

Reniform in U.S. Cotton: When, Where, Why, and Some Remedies¹

A. Forest Robinson

Agricultural Research Service, United States Department of Agriculture, College Station, Texas 77845; email: frobinson@cpru.usda.gov

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Key Words

cotton, crop losses, *Gossypium hirsutum*, emerging diseases, nematode, *Rotylenchulus reniformis*

Abstract

The reniform nematode, *Rotylenchulus reniformis*, is an emerging problem in U.S. cotton. The impact of this nematode and the extent to which it has and will continue to spread across the U.S. cotton belt are controversial. Long-term changes in cotton production and unique biological attributes of *R. reniformis* are key factors. Expert opinion surveys indicate that *R. reniformis* has replaced the root-knot nematode (*Meloidogyne incognita*) as the major nematode of cotton in Mississippi, Louisiana, and Alabama. In neighboring states the incidence of heavily infested fields has increased during the past 10 years. Estimated annual loss to the U.S. cotton crop is \$130M. Crop rotation and nematicides can reduce losses. Introgression of genetic resistance from primitive accessions of other cotton species offers the most promising opportunity to effectively control this pathogen in the long term. Laboratories in several institutions are currently pursuing this goal, with the promise of resistant cultivars adapted to U.S. cotton production regions within three years.

My family has been growing cotton in this field for 100 years, so why am I pickin' 400 pounds less cotton?

Query from North Alabama cotton farmer to Extension Nematologist W.S. Gazaway

INTRODUCTION

Cotton is a major crop on every continent except Antarctica. Globally, its returns are surpassed only by wheat, rice, soybean, and American corn (*Zea mays*). The bale, a tightly compacted rectangular bundle of lint weighing 218 kg (480 pounds) and worth ca. \$1.10 U.S./kg, is the production unit in the United States. In the year January 2006 to January 2007 world cotton production totaled 117 million bale equivalents with a \$U.S. 23 billion farm gate value (<http://www.fas.usda.gov/cotton/circular/Current.htm>). China, United States, India, Pakistan, and Brazil produced 31, 22, 21, 10, and 6 million bales, respectively. The U.S. crop farm gate value was \$6.5 billion.

How much is lost to pathogens and nematodes, which ones, and where? The best guess is provided by the primary cotton commodity organization in the United States, the National Cotton Council of America (NCCA). The Annual Report of the NCCA Cotton Disease Loss Committee (15) is based on expert opinion within each cotton-producing state regarding the number of cotton bales lost to pathogens and nematodes. Before 2000, losses due to all nematode species were lumped together, but since then these losses have been listed separately for *Meloidogyne incognita* (Kofoid and White) Chitwood (root-knot nematode), *Rotylenchulus reniformis* Linford and Oliveira (reniform nematode), and “other” species. The latter comprise for the most part *Hoplolaimus columbus* Sher (Columbia lance nematode) and *Belonolaimus longicaudatus* Rau (sting nematode), which are of great importance in relatively restricted areas with coarsely sandy soils within the Coastal Plains production region (37, 49, 82, 90–92, 113).

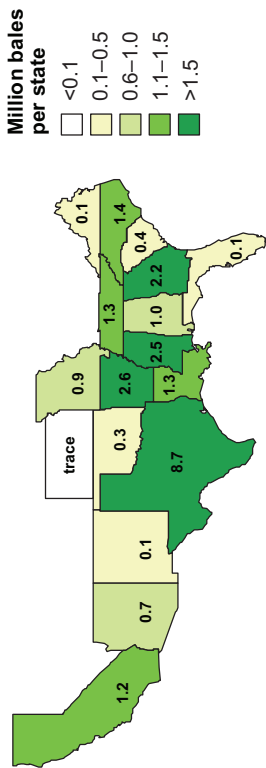
WHEN AND WHERE?

Over the past six years, the NCCA reports have shown a steady increase in losses due to *R. reniformis* (Figure 1), and in the last report, half the nematode losses in the U.S. cotton belt were attributed to *R. reniformis* (15, 17). In the 1970s, by contrast, *M. incognita* was widely regarded to be the most costly nematode by far in U.S. cotton (131). The NCCA report reflects a shift in expert opinion in the mid-South, and is coincident with the growth of a large body of supporting information over the past 15 years that progressively has included dozens of farm press articles, survey reports, nematocide test reports, and extension service bulletins. While some articles in the popular press have an alarmist tone, a growing number of technical reports and refereed journal articles over the past five years confirm the dispersal and impact of this nematode. These data dispute the contention that increased concern in the mid-South stems merely from “heightened awareness” of a “neglected” nematode, as suggested by Koenning et al. (69). *Rotylenchulus reniformis* typically occurs in exceptionally high numbers in positive samples, so that its presence is unlikely to be overlooked by a trained observer.

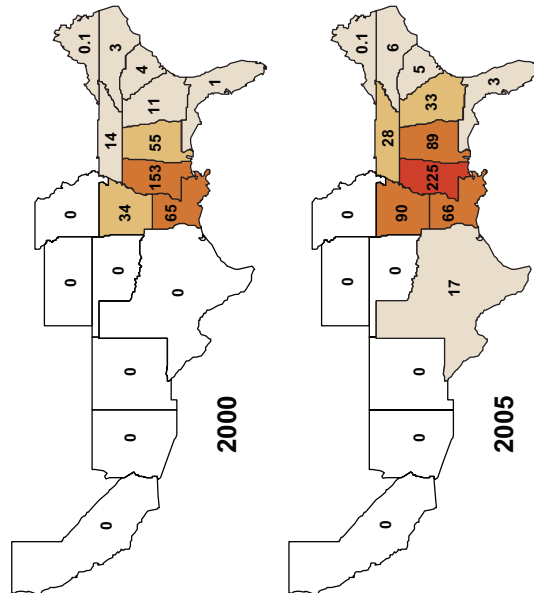
The geographical expansion of *R. reniformis* in cotton is illustrated in Figure 1, which compares state-based estimates of losses to *R. reniformis* and *M. incognita* in 2000 and 2005. In 2005, *R. reniformis* was rated the paramount nematode problem of cotton in Mississippi, Louisiana, Alabama, and Tennessee, and was considered to cause losses comparable to those caused by *M. incognita* in Arkansas, Georgia, and Florida. Coincident with the increased concern about *R. reniformis* in the mid-South came a general diminution of concern about *M. incognita*.

Scientific proof that gradual changes occur over a long interval requires data and time. First reports in specific states of the United States have accumulated gradually since *R. reniformis* was described as a new species from Hawaii in 1940 (79, 80), and progressively included Georgia in 1940 (138), Louisiana in

Cotton production, 2005



Cotton losses due to *Rotylenchulus reniformis*



Cotton losses due to *Meloidogyne incognita*

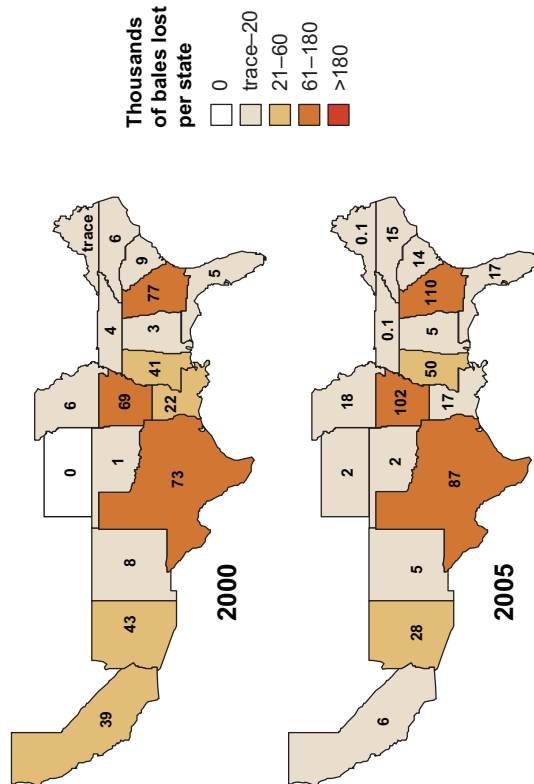


Figure 1

Total bales of cotton produced (*upper map*) and comparative losses to *Rotylenchulus reniformis* (reniform nematode) and *Meloidogyne incognita* (root-knot nematode) in each U.S. state in 2000 and 2005, as estimated by the Cotton Disease Loss Committee of the National Cotton Council of America.

Table 1 Alabama counties and comparative incidence of *Rotylenchulus reniformis* in cotton across a 10-year period

Region	County	Total fields sampled		Percentage of fields above threshold	
		1989–1990	1998–2000	1989–1990	1998–2000
Tennessee Valley	Colbert	20	46	20	13
	Lawrence	25	174	4	29
	Limestone	23	386	0	12
	Madison	30	181	0	90
Central Alabama	Autauga	14	94	0	12
	Elmore	22	36	23	56
	Dallas	20	0	10	NA
	Lee	20	0	20	NA
	Montgomery	1	3	0	0
	Total	175	920	9	30

1941 (139), Florida in 1942 (145), Alabama in 1959 (86), Texas in 1959 (98), South Carolina in 1967 (39), Mississippi in 1968 (56), Arkansas in 1982 (112), North Carolina in 1982 (69), Missouri in 1992 (157), Tennessee in 1996 (96), and Virginia in 2004 (35). Recently, survey data at 10- or 20-year intervals on infestation levels by *R. reniformis* in cotton in key counties or parishes in Alabama, Louisiana, and Mississippi have become available (**Tables 1–3**). Data for Alabama (46) show a steady increase not only in the number of infested farms but also in the percentage of fields above the economic threshold (**Table 1**). In Mississippi (16, 34, 133), all cotton-producing counties in the state are infested. Comparison of information between data for *R. reniformis* and *M. incognita* in 12 Mississippi counties (**Table 2**), albeit incomplete, suggests a coincident decrease in fields with damaging infestations of *M. incognita*. This observation agrees with frequent anecdotal reports of *R. reniformis* displacing *M. incognita* in specific fields over a period of years. In Louisiana (102), 3213 infested fields have been identified and represent all cotton-producing parishes (C. Overstreet, personal communication). Data on the percentage of samples infested, among those submitted to the Louisiana State University Diagnostic

Laboratory over 5-year intervals spanning ca. 20 years (**Table 3**), indicate a projected equilibrium approaching 100% infestation in four of the most productive parishes of the state.

