholds in 37% of fields sampled (80). Yield losses on cultivars of *G. barbadense* in Egypt have been attributed *H. columbus* (23).

Lance nematodes feed as migratory ecto-, endo-, or semi-endoparasites, and compared to most migratory plant parasites, are robust in size, being 0.9 to 1.9 mm in length. The nematodes in this genus all have large stylets and massive knobs with anterior projections (76,84). Factors influencing the feeding site preference of lance nematodes are not known, but infection by Columbia lance nematode generally results in necrosis with lesions developing on the root surface. The most severe damage occurs when *H. columbus* infection occurs early in the growing season on meristematic tissue at the tips of tap and secondary roots (78,86). Injury to the meristematic tissue as a result of nematode feeding causes severe stunting of the taproot and forking of secondary roots. Se-

verely affected cotton plants have shallow root systems with a concentration of roots in the upper soil profile. This limited root development prevents efficient water and nutrient uptake, resulting in stunted plants and suppressed yield (Fig. 9).

The life cycles, feeding habits, and many aspects of the basic biology of all lance nematodes differ significantly from those of root-knot and reniform nematodes. Lance nematodes remain vermiform and mobile throughout their life cycle. Reproduction is by mitotic parthenogenesis, and males are generally absent (76). Second-stage juveniles hatch from eggs after approximately 12 days, with an additional 33 days required for completion of the life cycle. All stages with the exception of the first-stage juvenile that remains in the egg require nutrition. The optimum temperature for development of *H. columbus* is approximately 30°C (92). The life cycle is of indeterminate length and may in fact exceed a year in some instances, since *H. columbus* has been documented to survive in a state of anhydrobiosis (76). Both *H. columbus* and *H. galeatus* have sublayers within their cuticle that thicken the cuticle compared to other nematodes and increase resistance to desiccation and chemical, pH, and osmotic stresses. Also, lance nematodes can overwinter as eggs, larvae, or adults. Eggs have been observed within the root tissue of cotton, but are probably deposited in the soil also.

Columbia lance nematode is most common in soils that have relatively high sand contents (57,77,80). Distribution across a field is normally in scattered pockets determined by soil texture. In a South Carolina study, population densities of *H. columbus* were positively related to sand content in fields where the sand content varied from 90 to 81%, and this nematode was not

detected in soils with less than 70% sand (57). Columbia lance nematode may occur in fields also infested with root-knot or reniform nematodes, but it has been reported to displace root-knot nematodes where concomitant populations were initially reported (71).

Reported damage thresholds for *H. columbus* are approximately 50 per 100 cm³ of soil (66,90). Yield losses typically range from 10 to 25%; however, losses of more than 50% can occur. Subtle yield losses may be caused by suppressed photosynthesis, the delayed onset of fruiting, and subsequent delays in harvest maturity (21,87).

The Sting Nematode

The sting nematode, *Belonolaimus longicaudatus*, is a migratory ectoparasite with a life cycle similar to lance nematode in that it remains vermiform and mobile throughout its life cycle (98). Sexual reproduction is obligatory (amphimixis), and adult sting nematodes are two to three times longer than lance nematodes. The combination of amphimictic reproduction and their large size limits their distribution to very sandy soils (greater than 85% sand content) (106). The requirement for very sandy soil restricts sting nematodes primarily to the coastal plains soils of the southeastern United States, primarily in Florida, North Carolina, South Carolina, Georgia, Virginia, Alabama, and Mississippi (6,17,47,60,69). The sting nematode exhibits a wide host range, including most field crops with the exception of tobacco (100,105,119).

Damage thresholds are very low for this pathogen, usually only 3 to 5 per 100 cm³ of soil are required to impact cotton yield (33,66). Sting nematodes feed strictly as ectoparasites on cotton roots and often produce visible lesions on the root surface.

Fig. 9. Stunting of cotton caused by the Columbia lance nematode, *Hoplolaimus columbus*, in North Carolina, courtesy of K. R. Barker.

Feeding by this nematode greatly limits cotton root biomass and can result in a proliferation of small rootlets. Damage can be severe with stunting, chlorosis, and even plant death common. Like root-knot nematode, sting nematodes can increase the incidence of Fusarium wilt observed in cotton (50).