Time sequence survey data for individual farms and counties were not found for states neighboring Alabama, Louisiana, and Mississippi, i.e., Texas, Arkansas, Tennessee, and Georgia. However, the number and geographical spread of reported infested sites in those states have also steadily grown during the past 20 years. In Texas, *R. reniformis* was long known only in four counties of the subtropical Lower Rio Grande Valley (LRGV) at the southern tip of the state (98). In 1982, it was first detected and determined to be uniformly and intensely distributed across a 40-acre cotton field 900 km to the north, on the Texas High Plains, but in none of the thoroughly sampled surrounding cotton fields; this farm belonged to a man who also farmed cotton in the LRGV, and may have moved equipment back and forth (A.F. Robinson, unpublished data). Since then, *R. reniformis* has been found in cotton fields in 12 additional counties of Texas (56, 142). *Rotylenchulus reniformis* was first reported from Arkansas in 1982 (112). It is now present in ten major cotton-producing counties in Arkansas from

LRGV: Lower Rio Grande Valley

Table 2 Some major Mississippi cotton-producing counties and comparative incidence of *Rotylenchulus reniformis* and *Meloidogyne incognita* in cotton across a 14-year period

	Percentage infested with <i>R. reniformis</i>		Percentage above threshold for <i>R. reniformis</i>		Percentage with root-knot (<i>M. incognita</i>)		Percentage with root-knot above threshold			
	1986–1987	2000–2001	1986–1987	2000–2001	1986–1987	2000–2001	1986–1987	2000–2001		
Coahoma	145	323	0	34	0	20	26	23	19	18
LeFlore	169	225	9	37	6	21	33	21	26	13
Sharkey	150	160	72	89	—	65	26	2	—	0
Entire state	2000	2400	25	39	13	15	19	13	12	6

Dashes indicate that data were unavailable. In the 1986–1987 survey, all cotton producing counties in Mississippi were sampled, and in the 2000–2001 survey, eight major counties were re-sampled. Statewide, *R. reniformis* was detected in 47 and *M. incognita* in 37 counties, with *R. reniformis* infesting 32.0% (301,320 acres) and *M. incognita* infesting 15.2% (141,360 acres) in 1986–1987, contrasted with a projection from the eight counties sampled in 2000–2001, that *R. reniformis* at that time infested 39.2% (490,000 acres) and *M. incognita* infested 13.0% (162,500) acres of the total Mississippi cotton acreage.

Table 3 Louisiana parishes and comparative incidence of *Rotylenchulus reniformis* in cotton across an 18-year period

	Total samples				Percentage infested			
	1980–1985	1986–1990	1991–1995	1996–1998	1980–1985	1986–1990	1991–1995	1996–1998
Caldwell	23	12	10	52	9	33	90	71
Franklin	122	151	634	1939	2	31	63	53
Morehouse	128	1021	914	248	3	23	41	75
Richland	56	159	701	648	4	50	58	61
Total	329	1342	2259	2887	4.5	34.3	63	65
				Mean				

Data provided by Charles Overstreet, Louisiana Cooperative Agricultural Extension Service.

the Louisiana line to the Missouri “boot heel.” A survey examining 2863 soil samples submitted from nine counties in 2005 revealed 247 positive samples spanning nine counties, with 116 samples in seven counties above the economic threshold (7). *Rotylenchulus reniformis* was found in Tennessee in 1996 on a single farm in the western part of the state, and in 1997, it was found in more than 80 fields. These fields were distributed across three of the six counties that accounted for 80% of the 445,000 bales of cotton produced in Tennessee in 1998, and thus put much of the cotton production land in the state near infested sites. Subsequent increase in the number of known infestations in Tennessee has been slow but steady. *Rotylenchulus reniformis* was discovered in Georgia in 1940 (138). In 1974, it was found in 2% of samples from 14 counties surveyed (89) and in 1995 was found in 14% of 780 samples, and present in 10 of 11 counties surveyed (6). In Jefferson and Washington Counties, 37% and 52% of the fields surveyed were infested.

WHY?

Why Is It Happening?

To formulate hypotheses regarding the cause, and consider remedies for the increased incidence, intensity, and geographical spread of

R. reniformis in the U.S. cotton belt, it will be helpful to review changes in cotton as a U.S. crop, and examine aspects of the biology of *R. reniformis* that distinguish it from other nematodes of cotton.

Cotton acreage in the United States peaked in 1926 (**Figure 2**), and subsequent improvements in farming and cotton genetics have made it possible to produce more cotton fiber on less ground. Data on distributions of cotton acreage at the county level in 1952 show cotton farms, even after significant acreage reductions since 1926, to remain densely distributed throughout the South (**Figure 3**), often in small operations of less than 320 acres. During the next 20 years as cotton acreage approached its all-time low in about 1982, acreage greatly diminished everywhere, but most notably in the Piedmont and Coastal Plain regions of the Carolinas and Georgia, in eastern Mississippi, throughout Louisiana, in the Blackland region of eastern Texas, the Coastal Bend of Texas, and the Pecos River Valley of western Texas and New Mexico. Much of this land probably went into soybean, corn, and sorghum production. After 1982, cotton acreage increased again, but production regions became more clearly compacted, so that by 1995, the Coastal Plain, but not the Piedmont, had become heavily planted back to cotton. As noted by Koenning et al. (69), the success of the USDA boll weevil eradication program and the advent of insect-resistant transgenic cotton cultivars were undoubtedly contributing factors. Increases in cotton acreage were also strikingly apparent in the Tennessee River Valley of northern Alabama, eastern Arkansas, western Tennessee, the Red River Valley of Louisiana, and the Coastal Bend, but not the Blackland region of Texas. Cotton acreage in those areas has continued to increase. Today, wide zones where cotton acreage is sparse clearly separate four distinct major production regions: (i) the Coastal Plain of North Carolina, South Carolina, Georgia, and southeastern Alabama; (ii) the “Mississippi Delta” region of Louisiana, Mississippi, Arkansas,

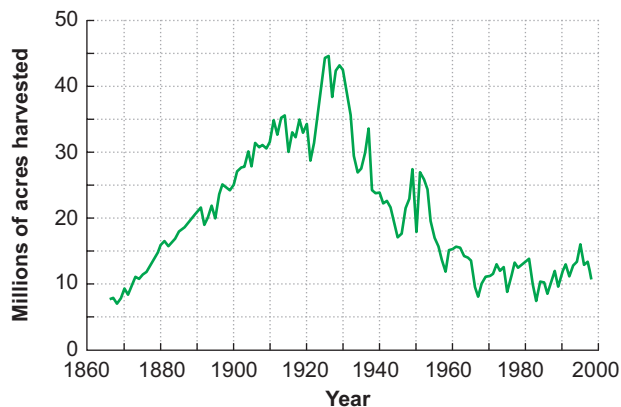


Figure 2

Cotton crop land area harvested in the United States during 130 years.

Tennessee and Missouri; (iii) the High Plains region of Texas and Oklahoma; and (iv) the San Joaquin Valley of California. Minor production regions today include the Tennessee Valley of northern Alabama; the Red River Valley of Louisiana; the Lower Rio Grande Valley (LRGV) of southern Texas; the Brazos and Trinity River Valleys of Texas; the Texas Rolling Plains; and southern Arizona.

In sum, land planted to cotton has increased almost everywhere since 1982, much more so in some regions than in others, and markedly in the Coastal Plain region of Alabama, Georgia, Florida, South Carolina, and North Carolina, during a time when the boll weevil eradication program was proving successful. Because cotton is an excellent host for *R. reniformis*, it is reasonable to expect more *R. reniformis* where there is more cotton. Returning to cotton cultivation after growing soybean varieties that are hosts to *R. reniformis* (69) may explain the increased incidence of this nematode on farms on the Coastal Plain. However, much of the land in the mid-South, particularly in the Mississippi Delta production region spanning Mississippi, Louisiana, Arkansas, and Tennessee, was continuously used for cotton production, in many cases since before the Civil War. Thus, any change in agricultural practices that may have introduced or aggravated the reniform nematode problem in this key region would lie within the limits of cotton monoculture. For example, there has been a gradual transition to larger farm operations, often with a corporate rather than family structure, which utilize larger, faster tractors and implements that routinely cover far greater acreages than in years past, in the same meteorological window. Larger, faster equipment could contribute to the spread of contaminated soil. *R. reniformis* is exceptional among the major nematodes of cotton for its ability to survive in dry soil (1, 13, 42, 53, 134, 135, 150, 156), and dispersal of *R. reniformis* in soil on farm equipment can spread the nematode over a field from a point of introduction within three

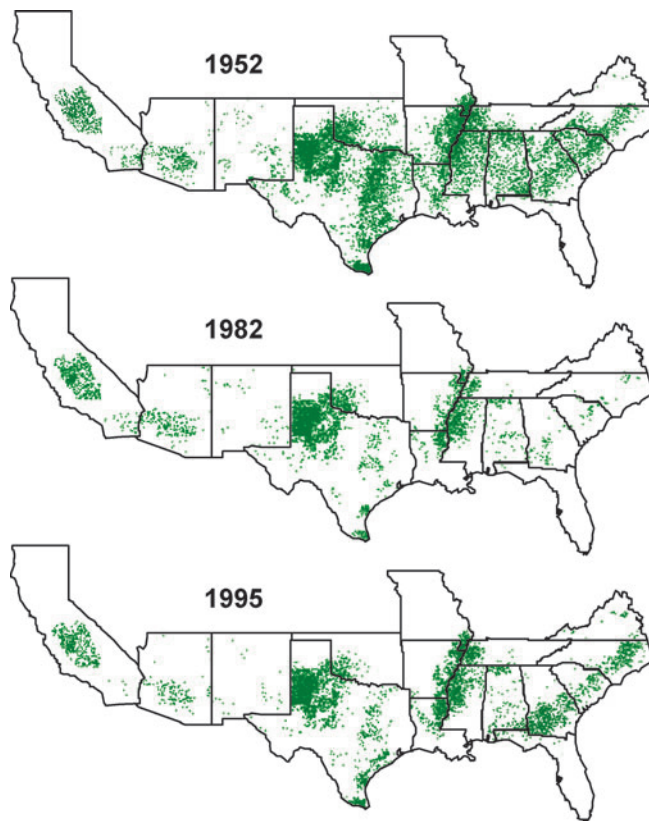


Figure 3

Geographical distribution of land planted to cotton in the United States at key points in history, comparing distribution in 1982, when the least area was planted, to distribution in 1995, when rapid geographical expansion of known infestations of *Rotylenchulus reniformis* became apparent. Dots are plotted randomly within each county. Each dot represents 1000 ha. Source: National Agricultural Statistics Service, United States Department of Agriculture.

years (57, 87; G.W. Lawrence, personal communication).

In seeking biological explanations for the buildup of *R. reniformis* populations, and its putative ability to displace *M. incognita*, at least six attributes of *R. reniformis* are noteworthy: (i) Cotton is an excellent host for *R. reniformis*. (ii) In addition to the ability noted above to survive desiccation in its vermiform stages, which occur exclusively in the soil, *R. reniformis* has a short life cycle, with as little as 17 days from egg to egg at 27°–32°C (41, 110, 127, 137) and 5–7 generations per year (73). In comparison *M. incognita* has a life

cycle of about 30 days. (iii) *R. reniformis* decrements taproot penetration and root colonization of the soil far less than does *M. incognita*, and (iv) establishes feeding sites all along primary, secondary, and tertiary roots, resulting in far more reproductive females on a root system. Hence, *R. reniformis* has a high potential rate of population increase compared to other nematode parasites of cotton, in spite of the small size of the sedentary adult females of *R. reniformis* and the relatively small egg clutch size (usually about 60 eggs per female are found in the surrounding gelatinous matrix, although up to 200 may be present) compared to *M. incognita* (which has a female volume several times that of *R. reniformis* and egg masses with more than 300 eggs). The high potential rate of population increase of *R. reniformis* in cotton is evident in the exceptionally high population densities typically measured—60 vermiform *R. reniformis*/cm³ soil is common and 490/cm³ have been reported (63)—and in the rapid reattainment of high populations consistently observed during the first year of cotton following rotation to a poor host (30, 43). Such high populations are virtually unheard of for *M. incognita* in cotton. *Rotylenchulus reniformis* exhibits deeper soil colonization of roots than permitted by *M. incognita* and, thus, often occurs at high population densities below the reach of nematicides (118, 124, 153), facilitating recolonization of the upper soil profile where most feeder roots develop following nematicide treatment. (v) The cuticles retained during the three juvenile molts of *R. reniformis* in the soil may provide protection from antagonists; the potent nematode biological control agent, *Pasteuria penetrans*, which is devastating to *Meloidogyne* spp., for example, has not been reported on *R. reniformis* to this author's knowledge. (vi) *R. reniformis* can build up high population densities in a wide range of soils, including soils with high silt and clay content, such as the deep alluvial soils of the Mississippi and Rio Grande flood plains. In contrast the root-knot, lance, and sting nematodes of cotton are strongly favored by, or are limited to,

sandy soils. Although results of early surveys indicated that *R. reniformis* was less common in sandy than in silty soils in Texas (126, 142), the nematode has been observed frequently in diverse soils with high as well as low sand content in other regions.

While these six biological attributes contribute to the biological success of *R. reniformis* in cotton, they cannot alone explain the temporal changes in distributions observed over broad geographical regions. They only indicate how this nematode might be expected to colonize new fields or certain kinds of fields faster than other nematodes would. As with any organism, *R. reniformis* undoubtedly has its weak points, and its fitness relative to competitors depends on the specific environment occupied, and the entire community of organisms present. Many biological, agricultural, and historical factors may have contributed to the increase in incidence and severity and the spread of the reniform nematode in cotton, and the relative importance of those factors likely differs among production regions. Cotton is grown in the South because the crop requires high temperatures and a long growing season. So do all important nematodes of cotton. The regions where cotton is grown not only have different cropping histories, but also a wide range of climates (mesic to arid), soils (coarse sands to pure clay), pests, and pathogens. These differences cumulatively necessitate different cultivars, pesticides, fertilizer rates, tillage and irrigation practices, and mechanical harvesting technology, provide different crop rotation options, and present different weed communities as alternative hosts for nematodes. The effects of those factors on nematode pests probably differ substantially depending on the species.

Changes in cotton cultivars over time are unlikely to have contributed to increased incidence of *R. reniformis* because the 55 predominant cultivars planted in all production areas from 1950 to 2000 were all highly susceptible (123). Nor is it likely that transgenic cultivars have contributed, as neither the delta-endotoxin transgenes in *Bacillus thuringiensis*

nor the herbicide-resistant transgenes in cotton appear to affect nematode resistance. However, the suite of weeds in a given field can, if unmanaged, substantially affect the ability of *R. reniformis* to maintain large populations, depending on the weeds present. Many weeds in cotton in the United States are very poor hosts, whereas others, such as several species of morning glory, are excellent hosts that support even greater populations than does cotton in pots (31, 34). The increasing usage of reduced and minimum tillage practices in cotton undoubtedly affects microorganisms within the soil and its influence on *R. reniformis* merits further study, but there are no data yet to indicate that minimum tillage augments populations of *R. reniformis*. The same observation can be made for pivot irrigation and chemigation, although the latter can be used in cotton, in conjunction with underground drip irrigation, to manage nematodes. Finally, long-term changes in weather, especially changes in seasonal rainfall patterns, could markedly influence *R. reniformis*, because dry soil favors nematode survival over winter (13, 134, 150, 156).

Symptoms: Why the Nematode Is a Problem

R. reniformis suppresses cotton yields to 40% of the yield potential; thus in heavy infestations, yield increases of more than 100% are obtained if uneconomically high rates and deep placement of fumigant are employed to kill the nematode throughout the soil profile (63, 124, 153). However, it is practicable to fumigate only the upper 30–45 cm of soil, and yield responses to the labeled, economic nematicide rates examined in nematicide efficacy tests on *R. reniformis* today are typically 5% to 20% (44, 66, 73, 75, 159, 160).

Newly infested fields typically have uneven, irregular stunting, whereas in old infestations larger areas of uniformly stunted plants are seen (**Figure 4**), or stunting can be so uniform that damage is not immediately apparent. Wilting from water stress is

not necessarily symptomatic of *R. reniformis* stunting. The onset of stunting is consistently early in plant development and appears hormonally controlled (12, 52, 54, 63, 74, 143). Rapid growth stops at the third or fourth leaf stage; leaves take on a uniform, slightly light- or off-green appearance, sometimes confused with potassium deficiency; and some leaves may have a purple cast. Flowering and fruit set is consistently delayed one or two fruiting branches up the main stem. After gentle rinsing of roots, soil particles can be seen sticking to the gelatinous egg masses embedding the kidney-shaped females protruding from the root surface, making roots look dirty.

There are more than 20 published histopathology studies on *R. reniformis* on various hosts, including several on cotton (1, 2, 10, 21, 23, 111, 128). The interaction between nematode and plant is similar on a wide range of hosts. Unlike *M. incognita*, the vermiform infective stage of *R. reniformis* (which is the immature fifth-stage female rather than the J2, or second-stage juvenile) does not migrate between cells through the cortex toward the root apex, but rather penetrates and disrupts cells of the cortex as it moves into the root perpendicular to the root axis, coming to rest with the lips appressed to the outer tangential wall of a single, usually endodermal, cell on which it feeds. This cell, sometimes called the nurse cell, and a curved sheet of contiguous cells of the pericycle undergo adnate cell wall dissolution and slight hypertrophy without hyperplasia, producing a simple syncytium that serves as a nutrient source for the developing female.

In contrast to the localized, globose giant cell induced by *M. incognita* (140), the syncytium of *R. reniformis* may extend several root diameters along the root axis, involving many, perhaps hundreds of cells, but a gall that is apparent to the unaided eye is not formed. Syncytial cells have enlarged nuclei and nucleoli, safraninophilic cytoplasm, and extensive proliferation of rough endoplasmic reticulum indicative of accelerated metabolism (111).

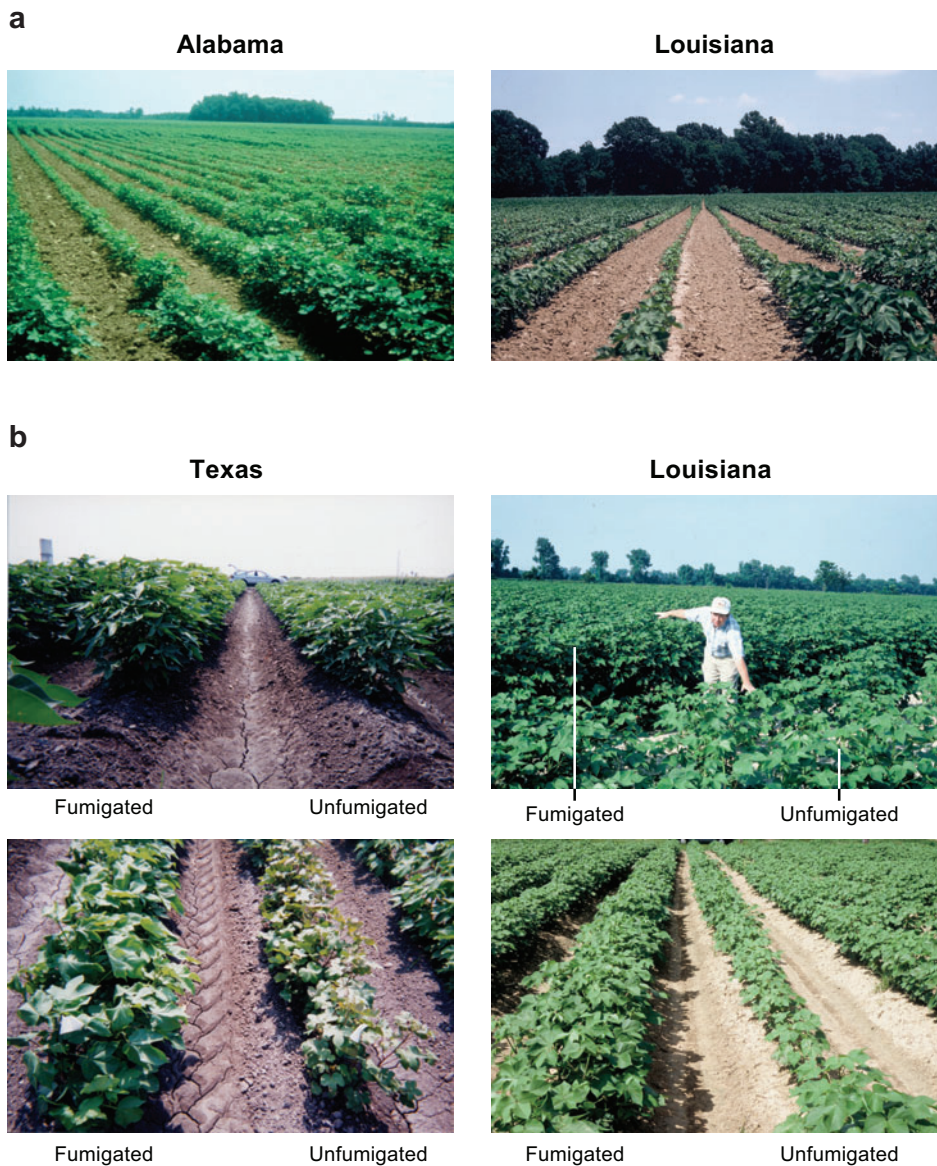


Figure 4

Field symptoms of *Rotylenchulus reniformis* in cotton, showing large areas of uniformly stunted plants (a) and marked growth responses to soil fumigation in four fields in Texas and Louisiana (b). Photo credits: Alabama, W.S. Gazaway; Louisiana, C. Overstreet; Texas, A.F. Robinson.

Because all water and minerals entering the root and moving apoplastically through the cortex must move symplastically across the endodermis, via active transport in many cases, in order to enter the vascular cylinder, disruption and/or dysfunction of a large curved sheet of endodermal and pericycle cells by each of the thousands of females that can feed on a single plant can profoundly alter overall root function.