Other Plant-Parasitic Nematodes on Cotton

Several other parasitic nematodes are known to reproduce on cotton, but their damage potential on this crop is not well understood. Three species of *Hoplolaimus* besides *H. columbus* have been identified in cotton fields, *H. galeatus*, *H. seinhorstii*, and *H. magnistylus*, but the pathogenicity of these nematodes to cotton is limited (6,76,84). In addition to lance nematodes, the stubby root, *Paratrichodorus minor*, the lesion nematode, *Pratylenchus brachyurus*, and various species of stunt nematodes, *Tylenchorhynchus* spp., are commonly found in cotton fields, but their economic importance on cotton has not been determined (23).

Disease Complexes of Nematodes and Fungal Pathogens

Interactions between nematodes and other plant pathogens have been documented in a number of crops (1,40,56,99,134,136,150,156). Synergism between nematodes and fungal pathogens in cotton is much more common, or perhaps better documented, than associations between nematodes and other pathogen groups (136). Atkinson's (4) 1892 observation of increased severity of Fusarium wilt of cotton in soils harboring root-knot nematodes was the first report of an interaction

between a fungal pathogen and a plant-parasitic nematode.

Interactions involving plant-parasitic nematodes and fungal pathogens in cotton fall into two general categories: interactions between nematodes and seedling disease pathogens, and interactions between nematodes and vascular wilt pathogens. In much of the U.S. Cotton Belt, interactions between nematodes and seedling disease pathogens are common. In the early 1950s, an increase in cotton seedling disease, caused by *Rhizoctonia solani*, was observed in the presence of *M. incognita* (103). Subsequent studies determined that environmental factors such as soil texture and temperature as well as the level of the pathogens can influence plant mortality (24,25,27,28,44,134). This association with *R. solani* is not limited to *M. incognita*. Studies have suggested that increasing populations of *R. reniformis* and *R. solani* result in a linear suppression in plant growth (117).

The presence of *M. incognita*, *R. reniformis*, or *Hoplolaimus* spp. has also been shown to increase the severity of seedling disease caused by certain fungal pathogens including *Pythium*, *Alternaria*, *Glomerella*, and *Fusarium* spp. (136). Recently, an interaction between *Thielaviopsis basicola*, which causes black root rot of cotton seedlings, and *M. incognita* has been reported (150,152). With this interaction, enhanced seedling mortality and delayed plant development occur with cotton seedlings in the presence of both organisms. In this situation, it appears that while each of these pathogens normally causes disease of a chronic nature, in combination they can cause significant plant mortality, and there is some evidence that infection by the

nematode allows *T. basicola*, which is typically a root cortex pathogen, access to vascular tissue that would not normally be invaded in the absence of the nematode (151).

The most familiar fungal–nematode interaction in cotton is the Fusarium wilt–root-knot complex that involves both *M. incognita* and *Fusarium oxysporum* f. sp. *vasinfectum* (Fig. 10). Symptoms of the interaction are the same as with each pathogen separate and include root galling due to nematode infection and plant wilting and vascular discoloration due to *F. oxysporum* f. sp. *vasinfectum* (134). A common misconception is that root-wounding caused by the nematode allows *F. oxysporum* f. sp. *vasinfectum* entry into cotton roots, leading to more severe wilt symptoms. Although root cracking due to the formation of galls has been implicated as a possible mechanism for increased infection by the fungus, it is more likely that physiological changes within the roots interfere with normal host resistance expression (51,136). The interaction between these organisms does not appear to affect the damage threshold for yield losses by the nematode, but greater yield losses occur where both organisms are present and nematode population densities are above the damage threshold (56,99,134).

A second misconception regarding this interaction has been that *M. incognita* infection may alter the expression of genetic resistance in cotton cultivars to *F. oxysporum* f. sp. *vasinfectum*. Because numerous breeding programs screen germ plasm for resistance to *F. oxysporum* f. sp. *vasinfectum* in nematode-infested fields, many cultivars now have relatively high levels of resistance even when infected by *M. incognita* (136). These cultivars may exhibit slightly greater wilt severity in the presence of the nematode than in its absence, but disease incidence is still considerably lower than with susceptible cultivars. The majority of *F. oxysporum* f. sp. *vasinfectum*–resistant and –susceptible cotton cultivars that are currently available, however, are still susceptible to the nematode, and significant crop damage due to the nematode alone may still occur (112,113).

Management approaches for most fungal–nematode disease interactions require a consideration of both pathogens. The use of nematicides has been shown to lower the amount of crop loss caused by both fungal and nematode pathogens (29,56). Seedling-disease pathogens, though, are capable of causing disease in the absence of the plant-parasitic nematodes, and the use of fungicides may also be necessary. Traditional disease management programs that utilize host plant resistance, crop rotation, and/or modification of the planting environment to enhance seedling vigor are also effective at limiting the damage caused by nematode–fungal interactions.