The female appears to continue to feed on the same nurse cell as the posterior two-thirds of its body extends out into the soil and swells into the kidney shape characteristic of the genus *Rotylenchulus* (115, 116, 140). Five days to 2 weeks after root penetration, males are found in the gelatinous egg matrix that the female secretes shortly before laying eggs, typically about 60 but sometimes as many as 200, into the matrix. Second-stage

juveniles (J2) hatch from eggs about 1 week after oviposition, and the emerging J2 undergo three superimposed molts, giving rise to equal numbers of vermiform females and males (14). Males have an indistinct stoma and esophagus and do not feed. The molting speed depends on environmental conditions and can be delayed by thermal stress (55); under ideal conditions at 27°–32°C, egg to egg life cycle may require as little as 17 days, although little or no development occurs at 16° and 36°C (110).

How Many Does It Take?

There are abundant data regarding the approximate population density threshold at which damage from *R. reniformis* can be expected in cotton with the understanding that many location-specific factors related to soil, temperature, and nutrient and water availability that can be integrated into a prediction only through experience, must also be considered. Several field and pot studies show that damage to cotton can be expected when soil populations during seedling growth are between 1 and 10 nematodes/cc soil, equivalent to 0.8 and 8 nematodes per gram soil at 1.25 specific gravity (36, 47, 103, 106, 148, 149). Pot studies evaluating resistance in plants have used inoculum densities between 2 and 11 nematodes/cm³ soil (27, 93, 129, 158). Because survival over winter in cotton-producing regions of the United States is high, end-of-season samples are typically used as the basis for nematode management decisions in the next year's cotton crop. Treatment thresholds in use by consultants and farmers vary with growing conditions from about 8 to 16 nematodes/g soil collected at the end of the previous season (67, 71, 100, 133). These values (8 and 16) are calculated based on a 1.3 soil specific density and the critical nematode densities in imperial units of 5000 to 10,000 nematodes/pint of soil. When spring samples are used, the treatment threshold employed is 20% of that in the fall, i.e., between 1.6 and 3.2 nematodes/g, and thus very similar to the values observed in quantitative studies.

Are There Interactions with Other Disease Problems in Cotton?

Several surveys have noted a low incidence of fields with high populations of both *M. incognita* and *R. reniformis*. From 1980 to 2005, the Louisiana Extension Service found *R. reniformis* in 12,095 field samples and of these, only 4.9% also contained *M. incognita* (C. Overstreet, personal communication). Results of two studies in Texas that examined soil texture indicate rare occurrence of *R. reniformis* in soils with >40% sand, in contrast with *M. incognita*, which is strongly favored by sandy soils. However, *Rotylenchulus reniformis* also can occur in soil with high sand content and occurs occasionally in the presence of high population densities of *H. columbus*, which like *M. incognita*, is strongly favored by sand. In pot studies examining competition between *R. reniformis* and *M. incognita* (32, 70), either species could suppress the other if its initial relative population density (i.e., relative primary inoculum level) was sufficiently high. However, *M. incognita* required a much higher competitive edge in primary inoculum to out-compete *R. reniformis* (32). Soil with high sand content favored *M. incognita*.

Neal (95) first observed that *R. reniformis* increased the severity of *Fusarium* (*Fusarium oxysporum* f. sp. *vasinfectum*) on wilt-susceptible but, in contrast to *M. incognita*, did not do so on wilt-resistant cotton cultivars. Thus, *R. reniformis* did not appear to predispose plants to the fungus as strongly as *M. incognita* did (65, 144). Information regarding interactions with Verticillium wilt is limited. Prasad & Padeganur (109) found higher populations of *R. reniformis* in fields with than in fields without wilt symptoms (144), and an interactive effect between *R. reniformis* and the fungus was observed to suppress shoot growth but not increase wilt incidence in pots.

In seedling disease studies, *R. reniformis* has been observed to exacerbate cotton seedling disease in some cases but not in others. Sankaralingham & McGawley (130) observed nematode populations to be augmented when

plants were co-inoculated with *R. solani*. Brodie & Cooper (19) tested different nematode population densities and found that an exceptionally high nematode inoculum density of 40 nematodes/cc soil was required under their conditions for the nematode to augment seedling disease symptoms caused by *Rhizoctonia solani*. Co-inoculation of cotton seedlings with one tenth as many *R. reniformis* (ca. 4 nematodes/cc soil) and either *R. solani*, *Thielaviopsis basicola*, or one of 10 species of Fusarium, consistently showed increased incidence of seedling disease over nematode-free controls (104). *Rotylenchulus reniformis* slows seedling growth, as do cool soil conditions favoring cotton seedling disease; a key factor common to cool conditions and *R. reniformis* feeding could be deceleration of taproot growth through soil, reducing the plant's ability to outpace fungal invaders.

REMEDIES

Undo It: Remove the Cause

As discussed above, many candidate causes of the increased incidence of *R. reniformis* in the United States cotton belt have been identified but none proven. Thus, until more information is available, we must consider known options, below, for reducing damages caused by the nematode as infested fields are discovered.

Kill Them

The statement made by Sasser (131) that "Chemical control of plant pathogenic nematodes in cotton is by far the most expedient and widely used method" has yet to be disproven, even though most of the means to achieve it are no longer accessible. The primary nematicides available for use in cotton include the fumigants 1,3-dichloropropene and metam sodium and the cholinesterase inhibitors aldicarb and oxamyl (44, 69, 73, 75, 77–79). Where it occurs naturally, cotton is a perennial with a fast-growing deep taproot. Today, as in 1972 (131), the nematicide strat-

egy for all nematodes in cotton is to save nematicide costs by focusing on protection of the young plant, and to target the soil zone that the taproot will grow through during the first few weeks. This is achieved by fumigant placement 25–45 cm deep under the center of the bed, or granular nematicide either in the seed furrow or band incorporated over the top of the planting bed, with the option to also side-dress later. Foliar applications of oxamyl have also been used in cotton with good success in some regions (73), and since 2004, seed coat formulations of the insecticide/anthelmithic avermectin compounds produced by the soil bacterium *Streptomyces avermitilis* have been extensively tested and are now commercially offered (22, 38, 64, 132). Commercially available formulations of resistance-inducing harpin proteins as seed and foliar treatments also have recently been evaluated and may have a place in management of *R. reniformis* in cotton (40).

Many nematicide efficacy tests have been conducted for a number of years in fields infested with *R. reniformis* in almost all cotton-producing states east of New Mexico, and the population suppression and yield responses obtainable with labeled nematicides and rates have been well characterized, as have the economics (44, 75–77, 101, 103, 149, 159, 160). Fumigants typically kill most *R. reniformis* 5 cm below and directly above the point of placement up to the soil surface, but populations always quickly rebound during the first half of the crop season and at harvest are often comparable to those in untreated plots (44, 66, 72). On average, fumigation provides an economic return in some areas, but not always, and yield boosts, when obtained, are often only 5% or 10%, in striking contrast to the 40%–60% yield suppressions measured in early studies examining the impact of *R. reniformis* (12, 63). Because granular in-furrow application of a subnematicidal rate of aldicarb is widely used prophylactically for early season insect control, the cost of stepping up the rate (5.6–7.8 kg a.i./ha) for nematode control is low. However, the benefits

typically are inferior to those obtained by fumigation (44, 99). Nonetheless, at appropriate rates, both 1,3-dichloropropene (1,3-D) and aldicarb can be profitable, if risky, for management of both *R. reniformis* and *M. incognita*. Aldicarb-degrading microflora could potentially develop following long-term use as a prophylactic, as demonstrated recently is occurring in Alabama (84). It is unlikely that suppression of seedling disease-causing microflora by 1,3-D and aldicarb is an important component of yield responses to fumigation observed in fields infested with *R. reniformis*, because careful studies have shown that the use of 1,3-D and aldicarb in cotton fields does not significantly affect plant pathogenic fungi or saprophytic fungal populations (5).

When comparing nematicides with other nematode management options, such as crop rotation, biological control, and host plant resistance, it is important to know how much of the total yield potential is recovered by nematicide treatment, and how much it costs. Analyses by Zimet et al. (159, 160) indicated that a substantial fraction of the yield potential could be tapped by fumigating shallow sandy soils in the Florida panhandle. The well-known superior efficacy of fumigants in sandy soils, however, should make these soils easier to fumigate than the more finely textured soils where *R. reniformis* more frequently occurs. Also, graduated deep nematode sampling has shown that in many fields large numbers of *R. reniformis* below the point of fumigant placement remain unaffected (81, 97, 124). Application of sufficiently high, intentionally uneconomic rates in two fields in the Texas LRGV consistently gave >50% increases in yield several years in a row (26, 124, 153). Deep injection of fumigant 81 cm below the surface in these fields suppressed nematode populations 90 cm deep in the soil throughout the season, strongly promoted deep root growth, and increased yield by 100%, in contrast to the 57% increase obtained by only fumigating 43 cm deep. This additional yield boost is very important because it is part of the yield potential that might be tapped by

planting a resistant cultivar, should one become available.

Several recent tests explored the potential of strategic placement of anhydrous ammonia, a widely used nitrogen fertilizer formulation, for *R. reniformis* management. Significant yield improvements over the alternative nitrogen control were measured, but consistent suppression of the nematode populations was not obtained (85).

Toxic amendments have been explored for management of *R. reniformis* on cotton in pots in India, and several are highly effective, including presmud, fresh Azolla, farm yard manure, and neem cake (105). Such studies have the potential to reveal new nematicide chemistry that could have important applications in large-scale American agriculture. Incorporation of crop residues that generate biofumigants, highly effective against plant nematodes, has shown economic potential in various crops in Alabama. Because *R. reniformis* symptoms in cotton mimic potassium deficiency, potassium supplementation has been explored as an amelioration strategy, but without significant effects on yields (108).

Eat Them

Biological control of nematodes is not practiced in cotton in the United States. However, several specific, identified and unidentified organisms have shown good potential against *R. reniformis* in controlled experiments. An unidentified fungus isolated from soybean cyst nematode *Heterodera glycines* was found to consistently suppress Arkansas populations of *R. reniformis* in pots by up to 98% (151). Three of 117 isolates of *Pochonia chlamydosporia* that were tested parasitized and suppressed an Arkansas population of *R. reniformis* in pots by up to 77% (152). Isolates of *Paecilomyces lilacinus* also have been tested against *R. reniformis* in pots (59), and *Pseudomonas fluorescens* suppressed Indian populations of *R. reniformis* by up to 70% (60). Unidentified agents in three soils from cotton fields in the Texas LRGV, whose effects were removable by

1,3-D:
1,3-dichloropropene

autoclaving, suppressed populations of *R. reniformis* in sand by 80% and 95% when field soil was added to sand at ratios of 1:20 and 1:10, respectively (A. Westphal & A.F. Robinson, unpublished data). Perhaps biological control will be an option for managing *R. reniformis* in the future.

Starve Them to Death

Crop rotation. The rotation crops recommended by the Cooperative Extension Service for managing *R. reniformis* in cotton include corn, peanut, sorghum, small grains, and resistant soybean. The ability of these crops to suppress *R. reniformis* has long been known (11, 18, 45, 47, 149, 155). In a typical trial (43), cotton yields in a reniform-infested field were increased by 31%, 27%, and 27% compared to cotton monoculture, following corn, peanut, and resistant soybean, respectively. Populations drop even further the second year into resistant soybean, suggesting protracted survival in the soil (47). Growing resistant soybean (47, 48, 50, 51, 114) suppresses populations 120 cm deep into the soil profile (154). Corn (43) is most commonly recommended in Alabama but can build up populations of *M. incognita*. None of these crops is currently as profitable as cotton in most of the areas where cotton is grown, and losses from not growing cotton the year of the rotation must be weighed against the benefit of increased cotton yields following the rotation. Numerous crop rotation experiments for management of *R. reniformis* have been conducted and generally, populations of *R. reniformis* completely rebound during the first year back into cotton, so that there are no residual benefits from the rotation the second year that cotton is planted. A good example is the comparative study of Davis et al. (30). In this study, comparisons of one-year rotations to corn and resistant soybean at four locations showed dramatic population suppression from both resistant crops with improved cotton yields four out of four times after resistant soybean, and three out of four times after corn. The

effect of the rotation on nematode populations was consistently undetectable in these tests by midseason of the first year back into cotton.

Weed management. More than 87% of 350 plant species tested have been found to support reproduction by *R. reniformis* (58, 127). Fortunately, although most dicotyledonous weeds in cotton in the southeastern United States appear to be hosts, only a few are better hosts than cotton (20, 31, 34). Some are sufficiently good hosts to sustain populations in fields planted to nonhost corn (34). The best hosts among 28 weeds tested in Alabama were three *Ipomoea* spp. (morning glory). Mixed morning glory species sustained the second highest *R. reniformis* populations during a corn rotation in microplots and sicklepod (*Senna obtusifolia*) sustained the highest. Other potentially problematic weeds in corn rotation included coffee senna (*Cassia occidentalis*), common ragweed (*Ambrosia artemisiifolia*), and velvetleaf (*Abutilon theophrasti*). Among 11 weeds examined in Georgia (31), only purple nutsedge (*Cyperus rotundus*), sicklepod, Florida beggar weed (*Desmodium tortuosum*), and smallflower morning glory were comparable to cotton, with populations (expressed as a percentage of that on cotton) 454%, 81%, 73%, and 33%, respectively. *Meloidogyne incognita* also reproduced well (35% of cotton) on purple nutsedge, but not as well as *R. reniformis*. Smallflower morning glory and ivyleaf morning glory were both good hosts for *M. incognita* (70% and 211% of cotton), but only prickly sida (*Sida spinosa*), which had 407% of *M. incognita* and only 10% of *R. reniformis*, differed strikingly in its suitability as a host for the two nematodes. These investigators examined their data in relation to the times of year when these plants tend to be present and illustrated that weed management guided by an understanding of which weeds support which nematodes, can be an important component of nematode management in cotton. No obvious explanations for long-term increases in *R. reniformis* over

wide geographical regions, however, were apparent.

Host plant resistance and tolerance. The cheapest and most complete way to avoid parasitism of cotton by *R. reniformis* is to identify a cotton cultivar or breeding line that is a non-host. Unfortunately, no known upland cotton cultivar is resistant to *R. reniformis* in pots (123) and none appears to substantially suppress populations of *R. reniformis* in the field. At least 11 tolerant (28) breeding lines have been released (24, 25, 62, 120). These lines yield well in infested fields under the growing conditions to which they are adapted and, in contrast to susceptible cultivars, exhibit little or no growth or yield response to fumigation in infested fields; however, the highest population suppression reported is only about 62% (8, 25, 27, 61, 68), and usually it is less; thus, they cannot be considered resistant when compared with rotational crops, which support virtually no nematode reproduction.

More than 2000 genotypes of *G. hirsutum* have been evaluated in the search for resistance to *R. reniformis* (121–123, 129, 158). Of these, only 19 were scored as potentially resistant in the first examination. Nine (158) were reclassified as susceptible in a subsequent screen (129), and four (TX-110, TX-502, TX-1347, and TX-1348) were reclassified as *G. barbadense*, leaving six primitive *G. hirsutum* accessions (TX-25, TX-748, TX-1586, TX-1828, TX-1860, and TX-2469) as possible resistance sources; all six of the latter were classified as moderately resistant, suppressing populations in pots to less than one third but not less than one tenth of the susceptible control. Several additional weak- to moderate-resistant primitive accessions of *G. hirsutum* have been found recently (D. Weaver, personal communication).

Stronger levels of resistance than that found in *G. hirsutum* have been observed in several other *Gossypium* species including *G. barbadense*, *G. arboreum*, *G. herbaceum*, *G. longicalyx*, *G. somalense*, and *G. stocksii* (21, 129, 146, 147, 158). Some suppress populations of

R. reniformis in pots 90% to 100% compared to susceptible upland cotton, and the ability of several of these to reduce populations in the field has been confirmed (117).

Currently, projects are under way at Alabama A&M University, University of Arkansas, Auburn University, Mississippi State University, Texas A&M University, and three laboratories of the Agricultural Research Service of the USDA to introgress resistance from the above sources into Upland cotton (4, 9, 33, 88, 121, 136; J.N. Jenkins, E. Sacks, D. Weaver, L.D. Young, personal communications). These are challenging, long-term projects, as the genetics of cotton is complex, involving differences in ploidy and the existence of various genomes and subgenomes, which in many cases have low or zero intercompatibility (107).

A program being carried out by the USDA at College Station, Texas, in collaboration with Texas A&M University, has employed two male-sterile, tri-species hybrids of *G. hirsutum* (9) with *G. longicalyx*, and either *G. armourianum* or *G. herbaceum* as bridge species, to introgress virtual immunity to *R. reniformis* from diploid *G. longicalyx* into allotetraploid *G. hirsutum* (119). Introgression was accomplished by recurrent backcrosses to *G. hirsutum* with cytogenetic analysis of early backcross generations to assess progress toward the euploid state ($2n = 52$) for *G. hirsutum*, selection for nematode resistance at each generation, and examination of self progeny at the first, third, sixth, and seventh backcross to identify and eliminate lineages with undesired recessive traits.

After attempting thousands of crosses, 689 first-backcross generation progeny were generated from the two hybrids. A small number of these were both resistant and fertile. Introgression was then pursued from 28 resistant backcross-one plants, each of which was backcrossed four to seven times to *G. hirsutum* to derive agronomically suitable types, selecting for nematode resistance by bioassay at each backcross, and within segregating progeny from selfed plants at selected generations.

This arduous process involved the evaluation of nematode resistance in more than 2600 plants. The resistance trait was consistently inherited in ratios (resistant:susceptible) of 1:1 in backcross progeny and 3:1 in self progeny, in repeated generations with no loss of resistance across generations and full recovery of resistance in plants where the resistance trait was fixed. This inheritance pattern indicates a single dominant gene, or a block of non-recombinant alien DNA that behaves like a single gene, providing plant breeders with an easy genetic system for development of resistant cultivars. Hundreds of backcross plants were indistinguishable from agronomic cotton under greenhouse conditions, as were 12 progeny sets in the field in 2006, which were descended from selfed mother plants with the resistance trait in the homozygous, fixed condition. Thus, the trait has been fixed genetically in the absence of any known unwanted characteristics. Fiber quality data are excellent (119).

More than 500 segregating phenotyped plants in the USDA-Texas A&M University *G. longicalyx* project were utilized to discover six SSR markers cosegregating with the trait. One of the markers is codominant, allow-

ing it to be used to distinguish homozygous from heterozygous resistant plants, and resides within ca. 1 cM of the resistance gene (33). Seed are currently being increased for a germplasm release to the public expected in 2007.

In other introgression projects, resistance to *R. reniformis* is being transferred into cotton from *G. barbadense* TX-110 (88, 136), *G. barbadense* GB-713 (125), *G. arboreum* (4; E. Sacks, personal communication), *G. barbadense* TX-1348 (L.D. Young, personal communication), or being approached via transgressive segregation within *G. hirsutum* (D. Weaver, personal communication; A.F. Robinson, unpublished data). Bringing resistance into cultivated cotton from different sources is important because in each case the likelihood of introgressing an alien segment with low rates of recombination between resistance genes and genes for agronomically unacceptable traits also on the alien segment is high. Moreover, multiple resistance sources may prove an invaluable resource if and when resistance-breaking nematode populations or races are encountered or develop. There already is ample evidence of variability within *R. reniformis* (3, 29, 83, 94).

SUMMARY POINTS

1. A growing body of information in commodity newspapers, expert opinion surveys, technical reports, published surveys, and refereed scientific journal articles documents the increasing effect of the reniform nematode, *R. reniformis*, on cotton production in the United States.
2. Infestations with damaging population densities of the nematode have been found in all states east of New Mexico. The highest incidence of severely infested fields occurs in Louisiana, Mississippi, and Alabama, where almost all cotton-producing counties and parishes are affected. The incidence of infested cotton fields in the surrounding states of Texas, Arkansas, Tennessee, Georgia, and Florida appears to be steadily increasing.
3. Current annual cotton losses to *R. reniformis* in the United States are estimated to be 525,697 bales, with a value of approximately \$130M.
4. The causes for recent spread of *R. reniformis* are not known but may include a slow, ineluctable natural progression, increased acreages planted to cotton, increased

movement of soil due to larger, faster farm equipment and more prevalent contract harvesting, long-term changes in climate or soils, introduction of the nematode to areas lacking suppressive agents, and introduction of conducive agents.

5. Biological factors that favor dispersal and buildup of *R. reniformis* over other problematic nematodes in cotton include the ability to survive in dry soil, deep occurrence, a high biotic potential on cotton, a wide host range, and the ability to maintain high population densities in a wide range of soil types.
6. The effects of *R. reniformis* on cotton include feeding-induced modifications of cells in the root endodermis and pericycle, leading to stunting, fruit delay, and up to 60% yield suppression. Cotton plant stunting is irregular in new infestations and uniform in old ones.
7. Current management is limited to nematicide application, weed control, and rotation with crops, primarily corn, peanut, and resistant soybean, which many cotton farmers will not or cannot plant, and which may or may not provide a profit greater than damaged cotton.
8. Acceptable levels of genetic resistance to *R. reniformis* are absent in upland cotton but present in related wild species, and active projects are under way at six or more public institutions to introgress resistance to *R. reniformis* from those species into Upland cotton. The most advanced of those projects expects to release seed of highly agronomic, resistant germplasm to the private sector within one year. A tightly linked codominant marker suitable for marker-assisted selection has been discovered and submitted for publication. The seed and marker are expected to allow cotton seed companies to develop resistant cultivars adapted to a wide range of production regions within three years.