Fig. 10. An Arkansas cotton field infested with the root-knot nematode, *Meloidogyne incognita*, and *Fusarium oxysporum* f. sp. *vasinfectum*. Inset: foliar and vascular symptoms as a result of Fusarium wilt of cotton and galling of roots caused by *M. incognita*.

Nematode Management Considerations

Few studies have focused on potential relationships of the initial population density (at planting or P_i) of *M. incognita*, *B. longicaudatus*, *H. columbus*, and *R. reniformis* in the soil to cotton yield (33,70,90). A difficulty with sampling for detection and quantification of plant-parasitic nematodes is their extremely variable distribution within fields (7,163). In addition to distribution patterns, detection of the nematode in the field immediately prior to the time the crop is planted is made more difficult due to the lack of precision currently possible in detecting low numbers of nematodes at planting time, especially with routine sampling and extraction procedures (7). Consequently, the potential risk of damage to a cotton crop due to plant-parasitic nematodes has traditionally been estimated based on soil samples collected in early autumn of the preceding year when population densities are greatest (8). Population densities of very damaging species of nematodes such as *M. incognita* and *B. longicaudatus* may be below the detection limits for various extraction techniques in the spring of the year. Fall sampling for nematodes also allows more time for processing samples, disseminating recommendations, and making management decisions. Typically, the extraction efficiency of the method employed and the attrition rate for the species in question must be determined for a given region before a recommendation is made. Since nematode assay procedures differ considerably among diagnostic labs, damage thresholds must be interpreted cautiously. Ideally, the decision to adopt a particular management tactic, the use of a nematicide in particular, is done after an economic analysis of costs and benefits (166,167).

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 nonhost, 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 on this crop (9,35,36,67,68,104). 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 resistant to the nematode species in question. In order for rotational crops to be practical, alternative crops also must provide an adequate return to the grower and production of the crop must result in sufficient cotton yield increases to justify removing land from cot-

ton production. Selection of a crop for inclusion in a rotation with cotton must be done on the basis of the nematode species that is present, and in the case of *M. incognita* the host race of the nematode must be known.

Peanut is highly resistant to the Columbia, lance, southern root-knot, and reniform nematodes, and provides an attractive rotational crop for managing these nematodes in parts of the United States where peanut is grown (13,77,100,115,139). Similarly, tobacco can be used effectively in rotation with cotton for suppression of *H. columbus* and *B. longicaudatus* population densities where this crop is economically feasible (100,105). Corn and grain sorghum are generally susceptible to *M. incognita*, whereas soybean cultivars vary from highly susceptible to immune (53). 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 concern, although host races 1 and 2 of *M. incognita* do not reproduce on cotton (139). In contrast to the southern root-knot nematode, reniform nematode reproduces minimally if at all on grain crops such as corn or grain sorghum (13,36,115,160). Reniform nematode-resistant soybean cultivars and winter grain crops can be included in rotation with cotton to achieve a reduction in the population density of *R. reniformis* (36). Rotation for suppression of reniform nematode with nonhost crops, however, is only effective for 1 year. Rotation is not generally an option in fields infested with *H. columbus* due to its wide host range (42,77,78,100). For example, corn and soybean are excellent hosts for this nematode, and corn hybrid or soybean cultivars resistant to Columbia lance nematode are not known (22,85,100,121). Peanut and tobacco can be used in rotation with cotton to achieve reductions in the population density of *H. columbus*, but the hectareage of these crops is limited. With the possible exception of root-knot nematodes, the sting nematode has perhaps a larger host range than any of the other cotton-parasitic nematodes. Only tobacco is considered to be resistant to this nematode, although some vegetables such as watermelon allow only limited reproduction, and populations of *B. longicaudatus* vary in their ability to reproduce on peanut (100). Vegetable or other crops may actually be grown in the same year as cotton in southern areas, and cotton is severely affected by *B. longicaudatus* in Florida following potato (34).