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LITERATURE CITED

1. Agudelo P, Robbins RT, Kim KS, Stewart JMD. 2005. Histological changes in *Gossypium hirsutum* associated with reduced reproduction of *Rotylenchulus reniformis*. *J. Nematol.* 37:185–89
2. Agudelo P, Robbins RT, Stewart JMD, Bell A, Robinson AF. 2005. Histological observations of *Rotylenchulus reniformis* on *Gossypium longicalyx* and interspecific cotton hybrids. *J. Nematol.* 37:44–47
3. Agudelo P, Robbins RT, Stewart JMD, Szalanski AL. 2005. Intraspecific variability of *Rotylenchulus reniformis* from cotton-growing regions in the United States. *J. Nematol.* 37:105–14

4. Avila CA, Stewart JMD, Robbins RT. 2006. Introgression of reniform nematode resistance into upland cotton. In *Proc. Beltwide Cotton Conf. Natl. Cotton Counc. Am.* 154. San Antonio, TX
5. Baird RE, Carling DE, Watson CE, Scruggs ML, Hightower P. 2004. Effects of nematocides on cotton root mycobiota. *Mycopathologia* 157:191–99
6. Baird RE, Davis RF, Alt PJ, Mullinix BG, Padgett GB. 1996. Frequency and geographical distribution of plant-parasitic nematodes on cotton in Georgia. *J. Nematol.* 28:661–67
7. Bateman RJ, Kirkpatrick TL, Howard SC. 2005. *Nematode Diagnostic Clinics 2005 Summary Report*. Fayetteville, AR: Univ. Arkansas Southwest Res. Ext. Cent. Bull. AG-968-06
8. Beasley JP. 1985. *Evaluation of cotton, Gossypium hirsutum L., genotypes for resistance to the reniform nematode, Rotylenchulus reniformis Linford and Oliveira*. PhD thesis. Louisiana State Univ., Baton Rouge
9. Bell A, Robinson AF. 2004. Development and characteristics of triple species hybrids used to transfer reniform nematode resistance from *Gossypium longicalyx* into *Gossypium hirsutum*. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 422–26. San Antonio, TX
10. Birchfield W. 1962. Host-parasitic relations of *Rotylenchulus reniformis* on *Gossypium hirsutum*. *Phytopathology* 52:862–65
11. Birchfield W, Brister LR. 1962. New hosts and nonhosts of the reniform nematode. *Plant Dis. Rep.* 46:683–85
12. Birchfield W, Jones JE. 1961. Distribution of the reniform nematode in relation to crop failure of cotton in Louisiana. *Plant Dis. Rep.* 45:671–73
13. Birchfield W, Martin WJ. 1967. Reniform nematode survival in air-dried soil. *Phytopathology* 57:804
14. Bird AF. 1983. Growth and moulting in nematodes: Changes in the dimensions and morphology of *Rotylenchulus reniformis*. *Int. J. Parasitol.* 13:201–6
15. Blasingame D. 2006. 2005 Cotton disease loss estimate. In *Proc. Beltwide Cotton Conf. Natl. Cotton Counc. Am.*, pp. 155–57. San Antonio, TX
16. Blasingame D, Patel MV. 1987. A population and distribution survey of cotton nematodes in Mississippi. *Plant Disease Dispatch*, Jan. 18. Mississippi State, MS: Mississippi Coop. Ext. Service
17. Blasingame D, Patel MV. 2001. Cotton disease loss estimate. In *Proc. Beltwide Cotton Conf. Natl. Cotton Counc. Am.* Anaheim, CA
18. Brathwaite CWD. 1974. Effect of crop sequence on populations of *Rotylenchulus reniformis* in fumigated and nontreated soil. *Plant Dis. Rep.* 58:259–61
19. Brodie BB, Cooper WE. 1964. Relation of plant parasitic nematodes to postemergence damping-off of cotton. *Phytopathology* 54:1023–27
20. Carter CH, McGawley EC, Russin JS. 1995. Reproduction of *Rotylenchulus reniformis* on weed species common to Louisiana soybean fields. *J. Nematol.* 27:494–95
21. Carter WW. 1981. Resistance and resistant reaction of *Gossypium arboreum* to the reniform nematode, *Rotylenchulus reniformis*. *J. Nematol.* 13:368–74
22. Cochran A, Long D, Beckett TH, Payan LA, Belles D. 2006. Efficacy of Avicta Complete Pak against nematodes and seedling diseases in western cotton. In *Proc. Beltwide Cotton Conf. Natl. Cotton Counc. Am.*, 131. San Antonio, TX
23. Cohn E. 1973. Histology of the feeding site of *Rotylenchulus reniformis*. *Nematologica* 19:455–58
24. Cook CG, Namken LN, Robinson AF. 1997. Registration of N220-1-91, N222-1-01, N320-2-91, and N419-1-91 nematode-resistant cotton germplasm lines. *Crop Sci.* 37:1028–29

25. Cook CG, Robinson AF. 2005. Registration of RN96425, RN96527, and RN96625-1 nematode-resistant cotton germplasm lines. *Crop Sci.* 45:1667–68
26. Cook CG, Robinson AF, Bridges AC, Percival AE, Prince WB, et al. 2003. Field evaluation of cotton cultivar response to reniform nematodes. In *Proc. Beltwide Cotton Conf. Natl. Cotton Counc. Am.*, pp. 861–62. Nashville, TN
27. Cook CG, Robinson AF, Namken LN. 1997. Tolerance to *Rotylenchulus reniformis* and resistance to *Meloidogyne incognita* race 3 in high-yielding breeding lines of upland cotton. *J. Nematol.* 29:322–28
28. Cook R, Evans K. 1987. Resistance and tolerance. In *Principles and Practice of Nematode Control in Crops*, ed. RH Brown, BR Kerry, pp. 179–231. New York: Academic
29. Dasgupta DR, Seshadri AR. 1971. Reproduction, hybridization and host adaptation in physiological races of the reniform nematode, *Rotylenchulus reniformis*. *Indian J. Nematol.* 1:128–44
30. Davis RF, Koenning SR, Kemerait RC, Cummings TD, Shurley WD. 2003. *Rotylenchulus reniformis* management in cotton with crop rotation. *J. Nematol.* 35:58–64
31. Davis RF, Webster TM. 2005. Relative host status of selected weeds and crops for *Meloidogyne incognita* and *Rotylenchulus reniformis*. *J. Cotton Sci.* 9:41–46
32. Diez A, Lawrence GW, Lawrence KW. 2003. Competition of *Meloidogyne incognita* and *Rotylenchulus reniformis* on cotton following separate and concomitant inoculations. *J. Nematol.* 35:422–29
33. Dighe N, Bell AA, Robinson AF, Menz MA, Cantrell RC, Stelly DM. 2007. Tagging and mapping of the reniform nematode resistance gene introgressed from wild diploid, *G. longicalyx*, into upland cotton, *G. hirsutum*. *Crop Sci.* Submitted.
34. Dismukes AL, Lawrence KS, Price AJ, Lawrence GW, Akridge R. 2006. Host status of noxious weed plants associated with *Gossypium hirsutum*–*Zea mays* rotation systems to *Rotylenchulus reniformis*. In *Proc. Beltwide Cotton Conf. Natl. Cotton Counc. Am.*, pp. 7–11. San Antonio, TX
35. Eisenback JD, Hopkins N. 2004. First report of the reniform nematode *Rotylenchulus reniformis* on cotton in Virginia. *Plant Dis.* 88:683
36. Elgawad AMM, Ismail AE, El-Metwally EA. 1997. Evaluation of cotton rotation for production in a nematode-infested field in Egypt. *Internatl. J. Nematol.* 7:103–06
37. Esser RP. 1976. *Sting Nematodes, Devastating Parasites of Florida Crops*. Gainesville, FL: Florida Dept. Agric. Cons. Svcs. Nematol. Cir. No. 18
38. Faske TR, Starr JR. 2006. Sensitivity of *Meloidogyne incognita* and *Rotylenchulus reniformis* to abamectin. *J. Nematol.* 38:240–44
39. Fassuliotis G, Rau GJ. 1967. The reniform nematode in South Carolina. *Plant Dis. Rep.* 51:557
40. French NM, Kirkpatrick TL, Colyer PD, Starr JL, Lawrence KS, et al. 2006. Influence N-Hibit and ProAct on nematodes in field cotton. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 137–42. San Antonio, TX
41. Gaur HS, Perry RN. 1991. The biology and control of plant-parasitic nematode *Rotylenchulus reniformis*. *Agric. Zool. Rev.* 4:177–212
42. Gaur HS, Perry RN. 1991. The role of the moulted cuticles in the desiccation survival of adults of *Rotylenchulus reniformis*. *Rev. Nematol.* 14:109–12
43. Gazaway WS, Akridge JR, McLean K. 2000. Impact of various crop rotations and various winter cover crops on reniform nematode in cotton. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 162–63. San Antonio, TX

44. Gazaway WS, Akridge JR, McLean K. 2001. Impact of nematicides on cotton production in reniform infested fields. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, 128. Anaheim, CA
45. Gazaway WS, Akridge JR, Rodriguez-Kabana R. 1998. Management of reniform nematode in cotton using various rotation schemes. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 141–42. San Diego, CA
46. Gazaway WS, McLean KS. 2003. A survey of plant-parasitic nematodes associated with cotton in Alabama. *J. Cotton Sci.* 7:1–7
47. Gilman DF, Jones JE, Williams C, Birchfield W. 1978. Cotton soybean rotation for control of reniform nematodes. *La. Agric.* 21:10–11
48. Gilman DF, Marshall JG, Rabb JG, Lawrence JL, Boquet DJ, Bartleson JL. 1979. Performance of soybean varieties in Louisiana, 1976–78. *La. Agric.* 22:22
49. Graham TW, Holdeman QL. 1953. The sting nematode, *Belonolaimus gracilis* Steiner: A parasite of cotton and other crops in South Carolina. *Phytopathology* 43:434–39
50. Hartwig EE, Epps JM. 1977. Registration of Centennial soybeans (Reg. No. 114). *Crop Sci.* 17:979
51. Harville BG. 1985. Genetic resistance to reniform nematodes in soybeans. *Plant Dis.* 69:587–89
52. Heald CM, Heilman MD. 1971. Interaction of *Rotylenchulus reniformis*, soil salinity and cotton. *J. Nematol.* 3:179–82
53. Heald CM, Inserra RN. 1988. Effect of temperature on infection and survival of *Rotylenchulus reniformis*. *J. Nematol.* 20:356–61
54. Heald CM, Orr CC. 1984. Nematode parasites of cotton. In *Plant and Insect Nematodes*, ed. WR Nickle, pp. 147–66. New York: Marcel Dekker, Inc.
55. Heald CM, Robinson AF. 1987. Effects of soil solarization on *Rotylenchulus reniformis* in the Lower Rio Grande Valley of Texas. *J. Nematol.* 19:93–103
56. Heald CM, Robinson AF. 1990. Survey of current distribution of *Rotylenchulus reiniformis* in the United States. *J. Nematol.* 22:695–99
57. Heald CM, Thames WH. 1980. Vertical distribution and dissemination of *Rotylenchulus reniformis* in field soils. *J. Nematol.* 12:255
58. Inserra RN, Dunn RA, McSorley R, Langdon KR, Richmer AY. 1989. *Weed Hosts of Rotylenchulus reniformis in Ornamental Nurseries of Southern Florida*. Gainesville, FL: Florida Dept. Agric. Cons. Svcs. Nematol. Circular No. 171
59. Jayakumar J, Ramakrishnan S, Rajendran G. 2002. Bio-efficacy of *Paecilomyces lilacinus* against reniform nematode, *Rotylenchulus reniformis* infesting cotton. *Curr. Nematol.* 13:19–21
60. Jayakumar J, Ramakrishnan S, Rajendran G. 2003. Bio-efficacy of fluorescent pseudomonad isolates against reniform nematode, *Rotylenchulus reniformis* infecting cotton. *Indian J. Nematol.* 33:13–15
61. Jones JE. 1987. Notice of release of La RN 4–4, La RN 909, La RN 910 and La RN 032 reniform and root-knot resistant registered breeding lines of upland cotton. *G. hirsutum*. Baton Rouge, LA: Louisiana Coop. Exp. Sta. Mimeo. Ser. 015
62. Jones JE, Beasley JP, Dickson JI, Caldwell WD. 1988. Registration of four cotton germplasm lines with resistance to reniform and root-knot nematodes. *Crop Sci.* 28:199–200
63. Jones JE, Newsom LO, Finley EL. 1959. Effect of the reniform nematode on yield, fiber properties of upland cotton. *Agron. J.* 51:353–56