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 since it is a perennial and could support reproduction of plant-parasitic nematodes in areas where soil temperatures remain above the activity threshold for pathogenic nema-

todes 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 in Georgia or North Carolina (35,68). In-row subsoiling or some other form of deep tillage appears to be necessary to optimize yields in fields infested with lance nematodes if a hardpan is present (52,121). Deep tillage allows the tap-roots to reach the clay layer, where higher levels of water and nutrients are present than in the sandy topsoils of the coastal plain. Many farmers, however, have adopted reduced tillage practices that eliminate or restrict routine subsoiling. The impact of reduced tillage practices on cotton-parasitic nematodes 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. Cotton planting date had no impact on Columbia lance nematode in North Carolina, and planting dates are not flexible in many areas because of the relatively long season used to produce cotton in the United States (68). Poultry litter has been shown to be suppressive to root-knot nematode in Georgia and Columbia lance nematode in North Carolina, but the rates at which it must be applied to effect control of these pathogens may exceed environmental regulations (67,104). Winter cover crops, particularly the small grains (wheat, rye, oats), 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 (9). However, many winter cover crops, including small grains, are hosts for *M. incognita*, *H. columbus*, and *B. longicaudatus*, but generally not for *R. reniformis* (10,13,77,100). 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 (10,35). 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 (S. R. Koenning, *unpublished*). Although small grain cover crops can serve as hosts for these nematode species, in many cases they are probably sowed and grow actively after the nematodes have entered a dormant or semidormant state as a result of low soil temperatures. Research in California demonstrated that wheat planted in soil 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 (110). In the coastal plain soils of the eastern and Gulf Coast states where *H. columbus* and *B. longicaudatus* are 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.

Resistance and Tolerance for Management of Nematodes

Resistance to plant-parasitic nematodes is usually defined as the ability of the plant to inhibit nematode reproduction relative to that on a standard susceptible host (108). Numerous cotton genotypes resistant to *M. incognita* have been identified (30,31,65, 94,112,113,116,122–126,135). Resistance levels vary from near immunity in the breeding lines Auburn 623 RNR, Auburn 634 RNR, and the M-series lines derived from these sources of resistance to breeding lines and other accessions having moderate levels of resistance that reduce nematode reproduction to about 10 to 30% of that found on a susceptible genotype (Fig. 6). Unfortunately, few root-knot nematode-resistant cultivars with yield potential and fiber quality comparable to popular susceptible cultivars have been developed. The rapid expansion in numbers of cotton cultivars containing transgenic insect- and herbicide-resistant traits has resulted in the use of cultivars with limited field data on nematode tolerance and/or resistance (30,65). Currently, the only root-knot nematode-resistant cotton cultivar available is Acala NemX, which is adapted to western cotton production areas. Even though the resistance of NemX is moderate, this cultivar provides increased yields in fields with moderate to severe infestations of *M. incognita* and suppresses nematode population densities (94). When NemX was planted in the same infested plots for three consecutive years, the yield was stable at nearly 1,100 kg lint/ha, while the yield in plots planted to a root-knot nematode-susceptible cotton cultivar declined from about 950 kg lint/ha in the first year to <600 kg lint/ha in the third year of the test (95). 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 density after production of 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 NemX (95). Nematode population densities in that study were about four times greater following the susceptible cultivar than following NemX.

Although much effort has been devoted to the development of advanced generation root-knot resistant breeding lines with improved agronomic characteristics, the fact that only a single resistant cultivar is available indicates a need for more effort by cotton breeding programs. More than 95% of all cotton cultivars planted today are products of seven commercial breeding programs (2), none of which appear to have the interest and/or expertise to introgress resistance to root-knot nematodes into their cultivars. Anecdotal evidence suggests that the effort required for phenotypic screening programs is a major impediment in the development of additional nematode-resistant cultivars. A molecular map of cotton is available (102), but no marker-assisted selection (MAS) systems have yet been developed for any *M. incognita* resistance genes. Since at least some of the available resistance is inherited as one or a few genes, it is likely that efficient, high-throughput MAS screening systems can be developed, which will hopefully increase the interest of commercial breeding programs in development of cultivars resistant to *M. incognita* (83,165).

Even after extensive screening of the germ plasm collection of *G. hirsutum*, no genotype with confirmed, appreciable resistance to *R. reniformis* is known (113,116,164). Resistance exists in other *Gossypium* species, and efforts are in progress to introgress this resistance into upland cotton. Unfortunately, *G. hirsutum* is an allotetraploid with the AD genome, whereas most of the wild *Gossypium* species are diploids (39). *Gossypium longicalyx* has near immunity to *R. reniformis* but is a diploid with an F-genome, making introgression of traits from this species into cultivated cottons extremely difficult. *G. barbadense*, a few accessions of which have moderate levels of resistance to *R. reniformis*, is also an AD genome allotetraploid and can be readily crossed with *G. hirsutum* (111,165). However, stable introgression of traits from *G. barbadense* into *G. hirsutum* is difficult. It will take considerable time to develop breeding lines with suitable agronomic characteristics and useful levels of resistance such that they can be used as a resistant parent in a breeding program. As with resistance to root-knot nematodes, it will also be important to develop suitable MAS systems for resistance to reniform nematodes to increase the likelihood of actual use by commercial breeding programs.