64. Kemerait RC, Jost PH, Davis RF, Brown SN, Green TW, et al. 2006. Assessment of seed treatments for management of nematodes in Georgia. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 144–49. San Antonio, TX
65. Khadr AS, Salem AA, Oteifa BA. 1972. Varietal susceptibility and significance of the reniform nematode, *Rotylenchulus reniformis*, in Fusarium wilt of cotton. *Plant Dis. Rep.* 56:1040–42
66. Kinloch RA, Rich JR. 2001. Management of root-knot and reniform nematode in ultra-narrow row cotton with 1,3-dichloropropene. *Suppl. J. Nematol.* 33:311–13
67. Koenning SR. 2002. Economics and ecology put to use—Action thresholds. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 143–47. Atlanta, GA
68. Koenning SR, Barker KR, Bowman DT. 2000. Tolerance of selected cotton lines to *Rotylenchulus reniformis*. *Suppl. J. Nematol.* 32:519–23
69. Koenning SR, Kirkpatrick TL, Starr JL, Wrather JA, Walker NR, Mueller JD. 2004. Plant parasitic nematodes attacking cotton in the United States: Old and emerging production challenges. *Plant Dis.* 88:100–13
70. Koenning SR, Walters SA, Barker KR. 1996. Impact of soil texture on the reproductive and damage potentials of *Rotylenchulus reniformis* and *Meloidogyne incognita* on cotton. *J. Nematol.* 28:527–36
71. Komar SJ, Wiley PD, Kemerait RC, Shurley WD. 2003. Nematicide treatment effects on reniform nematodes in cotton. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, 272. Nashville, TN
72. Lawrence GW, McLean KS. 1996. Reniform nematode and cotton production in Mississippi. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 251–53. Nashville, TN
73. Lawrence GW, McLean KS. 2000. Effect of foliar applications of oxamyl with aldicarb for the management of *Rotylenchulus reniformis* on cotton. *Suppl. J. Nematol.* 32:542–49
74. Lawrence GW, McLean KS. 2001. Reniform nematodes. In *Compendium of Cotton Diseases*, ed. TL Kirkpatrick, CS Rothrock, pp. 42–44. St. Paul, MN: APS Press
75. Lawrence GW, McLean KS, Batson WE, Miller D, Borbon JC. 1990. Response of *Rotylenchulus reniformis* to nematicide applications on cotton. *Suppl. J. Nematol.* 22:707–11
76. Lawrence KS, Uesry SR, Burmester CH. 2000. Evaluation of recommended and experimental compounds for reniform nematode management in cotton in North Alabama, 2004. In *2004 Cotton Research Report*, 39. Auburn, AL: Alabama Agric. Exp. Sta. Research Report No. 26
77. Lawrence KS, Uesry SR, Burmester CH, Lawrence GW. 2005. Evaluation of Telone II, Vapam HL, and Temik 15G for reniform nematode management in cotton in North Alabama, 2004. In *2004 Cotton Research Report*, 40. Auburn, AL: Alabama Agric. Exp. Sta. Res. Rep. No. 26
78. Lawrence KS, Uesry SR, Burmester CH, Lawrence GW. 2005. Evaluation of seed treatment nematicides for reniform nematode management in cotton in North Alabama, 2004. In *2004 Cotton Research Report*, 40. Auburn, AL: Alabama Agric. Exp. Sta. Res. Rep. No. 26
79. Linford MB, Oliveira JM. 1940. *Rotylenchulus reniformis*, nov. gen. n. sp., a nematode parasite of roots. *Proc. Helminth. Soc. Wash.* 7:35–42
80. Linford MB, Yap F. 1940. Some host plants of the reniform nematode in Hawaii. *Proc. Helminth. Soc. Wash.* 7:42–44
81. Lee HK, Lawrence GW, Kelley AT, Dubien JL. 2003. Seasonal variation in the spatial distribution of the reniform nematode in Mississippi cotton. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 245–46. Nashville, TN

82. Lewis SA, Smith FH. 1976. Host plant distribution and ecological associations of *Hoplolaimus columbus*. *J. Nematol.* 8:264–70
83. McGawley EC, Overstreet C. 1995. Reproduction and pathological variation in populations of *Rotylenchulus reniformis*. *J. Nematol.* 27:508
84. McLean KS, Lawrence GW. 2003. Efficacy of aldicarb to *Rotylenchulus reniformis* and biodegradation in cotton field soils. *J. Nematol.* 35:373–75
85. McLean KS, Lawrence GW, Overstreet C, Young LD. 2003. Efficacy of anhydrous ammonia on reniform nematode in cotton. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 282–83. Nashville, TN
86. Minton NA, Hopper BE. 1959. The reniform and sting nematodes in Alabama. *Plant Dis. Rep.* 43:47
87. Monfort WX, Kirkpatrick TL. 2005. Spread of reniform nematode (*Rotylenchulus reniformis*) in a southeastern Arkansas cotton field over a three-year period. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, 183. New Orleans, LA
88. Moresco E, Morgan E, Ripple KW, Smith CW, Starr JL. 2004. Resistance to *Rotylenchulus reniformis* in interspecific *Gossypium* hybrids. *J. Nematol.* 36:335
89. Motsinger RE, Crawford JL, Thompson SS. 1976. Nematode survey of peanuts and cotton in southwest Georgia. *Peanut Sci.* 3:72–74
90. Mueller JD. 1993. Lance nematodes. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 176–77. New Orleans, LA
91. Mueller JD, Lewis SA. 2001. Lance nematodes. In *Compendium of Cotton Diseases*, ed. TL Kirkpatrick, CS Rothrock, pp. 44–45. St. Paul, MN: APS Press
92. Mueller JD, Sullivan MJ. 1988. Response of cotton to infection by *Hoplolaimus columbus*. *Suppl. J. Nematol.* 20:86–89
93. Muhammad N, Jones JE. 1990. Genetics of resistance to reniform nematode in Upland cotton. *Crop Sci.* 30:13–16
94. Nakasono K. 1983. Studies on morphological and physio-ecological variation of the reniform nematode, *Rotylenchulus reniformis* Linford and Oliveira, 1940 with an emphasis on differential geographical distribution of amphimictic and parthenogenetic populations in Japan. *Bull. Natl. Inst. Agric. Sci. Jpn.* 38:63–67
95. Neal DC. 1954. The reniform nematode and its relationship to the incidence of Fusarium wilt of cotton at Baton Rouge, Louisiana. *Phytopathology* 44:447–50
96. Newman MA. 2005. *Cotton Disease and Nematode Control, 2005*. Jackson, TN: Univ. Tennessee Ext. Svc. Bull. E&PP Info24
97. Newman MA, Stebbins TC. 2002. Recovery of reniform nematodes at various soil depths in cotton. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 254–55. Atlanta, GA
98. Norton DC. 1959. *Plant Parasitic Nematodes in Texas*. College Station, TX: Texas Agric. Exp. Sta. Misc. Pub. No. 321
99. Orr CC, Brashears AD. 1977. Aldicarb and DBCP for root-knot nematode control of cotton. *Plant Dis. Rep.* 62:623–24
100. Overstreet C. 2001. *Survey of Reniform Nematodes in 2001*. Baton Rouge, LA: Louisiana Agric. Coop. Ext. Svc. Update No. 3
101. Overstreet C, Erwin TL. 2003. The use of Telone in cotton production in Louisiana. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 277–78. Nashville, TN
102. Overstreet C, McGawley EC. 2000. Geographical dispersion of reniform nematode in Louisiana. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 168–71. San Antonio, TX
103. Palanisamy S, Balasubramanian M. 1983. Assessment of avoidable yield loss in cotton (*Gossypium barbadense* L.) by fumigation with metam sodium. *Nematolog. Medit.* 11:201

104. Palmateer AJ, Lawrence KS, VanSanten E, Morgan-Jones G. 2004. Interaction of *Rotylenchulus reniformis* with seedling disease pathogens of cotton. *J. Nematol.* 36:160–66
105. Patel RR, Patel BA, Thakar NA. 2003. Organic amendments in management of *Rotylenchulus reniformis* on cotton. *Indian J. Nematol.* 33:146–48
106. Patel RR, Patel BA, Thakar NA. 2004. Pathogenicity of reniform nematode, *Rotylenchulus reniformis* on cotton. *Indian J. Nematol.* 34:106–07
107. Percival AE, Wendel JF, Stewart JM. 1999. Taxonomy and germplasm resources. In *Cotton: Origin, History, Technology, and Production*, ed. CW Smith, JT Cothren, pp. 33–63. New York: John Wiley & Sons
108. Pettigrew WT, Meredith WR Jr, Young LD. 2005. Potassium fertilization effects on cotton lint yield, yield components, and reniform nematode populations. *Agron. J.* 97:1245–51
109. Prasad KS, Padeganur GM. 1980. Observations on the association of *Rotylenchulus reniformis* with Verticillium wilt of cotton. *Indian J. Nematol.* 10:91–92
110. Rebois RV. 1973. Effect of soil temperature on infectivity and development of *Rotylenchulus reniformis* on resistant and susceptible soybeans, *Glycine max.* *J. Nematol.* 5:10–13
111. Rebois RV, Madden PA, Eldridge BJ. 1975. Some ultrastructural changes induced in resistant and susceptible soybean roots following infection by *Rotylenchulus reniformis*. *J. Nematol.* 7:122–39
112. Robbins RT. 1982. Phytoparasitic nematodes associated with soybean in Arkansas. *J. Nematol.* 14:466
113. Robbins RT, Barker KR. 1974. The effects of soil type, particle size, temperature, and moisture on reproduction of *Belonolaimus longicaudatus* from North Carolina and Georgia. *J. Nematol.* 6:1–6
114. Robbins RT, Shipe ER, Rakes L, Jackson LE, Gbur EE, Dombek DG. 2001. Host suitability in soybean cultivars for the reniform nematode, 2000 tests. *Suppl. J. Nematol.* 33:314–17
115. Robinson AF. 1999. Cotton nematodes. In *Cotton: Origin, History, Technology, and Production*, ed. CW Smith, JT Cothren, pp. 595–616. New York: John Wiley & Sons
116. Robinson AF. 2002. Reniform nematodes: *Rotylenchulus* species. In *Plant Resistance to Parasitic Nematodes*, ed. JL Starr, R Cook, J Bridge, pp. 153–74. Wallingford, UK: CABI Publishing
117. Robinson AF, Akridge JR, Bradford JB, Cook CG, Gazaway WS, et al. 2006. Suppression of *Rotylenchulus reniformis* 122 cm deep endorses resistance introgression in *Gossypium*. *J. Nematol.* 38:195–209
118. Robinson AF, Akridge JR, Bradford JM, Cook CG, Gazaway WS, et al. 2005. Vertical distribution of *Rotylenchulus reniformis* in cotton fields. *J. Nematol.* 37:265–71
119. Robinson AF, Bell AA, Dighe N, Menz MA, Nichols RL, Stelly DM. 2007. Introgression of resistance to nematode *Rotylenchulus reniformis* into upland cotton (*Gossypium hirsutum*) from *G. longicalyx*. *Crop Sci.* In press.
120. Robinson AF, Bowman DJ, Colyer PD, Cook CG, Creech RG, et al. 2001. Nematode resistance. In *Compendium of Cotton Diseases*, ed. TL Kirkpatrick, CS Rothrock, pp. 68–72. St. Paul, MN: APS Press
121. Robinson AF, Bridges AC, Percival AE. 2004. New sources of resistance to the reniform (*Rotylenchulus reniformis* Linford and Oliveira) and root-knot (*Meloidogyne incognita* (Kofoid & White) Chitwood) nematode in upland (*Gossypium hirsutum* L.) and sea island (*G. barbadense* L.) cotton. *J. Cotton Sci.* 8:191–97

122. Robinson AF, Cook CG. 2001. Root-knot and reniform nematode reproduction on kenaf and sunn hemp compared with that on nematode resistant and susceptible cotton. *Indust. Crops Prod.* 13:249–64
123. Robinson AF, Cook CG, Percival AE. 1999. Resistance to *Rotylenchulus reniformis* and *Meloidogyne incognita* race 3 in the major cotton cultivars planted since 1950. *Crop Sci.* 39:850–58
124. Robinson AF, Cook CG, Westphal A, Bradford JM. 2005. *Rotylenchulus reniformis* below plow depth suppresses cotton yield and root growth. *J. Nematol.* 37:285–91
125. Robinson AF, Gutierrez OA, LaFoe JM, McCarty JJC, Jenkins JN. 2005. Detection of reniform nematode resistance in primitive *Gossypium hirsutum* and *G. barbadense* during a survey of the U.S. National Cotton Collection and initiation of research to incorporate resistance into agronomic cotton. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, 934. New Orleans, LA
126. Robinson AF, Heald CM, Flanagan SL, Thames WH, Amador J. 1987. Geographical distributions of *Rotylenchulus reniformis*, *Meloidogyne incognita*, and *Tylenchulus semipenetrans* in the Lower Rio Grande Valley as related to soil texture and land use. *Ann. Appl. Nematol.* 1:20–25
127. Robinson AF, Inserra RN, Caswell-Chen EP, Vovlas N, Troccoli A. 1997. *Rotylenchulus* species: Identification, distribution, host ranges, and crop plant resistance. *Nematropica* 27:127–80
128. Robinson AF, Orr CC. 1980. Histopathology of *Rotylenchulus reniformis* on sunflower. *J. Nematol.* 12:84–85
129. Robinson AF, Percival AE. 1997. Resistance to *Meloidogyne incognita* race 3 and *Rotylenchulus reniformis* in wild accessions of *Gossypium hirsutum* and *G. barbadense* from Mexico. *J. Nematol.* 29:746–55
130. Sanaralingham A, McGawley EC. 1994. Interrelationships of *Rotylenchulus reniformis* with *Rhizoctonia solani* on cotton. *J. Nematol.* 26:475–85
131. Sasser J. 1972. Nematode diseases of cotton. In *Economic Nematology*, ed. JM Webster, pp. 187–214. London: Academic
132. Schwarz M, Graham C, Kleyla C. 2006. New seed-applied nematicides from Bayer Crop-science. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, 2284. San Antonio, TX
133. Sciumbato GL, Blessitt JA, Blasingame D. 2004. Mississippi cotton nematode survey: Results of an eight county survey. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, 451. San Antonio, TX
134. Sehgal M, Gaur HS. 1988. Survival and infectivity of the reniform nematode, *Rotylenchulus reniformis*, in relation to moisture stress in soil without host. *Indian J. Nematol.* 18:49–54
135. Sehgal M, Gaur HS. 1989. Effect of the rate of soil moisture loss on the survival, infectivity and development of *Rotylenchulus reniformis*, the reniform nematode. *Pak. J. Nematol.* 7:83–90
136. Silvey DT, Ripple KR, Smith CW, Starr JL. 2003. Identification of RFLP loci linked to resistance to *Meloidogyne incognita* and *Rotylenchulus reniformis*. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, 270. Nashville, TN
137. Sivakumar CV, Seshadri AR. 1971. Life history of the reniform nematode *Rotylenchulus reniformis* Linford and Oliveira, 1940. *Indian J. Nematol.* 1:7–20
138. Smith AL. 1940. Distribution and relation of the meadow nematode, *Pratylenchus pratensis* to Fusarium wilt of cotton in Georgia. *Phytopathology* 30:710
139. Smith AL, Taylor AL. 1941. Nematode distribution in the 1940 regional cotton-wilt plots. *Phytopathology* 31:771

140. Starr JL. 1998. Cotton. In *Plant and Nematode Interactions*, No. 36 in the Series Agronomy, ed. KR Barker, GA Pederson, GL Windham, pp. 359–79. Madison, WI: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America Publishers
141. Starr JL, Bridge J, Cook R. 2002. Resistance to plant parasitic nematodes, history, current use, and future potential. In *Plant Resistance to Parasitic Nematodes*, ed. JL Starr, R Cook, J Bridge, pp. 1–22. Wallingford, UK: CABI Publ.
142. Starr JL, Heald CM, Robinson AF, Smith RG, Krause JP. 1993. *Meloidogyne incognita* and *Rotylenchulus reniformis* and associated soil textures from some cotton production areas of Texas. *J. Nematol.* 25:252–56
143. Starr JL, Page SLJ. 1990. Nematode parasites of cotton and other tropical fibre crops. In *Plant Parasitic Nematodes in Subtropical and Tropical Agriculture*, ed. M Luc, RA Sikora, J Bridge, pp. 539–56. Wallingford, UK: CABI Publ.
144. Starr JL, Wheeler TA, Walker NR. 2001. Nematode fungal interactions. In *Compendium of Cotton Diseases*, ed. TL Kirkpatrick, CS Rothrock, pp. 46–48. St. Paul, MN: APS Press
145. Steiner G. 1942. Nematode control under Florida conditions. *Proc. Soil Crop Sci. Soc. Florida* 4:72–117
146. Stewart JM, Robbins RT. 1995. Evaluation of Asiatic cottons for resistance to reniform nematode. In *Proc. 1994 Cotton Res. Mtg*, ed. DM Oosterhuis, pp. 165–68. Fayetteville, AR: Arkansas Agricultural Experiment Station Special Report 166
147. Stewart JM, Robbins RT. 1996. Identification and enhancement of resistance to reniform nematode in cotton germplasm. In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, 255. Nashville, TN
148. Sud UC, Varaprasad KJ, Seshadri AR, Kher KK. 1984. Relationship between initial densities of *Rotylenchulus reniformis* and damage to cotton with fits to Seinhorst curves. *Indian J. Nematol.* 14:148–51
149. Thames WH, Heald CM. 1974. Chemical and cultural control of *Rotylenchulus reniformis* on cotton. *Plant Dis. Rep.* 58:337–41
150. Tsai BY, Apt WF. 1979. Anhydrobiosis of the reniform nematode: Survival and coiling. *J. Nematol.* 11:316
151. Wang K, Riggs RD, Crippen D. 2004. Suppression of *Rotylenchulus reniformis* on cotton by the nematophagous fungus ARF. *J. Nematol.* 36:186–91
152. Wang K, Riggs RD, Crippen D. 2005. Isolation, selection, and efficacy of *Pochonia chlamydosporia* for control of *Rotylenchulus reniformis* on cotton. *Phytopathology* 95:890–93
153. Westphal A, Robinson AF, Scott JAW, Santini JB. 2004. Depth distribution of *Rotylenchulus reniformis* under crops of different host status and after fumigation. *Nematology* 6:97–108
154. Westphal A, Scott JAW. 2005. Implementation of soybean in cotton cropping sequences for management of reniform nematode in South Texas. *Crop. Sci.* 45:233–39
155. Windham GL, Lawrence GW. 1992. Host status of commercial maize hybrids to *Rotylenchulus reniformis*. *J. Nematol.* 24:745–48
156. Womersley C, Ching C. 1989. Natural dehydration regimes as a prerequisite for the successful induction of anhydrobiosis in the nematode *Rotylenchulus reniformis*. *J. Exp. Biol.* 143:359–72
157. Wrather JA, Niblack TL, Milam MR. 1992. Survey of plant-parasitic nematodes in Missouri cotton fields. *Suppl. J. Nematol.* 24:779–82
158. Yik CP, Birchfield W. 1984. Resistant germplasm in *Gossypium* species and related plants to *Rotylenchulus reniformis*. *J. Nematol.* 16:146–53

159. Zimet DJ, Rich JR, LaColla A, Kinloch RA. 1999. Economic analysis of Telone II (1,3-D) and Temik 15G (aldicarb) to manage reniform nematode (*Rotylenchulus reniformis*). In *Proc. Beltwide Conf. Natl. Cotton Counc. Am.*, pp. 111–12. Orlando, FL
160. Zimet DJ, Smith JL, Rich JR, Kinloch RA. 2002. Improving returns using nematicides in cotton fields infested with reniform nematodes in northwestern Florida. *J. Cotton Sci.* 6:34–39



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Errata

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