No *Gossypium* species with resistance to the Columbia lance or sting nematodes is known (22). Because of the lack of readily available sources of resistance in cotton to the Columbia lance, reniform, and sting nematodes, there has been considerable interest in using tolerance to reduce yield losses due to these nematodes. Tolerant cultivars support reproduction by the nematode but sustain lower yield losses

than other cultivars with equal infection and reproduction levels (64). Frequently, cultivars are considered to be or reported as tolerant to various parasitic nematodes when little or no confirming data are available. A number of soybean cultivars have been reported to be tolerant to Columbia lance nematode, and this tolerance appears to be stable and consistent across environments (85,92,121). Tolerance to lance and reniform nematodes has been reported in cultivars or accessions of *G. hirsutum* (31,64,68,86,121). Some cultivars such as Deltapine Acala 90 may be tolerant of Columbia lance nematode infection (49,68). The evaluation of tolerance in cotton to Columbia lance nematode, however, is still preliminary. Tolerance may be related to the relative maturity of the cotton cultivar. Thus far, cotton cultivars identified as tolerant have tended to be of later maturity. Late-maturing cultivars, however, are less determinate in growth and fruiting pattern than early-maturing cultivars, and this could be related to their better performance in sandy soils where *H. columbus* is found. In a given year, especially in nonirrigated production, the relative maturity of a cultivar can have a large impact on yield, thus confounding apparent tolerance (68). Since evaluation of tolerance must be done in field trials with a large number of replications to accurately distinguish different levels of this quantitative trait, it is unlikely that breeding programs will actively seek to introgress increased tolerance into newly developed cultivars (22). Rather, researchers will need to continually evaluate newly released cultivars to identify those that have the highest levels of tolerance (64).

Management with Nematicides

Nematode management in cotton is largely dependent on nematicides, and these materials are reasonably effective in preventing cotton-yield suppression by plant-parasitic nematodes on cotton (131). The use of nematicides, however, has increasingly come under scrutiny by public and government agencies because of toxicological and environmental concerns (142).

Currently, the only nonfumigant nematicide/insecticide with a proven level of efficacy against nematodes that is labeled for at-planting use in cotton is aldicarb (BayerCrop Science, Research Triangle Park, NC). Aldicarb has historically been used on much of the cotton hectareage at relatively low rates for insect control. Rates of aldicarb considered adequate for insect control are from 0.5 to 0.8 kg a.i./ha applied in-furrow at planting, whereas rates used for nematode control are 0.8 to 1.2 kg a.i./ha in furrow. Lower rates of aldicarb are often considered inadequate for control of the various pathogenic nematodes and only serve to protect the roots for a limited period of time. Higher rates of aldicarb may be applied in a

banded application or split applications that include in-furrow applications at planting followed by a side-dress application later in the season. The use of banded or side-dress applications, however, is considered to be prohibitively expensive by most growers. Recent research has raised concerns that the efficacy of aldicarb may be reduced through biodegradation in some soils (82).

Another carbamate, oxamyl (DuPont Crop Protection, Wilmington, DE), is labeled for foliar application to cotton, provided a preplant or at-plant application of a nematicide was made. Foliar applications of oxamyl have proved effective for management of *R. reniformis* and *M. incognita* in Mississippi (72,73). The population density of reniform nematode following treatment with even high rates of 1,3-dichloropropene or aldicarb will often increase to levels equivalent to the untreated plots by the end of the growing season (74,64). Current fumigant nematicides labeled for use in cotton include the chlorinated hydrocarbon 1,3-dichloropropene (Dow AgroSciences, Indianapolis, IN) and metam sodium (Amvac Chemical Corp., Los Angeles, CA). Considerable data on the efficacy of 1,3-dichloropropene and aldicarb are available for control of the various cotton nematodes, but only limited information on the efficacy of metam sodium has been published (29,30,58,59,64,74,89,121,158,162). Results obtained from nematicide trials vary enormously from site to site and from year to year, and yield improvement in infested sites may range from less than 50 to several hundred kilograms per hectare.

Precision Agriculture and Nematode Management

Precision farming, a current area of interest in agriculture, is usually defined as a site-specific approach for tailoring soil and crop management to fit the different conditions found within a field (120). Precision farming relies on various recently developed technologies to guide the precise application of agricultural inputs to specific locations within fields. Fundamental parts of this approach to farming are a geographic information system (GIS) and a global positioning system (GPS), a network of satellites, controlled by the U.S. Department of Defense, designed to help ground-based units determine their real-time location using latitude and longitude coordinates (138). GPS has been used for various agricultural purposes, including the guidance of farming machinery and controlled delivery of varying rates of various pesticides and plant nutrients to previously specified zones within individual fields (variable-rate-input applications).

Site-specific application of aldicarb may not result in greater cotton yields than the uniform-rate treatment. Wheeler et al. (158) determined that site-specific applica-

tion of aldicarb did not consistently result in greater cotton yields than a uniform application in *M. incognita*-infested fields. Other research also determined there were few grid-intersection points where the rate of aldicarb applied for the site-specific treatment was greater than for the uniform-rate treatment (162). In some situations, site-specific application of a nematicide may save producers money and pose less environmental risk than the uniform-rate treatment because less nematicide will be applied on a per-hectare basis (41). However, a major impediment to this approach is the labor, expense, and equipment required to develop density distribution maps for plant-parasitic nematodes (43,163). Techniques such as aerial photography of growing crops, use of precision yield monitors to detect problem zones, or predictions based on certain edaphic factors such as soil texture also should be investigated (26,157). Precision farming technology may be useful both for the detection of spatial patterns of crop damage due to nematodes (41,43,91,96) and to develop precise maps of fields for more effective, economical, and environmentally appropriate application of nematicides. The spatial variability of *M. incognita* and most other nematode species within individual fields may be a definite complicating factor in development of treatment maps due to the intensity of sampling that may be necessary to determine high risk areas (155). Still, a less intensive approach might involve ground proofing, or more intensive sampling, of areas of low yield revealed by a yield map from a picker sensor. It may also be possible to utilize correlations of nematode population densities with field characteristics that are less difficult and expensive to measure, such as soil texture (57,162). Development of effective models for site-specific application of nematicides or other inputs could be tremendously beneficial in comparison to field-wide treatment in terms of both economics and environmental stewardship.

Outreach and Extension

Annual records of estimated cotton yield suppression due to diseases including plant-parasitic nematodes have been published in either the *Plant Disease Reporter* or the *Proceedings of the Beltwide Cotton Conference* since 1952, and the data were summarized in the Cotton Pest Loss Data Base (Fig. 3). Estimated cotton yield losses due to parasitic nematodes have increased over time for several reasons: increased monoculture of cotton, a limited number of tactics for nematode management, and a lack of knowledge or perception of the magnitude of nematode problems among growers and advisors. The Beltwide Cotton Nematode Research and Education Committee was formed in 1990 to educate cotton producers across the U.S. Cotton Belt about the biology, distribution, and management of cotton parasitic nematodes. The committee consists of university scientists from most land grant institutions in the Cotton Belt partnered with the National Cotton Foundation and Rhone-Poulenc Agricultural Products Company (now BayerCrop Science).

From 1990 to 2002, the committee has met annually to develop educational materials and programs aimed at increasing awareness of nematodes as a potential production constraint among cotton producers across the Cotton Belt. The committee has provided instruction to producers about cotton nematode management through individual consultations, small group presentations, news articles in the popular press, newsletters, pamphlets, field day presentations (Fig. 11), workshops held during the annual Beltwide Cotton Conference, class lectures, and the World Wide Web (17,32).

Circumstantial evidence for increased awareness of plant-parasitic nematodes as yield limiting factors in cotton can be found in the increased use of the nematicide/insecticide aldicarb (Fig. 3). Although progress on increasing the awareness of nematodes has been made, even among

Fig. 11. Cotton nematode education program: field day presentation in 2002 at the Upper Coastal Plain Research Station near Rocky Mount, NC.

growers who recognize nematodes as a potential constraint to their profitability, safe, highly effective tools for management of nematode problems are limited. While yield losses to nematodes have stabilized or declined in a few states, nematode-induced cotton losses appear to be on the increase in most parts of the country (Fig. 3). Increased cotton losses to nematodes are the result of several factors: (i) the continued spread of these organisms to new areas, (ii) the increased intensity with which cotton is currently produced in the United States, and (iii) the lack of practical, effective, and economical means for managing these pathogens in cotton.

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